

Movement patterns, home range size, and resource selection of brown bears near the Malaspina Glacier, Southeast Alaska

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Abstract

We studied movement patterns, home range size, and resource selection of brown bears (*Ursus arctos*) near the Malaspina Glacier, Southeast Alaska, during 2009 to 2013. The primary purpose of this research was to provide resource managers with spatial use and resource selection information useful for managing a sustainable population of brown bears in northern Southeast Alaska. We captured and equipped 18 brown bears with global positioning system (GPS) radio collars within a 990 km² study area in Wrangell-St. Elias National Park and Preserve, adjacent to the Malaspina Glacier. We estimated annual and seasonal home ranges using 2 methods, 100% minimum convex polygon (MCP) and 95% fixed kernel density estimation (KDE) using least-squares cross-validation to estimate bandwidths. We found no significant difference ($P = 0.20$) between male ($\bar{x} = 462.0$ SE = 175.5, $n = 7$) and female ($\bar{x} = 183.9$ SE = 36.6, $n = 4$) annual MCP home range size estimates. Seasonal KDE estimates of male home ranges, however, were larger than females ($P = 0.01$). Brown bear daily movement rates were calculated for each season, with bears traveling the shortest distances in the spring, and the furthest distances in late summer coinciding with salmon spawning. In the spring, the average daily movement rate of females with cubs was 1.0 km, while adult males traveled 4.6 km. In late summer, all cohorts increased movement rates, and we found females with cubs traveled 4.8 km and adult males moved 5.9 km per day. We developed a random mixed-effects model to investigate the influence of sex, reproductive status, season, and year on home range size. Both reproductive status and season were important predictors of home range size. Late summer home ranges were larger than spring home ranges, and subadult male home ranges were significantly larger than other cohorts. We also evaluated brown bear habitat selection in late summer using a resource selection function (RSF). The most parsimonious RSF model for brown bear habitat selection included resources that were at low elevation, near herbaceous habitats, and included a mosaic of conifer and deciduous forest, shrub and unvegetated habitats, and water. We provided recommendations for the continued management of brown bears near the Malaspina Glacier.

Key words: Brown bears, habitat selection, home range, Malaspina Glacier, movements, resource selection, Southeast Alaska, *Ursus arctos*.

Introduction

Brown bears (*Ursus arctos*) in Alaska are highly valued intrinsically, ecologically and economically (Miller et al. 1998, Titus et al. 1999, Holtgrieve et al. 2009). Given the demand for consumptive and non-consumptive uses of brown bears (Titus et al. 1994), we must understand brown bear ecology and collect pertinent biological data necessary to guide the management of Southeast Alaska's brown bear population. Over the past 4 decades, brown bear research in Southeast Alaska has focused on ecology, animal movements, population abundance, and genetic variation within and between bear populations (Wood 1976, Schoen and Beier 1990, Talbot and Shields 1996, Titus et al. 1999, Gende et al. 2001, Flynn et al. 2007, Flynn et al. 2010, Flynn et al. 2012). The results of these projects highlight the importance of understanding the dynamics in each study area and the variations among them, as mainland and island populations function differently across Southeast's various ecoregions. Until recently, relatively little has been known about the brown bear population inhabiting the remote landscape along the northern mainland coast near Yakutat from Glacier Bay National Park to Icy Bay in Wrangell – St. Elias National Park (WRST) (Game Management Unit (GMU) 5A and 5B). Consequently, the Alaska Department of Fish and Game (ADF&G) and the WRST unit of the National Park Service (NPS) have collaborated on a research project investigating brown bear spatial use patterns and habitat selection near the Malaspina Glacier (GMU 5B) to provide managers information for developing future brown bear management strategies.

Managers have expressed a need for better population information to help guide their management decisions. Commercial hunting guides have requested additional commercial guiding opportunities in GMU 5. In addition, the public has submitted proposals to the Alaska Board of Game (BOG) to increase brown bear harvest levels in GMU 5, the area surrounding the village of Yakutat. The NPS is involved in brown bear management in GMU 5 because the NPS permits subsistence harvest, allowing federally qualified users to harvest 1 bear per year, and also issues special use permits to commercial guides and outfitters for brown bear hunts. Knowledge of brown bear seasonal spatial use and movement patterns will help guide the timing and location of regulated activities.

The most recent population estimate of 108 bears in GMU 5B comes from a statewide brown bear population study by Miller et al. (1997). They calculated population size by applying density estimates derived in other regions of the state to assumptions about the amount and quality of available habitat in GMU 5B. ADF&G has used this estimate to manage brown bear harvest in GMU 5B, and harvest typically meets or exceeds established guideline harvest levels. Lacking more recent and definitive knowledge of brown bear numbers, spatial requirements, and harvest vulnerabilities, ADF&G has not endorsed the petitions for increased harvest.

The primary objectives of this research project were to provide information on brown bear seasonal habitat use and movement patterns, home range analyses, and habitat preferences for

bears near the Malaspina Glacier. The biological factors that affect movement patterns, home range size, and habitat selection are often useful indicators of the spatial and ecological requirements of species (Seaman and Powell 1996, McLoughlin et al. 1999). Factors that have been shown to affect home range size include sex, age, season (Burt 1943), population density (Dahle and Swenson 2003), body size (McNab 1963), social organization, habitat quality (McLoughlin et al. 2002), and risk of predation (Kie 1999). An inverse relationship exists between density and female home range size (Sandell 1989, Nagy and Haroldson 1990, Bjornlie et al. 2014).

Malaspina Glacier is a piedmont glacier covering approximately 2,200 km² on the flat coastal foreland of northern Southeast Alaska near Yakutat. Seismic explorations show that the ice, 600 m thick, lies in a basin up to 300 m below sea level (Sharp 1958). As glaciers recede and habitats transform, brown bear populations will likely be regulated by habitat quality and population density. If forage availability and distribution within an animal's home range do not meet energetic and nutritional requirements, then home range size must increase to meet the demands. Consequently, we expect that the quality and assembly of resources along the northern mainland coast to influence brown bear home range size and habitat selection. Determining habitat quality and population density was not within the scope of this project, however, recent studies of Southeast Alaska mainland brown bear populations indicate lower densities than adjacent island (i.e., Admiralty, Baranof, and Chichagof (ABC) islands) populations (Flynn et al. 2012). In this study, we investigated the role of sex, reproductive status, and season in determining home range size and resource selection in this unique glacial landscape.

Study Area

The 990 km² study area was located near the Malaspina Glacier along the northern mainland coast of Southeast Alaska, USA (lat 59°44'40"N, long 140°8'50"W) (Fig. 1) between Yakutat and Icy bays, about 30 km to the northwest of the community of Yakutat. The Malaspina Glacier, the world's largest piedmont glacier (ca. 5,000 km²), connects to the most expansive icefield complex in North America (Sharp 1958) (Fig. 2). The movement of this glacier from the foothills of the adjacent mountain range to the Gulf of Alaska has excavated and shaped the flat and narrow terrain of the forelands. We focused bear capture efforts on a 20 km section of shoreline from Point Manby to the Grand Wash River. The majority of lands within the study area were within the WRST National Park and Preserve. A small portion of study area lands to the west near Icy Bay is administered by the Chugach Alaska Corporation and Bureau of Land Management. The State of Alaska manages hunting and trapping on the lands between Yakutat Bay and Icy Bay with regulations specific to GMU 5B. Weather observations in nearby Yakutat reported by the National Climatic Data Center during 1981–2010, indicate the region has a maritime climate with mean temperatures ranging from -2.2° C in January to 12.2° C in July, and annual precipitation of 408 cm.

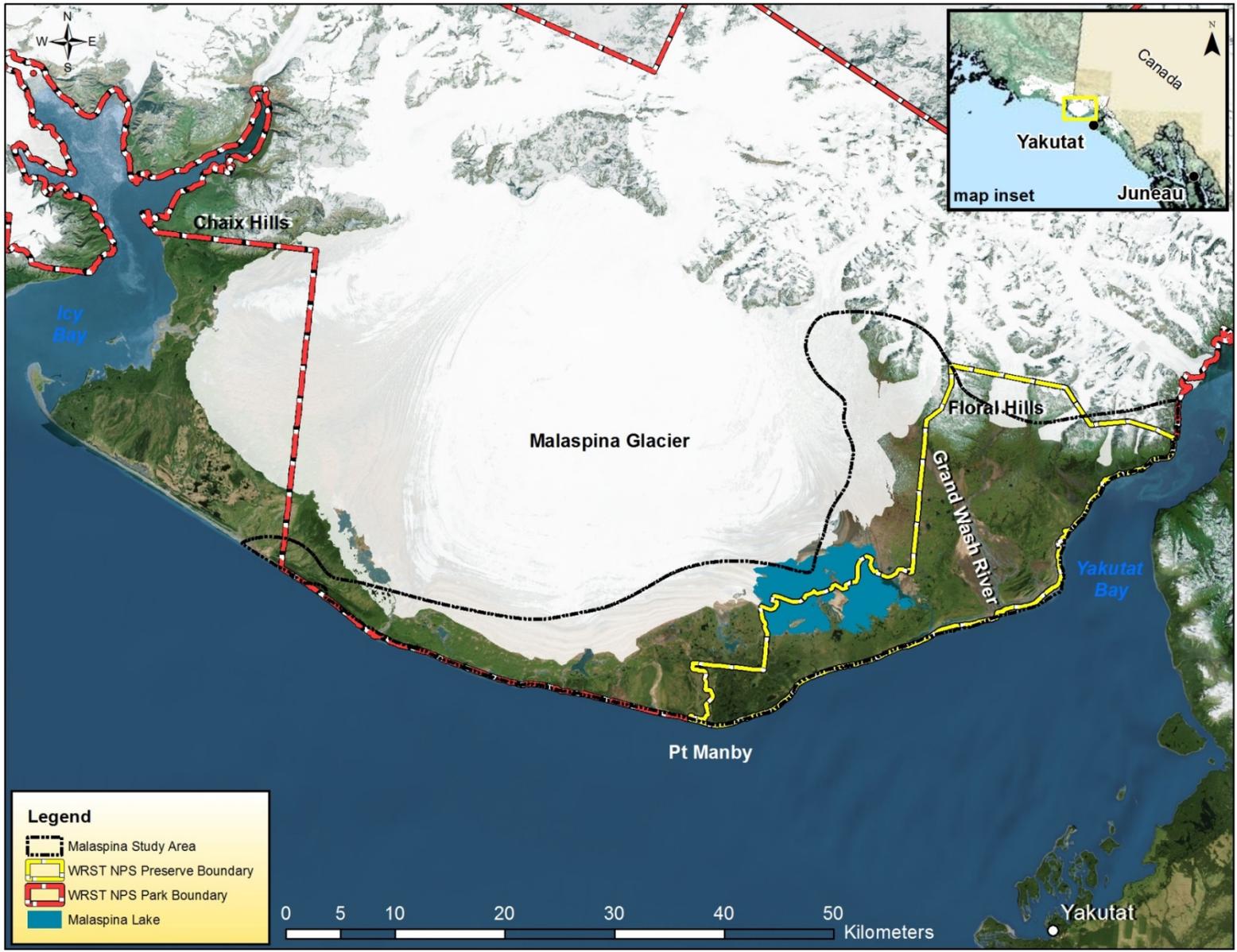


Figure 1. Location of Malaspina Forelands study area in Southeast Alaska where brown bear research was conducted, 2009–2013.



Figure 2. Photograph taken during an aerial telemetry flight in June 2013 depicting the character of the Malaspina Glacier landscape, with Mount St. Elias in the background.

The landscape between the glacier and the coastal beach habitat is characterized by sandy beaches, tidal mud flats, abundant wetlands, recently colonized Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) forests, and a mosaic of deciduous trees and shrubs including, cottonwood (*Populus* spp.), alder (*Alnus* spp.), and willow (*Salix* spp.) along the riparian margins. Glacial lakes, rivers, and streams provide important spawning and rearing habitats for fish species with 78 documented anadromous water bodies between Yakutat Bay and Icy Bay supporting 4 species of Pacific salmon (*Oncorhynchus*): sockeye (*O. nerka*), pink (*O. gorbuscha*), coho (*O. kisutch*), and king (*O. tshawytscha*), as well as eulachon (*Thaleichthys pacificus*) (Johnson and Blanche 2012). The distribution and timing of the Pacific salmon runs vary seasonally. Peak run timing for king salmon occurs between mid-June and late July, for sockeye from late June to mid-August, for pink salmon during August, and for coho from mid-August into October (Woods and Zeiser 2012).

Brown bear diet in this region is likely consistent with other coastal populations with the availability and abundance of resources varying seasonally. Graminoids (i.e., grass (Poaceae), rush (Juncaceae), or sedge (Cyperaceae)), berries (i.e., blueberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), dwarf nagoonberry (*R. arcticus*)), devil's club (*Oplopanax horridus*)), and

other herbaceous vegetation (i.e., skunk cabbage (*Lysichiton americanum*), northern rice root (*Fritillaria camschatcensis*), beach lovage (*Ligustichum scoticum*)) likely balance their primary diet of salmon and terrestrial meat such as moose, which browse this recently deglaciated landscape. During late summer, brown bears concentrate their activities along beach habitats that produce an abundance of coastal strawberry (*Fragaria chiloensis*) and ocean fishes (i.e., capelin (*Mallotus villosus*) and sand lance (*Ammodytes hexapterus*)) that have washed ashore, before moving to riparian streams and lake margins to eat salmon.

Methods

ANIMAL CAPTURE AND TELEMETRY

Between July 2009 and July 2012, we captured brown bears along the southeast shoreline of the study area using foot snaring and aerial darting techniques (Titus et al. 1999). In 2009 and 2010, we captured bears using modified Aldrich foot snares set along bear trails traversing the beach. We checked the snares daily by manually inspecting them or listening to snare-side VHF transmitters that indicated whether they were triggered. In 2011 and 2012, we used a Hughes 500D or Bell 206 Jet Ranger helicopter to opportunistically locate bears to collar or recapture. Each bear was chemically immobilized using tiletamine zolazepam (Telazol®, Fort Dodge Animal Health, Fort Dodge, IA, USA) at a dosage of 7–10 mg/kg estimated body weight (Taylor et al. 1989). We administered the anesthesia by a 3–5 cc projectile dart delivered from a Palmer Cap-Chur gun. All animal capture and handling protocols were approved by the department’s Animal Care and Use Committee under ACUC #07–14, and we adhered to cooperative project agreement COOP–09–128, and Scientific Research and Collecting Permit WRST–2009–SCI–011.

Each animal was marked with a unique numbered ear tag and an ear tissue sample was collected for DNA analysis. The tissue was subsampled and preserved in 95% ethanol for archival storage. We collected morphometric measurements on skull length and width, neck girth, total body length, chest girth, and estimated body weight. To determine bear age, we extracted a premolar tooth for cementum analysis (Matson et al. 1993) at Matson’s Laboratory (Milltown, Montana, USA). We grouped the age class of solitary bears as subadult (age class 1–4) or adult (\geq age 5), and bears that accompanied adult females as young of the year (age 0) or dependent cub (age class 1–3) (Barnes and Van Daele 2008). We determined adult female reproductive status as either solitary adult female or female with cubs, after observing cubs or evidence of lactation during capture, or observing cubs with the female on subsequent telemetry flights.

We deployed global positioning system (GPS) equipped radio collars (Telonics models TGW-3600, 3700, 3790, or 4700 Telonics, Inc., Mesa, AZ) on all captured adult brown bears, and on 3–4 year old subadults. The GPS collars were set to collect a location fix at 20 to 30 minute intervals from 16 April to 15 November, and then changed to an acquisition rate of 1 fix per day from 16 November to 15 April. Most collars stored location, activity and temperature data via

internal memory, yet some collars (model 3790) were capable of being downloaded remotely by transmitting this information to a laptop computer operated in a fixed wing aircraft when within 1 km of the bear. Each collar was also equipped with a standard VHF beacon in the 150–151 MHz range. Collars were fitted with a release mechanism (Telonics model CR–2a) programmed to detach from the bear 10–24 months after deployment. We selected release dates that we believed would best facilitate collar retrieval, although in several instances release mechanisms failed and we did not recover the collars.

Once collars were recovered we downloaded GPS locations on a personal computer using Telonics software (TDC version 2.18). We processed the output files and converted the data to a geodatabase for analysis. We mapped the spatial distribution of all GPS locations in a Geographic Information System (GIS) to determine the spatial extent of brown bear activity. We then screened GPS locations to improve location precision and minimize locations believed to be inaccurate or impossible (D'Eon et al. 2002). We used the activity and temperature sensors in the collars to determine the actual date and time that the collar released from the animal or when the animal died. For seasonal activity patterns, we divided the year into 5 seasons: 1) spring, 1 April to 31 May; 2) early summer, 1 June to 15 July; 3) late summer, 16 July to 15 September; 4) autumn, 16 September to 30 November; and 5) winter, 1 December to 31 March. These seasons correspond to expected changes in brown bear foraging behavior due to seasonally ephemeral food resources and denning chronology.

ANALYSES

Home Range

We used 2 methods to estimate multi-year male and female home ranges and space use from mapped locations of collared brown bears within the study area using the Geospatial Modeling Environment (GME; Beyer 2013) and ArcGIS (Version 10.1, ESRI 2013). First, we calculated 100% minimum convex polygons (MCP) to evaluate each bear's maximum spatial extent (Mohr 1947, White and Garrott 1990). Although this metric cannot be used to interpret the intensity of space use within an animal's home range, we nevertheless estimated the 100% MCPs for comparison with other studies. To address the limitations of 100% MCPs, we next used kernel density estimation (KDE) methods to estimate home range size, to define the probability of use of particular areas, and to determine concentrations of activity or utilization distributions within each home range (Worton 1989).

We generated a fixed kernel to estimate the 95% home range size using least-squares cross-validation (LSCV) to estimate the bandwidth (Seaman and Powell 1996, Horne and Garton 2006). We acknowledge that no single bandwidth estimator can be applied to all species (Hemson et al. 2005) and complications can arise due to spatial and temporal autocorrelation of GPS-collected location data (DeSolla et al. 1999, Fieberg 2007), yet we believe our methods are

biologically appropriate for this species given our sample size (Silverman 1986, Kie et al. 2010). We chose LSCV to estimate the smoothing parameter of the utilization distribution as it is robust to clumped location distributions (Gitzen et al. 2006), as is often observed with bears occupying daybeds and patchy habitats.

Only bears with a minimum of 1,000 annual locations were used in order to adequately describe the animal's temporal and spatial use of the study area. Furthermore, we defined home range following the long-standing definition of Burt (1943):

“that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.”

As such, we did not include the month-long sojourn of one adult male bear's circumnavigation of the Malaspina Glacier in our analyses. Finally, we truncated brown bear home range estimates that extended into ocean habitats by clipping the estimated home range polygon to the defined shoreline, similar to the approach used by Goodrich et al. (2010).

We compared male and female KDE annual and seasonal home range estimates using a one-way ANOVA using PROC GLM (SAS Institute Inc., Cary, NC, USA). We performed all statistical analyses at the 95% significance level, and means are presented \pm SE.

Effects of sex, age, and reproductive status on home range size

We examined repeated-measures mixed-effects models, using a Gaussian error distribution and variance component covariance structure, to evaluate the effects of age, sex, and reproductive factors on seasonal home range size. We treated each animal as a random effect to quantify and account for individual variation in seasonal home range size, as well as to investigate the contribution of the individual to the total variance of the dependent variable. The use of this random effect allows individual variation to be quantified and enables model interpretations to be extended to the entire population (Bolker et al. 2009). We assessed the random effects of our models using likelihood ratio tests, specifying the restricted maximum likelihood (REML) estimation method. We normalized the response variable, home range area (km²), with a root-root transformation. Model selection was based on the small-sample corrected Akaike's Information Criterion (AICc).

We assessed the effects of season, cohort (including adult females with offspring, adult females without offspring, adult males, and subadult males), and year, as well as all interactions, for animals with a minimum of 200 seasonal locations. As seasonal variation in habitat use reflects changes in bear diet, plant phenology, and salmon run timing, we defined season according to expected changes in available resources. Seasons were divided by date range into spring (1 April – 31 May), early summer (1 June – 15 July), late summer (16 July – 15 September), autumn (16 September – 30 November), and winter (1 December – 31 March). Coefficient estimates were

presented relative to the baseline reference category within each factor (season = autumn, cohort = subadult male, and year = 2013). We used a backward stepwise procedure to select the candidate models.

Given that we had multiple measures of the same individual varying in time and space according to season and year, we evaluated the seasonal, cohort and annual influence on brown bear home range size using the following mixed-effects model equation:

$$Y_{ij} = \beta_0 + \beta_1 X_{1ij} + \beta_2 X_{2ij} + \dots + \beta_n X_{nij} + u_{0j} + e_{0ij} \quad (1)$$

where:

Y_{ij} = estimated home range size of the j^{th} animal in the i^{th} group, n = number of predictors, β_0 = global intercept, β_n = coefficient of the n^{th} predictor variable, X_{nij} = i^{th} value of the n^{th} predictor variable for the j^{th} animal, u_{0j} = random intercept for the j^{th} animal, e_{0ij} = residual error term for j^{th} animal.

MOVEMENT PATTERNS AND HUNTING VULNERABILITY

We created daily movement paths between each point location for individual bears using GME. Using ArcGIS, we digitized the edge of the saltwater shoreline and Malaspina Lake to reflect current habitat conditions obtained from high-resolution satellite imagery collected in September 2011, and accessed via Bing Maps Services (Microsoft Corp. 2014). We calculated the Euclidean distance between bear locations and the saltwater shoreline. As we assumed bears would be most vulnerable to human activities within 1.0 km of the shoreline, we tallied the number and percentage of locations in this zone. We also calculated the Euclidean distance between bear locations and anadromous streams identified in the Anadromous Waters Catalog (Johnson and Blanche 2012).

DEN LOCATIONS

We examined GPS locations collected in the late-autumn to early-spring seasons to determine approximate den location, as well as den entrance and emergence dates. We determined locations and entrance dates based on several successive locations in a region and the evaluation of GPS collar activity and temperature sensor data. These locations were typically identified in the vicinity of the last successful fix prior to winter hibernation and the first series of successful fixes in the spring. We did not visit any of these potential den site locations, but given the unique aspects of the landscape, incorporating these locations into a future study of den site selection would be valuable.

HABITAT SELECTION

Resource Selection Function Model Development

To measure selection of habitat by brown bears, we developed a resource selection function (RSF). RSFs measure selection of habitat by statistically comparing the environmental attributes of animal GPS locations ('used' points) versus the attributes of the surrounding environment as characterized by random locations ('available' points). In this study, the available points were generated at the scale of the study area (1st-order selection, Johnson 1980), and habitat selection by each individual brown bear was contrasted with the available points (Design II approach, Manly et al. 2002). Then, individual brown bear models were averaged to obtain an overall, population-level RSF (Fieberg et al. 2010).

We chose to limit RSF models to the late-summer season (16 July–15 September), a period in which selection of habitats to optimize nutritional intake is particularly important for brown bears (Schoen et al. 1994, Hilderbrand et al. 1999). Additionally, this period included the greatest number of animals and GPS locations. Data for both male and female brown bears during late summer were combined to create a more robust data set with which to investigate habitat selection.

To delineate the extent at which habitat selection was assessed, we first created a polygon using the 99% isopleth of a kernel density estimation (KDE) function in GME constructed from all brown bear locations. We then constrained this polygon to focus on WRST lands surrounding the Malaspina Glacier, a region similar to the focus of our capture efforts and therefore most relevant to model prediction. Areas of little or no value as bear habitat—including saltwater and Malaspina Lake—were digitized using current satellite images accessed via Bing Map Services (Microsoft Corp. 2014) and then removed from this polygon to obtain the RSF study area (917.9 km², Fig. 1). Within the study area, 500,000 random points were generated to characterize habitat available to brown bears. Because of the limited use of ice- and snow-covered terrain in the study area by brown bears (< 0.3% of all locations, and only 3 of 13 bears had one or more locations in ice/snow), we excluded areas of ice and snow within the study area from the RSF analysis.

All used and available locations were attributed with a suite of both continuous and categorical environmental variables (Table 1). The continuous factors included elevation, derived from the Shuttle Radar Tomography Mission Digital Elevation Model (SRTM-DEM), and distances from ecologically relevant landscape features, including documented ADF&G anadromous waters catalog (AWC) streams (Johnson and Blanche 2012), digitized saltwater shoreline, and areas classified as herbaceous vegetation. These continuous variables were standardized prior to RSF analysis by subtracting the mean and dividing by the standard deviation. The categorical variables consisted of vegetation classes derived from an existing GIS landcover database (Fig.

3) (Boggs et al. 2014), which compiled landcover data from a classification derived from a Landsat image collected on 14 July 1999 (Stumpf et al. 2007) with the National Wetland Inventory (USFWS 2009).

Potential model factors were screened for collinearity using Pearson's correlation coefficient, and the 'distance to shoreline' factor was removed due to high collinearity ($r_s = 0.69$) with 'distance to AWC'. Models were built using the GLM function in the R statistical environment (R Development Core Team 2014), from which RSFs describing the relationship between animal use and model factors (Table 1) can be obtained via the equation:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n) \quad (2)$$

where $w(x)$ is proportional to the probability of use for each individual brown bear.

The factor coefficients ($\beta_1, \beta_2, \dots, \beta_n$) were then averaged across individuals using a method in which coefficients were weighted according to the inverse of their variance (Fieberg et al. 2010, Murtaugh 2007). This method ensures that the contribution of individual animal coefficients for which there is little confidence is reduced in the population-level model. We used a backward elimination model selection procedure to develop a final set of predictor variables, dropping factors with confidence intervals surrounding zero until a final model was achieved.

Model Validation

Late-summer habitat selection models were validated using the k -fold cross-validation method (Boyce et al. 2002, Johnson et al. 2006). In the k -fold cross-validation method, a set of validation data is removed from the total pool of data, leaving the training data. A new model is built using only the training data and the original model factors. This new model is then tested to see how accurately it predicts the removed validation data. The variable k represents the number of times this process is iterated. Typically (and here), $k = 5$ is chosen, the training data being built on $1 - (k/n)$ of the data and validated using k/n of the data, where n is the total number of bears ($n = 13$).

Each of the 5 resulting models was then used to generate RSF scores for all the available (random) points and for all of the point locations from the bears in the removed, validation set. The RSF scores for the available points were then split into 10 equal-sized bins ranked in increasing order, from low to high relative probability of selection. The mean RSF score of each bin was divided by the sum of these means to yield the *expected* proportion of locations in each bin. The RSF scores of the validation-set bears were similarly split using the same breakpoint values as used to split the available points. This yields the *observed* proportion of values in each bin.

These sets of expected and observed proportions were then analyzed against each other using Spearman's rank correlation and linear regression. Larger Spearman's rho values (approaching 1

Table 1. Terrain and landcover factors used in resource selection functions (RSF) for brown bears along the Malaspina Forelands, Southeast Alaska.

Variable	Definition	Source data
<i>Terrain factors</i>		
Distance from anadromous streams	Euclidean distance (m) to nearest Anadromous Waters Catalog (AWC) stream reach	ArcGIS Spatial Analyst
Distance from shoreline	Euclidean distance (m) to saltwater shoreline	ArcGIS Spatial Analyst
Distance from herbaceous	Euclidean distance (m) to herbaceous habitats	ArcGIS Spatial Analyst
Elevation	Elevation above sea level (m)	SRTM-DEM; ArcGIS Spatial Analyst
<i>Landcover classification</i>		
Conifer forest	Forest characterized by a combination of open and closed conifer forest assemblages	Alaska Natural Heritage Program landcover classification accessed 10 December 2013
Deciduous forest	Landcover type dominated by deciduous trees	Alaska Natural Heritage Program landcover classification
Shrub forest	Landcover types dominated by deciduous shrubs	Alaska Natural Heritage Program landcover classification
Herbaceous	Landcover types dominated by sedges, grass, and other herbaceous plants	Alaska Natural Heritage Program landcover classification
Unvegetated	Landcover type of rock, gravel, sand	Alaska Natural Heritage Program landcover classification
Water	Water: fresh, salt, turbid, shadowed	Alaska Natural Heritage Program landcover classification
Ice_Snow	Ice and snow	Alaska Natural Heritage Program landcover classification

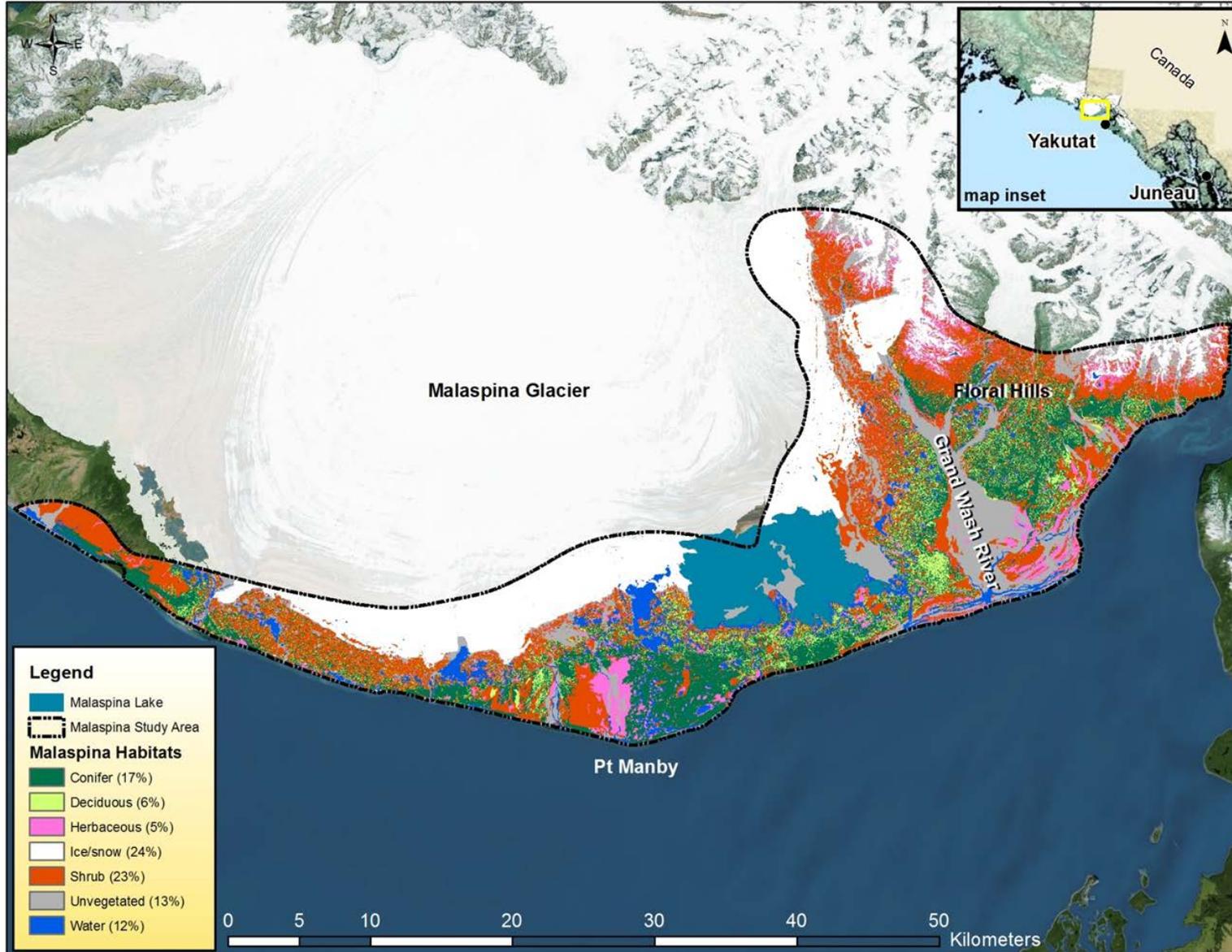


Figure 3. Distribution of predominant landcover classification habitat types, including percent occurrence used in RSF model of brown bear habitat selection along the Malaspina Forelands, Southeast Alaska, 2009–2013.

with low *P*-values) indicate concordance between the rankings of observed versus expected values (Boyce et al. 2002). Regression analysis results in optimum performance when the slope approaches 1, the *y*-intercept approaches 0, and the adjusted *r*-squared approaches 1. Such optimal results indicate proportionality between observed and expected results (Johnson et al. 2006, Wiens et al. 2006).

We generated an output surface map of relative probability of selection using the coefficients of factors included in the final model. The RSF score predictions were binned into 5 classes by sorting the raw RSF scores from lowest to highest, and then selecting breakpoints such that the values divided into bins that had an equal number of values in each of them. Because all pixels were identical in size, and each value represented a pixel, the RSF surface was divided into equal areas in each bin. Each binned habitat class was defined with the following upper limit breakpoint values, low (2.10), low-moderate (3.87), moderate (5.46), moderate-high (7.49), and high (68.67). We aim to understand brown bear habitat selection through an examination of these resource selection analyses.

Results

ANIMAL CAPTURE AND TELEMETRY

During 2009–2012, we captured 20 individual bears (10 males and 10 females) (Table 2) along the southeast portion of the Malaspina Forelands between Point Manby and the Grand Wash River (Fig. 4–5). The bears captured represented various age and sex cohorts comprised of 8 adult males, 6 adult females, 2 subadult males, and 4 subadult females. The mean age at capture for adult males was 12.6 years, and 8.2 years for adult females. The oldest male was aged at 20 years, and the oldest female was 13 years. The majority of captures ($n = 15$) occurred along the shoreline using foot snares, and the remainder were captured from a helicopter (Table 2).

We deployed GPS-equipped collars on 18 bears, 4 of which were subsequently recaptured and affixed with a second collar. Between July 2009 and October 2013, we collected 64,076 GPS locations (Table 3), recording data on 16 individual bears for varying duration ranging from 3 days to more than 3 years. Three collars were not recovered due to collar release mechanism malfunction. The data from these collars were not available for the analyses. Hence, we did not retrieve GPS data for captured subadult females. We recaptured 2 bears whose original collars didn't release correctly. For an additional 11 bear captures, we attached collars that had remote download capabilities. For the most part, these collars worked fine.

Although all bear GPS data were found to be informative and interesting, 2 animals in particular warrant description for their anomalous movements. One 6-yr old male bear, 722, was captured in Yakutat and later swam 5.25 km over 90 minutes (~2 mph) across Yakutat Bay from Latouche Point to the Malaspina Forelands. Concurrent with the typical mating season (May to July), he

Table 2. Brown bears captured along the Malaspina Forelands, Southeast Alaska, 2009–2013, indicating animal identification, sex, age, capture date, capture method, and female reproductive status.

Bear ID	Sex	Age	Capture date	Collar status	Bear status	Capture method	Female reproductive status at capture
705	F	3	7/21/2009	Did not release; EOL	Alive: 8/26/12	FS	No cubs; sub-adult, no estrus
706	M	5	7/21/2009	Released early; unknown	Alive: 10/17/09	FS	
707	F	5	7/24/2009	Did not release; EOL	Alive: 10/8/11	FS	No cubs; no estrus
708	M	3	7/24/2009	Released early; poss bear	Alive: 4/8/10	FS	
709	M	17	7/24/2009	Released early; unknown	Alive: 8/7/2009	FS	
710 ^a	M	10	7/25/2009	Collar failed	Recollared	FS	
710 ^b	M	10	8/8/2009	Released early; poss bear	Alive: 9/16/09	FS	
711 ^a	F	8	7/26/2009	Did not release; recaptured	Recollared	FS	No cubs; no estrus
711 ^b	F	10	6/17/2011	Did not release; downloaded	Alive: 10/11/13	H	2 0-yr cub; lactating
712	F	1.5	7/25/2009	Did not collar		FS	No cubs; sub-adult, no estrus
713 ^a	F	5	7/26/2009	Did not release; recaptured	Recollared	FS	No cubs; no estrus
713 ^b	F	7	6/19/2011	Did not release; downloaded	Alive: 10/11/13	H	No cubs; in estrus
714	M	15	7/26/2009	Released early; unknown	Dead: 10/7/09; hunter killed	FS	
715	F	4	7/26/2009	Did not release; EOL	Alive: 8/26/12	FS	No cubs; sub-adult, no estrus
718	F	0.5	8/8/2009	Did not collar		FS	No cubs; sub-adult, no estrus
724 ^a	M	9	8/10/2010	Released early; unknown	Recollared	FS	
724 ^b	M	10	8/4/2011	Did not release; MIA	Alive: 11/3/11	H	
725	M	20	8/12/2010	Released; bear	Alive: 4/26/11	FS	
731	M	8	6/18/2011	Released; bear	Alive: 5/21/12	H	
732	M	3	8/3/2011	Did not release	Alive: 10/10/13	H	
733	F	11	8/3/2011	Release unknown	Dead: 8/4/11 ^c	H	1 0-yr cub; lactating
734	F	7	8/4/2011	Did not release	Alive: 10/10/13	H	No cubs; no estrus
738	M	17	7/12/2012	Release unknown	Alive: 7/16/12	H	
739	F	13	7/28/2012	Did not release	Alive: 10/11/13	H	No cubs; no estrus

^a First capture of individual bear. ^b Second capture of same individual bear. Collar status when battery is at end of life (EOL). Capture methods are foot snare (FS) and helicopter (H). ^c Cause of death was another bear.

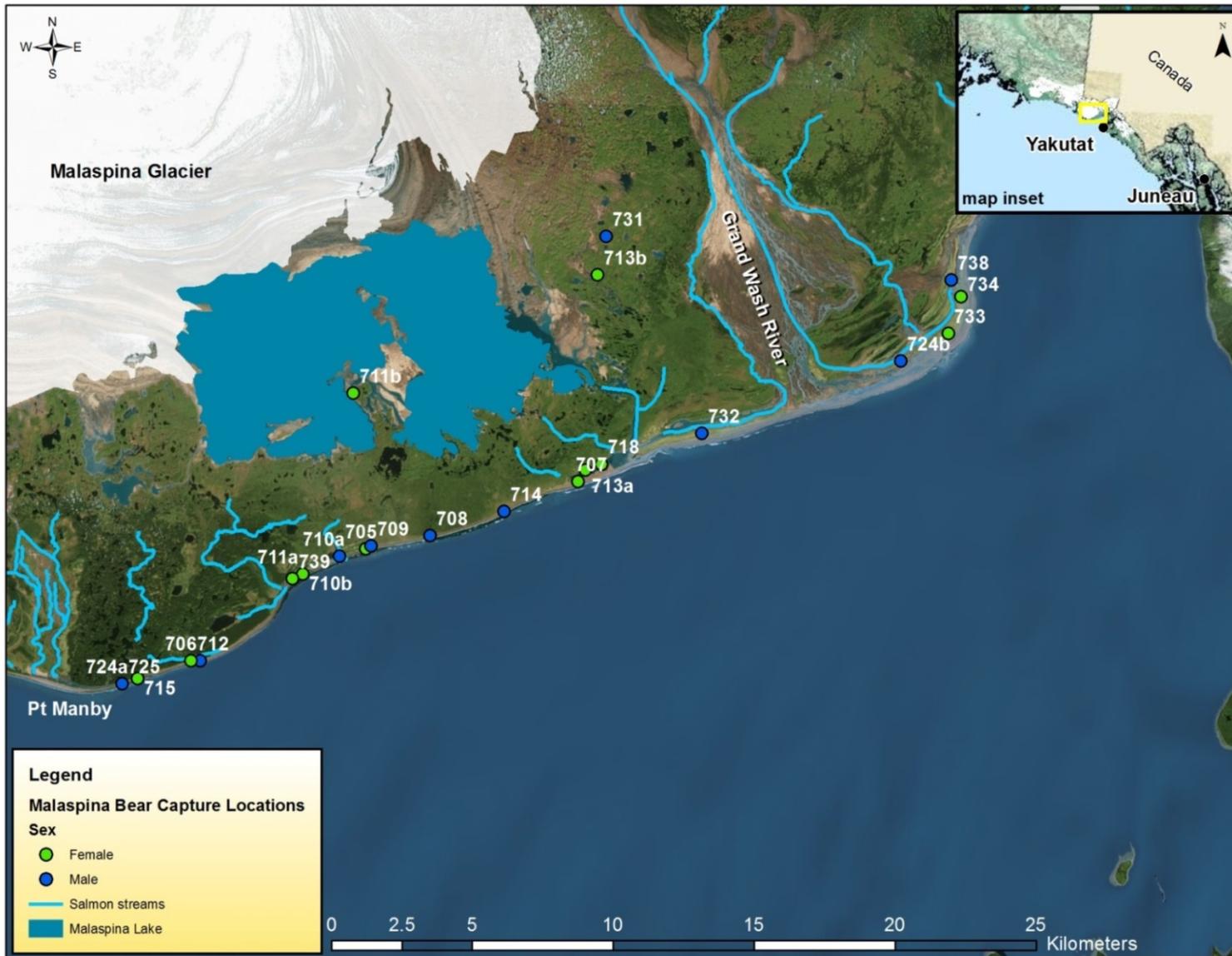


Figure 4. Brown bear capture locations in Wrangell-St. Elias National Preserve along the Malaspina Forelands, Southeast Alaska, 2009–2012.



Figure 5. Immobilized bear, adult male 724, captured in a foot snare by LaVern Beier and Anthony Crupi. Illustrated are the GPS collar and the forest character along the beach fringe near Pt. Manby, Southeast Alaska.

Table 3. Summary of brown bear GPS locations and home range estimates in the Malaspina Forelands study area, Southeast Alaska, 2009–2013. Annual home range estimates calculated for animals with a minimum of 1,000 locations using 2 methods, 100% minimum convex polygon (MCP) and 95% fixed kernel density estimate (KDE) with least-squares cross-validating generated bandwidths.

Bear ID	Sex	No. of successful locations	No. of days with locations	First day	Last day	Home range size km ² (100% MCP)	Home range size km ² (95% KDE)	Locations within 1 km shoreline (%)
706	M	3882	88	7/21/2009	10/17/2009	312.7	194.5	50.4%
708	M	2831	258	7/24/2009	4/8/2010	1257.7	637.0	45.6%
709	M	821	14	7/24/2009	8/7/2009	-	-	51.9%
710	M	2329	39	8/8/2009	9/16/2009	67.2	52.0	30.4%
711	F	15517	1167	7/25/2009	10/27/2012	174.0	57.4	6.2%
713	F	9979	916	7/26/2009	10/29/2012	143.5	77.9	7.6%
714	M	1138	34	7/26/2009	8/29/2009	87.9	75.8	34.6%
722	M	2500	68	5/11/2010	7/18/2010	404.4 ^a	-	46.6%
724	M	655	48	8/10/2010	8/18/2011	-	-	63.7%
725	M	1449	257	8/12/2010	4/26/2011	46.4	36.8	22.8%
731	M	3204	338	6/18/2011	5/21/2012	803.3	491.6	28.1%
732	M	7562	799	8/3/2011	10/10/2013	658.6	427.7	44.5%
733	F	6	3	8/3/2011	8/6/2011	-	-	83.3%
734	F	7877	798	8/4/2011	10/10/2013	128.1	73.6	12.5%
738	M	31	3	7/12/2012	7/15/2012	-	-	9.7%
739	F	4295	440	7/28/2012	10/11/2013	290.1	184.9	10.9%
Total		64076						22.1%

^a MCP home range of locations on the west side of Yakutat Bay.

explored a 200 km² area, over 68 days, along the eastern portion of the study area, primarily along the shoreline and riparian margins with some movements to higher elevation habitats. Later, the bear swam back to the Yakutat side of the bay. Location data from this bear while on the Malaspina Forelands were included in individual location analyses, such as mean distance to landscape features and RSF model, but not included in Malaspina bear home range estimates.

The movements of a second adult bear, 8-yr old male 731, involved a month-long counterclockwise circumnavigation of the Malaspina Glacier. This bear investigated the exposed mountainous terrain while following the north edge of the glacier, before descending the western portion of the glacier to Icy Bay. He spent a week foraging near Point Riou in Icy Bay, and then in 5 days traveled 100 km back along the coast to where he began along the Grand Wash River. The 781 locations collected during this foray were excluded from the late summer home range analysis.

We mapped bear locations for each season (spring – autumn) to depict the general seasonal habitat use patterns and summarized the number of locations collected in each season, including the proportion within 1 km of the shoreline (Table 4). In spring, bears concentrated activity in the eastern portion of the study area (Fig. 6). Adult females with young of the year cubs remained in close proximity to their low elevation den sites near Malaspina Lake for several weeks following den emergence. Adult single females and subadult males occupied habitats near the Grand Wash River and the east side of Malaspina Lake. Upon exiting the den, adult males began moving larger distances than other cohorts, transitioning through riparian habitats and typically remaining near the saltwater shoreline. In early summer, bears occupied similar portions of the study area, but locations were more dispersed from den sites, moving down in elevation and closer to both fresh and saltwater habitats where emergent vegetation is abundant (Fig. 7). The greatest number of locations was collected in late summer, corresponding to the time period when the most collars were deployed. Bears extensively used the entire study area, avoiding the unvegetated snow and ice of the Malaspina Glacier, and concentrated activities at low elevation, often foraging near riparian habitats and scavenging along the shoreline (Fig. 8). In autumn, bears focused their activities around the Grand Wash River, near the salmon streams adjacent to Pt. Manby. One subadult male bear traveled from Malaspina Lake to Icy Bay, and after 1 month fishing along salmon streams, moved up in elevation and denned in the Chaix Hills (Fig. 9).

HOME RANGE

We acquired an adequate sample to estimate multi-year annual home range sizes for 7 male and 4 female brown bears using 2 estimation methods, MCP and KDE. The average number of locations collected per individual was $5,389 \pm 1,336$, over a mean time span of 466.7 ± 118.0 days. Mean annual male MCP home range was 462.0 ± 175.5 km², which was 2.5 times larger than the female range size of 183.9 ± 36.6 km² (Table 5). Using the KDE method, the estimated

Table 4. Number of brown bear GPS locations collected within each season and the proportion within 1 km of the shoreline adjacent to the Malaspina Forelands, Southeast Alaska, 2009–2013.

Season	Dates	Number of successful locations	Within 1 km of shoreline	Within 1km shoreline (%)
Spring	04/01–05/31	9,597	965	10%
Early summer	06/01–07/15	9,936	3,002	30%
Late summer	07/16–09/15	26,011	9,773	38%
Autumn	09/16–11/30	18,486	1,164	6%
Winter	12/01–03/31	46	0	0%
Total		64,076	14,604	23%

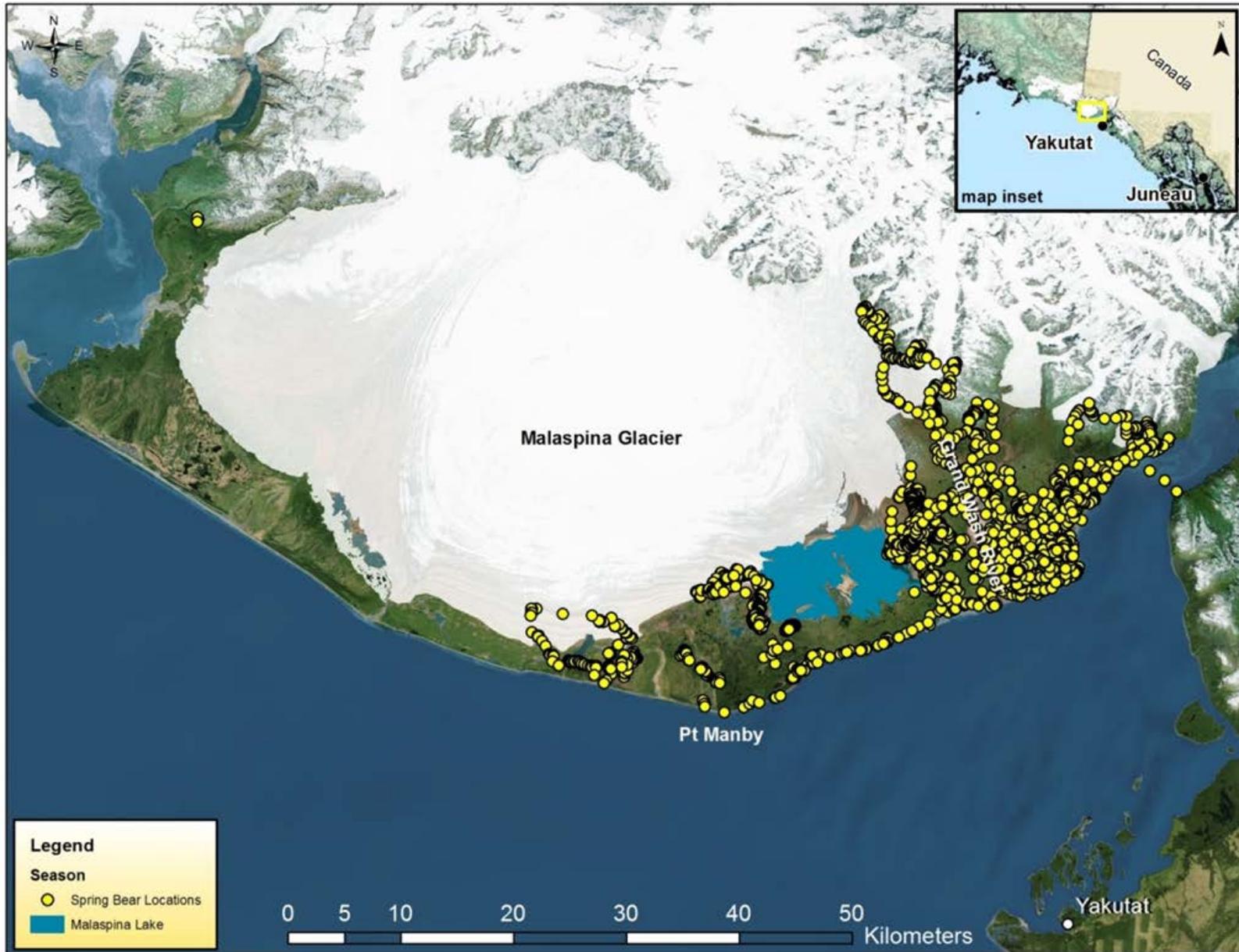


Figure 6. Brown bear locations collected during spring in the Malaspina Forelands study area, Southeast Alaska, 2010–2013.

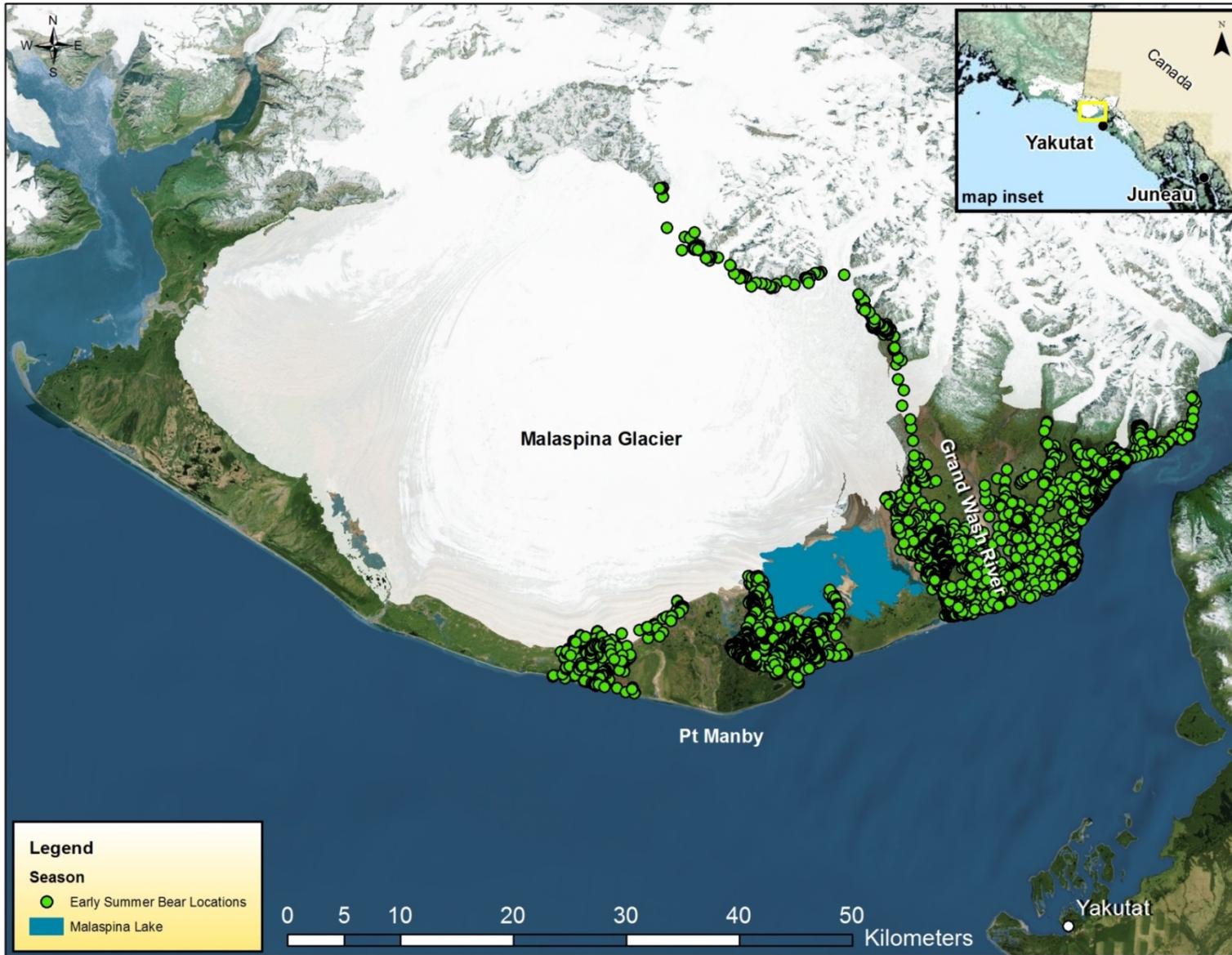


Figure 7. Brown bear locations collected during early summer in the Malaspina Forelands study area, Southeast Alaska, 2010–2013.

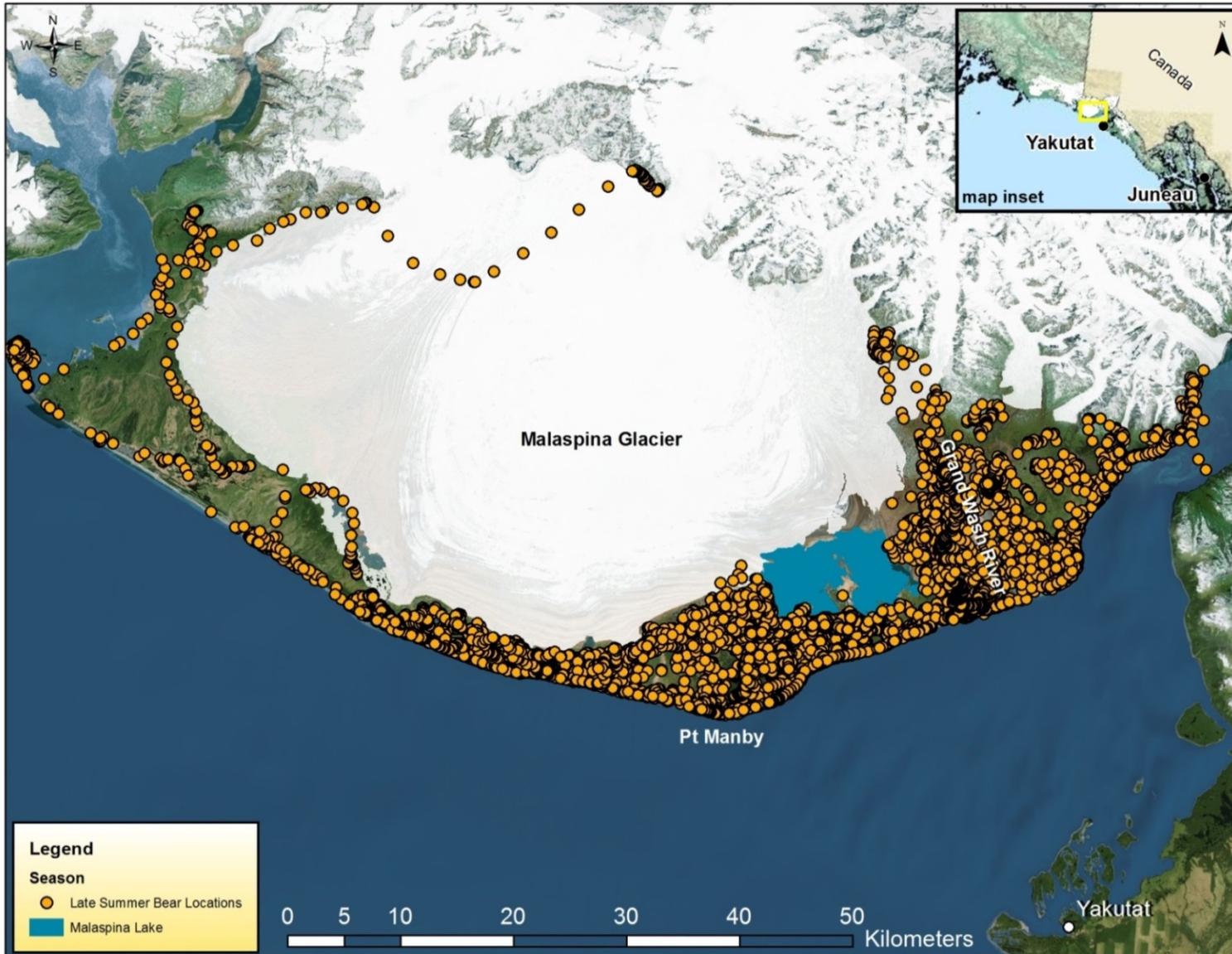


Figure 8. Brown bear locations collected during late summer in the Malaspina Forelands study area, Southeast Alaska, 2009–2013.

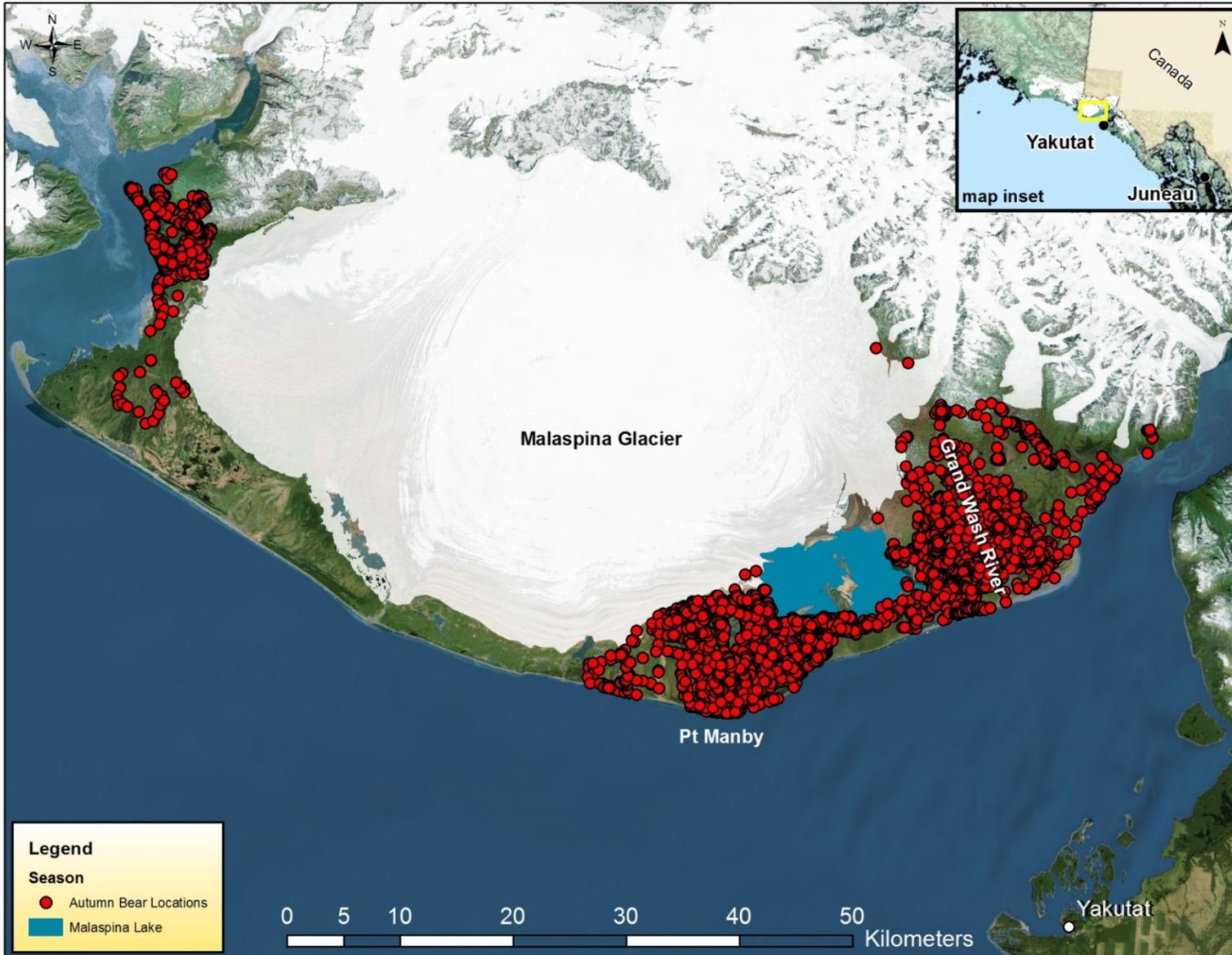


Figure 9. Brown bear locations collected during autumn in the Malaspina Forelands study area, Southeast Alaska, 2009–2013.

Table 5. Annual home range size estimates of brown bears in the Malaspina Forelands study area generated using 2 methods, 100% minimum convex polygon (MCP) and 95% fixed kernel density estimate with least-squares cross-validating generated bandwidths.

Sex	100% MCP home range (km ²)			95% KDE home range (km ²)	
	<i>n</i>	Mean±SE	Median	Mean±SE	Median
Male	7	462.0±175.5	312.7	273.6±91.8	194.5
Female	4	183.9±36.6	158.7	98.4±29.1	75.7
All bears	11	360.9±116.5	174.0	209.9±63.4	77.9
M:F ratio		2.5		2.8	

male annual 95% home range size was 2.8 times larger than females, with male home range size estimated at $273.6 \pm 91.8 \text{ km}^2$ and female range estimated at $98.4 \pm 29.1 \text{ km}^2$ (Fig. 10). However, due to small female sample size and combined reproductive classes, the effect of sex was not significant for annual home range estimates ($F_{1,10} = 1.93, P = 0.20$). The number of locations used to estimate home range size was not correlated to annual home range estimates of male or female brown bears (MCP: $r = -0.17, P = 0.61$; KDE: $r = -0.23, P = 0.49$).

We estimated 67 seasonal KDE home ranges from 13 individual bears from 2009–2013 (Appendix A). Seasonal home ranges were estimated for each sex and reproductive class for each year resulting in 42 home range estimates for females (27 adult females and 15 females with cubs) and 25 male home range estimates (17 adult male and 8 subadult males). The season with the greatest number of home ranges was late summer (24), followed by autumn (19), and an equal number of home ranges estimated in both spring, and early summer (12). Overall male seasonal home ranges were larger than females ($F_{1,65} = 6.58, P = 0.01$).

We estimated the mean seasonal KDE home range size for all cohorts within each season (Fig. 11). Female bears occupied fairly consistent-sized home ranges across seasons, with an increase in home range size for single adult females in the late summer and particularly small home ranges observed in adult females with offspring in the spring. We mapped seasonal home range estimates for each bear to illustrate the spatial extent occupied by subadult males, adult males, and female bears (cohorts combined for ease of interpretation, Fig. 12–16). Subadult male home range size was particularly pronounced in the late summer (Fig. 14). Adult male home range size remained relatively similar throughout the year, with the largest home ranges occupied in autumn (Fig. 16).

We examined a set of mixed-effects models to explain and predict the seasonal and annual variation between sex and reproductive class home range size. The best fitting mixed-effects model (Table 6) explained bear home range size with the factors of cohort, season, year, and interactions between year and season, and year, season and cohort (Table 7) ($\text{AICc} = 51.1$). Model covariance parameter estimates evaluating the random effects of individual bears indicated a significant amount of variation within individuals (Table 8), but that the variation between individuals did not help explain the model. Several fixed effects were important predictors of home range size, including cohort, season, year, and the interactions between year and season, and year, season and cohort (Table 9).

Given that the interaction between cohort and season was not significant, we developed a mixed-effects model which excluded year to generate pairwise comparisons between cohorts and seasons (Table 10). Both cohort and season were important predictors of home range size (Table 11). Subadult males had significantly larger home ranges than all other cohorts. We also found that late summer home range sizes were larger than spring home ranges.

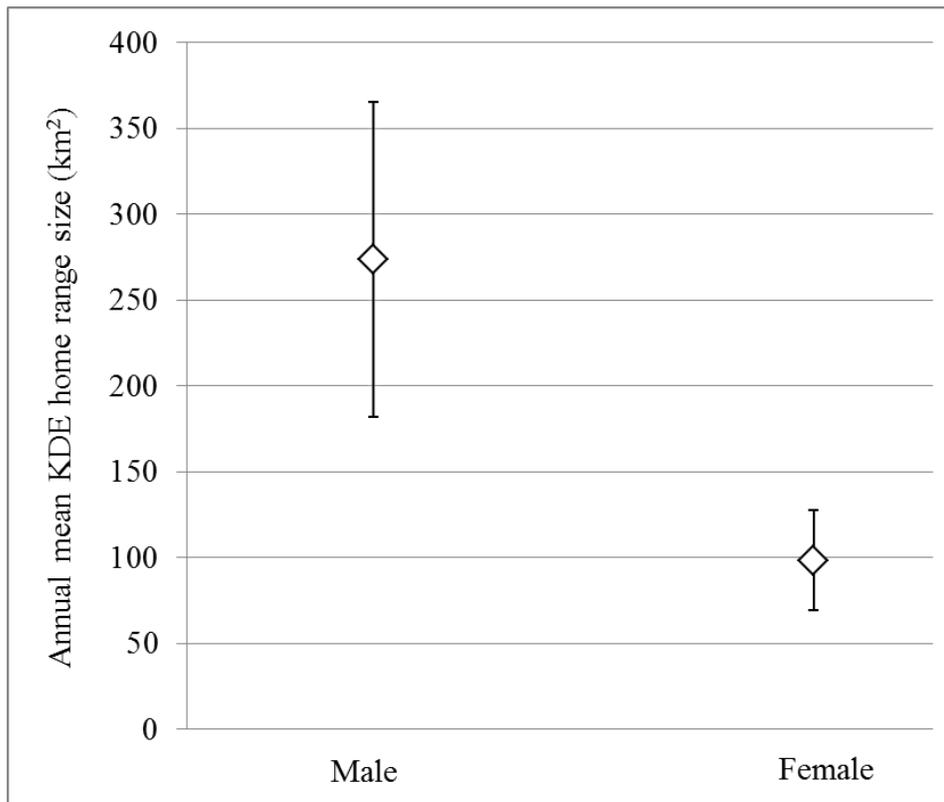


Figure 10. Mean annual KDE home range size estimated for male and female brown bears near the Malaspina Glacier, Southeast Alaska, 2009–2013. Error bars represent the SE.

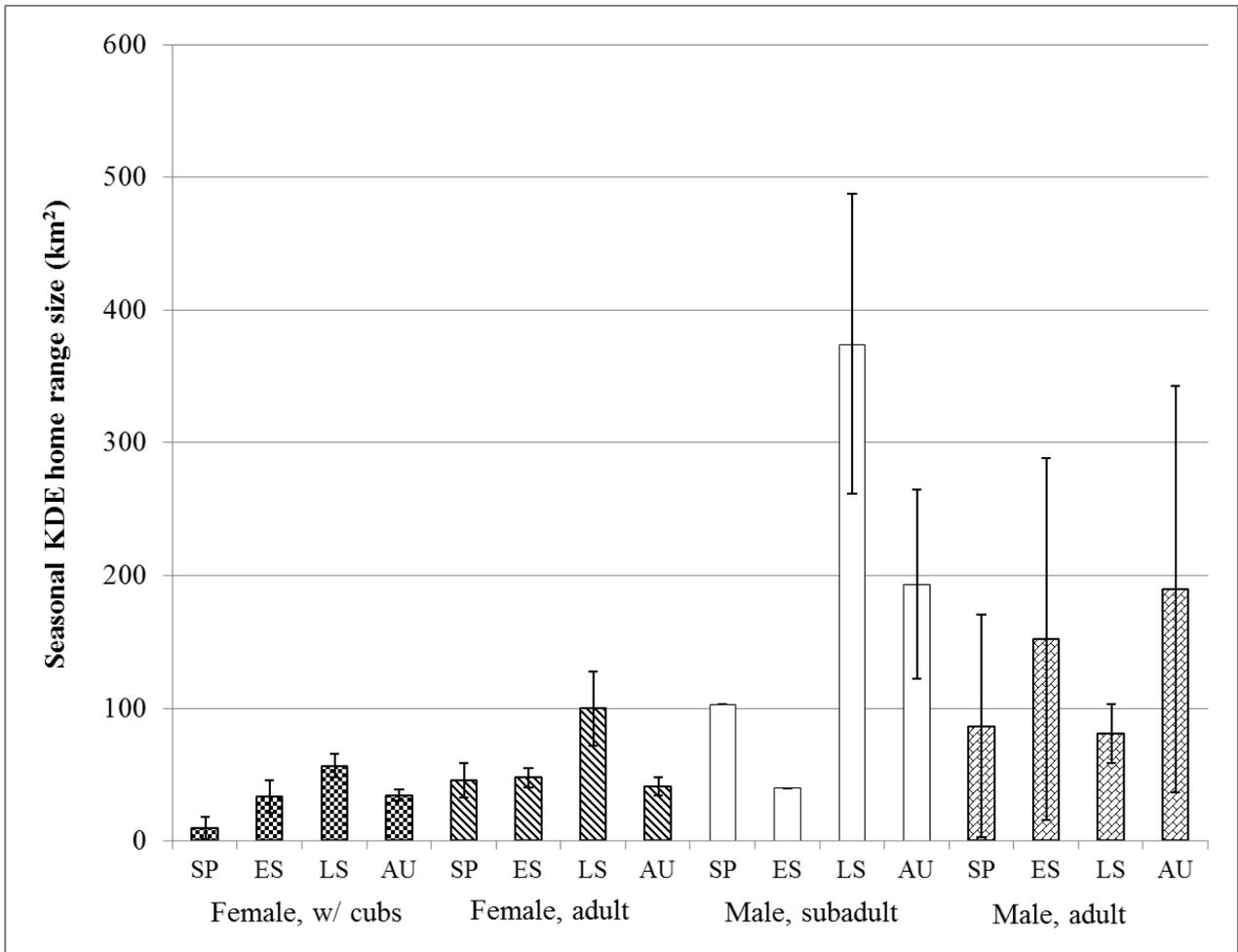


Figure 11. Seasonal KDE home range sizes of brown bear cohorts near the Malaspina Glacier, Southeast Alaska, 2009–2013 (SP = spring, ES = early summer, LS = late summer, AU = autumn).

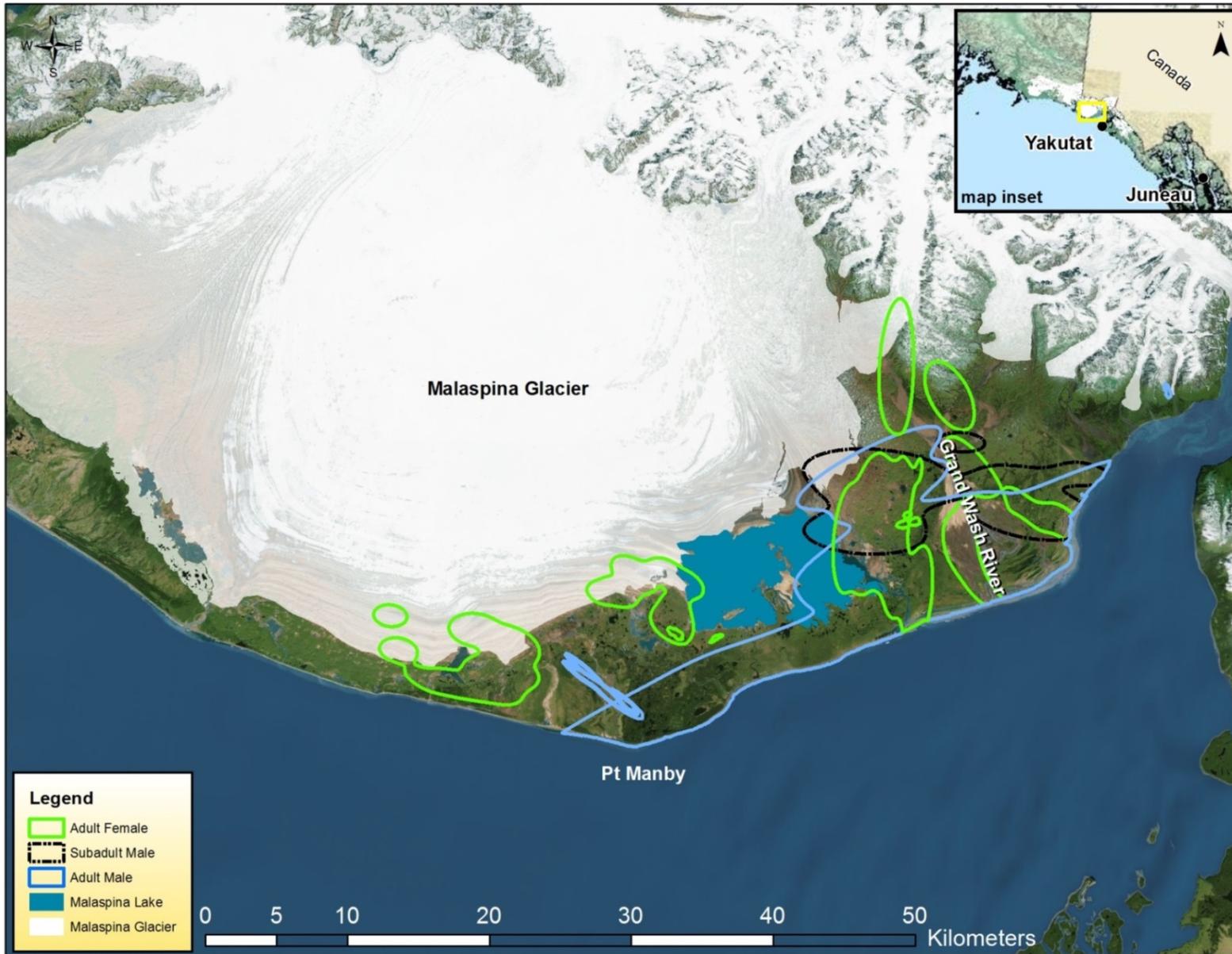


Figure 12. Brown bear seasonal home ranges during spring in the Malaspina Forelands study area, Southeast Alaska, 2010–2013.

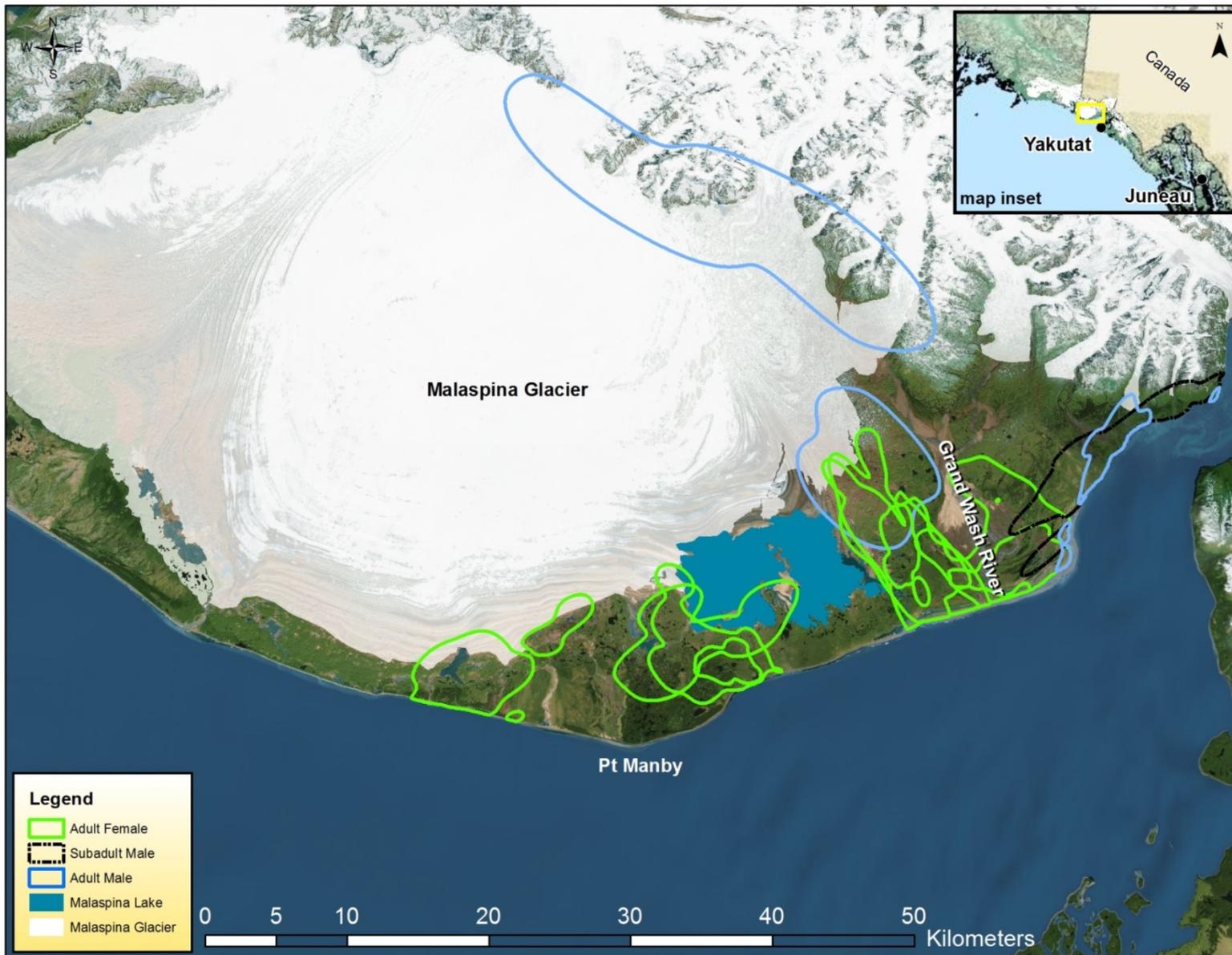


Figure 13. Brown bear seasonal home ranges during early summer in the Malaspina Forelands study area, Southeast Alaska, 2010–2013.

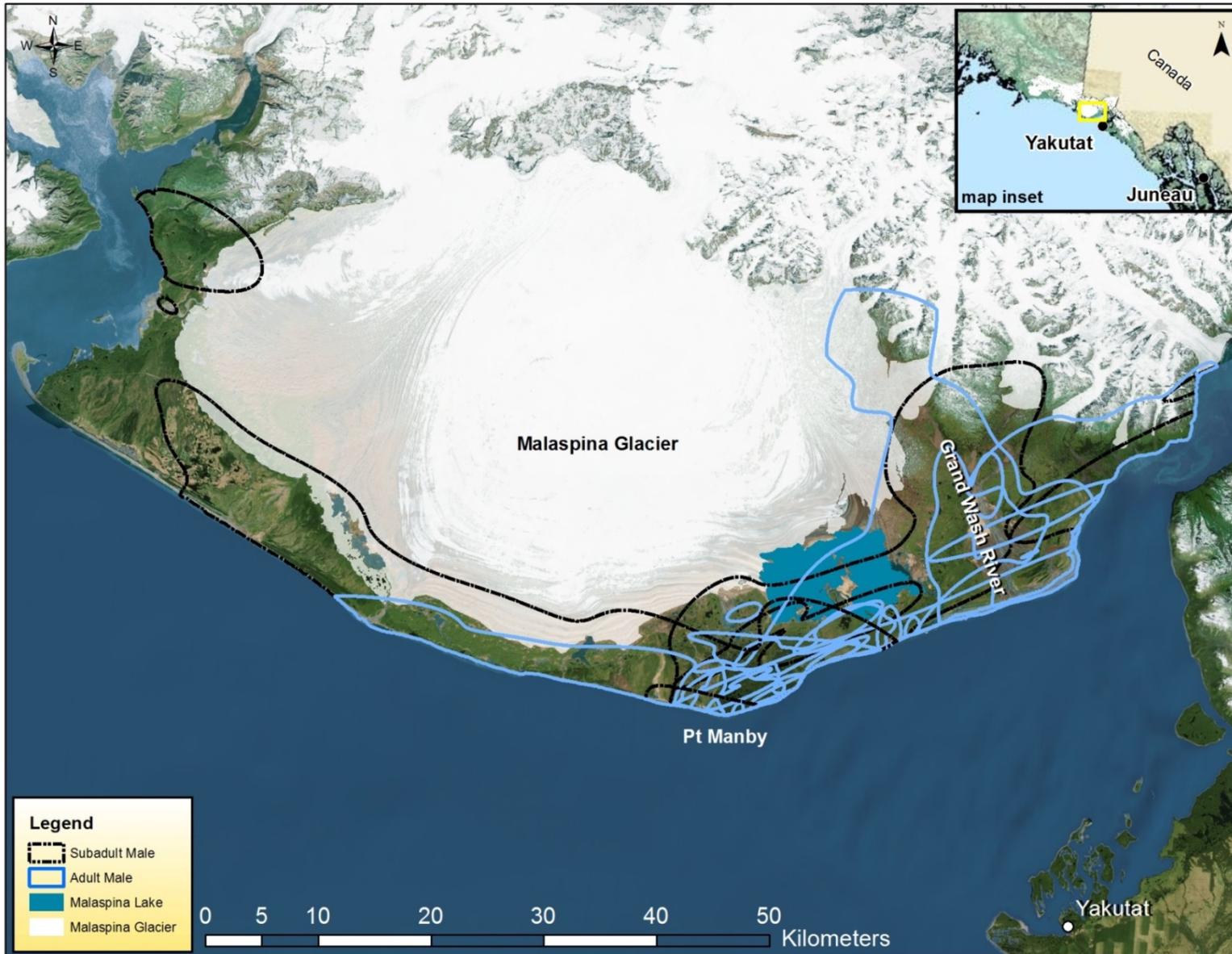


Figure 14. Male brown bear seasonal home range during late summer in the Malaspina Forelands study area, Southeast Alaska, 2009–2013.

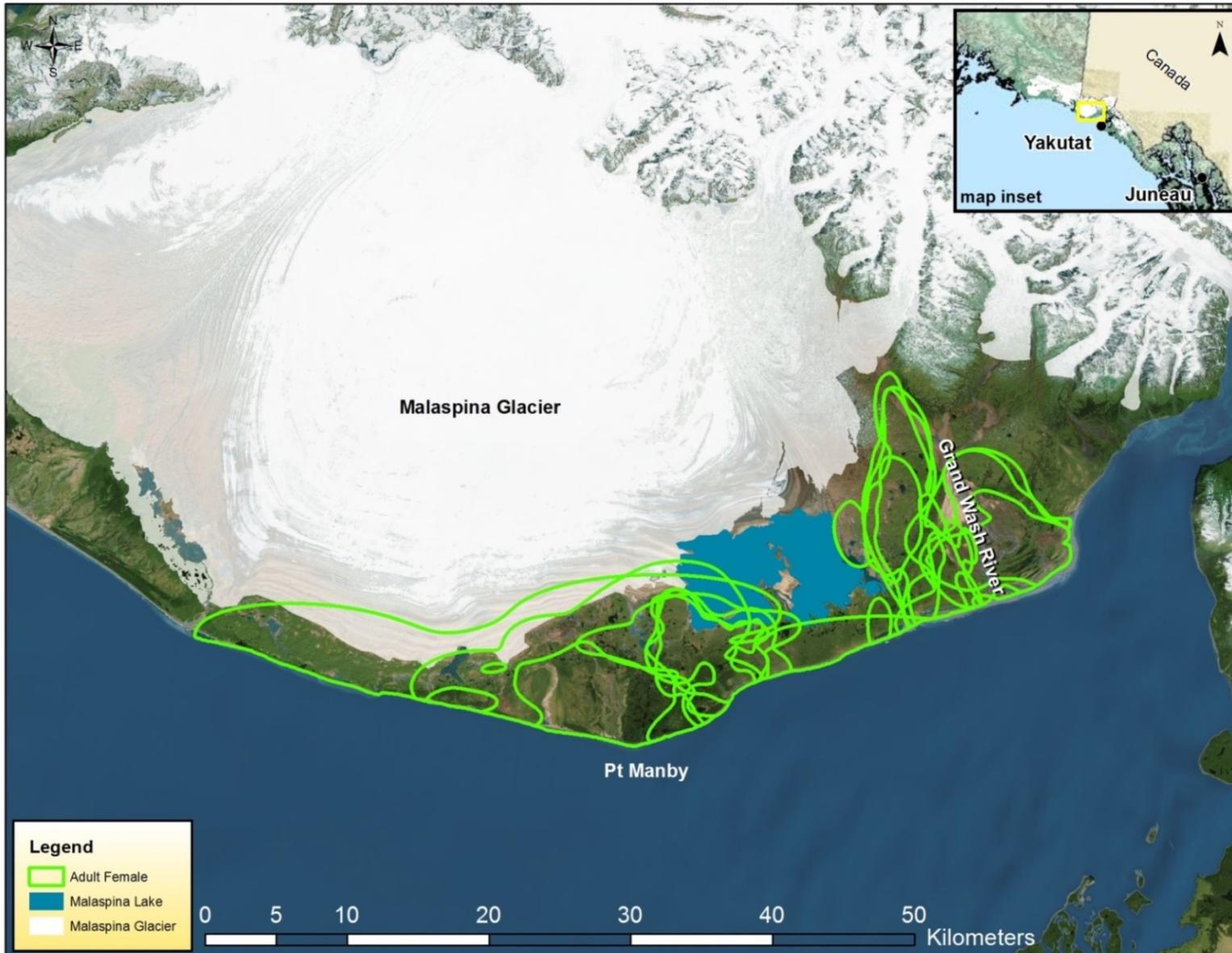


Figure 15. Female brown bear seasonal home ranges during late summer in the Malaspina Forelands study area, Southeast Alaska, 2009–2013.

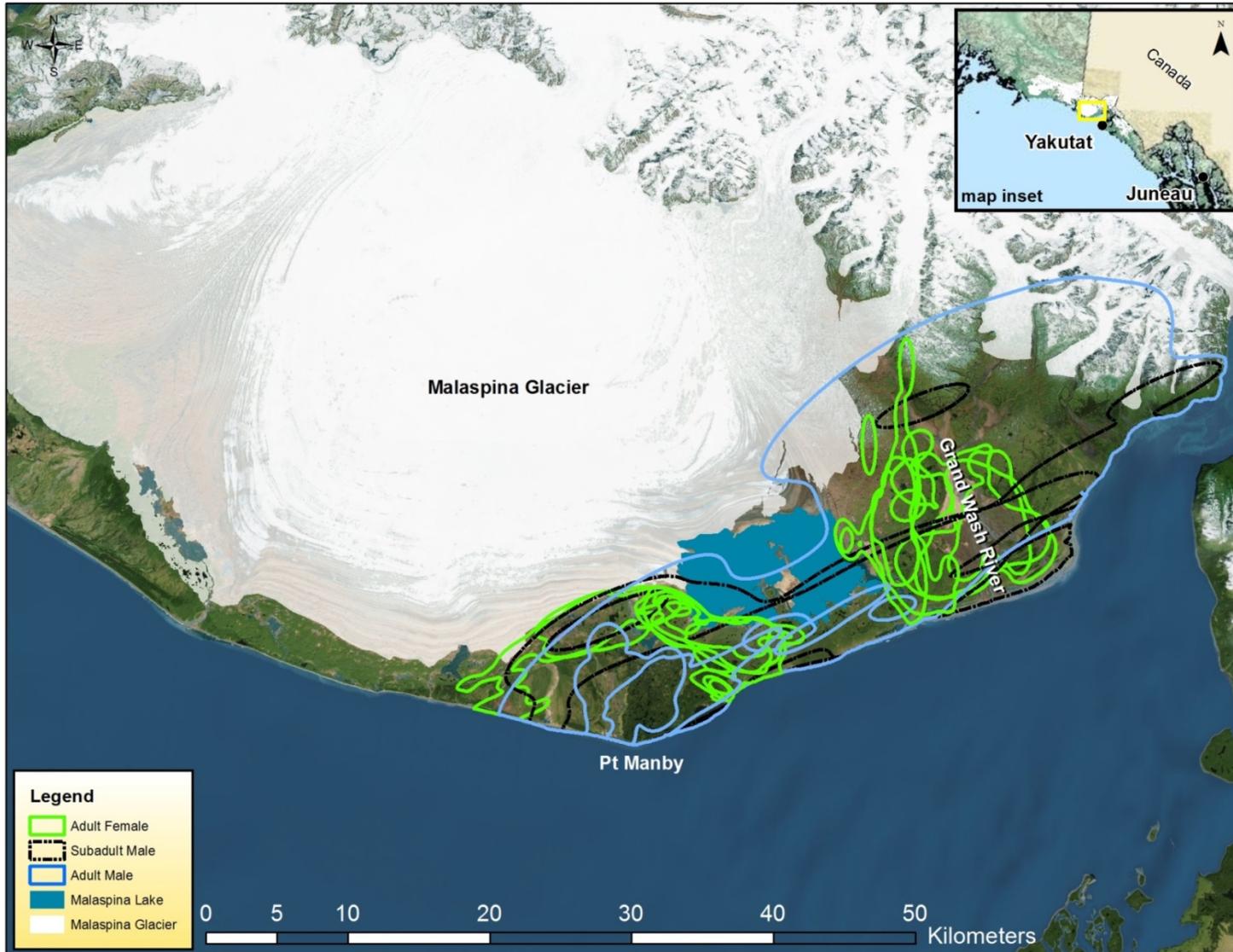


Figure 16. Brown bear seasonal home ranges during autumn in the Malaspina Forelands study area, Southeast Alaska, 2009–2013.

Table 6. Model variables and model selection criteria used in examining relationships in brown bear home range size. K represents the number of parameters estimated.

Model	AIC _c	K	ΔAIC _c	AIC _c weight
Cohort season year	51.1	9	0	1.0
Cohort season	136.3	5	85.2	3.2×10 ⁻¹⁹
Season year	141.4	5	90.3	2.5×10 ⁻²⁰
Cohort year	146.8	5	95.7	1.7×10 ⁻²¹
Cohort, season, year	150.4	5	99.3	2.7×10 ⁻²²
Cohort, season	154.4	4	103.3	3.7×10 ⁻²³
Cohort, year	160.2	4	109.1	2.0×10 ⁻²⁴
Cohort	160.7	3	109.6	1.6×10 ⁻²⁴
Season	161.4	3	110.3	1.2×10 ⁻²⁴
Season, year	163.8	4	112.7	3.4×10 ⁻²⁵
Year	172.9	3	121.8	3.6×10 ⁻²⁷

| indicates the inclusion of the individual variables and the interaction between them.

Table 7. Least-squared means from mixed linear model with root-root transformed home range size (km²) as the dependent variable, and season, sex with reproductive status (cohort), year, and the interaction (*) between these factors as explanatory variables. The individual animals were treated as a random effect. The variables included in this table were those significant at $\alpha < 0.05$.

Explanatory variables	β	df	SE	<i>t</i>	<i>P</i>
Intercept	2.69	6	0.53	5.10	0.002
Cohort (female with cubs)	-1.62	16	0.65	-2.50	0.020
Season (spring)	-5.73	16	1.54	-3.72	0.002
Season (early summer)	-6.03	16	1.50	-4.03	0.001
Season (late summer)	2.07	16	0.75	2.78	0.010
Season (spring) * cohort (adult female)	6.08	16	1.63	3.73	0.002
Season (early summer) * cohort (adult female)	6.37	16	1.58	4.02	0.001
Season (early summer) * cohort (adult male)	2.95	16	1.29	2.28	0.040
Year (2013)	2.34	16	0.75	3.15	0.006
Cohort (adult female) * year (2013)	-2.41	16	0.92	-2.63	0.020
Season (spring) * year (2011)	3.86	16	1.06	3.65	0.002
Season (spring) * year (2012)	4.97	16	1.35	3.69	0.002
Season (early summer) * year (2011)	5.32	16	1.06	5.03	0.0001
Season (early summer) * year (2012)	4.59	16	1.29	3.55	0.003
Season (late summer) * year (2012)	-2.52	16	1.06	-2.83	0.030
Season (spring) * cohort (adult female) * year (2012)	-5.47	16	1.59	-3.45	0.003
Season (early summer) * cohort (adult female) * year (2012)	-5.44	16	1.54	-3.53	0.003
Season (late summer) * cohort (adult female) * year (2013)	2.55	16	1.21	2.11	0.050
Season (late summer) * cohort (adult female) * year (2011)	-3.99	16	1.40	-2.85	0.010

Table 8. Mixed linear model random effect covariance coefficient estimates testing variation within and between individual bears.

Covariance parameter	Subject	β	SE	Z-value	<i>P</i>
Intercept	Animal_ID	0	.	.	.
Residual		0.2792	0.0842	3.32	0.0005

Table 9. Tests of fixed effects on root-root transformed brown bear home range size (km²) from the mixed-effects linear model with year effects.

Fixed effects	Numerator df	Denominator df	<i>F</i> -value	<i>P</i>
Cohort	3	16	13.48	0.0001
Season	3	16	12.68	0.0002
Season*cohort	9	16	2.04	0.1022
Year	4	16	3.79	0.0236
Year*cohort	7	16	2.2	0.0912
Year*season	10	16	2.58	0.0440
Year*season*cohort	8	16	3.11	0.0254

* indicates the individual fixed effect and the interaction between them.

Table 10. Least squared means from mixed linear model without year effects with root-root home range size (km²) as the dependent variable, and season and cohort as explanatory variables. The individual animal was treated as a random effect. The variables included in this table were those significant at $\alpha < 0.05$.

Fixed effects	β	df	SE	<i>t</i>	<i>P</i>
Intercept	3.62	11	0.30	12.23	<0.0001
Cohort (adult female)	-0.94	49	0.31	-3.06	0.004
Cohort (female with cubs)	-1.30	49	0.34	-3.86	0.0003
Cohort (adult male)	-0.91	49	0.32	-2.84	0.0065
Season (spring)	-0.59	49	0.27	-2.20	0.0327
Season (early summer)	-0.08	49	0.27	-0.30	0.7633
Season (late summer)	0.32	49	0.22	1.43	0.1592

Table 11. Tests of fixed effects on root-root transformed brown bear home range size (km²) from the mixed-effects linear model without year effects.

Fixed effects	Numerator df	Denominator df	<i>F</i> -value	<i>P</i>
Cohort	3	49	5.03	0.0041
Season	3	49	4.19	0.0102

MOVEMENT PATTERNS AND HUNTING VULNERABILITY

In spring, as brown bears emerged from their winter dens, daily movement rates were the least of any season. Daily movements of females with cubs were shortest, followed by subadult males, single adult females, and then adult males (Fig. 17). During the spring season, bears had the highest mean elevation (87.4 ± 1.3 m), as several bears occupied higher elevation habitats while descending from high elevation winter den sites. Bears were also found furthest from the shoreline ($5,786.6 \pm 45.18$ m) and AWC streams ($2,097.8 \pm 19.0$ m) (Fig. 18) during the spring season. In early summer, females with and without cubs, as well as subadult male bears, increased their daily movement rates with activity rates of females with cubs increasing the greatest, from 991 m to 1,830 m. During late summer, when strawberries ripen and become an important resource to bears, and salmon enter streams to spawn, all cohorts achieved maximum daily movement rates, with single females travelling the greatest distances, nearly 7 km/day. Bears in late summer also selected habitats closer to the ocean, as 38% of bear locations were found within 1 km of the shoreline. Adult males travelled fairly consistent distances throughout the year, with the maximum distances moved during the late summer. Movement rates of all cohorts slightly decreased between late summer and autumn, potentially a result of bears focusing their efforts on productive fishing locales. Bear distance to anadromous streams decreased in autumn as expected, and bears were found closer to salmon streams than in other seasons. In autumn, bears followed salmon upstream to their spawning reaches, and bear distances to saltwater shoreline therefore increased to the degree that only 6% of locations were found within 1 km of the shoreline.

With regard to hunting vulnerability, we identified 9 bears (6 males and 3 females) that used habitats within 1 km of the shoreline during the spring and autumn hunting seasons. Female bear vulnerability within this zone was highest near the mouth of the Grand Wash River in the spring and near Osar Creek, Spoon River and Alder Stream in the autumn. Overall, less than 10% of female locations were within 1 km of the shoreline, whereas male bears spent greater than 40% of their time in close proximity to saltwater (Table 3).

DEN LOCATIONS

GPS location data were available for 8 bears with collars affixed between late autumn and early spring, resulting in 12 den locations, with multiple den sites identified for 3 individuals. The mean date of den entrance was 24 November (range 13 November–10 December) and emergence was 22 April (range 29 March–3 May). Mean den elevation was 155.4 ± 54.3 m. Three dens were located at higher elevation (>300 m) in the Floral and Chaix hills, and 9 others were identified between the Malaspina Glacier and the shoreline, at lower elevation (<100 m), potentially excavated within ablative debris substrates or possibly in natural tree structures.

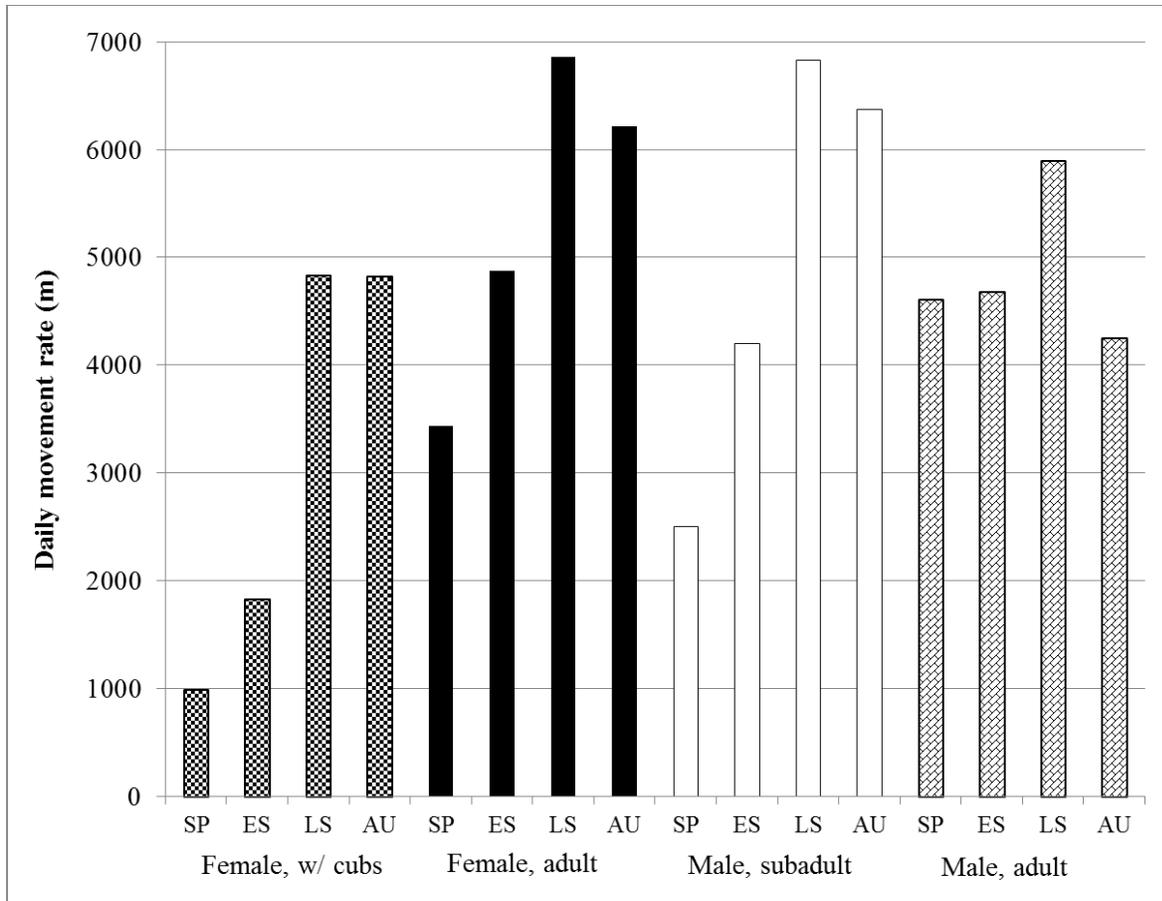


Figure 17. Seasonal daily movement rates of brown bear cohorts near the Malaspina Glacier, Southeast Alaska, 2009–2013 (SP = spring, ES = early summer, LS = late summer, AU = autumn).

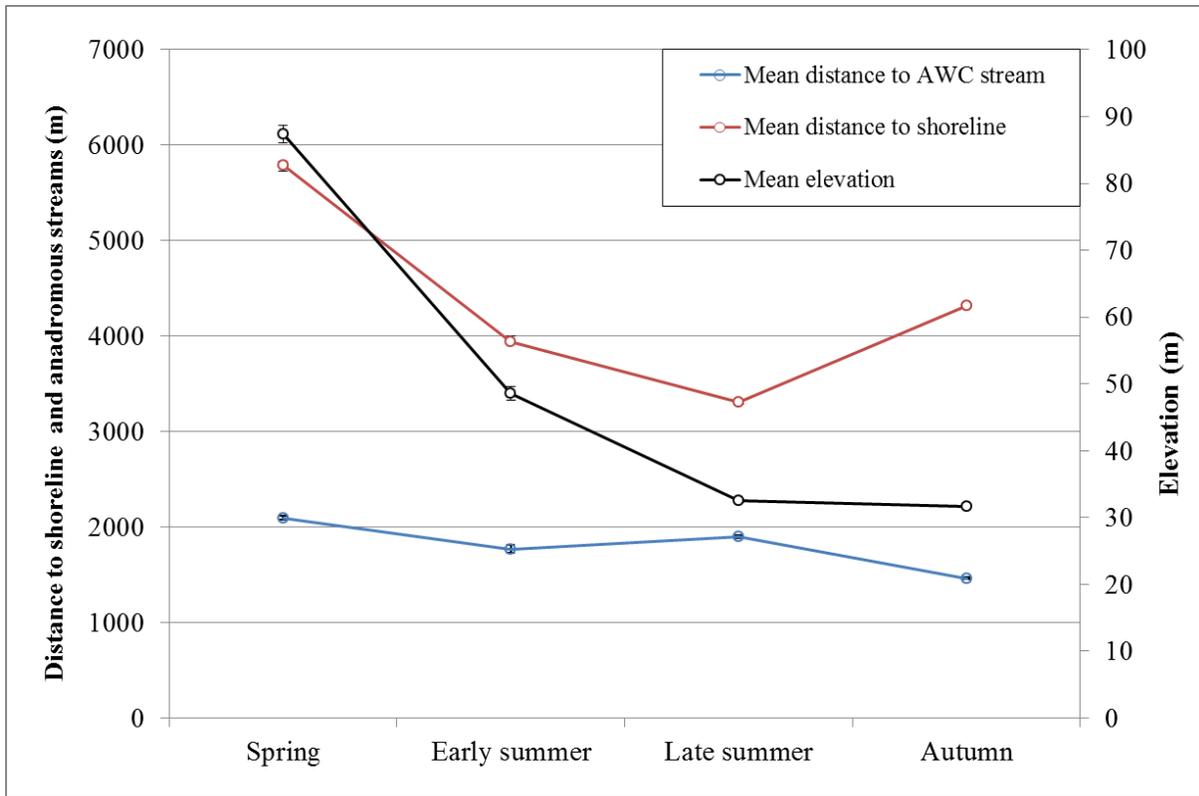


Figure 18. Seasonal movement patterns of brown bears near the Malaspina Glacier, illustrating mean distances to the saltwater shoreline and anadromous streams, and mean elevation.

HABITAT SELECTION

Resource Selection Function Model

From 2009–2013, we recorded 25,150 GPS locations in the late summer season on 9 male ($n = 12,704$) and 4 female ($n = 12,446$) brown bears within the study area for RSF analysis. We evaluated a suite of terrain features and landcover habitat characteristics that we believed were important seasonally to brown bear habitat selection (Table 1). Male and female bears exhibited a diversity of habitat selection ratios for each habitat type and terrain feature, although it was necessary to combine both sexes for the final RSF model. Terrain factors included in the final late summer RSF model included elevation, distance from herbaceous habitat, and distance from anadromous salmon streams. Habitat covariates in the RSF model comprised the complement of habitat types, including deciduous forest, conifer forest, shrubs, water, and unvegetated habitats. Weighted mean factor coefficients depict the contribution of each factor to the model (Table 12). The RSF model was strongly influenced by bears selecting habitats that were at low elevation and near herbaceous habitats. Brown bears positively selected a mosaic of habitat types relative to the reference herbaceous habitat. We mapped the resulting output surface depicting relative probability of selection symbolized by binned RSF scores (Fig. 19). The effect of elevation on the model was strong as RSF scores rapidly decreased as elevation increased, with RSF scores near zero as elevation approached 500 m. We graphed the effect of elevation combined with univariate habitat factors to evaluate the contribution of each habitat type on the model (Fig. 20). We also projected the univariate effects of individual habitats on distance from herbaceous habitat, which moderated the decline in RSF scores as distance from herbaceous habitats increased (Fig. 21).

Model Validation

We performed a cross validation of the RSF models to evaluate model performance. In the 5 models, the Spearman's rho values ranged from 0.79–0.96 with a mean of 0.89 with P -values < 0.01 , suggesting strong model performance (Table 13). Cross validation 5 showed the lowest performance, though it was still significant ($P < 0.01$). One explanation for the poor performance of this cross validation could be that the individual animals selected in this validation set preferred slightly different habitat than the average bear for which the model was constructed.

Discussion

MOVEMENT AND HOME RANGE

We chose to derive home ranges through kernel density estimates and used mixed-effects models to evaluate biological parameters associated with home range. Using LSCV as the bandwidth estimator was advantageous to other smoothing parameters as this method is suited for

Table 12. Weighted factor coefficients in late summer habitat selection RSF model for brown bears along Malaspina Forelands, Southeast Alaska, 2009–2013.

Factors	All bears
<i>Terrain factors</i>	
Distance from anadromous streams (s)	0.612
Distance from herbaceous (s)	-1.316
Elevation (s)	-1.833
<i>Landcover classification</i>	
Conifer forest	0.600
Deciduous forest	1.036
Shrub forest	0.609
Herbaceous	--
Unvegetated	0.432
Water	0.498
Ice/snow	NA

NA is not included in model, -- is reference factor, (s) is standardized variable

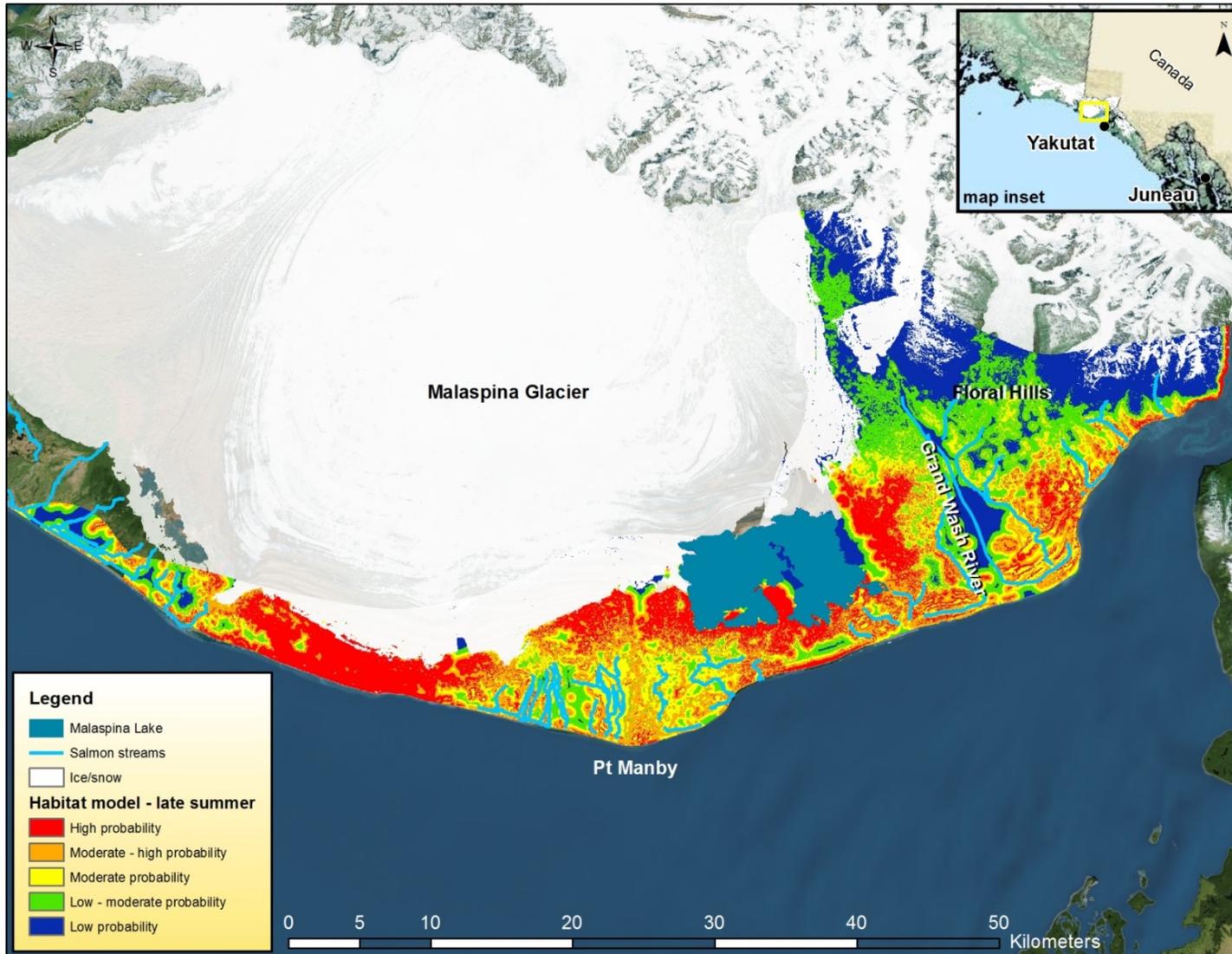


Figure 19. Map predicting relative probability of resource selection (RSF) during late summer for brown bears near the Malaspina Forelands, Southeast Alaska. Data collected from brown bears collared during 2009–2013. Because brown bears avoided ice and snow habitat within the study area, those areas were excluded from RSF analyses.

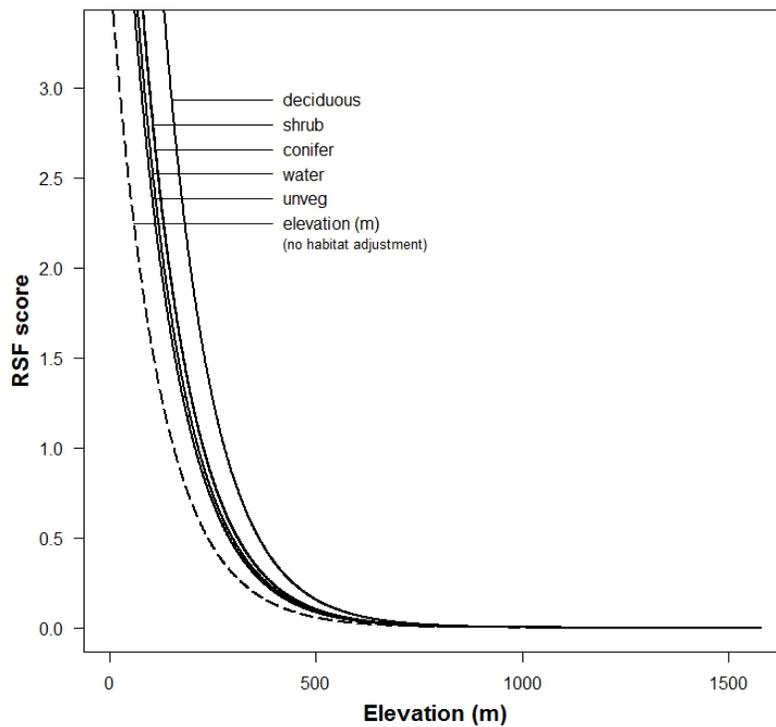


Figure 20. Effect of elevation on RSF scores combined with univariate habitat factors for all brown bears in late summer along the Malaspina Forelands, Southeast Alaska, 2009–2013.

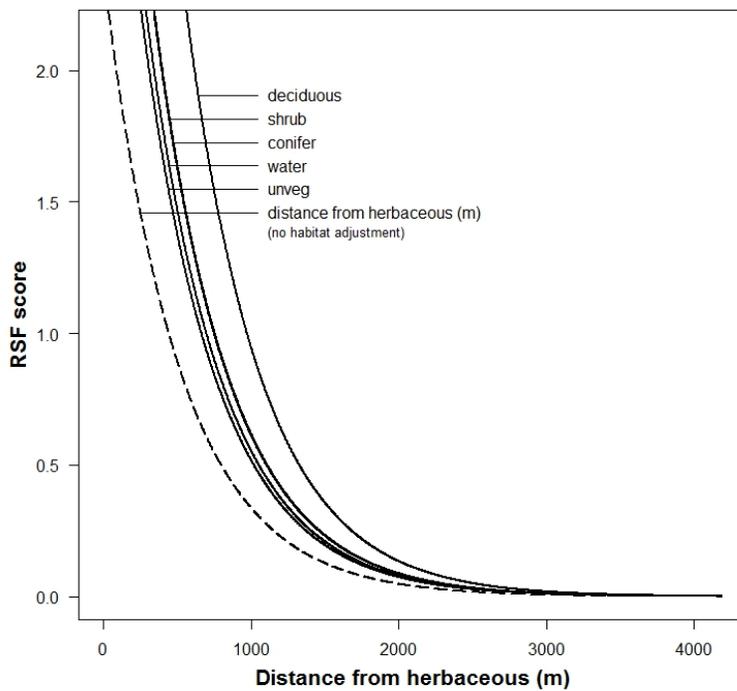


Figure 21. Relationship between brown bear resource selection and distance from herbaceous habitat combined with univariate habitat factors for all brown bears in late summer near the Malaspina Forelands, Southeast Alaska, 2009–2013.

Table 13. Late-summer RSF model performance on cross-validation for brown bears near the Malaspina Glacier, Southeast Alaska, 2009–2013.

Cross validation	Spearman's rho correlation (r_s)		Linear regression (R^2)				
	r_s	P -value	Slope		y-intercept		Adjusted R^2
			Coefficient	Significant ^a	Coefficient	Significant ^b	
1	0.95	<0.001	0.89	N	0.01	N	0.86
2	0.90	<0.001	1.36	N	-0.04	N	0.75
3	0.84	<0.004	0.61	Y	0.04	Y	0.76
4	0.96	<0.001	0.72	N	0.03	N	0.35
5	0.79	<0.01	0.46	Y	0.05	N	0.34
Mean	0.89						

If Y^a, slope significantly different than 1 ($P > 0.05$)

If Y^b, y-intercept significantly different than 0 ($P > 0.05$)

concentrations, such as foraging and resting sites. Desolla et al. (1999) suggested that autocorrelation does not reduce the validity of home range estimates as long as the interval between locations is relatively constant. Our sampling scheme of 20–30 minutes between relocations achieves this guideline, therefore maximizing the number of observations better estimates the precision of the home range estimates. Hemson et al. (2005) and others have discussed significant computing difficulties and failures with generating kernel density estimates (KDE) from large sample sizes. In our study, this only affected one animal with 15,000 locations, and successfully converged when we rarified the data to 11,000 locations. Ultimately, we were able to resolve this problem and generate a KDE for this animal, as well as the entire dataset of 64,076 locations. We resolved this issue by maximizing the RAM allocated to R using the function *memory.limit*, and report this solution to assist other researchers constrained by computer limitations.

Several shortcomings of the MCP approach have been identified (Seaman et al. 1999), yet we found it useful for comparison between studies, particularly older studies which relied on VHF relocations and limited sample sizes. We found that this population of brown bears on the northern mainland coast displayed some activity and home range patterns similar to other central mainland populations, yet dissimilar to Southeast island populations. Malaspina female bear MCP home range estimates were smaller (184 km²) than those found in Bradfield Canal and Unuk River (269 km²) (Flynn et al. 2010) and larger than those found in Berners Bay (147 km²) (Flynn et al. 2012). However, when compared to other high-density, salmon dependent, island populations such as Kodiak Island (71.0 km²) (Barnes 1990), Admiralty Island (37.3 km²) (Schoen and Beier 1990), Chichagof Island (35.1 km²) (Titus et al. 1999, Flynn et al. 2007), we found substantially larger female home range sizes on the northern mainland coast than those documented for island populations.

A reduced mobility hypothesis, whereby females with cubs are expected to occupy smaller home ranges since their ability to travel long distance is inhibited by the mobility of their offspring, has been tested by other researchers with mixed results (Dahle and Swenson 2003). Due to the limited sampling of females with cubs of various age classes, we combined them into one cohort, and did not find differences between female bears with and without offspring. However, we did observe that females with cubs of the year occupied the smallest home ranges, and had the shortest daily movement rates in the spring and early summer when mobility would be most challenging.

Malaspina MCP male home range estimates were smaller than other mainland populations studied in Bradfield Canal and Unuk River (519 km²) (Flynn et al. 2010), and Berners Bay (555 km²) (Flynn et al. 2012), though 4 times larger than Admiralty Island (99.7 km²) (Schoen and Beier 1990) and 7 times the size found on Chichagof Island (Titus et al. 1999). Subadult male home range size was substantially larger than other cohorts in late summer. The increased energetic demands of hyperphasia in late summer and autumn resulted in increased daily

movement rates and larger home range sizes. Adult males travelled fairly consistent distances throughout the year with the greatest distances moved in the late summer during the peak salmon run timing.

Similar to other brown bear studies (Barnes 1990, MacHutcheon 1993, Flynn et al 2012), male brown bears near the Malaspina Glacier occupied home ranges that were significantly larger than female home ranges. Previous researchers have suggested that male brown bears occupy greater ranges due to their increased energetic demand (McNab 1963), and prolific search for receptive females with which to mate (Gau 1998, Dahle and Swenson 2003). However, our data show that adult males occupied relatively consistent-sized home ranges, and they did not experience increased movement rates during the breeding season. The extent of male and female home range overlap and limited amount of available habitat likely enables male breeding opportunity in close proximity with adult females eliminating the need for them to increase travel distance and home range size.

Coastal brown bears are particularly dependent on highly digestible, high energy, lipid rich foods to maximize their energetic intake (Gilbert and Lanner 1997), while minimizing the constraints posed by foraging efficiency (Rode et al. 2001) to increase body mass and improve fitness (Hilderbrand et al. 1999). Nagy and Haroldson (1990) recognized that home range size was a function of both habitat quality and population density, and has also been found to be inversely proportional to the availability of food (Rogers 1977). Preliminary comparison of females captured on the Malaspina Forelands indicate lower body weights than the adjacent Yakutat Forelands study area (Crupi, unpublished data), possibly an indication that food abundance is limited. As density is inversely proportional to female home range size (Sandell 1989, Bjornlie et al. 2014), and female bears in this study occupied large home ranges, it is reasonable to assume that Malaspina bears exist at lower densities.

We provide a figure of male and female home range size estimates, labeled by study area, to provide context for the range estimates calculated in this study (Appendix B). Malaspina brown bear home ranges were among the largest of salmon dependent bears, potentially the result of dispersed salmon spawning streams with inadequate fishing locations, leading to increased movements necessary to track the phenological variation of spawning salmon (Schindler et al. 2013). Stream succession following glacial recession has been documented in Glacier Bay National Park, where vegetation began to grow after 30 years, and salmon colonization ensued after 40 years (Milner et al. 2008). Given the change in climatic conditions and the current recession of the Malaspina Glacier, we can expect changes in stream habitat available to spawning salmon. As salmon begin to occupy and spawn in these areas, we expect that bear movements in the future will shift to take advantage of this resource and population abundance will continue to be regulated by habitat quality and population density. Future studies could investigate the impacts of climate change, particularly projected variation in temperature and

snowfall, on spawning habitat as well as denning chronology. This study points to the potential implications of changing climate conditions on bear-salmon ecosystems.

HABITAT SELECTION

Habitat selection studies are important to understanding animal use of available resources as they occupy habitats and acquire resources that are necessary for survival. The terrain surrounding the Malaspina Glacier is a unique ecosystem with limited available bear habitat. We found that brown bears preferred habitats that were at low elevation, near herbaceous habitats, and they favored areas that were a matrix of available landcover classes. The RSF coefficients presented here are a valuable means for understanding habitat selection patterns, though it is important to recognize that the RSF model represents “average” resource selection patterns, and may not be indicative of the resources selected by the entire population. Ice and snow habitats were generally avoided as these habitats typically serve as barriers to movement. Saltwater crossings have also been found to limit dispersal of bears with distances as short as 2–4 km serving as barriers to females and 7 km for males (Paetkau et al. 1998). The closest distance between the Malaspina Forelands and Yakutat is 4 km, and 1 male bear was able to successfully cross over and back from this location, but his genetic contribution to the population is unknown. The expansive ice- and snow-dominated landscape combined with the saltwater between mainland habitats leads to the genetic isolation observed in our recent population structure analysis (Flynn et al. 2012).

The RSF model could potentially be improved with better mapping of the anadromous catalogued streams. In particular, information on spawning reach extent and salmon accessibility could influence the predictive power of the distance to anadromous streams factor. We have not yet determined the proportion of salmon in Malaspina brown bear diet, yet a preliminary assessment of stable isotope values indicates a strong marine signature with enriched levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, consistent with other mainland populations sampled (Rod Flynn, ADF&G, personal communication).

The Malaspina Glacier landscape is dynamic and subject to the effects of glacier movements, glacial uplift, hydrologic stream changes and climate change. Some regions of the study area have changed significantly since the Landsat image used for landcover classification was collected and this certainly influences the accuracy of current habitat conditions and the RSF model of brown bear habitat selection. We acknowledged this potential shortcoming, and we support efforts to improve the accuracy and resolution of the habitat classification.

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Appendices

Appendix A. Seasonal home range estimates of brown bears in the Malaspina Forelands study area generated using 95% fixed kernel density estimate with least-squares cross-validating generated bandwidths (SP = spring, ES = early summer, LS = late summer, AU = autumn).

Bear ID	Sex	Cohort	Year	Season	<i>n</i>	Area (km ²)
706	M	Adult male	2009	LS	2770	166.14
706	M	Adult male	2009	AU	1112	52.34
708	M	Subadult male	2009	LS	1429	516.70
708	M	Subadult male	2009	AU	1395	52.60
709	M	Adult male	2009	LS	821	18.80
710	M	Adult male	2009	LS	2317	50.61
711	F	Adult female	2009	LS	1471	41.03
711	F	Adult female	2009	AU	1823	26.64
711	F	Adult female	2010	SP	689	0.50
711	F	Adult female	2010	ES	1581	43.92
711	F	Adult female	2010	LS	2001	75.60
711	F	Adult female	2010	AU	1861	15.07
711	F	Female w/ cubs	2011	SP	1292	0.20
711	F	Female w/ cubs	2011	ES	389	56.53
711	F	Female w/ cubs	2011	LS	777	54.35
711	F	Female w/ cubs	2011	AU	760	34.51
711	F	Female w/ cubs	2012	SP	839	26.81
711	F	Female w/ cubs	2012	ES	632	10.21
711	F	Female w/ cubs	2012	LS	866	42.08
711	F	Female w/ cubs	2012	AU	536	38.50
713	F	Adult female	2009	LS	1270	63.11
713	F	Adult female	2009	AU	1282	40.70
713	F	Adult female	2010	SP	1236	77.02
713	F	Adult female	2010	ES	850	64.69
713	F	Adult female	2010	LS	760	61.32
713	F	Female w/ cubs	2011	ES	345	52.17
713	F	Female w/ cubs	2011	LS	711	80.77
713	F	Female w/ cubs	2011	AU	897	41.36
713	F	Female w/ cubs	2012	SP	481	0.89
713	F	Female w/ cubs	2012	ES	620	12.97
713	F	Female w/ cubs	2012	LS	881	47.83
713	F	Female w/ cubs	2012	AU	626	22.02
714	M	Adult male	2009	LS	1138	75.82
724	M	Adult male	2010	LS	481	46.27

724	M	Adult male	2011	LS	174	108.62
725	M	Adult male	2011	SP	214	3.95
725	M	Adult male	2010	LS	490	7.33
725	M	Adult male	2010	AU	739	43.75
731	M	Adult male	2012	SP	663	254.04
731	M	Adult male	2011	ES	479	288.01
731	M	Adult male	2011	LS	1065	2702.95
731	M	Adult male	2011	AU	970	12.47
732	M	Subadult male	2011	LS	628	455.14
732	M	Subadult male	2011	AU	946	283.89
732	M	Subadult male	2012	SP	531	103.07
732	M	Subadult male	2012	ES	776	39.99
732	M	Subadult male	2012	LS	1192	150.59
732	M	Subadult male	2012	AU	1059	242.64
732	M	Adult male	2013	SP	474	0.26
732	M	Adult male	2013	ES	691	15.07
732	M	Adult male	2013	LS	962	169.56
732	M	Adult male	2013	AU	297	648.79
734	F	Adult female	2011	LS	617	80.84
734	F	Adult female	2011	AU	1169	75.23
734	F	Adult female	2012	SP	823	40.95
734	F	Adult female	2012	ES	858	22.77
734	F	Adult female	2012	LS	1191	43.07
734	F	Adult female	2012	AU	1171	60.64
734	F	Adult female	2013	SP	944	65.32
734	F	Adult female	2013	ES	632	60.25
734	F	Adult female	2013	LS	296	81.69
734	F	Adult female	2013	AU	174	33.04
739	F	Adult female	2012	LS	860	136.44
739	F	Adult female	2012	AU	1245	43.76
739	F	Adult female	2013	SP	574	42.22
739	F	Adult female	2013	ES	465	45.03
739	F	Adult female	2013	LS	758	310.96
739	F	Adult female	2013	AU	393	27.75

Appendix C. Brown bear mortality.

The Malaspina Forelands present unique management issues for brown bears. One animal captured on the Malaspina Forelands, a 15-year-old male (#714), was harvested during the course of the study. During 2000–2012, ADF&G staff sealed 86 bears. Hunters harvested 83 brown bears, nearly 97% of Unit 5B mortality, and averaged approximately 6 bears/year (Table C.1). In addition to those harvested by hunters, 3 bears were reportedly killed in defense of life or property (DLP): 2 in 2010, and 1 in 2011. Male harvest averaged 5 bears/year and mean annual female harvest was 1.5 bears, reaching a peak of 5 females in 2011. Alaska residents harvested 13 bears, 16% of the total, taking 1 bear/year, while guided nonresident hunters accounted for the remaining 84% of the harvest, 70 bears (Fig. C.1).

The population estimate for GMU 5B was 108 brown bears given a density of 0.2 bears/mi² (Miller 1993, Miller et al. 1997). Recent human-caused mortality averaged 6.6 bears/year, or 6.1% of the population. Although the age structure of the harvest and the skull sizes have not indicated any significant trends over this period, ADF&G management staff will continue to monitor the current harvest levels to ensure that the population is managed for sustained yield (Miller 1990). Although the Malaspina bear population is small and demographically isolated, it appears to be productive. However, managers should be cautious managing this population to assure that viability is maintained, as overharvest could result in decreased recruitment and population decline, and generate conservation concerns.

Table C.1. Human-caused mortality of brown bears, including DLPs, based on ADF&G sealing records, near the Malaspina Glacier, GMU 5B, Southeast Alaska by regulatory years 2000–2012.

Year	Female	Male	Annual total
2000	1	8	9
2001	0	5	5
2002	1	3	4
2003	0	8	8
2004	1	6	7
2005	1	5	6
2006	2	7	9
2007	3	5	8
2008	3	10	13
2009	2	2	4
2010	2	0	2
2011	6	5	11
2012	0	0	0
Total	22	64	86
Average	1.7	4.9	6.6

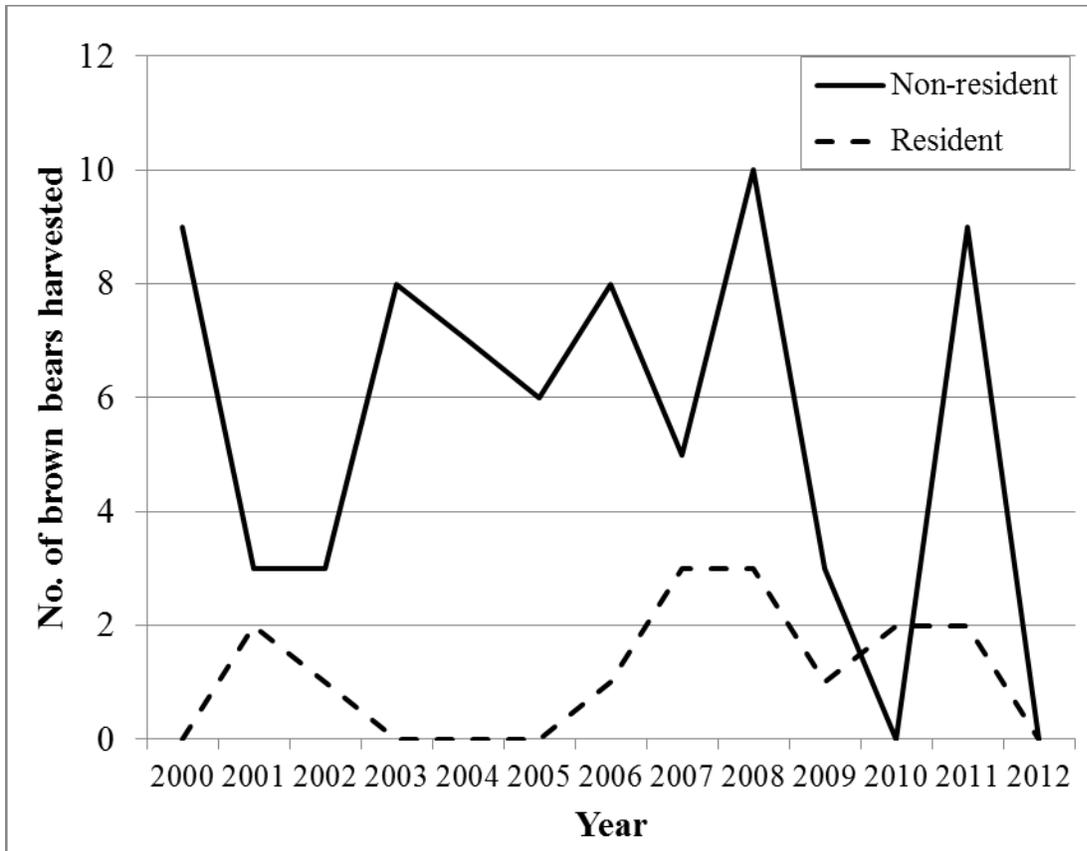


Figure C.1. Brown bear harvest by resident and nonresident hunters in GMU 5B, Southeast Alaska, regulatory years 2000–2012.

