Tribal Wildlife Grant Final Report
Makah Cougar and Bobcat Research
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INTRODUCTION

Mountain lions or cougars (*Puma concolor*) and bobcats (*Lynx rufus*) are both native mammals of the family Felidae. Mountain lions are large solitary cats with the greatest range of any large wild terrestrial mammal in the Western Hemisphere (Iriarte et al. 1990). Bobcats are also solitary cats that range from southern Canada to northern Mexico, including most of the continental United States. Both species are predators and as such play a prominent role in Native American mythology and culture due to their perceived attributes such as grace, strength, eyesight, and hunting ability. Similar to other Native American Tribes, predators have played a key role in the culture and ceremonies of the Makah people. Gray wolves (*Canis lupus*), black bear (*Ursus americanus*), cougars, and bobcats all are important components of Makah culture both historically and in contemporary times. For example, black bears and gray wolves both represented important clans in Makah history. Gray wolves exhibited cooperative behavior that provided guidelines for human behavior and "Klukwalle," or wolf ritual, was a secret society that required a 6 day initiation period (G. Arnold, personal communication). Wolf hides were also used in dance and costume regalia. Bear hides were worn by men of status (Chapman 1994) and as regalia during whale hunts (G. Ray, personal communication). Cougars and bobcats play a smaller, but still important role in Makah history and contemporary culture. During naming ceremonies a Makah name is given which best reflects an individual, often an animal such as the mountain lion is used as it represents intelligence and power. Additionally, their hides were traded and used as décor in longhouses (G. Ray, personal communication). Bobcat hides were traded, used as rugs, or their head, skull, and feet were placed on walking or 'talking sticks' and used at longhouse gatherings to signify who had the floor for discussions (G. Ray, personal communication).

Studies of cougar biology have provided information regarding their social system (Logan and Sweanor 2001, Beausoleil et al. 2013), home ranges and influencing factors (Pierce et al. 1999, Logan and Sweanor 2001, Dickson and Beier 2002), habitat use (Logan and Irwin 1985, Dickson and Beier 2002, Dickson et al. 2005, Kertson et al. 2011), reproduction (Logan and Sweanor 2001), survival (Logan and Sweanor 2001, McKinney et al. 2009), and prey selection (McLean et al. 2005, Atwood et al. 2007, Knopff et al. 2010, Clark et al. 2014). These studies have provided tremendous insight into cougar ecology in various ecosystems, but lack focused research within coastal rainforests on the Olympic Peninsula of Washington.

Similarly, studies of bobcat biology have provided information regarding their social system (Bailey 1974, Litvaitis et al. 1987, Anderson 1988, Lovallo and Anderson 1995, Benson et al. 2004), home ranges and influencing factors (Knick 1990, Chamberlain and Leopold 2001, Anderson and Lovallo 2003, Benson et al. 2006), habitat use (Kowolski and Woolf 2002, Roberts 2007), reproduction (Boyle and Findley 1987, Anderson and Lovollo 2003, Diefenbach et al. 2006, Roberts 2007), survival (Fuller et al. 1995, Griffin 2001), and prey selection (Kowalski and Woolf 2002, Anderson and Lovello 2003, Roberts 2007). Bobcats have been studied extensively throughout the eastern United States, but there is little documentation on bobcats and other furbearers on the Olympic Peninsula or anywhere else in Washington (Washington Department of Fish and Wildlife 2008).

Management by the Makah Tribe has been hampered by the lack of biological data on cougar and bobcat populations within the lands used for Tribal hunting. Tribal hunting regulations provide for harvest of both species, but the efficacy of these regulations is unknown. The current Makah Tribal Wildlife Plan (MTWP, Chapman 1994) covers furbearers collectively and cites a significant lack of data for effective management and establishes goals to improve understanding of species such as cougars and bobcats. Past research by the Makah Tribe has collected indirect information on prey use by these species through long term research projects with black-tailed deer (*Odocoileus hemionus columbianus*) and Roosevelt elk (*Cervus elephus roosevelti*). Cougars were the primary predator on adults of both species but, rates of predation were relatively low (McCoy and Gallie 2005, McCoy and Murphie 2012). Conversely, black-tailed deer fawn mortality rates were high, over 4 years of study, due partly to the combined effects of cougar and bobcat predation (McCoy et al. 2014). Similarly, elk calf mortality rates were high, over 2 years of study, with cougar predation accounting for 74% of all deaths (McCoy and Murphie 2012). The Makah Tribe suspected that the combined effects of multiple predators on deer fawns played a role in restricting black-tailed deer population growth (McCoy et al. 2014) and likely minimized elk population growth. However, specific information on prey selection and preference of bobcats and cougars as it pertained to ungulates and whether there were individual, sexual, or seasonal differences was unknown. Answers to these questions would help Tribal efforts to manage ungulate populations through annual hunting regulations. Proper management of ungulates is essential as Makah use of land mammals for subsistence foods is heavily concentrated on black-tailed deer and Roosevelt elk, which provide meat to 64% of Tribal households (Sepez 2001).

In addition to managing ungulate populations, baseline cougar and bobcat data will be essential for understanding impacts that recolonization of wolves may have on ungulate, cougar, and bobcat populations. The Washington Department of Fish and Wildlife developed a Wolf Conservation and Management Plan for Washington (Wiles et al. 2011) to manage a future statewide population. Wolf distribution has expanded in eastern Washington and will likely result in recolonization of the Olympic Peninsula from dispersal or translocation. The future presence of wolves would be a tremendous benefit to the Makah Tribe culturally (as cited previously), particularly as wolf hides and parts used for ceremonial purposes have been unavailable for decades. Additionally, it would alleviate further erosions of Makah traditions associated with extinction of a culturally significant species of wildlife (Preston and Harcourt 2009). Conversely, wolf recolonization may negatively affect Makah subsistence hunting of deer and elk through the introduction of a new predator. Research in Yellowstone National Park found that in multi-predator ecosystems including wolves, predation on elk calves was mainly additive (Barber-Meyer et al. 2008). The future establishment of wolves provides the impetus for a more thorough understanding of the current habitat use patterns, home range size, relative abundance, productivity, prey selection, and survival rates of both bobcats and cougars to measure changes after wolf recolonization. In areas where wolves and cougars interact, research suggests competition for similar prey may result in cougars moving away from kills to avoid wolf contact, avoidance of areas used by wolves, shifts in prey use, or increases in kill rates to replace lost prey (Akenson et al. 2005, Kortello et al. 2007). In central Idaho, cougars had lower recruitment, fewer adults, and a disrupted social structure several years after recolonization by wolves (Akenson et al. 2005). Effects on bobcats from wolf recolonization are undocumented. Speculation is that other carnivores, such as bobcats may be affected similarly to coyotes (*Canis latrans;* Ballard et al. 2003) including reductions in population size. Alternatively, bobcats may

benefit from wolf-killed carcasses by providing more food for scavenging, particularly during the winter months.

Bobcats have been identified as a primary source of mortality for fisher (*Martes pennanti*) recently reintroduced to Olympic National Park (P. Happe, personal communication). Concern over bobcat impacts to recovery efforts have generated interest in research on bobcat populations, especially since they are likely sharing similar foraging habitats, resulting in increased encounters with fisher. An understanding of bobcat prey use and predatory behavior, both present and future, will aid in determining what those impacts are, if any.

We collected baseline data on cougar and bobcat populations in western Washington that built upon existing research from cougars in eastern Washington, provided site specific data for western Washington, and produced significant insights into bobcat biology that can be used to improve both State and Tribal management of these species. A better understanding of cougar and bobcat prey selection and preference benefits management of ungulate populations important to tribal subsistence. Data collected prior to wolf recolonization of the Olympic Peninsula provides a foundation for future research on how wolves affect bobcats, cougars, and ungulate populations. Our specific research goals for each species were:

Cougars:

1) To determine prey selection, species composition and predation rates.
2) To determine cougar preference of prey in regards to deer and elk.
3) Document den sites for adult females and determine reproductive effort.
4) To determine annual survival rate, home range size, and habitat use.
5) To determine the minimum relative density of adult resident cougars.

Bobcats:

1) To determine prey selection, particularly for larger prey.
2) Document den sites for adult females and determine reproductive effort.
3) To determine annual survival rate, home range size, and habitat use.
4) To determine population density.

STUDY AREA

The study area was the Hoko Game Management Unit (GMU), Dickey GMU, Pysht GMU, and adjacent Makah Reservation in Clallam County, Washington (Figure 1) for cougars and the Hoko GMU for bobcats. The majority of lands were industrial timberlands with some public timberlands administered by the Washington Department of Natural Resources (WDNR) and protected forests within the coastal strip of Olympic National Park (ONP). A smaller component of the landscape encompassed small towns, dispersed housing, or small ranching operations, primarily along Highways 112 and 113 and along the Hoko-Ozette Road.

Elevations ranged from sea level to nearly 610 m. The climate was markedly influenced by the orographic interaction of maritime air masses and the mountainous topography; it was characterized by warm, dry summers and cool, wet winters. Temperatures were typically mild and, on average, ranged from 3 to 12° C in January and 10 to 19° C in August. The average

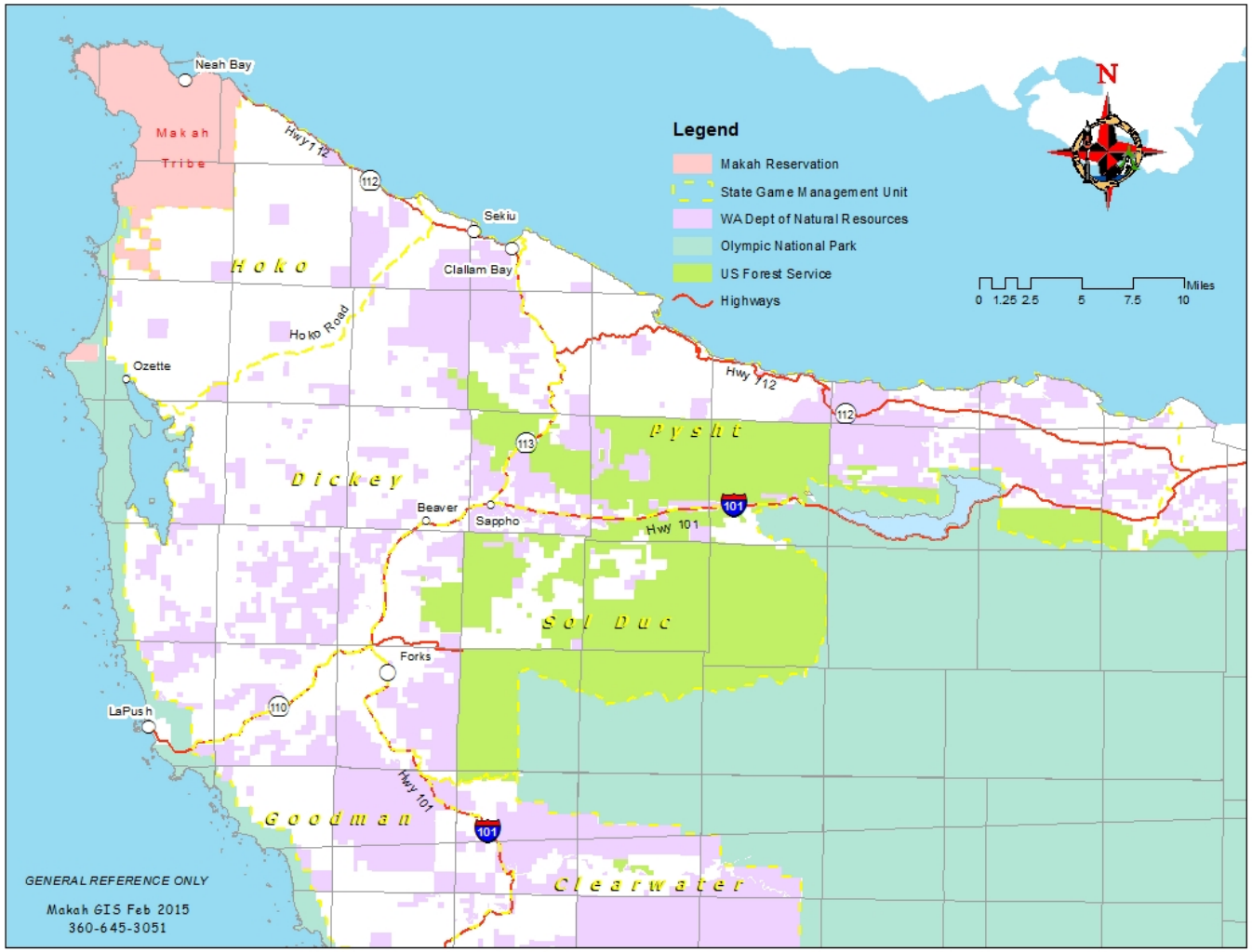

Figure 1: Study area including the Makah Reservation, Hoko Game Management Unit (GMU), and portions of the Dickey and Pysht GMUs on the northwest Olympic Peninsula, WA.

annual precipitation was 254 cm (Dion et al. 1980). Approximately 75% of the yearly precipitation historically occurred from October to March, and 8% occurred from June-August. Winter storms were commonly accompanied by severe winds that routinely exceeded 64 km/hr at the coast and commonly were 80 to 96 km/hr in mountain valleys. Warm westerly winds restricted snowfall to the higher elevations, usually above 610 m, except when the westerly winds were disrupted between December and February (Schultz 1990). Snow in the lowlands rarely exceeded 8 cm and was transient.

The northern Olympic Peninsula is dominated by temperate coniferous forests and is characterized by the *Picea sitchensis* (Sitka spruce) zone. Constituent tree species are the Sitka spruce, western hemlock (*Tsuga heterophylla*), western red-cedar (*Thuja plicata*), Douglas fir (*Psuedotsuga menziesii*), and Pacific silver fir (*Abies amabilis*). Red alder (*Alnus rubra*) is one of the most abundant trees on disturbed sites. Understory vegetation typically consists of red huckleberry (*Vaccinium parvifolium*), salmonberry (*Rubus spectabilis*), thimbleberry (*Rubus parviflorus*), devil's club (*Oplopanax horridus*), salal (*Gaultheria shallon*), red elderberry (*Sambucus recemosa*), sword fern (*Polystichum munitum*), lady fern (*Athyrium felix-femina*), deer fern (*Belchnum spicant*), Oregon oxalis (*Oxalis oregana*), trillium (*Trillium ovatum*), and Oregon grape (*Berberis nervosa*) (Franklin and Dyrness 1973, Makah Forestry 1999). Intensive timber harvest has converted what was historically extensive old growth to primarily second growth forests with stand conditions ranging from grass-forb following clear cutting to closed-sapling-pole saw timber (Hall et al. 1985). Timber harvest typically occurs in second growth stands at 40-70 years. A mosaic of stand conditions existed within our study area, but younger stands dominated, as the area has been subject to significant timber harvest over the past 10 years.

Timber harvest has resulted in high road densities, which were generally open to public access prior to 1987 on both private and WDNR timberlands for hunting and other uses. Since 1987, roads accessing private timber lands have primarily been gated and public use is limited to non-motorized transportation. Motorized public access to WDNR timber lands has remained open where accessible from public highways or roads, but not allowed where WDNR holdings are alienated within private property. On the Makah Reservation, access was limited by gates in some areas, but was largely unrestricted over most of the Reservation. Hunting and other uses was limited to tribal members only.

METHODS

Animal Capture and Handling

Cougars were pursued with hounds either by striking from an ungulate predation event identified as a cougar kill or by following tracks after a snow event. Ungulate predation events were determined from field examination of kill sites associated with radio-tagged deer or elk that were generally $\leq$ 2 days old. Once a cougar was treed, large nylon nets were attached to the tree beneath the cougar and to adjacent trees within a 3-5 meter radius to catch immobilized animals that fall from the tree. Cougars were darted with a mix of Telazol (5.5 mg/kg) and sterile saline solution, using an X-calibur gauged $C0_2$ projector and Type P disposable darts (Pneu-dart, Inc., Williamsport, Pennsylvania). When a cougar did not fall from a tree, the tree was ascended and a rope was attached to 2 legs and lowered to the ground using a secure nylon rope (Logan et al.

1986). Immobilized animals were blindfolded, aged, measured, and sexed. Vital signs including heart rate and respiration were monitored throughout the processing procedures. Adult cougars were fitted with a Lotek 4400S GPS collar (Lotek Engineering, Newmarket, Ontario, Canada), a numbered plastic ear tag (Figure 2a), and tattooed with a unique number. Sub-adult cougars received a numbered plastic ear tag and a unique ear tattoo only. Age was estimated by tooth wear, tooth color and gum line recession (Figure 2b) based on techniques by Laundré et al. (2000). Measurements collected for all cougars included weight, total length (from nose to tip of tail), length of tail, height (from front toe to top of shoulder), girth, right hind foot length, head length and width, and length and width of front and hind paw. Reproductive status of females at capture was determined by presence of milk, or color and size of nipples (Lambert 2003). Immobilized cougars were monitored until they recovered.

Figure 2. Photos showing procedures including collaring and ear-tagging (a), and gum line recession measurement (b) during cougar captures on the northwest Olympic Peninsula, WA 2012-2014.

Bobcats were captured using either hounds or custom cage traps between December and April each year. Hound captures were employed during snow events and dry weather throughout the capture timeframe. Dry weather captures involved traversing the study area with hounds, when a scent determined to be bobcat was struck by the hounds they were engaged in pursuit. Once treed, bobcats were captured using the same protocol established for cougar. Cage captures initially used Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin), which failed to work over the first capture season. During subsequent seasons, larger custom cage traps (0.9 x 0.9 x 1.5 m) were employed that were more effective. Traps were baited with a variety of meat and used visual attractants and lures in combination. Traps were checked at least once every 24 hours, typically within 2 hours of sunrise. Captured bobcats were chemically immobilized with a combination of Telazol (5.5 mg/kg) and sterile saline solution administered via hand syringe or jab-stick for traps and using darts for hound captures as described for cougars. Immobilized animals were blindfolded (Figure 3a) and vital signs, including heart rate and respiration, were monitored. Each bobcat was sexed, weighed (Figure 3b), measured, and classified as adult (>2 years), subadult (1-2 years), or juvenile (<1 year) using body size (Crowe 1975), teat condition of females, and scrotum size of males. Due to collar weight, only bobcat that weighed greater than 4.5 kg were collared. Bobcats meeting the weight criteria were fitted with a Vectronic GPS PLUS Mini-1C collar (Vectronic Aerospace GmbH, Berlin, Germany) and ear-tagged.

Juveniles and sub-adults not meeting the weight criteria received an ear-tag only. Measurements collected for all bobcats were the same as described for cougars, as was reproductive status of females. Immobilized bobcats were placed in a portable pet kennel or monitored at site of capture until recovered and then released.

Figure 3. Photos showing procedures including blindfolding (a), and weighing (b) during bobcat captures on the northwest Olympic Peninsula, WA 2012-2014.

Monitoring and Kill Site Investigation

GPS collars for cougars and bobcats were programmed to acquire a location fix 8 and 6 times per day, respectively. Fix locations were remotely downloaded from the ground every 2-6 weeks. GPS clusters with a probability of greater than 20% were identified using the program developed by Knopff et al. (2009) for cougars. There was no previous research that indicated minimum GPS cluster probabilities that would reliably identify bobcat kills. Therefore, we initially used a modified algorithm adjusted to 50 m for bobcats to select GPS clusters for field investigation. Preliminary field investigations and further screening of cluster data resulted in modified criteria, including 3 or more points within a 3 day timeframe and a probability of greater than 20% that were selected for field investigation.

Geometric centers of clusters were programmed into handheld GPS units to locate clusters in the field, similar to Kertson et al. (2011*a*). Sites of potential kills were visited within 2-6 weeks. Kill sites were identified based on characteristics consistent with drag trails, caching of remains, cougar/bobcat tracks or scat, and punctures in head or neck consistent with cougar/bobcat. At sites where prey remains appeared to predate cluster initiation, the site was designated as a scavenging event. Prey remains were identified to species and a GPS location was recorded. When deer or elk were found at kill sites, the sex and age class (adult, yearling, juvenile) were determined from the skull and lower jaw dentition (Severinghaus 1949) when possible. Additionally, signs of scavenging from other species were documented.

We estimated predation rates for cougar as the average interval between kills by assigning the kill date as the first day a cougar was located at the kill site then calculated the number of days

between 2 consecutive kills (Cooley et al 2008). Deer and elk specific predation rates were estimated by dividing the total number of days on-air by the total number of deer or elk killed; this was extrapolated out to estimate the total number of animals killed annually. We estimated the average number of days each individual spent at a kill by subtracting the end date from the start date of each cluster. We tested the difference between winter and summer predation rates and number of days on a kill using a one-tailed t-test assuming that summer would have shorter kill intervals and fewer days spent at a kill. We considered summer as the period of time between 1 May and 31 October and winter as 1 November to 30 April. Prey composition was determined for each cougar individually by calculating the number of prey species identified at kill sites divided by the total number of kills. Predation rates and prey composition was also determined collectively for all cougars and separately for each sex. Specific predation rates were developed for both deer and elk at the individual, collective, and sex scale to gauge impacts to ungulates specifically and included differences for adult and young-of-year age classes.

Bobcat prey composition focused on larger species of prey that were presumed to be the only prey items that would be detected at GPS clusters. This was based on larger prey requiring more time to consume resulting in identifiable clusters. Predation rates were not identified as all prey could not be accounted for from GPS data. Prey composition was determined individually and collectively for all bobcats for prey species identified at clusters, but did not represent actual proportions of prey consumed by bobcats since not all prey was detected. Selection of deer, particularly fawns, was predicted to occur seasonally during the late spring and summer when young fawns were widely available on the landscape. Thus, we used chi-square to test for differences in use of deer by bobcats between seasons.

Prey Selection by Cougars

Selection of deer or elk was determined by estimating the overall proportion of each species observed at kill sites relative to the proportion of each species available to cougars. We estimated both population and individual prey selection of deer and elk using a standardized selection index (Manly et al. 2002), assuming a constant prey population, following methods of Cooley et al (2008). We used the average annual number of deer and elk killed over 3 years of study for these estimates. We calculated standard errors, confidence intervals, and a chi-square log-likelihood estimate (Zar 1999). We also calculated selection preference for young-of-year, both deer and elk, for the entire cougar population. Finally, we evaluated individual selection relative to a) other cougars, b) the availability of prey at the population level, and c) females and males separately using methods from Cooley et al. (2008) and equations from Manly et al. (2002). We tested whether cougars were on average selecting prey consistently using log-likelihood chi-square tests, and whether they were using prey in proportion to availability regardless of whether individuals were selecting consistently by subtracting the log-likelihood chi-square of the used resources (χ^2_{L1}) from the log-likelihood chi-square of the available resources (χ^2_{L2}).

Prey availability of deer was determined by estimating the 2012 pre-hunting season deer population (deer/km^2) in the Hoko GMU using the Sex-Age-Kill (SAK) model (Skalski and Millspaugh 2002). The model inputs included reported State and Tribal deer harvest in 2011 and 2012 (Northwest Indian Fisheries Commission 2012, 2013) and observed parameters from deer composition flights collected in 2012 (fawn:doe ratios). Composition flights for deer were

conducted in September of 2012 using a helicopter to fly early seral habitats where deer could be observed and classified as adults or fawns. Adults were further classified as buck or doe. We applied the deer density estimate calculated for the Hoko GMU throughout the study area as habitat and environmental conditions were similar throughout. Deer density was calculated to reflect total deer as well as does, bucks, and fawns per km^2.

Availability of elk was determined by estimating the 2012 pre-hunting season elk population (elk/km^2) in the Hoko and northern portion of the Dickey GMU's (Figure 4), which overlapped significantly with the observed cougar home ranges. The elk population was determined using a Lincoln-Peterson estimate based on the ratio of marked to un-marked groups (Eberhardt et al. 1998). Marked groups were denoted by the presence of at least one radio-collared elk. Elk within the Hoko and Dickey GMU's had been radio-collared prior to flights by ground darting using a mixture of Carfentanil (1.5 mg) and Xylazine (390 mg) and reversed with Naltrexone (150 mg) and Tolazine (1,000 mg). Telemetry darts (Pneu-dart, Inc.) were used to aid in location of darted elk. Two flights were conducted the last week of August in 2012, one in the Hoko GMU and another in the northern Dickey GMU. During flights, each area was systematically covered; once a group of elk was encountered it was recorded as marked or unmarked and the number of cows, calves, and bulls were documented. Immediately after the flight, radio-collared elk that were not encountered were located to determine how many marked groups were available in the GMU surveyed. The estimated population was calculated using Program R (R Core Team 2012). The estimated population size for each GMU was calculated to reflect total elk as well as cows, bulls, and calves per km^2.

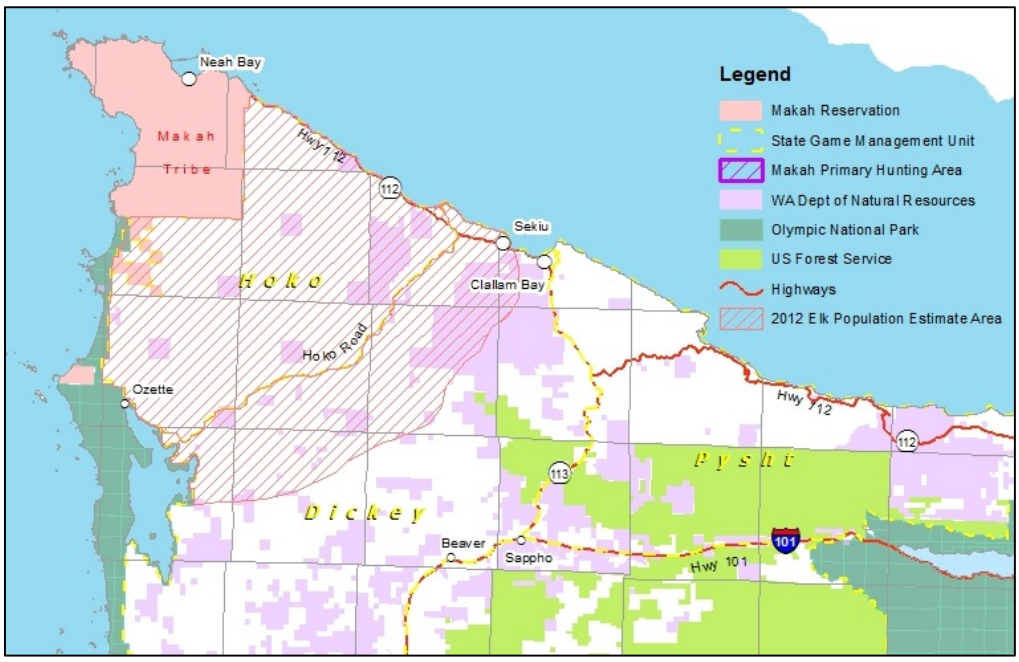

Figure 4: Area where elk population estimate was conducted in 2012 including the Hoko and northern portion of Dickey Game Management Units on the northwest Olympic Peninsula, WA.

Female Reproduction

Female cougar fix locations were constantly monitored for decreased movements indicative of denning activity (Beier et al. 1995, Logan and Sweanor 2001) as cougars can give birth at any time of the year. When denning was suspected, the sites were visited to locate den sites and confirm reproduction. A GPS location was established for the determined den site and vegetation structure was noted (open forest, dense regenerating forest, riparian, etc.). Litter size was determined and individual kittens were sexed, weighed, and ear tagged (if old enough). Kittens were removed from dens to acquire biological data and returned as quickly as possible to minimize disturbance. Handling of kittens was performed with latex gloves to minimize scent transferal.

The peak of bobcat breeding in Washington was reported to occur between April and July (Maser 1998). From March to August each year, the successive telemetry locations of female bobcats were monitored for evidence of restricted or centralized movements. There was no evidence from GPS data indicating den activity throughout the entire study period. Therefore, we were unable to collect this information as intended and will discuss potential issues that limited our ability to discern denning further in the discussion section.

Survival Analysis

We used the known fate model in Program MARK (White and Burnham 1999) to estimate annual survival rates and 95% confidence intervals to investigate factors influencing survival for both cougars and bobcats. We developed 8 a priori models for cougars that reflected season, year, and hunting pressure differences in survival (Table 1). We developed 9 a priori models for bobcats that reflected season and year differences in survival and incorporated sex as an individual covariate (Table 2). Hunting pressure was defined as the months when cougars, a highly sought after big game species by hunters, were considered most vulnerable due to overlapping State and Tribal big game seasons. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to judge support among the candidate models. We considered cougars at risk from February and bobcats from March for the first year of analysis and added subsequent captures using a staggered entry format.

Table 1. A priori models used to determine the influence of season, year, and hunting pressure on cougar survival from 2011-2015.

Model	K[a]	Description
$S_{constant}$	1	Survival is constant.
$S_{monthly}$	12	Survival varies by month.
S_{season}	4	Survival varies seasonally (winter, spring, etc.).
S_{year}	4	Survival varies by year.
$S_{month\ x\ year}$	48	Survival varies by month and year.
$S_{hunting}$	2	Survival varies between big game hunting season and rest of year.
$S_{hunting\ year}$	5	Survival varies during each big game hunting season with rest of each year held constant.
$S_{hunting\ x\ year}$	8	Survival varies by big game hunting season and year.

[a]Number of parameters in model.

Table 2. A priori models used to determine the influence of season, year, and sex as an individual covariate on bobcat survival from 2012-2015.

Model	K^a	Description
S_{season}	4	Survival varies seasonally (winter, spring, etc.).
$S_{constant}$	1	Survival is constant.
S_{year}	3	Survival varies by year.
S_{sex}	2	Survival varies between sexes.
$S_{year\ x\ sex}$	4	Survival varies between years and sexes.
$S_{season\ x\ year}$	12	Survival varies by season and between years.
$S_{season\ x\ year\ x\ sex}$	13	Survival varies by season, between years, and sexes.
$S_{season\ x\ sex}$	5	Survival varies by season and sexes.

[a]Number of parameters in model.

Home Range and Resource Use

Locations from GPS collars were downloaded and maintained in a database where they were imported into ArcMap 10.1 (Environmental Systems Research Institute, Redlands, CA, USA). We estimated annual and lifetime Utilization Distributions (UD; Worton 1989, Kernohan et al. 2001) for all cougars and a single lifetime UD for all bobcats, as we generally did not have bobcats on-air longer than 1 year. We used the fixed Kernel Density Estimate (kde) in Geospatial Modelling Environment (GME; Beyer 2012) with the PLUGIN estimate of bandwidth (Kertson and Marzluff 2010, Kertson et al. 2013), and a designated cell size of 30 m (Kertson et al. 2011a, b; 2013). We used the isopleth tool and the addarea tool in GME to estimate the 99% and 50% contours and area of use in each animal's home range. We used the 99% area to compare home range size and overlap between individual cougars and bobcats, and among years for cougars that were monitored for more than 1 year. We used the 50% area of bobcat home ranges to estimate core area overlap between individuals and to estimate the bobcat population within the study area (Nielsen and Woolf 2001; see below).

We used methods similar to Logan and Sweanor (2001) to estimate a fidelity index (FI) and an association index (AI) among and between cougars over the course of the study. The fidelity index was calculated for each cougar during pairs of years where annual home range estimates were obtained. The equation: $FI_x = n_1 + n_2 / N_1 + N_2 \times 100$, was used where x was the time span between pairs of years, n_1 and n_2 were the number of locations recorded within the overlap zone of the two years, and N_1 and N_2 were the total number of locations within each annual home range (p.212; Logan and Sweanor 2001). A shift was indicated by an overlap zone of less than 40%. The association index was calculated as the percent overlap between pairs of cougars using the 99% fixed kernel for each year. We also estimated the average overlap between F:F and M:F pairs for 2011-2012. The equation for AI is equivalent to the FI equation above, except n_1 and n_2 were the number of locations within the overlap zone for a pair of cougars in a given year, and N_1 and N_2 were the total number of locations within each cougars home range in that same year (p.249; Logan and Sweanor 2001).

We defined the area used by cougars as the 99% fixed-kernel boundary and assigned each 30×30 m pixel a value between 1 and 99, lowest to highest use respectively, based on the volume (height) of the UD (Marzluff et al. 2004, Kertson and Marzluff 2010, Kertson et al. 2013). We used the lifetime home ranges in resource use analysis because the FI (as above) indicated that

there was no shift in home range over years among individual cougars and for bobcats because we rarely had more than 1 year of home range data for individuals. We used the Ruf.fit package (Handcock 2004) in Program R (version 2.13.0) to estimate resource utilization functions (RUFs) for all cougars to determine the influence of landscape features on use within the home range and at the population level (Level II and III; Johnson 1980). We selected landscape features consistent with those important for prey species including the proportion of land-cover within a 150 m moving window (McGarigal and Marks 1995), distance to publicly accessible roads, distance to non-public roads, distance to perennial streams and freshwater bodies, and slope (degree). Land-cover classes included wetlands, urban areas, fields, regenerating forests 0-5 years of age, 6-15 years of age, 16-30 years of age, and >30 years of age. Distances to roads and water were derived using Spatial Analyst Euclidean Distance, and slope was derived using United States Geological Survey's 10 m digital elevation model for UTM zone 10 in ArcMap 10.1 (Kertson and Marzluff 2010). Habitat type was delineated in ArcMap 10.1 using subsequent orthophotos of Clallam County from 1983-2011, then converted to a TIF image for moving window analysis (Hepinstall et al. 2008), which was performed using Fragstats (version 4.2, McGarigal et al. 2012). The percent land-cover classes were imported back into GIS where all landscape features were extracted using a point grid generated in GME (genvecgrid) for all 30 x 30 m pixels within the 99% UD. We used the Extract Multi-values to Points tool in ArcToolBox to simultaneously extract relative use and covariates associated with resource units (Kertson and Marzluff 2010).

We analyzed both standardized and unstandardized partial regression coefficients generated by the Ruf.fit package in R for both cougars and bobcats. We averaged standardized coefficients and constructed 95% confidence intervals using a standard error estimate derived by subtracting the variance of individuals (Eq. 2; Marzluff et al. 2004) from the total variance, which included inter-animal variation (Eq. 3; Marzluff et al. 2004). Confidence intervals that did not include zero were considered significant predictors of use for the entire population (Kertson et al. 2011*b*) and coefficients were tested for differences from zero using a Student's *t* statistic (Zar 1999). The relative importance of landscape features were ranked according to the absolute value of the mean standardized coefficients and the number of cougars with significant use either positively or negatively associated with each resource was quantified (Marzluff et al. 2004, Kertson et al. 2011*b*). Average unstandardized coefficients and conservative standard errors were estimated similar to those for standardized coefficients as above. Unstandardized values were used to model predicted use within the study area.

Population Density

Relative minimum density (RMD) estimates were derived for cougars similar to methods by Lambert et al (2006). We used the composite 99% fixed kernel home range estimate (as above) of all adult females and divided the total area by the number of females to get adult females/100 km^2, then we added the proportion of adult male 99% fixed kernel home ranges that overlapped the female composite during the same timeframe. We estimated the RMD using cougar home ranges from 2012 since this is when we had the majority of adult male and female cougars collared. We extrapolated the RMD to include the Makah Reservation, Hoko GMU, and portions of the Dickey and Pysht GMUs (Figure 5) to estimate the total number of cougars within the study area. These estimates did not include juveniles or sub-adults.

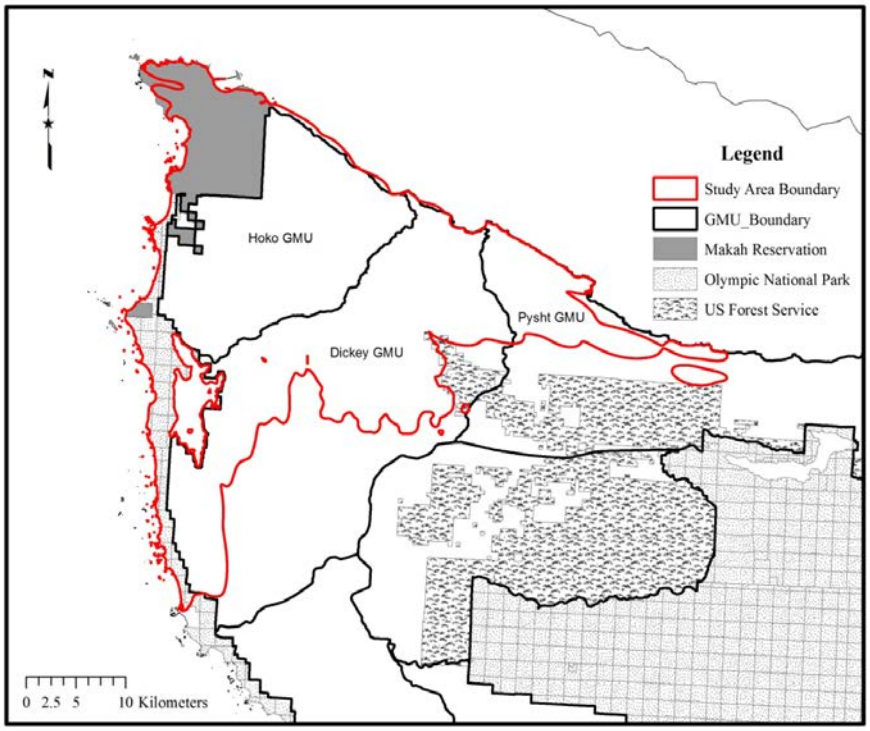

Figure 5. Map showing the total area used for population estimates (red) in 2012, and the relationship to the Hoko Game Management Unit (GMU), Dickey GMU, Pysht GMU, and Makah Reservation (gray), on the northwest Olympic Peninsula, WA.

We estimated population density of bobcats, similar to methods of Nielsen and Woolf (2001), using the pooled average 50% core area fixed kernel home range estimates of males and females and core area overlap of male and female pairs. We used the formula in Nielsen and Woolf (2001) to calculate bobcats/km^2:

Density = (1/mean core-area size [km^2]) + (1/mean core-area size x percent core-area overlap).

We extrapolated the density estimate to include the Hoko GMU and Makah Reservation to estimate the total number of bobcats within the study area. These estimates did not include juveniles or sub-adults.

RESULTS

Animal Capture

We captured 17 cougars: 4 adult females, 3 adult males, 1 sub-adult female, 5 sub-adult males, and 4 cubs (1 male, 3 female), and 21 bobcats: 6 adult females, 12 adult males, 1 sub-adult female, and 2 sub-adult males. For cougars, individual measurements were variable (Appendix A), but on average, adult males weighed approximately 60% more than adult females and 30% more than sub-adult males (Table 3), while other measurements showed that adult males were generally 15-20% and 5-15% larger, respectively. The adult female population was about twice as old as the adult male population based on age at capture, and consisted of 2 females over the estimated age of 9.5 years (Table 4).

Table 3. Average values with standard error (SE) and ranges for weight, length, height, and girth for all female, male and sub-adult (SA) male cougars on the northwest Olympic Peninsula, WA, 2011-2014.

	Weight (kg)			Total Length (cm)			Height (cm)			Girth (cm)		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Females	46.6	3.34	37-58	199.8	3.54	192-210	62	3.80	47-67	64	4.5	56-81
Males	74	4.58	65-80	230.2	4.04	223-237	67	4.44	59-74	77	2.0	75-81
SA Males	52.2	0.8	50-55	218.8	3.57	210-227	62.5	2.61	53-68	71	2.03	65-76

Table 4. Average values with standard error (SE) and ranges for age at capture of all female, male, and sub-adult male cougars on the northwest Olympic Peninsula, WA, 2011-2014.

	Age (years)		
	Mean	SE	Range
Females	6.7	1.33	3.3-9.5
Males	3.5	0.47	2.9-4.5
Sub-adult Males	1.8	0.27	1.4-2.5

For bobcats, individual measurements were also highly variable (Appendix B), but on average, adult males weighed approximately 52% more than adult females and were generally larger by 10-30% in other measurements (Table 5).

Table 5. Average values with standard error (SE) and ranges for weight, length, height, and girth for all female and male bobcats on the northwest Olympic Peninsula, WA, 2011-2014.

	Weight (kg)			Body Length (cm)			Height (cm)			Girth (cm)		
	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Female	7.2	0.7	5.1-9.5	77.9	1.2	74.0-82.0	39.2	1.4	32.5-43.4	29.2	1.5	25.2-34.2
Male	11.1	0.7	6.8-15.0	86.5	1.5	79.2-94.0	45.9	1.1	38.5-50.5	37.2	1.4	29.5-44.0

Prey Use and Selection

Over 35,770 locations were collected by cougar GPS collars resulting in an overall fix success of 81%. We visited 994 cougar clusters, with recovery of 812 clusters (82%) where prey remains were found, identified, and analyzed (Figure 6). Mean prey interval and mean number of days at a cluster varied by individual cougar (Table 6), and was 5.8 ± 0.9 and 4.0 ± 0.6 for all cougars, respectively. Prey interval was shorter during the summer by an average of 1.05 (±0.29) days ($t_{\infty} = -3.63$, $P < 0.001$) and the number of days spent on a kill was shorter during the summer by an average of 0.67 (±0.16) days ($t_{\infty} = -4.09$, $P < 0.001$) for all cougars combined.

Figure 6. Remains of an elk calf at a cougar cluster on the northwest Olympic Peninsula, WA, 2011-2015.

Table 6. The average number of days between cougar kills (prey interval) and number of days spent at a cluster for individual cougars on the northwest Olympic Peninsula, WA, 2011-2014.

Cougar ID No.	Prey Interval	Days at cluster
F01	7.1	5.0
F02	4.8	3.9
F03	6.9	4.4
F04	5.6	3.8
F05	4.9	3.1
M01	4.9	3.6
M02	6.6	4.4

Overall, deer made up 66% of cougar diets, elk 16.9%, and other 17.1%. However, the proportion of deer and elk in male diets was different than that for females (Figure 7); female diets were dominated by deer followed by other species then elk, whereas male diets were dominated by elk, followed by deer then other species (Figure 8). Out of 476 deer found at kill sites that could be identified to age, 55.3% were fawns, 34.7% were adults, and 10% were juveniles. Out of 119 elk found at kill sites, 60.5% were calves, 26.1% were adults and 13.4% were juveniles. Only 5% of elk were scavenged by male cougars whereas, 22% of elk were scavenged by females. Other species were important, accounting for 17% of diets, and included beaver (*Castor canadensis*), raccoon (*Procyon lotor*), coyote (*Canis latrans*), bobcat, black bear (*Ursus americanus*) cub, spotted skunk (*Spilogale gracilis*), river otter (*Lontra Canadensis*), grouse (*Dendragapus fuliginosis, Bonasa umbellus*), mallard duck(*Anas platyrhynchos*), red-tail hawk(*Buteo jamaicensis*), other birds, mountain beaver (*Aplodontia rufa*), snowshoe hare(*Lepus americanus*), and fish (*Oncorhynchus sp*.; Figure 9).

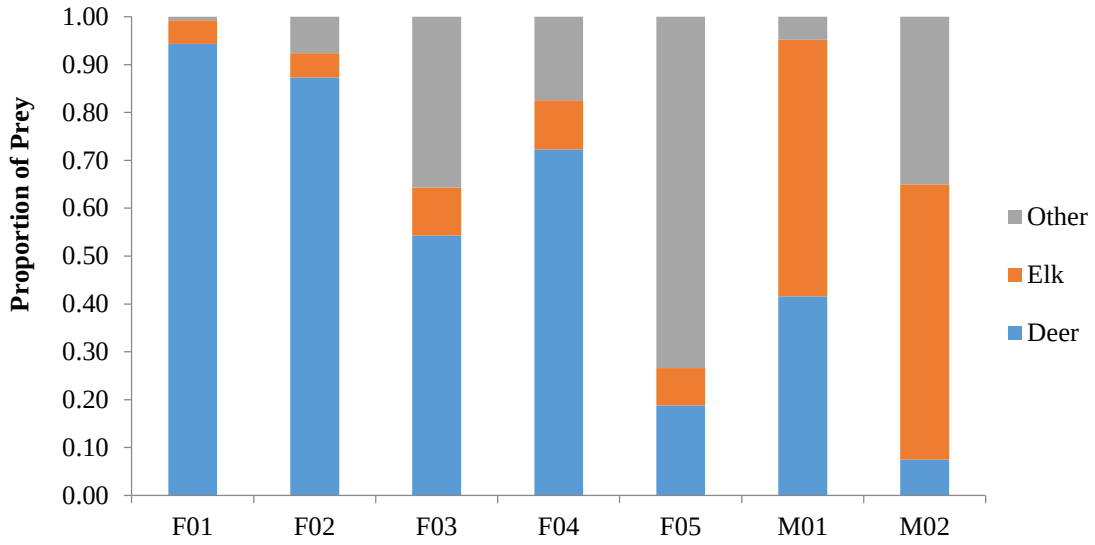

Figure 7. The proportion of deer, elk, and other prey species found at individual cougar clusters from January 2011-September 2014, on the northwest Olympic Peninsula, WA.

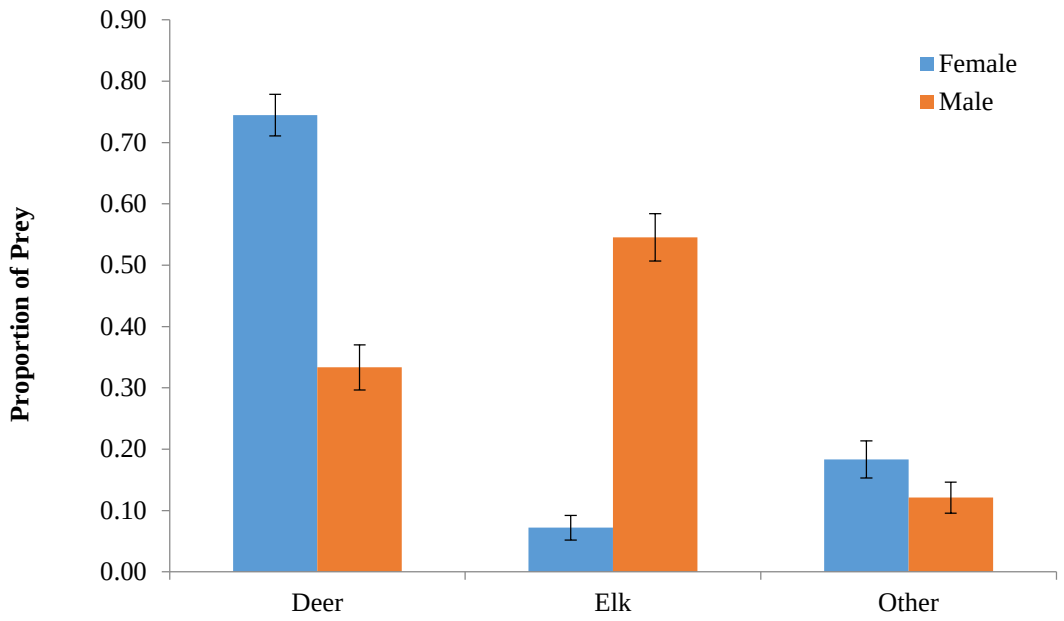

Figure 8. The proportion of deer, elk, and other prey species in diets of female cougars compared to male cougars from January 2011-September 2014, on the northwest Olympic Peninsula, WA.

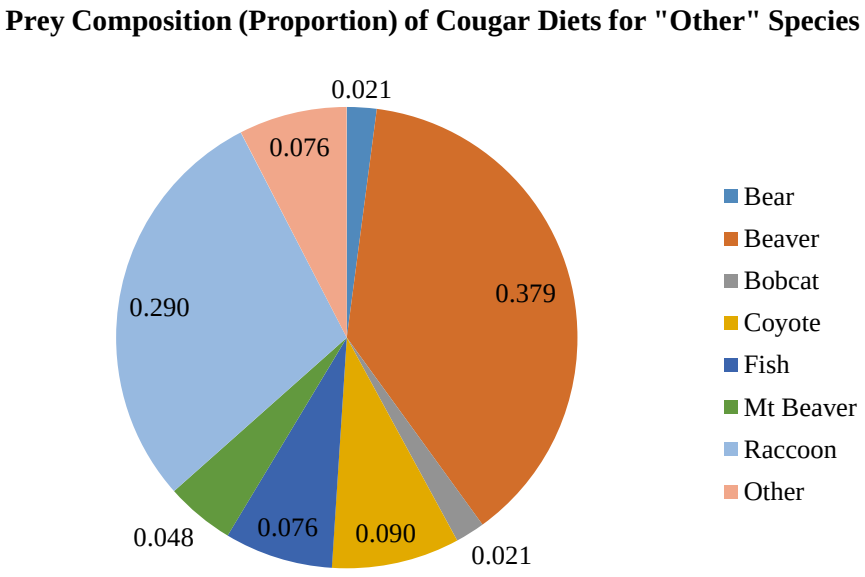

Figure 9. The proportion of other species found at cougar clusters from January 2011-September 2014, on the northwest Olympic Peninsula, WA. Other includes less than 2% of each various bird species, rabbit, river otter, cougar and unknown.

Bobcat GPS collars collected approximately 15,160 locations resulting in an overall fix success of 56%. We visited 174 bobcat clusters, with recovery of 60 clusters (34%), where prey remains were found, identified, and analyzed. Deer were the most abundant species recovered at clusters (50.8%) but nearly half (47%) of those were either scavenged from a cougar kill or natural mortality. Deer that were killed consisted of 14 fawns and 2 adults and were only found at clusters of male bobcats. Removing scavenged deer from the total proportion of prey resulted in a diet of deer (39%) mountain beaver (24.4%), other small prey (24.4%) such as small birds and rodents, grouse (5.1%), and rabbits (3.4%). Elk were scavenged on by bobcats on 3 occasions but there was no indication of bobcats killing any elk. There was no difference in the number of deer killed over summer compared to the winter (χ^2=2.42, P = 0.12).

Deer density was estimated at 3.3/km^2, with the proportion of fawns to adults as 0.298. The total population estimate of deer in the study area for prey availability was 3,554 (75.5%). Elk density was estimated at 1.07/km^2, with the proportion of calves to adults as 0.286. The total population estimate of elk in the study area for prey availability was 1,152 (24.5%). At the population level the deer selection ratio w_i = 0.997 (standardized β_i = 0.50) and the elk selection ratio w_i = 1.01 (standardized β_i = 0.50), indicated no selection for deer or elk based on population availability (log-likelihood χ^2_1 = 0.065, P = 0.80). However, there was significant selection for young-of-year compared to adults based on availability for both deer (w_i = 1.85; log-likelihood χ^2_1 = 50.6, P <0.001) and elk (w_i = 2.99; log-likelihood χ^2_1 = 54.0, P <0.001), for all cougars. At the individual level, 4 of 7 cougars (all females) selected in the direction of deer (selection ratio >1.0) but only 2 of those were significant (P < 0.001), and only 2 of 7 cougars (both males) selected for elk (P < 0.001; Table 7). Individual cougars, both male and female, did not show consistency when selecting resources ($\chi_{L1}{}^2{}_6$ = 103.3, P <0.001), with some more selective than others based on prey availability ($\chi_{L2}{}^2{}_7$ = 103.4, P < 0.001). However, for all cougars combined, the difference between the 2 scales of analysis ($\chi_{L1}{}^2$ - $\chi_{L2}{}^2$ = -0.1, P = 0.85) indicated on average that cougars were not selective. Individual female cougars did show consistency with all other females when selecting resources ($\chi_{L1}{}^2{}_4$ = 6.85, P = 0.11) even though some were more selective than others ($\chi_{L2}{}^2{}_5$ = 38.7, P < 0.001), for example F01 and F02 were more selective toward deer than F05 (w_i = 1.29 and 1.25, respectively, compared to w_i = 1.02; Table 7). Females on average were considered to be selective toward deer (w_i = 1.18; $\chi_{L1}{}^2$ - $\chi_{L2}{}^2$ = -31.9, P < 0.001). Individual male cougars were not consistent with each other regarding selection of resources ($\chi_{L1}{}^2{}_1$ = 161.2, P < 0.001), one male was more selective than the other ($\chi_{L2}{}^2{}_2$ = 64.6, P < 0.001) but on average males selected toward elk (w_i = 2.87; $\chi_{L1}{}^2$ - $\chi_{L2}{}^2$ = 96.6, P < 0.001).

Table 7. Average annual deer and elk killed by cougars and associated selection indices, from individual use and population availability showing means for females only, males only, and all cougars combined, on the northwest Olympic Peninsula, WA, 2011-2014.

Cougar No.	Prey	Total		Selection Ratios		SEs, CIs, and χ^2 tests				
		Obs[a]	Exp[b]	w_i[c]	β_i[d]	SE(w_i)	CI Lower	CI Upper	χ^2 LL[e]	*P*
F01	Deer	42	32.47	1.29	0.93	0.032	1.230	1.357	16.900	<0.001
	Elk	1	10.54	0.09	0.07	0.094	-0.089	0.279		
F02	Deer	53	42.28	1.25	0.85	0.041	1.172	1.334	14.808	<0.001
	Elk	3	13.72	0.22	0.15	0.123	-0.022	0.460		
F03	Deer	19	15.86	1.20	0.76	0.085	1.031	1.365	3.090	0.111
	Elk	2	5.15	0.39	0.24	0.262	-0.124	0.902		
F04	Deer	36	30.96	1.16	0.70	0.068	1.029	1.297	3.883	0.067
	Elk	5	10.05	0.50	0.30	0.209	0.088	0.908		
F05	Deer	10	9.82	1.02	0.52	0.155	0.715	1.322	0.014	0.906
	Elk	3	3.19	0.94	0.48	0.478	0.006	1.880		
Mean F	Deer			1.19	0.75	0.028	1.130	1.241		
	Elk			0.43	0.25	0.110	0.212	0.645		
M01	Deer	23	36.24	0.63	0.23	0.096	0.447	0.822	16.823	<0.001
	Elk	25	11.76	2.13	0.77	0.300	1.541	2.715		
M02	Deer	3	19.63	0.15	0.04	0.083	-0.010	0.315	47.826	<0.001
	Elk	23	6.37	3.61	0.96	0.272	3.080	4.147		
Mean M	Deer			0.39	0.14	0.062	0.272	0.516		
	Elk			2.87	0.86	0.256	2.366	3.370		
Mean All	Deer			0.96	0.58	0.038	0.884	1.035		
	Elk			1.13	0.42	0.119	0.892	1.359		

[a] Observed average annual number of kills for each species.
[b] Expected number of kills (total kills × proportion available for each species).
[c] Selection index (Manly et al. 2002).
[d] Standardized selection index.
[e] χ^2 log-likelihood statistic.

Female Reproduction

We documented 6 cougar dens and captured cubs on 2 separate occasions. Dens for F01 were located in >30 year timber stands, with a complex understory structure at den#1, including dense regenerating western hemlock and large blow-down trees, and with a more open understory at den#2 within riparian habitat. Three cubs (1 male, 2 females), approximately 5 weeks old, were captured on 28 September 2012 at den#1, with an average weight of 2.3 ± 0.19 kg (5.1 ± 0.42 lbs; Figure 10a). We suspected survival of these cubs was 0%, as F01 denned again 1 year later on 20 August 2013; we were unable to recover cubs from den#2. Dens for F02 were located in 6-15 year old stands, with extremely dense regenerating western hemlock (Figure 10b). We were unable to recover cubs from den#1 or den#2. Dens for F03 were located in a 16-30 year old stand (den#1) and a 6-15 year old stand (den#2). Both den locations had been thinned leaving a significant amount of slash among semi-dense understory. We suspected survival of

cubs from den#1 was 0% as F03 denned again approximately 5 months later on 15 April 2012. We captured 1 female cub, about 10 days old, weighing 0.65 kg (1.4 lbs). We never documented den activity for F04 or F05, nor did we ever document den activity for any female bobcats throughout the entire study.

Figure 10. Photo of 5 week old cougar cub from female F01 (a) and example den site cluster from female F02 (b) on the northwest Olympic Peninsula, WA, 2011-2014.

Survival Analysis

Two cougars and 3 bobcats died during the course of this study. Female cougar F03 was harvested by a state hunter on 30 October 2012, and male cougar M02 was harvested by a tribal hunter on 15 October 2012. Male bobcat BC01 was killed by a cougar on 9 October 2012, female bobcat BC08 died from unknown natural causes on 10 March 2013, and female bobcat BC15 was killed by a predator on 20 October 2014.

The average annual survival rate (S) of cougars was 0.905 (95% CI = 0.76 – 0.97). The top 2 models were not statistically different based on the likelihood ratio estimate ($\chi^2_2 = 2.25$, $P = 0.324$) and had AIC_c weights and ΔAIC_c values that prompted model averaging (Table 8). These models indicated that survival varied based on season, especially during the hunting season (Sept-Dec), when cougars were most susceptible to mortality.

Table 8. Performance of top 2 models describing cougar survival on the northwest Olympic Peninsula, WA from 2011-2015.

Model	***K*[a]**	**AIC_c[b]**	**ΔAIC_c[c]**	**AIC_c weight[d]**
$S_{hunting}$	2	41.48	0.0	0.66
S_{season}	4	43.28	1.8	0.27

[a] Number of parameters in model.
[b] Akaike's Information Criterion, corrected for small sample size.
[c] Change in AICc value from model 1 to model 2
[d] Relative weight attributed to model.

The average annual survival rate (*S*) of bobcats was 0.89 (95% CI = 0.68 – 0.97). The top model was statistically superior to the next best model (Table 9), based on the likelihood ratio estimate (χ^2_2 = 9.4, *P* = 0.024), it had the lowest AIC_c value, and the weight supporting it was 5 times greater than the 2nd best model. The top model indicated that survival varied based on season, especially during the September-November time frame, and sex, with males having a greater probability of survival.

Table 9. Performance of top 2 models describing bobcat survival on the northwest Olympic Peninsula, WA from 2012-2015.

Model	***K*[a]**	**AIC_c[b]**	**ΔAIC_c[c]**	**AIC_c weight[d]**
$S_{season\ x\ sex}$	5	56.39	0.00	0.743
S_{sex}	2	59.67	3.28	0.144

[a] Number of parameters in model.
[b] Akaike's Information Criterion, corrected for small sample size.
[c] Change in AICc value from model 1 to model 2
[d] Relative weight attributed to model.

Home Range and Resource Use

Home range sizes varied between individuals for both cougar (Appendix C) and bobcat (Appendix D) and were also variable between years for individual cougars (Appendix C). Female cougars had a smaller (F_{18} = 9.3, *P* = 0.007) mean annual home range size (169 ± 41 km^2) compared to males (369 ± 362 km^2), based on the 99% fixed kernel estimate. There was no significant difference in mean home range size between female (9 ± 7 km^2) and male (13 ± 4 km^2) bobcats (F_{11} = 2.63, *P* = 0.14), based on the 99% fixed kernel estimate.

Cougars showed high home range fidelity between all pairs of years analyzed based on the fidelity index (FI; Table 10). For all 1-year intervals the mean FI = 91% (n=9) for females and 96% for the one male monitored over 1 year. For all 2-year intervals the mean FI = 88% (n=5) for females and 89% for the one male monitored over 2 years. For all 3-year intervals, the mean FI = 70% (n=2) for females and 89% for the one male monitored over 3 years. Only F02 had a FI < 84% among all females and males (Figure 11). The mean association index (AI; percent overlap) between F:F pairs was 24% and M:F pairs was 35% in 2011 and 25% and 37% in 2012, respectively (Table 11).

Table 10. Fidelity Index (FI), percent overlap among individuals for 1-, 2-, and 3-year intervals for cougars on the northwest Olympic Peninsula, WA, 2011-2014.

	F01	**F02**	**F03**	**F04**	**F05**	**M01**
FI1	94.7	62.5	92.1	97.8	83.7	95.6
	94.5	95.7		97.6		
		95.5		95.4		
FI2	92.0	59.0		95.8		88.8
		95.4		95.5		
FI3		46.8		92.6		88.6

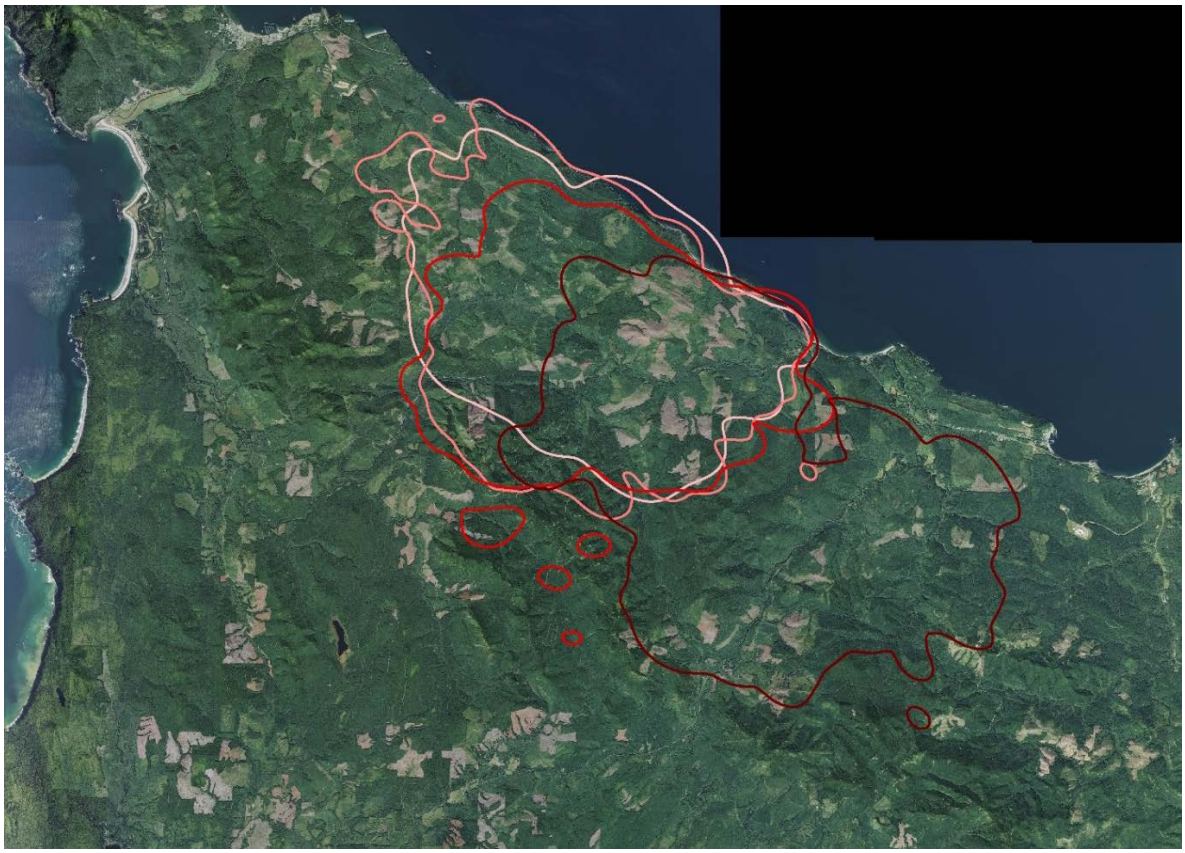

Figure 11. Home range boundaries (99% fixed kernel estimate) for F02 in 2011 (dark red), 2012 (light red), 2013 (dark pink) and 2014 (light pink) showing the overlap between years and the shift from 2011 to all subsequent years on the Olympic Peninsula, WA.

Table 11. Association index (percent overlap) between all F:F (red), F:M (green) and M:M (blue) pairs in 2011(a) and 2012 (b) on the northwest Olympic Peninsula, WA.

a.

2011	F01	F02	F03	F04	M01
F01		86.2	12.2	25.6	61.9
F02			2.7	12.95	57.4
F03				3.6	17.9
F04					0.6
M01					

b.

2012	F01	F02	F03	F04	F05	M01	M02
F01		58.9	9.8	41.5	0	43.2	52.4
F02			4.1	0	0	88.8	79.7
F03				2.4	34	18.6	46.7
F04					0	0.30	18.4
F05						0.80	20.6
M01							57.1
M02							

The mean percent overlap between all bobcat pairs was 16% for both spatial and volume of intersection for the 99% kernel home ranges (Appendix E). However, the mean overlap among M:F (n = 14) pairs (25%) was greater than that for either M:M (n = 13) or F:F (n = 2) pairs (7.5%; t_{15} = -2.24, P = 0.04). The mean core area size (50% fixed kernel estimate) for bobcats was 2.2 km^2 and there was no difference between males and females (F_{11} = 0.44, P = 0.52). The mean percent overlap between all M:F bobcat pairs (n = 7) for the 50% kernel core area was 28% (Appendix E; Figure 12).

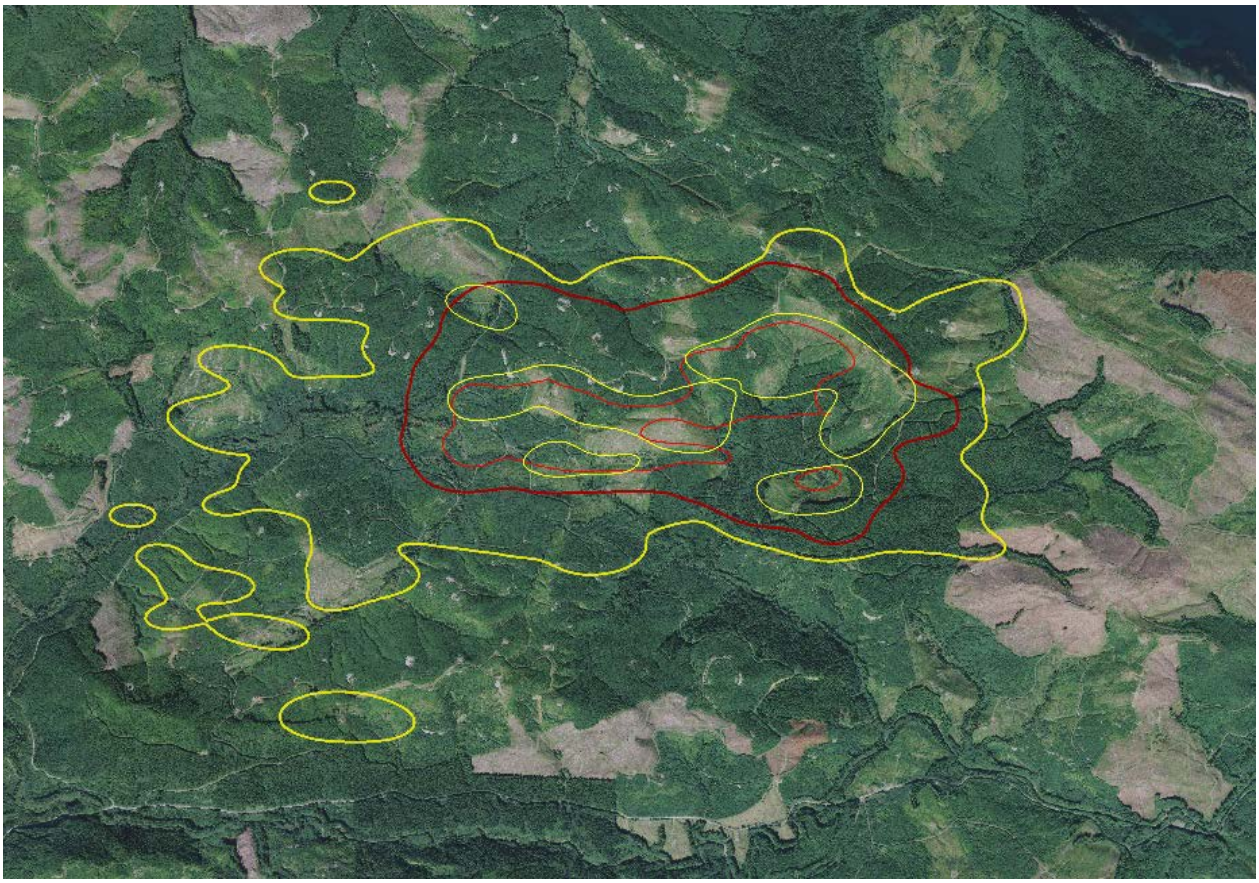

Figure 12. Example home range overlap of 99% fixed kernel estimate (bold line) and 50% fixed kernel estimate (thin line) for male bobcat BC09 (yellow) and female bobcat BC10 (red) on the northwest Olympic Peninsula, WA, 2012-2014.

The population level RUF indicated that use of habitat was positively associated with all land-cover classes, and highest use of areas within home ranges had a greater percentage of 6-15 year stands, closer distances to perennial streams and non-public roads, farther distances to publicly accessible roads and gentler slopes for both cougar (Table 12) and bobcat (Table 13).

Table 12. Estimated resource utilization function mean unstandardized coefficients for cougars (*n*=7) on the northwest Olympic Peninsula, WA from 2011-2014.

Landscape Attribute	Unstandardized RUF Coefficients	
	β	SE
Intercept	4.02289	4.07733
% Wetland	0.00582	0.12411
% Urban	0.02747	0.52332
% Field	0.22361	0.08286
% 0-5 age	0.24478	0.05015
% 6-15 age	0.26613	0.05951
% 16-30 age	0.14652	0.05456
% >30 age	0.15545	0.05759
Slope (Degree)	-0.00212	0.00265
Distance to Public Road	0.00049	0.00049
Distance to Non-Public Road	-0.00307	0.00126
Distance to Perennial Streams	-0.04373	0.02211

Table 13. Estimated resource utilization function mean unstandardized coefficients for bobcats (*n*=11) on the northwest Olympic Peninsula, WA from 2011-2014.

Landscape Attribute	Unstandardized RUF Coefficients	
	β	SE
Intercept	-21.20793	8.06381
% Wetland	0.88548	0.01459
% Urban	0.18950	0.02448
% 0-5 age	0.40443	0.07110
% 6-15 age	0.48966	0.06363
% 16-30 age	0.25217	0.05719
% >30 age	0.28564	0.05253
Slope (Degree)	-0.00982	0.01883
Distance to Public Road	0.00092	0.00067
Distance to Non-Public Road	-0.00284	0.00292
Distance to Perennial Streams	-0.00073	0.01358

Individual level RUFs showed that resource use was highly variable among all cougars and bobcats (Appendix F). Each of the 11 landscape features was significantly correlated with use for a majority of cougars (57-100%), and each of the 10 landscape features was significantly correlated with use for a majority of bobcats (73-100%). However, use was only consistent within the population for percent 0-5 year stands (86% positive), and percent 6-15 year stands (100% positive) for cougar (Table 14), and for percent 0-5 year stands (91% positive), percent 6-15 year stands (100% positive), percent 16-30 year stands (82% positive), and percent > 30 year stands (82% positive) for bobcat (Table 15).

Table 14. Standardized RUF mean coefficients for cougars (n=7) on the northwest Olympic Peninsula, WA from 2011-2014, with 95% confidence levels, the number of individuals with significant positive (+) or negative (-) use ($P < 0.05$) associated with each landscape attribute, and the rank of the absolute value of all coefficients.

Landscape Attribute	Standardized	95% CL			No. Cougars with use significantly associated with attribute		
	β	upper	lower	*P*	+	-	Rank
% Wetland	0.779	1.62	-0.06	0.05	4	0	8
% Urban	0.451	1.02	-0.11	0.10	4	2	9
% Field	0.987	2.46	-0.48	0.14	3	1	6
% 0-5 age	5.737	8.33	3.14	0.002	6	0	3
% 6-15 age	8.413	11.59	5.24	0.001	7	0	1
% 16-30 age	4.621	9.71	-0.47	0.07	5	1	4
% >30 age	5.928	12.83	-0.98	0.08	5	1	2
Slope (Degree)	-0.810	0.62	-2.24	0.21	2	2	7
Distance to Public Road	1.906	7.43	-3.62	0.43	2	3	5
Distance to Non-Public Road	-0.043	3.76	-3.85	0.98	1	6	11
Distance to Perennial Streams	-0.350	0.73	-1.43	0.46	1	5	10

Table 15. Standardized RUF mean coefficients for bobcats (n=11) on the northwest Olympic Peninsula, WA from 2011-2014, with 95% confidence levels, the number of individuals with significant positive (+) or negative (-) use ($P < 0.05$) associated with each landscape attribute, and the rank of the absolute value of all coefficients.

Landscape Attribute	Standardized	95% CL			No. Bobcats with use significantly associated with attribute		
	β	upper	lower	*P*	+	-	Rank
% Wetland	1.513	12.55	-9.53	0.332	2	0	7
% Urban	1.744	4.04	-0.55	0.082	3	0	6
% 0-5 age	10.969	15.93	6.01	<0.001	10	0	3
% 6-15 age	17.311	21.76	12.87	<0.001	11	0	1
% 16-30 age	6.016	10.83	1.20	0.019	9	2	4
% >30 age	11.231	16.04	6.42	<0.001	9	1	2
Slope (Degree)	-0.439	0.56	-1.43	0.791	3	5	10
Distance to Public Road	1.808	5.07	-1.46	0.245	7	4	5
Distance to Non-Public Road	-0.749	0.54	-2.04	0.226	3	6	8
Distance to Perennial Streams	0.584	5.36	-4.20	0.349	6	5	9

Population Density

Cougar relative minimum density was estimated at 0.0215/km^2, for a population estimate within the study area of 23 adult resident cougars. Bobcat population density was estimated at 0.58/km^2, for a population estimate within the reduced study area of 263 adult resident bobcats.

DISCUSSION

Captured animals were similar in size to other studies of cougars (Logan and Sweanor 2001) and likewise, adult males were on average larger than females. The age structure was different than that found by Logan and Sweanor (2001), where our cougar population consisted of older females (6.7) and younger males (3.4) similar to that seen in protected populations by Stoner et al. (2006). Our age structure would suggest higher female survival compared to males, and a population that is not heavily exploited. We did not identify differences in survival between males and females and hunting (the only source of mortality documented over 4 years of study) was opportunistic since hound hunting was illegal and access to the study area was strictly non-motorized. Our inability to capture all animals within our study area and the failure of some collars may have hindered our ability to detect other sources of mortality, for example, we found a cougar carcass at one of the clusters for M01, and we assume that he killed (and ate) it. In areas without hunting, intraspecific predation was a common source of mortality (Stoner et al. 2006, McKinney et al. 2009).

Capture efforts were successful during the first winter due to an adequate amount of snowfall, but in subsequent years capture efforts of new animals were hampered by a general lack of snow and copious amounts of rain. We captured more sub-adult males (n=5) compared to sub-adult females (n=1), with 3 sub-adult males under the age of 2 and 2 sub-adult males around the age of 2.5 years old. Males begin dispersing prior to sexual maturity at the age of 2 (Logan and Sweanor 2009) so we suspect that the 3 younger sub-adults were offspring of resident females that hadn't yet dispersed. The other 2 sub-adult males were likely recent immigrants into the population. We collared one of these males but the collar failed after only 1 month and the other male was harvested a few months after capture by a state hunter. In addition, M01 and M02 were similar in age at capture; while M02 showed behavior similar to a transient adult (Logan and Sweanor 2001), his home range significantly overlapped that of M01 and was twice as large. We only captured one other adult resident male and his collar failed after 2 months. The younger male age structure likely resulted from opportunistic hunter harvest of resident adult males or intraspecific competition among mature resident adult males and younger immigrating or transient males (Stoner et al. 2006). Additional research including a greater sample of adult and sub-adult males will be necessary to better understand the mechanism driving the age structure as well as immigration and emigration of our population.

Transient behavior in cougars may result from 4 conditions (p. 244, Logan and Sweanor 2001); two of these conditions (population isolation or inability to compete) may explain the behavior of M02 and the young age structure we experienced. Male M02 may have simply been unable to compete with M01 and traveled greater distances waiting to establish residency. Alternatively, Beier (2009) indicated a potential genetic bottleneck among the cougar population on the Olympic Peninsula. The limited immigration and emigration access from the south to southeast (Figure 1) may be contributing to this type of behavior. As new males immigrate into the area, they cannot continue traveling north or west, setting up home ranges between resident males and biding their time until they are strong enough to compete with stronger, more mature males or until vacancies open up. We collected DNA samples from all adults and sub-adults; this with an extensive genetic analysis throughout the Olympic Peninsula would be beneficial in identifying

recruitment into the population (Quigley and Hornocker 2009) or genetic isolation that may be present (Beier 2009).

Initial bobcat captures were plagued with problems. We implemented captures using collapsible bobcat traps. Cameras were placed on some trap sites and recorded bobcat interest, however, pictures consistently displayed an unwillingness to enter the trap. Therefore, we solicited the building of custom traps that were larger (see Methods) and improved trap success. We originally planned on using primarily live traps to obtain a sample of bobcats, but with the small number of custom traps available we used hounds to improve our capture rates and meet the sample size. We also experienced issues with obtaining a representative sample of female bobcats, which is difficult to explain. Of the total captures the ratio of male to female was 2:1. The majority of our female captures were from the custom cage traps, while the males were primarily captured using hounds. This suggests that, had we increased the number of large custom cage traps early on, our sample would not have been as skewed toward males. Females may have been able to escape hounds due to small body size and ease of movement in brushy conditions with a greater ability to seek refuge in structures other than trees (e.g. slash piles, blowdown, etc.). Males were more likely to be pursued successfully due to larger body size and propensity to use trees for refuge.

Prey Use and Selection

Prey species used by cougars on the Olympic Peninsula were diverse, similar to other studies (Murphy and Ruth 2009, Knopff et al. 2010) including those found by Kertson et al. (2011a) in the western Cascade Mountains. Deer and elk combined made up 82% of cougar diets whereas beaver and raccoon made up another 12%. We documented several interesting prey items (Figure 9) including bobcat, bear, cougar, coyote, river otter, mountain beaver, fish, mallard duck, red-tailed hawk, and an unknown marine mammal that was scavenged on by F05. The species specific predation rates that we report were within the ranges compiled by Knopff et al. (2010) and similar to their ungulate specific predation rates of 0.8 per week. The amount of time spent on a kill that we report was similar to those in wildland populations of cougars studied by Kertson et al. (2011a). We found a difference in these estimates between the winter and summer, where intervals and days on a kill were shorter during the summer timeframe and should be considered when estimating predation rates on ungulate populations (Knopff et al. 2010).

When comparing males and females together, cougars selected deer and elk according to their availability at the population level. Females consistently selected for deer compared to elk even though only 2 females (F01 and F02) showed significant selection, indicating that these 2 females exhibited individual specialization toward deer (Knopff and Boyce 2007) compared to the other 3 females in our study. In contrast, F05 may be considered an “other” species specialist, particularly for raccoon, as her deer and elk selection ratios showed no real preference or avoidance of either species and her diet was comprised of 73.4% “other;” of which over 60% was raccoon, 31% beaver. Unfortunately, we didn’t have availability data for “other” species and could not estimate the true selection (specialization) of these alternative prey species. There seemed to be a greater number of “other” species in diets of older females (>9.5 years old) compared to younger females, potentially indicating their preference for easier prey. Males did not select consistently for elk and deer, where males on average selected for elk, M02 had a

greater selection ratio for elk and a much lower selection ratio of deer compared to M01 (Table 7). Male M02 also had a greater proportion of "other" species in his diet, which was not included in this analysis, suggesting that he selected elk and avoided deer based on their availability, replacing deer with other species such as beaver and raccoon. A larger sample of males would be beneficial for analyzing diets and identifying any individual specialization that may occur.

Both males and females selected for young-of-year in both deer and elk species at approximately 2 times their availability. While selecting deer and elk according to availability at the population scale, as long as cougar densities remain stable, male-to-female ratios similar, and potentially an older female cougar age structure, deer and elk populations should also remain relatively stable as current research suggests they are (McCoy and Murphie 2012, McCoy et al. 2014). However, the selection of young animals will likely interfere with any efforts to increase ungulate populations by suppressing recruitment unless other management techniques are employed (i.e. harvest modifications either to deer and elk populations or cougar populations). White et al. (2011) also found that males and females used prey differently, potentially having different effects on prey population growth, where males would have a greater effect on elk and females a greater effect on deer. They suggested using sex-specific prey use to tailor decisions based on management goals.

Recovery of bobcat prey at identified clusters was hampered by the low fix success rate of GPS collars (56%). Even with the modifications of the algorithm developed for cougar prey recovery, we still identified prey remains at only 34% of the investigated sites. The low fix success rate resulted in many clusters containing only a small number of actual points with a significant number of missing points during the cluster timeframe. This may have resulted in searches not focused in the correct location in some instances or prey may have been smaller and completely consumed. The habitat where many of the potential clusters were identified was commonly composed of young, dense, regenerating forests that were difficult to search. Our ability to find remains of small prey species was probably compromised.

Bobcat diets of most studies were primarily comprised of rodents and lagomorphs (Brittell et al. 1979, Knick et al. 1984, Witmer and deCalesta 1986, Neale and Sacks 2001, Hass 2009), although deer were reported to provide significant dietary contribution as well (Knick et al. 1984, Hass 2009). We found that deer and mountain beaver were the primary species utilized by bobcats in our study. However, this likely reflects the methods used for determining prey selection (GPS clusters), rather than stomach content or scat analysis, which biases our results to larger prey that require greater handling and feeding time. Considering that smaller prey like mountain beaver, small birds and rodents, grouse, and snowshoe hare together comprised approximately 57% of the diet; these species likely provide a greater contribution to the actual diet and are presumably the focus of bobcat predation.

Deer were the most common species of prey found at identified clusters, even after adjusting for scavenging, which was prevalent. This wasn't unexpected as bobcats were identified as a major source of predation on black-tailed deer fawns in the same study area (McCoy et al. 2014). We also expected bobcat predation to be most pronounced on fawns during the first few months of life, similar to other studies (Carroll and Brown 1977, Trainer et al. 1981, Temple 1982,

Vreeland 2002, Roberts 2007, Rohm et al. 2007). However, we didn't detect a difference in deer use between summer and winter suggesting that bobcat predation occurs throughout the year, similar to Anderson (1987) and Blankenship (2001). Male bobcats accounted for all of the confirmed deer predations suggesting an influence of body size on prey selection, similar to Knick et al. (1984) and what we observed for cougars. Deer less than one year of age comprised 87.5% of the predation events which indicate that impacts to deer populations are limited to recruitment level effects not adult survival.

We were surprised that predation on deer was not most pronounced during the summer when fawns are smallest and most vulnerable. Rather, we observed 69% of predation on deer to occur during the winter, including the only 2 adults documented. This is likely due to two factors that increase the vulnerability of deer during the winter timeframe. The low digestible energy available in common species of forage used by deer (Hutchins 2006), contributes to weight loss during the winter. This leads to malnutrition, which was reported prevalent in black-tailed deer fawns (McCoy et al. 2014). This is compounded by the high prevalence of hair loss syndrome (HLS), which was first documented in 1996 in western Washington (Bender and Hall 2004). Bildfell et al. (2004) found that HLS was caused by an exotic species of chewing louse, *Damalinia* (*Cervicola*), which is not native to the Pacific Northwest and is a new parasite of black-tailed deer. Fawns are particularly prone to the condition. HLS is principally apparent in deer during the winter and spring months and results in hair loss from excessive licking and scratching of affected areas. HLS afflicted fawns have been documented to reduce feeding time (Murphie 2010) and suffer greater rates of mortality than non-afflicted fawns (McCoy et al. 2014). Both of the adult deer predated had health issues that likely increased their vulnerability. One had a significant hoof deformity and the other was malnourished, based on bone marrow examination, and afflicted with HLS. Eight of the 9 fawns that were predated during the winter had bone marrow indicative of nutritional stress and 4 were confirmed to have HLS. Historical data for bobcat prey use in Washington (Brittell et al. 1979, Knick et al. 1984) pre-dated the on-set of HLS and likely influenced the contribution of deer in the diet. Our results suggest that deer may currently be a more important contribution to bobcat diets due to the relatively recent onset of HLS, which increases the vulnerability of fawns to predation during the winter.

Mountain beavers were a significant contributor to bobcat diets in this study, similar to other studies in Oregon and Washington (Brittell et al. 1979, Knick et al. 1984, Witmer and deCalesta 1986). Mountain beavers inhabit densely vegetated areas with high annual precipitation and commonly occur in the initial seral stages after clearcutting of forests (Feldhamer et al. 2003). Population densities were reported to vary from 6.7 to 8.7/ha in logged areas in the Coast Range of Oregon (Lovejoy 1972). Our study area was comprised primarily of industrial timberlands that are actively logged, resulting in a mosaic of regenerating stands of various ages that provide optimal habitat for mountain beaver. We noted a high density of mountain beaver burrows and activity (fresh vegetation at burrow entrances) on many of the clusters where prey were not found. We suspect that mountain beaver was likely the most common species of prey utilized and that we struggled to find remains due to the brushy conditions limiting our search effort.

We were surprised that snowshoe hare was not a higher dietary contributor for bobcats. Previous studies in western Washington found this species to be common in the diet (Brittell et al. 1979, Knick et al. 1984). Snowshoe hares are larger than mountain beaver and should have required

sufficient handling time to be detected more frequently by GPS clusters. Forest structure may explain the lack of hare we documented, as research by Berg et al. (2012) found that snowshoe hares were more abundant in late seral multi-storied forests than regenerating even-aged forests. Our study area was dominated by younger stands that lack the diversity of older forests, and late successional forests are almost non-existent. Considering that timber harvest today occurs commonly in even aged stands younger than 50 years, development of optimal habitat for snowshoe hares is not occurring. We believe that snowshoe hare density is likely lower on the managed landscape today than when Brittell et al. (1979) and Knick et al. (1984) studied bobcat diets. This may have shifted contemporary bobcat diets toward more dependence on mountain beaver and other small prey.

Female Reproduction

We were unable to estimate annual reproductive effort by female cougars in our study. We did identify 6 dens from 3 females and we were successful at finding cubs on 2 occasions. We searched each location multiple times but our ability to locate and capture cougar cubs at the other 4 dens was hampered by dense vegetation and the age of cubs by the time we were able to search for them. Cubs are relatively mobile by 4 weeks of age (Logan and Sweanor 2009), and were able to avoid capture by hiding in dense understory, typically consisting of regenerating hemlock or pre-commercially thinned units, with significant understory debris that was extremely challenging to navigate. In the future, we recommend downloading data more frequently to get to den sites before cubs are more mobile, and assembling larger search parties or using a leashed dog to assist in locating cubs.

We observed 2 resident adult females that never seemed to produce offspring during our study. Both F04 (approximately 7 years old at first capture) and F05 (approximately 9.5 years old at first capture) did not have any clusters that would indicate den activity, and neither of them showed signs of rearing cubs. Female F04 was in good condition and was the largest female that we caught (Appendix A); she was monitored for over 3 years. Female F05, appeared to be in good condition, though one of the smallest females we captured (Appendix A); she was monitored for approximately 15 months. Female F04 appeared to have nursed previously and shared a kill with F01 on 2 occasions indicating that they were related in some manner. It is unlikely that we missed den activity for F04 as we were able to recapture her within 1 month of GPS battery failure in 2012 and within 4 months in 2013. The equation used to age cougars (Laundre et al. 2000) was estimated and most accurate for animals 3-7 years old; it is possible that F05 was older than we estimated and may have been unable to successfully reproduce. Alternatively, it is possible that we simply missed her den, as there were 2 months between when her GPS battery failed and when we recaptured her, and there were collar malfunctions between May and November 2013, at which point we lost contact with her. Logan and Sweanor (2001) documented non-reproducing females but all were less than 3 years old, likely prior to breeding, even though they captured females up to 12 years of age. They considered cougars between the ages of 8-13 years as old, but they found no evidence that aging females had reduced litter sizes and the oldest reproducing female in their study was about 10.5 years old (Logan and Sweanor 2001). Also, in our study F03 produced a single female cub at almost 11 years old. We only monitored 5 resident adult females throughout our study, but it seems unusual that 2 of those did not reproduce. Further investigation is necessary; potentially analysis of blood parameters would provide insight into factors related to sudden or ultimate lack of productivity.

Female bobcats are capable of reproducing yearly throughout their life span (Crowe 1975a). Litter sizes range from 1-5 kittens, but usually average 2-3 (Anderson and Lovello 2003). Unfortunately, we did not detect denning from the adult females monitored and subsequently did not document reproduction. However, as the population studied had characteristics of an unexploited population (Nielsen and Woolf 2001), such as high rates of survival (89%) and population density (0.57/km^2) we suspected reproduction may be low. Diefenbach et al. (2006) reported declining reproduction with increasing population density. Density of bobcat populations is known to affect sex ratios. An unharvested population in California at high density had a sex ratio of 2.1 males per female. The ratio reduced to 0.89 males per female when density was low (Lembeck and Gould 1979). Similarly, Zezulak and Schwab (1979) observed 7 males per female and suspected that males were selected for at high densities, resulting in limited reproduction until mortality, emigration, or environmental shifts reduced population density. The population studied may also be comprised of older bobcats with lower reproductive rates. Unexploited populations are largely composed of older individuals, whereas younger animals dominate exploited populations (Anderson and Lovello 2003). Lembeck and Gould (1979) found 16% of the bobcats in an unexploited population were <2 years old, compared to 43% in an exploited population in similar habitat. This suggests lower reproduction is typical at higher bobcat density, with an older age structure. We did not determine the ages of captured bobcats, but the age distribution was likely older.

Intrasexual home range overlap influenced by prey availability may be another factor influencing reproduction. Female bobcats are solely responsible for rearing offspring, and their home ranges must provide an abundance of prey to meet energetic demands of the female and kittens (Anderson and Lovello 2003). Core areas of female bobcats have been reported to be nearly exclusive to conspecifics of the same sex (Nielson and Woolf 2001, Chamberlain and Leopold 2001). Woolf (1997) proposed that females seek exclusive use of home range areas to prevent infanticide from conspecific females. However, intraspecific home range overlap has been reported to increase in female bobcats with reduced prey density (Knick 1990, Litvaitis et al. 1986). This suggests that prey availability can influence reproduction through intraspecific interactions or simply females may reduce their reproductive effort in response to declining food availability. We did not observe significant overlap at the core area or 50% kernel home range (Appendix E), which suggests that our female bobcats were maintaining exclusive use areas within their home range. A wide variety of prey species were available on the landscape based on the prey selection data. We suspected the mountain beaver was ubiquitous in our study area and likely the most used species of prey. This suggests that neither prey availability nor infanticide was a contributing factor. However, our sample of female bobcats was low and represents an unknown proportion of the population. Consequently, we may have failed to monitor enough of the females in the population to understand the true relationship of bobcat density to degree of overlap (Anderson 1987). We also have no information on population size and trend for many common species of prey utilized by bobcats which may play a role in bobcat reproduction.

Despite our failure to document reproduction, we suspect it did occur. While reproduction is typically lower in unexploited populations, reproduction has been documented under those conditions (Diefenbach et al. 2006, Roberts 2007). Our ability to document female bobcat

reproduction was likely compromised by the poor GPS fix rate. Bobcats are associated with thick vegetative cover (Kolowski and Woolf 2002, Roberts 2007) and dens are typically in hollow stumps, uprooted trees, or areas of thick understory (Roberts 2007). We may have failed to note denning behavior due to missing data associated with heavy cover at den sites and misinterpreted hunting forays away from the den as movements not indicative of denning. Additionally, den sites of bobcats are moved several times while females are rearing kittens (Bailey 1979), which may have further complicated documenting reproduction from inconsistent GPS data. We recommend triangulating female bobcat positions a couple of times per week, during the denning timeframe, using the collar VHF signals to note potential denning, rather than relying on GPS fixes.

Survival Analysis

Survival of cougars was relatively high, similar to rates seen in protected or non-hunted populations (Logan and Sweanor 2001) and higher than rates seen in lightly hunted populations of Washington (0.71±0.06; Cooley et al. 2009). We suspected that dense forested conditions prevalent in the study area lowered vulnerability of cougars to hunters. The lack of difference in survival between males and females, given the age structure of our population, however, was not expected (see discussion above) and seems contradictory. The only source of mortality documented over 4 years was hunting, both 1 male and 1 female were harvested in October of the same year. Other studies documented hunting mortality as the primary cause (Stoner et al. 2006, Lambert et al. 2006, Robinson et al. 2008, Clark et al. 2014) but only Clark et al. (2014) had similar management practices in one of their study areas, where hunting with dogs was prohibited. In this area of southwest Oregon, habitat was similar to that in our study area and survival rates of cougars were slightly lower but within the 95% confidence interval that we reported. They documented natural mortality as the leading cause after the ban of hound hunting, whereas we did not. We believe that small sample size of males affected our ability to document other sources of mortality.

We believe that cub(s) from F02 survived to independence based on predation events including kill intervals and evidence at kill sites. Unfortunately, we do not know how many or what sex these cubs were, but 2 of the sub-adult males we captured were within her home range prior to their dispersal. We were unable to confirm mortality or cause of death for the 4 cubs that we captured, even though we suspect that they all died. Infanticide was a potential threat as kitten survival is low when male turnover is high or if males are newly established (Ruth et al. 2011), especially given the young age structure of males in our study area and the number of sub-adult males we captured. Cougar cub mortality averaged 0.41 and 0.43 in other studies (Logan and Sweanor 2001, Lambert et al. 2006), and in a few instances entire litters of cubs were lost. In these cases, Logan and Sweanor (2001) documented successful breeding again 23-307 days later; similar to that seen in our study by F01 (approximately 300 days) and F03 (approximately 120 days). Most cub mortality (65%) occurs before the age of 3 months (Logan and Sweanor 2001) and we suspect that in both instances where litters were lost, this was the case. Female F01 was a new mother, which may have contributed to the loss of her first litter considering that younger mothers may have lower success at rearing their young to independence than older, more experienced mothers (Logan and Sweanor 2001).

The bobcat mortalities we documented were limited to natural causes and predation by other carnivores. Cougar predation was the culprit in one predation event and has been documented in previous studies (Young 1958, Koehler and Hornocker 1991). The cougar predation we documented was from one of our female cougars (F02). The other predation event was unknown, but could have been from coyotes that have been directly identified as bobcat predators (Young 1958, Knick 1990). The female dying from natural causes appeared to be severely emaciated, which may have been related to disease (Anderson and Lovallo 2003).

The survival rate we documented (89%) is consistent with an unexploited population. Anderson and Lovallo (2003) indicated that exploited bobcat populations (excluding heavily exploited populations) had an average annual adult survival of 56-76%. Adult survival in unexploited populations has been reported to be much higher, ranging from 78-97% (Crowe 1975b, Knick 1990, Chamberlain et al. 1999). Human exploitation, including legal and illegal harvest, is the most prevalent source of mortality in many studies (Hamilton 1982, Fuller et al. 1985, Rolley 1985, Fuller et al. 1995). In Washington, the use of body gripping traps has been restricted since Initiative No. 713 was passed in 2000 which dramatically lowered furbearer harvest (http://ballotpedia.org/Washington_Animal_Trapping_Act,_Initiative_713_%282000%29). In 2009 the harvest of furbearers in Washington was 3,180 compared to 12,116 in 1999 prior to Initiative No. 713 (Washington Department of Fish and Wildlife 2014). While the use of live traps to pursue furbearers is still legal, the elimination of body gripping traps for legal harvest has dramatically reduced trapping effort. We knew of no licensed trappers operating in our study area before or during our field data collection. Bobcats were legal game that could be taken by hunters using legal weapons during established hunting seasons, however, we did not document any harvest. It appears that hunters pursuing other game are not significantly interested in harvesting bobcats.

Modeling indicated that bobcat survival was explained by increased vulnerability during the September-November timeframe, with males having a greater probability of survival. Male bobcats in particular are known to have greater movement rates and distances than females, particularly during the fall-winter timeframe (Bailey 1974), which increases their susceptibility to hunting (Edwards 1996). However, hunting was not a factor for either sex, even though the number of hunters in the study area peaks during this time as it corresponds with both State and Tribal big game hunting seasons. The lower survival rate for females may be explained by the demands of reproduction and kitten rearing (Chamberlain et al. 1999). While Chamberlain et al. (1999) reported lower female survival during parturition-kitten rearing (June 1- September 30), kittens generally stay with the female until the subsequent breeding season (Anderson and Lovello 2003). Females in our study area (despite our lack of documentation of denning) may have been more susceptible to mortality than males due to the costs associated with reproduction and those costs may have been most pronounced during the fall-winter timeframe. Contrarily, the lower female survival we observed could be an artifact of low sample size. We only recorded 3 mortalities over the course of the study which provides little evidence to establish definitive trends or differences in survival between the sexes or time of year. However, the lack of mortality from hunting, higher survival of males than females (Frits and Sealander 1978), and the documented mortality sources all suggest that the population studied is regulated by natural processes.

Home Range and Resource Use

The variation we documented in home range size between individuals and between years is typical and may be related to habitat quality; prey availability, distribution and movements; and cougar abundance and interactions (Pierce and Bleich 2003, Logan and Sweanor 2009). Home range sizes fell within the ranges reported in other studies (females: 55-300 km^2, males: 150-700 km^2; Logan and Sweanor 2009), but were smaller than those estimated in other areas of western Washington by Kertson et al. (2013) and in eastern Washington by Lambert et al. (2006). Home range overlap between years indicated high fidelity for individuals despite differences in size and small shifts over time (Table 10). Female F02 was the only cougar with an FI index below 84%, which was represented by a movement from her 2011 home range (where she denned) to subsequent home ranges in 2012, 2013 and 2014 (Figure 11). She never returned to the area where she denned in 2011 for any of the subsequent years of monitoring. The FI index reached 46.8% for the 3-year interval between 2011 and 2014, above the 40% threshold indicated by Logan and Sweanor (2001), which was not considered to be a significant shift in home range. The high fidelity among adult resident cougars indicates adequate resources for the current population. The percent overlap among females suggested close relationship with some, such as matrilineal lines common in philopatric female populations (Logan and Sweanor 2001, 2009); for example F01 and F02 (Table 11), contrary to overlap with F05 which only occurred with F03. The percent overlap between males and multiple females is consistent with male territorial behavior including access to mates (Logan and Sweanor 2001, 2009). The overlap documented between M01 and M02 was likely due to M02's age and status within the population (see discussion above).

Cougars showed high variability in selection of resources at the individual level, which is consistent with the habitat generalist behavior observed in cougars (Pierce and Bleich 2003, Kertson et al. 2011b, Ruth et al. 2011). The percent of regenerating forests in the 0-5 year and 6-15 year age class were the most important land-cover attributes in cougar habitat use at the population level. At this scale, cougars selected habitats that provided the greatest opportunity for prey, and it was in these land-cover classes that we found the majority of kill sites (12% and 46%, respectively). This is similar to findings of Kertson et al. (2011b) in the western Cascade Mountain range of Washington and follows consistently with prey populations (Goh 2000, Nelson et al. 2008, Boyd 2009) and cover characteristics of those habitats (Hall et al. 1985).

Distance to roads was not significant at the population level, but for individual cougars use increased as distance from non-public roads decreased, indicating the potential importance of unpaved roads as travel corridors (Dickson et al. 2005). The only exception to this was F05 (Appendix F), who used the coastal strip of Olympic National Park (ONP), a significant amount of area without any roads. Female F05 was a unique individual considering that the coastal strip of ONP was within the core area of her home range, which was associated with mature timber >30 years old, and resulted in a significant number of kills comprised of raccoon. Her individual RUF coefficients revealed that the >30 year age class was most important followed by 16-30 year then 6-15 and 0-5 year, which was different than all other cougars in our study. Riparian habitat was an important factor in cougar use of habitat in California (Dickson and Beier 2002, Dickson et al. 2005), and while still important for a majority of individuals in our study, it was not significant in selection of resources at the population level. However, there was generally greater use of areas with shorter distances to perennial streams (with the exception of F05), and

for 4 individuals there was a significant increase in use as the proportion of wetland habitat increased. This was likely associated with the importance of beaver in the diet of some individuals. Likewise, Kertson et al. (2011b) found cougars in close proximity to water and associated its use with abundant beaver, raccoon and mountain beaver populations. Access to water is not limited in the Pacific Northwest, there is availability year-round and may explain the lack of significance for selection at the population level in our study.

Slope was not important at the population level, and was generally the least important variable for most individuals, similar to results from other studies (Goh 2000, Dickson and Beier 2002). This was evident by the coefficients of individuals (Appendix F1) where some were significant in one direction while others were significant in the other direction or not at all. This was also the case for distance to publicly accessible roads, though an extremely important variable for F02 and F04. Public roads included both paved and unpaved roads where access by the public was possible and weren't considered separately in resource use analysis, contrary to studies by Dickson and Beier (2002) and Dickson et al. (2005). Those studies identified an importance at the population level but not at the individual level, which we may have found if we had considered paved roads alone.

Bobcats are similar to cougars regarding home range and social organization, where they are essentially solitary except for females with kittens and during the breeding season. Social classes include resident adults, transients, and juveniles, with varying degrees of spatial overlap. Variation in home range sizes of bobcats was typical throughout their range from 1.0-112.2 km^2 as compiled by Anderson and Lovallo (2003). Home range sizes we report were most similar to those in a high population density area in Idaho (Knick 1990), even though they used MCP and our estimates were based on the 99% fixed kernel estimate. Unlike other studies, we did not see differences in home range sizes between males and females for the 99% or the 50% fixed kernel estimates. Female home ranges may be more related to prey availability, whereas male home ranges may be more influenced by the number of mates (Anderson and Lovallo 2003). Similar home range size among the sexes indicated that adequate prey existed within relatively small areas and that female density was high enough to keep male home range sizes relatively small as well.

Anderson and Lovallo (2003) reported that most studies found significant intersexual overlap (M:F pairs) with varying degrees of intrasexual overlap (M:M or F:F pairs), including that generally females exclude other females whereas males overlap each other encompassing ranges of 2-3 females. We had significant overlap among M:F pairs (25%) and varying degrees of F:F and M:M overlap (averaging <8%) that followed the general rule. The low levels of intrasexual overlap in our study area supports territorial behavior and suggest abundant and evenly spaced prey and cover. We reported both spatial overlap (99% fixed kernel estimate) and the volume of intersection (99% utilization distribution). Spatial overlap (SO) simply estimates the area of overlap between 2 home ranges and does not account for the third dimension (i.e. height of the UD). The volume of intersection (VI) quantifies the degree of overlap in shape and location between 2 UDs (Millspaugh et al. 2004), such that overlapping areas with greater use receive a greater weight. For example, if we consider the pair BC09 and BC10 the SO is 45.1% whereas the VI is 72.14% (second line, Appendix E). The overlap for these bobcats occurred within areas of greater use for both, indicating that they were using areas similarly (greater overlap of core

areas); whereas a comparison of SO only would indicate that they used similar areas less than 50%. For a majority of bobcats the VI was less than the SO, suggesting overlap of peripheral boundaries where degree of use was less. For bobcats where VI was greater than SO there was more of an overlap in locations with greater use, such as core areas.

Bobcats used habitat similarly to cougars (greater percentages of 0-5 and 6-15 year regenerating forests) except that they also used areas with greater percentages of 16-30 and >30 year old timber stands. This likely reflects the distributions of their prey populations where small prey are likely abundant in all age classes and deer are most abundant in 0-5 and 6-15 year stands resulting in overlap with cougar as deer are their primary prey. There was no evidence of spatial avoidance between cougar and bobcat, similar to Hass (2009), but interference competition may have influenced their use of habitat either temporally or at a finer scale (such as shorter increments in forest age structure). Bobcats in Michigan also used multiple habitats within their core areas, indicating the importance of landscape patchiness (Preuss and Gehring 2007), a common attribute in managed forests of the Pacific Northwest. Other landscape characteristics were not significant at the population level, but were highly variable between individuals. Observed variability in resource use could potentially be explained by differences in age, sex, and social characteristics (Anderson and Lovallo 2003) or as a function of differences between resource abundance and distribution within home ranges coupled with innate or learned behavioral adaptations that might stem from the land tenure structure (Diefenbach et al 2006, Lynch et al. 2008). Bobcats appeared to be more generalist than cougars based on the significance of 4 land-cover classes compared to only 2 for cougars. Otherwise, all other landscape characteristics were similar between the 2 species (at the population level) including slope, distance to public roads, and distance to non-public roads.

At the individual level, the majority of bobcats showed a greater use of areas as distance to public roads increased, and as distance to non-public roads decreased (Appendix F2). This suggests that bobcats do not prefer roads with greater amounts of traffic, especially as it could increase their risk of mortality. Alternatively, non-public roads, typically logging roads with limited motorized vehicle access or non-drivable roads, provided travel routes to bobcats within their home ranges, especially since road densities in this area are relatively high. Similar to cougars in our study, slope was the least significant landscape attribute in areas used by bobcats both at the population level and at the individual level; five bobcats used gentler slopes, 3 bobcats used steeper slopes, and 3 showed no significance in use of slopes either way. The fact that slope was not important at the population level, may indicate a lack of variability among individual home ranges. Some studies have shown that male and female bobcats use habitat differently (Anderson and Lovallo 2003, Chamberlain et al. 2003), unfortunately, we did not feel that we had enough females to evaluate differences in habitat use between the sexes in our study. However, anecdotal evaluation of standardized RUF coefficients shows a slightly greater use in the 0-5 year stands compared to >30 year stands for males, whereas females used >30 year stands more than 0-5 years stands. This likely reflects the greater proportion of deer in male diets compared to females, as deer were more abundant in 0-5 years stands.

Population Density

The estimated adult resident cougar population density in our study area (2.15/100km^2) is higher than densities estimated in eastern Washington (Lambert et al. 2006) and higher than the

Washington Department of Fish and Wildlife goal of 1.7/100km^2 (Beausoleil et al. 2013), though not by much. Population density estimates have been shown to vary widely (0.44-13.03 cougars/100 km^2; Smallwood 1997), based on the scale of measurement. Our study area was smaller than most in the reported literature and may have been correlated to the density estimates we obtained. Our estimate was for resident adults only and does not account for sub-adults. If our study area is experiencing higher immigration rates than emigration rates of males, this would result in a greater density than we report. The management strategy based on cougar behavior and social organization put forth by Beausoleil et al. (2013) is designed to maintain an older age structure that should promote population stability. We believe the cougar population that we studied is essentially stable, but more information is needed on all age classes of males, including immigration and emigration rates and the extent to which transients exist.

Bobcat density on our study was higher than reported for exploited populations (0.05-0.10/km^2; Anderson 1987), higher than an unexploited population in Illinois (0.34/km^2; Nielson and Woolf 2001), but lower than other unexploited populations (0.77-1.53/ km^2; Miller and Speake 1979, Lembeck and Gould 1979). The bobcat density we report in conjunction with the high survival of territorial adults provided a high degree of certainty that the population studied can be characterized as unexploited.

Bobcat social organization, particularly core area (50% kernel) overlap and core area size, played a key role in determining population density in our study area. Bobcats are thought to be territorial, operating under a land tenure system based on prior rights with little displacement apart from changes created by mortality. Vacancies created by the death of resident individuals are filled by transients or adjacent residents (Anderson and Lovello 2003). Territoriality in bobcats has been the subject of research and the degree of territoriality as measured by home range overlap has varied. Intersexual home range overlap is common in bobcats. Male home ranges are influenced by the number of mating opportunities or females within their range (Anderson and Lovello 2003). We found high levels of intersexual overlap within the core areas of our bobcats. However, our home ranges were significantly smaller than typically reported for northern latitudes (Litvaitis et al. 1987) and played a key role in our estimated density. For example, Nielson and Woolf (2001) reported similar intersexual core area overlap to ours, but their density estimate was lower. This is due to the average core area size for our bobcats which was approximately 37% lower than reported by Nielson and Woolf (2001).

We found little intrasexual overlap for both males and females within the core areas which suggested exclusive use within the sexes, similar to Nielson and Woolf (2001). We believe that at our current densities, core areas represent areas of more aggressive territoriality (Chamberlain and Leopold 2001) that mimic conditions occurring in denser populations (Nielson and Woolf 2001). This implies that female and male bobcats are reducing competition for resources within their core areas. Core areas represent where individuals spend the most time and are more familiar with resources compared to the rest of the home range. Thus, territoriality is more pronounced within the core area than the rest of the home range.

One possible criticism of our density estimate is the assumption that sex ratios are 1:1. We did not have any ancillary data such as trapping records to validate this assumption. Other studies found skewed sex ratios with high density populations (Lembeck and Gould 1979, Zezulak and

Schwab 1979) and we had a low capture rate of female bobcats in this study suggesting fewer females in the study area. This suggests the density we reported may be an overestimate. However, we felt capture methods may have played a role as described previously (Animal Capture) and the fact we had pictures from remote cameras of smaller female bobcats at trap sites that we were never able to capture. Also, our density estimate, while indicative of unexploited populations, was not as extreme as reported in other studies (Miller and Speake 1979, Lembeck and Gould 1979).

Conclusion

The northwest Olympic Peninsula provided a unique opportunity to study cougars and bobcats to assess their impacts on local prey populations and identify resource use at both the population and individual level. Our study area consisted of year-round water resources, non-migratory ungulate populations, abundant alternative prey for cougars, such as beaver, raccoon, and mountain beaver, abundant primary prey for bobcats, immigration and emigration access that is limited by the Pacific Ocean to the west and the Strait of Juan de Fuca to the north/northeast, patchy habitat mosaics consistent with managed forests of the Pacific Northwest including adequate cover for stalking, hiding and rearing young, and limited hunting access through restriction of motorized vehicles in most areas of research. Cougar and bobcat populations both showed high rates of survival and similar spatial use of habitat at the population level, whereas individuals were highly variable in their selection of resources. Prey species differed between the 2 species with female cougars selecting deer, male cougars selecting elk and bobcats selecting smaller prey. Overall, we believe both populations are relatively stable at this time, and are likely maintaining ungulate prey populations at current levels.

The opportunity for additional research exists for both cougar and bobcat. For cougar, a greater sample of males (all age classes) is needed to understand the younger male age structure, estimate immigration and emigration rates within the study area, and identify other potential sources of mortality. A larger sample of female cougars is necessary to estimate productivity and obtain better estimates of survival and natality. Both would benefit efforts for a more accurate density estimate of cougars based on a larger scale. For bobcats, a greater sample of females is needed to estimate productivity, along with survival and sources of mortality for young.

We have collected valuable information on cougar and bobcat populations within our study area that includes resource use among populations and individuals. As the population of wolves in eastern Washington continues to increase, the likelihood of re-colonization on the Olympic Peninsula also increases. We now have baseline data for these 2 relatively stable populations, which will likely be altered with the return of wolves to the study area. Wolves have been responsible for affecting cougar populations through direct mortality, and by altering diet and space use patterns through interference and exploitative interactions (Kortello et al. 2007). In addition, wolves are suspected to be bobcat predators and may have similar influences on their populations, or alternatively, bobcats may benefit from wolves by reducing competition with cougars or coyotes (Anderson and Lovallo 2003). Ungulate prey species will also be affected by wolves and documenting changes in baseline populations will be necessary to determine any impacts that may be experienced, both short term and long term.

Some research has found that competition with fisher populations may result in increased bobcat kitten mortality (Gilbert and Keith 2001), but local research suggests that bobcats may have an impact on fisher populations through predation on female fishers (Lewis et al. 2011, Lewis 2014). Though we did not identify fishers in bobcat diets, the density of fishers in our study area is likely very low as their re-introductions only began in 2008-2010. More likely, they would compete for similar food resources, including mountain beaver (Feldhammer et al. 2003) and other small prey selected by bobcats. As fisher populations become re-established, it will be important to monitor interactions between fishers and bobcats to quantify any impacts that may result.

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APPENDIX A. All measurements of cougars taken at initial capture (except F01, taken on 2nd recapture as full grown adult) on the northwest Olympic Peninsula, WA, 2011-2014.

Capture Date	Animal ID	Weight (kg)	Sex	Age[a] (years)	Total Length[b] (cm)	Shoulder Height (cm)	Girth (cm)	Neck (cm)	RHFL[c] (cm)	UCG[d] (mm)	LCG[e] (mm)	Head Length (cm)	Head Width (cm)
2/10/2013	F01	46	F	3.28	195.5	63.5	64	29.4	26	36.8	31.8	21.6	13.5
2/18/2011	F02	46	F	4.06	206.5	67	61.5	33.8	28	39.6	34.7	24.4	13
2/24/2011	F03	37	F	9.55	195	66.5	56	31	26	39.7	33.2	24.3	11.5
2/26/2011	F04	58	F	7.20	210	66	81	37	31	41.5	35.6	25	15.8
1/18/2012	F05	46	F	9.55	192	47	58	33.5	28	43.2	37.8	24	13
2/17/2011	M01	80	M	2.89	230.5	69	81	46.7	29	45	32.9	31	17
12/6/2011	M02	65	M	3.28	237	58.5	75	40	30	49.4	37.9	26	16.5
11/29/2012	M03	77	M	4.45	223	73.5	75	42.5	28.8	46.5	41	28.5	17.4
2/18/2011	SAM01	50	M	1.37	210.5	66	76	35.3	28.5	48.2	37.6	26.2	14.6
2/23/2011	SAM02	52	M	1.42	222.5	63.5	70.5	35.5	29.7	43.9	38.8	25.5	13.5
3/9/2013	SAM03	55	M	1.45	227	53	68.5	36.5	30	43	40.5	25	13
6/8/2013	SAM04	52	M	2.50	210	68.2	65.1	32.8	27.5	43.6	37.9	13.5	28.5
6/9/2013	SAM05	52	M	2.50	224	62	75	40	28	42.5	36.9	27	15

[a] Estimated age at capture
[b] Total length includes tail length
[c] RHFL = Right Hind Foot Length
[d] UCG = Upper Canine Gap
[e] LCG = Lower Canine Gape

APPENDIX B. All measurements of bobcats taken at initial capture on the northwest Olympic Peninsula, WA, 2012-2014.

Animal ID	Sex	Weight (kg)	Body Length (cm)	Tail Length (cm)	Shoulder Height (cm)	Girth (cm)	Neck (cm)	Hind Foot Length (cm)	Head Width (cm)	Head Length (cm)	UCG[a]	LCG[b]
BC01	M	10.0	88	15.8	48.2	34.7	22.3	17.3	8.2	15	29.6	16.8
BC02	M	6.8	82.1	15.8	38.5	29.5	18.5	17	10.1	15.4	24.1	21.1
BC03	F	5.1	82	12.5	37.5	25.2	17	16.2	9.4	15.7	22.4	21.3
BC04	M	11.5	82.5	12.2	49	37.3	23.3	na	12.3	17.2	25.8	23
BC05	M	15.0	86.5	15	46.3	41	24.3	18.8	10.3	17.6	26.4	23.8
BC06	M	12.3	91	16.5	46	39.5	26.6	18.5	11.5	19	26.9	25.5
BC07	M	9.5	84	16.3	44.7	34.5	21	18.5	11.6	17.5	26.4	23
BC08	F	6.0	75.8	12.8	43.4	27.5	19	16.3	8.5	14	22.8	20.9
BC09	M	10.0	82.5	14.1	41.4	32	20.8	17.7	9.8	19.5	25.5	23.3
BC10	F	9.5	79.5	11.7	32.5	na	18.5	17.0	10.0	16.6	22.9	21.1
BC11	F	9.5	81.5	11	42.5	34.2	20.8	16.5	9.2	17.4	24.5	20.2
BC12	F	6.5	75	15.6	38.8	28	17.8	17.5	9	15.5	25.5	21
BC13	M	13.5	94	15	49	44	31	19	11	18	18	15
BC14	F	8.0	77.5	16	41	33	20.3	15	8	14	26.5	23.8
BC15	F	6.0	74	12.5	39	27.2	19.1	16.5	9.5	15.5	21.6	19.3
BCUAM1	M	12.0	87.2	14	50.5	35.5	22	18.5	11.2	17.4	25.7	25.5
BCUAM2	M	11.0	79.2	13.5	43	37.5	23.5	17.5	9.8	15.6	23.5	22.6
BCUAM3	M	10.0	94	15	48.5	44	25	16.5	10.3	16.8	20	18
BCUSAF1	F	4.5	69.5	11.5	40.4	25.1	16	14.4	8.4	17.2	21.5	18.3
BCUSAM1	M	6.0	75.5	13.6	39	28	17.5	17.5	8.2	14.5	21.8	17
BCUSAM2	M	7.0	81.3	11.2	42.2	30	19.2	16.3	10	15.4	24	21.2

a UCG = Upper Canine Gap
b LCG = Lower Canine Gap

APPENDIX C. Annual home range sizes (km^2) for 99% utilization distributions (UD) of cougars on the northwest Olympic Peninsula, WA, 2011-2014.

YEAR	F01	F02	F03	F04	F05	M01	M02
2011	201.16	116.36	199.64	151.38		237.43	
2012	167.13	80.54	249.57	141.55	339.15	219.32	704.72
2013	156.76	91.24		147.46	275.09		
2014		81.30		133.49		315.14	

APPENDIX D. Home range sizes for 99% utilization distribution (UD) and 50% UD fixed kernel estimates of bobcats on the northwest Olympic Peninsula, WA, 2012-2014; blue indicates male bobcats and black indicates female bobcats.

Bobcat ID	99% Home Range (km^2)	50% Home Range (km^2)
BC01	9.15	2.18
BC02	13.15	2.09
BC04	15.08	2.83
BC05	21.23	2.57
BC06	8.76	1.9
BC07	16.32	2.39
BC09	8.63	1.44
BC13	14.69	2.85
BC10	3.89	1.1
BC11	11.74	2.52
BC14	13.57	3.04
BC15	6.69	1.42

APPENDIX E. Percent spatial overlap and percent volume overlap for bobcat 99% fixed kernel density estimates (KDE) and percent spatial overlap for bobcat 50% fixed KDE on the northwest Olympic Peninsula, WA, 2012-2014; blue indicates M:F pairs, red indicates M:M pairs, and black indicates F:F pairs.

Bobcat Pairs	Spatial Overlap (99% KDE)	% Volume Overlap	Spatial Overlap (50% KDE)
BC02-BC11	82.40%	76.31%	42.88%
BC09-BC10	45.10%	72.14%	39.06%
BC05-BC14	63.07%	71.48%	59.84%
BC06-BC15	64.27%	66.32%	28.09%
BC05-BC13	29.52%	47.17%	30.80%
BC13-BC14	38.68%	42.44%	25.01%
BC05-BC04	16.70%	8.60%	0
BC11-BC06	10.84%	7.37%	0.39%
BC06-BC05	17.17%	6.98%	0
BC14-BC04	7.39%	6.84%	1.20%
BC02-BC06	12.29%	6.73%	0
BC11-BC15	7.69%	6.58%	0.43%
BC02-BC15	9.19%	5.73%	0
BC15-BC05	14.37%	5.26%	0
BC13-BC04	8.32%	4.32%	0
BC15-BC04	7.36%	3.25%	0
BC01-BC02	5.14%	3.23%	0
BC06-BC14	3.38%	2.39%	0
BC06-BC04	5.39%	1.99%	0
BC07-BC11	2.31%	1.17%	0
BC15-BC14	1.78%	1.00%	0
BC06-BC13	2.74%	0.91%	0
BC07-BC02	3.50%	0.72%	0
BC15-BC13	1.34%	0.33%	0
BC04-BC09	1.19%	0.27%	0
BC01-BC04	0.58%	0.13%	0
BC02-BC05	0.34%	0.07%	0
BC04-BC10	0.03%	0.01%	0
BC07-BC06	0.06%	0.01%	0

APPENDIX F. Individual RUF coefficients and standard errors (se, in parentheses) for cougars (1) and bobcats (2) on the northwest Olympic Peninsula, WA, 2011-2014; numbers in red indicate landscape attributes that are not significant at the individual level.

1.

Cougar ID	% Wetland	% Urban	% Field	% 0-5	% 6-15	% 16-30	% >30	Distance Perennial Streams	Distance Public Road	Distance Non-Public Road	Slope (Degree)
F01	0.94(0.06)	-0.02(0.09)	-0.34(0.16)	7.21(0.50)	12.15(1.0)	6.01(0.74)	11.32(1.06)	-0.47(0.33)	0.06(0.18)	-1.74(0.18)	-0.45(0.35)
F02	0.03(0.06)	0.45(0.08)	0.14(0.08)	6.66(0.83)	10.59(1.32)	4.13(0.84)	6.61(1.32)	-0.98(0.20)	7.55(0.15)	-1.05(0.13)	0.03(0.33)
F03	0.37(0.29)	1.36(0.21)	0.55(0.45)	3.70(1.09)	5.01(1.62)	1.07(1.28)	1.76(1.82)	-1.03(0.13)	-0.88(0.24)	-0.68(0.24)	-0.59(0.27)
F04	0.82(0.21)	-0.10(0.03)		8.88(0.24)	11.51(0.39)	4.81(0.21)	5.66(0.26)	-1.22(0.15)	11.65(0.41)	-0.99(0.14)	0.58(0.23)
F05	1.52(0.12)	0.56(0.05)	0.26(0.03)	6.81(0.25)	9.19(0.34)	14.28(0.48)	16.10(0.55)	1.82(0.10)	-3.80(0.11)	8.24(0.14)	-2.34(0.19)
M01	-0.33(0.25)	-0.09(0.10)	2.40(0.18)	0.77(0.47)	3.09(0.66)	-2.50(0.47)	-6.09(0.71)	-3.03(0.06)	-0.17(0.16)	-3.63(0.15)	1.00(0.14)
M02	2.10(0.48)	1.00(0.47)	2.92(0.45)	6.13(1.2)	7.36(1.94)	4.54(1.86)	6.13(2.38)	-0.77(0.14)	-1.08(0.22)	-0.46(0.17)	-0.69(0.40)

2.

Bobcat ID	% Wetland	% Urban	% 0-5	% 6-15	% 16-30	% >30	Distance Perennial Streams	Distance Public Road	Distance Non-Public Road	Slope (Degree)
BC01			-0.39(0.29)	4.02(0.55)	-1.57(0.51)	-1.64(0.39)	7.47(0.36)	0.99(0.16)	0.22(0.24)	0.11(0.23)
BC02			6.02(0.36)	13.98(0.45)	2.76(0.26)	13.45(0.58)	-8.48(0.13)	5.84(0.18)	-2.65(0.12)	0.88(0.16)
BC04		1.68(0.15)	9.67(0.37)	24.73(0.61)	9.17(0.26)	12.65(0.70)	-5.93(0.18)	-5.77(0.16)	-0.11(0.17)	0.49(0.22)
BC05		0.52(0.12)	12.72(0.54)	14.68(0,87)	10.17(0.66)	13.37(0.92)	-3.22(0.12)	-4.04(0.19)	-1.71(0.14)	-1.23(0.16)
BC06			4.64(0.40)	17.90(0.39)	-1.52(0.25)	0.03(0.38)	8.79(0.13)	-0.25(0.10)	1.91(0.14)	0.25(0.17)
BC07	2.62(0.06)		17.51(0.32)	17.10(0.27)	3.55(0.10)	11.41(0.26)	0.69(0.19)	4.49(0.18)	-1.07(0.14)	-0.69(0.15)
BC09			7.77(0.35)	12.79(0.55)	6.56(0.35)	10.67(0.47)	14.01(0.24)	9.74(0.16)	1.95(0.15)	-0.36(0.18)
BC13	0.40(0.06)	3.03(0.21)	20.09(0.50)	18.35(0.39)	8.42(0.28)	14.10(0.49)	0.90(0.18)	-0.97(0.20)	-3.44(0.17)	-0.34(0.30)
BC11			3.90(0.33)	16.25(0.46)	0.81(0.12)	13.44(0.53)	-7.07(0.23)	0.43(0.16)	-3.24(0.18)	1.35(0.24)
BC14			22.65(0.53)	29.89(0.78)	23.88(0.97)	25.42(1.13)	-2.68(0.12)	1.07(0.20)	-1.12(0.15)	-1.08(0.12)
BC15			16.06(0.42)	20.74(0.65)	3.95(0.24)	10.63(0.52)	1.95(0.18)	8.36(0.11)	1.00(0.15)	-4.21(0.22)