

Resource selection by coastal wolves reveals the seasonal importance of seral forest and suitable prey habitat

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ARTICLE INFO

Keywords:

Canis lupus

Habitat selection

Odocoileus hemionus sitkensis

Successional forest

Temperate rainforest

Thinning treatment

ABSTRACT

Wolves (*Canis lupus*) in Southeast Alaska inhabit temperate rainforests characterized by patchworks of old-growth and harvested forest stands in various stages of regeneration. Investigating wolf space-use patterns in this landscape may yield information on their tolerance of anthropogenic disturbance in forest ecosystems. Furthermore, identifying shifts in habitat selection throughout the year can provide insights into wolves' ability to exploit seasonally available resources. We examined seasonal habitat selection of wolves on Prince of Wales Island, Alaska with respect to forest structure, succession, land cover, topography, road densities and habitat predicted to support Sitka blacked-tailed deer (*Odocoileus hemionus sitkensis*) and salmon (*Onchorynchus* spp.), the primary and a secondary prey species. We used GPS locations from 13 wolves during 2012–2016 to develop resource selection functions (RSFs). Within their home ranges, wolves selected low elevation, flat terrain with open land cover and low-volume old-growth forests across seasons. During fall and winter wolves preferred clearcuts ≤ 30 years old, but avoided clearcuts > 30 years old and thinned young-growth relative to medium-volume old growth. Habitats with predicted high deer carrying capacities were selected during late summer and fall, and areas close to anadromous streams were important only during summer when salmon were spawning. Areas of high road densities were avoided during denning season and summer, but strongly selected during winter. Our study reveals the potential of coastal wolves to seasonally target prey habitat and adjust to altered landscapes, but successional forests had a limited period of use (< 30 years), thus forestry practices could reduce availability of wolves' preferred habitat.

1. Introduction

Wolves in coastal Southeast Alaska and British Columbia inhabit temperate rainforests distributed across island archipelagos (except for Admiralty, Baranof and Chichagof islands) and a narrow region of the mainland coast separated from the continental interior by mountains and icefields. Coastal wolves are considered distinct from continental populations due to morphological (Goldman, 1944; Nowak, 1983), genetic (Weckworth et al., 2010, 2011; Cronin et al., 2014), and ecological characteristics (Weckworth et al., 2005; Muñoz-Fuentes et al., 2009). Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) constitute the primary prey of coastal wolves throughout most of their naturally fragmented range, in addition to marine resources such as salmon (*Onchorynchus* spp.) and marine mammals (Szepanski et al., 1999; Darimont et al., 2004). This ecosystem has supported wolves for approximately 12,000 years when glacial ice retreated and opened colonization routes from southern Pleistocene refugia (Nowak, 1995). In contemporary times, large-scale industrial logging has transformed

forested sections of this landscape into a mosaic of productive old-growth forest and clearcuts in various stages of succession (i.e., young-growth). Intensive industrial-scale logging has occurred since the 1950s, and the resulting forest alteration, habitat fragmentation, and development of a network of roads have raised concerns about the impacts on wildlife populations (Schoen and Kirchhoff, 1988; Cook et al., 2006; Albert and Schoen, 2013).

Temperate rainforests transition through stages of succession post-logging and the consequences to resident wildlife are best understood for deer (Doerr et al., 2005; Hanley et al., 2005; Farmer et al., 2006; Farmer and Kirchhoff, 2007), and affect coastal wolves directly through habitat changes and indirectly through their deer prey. Old-growth forests are heterogeneous in stand age and canopy structure, allowing sufficient light to penetrate to the forest floor and support diverse understory species including shrubs, forbs, and lichens that are important deer forage (Alaback, 1982). Understory shrubs regenerate in young clearcuts (age 0–25–30 years), particularly during summer and mild winters (Alaback, 1984; Farmer and Kirchhoff, 2007; Cole et al., 2010),

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but during severe winters, early successional forests lack a canopy capable of intercepting snow (Kirchhoff and Schoen, 1987), allowing shrub burial (White et al., 2009) and increasing energetic costs of deer movement (Parker et al., 1999). Older clearcuts (> 25–30 years) grow into even-aged stands with dense canopies which block sunlight and impede growth of deer forage (Alaback, 1982; Schoen et al., 1988, Farmer and Kirchhoff, 2007). This is also known as the stem-exclusion phase and may last > 100 years (Wallmo and Schoen, 1980; DellaSala et al., 1996). These second-growth forests are unproductive for many old-growth associated wildlife species, and the delayed effects of past timber harvest (termed “succession debt”) predicts long-term and large-scale declines of deer, and subsequently wolves (Person, 2001).

Wolves in Southeast Alaska have been a focal point of conservation concerns since the 1990s, with heightened attention to the negative consequences of timber harvest on wolf and deer habitats, and increased access from roads built to support the timber industry resulting in higher wolf harvest by humans (Person et al., 1996, 2001; Swanston et al., 1996; Wolf Technical Committee, 2017). In 1993 and 2011 the U.S. Fish and Wildlife Service (USFWS) was petitioned to list Southeast Alaskan wolves under the Endangered Species Act. The most recent petition outlined specific concerns for wolves on Prince of Wales Island (POW), reflecting increased alarm over the effects of continued old-growth logging, as the most intense logging activity in Southeast Alaska occurs on POW (Albert and Schoen, 2013). After completing status reviews, the USFWS determined that listing was not warranted in 1995, in 1997 (after the finding was remanded), and again in 2015. Despite the recent finding, concerns were raised in the species status assessment about the sustainability of POW wolves due to reductions in habitat capability of deer resulting from timber harvest management (USFWS, 2015; FR 32473, 5 Jan 2016).

The majority of the land in Southeast Alaska is within the Tongass National Forest managed by the U.S. Forest Service (USFS). Recently, the USFS developed habitat and access management recommendations to the Tongass National Forest Land and Resource Management Plan (USFS, 1997; USFS, 2008) to maintain long-term, sustainable wolf populations (Wolf Technical Committee, 2017). The key recommendations relating to habitat included enhancement of the deer populations by increasing forage, maintaining corridors to facilitate movement, and increasing heterogeneity within young-growth forest stands, especially in winter habitats (Wolf Technical Committee, 2017). One management action proposed to accomplish these objectives is treating young-growth forest with thinning, with the intended effects of delaying the development of stem exclusion and hindrance of understory forage growth from shading (Hanley, 2005; Cole et al., 2010). The USFS recently implemented a strategy to transition harvest from old-growth forest to young-growth forest with the goal of establishing ecologically, economically, and socially sustainable management practices (81 FR 88657, 8 Dec 2016). The first large-scale effort towards this transition began on POW in 2017; old-growth logging will constitute the majority of the harvest for the first decade of the transition, followed by an increasing proportion of young growth until reaching nearly 100% by the end of the 16 year period.

Wolves are considered habitat generalists (Mladenoff et al., 1995; Fritts, 2003), able to survive in a broad range of ecological conditions, limited mainly by prey availability and mortality risk (Fuller et al., 2003). Furthermore, wolves demonstrate marked dietary plasticity (Peterson and Ciucci, 2003), which suggests the possibility of weak habitat selection patterns and the potential for resilience despite changing habitat conditions. However, patterns of habitat preference may be revealed at finer scales (within the home range; Ciucci et al., 2003) and may shed light on thresholds of tolerance or avoidance of habitat types. Previous research of coastal wolf habitat selection has focused primarily on den sites (Person and Russell, 2009) and the pup rearing period (Person, 2001). Wolves did not demonstrate distinct patterns of habitat selection outside of the denning season (Person, 2001); however, this research relied on VHF radio collar locations at

course time intervals. Furthermore, as most attention has been paid to wolves' use of deer habitat, little is known about seasonal changes in wolf habitat selection reflecting use of other prey in temperate rainforests.

Wolves are expected to display preferences for different habitat types among seasons because of variation in behavior throughout the year. For example, during denning season, wolf activity is focused around the den site (Ruprecht et al., 2012) generally located in protected areas because of pup vulnerability (Mech and Boitani, 2003; Szatornil et al., 2016), whereas territorial behavior increases during winter requiring more movement (Jędrzejewski et al., 2001; Smith et al., 2015) and potentially different habitat selection patterns (Ehlers et al., 2014). Foraging behavior may change throughout the year as wolves have been demonstrated to shift habitat selection seasonally, reflecting variability in prey availability or vulnerability (Peterson et al., 1984; Metz, 2012; Latham et al., 2013). Investigations of variation in seasonal foraging patterns have proved important for understanding predator-prey dynamics (Sand et al., 2008; Knopff et al., 2010; Metz et al., 2012) including apparent competition (Latham et al., 2011) and prey-switching behavior (Latham et al., 2013). Indeed, research using stable isotope ratios suggests coastal wolves switched dietary preference to salmon, a seasonally available resource, when deer became less abundant (Szepanski et al., 1999), or during periods of availability (during late summer and fall), regardless of ungulate abundance (Darimont et al., 2008).

Considering the concerns for coastal wolf viability, determining how wolves select specific forest successional stages is necessary to understand the effects of logging practices, and can inform evaluation of measures taken to mitigate negative consequences of timber harvest and enhance wolf habitat. Moreover, identifying differences in use of primary and alternate prey habitat throughout the year can reveal seasonal targeting of prey species. To address these issues, we investigated seasonal habitat selection of wolves on Prince of Wales Island, Alaska. To understand shifts in patterns of landscape preference throughout the year, we modeled the relative probability that certain resources were selected in relation to the distribution of forest type, land cover classes, topographical variables, road density, and availability of primary and alternate prey. We specifically tested for preferences in selection of productive old-growth forest classes, age of successional forest, and forests that had been treated to enhance deer habitat. We hypothesized that wolves would select habitats that best support deer, including old-growth forests and young successional clearcuts, and would avoid habitats that are unproductive for deer including clearcuts > 30 years old, particularly during winter. Second, we predicted that use of areas near salmon streams would increase with seasonal (late summer) availability of this alternative prey resource. Finally, we predicted that wolves would avoid areas of high road densities during the denning season because pups are vulnerable and less mobile at that time (Person and Russell, 2009; Benson et al., 2015). Conversely, we predicted that wolves would select high-density roaded areas during winter because of increased movement during this period, as roads have been demonstrated to facilitate movement and prey acquisition by wolves (Whittington et al., 2011; Dickie et al., 2016). Greater knowledge of variation in seasonal resource selection is important for understanding coastal wolf ecology and will help evaluate their potential to adjust to altered landscapes.

2. Materials and methods

2.1. Study area

The study area covered 3570 km² of temperate rainforest on POW, the largest island (6670 km²) in the Southeast Alaska Archipelago (Fig. 1). The POW Island complex (9025 km²) is characterized by an extensive coastline with long fjords, rugged mountains ≤ 1160 m, and multiple watersheds. A variety of habitat types are represented in this

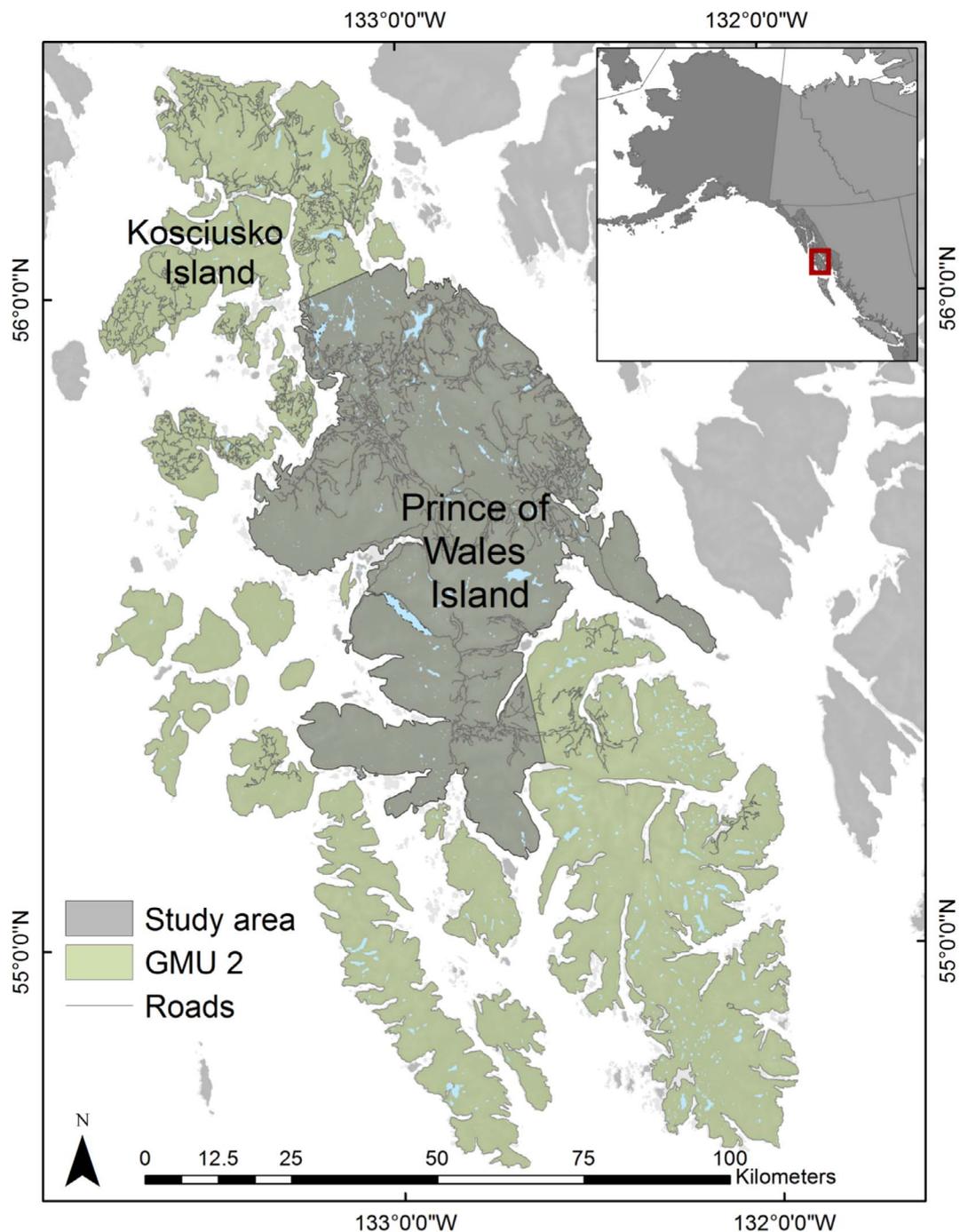


Fig. 1. Wolf seasonal resource selection study area (2012–2016) on Prince of Wales Island, Alaska, and the boundaries of Game Management Unit 2 (GMU 2).

area (Table 1). Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) are the dominant tree species with large forested areas common at lower elevations (< 600 m; Alaback, 1982). Old-growth (> 300 years) forest patches are structurally complex and diverse in understory species. On POW, old-growth forests are intermixed with blocks of even-aged forest stands at varying successional stages resulting from clearcut logging. Clearcuts ≤ 30 years after logging are brushy with young conifers and shrubs, and clearcuts > 30 years old have a homogenous structure with sparse understory and low species diversity (Wallmo and Schoen, 1980; Albert and Schoen, 2013). Other habitats include muskegs, marine estuaries, riparian and alpine zones. Annual precipitation ranges between 130 and 400 cm mostly in the form of rain, with intermittent snow during the winter months. Prince of Wales Island has had the highest rates of logging in Southeast Alaska,

where contiguous high-volume forests have been reduced by 93.8% between 1954 and 2004 (Albert and Shoen, 2013). Approximately 4800 km of roads, the majority of which are graveled, secondary roads, have been built throughout POW to facilitate logging, with the highest road densities in northern POW (0.49–1.04 km/km²; Person and Russell, 2008).

Wolves have been studied intensively on POW during 1993–1995 and 1999–2004 (Person, 2001; Person and Russell, 2008), and 2012 to the present. Wolf density on POW and the surrounding islands during these periods ranged from 39.5 wolves/1000 km² in 1994 on POW and Kosciusko Islands (6808 km²; Person et al., 1996), to 9.9–24.5 wolves/1000 km² during 2013–2015 in Game Management Unit 2 (GMU 2), which includes POW and the surrounding complex of islands (9025 km²; Roffler et al., 2016). Sitka black-tailed deer are the primary

Table 1

Habitat covariates used in wolf seasonal resource selection function models, % availability (for categorical covariates), and range and mean of values (for continuous covariates) within wolf pack home ranges on Prince of Wales Island, Alaska, USA, 2012–2016.

Abbreviation	Variable	Description	% , Range, Mean
<i>Land cover</i>			
ALP	Alpine	High elevation vegetation including sparse tree cover, herbs, shrubs, and lichens, also rock and snow	1%
LVPOG	Low-volume productive old-growth forest	Forest older than 150 years, trees $\geq 9''$ dbh ^a , 8–20 MBF ^b /acre on hydric soils, (also young growth from natural disturbance, and unproductive for timber harvest)	38%
MVPOG	Medium-volume productive old-growth forest	Forest older than 150 years, trees $\geq 9''$ dbh, 8–20 MBF/acre on non-hydric soils, 20–30 MBF/acre on hydric soils	12%
HVPOG	High-volume productive old-growth forest	Forest older than 150 years, trees $\geq 9''$ dbh, 20–30 MBF/acre on non-hydric (north aspect or flat) or hydric soils, 30 to ≥ 50 MBF/acre	17%
CC ≤ 30	Young clearcut forest ≤ 30 years	Young clearcut forest, 0–30 years after harvest	6%
CC > 30	Old clearcut forest > 30 years	Old clearcut forest, > 30 years after harvest	4%
OPEN	Open vegetated	Meadows, grasslands, and muskegs	3%
OTHER	Other non-forest	Freshwater lakes and wetlands, brush, urban areas	13%
THIN	Thinned forest	Precommercially thinned stands with at least 50% of total area thinned	6%
<i>Topographic</i>			
ELV	Elevation	Meters above sea level	0–1168, 239
SLP	Slope	Degrees	0–63, 14
ASP	Aspect	Four cardinal directions and flat	North = 23% East = 25% West = 27% South = 24% Flat = 1%
<i>Landscape</i>			
RDENS	Road density	Kernel density estimate of all road types at 100-m and 1000-m scales (km road/km ²)	0–4.439, 0.647
EDENS	Edge density	Kernel density estimate of edges at 100-m and 1000-m scales	0–10.02, 3.19
DISTFRESH	Distance to freshwater	Distance in meters to freshwater lakes and wetlands	0–8570, 1870
<i>Prey</i>			
DEER	Deer HSI	Habitat suitability index of deer carrying capacity	1–252, 123
DISTSS	Distance to salmon stream	Distance in meters to anadromous streams with documented salmon runs	0–5006, 1047

^a Diameter at breast height.

^b Thousand board-feet.

prey species of POW wolves, and beaver (*Castor canadensis*) and seasonally-available salmon are important secondary prey species (Kohira and Rexstad, 1997; Szepanski et al., 1999). Other mammals that are present and constitute a lesser portion of the diet include river otters (*Lontra canadensis*), black bears (*Ursus americanus*), other mustelids, marine mammals, and small rodents (Kohira and Rexstad, 1997; MacDonald and Cook, 2007).

2.2. Wolf location data

We modelled habitat selection within seasonal home ranges for 13 radiocollared wolves (8 females and 5 males) in 7 packs with 1–5 wolves radiocollared in each pack home range. We captured and radiocollared wolves during 2012–2016 using modified padded long spring (Easy-Grip® #7, Livestock Protection Company, Alpine, TX) and unpadded coil spring foothold traps (MB750, Minnesota Brand Inc.) set along the road system with commercially-produced lures and canid urine used as attractants. We immobilized restrained wolves using either tiletamine HCl and zolazepam HCl, or a combination of ketamine and medetomidine. We recorded sex, morphological data, and age category for each wolf. We ensured that capture and handling procedures conformed to guidelines established by the ADF&G Animal Care and Use Committee (ACUC #2012–028 and #2014–15) and the American Society of Mammalogists (Sikes and Gannon, 2011). We fit each captured wolf with a spread-spectrum, Global Positioning System (GPS) radio collar (Mod 4500, Telonics, Inc.) programmed to obtain a location every 6 h during 1 January–31 August, and every 2 h 1 September–31 December to coincide with the period of population estimation. We thinned wolf relocations during September–December to every 6 h to be consistent with the rest of the year. Collars were programmed to automatically release after 24 months, and had a VHF component for radiotelemetry and collar recovery after release.

We defined 4 seasons based on the life history of wolves in our study

area: denning season (15 April–31 July), late summer (1 August–14 October), fall (15 October–31 December), and late winter (1 January–14 April). During the denning season wolf activity is focused around den sites until early to mid-July when wolf movements shift to rendezvous sites (Mech and Boitani, 2003; Person and Russell, 2009). Late summer encompasses the period when activity centers shift from dens to rendezvous sites from which wolves make forays within their home range. Pups become more mobile during this time and have changing nutritional requirements, therefore wolf resource selection may be substantially different than during the denning season (Benson et al., 2015). Previous investigations of radiocollared wolves on POW demonstrated that rendezvous sites are generally < 1 km from the den, and the wolves used the rendezvous sites as late as October (Person and Russell, 2009). Late summer is also the period when spawning salmon become available in streams on POW (Campell et al., 2012). Salmon are a seasonally-important part of the diet of coastal wolves (Kohira and Rexstad, 1997; Szepanski et al., 1999; Darimont et al., 2008), thus wolves may localize on anadromous streams during salmon spawning from late summer through October (Person, 2001; Person and Russell, 2009). Wolves become more mobile during the fall period and have larger home ranges (Person, 2001). During late winter wolves are nomadic, and breeding also occurs during this season (Mech and Boitani, 2003).

2.3. Habitat covariates

Our habitat selection models included covariates based on previous wolf habitat selection studies on POW (Person and Russell, 2009). We considered terrestrial habitat features representing variation in land cover, topographic features, and the landscape (Table 1). Land cover classifications were included as categorical covariates and were derived from the ‘Size Density’ (Caouette and DeGayner, 2005), ‘Cover Type’, and ‘Activity’ (i.e., thinning data), GIS layers from the USFS Tongass

(Southeast Alaska GIS Library; <http://seakgis.alaska.edu/index.html>). In these classifications we differentiated between young clearcuts (≤ 30 years since cut) and old clearcuts (> 30 years) because these successional stages are structurally distinct (Wallmo and Schoen, 1980; Albert and Schoen, 2013). We also classified forests that contained at least 50% precommercially thinned forest stands. The mean age of the forest stands at the time of treatment was 24 years (range 6–52 years). Vegetation classifications included low-, medium-, and high-volume old-growth forests, open vegetation (meadows, grasslands, and muskgs), other non-forest (freshwater, brush, urban areas), and alpine. We used medium-volume old-growth forest as the reference category.

We derived the topographic covariates slope, elevation (continuous covariates), and aspect (categorical covariate, with north and flat terrain as the reference category) across the study area using the Shuttle Radar Topography Mission (SRTM) digital elevation model (Farr et al., 2007). We included road and edge density (calculated using a kernel density estimate at 100-m and 1000-m scales) as continuous covariates. Edges were defined as the boundary between land cover classifications categorized as open (e.g. alpine, meadows, young clearcuts), and closed (e.g., old-growth forests, old clearcuts), and density was calculated with ArcGIS Spatial Analyst 'Line Density' function. We also included distance to freshwater lakes and wetlands as continuous landscape covariates.

We also included covariates related to habitat suitable to wolf prey species because landscape-level abundance estimates of deer and salmon are not available. A habitat suitability index (HSI) for deer (Suring et al., 1993) was based on a spatial model to estimate habitat capability of Sitka black-tailed deer during winter and served to provide an index of deer carrying capacity with the highest scores attributed to southern aspects, lower elevations, low snow level, and old growth stands (high-volume forests received the highest scores, whereas medium-, and low-volume forests ranked lower, but still substantially higher than other forest categories). Winter is considered to be the most restrictive time of the year for deer physically (Parker et al., 1996, Parker et al., 1999), and thus conserving high quality winter habitat would help sustain deer populations (Suring et al., 1993). Critical winter deer habitat is also considered to be a good measure of wolf habitat quality for wolves in Southeast Alaska (Person, 2001) where both species occur, and deer habitat capability is directly tied to models for wolf habitat capability (Suring et al., 1993). The deer HSI estimates habitat quality and is not intended to predict absolute deer numbers; instead, the HSI provides a relative index of carrying capacity. Given the assumptions that the HSI model indicates the relative ability of habitat to support deer, and that habitat suitability is correlated with abundance over the long-term, and that deer constitute the primary prey of wolves in this region, the HSI model has been used to estimate wolf population abundance across Southeast Alaska (Person et al., 1996, USFWS, 2015) and in population viability analyses related to management considerations such as the ESA (Gilbert et al., 2015, USFWS, 2015). Considering the ongoing application of this model to management, we wanted to explicitly investigate the relationship of seasonal wolf habitat selection to the deer HSI model. We expected HSI would indicate relative abundance of deer during winter and fall, as old growth forests, low elevations, and southern aspects are important to deer during these seasons, but that HSI would be less predictive of deer habitat during late spring and summer, when deer use higher elevations and young clearcuts in addition to old growth forests (Schoen and Kirchhoff, 1990; Person, 2009; Gilbert, 2015). We included deer HSI as a continuous covariate in models along with its components, as we wanted to investigate wolf response to the individual factors as well as the deer HSI, which was viewed as a more integrated perspective of wolf response to deer. Tests for multi-collinearity between HSI and its component factors did not reveal any significant correlations. We also included distance to anadromous streams as a continuous prey habitat covariate. We resampled all GIS data to a 30 m² cell resolution for spatial analysis. We used the R statistical environment and ArcMap

10.2.1 (ESRI 2013) to conduct all spatial and statistical analyses.

2.4. Habitat selection modelling

We evaluated wolf habitat selection at the third order (within the home range), following Johnson's (1980) hierarchy of scales of selection to compare locations used by wolves to those available within their seasonal home ranges. We estimated wolf habitat selection for each of the 4 seasons with resource selection functions (RSFs; Boyce and McDonald, 1999; Boyce et al., 2002; Manly et al., 2002) using generalized linear mixed models (Bolker et al., 2009) with the logit link. We evaluated models that included a random intercept for individual wolves nested within each pack. These random effects were included to accommodate the hierarchical structure of wolves (Hebblewhite and Merrill, 2008) and to mitigate effects of uneven sample sizes of pack home range locations and possible autocorrelation of used locations within packs (Pinheiro and Bates, 2000; Gillies et al., 2006).

We calculated seasonal home ranges to estimate habitat availability for each wolf pack using 95% minimum convex polygons (MCP; Mohr and Stumpf, 1966). Although MCPs do not provide information regarding variance of use of space within the polygon border, they are suitable for defining the extent of area used, and thus an appropriate method for characterizing available habitat within the home range. We used the rhr package (Signer and Balkenhol, 2015) in R 3.3.2 (R Core Team, 2016) to estimate 95% MCP seasonal home ranges for each wolf pack, and to calculate the minimum number of relocations necessary for home range areas to reach an asymptote. Following Laver and Kelly (2008) the asymptote was reached if the 95% confidence interval of bootstrapped home-range sizes fell within 5% of the total home range area (using all relocations) for at least 5 estimates. We clipped all MCP seasonal home ranges to the shoreline of POW, thus home range and habitat selection in this study are specific to terrestrial resources. We excluded wolf GPS relocations outside of 95% MCP home ranges calculated from locations of all collared pack members from analysis, including extraterritorial forays (temporary movements outside of home range that are markedly separate from their previous locations; Ballard, 1997; Burch et al., 2005), or dispersal events (permanent movement away from natal pack home range, not remaining in one place for > 14 days; Person and Russell, 2008). We also excluded wolves that did not exhibit fidelity to a home range (dispersers) as indicated by lack of a well-defined core area (Appolonio et al., 2004), as home-range estimation is not appropriate for such individuals. We randomly drew available habitat for each individual wolf within their respective 95% MCP at a ratio of 20 locations for every used location to ensure accurate habitat representation and reliable coefficient estimation, as recommended by Northrup et al. (2013). In addition to excluding locations of wolves outside of the seasonal 95% MCPs, we included used locations for only adult or yearling resident wolves within a given season. Resident wolves had well-defined home ranges that did not overlap those of neighboring packs and associated with other wolves in their pack.

We first screened individual habitat covariates for collinearity using a threshold cut-off of $r = 0.6$ (Hosmer and Lemeshow, 2000) or with variance inflation factors (VIF) > 10 (McCullagh and Nedler, 1989) to exclude collinear habitat covariates. We further assessed VIF for the global model (all covariates included) and combinations of potentially collinear covariates (McCullagh and Nedler, 1989). We standardized continuous covariates to enable comparison of their relative effect on wolf seasonal habitat selection. We determined the most predictive scale for road and edge density by conducting univariate analyses and selecting the scale with the lowest Akaike's Information Criterion, corrected for sample sizes (AIC_c) score. We examined potential quadratic linear distributions for nonlinear continuous covariates.

We then conducted model selection using AIC_c (Burnham and Anderson, 2002). We first developed a global model and evaluated biologically plausible candidate models that included subsets of the

Table 2
Number of radiocollared wolves, monitoring period, number of GPS collar locations by pack and season (denning season [15 April–31 July], late summer [1 August–14 October], fall [15 October–31 December], and late winter [1 January–14 April]), Prince of Wales Island, Alaska, USA, 2012–2016.

	Pack	Number radiocollared wolves	Monitoring period	Number locations
Denning	Honker	5	2012–2014	1007
	Hydaburg	1	2013	196
	Nossuk	1	2013	186
	Ratz	1	2012	179
	Sandy Beach	2	2015–2016	594
	Staney	2	2012–2015	518
	Trocadero	1	2016	227
	Mean	1.9		415
Summer	Honker	4	2012–2014	119
	Hydaburg	1	2013	190
	Nossuk	1	2013	119
	Ratz	1	2012	217
	Sandy Beach	2	2015	386
	Staney	2	2013–2014	434
	Trocadero	–	–	–
	Mean	1.8		244
Fall	Honker	6	2012–2014	1129
	Hydaburg	1	2013	126
	Nossuk	1	2013	205
	Ratz	1	2012	346
	Sandy Beach	2	2015	563
	Staney	1	2012–2013	689
	Trocadero	–	–	–
	Mean	2		510
Winter	Honker	4	2012–2014	988
	Hydaburg	–	–	–
	Nossuk	1	2012	407
	Ratz	1	2012	337
	Sandy Beach	2	2014–2015	234
	Staney	1	2012–2014	369
	Trocadero	1	2016	317
	Mean	1.7		442

Table 3
Standardized selection coefficients (β), standard errors (SE), and significance level for seasonal resource selection functions for wolves on Prince of Wales Island, Alaska, USA, 2012–2016. Covariate values in bold are significant at $\alpha = 0.05$. Elevation (ELV), slope (SLP), aspect (ASP), road density at the 1000-m scale (RDENS), edge density at the 1000-m scale (EDENS), distance to freshwater (DISTFRESH), deer habitat suitability index (DEER), distance to anadromous stream (DISTSS²), low-volume productive old-growth forest (LVPOG), young clearcut forest ≤ 30 years (CC ≤ 30), old clearcut forest > 30 years (CC > 30), open vegetation (OPEN), other land classification (OTHER), thinned forest (THIN).

Covariate	Den			Late summer			Fall			Winter		
	β	SE	p									
ELV	-0.787	0.036	< 0.001	-0.378	0.040	< 0.001	-0.400	0.028	< 0.001	-0.407	0.036	< 0.001
SLP	-0.423	0.035	< 0.001	-1.025	0.049	< 0.001	-0.800	0.035	< 0.001	-0.441	0.039	< 0.001
ASP – South							0.146	0.042	< 0.001	5.254	0.150	< 0.001
ASP – East										-1.284	0.060	< 0.001
ASP – West										-0.902	0.059	< 0.001
RDENS	-0.269	0.025	< 0.001	-0.397	0.036	< 0.001	-0.055	0.022	0.014	0.197	0.030	< 0.001
EDENS	-0.060	0.025	0.007	0.018	0.030	0.549	-0.095	0.022	< 0.001			
DISTFRESH										0.201	0.026	< 0.001
DEER				0.189	0.033	< 0.001	0.111	0.023	< 0.001			
DISTSS ²				0.115	0.034	0.001						
LVPOG	0.411	0.047	< 0.001	0.692	0.064	< 0.001	0.490	0.047	< 0.001	0.470	0.066	< 0.001
CC ≤ 30							0.357	0.074	< 0.001	0.286	0.094	0.002
CC > 30							-0.101	0.092	0.273	-0.421	0.125	0.001
OPEN	0.594	0.104	< 0.001	0.796	0.132	< 0.001	1.428	0.072	< 0.001	1.334	0.097	< 0.001
OTHER				0.676	0.098	< 0.001				0.282	0.136	0.038
THIN										-0.489	0.113	< 0.001
EDENS:OPEN				0.230	0.078	< 0.001						
RDENS:OPEN	-0.284	0.120	0.018	-0.605	0.143	< 0.001						
DISTSS:OPEN				-0.579	0.139	< 0.001						
RDENS:DEER							-0.063	0.019	0.001			
RDENS:OTHER										-0.389	0.143	0.007

best-supported covariates and interactions. These same 24 candidate models were evaluated for each season. We examined interactions hypothesized to be biologically meaningful, including the interactions between preferred habitats and road density, edge density, and distance to anadromous salmon streams (which was included as second-order polynomial). To evaluate the fit of the seasonal RSF models we used k-fold cross validation and Spearman’s rank correlation (r_s) across 10 subsamples (Boyce et al., 2002). Analyses were conducted using the lme4 package with R software.

3. Results

3.1. Wolf habitat selection

GPS collars recorded on average 809 locations (SD = 415) per wolf, over a time interval of 401 days/collar. The average number of relocations per wolf per season was 242 (SD = 59) for the pup-rearing season, 186 (SD = 57) for late summer, 265 (SD = 194) for fall, and 276 (SD = 129) for late winter (Table 2). All 95% MCP home range areas reached an asymptote within the number of relocations available for each pack, thus all were retained for defining available habitat in the resource selection function models.

Wolf resource selection was a function of topographic and land cover covariates, as wolves consistently selected low elevation (mean = 143 m, SD = 142 m), flat terrain with open vegetation or low-volume old-growth forests across seasons. Selection for low elevations was strongest during the denning season, and flat terrain was most important during late summer and fall, although both habitat covariates were highly significant in all top-ranked seasonal habitat selection models (Table 3). Open vegetation and low-volume old-growth forests were selected more than the other land cover covariates in relation to medium-volume old-growth forest (the reference category). The open vegetation class (including muskegs, meadows and grasslands) was one of the most important habitat covariates in all seasonal models, especially in late summer ($\beta = 0.796$, SE = 0.162, $P < .001$), fall ($\beta = 1.428$, SE = 0.072, $P < .001$) and winter ($\beta = 1.334$, SE = 0.097, $P < .001$), although still significant during the denning season ($\beta = 0.594$, SE = 0.104, $P < .001$). Low-volume old-growth forests

were most strongly selected during fall and winter relative to medium-volume old-growth, and high-volume old-growth did not contribute to the top models for any season (Table 3).

During the denning season and late summer, wolf habitat selection was negatively correlated with high road density at the 1000-m scale (Table 3). In areas with high road densities wolves avoided open land cover during late summer even though this habitat type was one of the most important predictors of wolf habitat selection across all seasons. Wolves used areas with a mean road density of 0.772 km/km² during denning season, 0.686 km/km² during late summer, and 0.406 km/km² in open habitats during late summer (road density in the study area ranged from 0 to 4.439 km/km² at the 1000-m scale). Wolves weakly avoided areas of high road densities during fall ($\beta = -0.055$, SE = 0.022, $P = .014$), but this relationship switched during winter when wolves strongly selected highly roaded areas (Table 3). Areas of high edge densities at the 1000-m scale were also avoided by wolves during the denning season and fall, but selected during late summer in areas where they coincided with open vegetation classes (Table 3). Road density and edge density at the 100-m scales were not significant in the top-ranking seasonal habitat selection models (Table S1, Supplementary materials).

During fall and winter wolves selected clearcuts ≤ 30 years old, and strongly avoided clearcuts > 30 years old more than medium-volume old-growth forest, particularly during winter ($\beta = -0.421$, SE = 0.125, $P < .001$). Wolves also strongly avoided forest stands during winter that had received thinning treatments. This forest management category was not a significant habitat covariate in any of the other seasonal RSF models. Wolves selected areas of predicted high deer carrying capacity (high HSI values in south-facing, low elevation, high-volume old growth forest) only during late summer and fall. In areas of high road densities during fall, the relationship reversed and wolves instead avoided high suitability deer habitat in these areas (Table 3). Distance to anadromous salmon streams entered only the late summer resource selection function models. Wolves used areas at a mean distance of 917 m to anadromous streams during late summer, and selection of areas close to streams increased in areas of open vegetation classes ($\beta = -0.579$, SE = 0.139, $P < .001$). The other non-forest land cover category (including freshwater lakes, wetlands, brush, and urban areas; Table 1) was selected by wolves during late summer ($\beta = 0.676$, SE = 0.098, $P < .001$) and winter ($\beta = 0.282$, SE = 0.136, $P = .038$). Examination of used locations in this category revealed that during late summer, wolves selected areas adjacent to lakes and anadromous streams. During winter, the majority of used locations in this land cover category were in close proximity to the shore line (< 1.5 km), or on the edges of freshwater lakes.

Aspect was a significant habitat covariate only for the fall and winter resource selection functions, when wolves selected south facing terrain (in relation to north aspects and flat terrain, the reference category). Indeed, southern topography during winter was the most strongly selected covariate based on standardized coefficients of any habitat type for any season (Table 3). Wolves avoided eastern and western aspects during winter. The top models for each season performed well in the Spearman rank correlation from the k-fold cross-validation ($r_s = 0.951$ – 0.966).

4. Discussion

Within their seasonal home ranges, wolf habitat was defined by topography (low elevation, flat terrain) and mostly unmodified land cover (open vegetation and low-volume old-growth forests) across all seasons. Our results supported the hypothesis that wolves select forest categories indicative of high quality deer habitat (low-volume old-growth forests and young successional clearcuts) in relation to the reference category, but not those presumed to be the highest quality deer habitats (high-volume old-growth). Wolves avoided low-quality deer habitat (old clearcuts) especially during winter. Wolf selection of areas

near salmon streams was significant only during late summer, providing evidence supporting our second hypothesis. Finally, our results confirm that wolves avoided areas of high road densities during the denning season but selected high-density roaded areas during winter.

Seasonal resource selection by wolves indicated a strong preference for certain high-quality deer habitat and demonstrated that wolves shift habitat use seasonally especially with regard to road density. We found the strength of selection by wolves increased with suitability of deer habitat within their late summer and fall home ranges (Table 3). During the denning season, despite an affinity for low-volume old-growth forest and low elevations, selection for high quality deer habitat (measured by the deer HSI, Suring et al., 1993) was less apparent than for other seasons. There are two non-mutually exclusive potential explanations for this pattern. First, as the deer HSI was intended to predict carrying capacity of deer considering physiological limitations imposed during winter, results could indicate this index is a poor predictor of seasonal deer habitat use during early summer. While deer select old growth forests, low elevations, and southern aspects year-round, during late spring and summer deer also make use of higher elevations and young clearcuts (Schoen and Kirchoff, 1990; Person, 2009; Gilbert, 2015). Deer movements are relatively less restricted during this time than other seasons, and use of higher elevations by some deer begins as early as May (Schoen and Kirchoff, 1985), a strategy with demonstrated fitness advantages including larger body size and higher reproductive rates (Klein, 1965). Another fitness-conferring strategy for deer is to use young clearcuts to maximize forage intake during summer, which enables energetically demanding lactation (Parker et al., 2009), and ability to increase body reserves as a buffer against nutritional stress experienced during winter (Parker et al., 1999). Deer on POW favor clearcuts 10–25 years old (Yeo and Peek, 1992; Person et al., 2009; Gilbert, 2015) during summer, as this age class of clearcut provides the highest abundance of summer forage, relative to other habitats (Alaback, 1982; Farmer et al., 2006). Wolves did not select young clearcuts during the denning period, indicating little overlap with preferred deer habitat during this season.

Second, patterns of wolf habitat selection during the denning season could indicate that reproductive activities (i.e., den site selection, pup rearing) took precedent over deer hunting. Wolves have restricted movements and foraging patterns during the denning season (Mech and Boitani, 2003). Earlier studies (Person, 2001) provide evidence that wolf home ranges in this area are significantly constrained during the denning season compared to fall (mean MCP pup-rearing [15 April–15 August] = 104.7 km²; mean annual MCP = 259.7 km²), and results from the current study also indicate smaller home ranges during denning season than fall and winter. While the highly synchronized birthing period of deer occurs the third week of May (Gilbert, 2015), providing an influx of vulnerable prey, the majority of neonate fawn mortality on POW was from black bear predation, not wolves (Gilbert, 2015). In order to remain in close proximity to their den sites, wolves may be targeting alternative prey that are more accessible, including beaver (Person and Russell, 2009). Indeed, most den sites were adjacent to freshwater and had evidence of recent beaver activity nearby (Person and Russell, 2009; ADF&G, unpublished data). By mid-July, wolves move to rendezvous sites (Person and Russell, 2009), and as pups become more mobile and require less attendance, wolves may increase hunting activities of deer, reflected in wolf selection of high suitability deer habitats during summer and fall.

Wolf predation is the primary cause of deer mortality during winter aside from malnutrition and human harvest (Farmer et al., 2006; Person, 2009), indicating wolves may select habitats during this season to increase their encounters with deer. Our results demonstrated strong preference by wolves for the components of certain critical winter deer habitat (southern aspects, low elevation, old-growth forest), which were better predictors of wolf habitat selection than the integrated deer HSI. In Southeast Alaska, critical winter deer habitat is composed of old-growth forest on southern aspects below 250 m (Wallmo and

Schoen, 1980; Kirchoff and Schoen, 1987; Suring et al., 1993), and the deer HSI model incorporates these attributes with variation in snowfall to predict the deer carrying capacity (Suring et al., 1993). Because deer habitat selection is modified by deep snow, the HSI become less predictive during severe winters. High-volume old-growth forests with snow-intercepting canopies are more important for deer in areas of higher snowfall (Schoen and Kirchoff, 1985), or during severe winters (Doerr et al., 2005; Gilbert et al., 2017), compared to areas with milder winter climates (Yeo and Peek, 1992). Conversely, deer make greater use of young clearcuts during winters with less snow fall (Yeo and Peek, 1992; Gilbert, 2017), although this strategy comes with consequences for survival as selection of young clearcuts during low-snow periods by deer was positively associated with risk of death by wolf predation (Farmer et al., 2006).

During our study, Prince of Wales Island experienced relatively mild winters with little snowfall (NOAA online weather data), and wolves selected young clearcuts during fall and winter (although less than for low-volume old-growth). Previous wolf research demonstrated variation in selection for closed-canopy (snow-intercepting) old-growth during winter, and attributed spatial patterns of selection by different wolf packs to variation in snow accumulation across POW (Person, 2001). During his study, wolves in the northcentral regions of POW (overlapping the contemporary home ranges of the Honker and Ratz packs; Fig. 2) experienced deep snow during the winters of 1993–1995 (> 60 cm) and selected closed-canopy old growth forest relative to its availability (Person, 2001). In comparison, Koskiusko Island and the west side of POW received less snow (< 20 cm), and the resident wolf packs either weakly selected open-canopy old-growth (abundant understory vegetation but poor snow-interception qualities), or had no distinct patterns of selection (Person, 2001). Wolf packs avoided ($n = 3$) clearcuts and seral forest or demonstrated no pattern of selection ($n = 4$) for these habitats. In comparison, our results reveal strong selection for clearcuts and low-volume old-growth during winter (Table 3).

The most parsimonious wolf winter model was largely driven by strong selection for southern aspects (relative to northern aspects and flat terrain), which had the highest standardized coefficient of selection for any covariate in any seasonal model (Table 3). These results suggest wolves shift selection seasonally to target the most important deer habitat. Previous research showed southern aspects near shore line were better predictors for deer habitat use than forest type due to increased exposure of warm southeast winter storms that reduce the snow pack (Doerr et al., 2005). Further, southern aspect is an important modifying factor determining selection of open-canopy forests by deer in winter (Person et al., 2009), illustrating interactions between variation in snow depth and forest stand age (i.e., old-growth, young clearcut, old clearcut).

The most wide-spread anthropogenic effect on northern temperate forest ecosystems is silviculture, resulting in habitat fragmentation and long-term modifications of forest structure. The ability of wolves to persist in altered ecosystems depends in part on their ability to adapt their behavior to accommodate potential changes in prey distribution. In this research, we found wolf habitat selection patterns favored natural forest and land cover, mixed use of roads, and limited use or avoidance of human-caused seral forests. In relation to the landcover reference category wolves consistently selected low-volume old-growth forest, the forest class containing the lowest density of large diameter trees of all classes, but the highest forage biomass (Alaback, 1982). Our work corroborates previous research indicating that wolves selected this forest type significantly more than expected based on its availability (Person and Ingle, 1995; Person et al., 2001). Although wolves selected young clearcuts during fall and winter, this young-growth forest category did not factor into the denning and summer RSF models, demonstrating limited seasonal use. More importantly, wolves avoided old clearcuts during fall and winter, indicating that young-growth forest has a limited time frame of potential use by wolves, similar and likely

related to predictions for use by deer (≤ 30 years post clearcut). Young-growth treated with precommercial thinning is intended to enhance deer habitat by delaying stem exclusion and prolonging forage production (DellaSala et al., 1996; Hanley, 2005; Cole et al., 2010). However, wolves avoided thinned forest during winter, and did not display patterns of selection for thinned forest stands during other seasons (Table 3) confirming previously described patterns of avoidance of second growth in the stem exclusion phase, in particular pre-commercially thinned stands (Person, 2001). Thus far, the benefits of thinning treatments on maintaining understory vegetation have proven to be short-term (5–10 years), diminishing the potential for sustaining wildlife through the long-lasting stem exclusion phase (Hanley, 2005; Farmer et al., 2006; Cole, 2010). In this study we demonstrate that thinning treatments do not thus far appear to enhance habitat for wolves. Thinning treatments recommended by the interagency Wolf Technical Committee (2017) for Prince of Wales Island include thinning prior to 25 years post-harvest in medium to high productive stands, prioritizing landscapes with low proportions of high quality winter deer habitat, and conditions that would favor understory regeneration. These treatments warrant continued evaluation for the benefits provided to both deer and wolves. Approximately 1500 km² of forest (representing over one third of the old-growth available prior to industrial logging) is predicted to enter the stem exclusion phase over the next two decades on POW and the surrounding islands (Smith et al., 2016) raising concern for the long-term abundance of predator and prey populations in logged temperate forests.

Use of alternate prey may indicate wolves' ability to tolerate landscape-level changes such as succession debt that could diminish the abundance of their primary prey. Wolves in Southeast Alaska have access to spawning salmon during late summer through early autumn (Kohira and Rexstad, 1997; Szepanski et al., 1999; Person, 2001), providing a seasonal source of prey that is spatially and temporally predictable, and requires relatively little handling time (Willson and Halupka, 1995). Salmon are present in approximately 2000 streams throughout Southeast Alaska (Sugai and Burrell, 1984), and northern POW contains the highest quantity of anadromous freshwater habitat in this region (Schoen and Dovichin, 2007). The primary salmon runs on POW are pink (*O. gorbuscha*) and chum (*O. keta*), occurring in late summer. Other salmon species present are sockeye (*O. nerka*) and coho (*O. kisutch*), which are less abundant, but the fall coho run extends the period of availability. Our results indicated that wolves select areas near anadromous salmon streams only during late summer (August–mid-October), coinciding with the salmon spawning period. Previous research also demonstrated selection by wolves of habitats near the mouths of anadromous streams during August–September (Person, 2001). Selection of areas near salmon streams increased in open habitats, which in our study area included meadows and grasslands, common in estuarine areas. Changes in wolf habitat selection to access spawning salmon indicate seasonal prey switching, and corroborates previously identified shifts in the proportions of primary and alternate prey consumed during summer. Kohira and Rexstad (1997) determined fish were the second most important prey species after deer during September–November and occurred in 21% of POW wolf scats. However, fish were not found in scats during the remainder of the year, and thus annual occurrence of fish in wolf scats was 5%, in comparison to other alternate prey species such as beaver (31%), black bear (8%), river otter (8%), and small mustelids (9%) that were consumed throughout the year. Despite the relatively narrow window of availability, Szepanski et al. (1999) determined that salmon made up 19.1% of the lifetime diet of POW wolves. Thus, although the season is limited temporally, the dietary contribution of salmon is large. Our results suggest the ability of wolves to shift seasonal foraging patterns spatially, and prioritize selection of specific resources corresponding with periods of prey availability.

Flexibility by wolves in spatial responses to anthropogenic features was demonstrated by seasonal patterns of selection and avoidance of

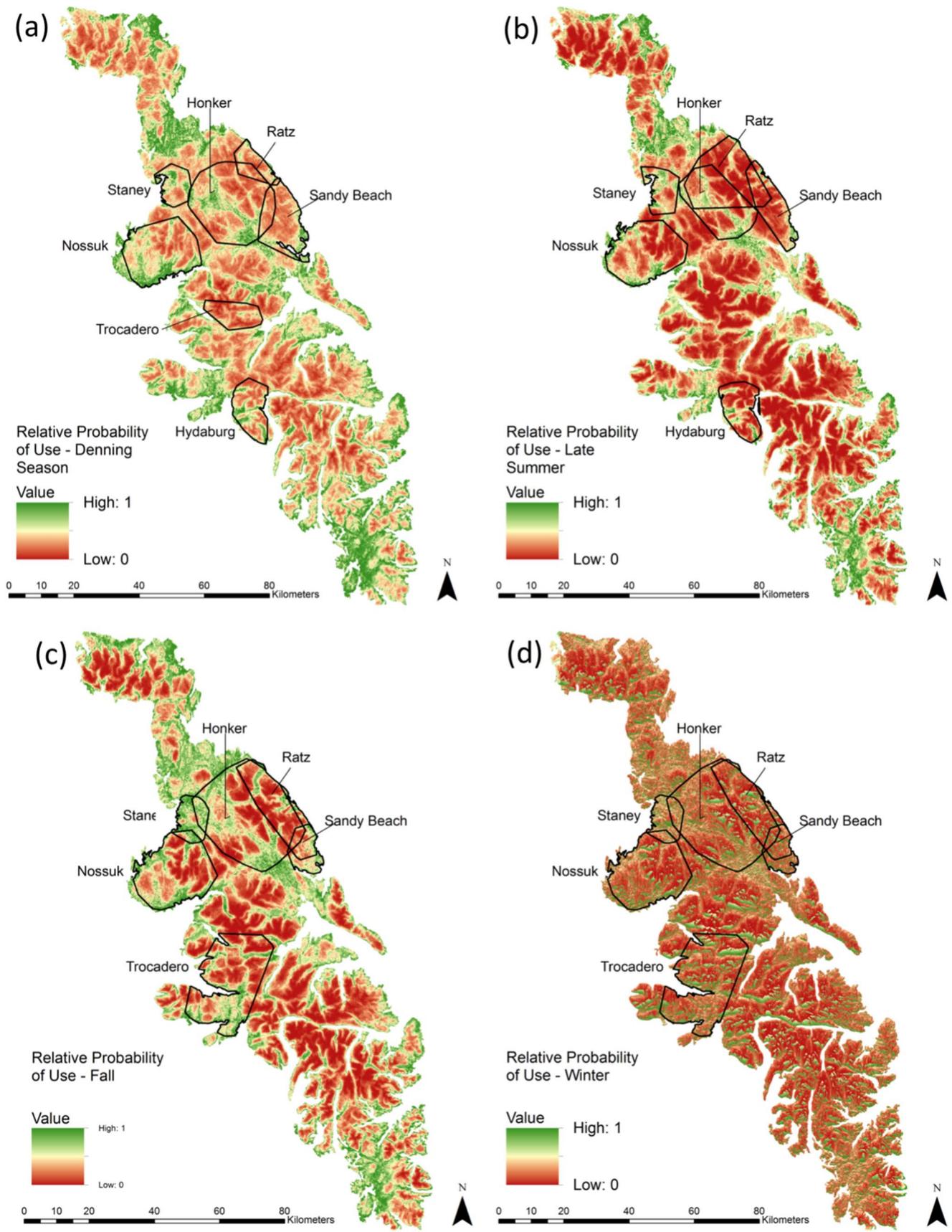


Fig. 2. Relative probability of use predicted by seasonal resource selection functions and wolf pack home ranges estimated using minimum convex polygons (MCPs) during (a) denning season, (b) late summer, (c) fall, and (d) winter on Prince of Wales Island, Alaska, USA, 2012–2016.

roads. Wolves have been shown to avoid roads when they coincide with areas of high human density (Dellinger et al., 2013), select roads to increase movement efficiency for territorial behavior and prey acquisition (Whittington et al., 2011; Zimmerman et al., 2014; Dickie et al., 2016), display flexibility in their responses to roads with higher use during night (Hebblewhite and Merrill, 2008; Zimmerman et al., 2014; Benson et al., 2015), or demonstrate differential responses to paved and unpaved roads (Ciucci et al., 2003). Seasonal differences in use of roads have also been documented with higher selection during fall and winter when wolves are nomadic (Houle et al., 2010; Lesmerises et al., 2013), and avoidance during the denning and rendezvous period (Person and Russell, 2009; Benson et al., 2015). Our results are similar to patterns detected in other areas of human disturbance as wolves on POW avoided areas of high road density during denning season and late summer but selection increased with increasing road density during winter. Wolves on POW have demonstrated aversion to human contact during denning season (Person and Russell, 2009) and responded to nearby disturbance from logging (low-level helicopter flights) by relocating a den site 0.36 km (G.H. Roffler, unpublished data). Active den sites on POW during 2012–2016 were on average 0.91 km from the nearest road (range = 0.17–3.83 km, SD = 1.07 km). In contrast, during the fall and winter, wolves were commonly documented on or near secondary roads with trail cameras and at hair snare stations established for estimating fall population densities with noninvasive capture-recapture methods (Roffler et al., 2016).

Road density was an important interaction term in seasonal habitat selection models. Whereas wolves selected habitats consistent with high-quality deer habitat during fall, and weakly selected areas of high road densities, when these two habitats coincided they were instead avoided (Table 3). A possible explanation for this modification of behavior is heavy deer hunter traffic on the POW road system during fall, with use peaking in late October but continuing through the end of December. During the 2012–2015 deer hunting seasons, an annual average of 1569 (SD = 8.22) hunters used road vehicles, off-road vehicles, or ATVs to travel along the road system (ADF&G, unpublished data). As hunters were likely also targeting high-quality deer habitat, wolves were possibly avoiding human contact at this time due to disturbance from noise, or avoiding risk of mortality by humans. Although wolf mortality from ground shooting (19.4% of wolves harvested during 2012–2015) on POW is less common than trapping or snaring, wolves may be shot opportunistically while hunters are targeting deer or other game species, as half the wolves shot during our study occurred during the deer hunting season. Road avoidance also increased during late summer in open vegetation habitats including muskegs and estuarine meadows which are used by POW wolves as rendezvous sites as late as October (Person and Russell, 2009). Selection of this habitat type was significant during the rendezvous period, as it provides important habitat for wolf pack interactions, and our results suggest wolves prefer these sites in areas of low road density.

5. Conclusion

Wolves appear to have the ability to use a variety of habitat types, although use of human-caused early succession forests had a short time frame, seral forests > 30 years were avoided, and forestry management to enhance habitat value in older seral forests did not extend the period of favorable conditions. Thus, the amount of habitat available to wolves could decline with an increasing proportion of the forest transitioning to the stem exclusion phase, with potential population-level consequences for wolves. Wolves displayed a variable response to road density confirming a high degree of adaptability to certain human-modified features. Wolves also shifted patterns of habitat selection towards alternate prey habitat (salmon) when seasonally available confirming flexibility in predation patterns (Peterson and Ciucci, 2003). However, to better forecast wolf resilience to the predicted decline of deer abundance resulting from succession debt, it is necessary to gain

further knowledge about wolves' use of alternate prey such as beaver, mustelids, black bears, and marine mammals throughout the year. The results of this work provide insights for understanding the potential consequences of landscape-level management practices on coastal wolves.

Acknowledgements

This work was funded by the Pittman-Robertson Federal Aid in Wildlife Restoration Program, the State of Alaska general funds, Cooperative Endangered Species Conservation Fund (Section 6 of the Endangered Species Act) Grant Program, and the U.S. Forest Service, Tongass National Forest. For fieldwork assistance, we thank L. Beier, S. Bethune, M. Douville, M. Kampnich, B. Porter, J. Terenzi, R. Slayton, and J. Whitman. D. Albert of the Nature Conservancy provided spatial data. D. Doyon was instrumental in conducting timely and safe radio-tracking flights. K. McCoy provided snow data summaries. B. Dale, C. Krenz, K. Titus, and S. Woodruff, and 2 anonymous reviewers provided helpful comments on early drafts of the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.11.025>.

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