Vegetation influences wolf fine-scale habitat selection and movement rate in a logged coastal rainforest

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Abstract

Vegetation and its modification by humans can shape wildlife habitat selection and movement. A better understanding of how wolves select and move through natural and human modified vegetative cover can be used to implement forest management that considers impacts on wolves and their prey. We analyzed fine-scale wolf habitat selection and movement in a coastal temperate rainforest (Prince of Wales Island, Alaska, USA) in relation to: (1) young (≤ 30 years) and old (> 30 years) logged areas, (2) continuous measures of vegetative cover (as estimated via LiDAR), and (3) distance to roads, using integrated step-selection analysis (iSSA). Wolves selected areas with less forest canopy and understory cover at the population level, although they switched to selecting understory when within logged forest stands. The continuous canopy and understory measures vary at a fine spatial scale and thus appear to better explain fine-scale wolf selection and movement than categorical landcover classes representing the age of logged stands. Wolf selection of young (≤ 30 years) and old (> 30 years) successional logged areas, and areas near roads, was mixed across individuals. All individual wolves avoided canopy cover, but varied in their selection of logged stands, understory, and roads. Similarly, there was variability in movement rate response across individual wolves, although at the population level wolves moved faster through old (> 30 years) logged areas and through areas with less understory vegetation. Open vegetation including that present recently after logging is selected by wolves, and facilitates wolf movement, but this effect may be ephemeral as vegetation undergoes succession.

Introduction

Where animals live and how they move across the landscape are shaped by biotic and abiotic factors that vary spatially (Guisan and Zimmerman 2000; Kearney and Porter 2009). Vegetation is salient among these factors, because it governs available food in the form of forage or, in the case of secondary consumers, herbivorous prey (Smith et al. 2019), as well as cover from predators, including humans (Suraci et al. 2020). Nutritional intake, efficient movement, and predator avoidance are animal fitness requirements that affect survival

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rate, and hence population dynamics (Plard et al. 2019), and are influenced by landscape vegetation patterns (Losier et al. 2015; Kane et al. 2017). Humans modify natural vegetation patterns (e.g., via infrastructure development, agriculture, and timber harvest), and this modification in turn affects ecosystems and the species within them, including by shaping animal habitat selection (Suraci et al. 2020; Northrup et al. 2021) and movement patterns (Plante et al. 2018; Quiles Quiles and Barrientos 2024). Here, we model the response of an apex predator, *Canis lupus*, to modification of natural vegetation by timber harvest and associated roads.

Human alteration of vegetation includes extensive timber harvest in temperate forests (Kennedy and Spies 2004; Knorn et al. 2013) which affects wildlife space use (Lesmerises et al. 2012; Pinard et al. 2012) and movement (Boucher et al. 2022; Gagnon et al. 2024). Logged stands in temperate, coniferous rainforests undergo succession from initially open vegetation, through a stage of productive understory, to a long-lasting (from 30 to 200 years post-logging) densely canopied forest with little understory production (Alaback

1984). The impact of the post-logging successional trajectory on wildlife varies depending on individual species' environmental niche and life history (Jones et al. 2024). Species favored initially post-logging may be disadvantaged later in the second-growth successional trajectory (Schlossberg & King 2009; Le Borgne et al. 2018).

The ability of wolves (*Canis lupus*) to hunt effectively is influenced by spatial patterns of vegetation (Dickie et al. 2017). Areas devoid of thick vegetation are associated with longer sight distance and increased movement rates and hence increased prey encounter rates (McPhee et al. 2012; Toretta et al. 2018). Wolf prey encounter rates may be greater in areas with greater ungulate prey density (Kittle et al. 2017; but see Zabihi-Seissan et al. 2022), which is promoted by abundant ungulate plant forage (Potvin et al. 2005; Gagnon et al. 2024), which is often present in early successional forests (Fisher and Wilkinson 2005; Hayes et al. 2022) but may diminish through time. Hence, timber harvest could initially benefit wolves by resulting in increased forage attractive to ungulate prey species (Farmer et al. 2006; Kittle et al. 2017). Similarly, logging roads are initially devoid of vegetation and may facilitate wolf hunting but often become revegetated over time (Waga et al. 2020). These initially unvegetated roads promote wolf prey detection and ease of travel but expose wolves to risk in the form of human hunters and trappers (Zimmerman et al. 2014) and vehicles (Dennehy et al. 2021). Logging roads may alternatively be maintained for continued use for logging or for other purposes, including as recreational trails or eventual upgrade for passenger vehicle use, thereby constituting risk avoided by wolves (Gurarie et al. 2011; Dennehy et al. 2021). Hence, there are conflicting forces that may result in wolf selection (Houle et al. 2010; Dickie et al. 2020) or avoidance (Whittington et al. 2005; Lesmerises et al. 2013) of roads, depending on revegetation and other road characteristics.

Coastal temperate rainforests, including those of Southeast Alaska, have been the target of industrial timber harvest that occurs to the present and has drastically reduced the coverage of old-growth forests (Albert and Schoen 2013). Prince of Wales Island (POW) in Southeast Alaska has been particularly targeted by the timber industry due to a high density of large trees, and now holds < 6% of the contiguous high-volume forest that existed before large-scale logging began in the 1950s (Albert and Schoen 2013). Wolves are of conservation concern in the region and have been petitioned for listing under the U.S. Endangered Species Act (ESA) three times in the past 30 years. The impacts of logging on these wolves and their Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) prey are a focus of conservation and management policy. Recently, the U.S. Forest Service (USFS) stated they will transition away from old-growth timber harvest to rotational harvest of second-growth forest (USFS 2016). The 2020 repeal of the Tongass National

Forest (TNF) exemption of the Roadless Area Conservation Rule (Executive Office of the President, Roadless Rule Revision 2021) further increases the focus of future logging in areas that have experienced previous harvest. The effect of historic timber harvest patterns and future harvest strategies on wolves and their ecosystem remains unclear.

Building on previous work studying the effects of logging on wildlife on POW (Farmer et al. 2006; Person and Russell 2008; Pyare et al. 2010; Porter et al. 2021; Roffler et al. 2023), we modeled fine-scale selection and movement of wolves in relation to spatial patterns of vegetation, logging, and roads. Based on our knowledge of wolf biology and with support from previous literature (including that presented above) we formulated hypotheses regarding wolf habitat selection and movement rate in relation to environmental covariates representing logging, vegetation, and road proximity (Table 1) to be tested via integrated step selection analysis (iSSA) model coefficients.

Methods

Study area

We studied wolves on POW in the coastal rainforest of Southeast Alaska (Fig. 1). POW is the largest island in an extensive archipelago and has a maritime climate with high precipitation (> 200 cm/year) and moderate temperatures—daily mean ranging from 1.3 °C (January) to 57.4 °C (August)—though cooler at elevation. The forest is dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*), with Alaska yellow cedar (*Callitropsis nootkatensis*) and western redcedar (*Thuja plicata*) also common. Some common understory woody plants include devil's club (*Oplopanax horridus*), blueberries (*Vaccinium* spp.), and salal (*Gaultheria shallon*), and ground cover species include bunchberry (*Cornus unalaschkensis*), foamflower (*Tiarella trifoliata*) and twisted stalk (*Streptopus* spp.). Wolves on POW co-occur with American black bear (*Ursus americanus*) and Sitka black-tailed deer. Seasonal anadromous runs of Pacific salmon (*Onchorynchus* spp.) provide large subsidies of marine-derived nutrients to the terrestrial ecosystem.

Logging on POW started in the early 1900s but became much larger in scale in the 1950s and continued through the time of the study. Logging has focused on high-volume coniferous forests (Albert & Schoen 2013), resulting in a mosaic of old- and second-growth forests interspersed with less productive forests and unforested lands. Logged areas vary in age and condition from initially open vegetation, transitioning to a mix of dense understory and young conifers, and followed (~ 30 year post-logging) by a longer lasting, 'stem-exclusion' phase of dense conifer canopy and

Table 1 Hypotheses related to wolf habitat selection and movement rate relative to environmental covariates, Prince of Wales Island (POW), Alaska, USA, 2012–2017

Habitat covariate	Habitat selection (selection or avoidance)		Movement rate (faster or slower)	
	Wolf behavior hypothesis	Literature support	Wolf behavior hypothesis	Literature support
Young (≤ 30 yr) logged stands	*Select*: higher value prey habitat and increased prey encounters attract wolves	Farmer et al. (2006); Pojarska et al. (2017); Kittle et al. (2017)	*Slower*: young logged stands contain shrubs and logging debris impeding movement	Person and Russell (2008); Gurarie et al. (2011); Kittle et al. (2017)
Old (> 30 yr) logged stands	*Avoid*: due to lower value prey habitat and decreased prey encounters	Roffler et al. (2018); Gregovich et al. (2024)	*Faster*: old logged stands with little vegetative structure (understory and down wood) and low prey density promote wolf movement	Farmer et al. (2006); Pojarska et al. (2017);
Forest canopy (LiDAR-based)	*Avoid*: due to lower value prey habitat and decreased prey encounters	McPhee et al. (2012); Lesmerises et al. 2012; Gregovich et al. (2024);	*Slower*: canopy has limited direct effect on wolf speed while travelling, but provides cover associated with wolf resting sites	Capitani et al. (2006); Llaneza et al. (2016)
Forest understory (LiDAR-based)	*Select*: understory represents ungulate prey forage and wolf hunting opportunities	Wilkinson (2005); Kittle et al. (2017); Hayes et al. (2022);	*Slower*: wolves target areas with higher ungulate forage, hence prey density, while denser understory impedes movement	Dickie et al. (2017); Kittle et al. (2017);
Proximity to logging roads	*Select*: roads promote ungulate forage and wolf prey detection	McKenzie et al. (2012); Zimmerman et al. (2014); Dickie et al. (2020); Waga et al. (2020)	*Faster*: roads generally provide a barrier-free surface, but represent risk from humans, both increasing movement rate	McKenzie et al. (2012); Zimmerman et al. (2014); Dickie et al. (2017, 2020)

Fig. 1 Study area for fine-scale habitat selection analysis of wolves, showing autocorrelated kernel density estimate (AKDE) pack home ranges, Prince of Wales Island (POW), Alaska, USA, 2012–2017
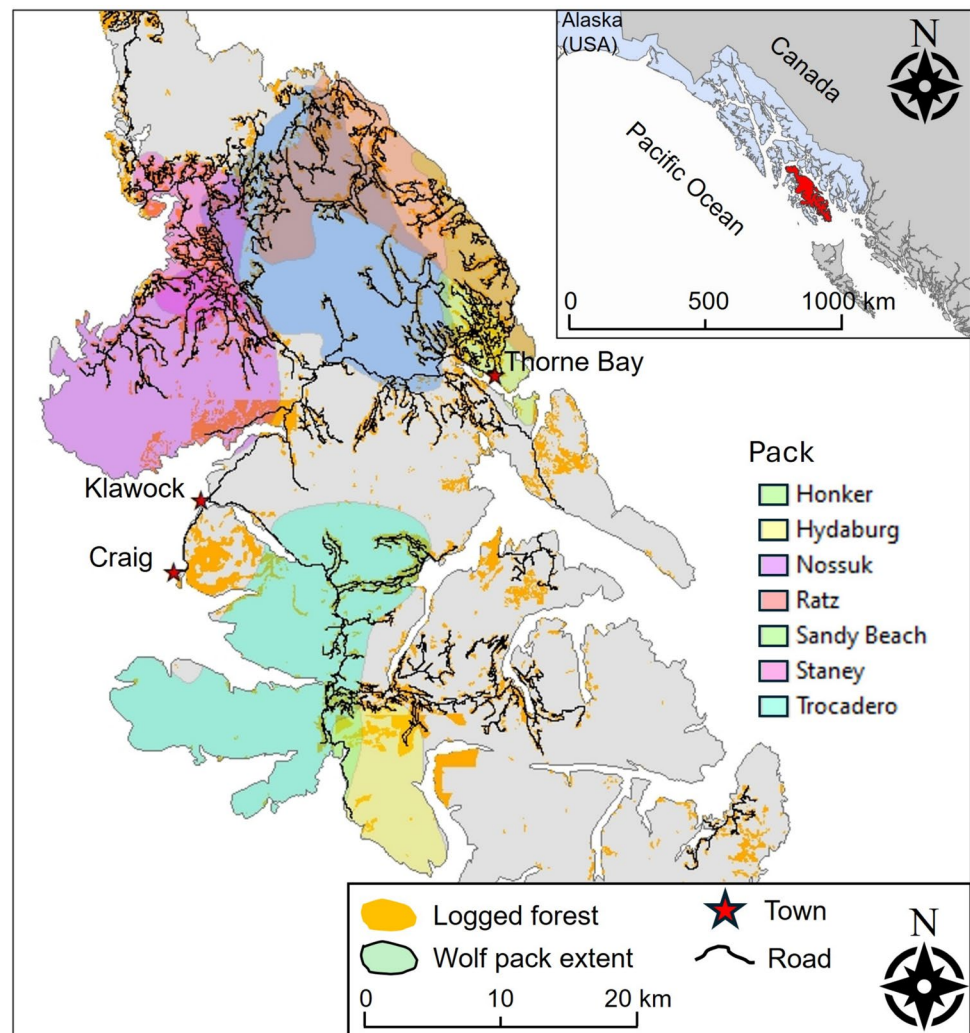
relatively little understory (Alaback 1984). The focus of the timber industry on larger tree stands has reduced contiguous patches of highly productive old-growth forest present before 1954 by 94% (Albert & Schoen 2013). Most of the existing roads (> 5000 km in length; USFS 2019a) were initially built to access timber but ranged in current status from revegetated (undrivable), to accessible only by off-road vehicles, to improve for passenger vehicle use. Road densities ranged from 0 to 0.44 km/km^2 (Roffler et al. 2018). The resulting landscape is thus fragmented by logged areas and roads of various condition, with consequences for wildlife species (Pyare et al. 2010; Smith and Flaherty 2023).

Wolf captures

We captured and radiocollared wolves ($n = 13$) from 2012 to 2017 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 logging roads and baited with

commercially-produced lures and canid urine. We checked wolf traps daily. We immobilized captured wolves using either tiletamine HCl and zolazepam HCl, or a combination of ketamine and medetomidine. 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. We programmed collars to automatically release after 24 months, and they included a VHF component for radiotelemetry and collar recovery after release.

Habitat and disturbance covariates

We analyzed the effects of two main features of timber harvest, logged forest stands and associated roads, on wolf habitat selection and movement rate. We calculated the distance to roads in two categories: open and closed

to vehicle traffic. We separated logged stands into young (≤ 30 years) and old (> 30 years) successional categories. As a contrast to these logging age categories, we used airborne Light detection and ranging (LiDAR)-derived vegetative cover metrics affected by timber harvest but varying continuously across the landscape (both inside and outside of logged areas).

Initial models using the categorical logged stand covariates failed to converge. This led us to explore the use of continuous covariates representing the proportion of logged stands within buffers of increasing radius (50–1000 m in increments of 50) around each wolf location and available point, and contrasted these with the unbuffered (binary) landcover classes, choosing the optimum representation (ultimately, 50-m radius) via model concordance scores (Therneau 2024; Online Resource Fig. S1). The model used for this purpose was based on model 1 (Table 2), but with landcover covariate mean values calculated within buffers of the varying radii. Often, coefficients derived from binary landcover classes used in habitat selection models refer to a 'reference category' not included in the model against which coefficients are contrasted. In our models, proportions of these binary landcover types within a 50-m radius of wolf locations were calculated, and the concept of a reference category is not relevant. However, the covariate for the proportion of noncommercial forest within a 50-m buffer of locations was excluded from models due to a high variance inflation factor (VIF; 8.42) when included in models with the other landcover covariates. For consistency, we also calculated the mean values of LiDAR-derived vegetation cover within a 50-m radius of used and available points.

We obtained landcover classes from USFS databases of timber harvest and associated roads in the study area (Online Resource Table S1). We defined young logged stands as those where logging occurred ≤ 30 years prior to 2014, the median year of wolf data collection, and old logged stands those harvested > 30 years prior. We refer to these classes as young and old logged stands, respectively, although some of the youngest (i.e., < 10 years) did not always harbor stands of trees. Distance to roads was log-transformed, as we expected a stronger effect near roads to diminish with distance. All other covariates were derived from LiDAR point cloud data collected in 2017 and 2018 under U.S Geological Survey QL1 specifications (point density = 8/m²; Heidemann 2014), and further processed to calculate vegetation structural metrics at a 30-m pixel resolution via LiDAR FUSION software (McGaughey 2008). The suite of LiDAR-derived vegetation metrics processed by the FUSION software available to us included many strongly correlated, difficult to interpret covariates. We chose two metrics representing canopy and understory cover due to their ease of interpretation and ecological relevance. Canopy cover was defined as the proportion of LiDAR returns > 2 m above ground; above a height which might impede wolf travel but low enough to account for nearly all existing forest canopy. Forest canopy is associated with light penetration, density of trees, and snow interception, measures that plausibly affect wolves and their Sitka black-tailed deer prey. We defined understory cover as the proportion of LiDAR returns in the range 0.5–1.0 m above ground relative to all points below that stratum. This corresponds roughly to the height distribution of Vaccinium spp. ('blueberries') important as food for wolf deer prey and other woody plants—e.g., salal (*Gaultheria shallon*) and false azalea (*Menziesia ferruginea*)—that potentially restrict wolf movement (see Dickie et al. 2017). We use the term understory here realizing that other plants conventionally

Table 2 Models and covariates used for fine-scale wolf habitat selection on Prince of Wales Island (POW), Alaska, USA, 2012–2017

Model#	Model name	Covariate groups included in model (in addition to core covariates)
1	Logging	Categorical land cover classes
2	Vegetative cover	Canopy and understory cover (%) as measured by LiDAR
3	Logging:vegetation interaction	Categorical land cover classes + vegetative cover + (Logging age):(vegetative cover) interactions
4	Movement rate versus logged stand age	Categorical land cover classes + (Movement rate):(logged stand) interactions
5	Movement rate versus vegetative cover	Vegetative cover + (Movement rate):(vegetative cover) interactions

Covariate group	Covariates included in group
Core covariates	ln(step length) + slope + elevation + ln(distance to road)
Categorical land cover classes	Young logged stands + old logged stands + unharvested commercial forest + open terrain
Vegetative cover	LiDAR derived canopy and understory (%)
(Logging age):(vegetative cover) interactions	young_logged_stands:canopy + young_logged_stands:understory + old_logged_stands:canopy + old_logged_stands:understory
(Movement rate):(logged stand) interactions	ln(step length):young_logged_stands + ln(step length):old_logged_stands + ln(step length):ln(distance to road)
(Movement rate):(vegetative cover) interactions	ln(step length):canopy + ln(step length):understory

referred to as 'understory' (shorter ground-cover plants and taller shrubs) likely fall outside this 0.5–1.0 m height stratum. However, similar available measures of LiDAR returns in the 0.0–0.5 and 1.0–2.0 m range were strongly correlated with the 0.5–1.0 m vegetation stratum ($r = 0.77$ and 0.81, respectively), and so are represented in models to some extent by proxy.

We did not know the LiDAR-derived structural attributes of historically logged forests prior to logging, as the LiDAR data were not collected until 2017–2018. Therefore, unharvested commercial forest was defined as that with a mean canopy height equal to the 25th-percentile of timber logged, since LiDAR data were collected in the study area in 2017–2018 (18.6 m). We believe that this threshold balances the fact that historic timber harvest targeted large trees (Albert & Schoen 2013) but that even within stands of trees targeted by logging there existed a wide range of canopy heights previous to logging. We defined an open vegetation class as lands with < 25% canopy coverage, and all remaining land—canopy cover ≥ 25% with tree height > 18.6 m (the threshold we used for commercial timber)—as noncommercial forest.

Open and closed road classes were delineated using two USFS roads databases (USFS 2019a; , b): (1) a main database including all USFS 'system' (permanent) roads (though many of these are in various stages of disrepair and vegetated to some extent), and (2) an ancillary database of decommissioned and non-USFS roads of varying characteristics, although most are closed to vehicle traffic. The system roads are further classed as (1) closed to vehicle traffic, (2) accessible to high-clearance vehicles, or (3) accessible to passenger vehicles. We defined closed roads as the combination of those system roads closed to any vehicles and all non-system roads, and open roads as all roads with at least some vehicle access per the USFS system roads database.

The road system on POW is extensive, discontinuous, and partially inaccessible to vehicles, which made ground-truthing site-specific road characteristics (vegetation, level of human use) not feasible for this study. Generally, the closed road class was in some state of revegetation, but this varied depending on site characteristics (Online Resource Appendix S1, Fig. 1). For instance, some closed roads experience foot traffic from human hunters and fishers, and so, although the road surface is vegetated, a foot trail is maintained, which may facilitate wolf movement and human use. Although an exhaustive characterization of roads was not possible, to understand the existing variability in road revegetation, we photo-interpreted road conditions at random points along open and closed roads ($n = 200$) and along both classes combined ($n = 400$), and categorized the surrounding road (100 m in each direction of a random point) into one of four classes: (1) Road paved and with no vegetation on road surface, (2) < 50% of road surface vegetated, (3) > 50% of

exposed road surface vegetated with herbs, shrubs, or trees, and, (4) 100% of road surface vegetated with trees (Online Resource Appendix S1, Table 1).

Modeling

We performed integrated step-selection analysis (iSSA; Avgar et al. 2016) to study the fine-scale influence of the vegetation and logging-related covariates on wolf habitat selection and movement rate. iSSAs contrast the environmental attributes of each animal location with a set of random locations drawn from the overall distribution of steps the animal took (Avgar et al. 2016), and availability is thus constrained to a localized area near the starting position of each step. We drew available points generated from the gamma distribution of step lengths of each wolf in each season. The distribution of turn angles of wolves did not show any deviation from random, and so was not used to constrain the location of available points as often done in iSSAs (Fieberg et al. 2021). We estimated coefficients of habitat selection via the main effects of environmental covariates, and movement via interactions of ln(step length) and the environmental covariates (Avgar et al. 2016). We generated 10 available points from a gamma distribution based on the step lengths each wolf took in an individual season using the amt package (Signer et al. 2019) and attributed these and the used locations with environmental (GIS) covariate data. We then built iSSA models using Cox proportional hazards models with the fit_issa function in amt, a wrapper for the clogit (R package survival) function. We used the covariate value at the end point of each step to describe wolf habitat selection and at the start point of each step to interact with step length to describe wolf movement (Avgar et al. 2016). We used R package targets to create a reproducible modeling workflow.

We included specific covariates in each of the 5 models built to ask different questions (Table 2). One exception to this conceptually was ln(distance to road), which we included in all models, as we thought it may influence both habitat selection and movement, but was not strongly related to other covariates. We chose to use the coefficients for ln(distance to road) and its interaction with ln(step length) from Model 5 to calculate predictions of movement rate, although the sign and magnitude of the coefficient for ln(distance to road) and the ln(step length):ln(distance to road) interaction did not vary greatly between models.

We modeled wolf step selection across the year, but also built seasonal models corresponding to environmental and wolf life-history transitions (Roffler et al. 2018): late winter (1 Jan–14 Apr), denning season (15 Apr–31 Jul), late summer (1 Aug–14 Oct), and fall (15 Oct–31 Dec). There were several preliminary analytical steps we performed (Online Resource Appendix S2) that resulted in our final

model specifications. We built simple, plausible base models to which covariates of interest were added. Specifically, we included a core group of covariates—ln(step length), ln(distance to road), elevation, and slope—in all models (Table 2). In models built to assess the effects of the categorical landcover classes or continuous LiDAR-derived covariates on wolf habitat selection, we did not include the two types together in the same model, as they were often strongly correlated ($r > 0.7$).

To estimate the effect size of model coefficients, we calculated wolf relative strength of selection (RSS) and movement rate predictions across the typical range of covariate values experienced by wolves. We made predictions of log-RSS (Avgar et al. 2017) to assess the relative likelihood of wolf habitat selection across a range of values of covariates of interest as the ratio x_2/x_1, where x_1 and x_2 are calculated from model coefficients β across a range of target covariate values x and holding all other covariate values at their mean (zero for scaled covariates), where $x_2 = \beta_1 x_1 + \beta_2 x_2 + \ldots \beta_n x_n$ (Avgar et al. 2017). The denominator x_1 was similarly calculated but with all covariates set to their mean, including the target covariate. We predicted log-RSS across the range of values each covariate of interest took in the wolf location data except for distance to road, as distances from roads > 5 km were rare, and we did not have an ecological rationale for an effect beyond this distance. Movement rate predictions were calculated by multiplying the shape and modified scale parameters of the gamma distribution used to generate the available step lengths (Avgar et al. 2016; Prokopenko et al. 2017).

We used the two-stage (sensu Fieberg et al. 2021) approach of constructing models for each individual wolf and calculating population-level coefficients using the inverse-weighted means of the coefficients from each individual wolf model (Murtaugh 2007). While these population-level coefficients are useful in summary, they obscure individual variability in habitat selection and movement. Hence, we also reported the proportion of individuals sharing direction (sign) of selection with the population-level coefficient, as well as the proportion of individuals for which coefficients excluded zero. To investigate the biological basis for individual differences in response, we classed individuals according to their life history attributes: (1) sex, (2) breeding status (breeding versus nonbreeding), and (3) residency—member of pack (resident) versus disperser (nonresident). Individual wolves switched breeding and residency classes during the study, and so we summarized year-round and seasonal results using the majority of time an individual spent in one of the two classes, although this led to some classes not being represented in some seasons. When > 1 individual was present in each class in a season, we tested for statistical differences in class response to environmental covariates with univariate linear models run iteratively with the

selection coefficient for each step-selection model covariate as the response and class membership as the independent variable (1 = male, 0 = female; 1 = breeding, 0 = nonbreeding; 1 = resident, 0 = nonresident). We also plotted RSS for wolves belonging to each life history class across the typical range of covariate values experienced by wolves.

Results

We analyzed data from 13 wolves, for which the mean number of year-round GPS locations was 1024 (range: 355–2279). Within seasons, the mean number of analyzed wolf locations was 292 (range: 250–355). Some wolves did not have locations for all seasons; therefore, the number of wolves included in each season was as follows: late winter, $n = 10$; denning season, $n = 12$; late summer, $n = 12$; and fall, $n = 12$. We classified wolves by breeding status, determined from field data and observations, and by resident status (i.e., resident wolves are members of a pack with a well-defined home range, and nonresident wolves are dispersers, or extraterritorial wolves, as defined in Roffler et al. 2018) and summarized the data in Online Resource Table S3.

Wolf habitat selection

Wolf population-level response to young (≤ 30 years) logged stands was mixed across individuals (population-level confidence interval included 0; $\beta = 0.050$, 95% CI −0.029, 0.130; Fig. 2a, Table 3) except in fall ($\beta = 0.117$, 95% CI 0.007, 0.197; Table 3). Individual wolf coefficients for selection of young logged stands tended to be positive across the entire year (77% of individuals) and in each season (58–83% seasonally; Table 4), with the greatest percentage of individual wolves selecting young logged stands occurring in the fall. Wolf population-level response to old (> 30 years) stands was mixed across individuals (population-level CI included 0; $\beta = -0.057$, 95% CI −0.201, 0.071; Table 3) over the entire year (Fig. 2b), reflecting variability in individual wolf response (Fig. 2b, Table 4). Seasonally, the maximum percentage of individuals with a positive selection coefficient for old logged stands (70%; Table 4) occurred in late winter.

Wolf response to the LiDAR-derived vegetative cover metrics was stronger than in relation to the categorical logged-stand covariates. Wolves consistently avoided canopy cover over the entire year ($\beta = -0.450$, 95% CI −0.534, −0.269; Table 3, Fig. 2c) and in each season (Online Resource Appendix S3, Fig. 1c) at the population level, and all individual wolves avoided canopy cover over the entire year (Table 4). In addition, in no season did more than one individual wolf display positive selection for canopy cover (Table 4). Wolves also avoided understory cover over the entire year at the population ($\beta = -0.086$, 95% CI −0.174,
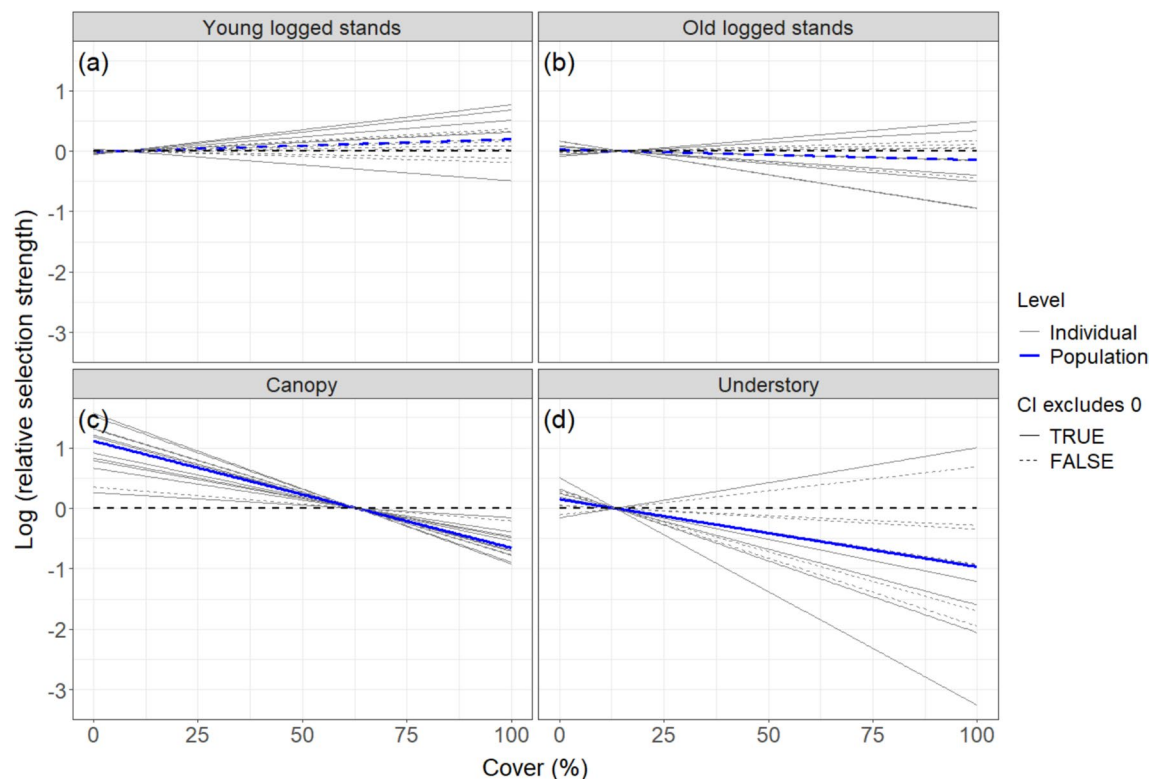
Fig. 2 Modeled wolf population-level and individual selection (log-RSS) versus percent cover (0–100%) of **A** young (≤30 years) logged stands, **B** old (>30 years) logged stands, **C** canopy cover, and **D** understory cover, Prince of Wales Island (POW), Alaska, USA, 2012–2017. Black dashed line (log-RSS=0) indicates neutral selection

−0.025; Fig. 2d) and individual level (85% of individuals; Table 4). Wolves tended to avoid understory seasonally at the population level, although confidence intervals for each season included 0 (Table 3). Individual wolves tended (50–80%) to avoid understory seasonally, with the maximum percentage occurring in late summer (Table 4). Wolves also avoided canopy cover within logged stands over the entire year at the population level (Fig. 3a, b), as indicated by the interaction coefficients between canopy and logged stands. Contrary to their general response to understory (irrespective of location), wolves selected understory cover within logged stands (Fig. 3c, d).

Roads displayed wide variability in their individual characteristics (Online Resource Appendix S1, Fig. 1, Table 1), the potential cause of wide variability in wolf individual wolf response to roads. Over the entire year, wolf individual response to roads was mixed (population-level $\beta = 0.043$, 95% CI −0.061, 0.211; Fig. 4), although wolves avoided roads in late summer at the population level (Table 3, Online Resource Appendix S3, Fig. 2) and across every individual (Table 4). Wolves selected areas of less slope and lower elevation across the entire year at the population level (Table 3). Wolves also selected areas of less slope and lower elevation in each season over the entire year at the

population level, although elevation coefficient confidence intervals only excluded 0 in fall (Table 3). Wolves avoided unharvested commercial forest over the entire year and seasonally (although late-winter and late-summer coefficient confidence intervals included 0; Table 3) and selected unforested areas over the entire year and seasonally (although the denning season coefficient confidence interval included 0).

Life history status (sex, breeding status, or residency) did not affect selection patterns of wolves. In linear models of step-selection model coefficients versus wolf status, no significant ($p \leq 0.05$) differences were observed in wolf habitat selection between classes in any season (Online Resource Appendix S4, Fig. 1a–c), despite 36 total linear models—4 covariates X 3 life history classes X 4 seasons (but excluding combinations for which <2 individuals were represented in a class)—used to detect differences (1–2 comparisons would be expected to yield p-values ≤0.05 by random chance). However, the lowest two p-values ($p = 0.07$) indicated a potential tendency for males to avoid young logged stands and understory relative to females in late winter.

Table 3 Coefficients from each of 5 fine-scale wolf habitat selection models, all seasons combined and seasonal, Prince of Wales Island (POW), Alaska, USA, 2012–2017

Covariate	All seasons			Late winter			Denning season			Late summer			Fall		
	β	LCL	UCL	β	LCL	UCL	β	LCL	UCL	β	LCL	UCL	β	LCL	UCL
Model 1															
ln(step length)	**0.111**	0.045	0.134	**0.105**	0.034	0.170	**0.109**	0.060	0.117	**0.095**	0.086	0.151	**0.135**	0.073	0.168
ln(distance to road)	0.026	−0.035	0.190	−0.078	−0.155	0.051	0.108	−0.093	0.296	**0.204**	0.098	0.292	0.024	−0.063	0.109
Elevation (m)	**−0.233**	−0.337	−0.017	−0.175	−0.454	0.043	−0.062	−0.243	0.042	−0.135	−0.418	0.034	−0.243	−0.492	0.025
Slope (°)	**−0.520**	−0.626	−0.330	**−0.403**	−0.914	−0.168	**−0.535**	−1.049	−0.233	**−0.460**	−0.663	−0.294	**−0.623**	−0.730	−0.442
Young logged stands	0.050	−0.029	0.130	0.010	−0.082	0.120	0.032	−0.163	0.137	0.029	−0.097	0.163	**0.117**	0.007	0.197
Old logged stands	−0.057	−0.201	0.071	−0.233	−0.401	0.035	−0.094	−0.437	0.143	−0.043	−0.259	0.139	0.019	−0.120	0.164
Unharvested commercial forest	**−0.135**	−0.207	−0.027	−0.220	−0.349	0.032	**−0.125**	−0.252	−0.040	−0.162	−0.272	0.015	**−0.155**	−0.237	−0.008
Unforested	**0.263**	0.134	0.360	**0.256**	0.142	0.337	0.163	−0.059	0.302	**0.237**	0.098	0.467	**0.331**	0.187	0.555
Model 2															
ln(step length)	**0.116**	0.041	0.141	**0.112**	0.036	0.179	**0.105**	0.059	0.132	**0.095**	0.082	0.144	**0.141**	0.066	0.177
ln(distance to road)	0.043	−0.061	0.211	−0.050	−0.157	0.068	0.131	−0.116	0.309	**0.175**	0.059	0.344	0.034	−0.111	0.079
Elevation (m)	**−0.265**	−0.360	−0.047	−0.199	−0.501	0.006	−0.089	−0.274	0.019	−0.164	−0.401	0.003	**−0.288**	−0.493	−0.059
Slope (°)	**−0.409**	−0.519	−0.237	**−0.372**	−0.797	−0.156	**−0.461**	−0.976	−0.227	**−0.409**	−0.573	−0.271	**−0.492**	−0.612	−0.336
Canopy	**−0.450**	−0.534	−0.269	**−0.399**	−0.650	−0.287	**−0.273**	−0.520	−0.098	**−0.387**	−0.535	−0.131	**−0.485**	−0.605	−0.342
Understory	**−0.086**	−0.174	−0.025	−0.027	−0.290	0.007	0.001	−0.106	0.098	−0.177	−0.318	0.148	−0.163	−0.311	0.052
Model 3															
ln(step length)	**0.120**	0.048	0.143	**0.115**	0.053	0.190	**0.122**	0.066	0.138	**0.113**	0.102	0.158	**0.145**	0.097	0.178
ln(distance to road)	0.010	−0.048	0.194	−0.102	−0.175	0.054	0.102	−0.089	0.306	**0.167**	0.093	0.284	0.028	−0.087	0.100
Elevation (m)	**−0.279**	−0.360	−0.045	**−0.246**	−0.513	−0.010	−0.093	−0.279	0.061	−0.174	−0.474	0.015	**−0.278**	−0.519	−0.013
Slope (°)	**−0.385**	−0.493	−0.267	**−0.286**	−0.717	−0.093	**−0.444**	−0.917	−0.212	**−0.388**	−0.527	−0.192	**−0.432**	−0.629	−0.342
Canopy	**−0.298**	−0.661	−0.264	**−0.564**	−0.767	−0.255	−0.113	−0.680	0.148	**−0.414**	−0.651	−0.246	**−0.240**	−0.882	−0.072
Understory	**−0.089**	−0.241	−0.033	−0.121	−0.313	0.025	−0.061	−0.187	0.055	**−0.202**	−0.528	−0.004	**−0.297**	−0.345	−0.113
Young logged stands	−0.010	−0.111	0.096	−0.097	−0.274	0.064	−0.103	−0.317	0.185	−0.110	−0.270	0.114	0.032	−0.110	0.149
Old logged stands	−0.029	−0.223	0.196	−0.070	−0.237	0.161	0.030	−0.733	0.147	−0.064	−0.653	0.212	0.055	−0.179	0.259
Unharvested commercial forest	−0.041	−0.060	0.054	−0.075	−0.139	0.081	**−0.107**	−0.197	−0.036	−0.026	−0.200	0.123	0.023	−0.171	0.105
Unforested	−0.065	−0.231	0.133	−0.195	−0.283	0.075	−0.017	−0.166	0.096	−0.109	−0.291	0.229	0.088	−0.411	0.209
young_logged:cover	0.016	−0.033	0.067	0.013	−0.018	0.146	−0.053	−0.123	0.055	**0.055**	0.028	0.275	0.018	−0.077	0.136
young_logged:understory	**0.058**	0.000	0.090	0.055	−0.009	0.152	0.104	−0.038	0.142	0.065	−0.159	0.264	0.062	−0.022	0.094
old_logged:canopy	−0.073	−0.258	0.023	−0.108	−0.295	0.076	−0.118	−0.370	0.193	−0.129	−0.376	0.174	−0.037	−0.188	0.098
old_logged:understory	**0.176**	0.040	0.249	0.179	−0.029	0.394	0.038	−0.193	0.188	0.190	−0.337	0.401	**0.165**	0.003	0.367
Model 4															
ln(step length)	**0.221**	0.134	0.333	0.208	−0.155	0.571	**0.247**	0.161	0.437	**0.172**	0.043	0.588	**0.300**	0.220	0.494
ln(distance to road)	0.041	−0.040	0.156	−0.053	−0.172	0.055	0.093	−0.100	0.357	**0.220**	0.086	0.253	0.000	−0.074	0.109

Table 3 (continued)

Covariate	All seasons			Late winter			Denning season			Late summer			Fall		
	β	LCL	UCL	β	LCL	UCL	β	LCL	UCL	β	LCL	UCL	β	LCL	UCL
Elevation (m)	**−0.228**	−0.325	−0.020	−0.164	−0.473	0.035	−0.125	−0.237	0.058	−0.145	−0.401	0.042	−0.248	−0.485	0.016
Slope (°)	**−0.525**	−0.628	−0.331	**−0.410**	−0.909	−0.187	**−0.568**	−1.039	−0.235	**−0.446**	−0.648	−0.381	**−0.630**	−0.730	−0.434
Young logged stands	0.049	−0.051	0.130	0.001	−0.103	0.161	0.022	−0.141	0.202	−0.025	−0.118	0.113	0.077	−0.003	0.182
Old logged stands	**−0.116**	−0.243	0.000	−0.223	−0.429	0.020	−0.144	−0.533	0.003	−0.064	−0.344	0.013	−0.028	−0.140	0.134
Unharvested commercial forest	**−0.135**	−0.203	−0.028	−0.219	−0.348	0.031	**−0.121**	−0.253	−0.039	−0.163	−0.282	0.017	**−0.160**	−0.235	−0.005
Unforested	**0.270**	0.139	0.357	**0.245**	0.142	0.338	0.155	−0.055	0.282	**0.242**	0.100	0.462	**0.334**	0.187	0.553
ln(step length):young_logged	−0.014	−0.037	0.014	0.002	−0.057	0.129	0.028	−0.031	0.168	−0.051	−0.067	0.036	−0.019	−0.054	0.038
ln(step length):old_logged	**−0.046**	−0.087	−0.026	−0.035	−0.070	0.097	−0.003	−0.102	0.041	−0.090	−0.158	0.029	−0.041	−0.075	0.049
ln(step length):ln(distance to road)	**−0.019**	−0.041	−0.012	−0.024	−0.093	0.044	−0.022	−0.045	0.002	−0.011	−0.074	0.017	−0.024	−0.043	0.014
Model 5															
ln(step length)	**0.176**	0.005	0.337	0.229	−0.201	0.515	**0.285**	0.127	0.457	0.112	−0.113	0.302	**0.237**	0.008	0.611
ln(distance to road)	0.044	−0.069	0.182	0.007	−0.195	0.057	0.141	−0.138	0.281	**0.187**	0.067	0.350	0.022	−0.123	0.058
Elevation (m)	**−0.271**	−0.386	−0.042	**−0.188**	−0.529	−0.020	−0.171	−0.339	0.040	−0.191	−0.393	0.001	**−0.296**	−0.520	−0.055
Slope (°)	**−0.390**	−0.520	−0.236	**−0.396**	−0.812	−0.167	**−0.462**	−0.999	−0.230	**−0.386**	−0.538	−0.267	**−0.491**	−0.564	−0.332
Canopy	**−0.467**	−0.566	−0.312	**−0.423**	−0.666	−0.286	**−0.384**	−0.565	−0.134	**−0.419**	−0.575	−0.162	**−0.491**	−0.658	−0.347
Understory	**−0.136**	−0.226	−0.046	−0.059	−0.338	0.011	−0.048	−0.163	0.073	**−0.214**	−0.350	−0.047	−0.190	−0.286	0.006
ln(step length):canopy	−0.040	−0.089	0.003	−0.051	−0.117	0.028	−0.087	−0.155	0.020	−0.040	−0.088	0.007	−0.025	−0.103	0.019
ln(step length):understory	**−0.046**	−0.099	−0.021	−0.050	−0.086	0.022	**−0.055**	−0.089	−0.011	**−0.087**	−0.138	−0.025	−0.036	−0.116	0.071
ln(step length):ln(distance to road)	−0.008	−0.033	0.012	−0.024	−0.074	0.055	**−0.025**	−0.060	−0.014	0.002	−0.035	0.038	−0.018	−0.049	0.020

Coefficients with confidence interval not including 0 are in bold

Table 4 Proportion of individual wolves with model coefficient sign concordant (Conc.) with the sign of the population-level coefficient (Sign), and with confidence interval of random coefficient excluding 0 (CI 0), in fine-scale habitat selection models, Prince of Wales Island (POW), Alaska, USA, 2012–2017

Covariate	All seasons			Late winter			Denning season			Late summer			Fall		
	Sign	Conc	CI 0	Sign	Conc	CI 0	Sign	Conc	CI 0	Sign	Conc	CI 0	Sign	Conc	CI 0
Model 1															
Young logged stands	+	0.77	0.38	−	0.60	0.20	+	0.58	0.17	+	0.60	0.10	+	0.83	0.42
Old logged stands	−	0.54	0.54	−	0.70	0.60	−	0.67	0.25	−	0.60	0.10	−	0.58	0.25
Unharv. commercial forest	−	0.92	0.46	−	0.80	0.30	−	0.92	0.33	−	0.70	0.30	−	0.83	0.08
Unforested	−	1.00	0.85	−	0.90	0.80	−	0.75	0.58	−	1.00	0.70	−	1.00	0.92
Model 2	−			−			+			−			−		
ln(distance to road)	+	0.69	0.46	+	0.70	0.30	+	0.75	0.42	+	1.00	0.60	+	0.58	0.17
Elevation (m)	−	1.00	0.54	−	0.80	0.50	−	0.58	0.33	−	0.80	0.30	+	0.83	0.67
Slope (°)	−	0.92	0.92	−	0.90	0.70	−	0.92	0.92	−	1.00	0.80	−	1.00	0.67
Canopy	+	1.00	0.92	+	0.90	0.90	+	0.92	0.42	+	1.00	0.70	+	1.00	0.92
Understory	+	0.85	0.38	+	0.70	0.20	−	0.50	0.17	+	0.80	0.40	+	0.75	0.33
Model 3	+			+			+			+			+		
Young_logged:canopy	−	0.62	0.08	−	0.70	0.00	−	0.58	0.00	−	0.90	0.10	−	0.50	0.08
Young_logged:understory	+	0.77	0.38	+	0.80	0.10	+	0.67	0.00	+	0.60	0.10	+	0.67	0.00
Old_logged:canopy	−	0.77	0.08	−	0.80	0.10	−	0.67	0.08	−	0.60	0.10	−	0.75	0.08
Old_logged:understory	−	0.92	0.46	−	0.70	0.40	−	0.58	0.08	−	0.70	0.40	−	0.83	0.08
Model 4	−			+			+			−			−		
ln(step length):young_logged	−	0.62	0.23	−	0.50	0.20	−	0.58	0.08	−	0.80	0.00	−	0.58	0.17
ln(step length):old_logged	−	0.85	0.46	−	0.60	0.20	−	0.50	0.17	+	0.80	0.20	−	0.75	0.17
Model 5	−			−			−			−			−		
ln(step length):canopy	−	0.77	0.38	−	0.70	0.10	−	0.75	0.33	−	0.80	0.10	−	0.67	0.17
ln(step length):understory	−	0.92	0.46	−	0.60	0.30	−	0.83	0.08	−	0.90	0.30	−	0.67	0.25
ln(step length):ln(dist to road)	−	0.69	0.31	−	0.60	0.40	+	0.92	0.17	−	0.50	0.00	−	0.67	0.08

Covariates shared by multiple models not shown

Wolf movement rate

Wolf movement rate was not influenced by young logged stands over the entire year at the population level (Fig. 5a) but slowed in old logged stands (Fig. 5b). In each individual season, the confidence intervals for ln(step length) interactions with young and old logged stands included 0 (Table 3; Online Resource Appendix S3, Fig. 3a, b), indicating no significant effect on movement rate. There was a tendency for wolves to move more slowly in old logged stands in each season, as the ln(step length):old logged stand interaction coefficient was consistently negative across seasons at the population level (but with confidence interval including 0; Table 3). In addition, 85% of individuals tended to move more slowly in old logged stands over the entire year (Table 4). Seasonally, the percentage of individuals displaying a tendency for slower movement in old logged stands was at its maximum in late summer (80%).

Canopy cover tended to slow wolf movement rates at the population level over the entire year (Fig. 5c) and in each season (Online Resource Appendix S3, Fig. 3c), although seasonal confidence intervals included 0. Individual wolves corroborated this tendency for slower movement in old logged stands; 75% of individuals over the entire year, and 67–80% seasonally, displayed negative coefficients for ln(step length):old logged stand interactions. Compared to canopy cover, understory slowed wolf movement to a greater extent at the population level over the entire year (Fig. 5d), seasonally (Online Resource Appendix S3, Fig. 3d), and across individuals (Table 4).

Contrary to our expectations, we did not observe an effect of roads on wolf movement rate at the population level ($\beta = -0.008$, 95% CI -0.033, 0.012) over the entire year (Fig. 6), although 69% of individuals moved faster near roads (Table 4). Wolves did, however, move faster near roads in the denning season at the population level ($\beta = -0.025$, 95% CI -0.060, -0.014), and in the denning season, all but one wolf moved faster near roads (Table 4).

As with wolf selection patterns, we saw no significant effect of different wolf life history classes (sex, breeding status, or residency) on seasonal wolf movement rate. In linear models of step-selection model coefficients versus
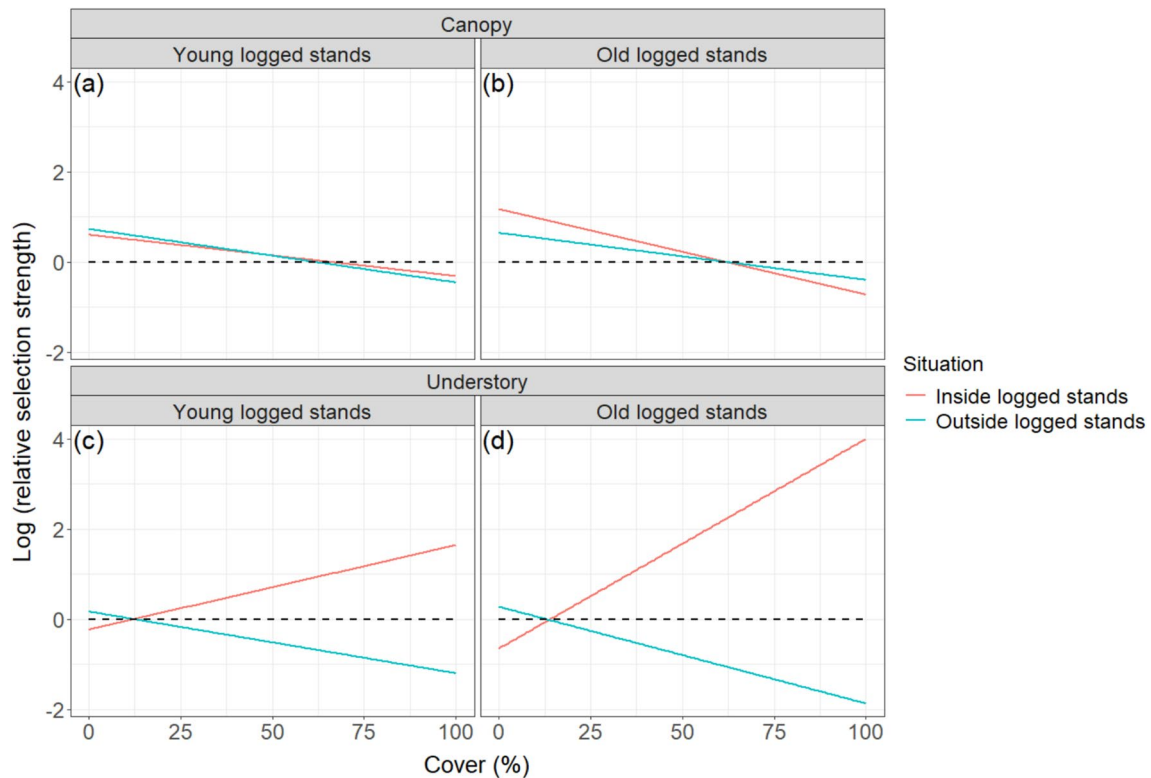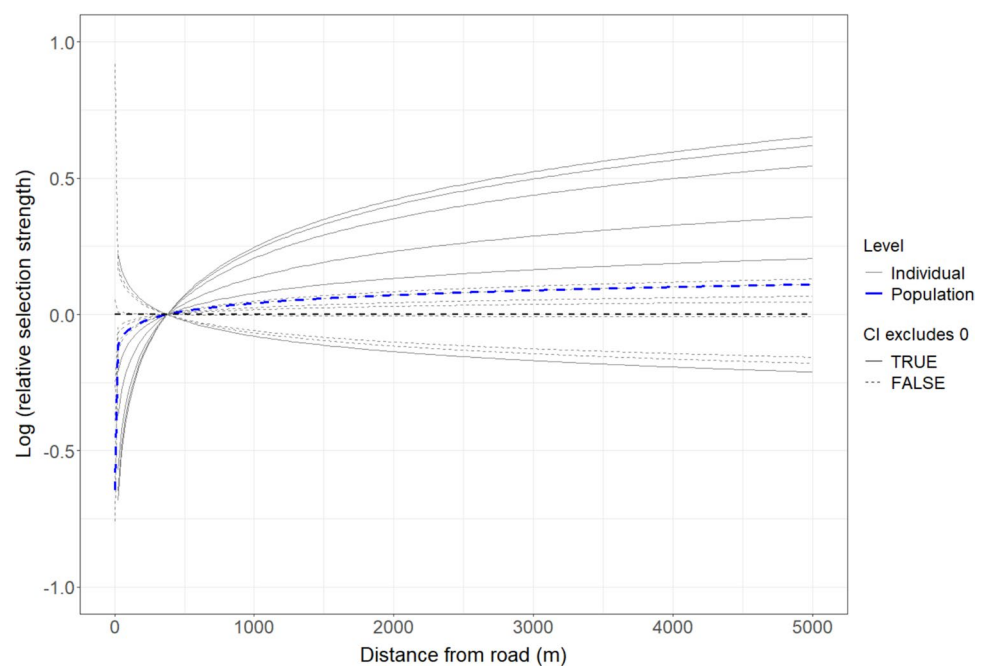
Fig. 3 Modeled wolf population-level selection (log-RSS) versus percent canopy cover (0–100%) inside and outside of **A** young (≤ 30 years) logged stands and **B** old (> 30 years) logged stands, and versus percent understory cover in **C** young and **D** old logged stands, Prince of Wales Island (POW), Alaska, USA, 2012–2017. Black dashed line (log-RSS = 0) indicates neutral selection
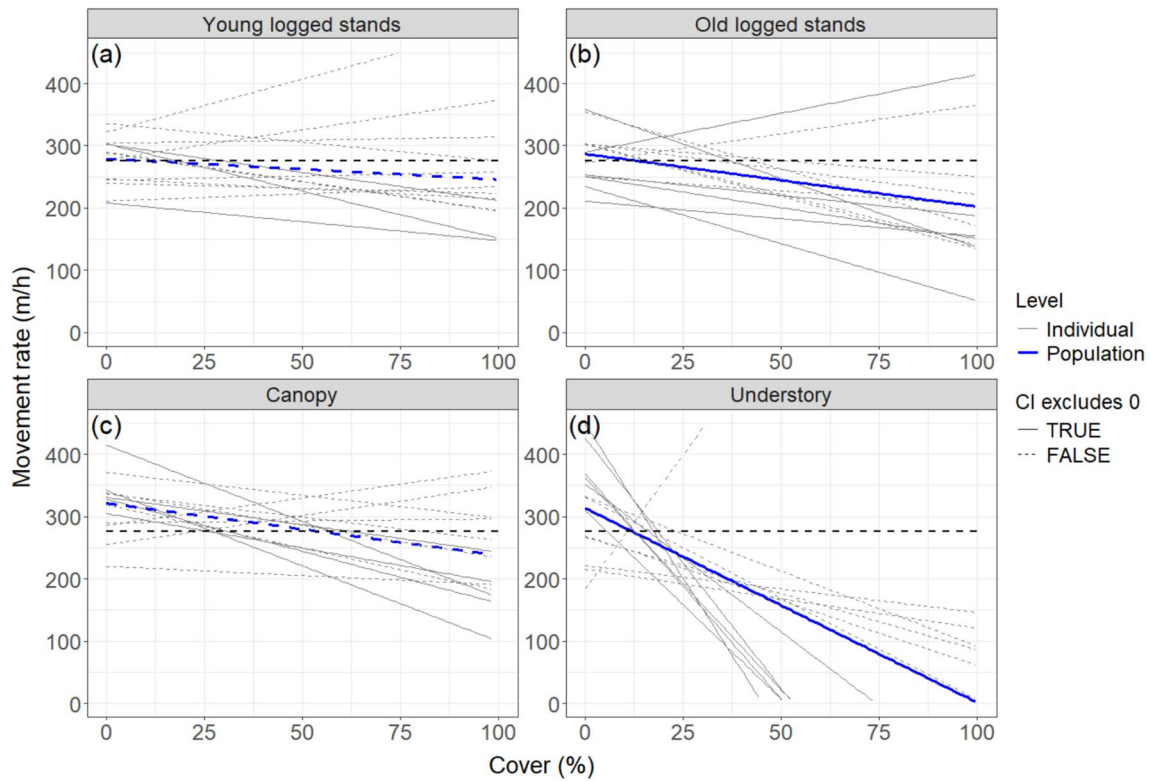
Fig. 4 Modeled wolf year-round, population-level and individual selection (log-RSS) versus distance to nearest road, Prince of Wales Island (POW), Alaska, USA, 2012–2017. Black dashed line (log-RSS = 0) indicates neutral selection

Fig. 5 Modeled wolf population-level and individual movement rate versus percent cover (0–100%) of **A** young (≤30 years) logged stands, **B** old (>30 years) logged stands, **C** canopy cover, and **D** understory cover, Prince of Wales Island (POW), Alaska, USA, 2012–2017. Black dashed line (log-RSS=0) indicates the mean wolf population movement rate (274 m/h^{-1})

Fig. 6 Modeled wolf population-level and individual movement rate versus distance to road, Prince of Wales Island (POW), Alaska, USA, 2012–2017. Black dashed line (log-RSS=0) indicates the wolf mean population movement rate (274 m/h^{-1})
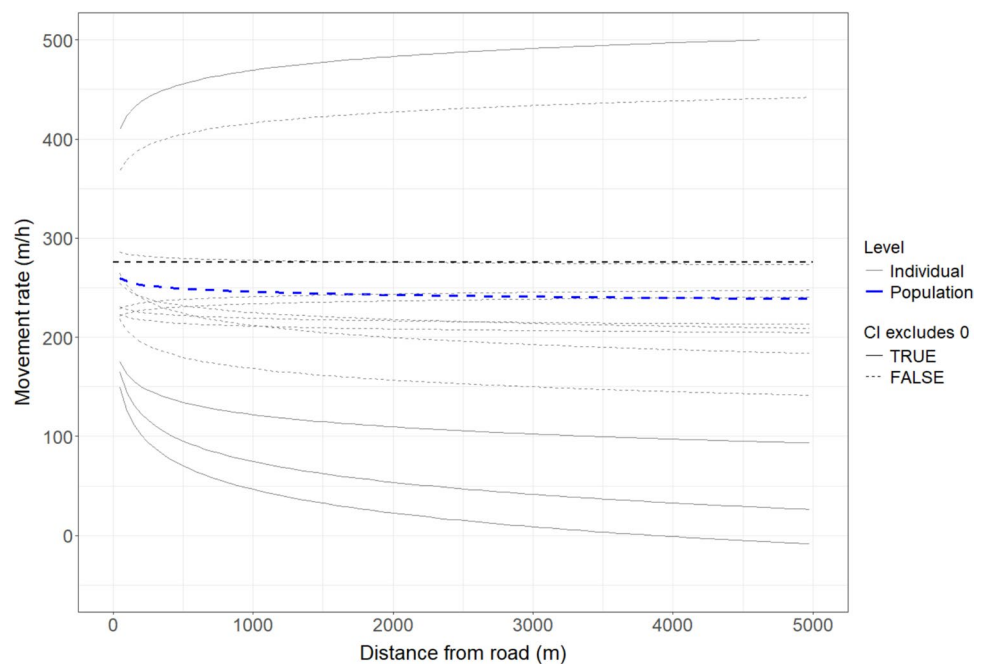
wolf status, no significant ($p \leq 0.05$) differences were observed in wolf movement rate relative to covariates between classes in any season (Online Resource Appendix S4, Fig. 2a–c).

Discussion

We found that wolves respond to continuous vegetative cover (measured by LiDAR) that captures fine-scale variability not reflected in 'all-or-nothing' categorical representations of logged stands. Contrary to our predictions, wolves did not select young (≤ 30 years) logged stands, nor avoid old (> 30 years) stands. Unexpectedly, wolves did not move faster through young logged stands, and their movement was slowed by old logged stands. In contrast, in accordance with our predictions, wolves selected and moved faster through areas of less canopy and understory cover (although the effect of canopy on movement rate was not significant). Modeling animal selection of one discrete landcover class over another is appealing in its simplicity, but the continuous covariates used for vegetative cover in this study captured gradients in vegetation lost in homogeneous logged stand classes (see Boyce et al. 2017).

The wolves we studied selected and moved through areas of less vegetative cover that potentially promote efficient hunting by wolves (Dickie et al. 2017; Finnegan et al. 2018). The ability of wolves to visually detect prey (Kauffman et al. 2007; Boucher et al. 2022), and to move efficiently (Dickie et al. 2017, 2020) can be reduced in heavy vegetation, potentially leading to decreased prey encounter rates. At the same time, wolves may perceive greater risk due to the presence of human deer hunters and wolf trappers visible in open terrain lacking cover (Person and Russell 2008) such as results from logging. In addition, in some cases, young seral forests resulting from logging are preferred by ungulate species preyed on by wolves (Boucher et al. 2022), and wolves with greater coverage of recently logged stands in their home range have a greater proportion of deer in their diet (Roffler et al. 2023). These factors that potentially affect wolf fitness may exert opposing forces on wolf habitat selection and could result in individual wolves' mixed selection toward logged stands in this study. While we did not find strong direct evidence for the influence of timber harvest on wolves, the vegetative cover metrics correlated with wolf habitat selection and movement are strongly affected by logging (Gregovich et al. 2024) and undergo a trajectory of reestablishment post-logging. Generally, forest canopy cover removed by logging increases in the period 0–30 year post-logging and then plateaus at percentages greater than that of the original old-growth forest for > 150 years (Alaback 1984). Understory that initially increases 0–30 year post logging is suppressed concurrent with the establishment of dense conifer canopy. Despite these general trajectories, there is likely fine-scale variability in post-logging vegetation that is dependent on site-specific conditions (Banner and LePage 2008) and influences wolf habitat selection and movement.

Although wolves generally avoided understory cover, they selected understory when in logged areas; the underlying mechanism for this is not clear from our analysis. A peak in understory cover is observed in the study area 10 years after logging which is a time when canopy cover is sparse. We suspect wolves are attracted to these recently logged areas with relatively open canopy that potentially provide forage for their Sitka black-tailed deer prey (see Boucher et al. 2022). By around 30 years after logging understory decreases and canopy increases, and so this situation favored by wolves post-logging appears short-lived.

Sitka black-tailed deer are wolves' main prey in our study area (Roffler et al. 2023), and vegetation patterns influence the risk of wolf predation to which deer are exposed in the region of this study (Farmer et al. 2006). Farmer et al. (2006) identify areas of open vegetation as high-risk for deer and highlight the importance of thick understory as cover from wolf predation. While vegetative cover undergoes rapid changes after logging occurs, natural areas not targeted by logging (e.g., wet bogs, forested wetlands, alpine meadows) are relatively stable in their characteristics through time. Such areas of little vegetative cover are selected by wolves, promote their movement, and are associated with increased mortality risk for deer (Farmer et al. 2006). In addition, Farmer et al. (2006) found deer more exposed to wolf predation in flat areas that wolves strongly selected in the current study. The configuration of natural features and vegetation outside the matrix of logged stands represents a temporally stable yet spatially variable landscape of risk for deer that is largely unaffected by land management.

The use of LiDAR to measure and map landscape vegetation patterns to describe wildlife-habitat relationships is becoming more common (Shanley et al. 2021; Sergeyev et al. 2024), and in this study, LiDAR-derived, continuous measures of vegetation better explained wolf selection behavior than categorical land classes. iSSAs contrast environmental covariates within clusters consisting of a single used location and multiple (here, 10) random points. Continuous covariate values are likely to vary at the fine scale of these data clusters, but land classes may not, depending on their spatial distribution (see Boyce et al. 2017). Wolves are likely responding to fine-scale variability in three-dimensional vegetative structure as captured by LiDAR (Davies and Asner 2014) but lost in monolithic, categorical representation.

A limitation of the current study is that the canopy and understory measures we used have not been validated on-the-ground. We recommend collection of vegetation plot

data to validate LiDAR-derived cover measures to on-the-ground measurements of vegetative characteristics in any future studies. In addition, the aerial collection of LiDAR measurements took place in 2017–2018, at the tail end of wolf GPS location collection, and 5 years after the first wolf GPS locations were obtained in 2012. The maximum mismatch between vegetation as it existed at the beginning of the study and when LiDAR was collected likely occurs in recently logged stands, as the greatest rate of change in canopy cover and understory occurs within 0–10 years (see Gregovich et al. 2024) after logging. Logged areas this recent are not prevalent in the study area, and so our results may not be greatly affected. Outside of logged areas, natural catastrophes (e.g., fire, large-scale windthrow) affecting vegetation are rare in the study area, and climax vegetation communities likely did not change appreciably during the 6 years of the study.

Overall, the population of wolves in this study did not behaviorally respond to roads, counter to our predictions. We expected roads would be associated with increased wolf movement (Zimmerman et al. 2014; Dickie et al. 2020), avoidance of risky areas (Gurarie et al. 2011), or selection as movement corridors (Boucher et al. 2022). In this study, we did not detect a difference in wolf response to roads open and closed (as classified via a USFS GIS database) to vehicle traffic. Roads (including within these two classes) vary widely in characteristics influential to wolves, and this may have led to the mixed response we observed. Roads in the study area exist in various combinations of human accessibility and revegetation, likely affecting wolf behavior in ways that are ambiguous and site dependent. For instance, roughly 1/3 of roads in the study area are fully revegetated with trees, which likely impedes both human and wolf use, while we estimated 4% of roads are paved and receive high-speed passenger use, and thus may be risky and avoided by wolves. The remainder of roads are gravel and in varying stages of revegetation, and hence vary widely in use by humans and potential effect on wolf behavior. However, while we did not observe significant overall effects of roads on wolf habitat selection there was some evidence for selection of roads as movement corridors. Wolves selected areas near roads during late summer at the population level, and in each season there were individuals that selected areas closer to roads. It is possible that snow deposition on roads in winter impedes wolf movement rate, though some individual wolves moved faster near roads year-round. Roads in the study area might benefit from a thorough description (perhaps via LiDAR, see Waga et al. 2020) and accurate classification based on characteristics relevant to wolf behavior.

In future studies, a shorter GPS fix interval than the 6-h rate used here may also reveal patterns of road use not evident in the current study. Greater spatio-temporal resolution of wolf locations could allow identification of wolf behavioral states (e.g., encamped, traveling; Zimmerman et al. 2014), that are difficult to obtain from data collected at this coarse, 6-h time interval (see Creel et al. 2013; Cristecu et al. 2015). Discerning behavioral states may help reveal road influence not evident in this study. For instance, the effect of roads on wolf movement rate may be confounded if wolves move faster on or near roads while hunting, but also stop to kill and consume prey there. Finally, a shorter GPS fix interval would more generally elucidate wolf habitat selection and movement behavior at a finer spatial scale; the combination of 6-h GPS fixes and the high mobility of wolves in this study resulted in a spatial scale of analysis on the larger end of that considered in most step selection analyses.

Wolves have long been recognized for their behavioral plasticity, which has facilitated adaptation to a variety of habitats worldwide (Boyd et al. 2023), differences in prey availability (Newsome et al. 2016), and varying effects of anthropogenic disturbance (Ferreiro-Arias et al. 2024). Although individual differences in behavior have been attributed to breeding status (Gable et al. 2023), sex (Eriksson et al. 2024), and resident status (Thompson et al. 2024), we did not find clear patterns in our study system. Wolf response to logging-related disturbance and vegetation patterns varied across individuals in this study, but we likely did not have enough data from different population segments (e.g., packs, sexes, residents versus non-residents) to determine a basis for this variability in individual wolf response. Individual variation in behavior may be the result of differences in personality (Bump et al. 2022), defined as consistent differences in individual behaviors across time, space, and ecological contexts (Young et al. 2015), which may be influenced by the individual's experiences early in life, or due to neuroendocrine activities (Packard 2003). In addition, individual personality may be altered by individual diet specialization (Toscano et al. 2016) as specific behaviors including boldness and innovation may be associated with foraging strategies (Parsons et al. 2022). In this study, individual wolves displayed a range of responses in different forest habitats exemplified by the percentage of wolves sharing behavior (avoidance or selection) toward covariates, which ranged from ~50% (expected by random chance) in relation to old logged stands to 100% avoidance of canopy cover. This suggests lack of a one-size-fits-all view of wolf habitat selection, and the potential that management actions may not affect all individuals in the same way.

Logging has resulted in a mosaic of natural habitat and second-growth forest in various stages of succession in coastal temperate rainforests (Albert and Schoen 2013). While natural vegetation patterns in areas not targeted for timber harvest are relatively stable through time, succession of previously logged forests, future timber harvest, and second-growth remediation (e.g., precommercial thinning)

will influence forest vegetative cover and, in turn, wolf habitat selection and movement rate. Wolves in this study generally selected and moved faster through areas of less canopy and understory cover present in unforested wetlands, alpine areas, and recently logged forests, the latter of which is a short-lived successional stage giving way (~ 30 year post-logging) to heavier vegetative cover wolves avoid. Forest precommercial thinning can decrease canopy cover but increase understory (Crotteau et al. 2020), with potentially opposing effects on wolf habitat selection. It is not clear how long these changes last after thinning occurs (Cole et al. 2010). Forest management activities may initially benefit wolves by providing open habitat they select, but this successional stage is short-lived, and as these stands transition to closed-canopy stages avoided by wolves, there may be negative consequences for wolf populations.

Data availability The data are the property of the State of Alaska. AS 16.05.815(d) mandates confidentiality of the specific location of fish and wildlife species, we, therefore, do not have authority to publicly share them.

Code availability The code is available on GitHub: (https://github.com/sculpin99/POW-wolf-iSSA).

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Ethical approval This study followed the guidelines established by the ADF&G Animal Care and Use Committee (ACUC #2012–028 and #2014–15) and the American Society of Mammalogists.

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