Behavioral plasticity in a variable environment: snow depth and habitat interactions drive deer movement in winter

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In seasonally varying environments, animals should alter habitat selection through time to avoid the harshest conditions. Winter severity is limiting for many ungulates in high-latitude ecosystems, and quality of habitat is an important determinant of winter survival. Previous studies in Southeast Alaska indicated that Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) selected old-growth forest that provides both snow interception and forage, but with great variability among studies, years, and geographic areas. Clearcut timber harvest has greatly reduced the extent and quality of old-growth forest. The value of 2nd-growth and old-growth forest types to deer likely depends on snow depth, which is highly variable in space and time. We measured selection for vegetation classes, landscape features, and forage biomass by monitoring 56 GPS-radiocollared adult female deer from 1 January to 1 April between 2011 and 2013. Simultaneously, we measured snow depth across deer home ranges daily. We determined that snow depth had a strong effect on selection for vegetation classes. During periods of low snow, deer selected young 2nd growth but avoided old 2nd growth and high-volume old growth. As snow depths increased, young 2nd growth was avoided and deer selected old 2nd-growth and productive old-growth forests. The composition of vegetation classes within the landscape influenced selection, with deer selecting locally abundant habitats. These behaviors suggest that the widespread distribution of forest patches that provide snow interception and forage biomass may be critical to fulfilling the energetic requirements of deer during winters with snow. Such context-dependent habitat selection is likely widespread among wildlife species in variable environments and should be incorporated into study design and analysis.

Key words: Alaska, deer, functional response, habitat selection, snow depth, Tongass National Forest, ungulate, winter

Fluctuating environmental conditions in time and space may alter the values of habitat to animals by imposing fitness costs or offering fitness benefits (Douhard et al. 2014; Long et al. 2014). Animals should respond by shifting habitat selection to maximize fitness (Mason et al. 2014), yet variable environmental conditions are rarely accounted for in studies of habitat selection (but see Hundertmark et al. 1990; Boyce et al. 2003; Long et al. 2014). Further, when such interactive effects of the environment on habitat selection are addressed, environmental conditions are often treated as categorical (e.g., "high" versus "low" snow winters or "hot" versus "cold" temperature). The effects of environmental conditions on animal behaviors such as habitat selection are likely to be continuous rather than discrete, because values of habitat and animal responses shift with environmental

fluctuations (Long et al. 2014). Similarly, habitat classifications also are often simplifications of continuous processes (i.e., successionally driven changes in forage—Stephenson et al. 2013).

Animals living in seasonal environments must contend with fluctuating resource availability, with survival and population growth often limited by a season in which resources are scarce (Fretwell 1972; Wolff 1997; Both et al. 2010). Seasonally limiting resources include plant phenology (Post and Forchhammer 2008; Monteith et al. 2011; Hurley et al. 2014) and many climate variables (Stein et al. 2010; van Beest et al. 2012). As such factors vary through time, they likely change the value of discretely defined habitat types for wildlife, as animals shift selection among habitats to satisfy nutritional needs, reduce energetic costs, and reduce predation risk (Parker 2003; Stein

et al. 2010). Most habitat selection studies do not incorporate fluctuating environmental variables into study designs or analyses but instead rely on seasonally averaged data (but see Parker et al. 1996; Fortin et al. 2005; Stein et al. 2010; Long et al. 2014). As a result, time-varying environmental conditions within seasons or across years likely will result in ambiguous and possibly contradictory patterns of selection (e.g., Schoen and Kirchhoff 1985; Yeo and Peek 1992; Doerr et al. 2005). In areas where environmental conditions are variable within and among years, incorporating time-varying versions of important variables is likely key to obtaining reliable and interpretable measures of habitat selection. Failure to do so could result in undervaluing the use of important habitats when conditions are severe and could have negative consequences for management if those habitats are not conserved adequately.

For ungulates at temperate and higher latitudes, winter is often the limiting season for survival, when cold temperatures and snowfall restrict the availability of forage and increase costs of movement (Messier 1991; Parker et al. 2009; Robinson and Merrill 2012). In addition, vulnerability of ungulates to predators can be higher in snow-covered landscapes because of reduced nutritional condition and increased cost of movements for prey relative to predators (Nelson and Mech 1986; Huggard 1993; Sand et al. 2006). Subsequently, habitat selection of ungulates in winter can be strongly shaped by the landscapes of energetic cost and risk of death (Farmer et al. 2006; Gustine et al. 2006; Monteith et al. 2011). As snow depth increases, values of habitat to wildlife may be completely reversed from low-snow conditions. As habitat types with abundant forage but little canopy cover to intercept snow become unusable, habitats with adequate forage and good canopy cover become preferred (Hundertmark et al. 1990).

In Southeast Alaska and northern coastal British Columbia, Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) contend with a highly variable snowpack in winter, and large areas of 2nd-growth forest produced by industrial timber harvest (Albert and Schoen 2013; Shanley et al. 2015). The values of these forest landscapes to deer depend on the composition of forest patches in various stages of forest succession, climate, and predation regime. Clearcut logging is the predominant method of harvesting timber and young 2nd-growth forests (< 30 years post-logging) produce abundant forage, whereas older clearcut stands with high levels of light interception by the canopy are typically forage depauperate (Fig. 1; Alaback 1982). Conversely, the thick canopy of old 2nd growth (> 30 years post-logging) intercepts most snowfall, whereas there is almost no canopy interception of snow in young 2nd growth (Kirchhoff and Schoen 1987; Hanley et al. 2012; Alaback and Saunders 2013). Subsequently, forage availability and cost of movement in 2nd-growth stands depends strongly on snowfall, and the value of timber-harvested landscapes to ungulates and other wildlife will vary across regions, climate cycles, and within and across years as dictated by snowfall. The coastal temperate rainforest presents an excellent study system to examine the interactive, time-dependent effects of habitat and climate. In previous studies, deer strongly selected old-growth forest on south-facing slopes in winters with deep snow (Schoen and Kirchhoff 1985), but selection of those habitats was weaker during winters with more intermittent snowfall and shorter duration of snow cover (Yeo and Peek 1992; Doerr et al. 2005; Person et al. 2009). Across these studies, snow depth was averaged seasonally, whereas deer undoubtedly respond to changing snow depth at much finer temporal and spatial scales (Parker et al. 1999).

Here, we examined the effects of snow depth on fine-scale selection by Sitka black-tailed deer relative to vegetation classes and landscape features. We hypothesized that as snow depth increased, deer would increasingly select locations with
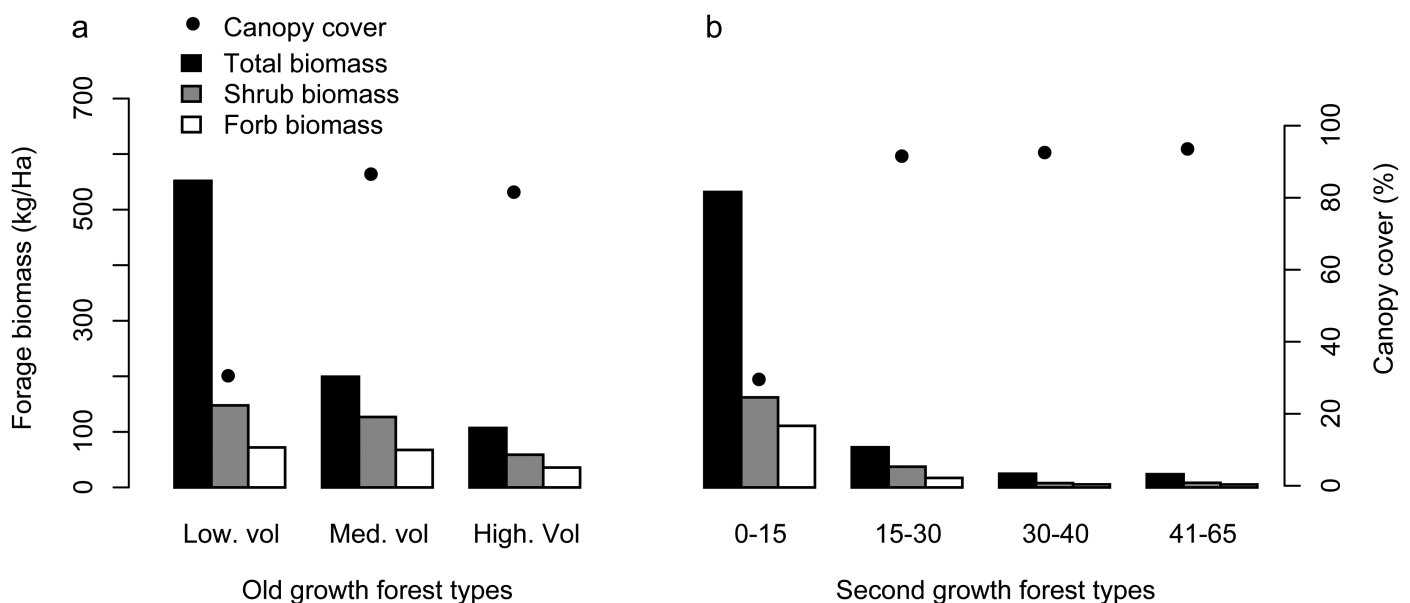

Fig. 1.—Differences in winter forage biomass (total, shrubs, and forbs, in kg/ha) among vegetation classes in the study area on Prince of Wales Island. Vegetation classes are a) old-growth forest types, shown for low-volume, medium-volume, and high-volume types, and b) 2nd-growth forest types, shown for age classes 0–65 years after original timber harvest. Values were derived from the published FRESH forage model (Hanley et al. 2012).

more canopy interception (i.e., higher-volume old-growth and older 2nd-growth forests), but locations that provided both canopy interception and forage would be preferred (i.e., higher-volume old growth; Fig. 1). We tested predictions at the scale of deer movements every 2 h, because snow depth strongly affects cost of movement and deer home ranges are greatly restricted in winter compared to summer (Schoen and Kirchhoff 1985; Yeo and Peek 1992). Deer also may respond behaviorally to the availability of habitats (i.e., a functional response in selection—Mysterud and Ims 1998), particularly if some habitats are of higher value than others but availability of high-quality habitats is limited (Moreau et al. 2012; Knopff et al. 2014), or potentially if animals prefer abundant or unfragmented habitats compared to rare habitats of the same quality. We therefore tested for functional responses in selection patterns of individual deer to availability of habitat types.

MATERIALS AND METHODS

Study area.—Our study area was the central portion of Prince of Wales Island, the largest island in the Alexander Archipelago of Southeast Alaska and the third largest in the United States

Prince of Wales Island
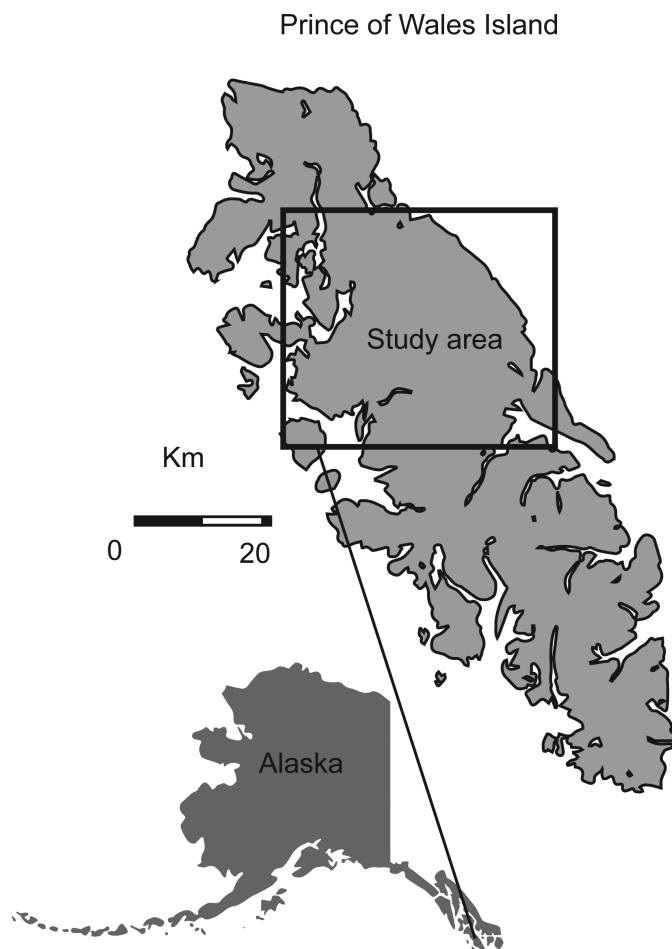
Fig. 2.—Map of the study area, which was conducted from 1 January to 1 April during 2011, 2012, and 2013 on the central portion of Prince of Wales Island, in the Alexander Archipelago of Southeast Alaska.

(Fig. 2). The ecosystem was coastal temperate rainforest, with natural habitats spanning a variety of old-growth forest types, as well as muskeg heaths, wet meadows, estuaries, beaches and shorelines, and numerous lakes and rivers. In addition, since 1954, Prince of Wales was been the focus of much of the commercial timber harvest in the region (Albert and Schoen 2013), which created extensive even-aged stands of varying successional stages and value to wildlife (Alaback 1982). Much of the land area in Southeast Alaska, including the entirety of the study area, was part of the Tongass National Forest. Annual precipitation was in excess of 300 cm per year in many areas, with average winter snowfall varying across the region (Shanley et al. 2015). In the study area on Prince of Wales, snow levels were relatively low in comparison with areas of the archipelago farther northward (Shanley et al. 2015). Nevertheless, heavy snowfall has occurred and persisted in the past, and deer populations declined sharply in response (Brinkman et al. 2011).

There were multiple sources of mortality for deer in the study area, primarily human hunters, malnutrition, and predation by wolves (*Canis lupus*) and black bears (*Ursus americanus*—Person et al. 2009; Gilbert 2015). Wolf densities were low on Prince of Wales Island (Alaska Department of Fish and Game 2015), and we observed no predation by wolves on adult study animals (Gilbert 2015). Nevertheless, Sitka black-tailed deer can exhibit antipredator behavior in response to fresh wolf sign even after 100 years of absence, indicating that avoidance of wolf predation risk is likely to continue to affect deer behavior (Chamaillé-Jammes et al. 2014). Bear predation was absent during winter months while bears hibernate, and deer hunting season closes in December. During the course of our study, malnutrition was the major cause of death for adult female deer in winter and occurred primarily during periods with deep snow (Gilbert 2015).

Animal capture and handling.—We captured 62 adult female deer between 2010 and 2012, following procedures described in Gilbert et al. (2014). All captures were carried out with approval of the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC #136040-14) and conformed with guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011). Deer were called using a fawn bleat (the squeaker removed from dog toys), or spotted from a vehicle, and stalked or ambushed on foot. All deer were free-range darted from a distance < 30 m and were immobilized using a mixture of Ketamine and Medetomidine. Deer captures were carried out in 6 watersheds, 3 with extensive timber harvest and 3 with little or no timber harvest, to characterize deer behavior across a range of habitat availability. Each deer was fitted with a GPS tracking radiocollar (Telonics, Isanti, Minnesota) that recorded locations every 2 h for 1 year. For this winter-focused analysis, we considered relocations between 1 January and 1 April of each year. We excluded from analysis 4 deer that died and 1 deer whose GPS collar failed before this winter period, along with an additional deer that resided primarily on state lands where GIS landscape and vegetative data were incomplete or unreliable.

Vegetation and landscape predictive variables.—We considered vegetation classes, topography, landscape variables, and

Table 1.—Groups of spatial predictive variables used in models of spatial selection by adult female deer (*Odocoileus hemionus sitkensis*) in winter. USFS = United States Forest Service.

Variable group	Variable	Description
Vegetation class[a]	Low-volume old growth	Intact forest classified by USFS as unproductive
Vegetation class	Medium-volume old growth	Intact forest classified by USFS as size density 4 or 5
Vegetation class	High-volume old growth	Intact forest classified by USFS as size density 6 or 7
Vegetation class	Young 2nd growth	Clearcut forests, 0–30 years after harvest
Vegetation class	Old 2nd growth	Clearcut forests, > 31 years after harvest
Landscape	Southing	Average degrees that face south (0 = 100% north facing, 180 = 100% south facing) within moving windows
Landscape	Edge density	Density of edges within moving windows
Landscape	Road density	Density of roads within moving windows
Forage	Total biomass	Total biomass of forage plants in winter (kg/km^2) within moving windows
Forage	Forb biomass	Biomass of forbs in winter (kg/km^2) within moving windows
Forage	Shrub biomass	Biomass of shrubs in winter (kg/km^2) within moving windows

[a] Proportion of vegetation classes within moving windows. Windows were set to 100-m-diameter circular buffers.

forage variables in spatial analyses (Table 1). In addition, we considered possible interactions between those predictive variables and daily snow depth across the landscape. Vegetation classes were derived from the community types developed for the Forage Resource Evaluation System for Habitat (FRESH—Hanley et al. 2014) model for predicting forage biomass within deer habitats in Southeast Alaska, created by the United States Forest Service and described in detail by Hanley et al. (2012). We combined several vegetation community types to reduce the numbers of vegetation classes for spatial analyses. Resulting vegetation classes included several old-growth and 2nd-growth forest types, as well as many other naturally occurring vegetation classes (Table 1). Here, we focus on forest vegetation classes only, because forest is fundamental winter habitat for deer in this northern system. Landscape variables included edge and road density and degree of southing (i.e., ranging from 0 if facing north to 180 if facing south; Table 1). We did not include landscape variables used in calculations of snow depth in models (i.e., elevation, aspect, and slope), because snow depth itself was included in all models.

Available forage depends on the height of plants, the snow depth at plant locations, and the resistance of plants to burial (i.e., plants bending under the weight of snow). Although there are several published equations that relate snow depth to forage burial (White et al. 2009; Hanley et al. 2012), we did not explicitly calculate forage burial by snow. Rather, we inferred levels of snow interception, snow accumulation, and duration of burial by 1) using canopy interception of vegetation classes to modify daily snow depth maps used in deer models and then 2) allowing snow depth to modify deer selection for forage and other habitat variables by fitting snow by habitat variable interactions within deer selection models. To create spatial maps of winter-specific total biomass, shrub biomass, and forb biomass, we used the FRESH model values for forage biomass in each community type in winter (Hanley et al. 2014), along with GIS maps of FRESH vegetation community types provided by the United States Forest Service.

Snow depth.—Snow levels can be highly variable across the Southeast Alaskan landscape, with effects of elevation, aspect, slope, and canopy cover. In addition, weather stations were sparsely distributed across the landscape (Simpson et al. 2005), making projections of snow depth to specific locations such as deer GPS relocations difficult. Consequently, we deployed 23 snow stations located systematically within the study area, each consisting of a vertical stake with an array of 3 pendant-style temperature loggers (Hobo tidbit loggers, Onset Computer Corporation, Bourne, Massachusetts) attached at 10, 25, and 50 cm above ground level (henceforth called snow loggers). Snow stations included another pendant logger (at 1 m above ground level) encased in a solar radiation shield (Ambient Weather, Chandler, Arizona) to measure air temperature (Lewkowicz 2008), henceforth called air loggers. Stations were placed in open, flat muskegs or meadows, and at least 25 m from forest edges to avoid potential edge effects on snow depth. Temperatures were recorded every 3 h throughout the year.

We used several filtering criteria to translate temperatures measured by the array of temperature loggers into snow coverage for each logger in the array. For each station, we calculated mean and *SD* of temperature of the air and snow loggers based on a 24-h moving window. The filtering criteria applied to these data included the temperature differential between means of air and snow loggers (i.e., differences > 1°C), and the mean and *SD* of the snow loggers (i.e., $\overline{X} \leq 1.4$°C and *SD* ≤ 0.55°C). These filtering criteria threshold values were developed using the period of 6–24 January 2012, when snow depth was recorded manually once per day during field visits to 10 stations. We tested a wide range of filtering values and chose final filtering values based on classification success (i.e., snow-covered or noncovered in the validation data set). The resulting data, reflecting whether the 10-, 25-, and 50-cm temperature loggers at each station were covered with snow or not, were then translated into minimum snow depths of 0.10, 0.25, or 0.50 m at each station every 3 h.

We calculated daily snow coverage at each station as the median of the 8 minimum snow depths logged each day. Using an equation relating elevation to snow depth developed in Juneau, Alaska (Hanley et al. 2012), we corrected daily snow-level data for elevation to produce sea-level snow equivalents (cm). Subsequently, we interpolated the corrected daily snow levels for each station across the extent of the study area using inverse distance weighting among stations in the gstat

package (Pebesma 2004) in program R (R Core Development Team 2014), at a 30 m × 30 m raster pixel scale. To account for elevation (m), slope (degrees), aspect (degrees), and canopy cover (%), we modified the raster layer of daily snow depth at sea level using linear relationships developed in Southeast Alaska and described in detail in FRESH (Hanley et al. 2012). We applied the FRESH linear relationships described above using raster-based, cell-by-cell regressions and the 30 m × 30 m FRESH vegetation community GIS rasters provided by the United States Forest Service.

Habitat selection by deer.—To evaluate habitat selection by deer, we used the scale of deer movements between relocations (i.e., every 2 h). During winter, deer in the study area should be strongly affected by the cost of movement through deep snow (Parker et al. 1984), which constrains both use and availability of locations. Parker et al. (1996) found that Sitka black-tailed deer in a similar forest environment foraged in bouts typically shorter than 250 min (4 h), with most bouts shorter than 2 h, at the same scale as the movements we define and analyze here. We defined habitat availability using step-selection functions (SSFs—Fortin et al. 2005). SSFs use movements of study animals during discrete time steps to generate used and randomly matched available steps and can compare either line segments between locations (i.e., steps) or the endpoints of segments (i.e., locations) to steps or locations that could have been chosen at that time-step. By using movement patterns to define the set of available steps or locations, the definition of availability is refined and may result in better models of actual selection by animals (Thurfjell et al. 2014). Once matched sets (i.e., strata) of used and available steps are generated for each individual (i.e., cluster), the contrast between use and availability is modeled using conditional logistic regression, to estimate coefficients for the same exponential form as a resource selection function with a log link function:

$$\hat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n)$$

where $\hat{w}(x)$ represents the response variable, the relative probability of a step or location being selected (hereafter, all probabilities of selection discussed are relative). The coefficients, β_n, are estimated by conditional logistic regression (conditioned on step-specific strata) and associated with predictive variables x_n (Fortin et al. 2005). We chose to analyze used and available locations rather than steps between locations because deer likely make circuitous movements or rest between the 2-h relocations, particularly with increasing snow depth (Parker et al. 1996, 1999). We generated 5 available points per used point using matched, randomly chosen turning angles and step lengths, drawn from distributions based on the combined movements of all deer in the study (Thurfjell et al. 2014).

Step-selection functions limit availability to the relatively small spatial scope defined by the scale of the step lengths between GPS relocations. As a result, habitat variables were not available to all deer uniformly. Model fitting is not possible if a covariate is not available to an individual animal, yet Akaike's information criterion (AIC)-based model selection dictates that underlying data (i.e., relocations of individuals)

be identical across the models being compared (Burnham and Anderson 2002; Burnham et al. 2011). Therefore, candidate models were developed within 3 model groups, with subsets of individual deer for each model group based on availability of predictive variables: old-growth forest vegetation classes, 2nd-growth forest vegetation classes, and landscape characteristics (which included forage). We did not add landscape variables to old- or 2nd-growth forest models because the forage biomass measures were strongly correlated with vegetation classes. Whereas all deer had all landscape variables available to them, within the vegetation class variables we subdivided data on females so that each female included in old- and 2nd-growth models had all old-growth or 2nd-growth classes available to them. As a result, landscape model sets included all 56 deer, old-growth vegetation model sets included 41 deer, and 2nd-growth vegetation model sets included 18 deer. We considered all subsets of variables within model groups to produce basic model formulas, and for each basic model formula, we considered 3 versions: with parameters for non-snow variables only; with parameters for non-snow and snow depth; and with parameters for non-snow, snow depth, and interactions between all non-snow variables and snow depth. Including these main and interactive effects resulted in 21 old-growth vegetation models, 9 second-growth vegetation models, and 45 landscape models. In addition, we did not include highly correlated predictive variables ($|r| > 0.7$) in the same models; among highly correlated variables, we used the most predictive variable based on average AIC scores of univariate models across individuals.

We used a 2-step modeling approach, as described by Fieberg et al. (2010). Although mixed-effects models with random effects of individuals are commonly used to account for heterogeneity within and between individual animals (Gillies et al. 2006; Fieberg et al. 2010), such models become complex and difficult to fit when random effects for each spatial covariate (i.e., different coefficients for individuals) are included and number of parameters is relatively large (Craiu et al. 2011). Successful model fitting is yet more computationally challenging when conditional logistic regression with conditioning on each relocation is used (i.e., available points conditional on each used point—Fieberg et al. 2010). Consequently, we followed a series of steps in modeling, with all statistical analyses carried out in program R. First, within each group of models, we fit conditional logistic regression models for each deer, with a unique condition for each relocation and associated available points, using the survival package (Therneau 2014). We fit all models in the group to each individual deer and calculated AIC values and weights (Burnham and Anderson 2002; Burnham et al. 2011) for each individual-level model, and an average AIC weight ($\bar{w}_i$) or each model across individuals. This average AIC weight for given model structure in a group, across individual models, can be expressed as:

$$\bar{w}_i = \frac{1}{n} \sum_{N=1}^{N} \left[\frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta_r\right)} \right]$$

where N is the number of individuals, R is the number of models in the candidate set, and Δ_i is the change in AIC score of model i from the best (i.e., lowest AIC score) model.

Next, to estimate coefficients and *SE*s at the population level, we fit mixed-effects conditional logistic regressions with random coefficients for each individual using the TwoStepCLogit package (Craiu et al. 2011). The TwoStepCLogit statistical package bypasses the computational complexities discussed previously by using a global 2-step approach, first fitting individual-specific parameters (i.e., random coefficients), then estimating population-level parameters using the expectation–maximization algorithm in conjunction with conditional restricted maximum likelihood (Craiu et al. 2011). Because the TwoStepCLogit functions currently do not provide a likelihood

estimate (or similar measure) to the user, we used the values of $\bar{w}_i$ from the individual-level models to rank the level of support for each model. Although we took an all-subsets approach to model evaluation, the inclusion of interactive terms with snow depth in some but not all models in the model sets precluded model averaging because main effects coefficients can be quite different when interaction terms are included compared to when they are not (Arnold 2010; Cade 2015). We therefore present all models with $\bar{w}_i$ greater than 0.10 from each model set in our reported results (Burnham and Anderson 2002).

To evaluate the potential mechanisms driving variation of selection among individual deer, we tested for functional responses in selection of each spatial variable to the availability of that variable. We compared individual coefficients of
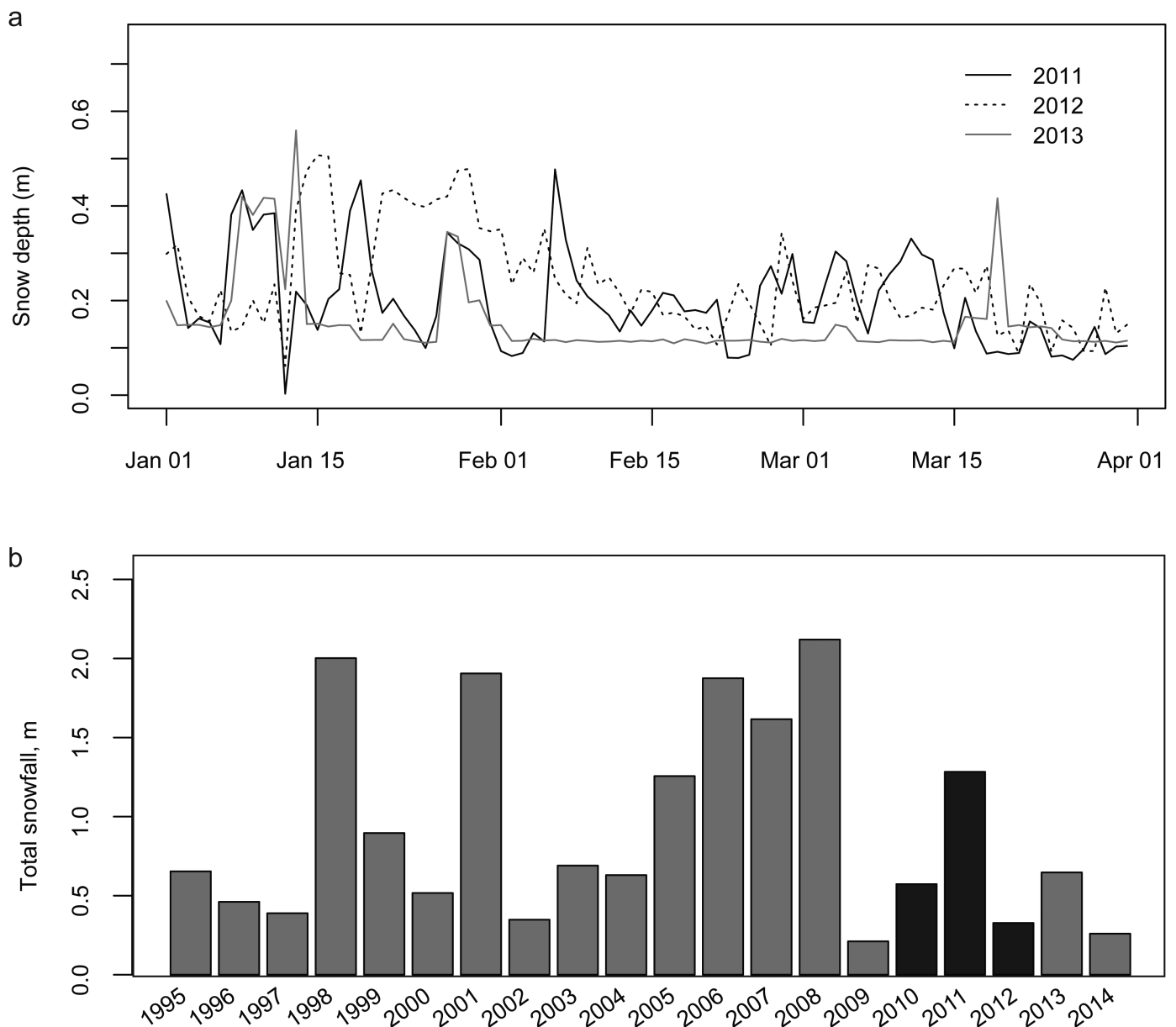
Fig. 3.—Variability in snow depth in the Prince of Wales Island, Alaska, study area. a) Daily mean of snow depths (m) across winter home ranges for female deer (Odocoileus hemionus sitkensis) monitored from 1 January to 1 April during 2011, 2012, and 2013 and b) total annual snowfall at an adjacent long-term weather station from 1995 to 2014, with study winters shown in black.

selection to mean values of the corresponding predictive variable at available points for each individual (Arthur et al. 1996; Moreau et al. 2012; Knopff et al. 2014). As a measure of the functional response in selection, we used the coefficients of individual deer from the best-ranked model in which that coefficient appeared (i.e., random effects plus mean population beta coefficient). In addition, we examined whether covariance of spatial variables, combined with functional responses in selection with changing availability, produced correlated selection for variables that covaried. We tested for associations between individual coefficients and availability using rank-based correlation tests (i.e., Spearman's rho), as some distributions of mean availability of predictive variables across individuals were not normally distributed and sample sizes (i.e., numbers of individuals) were low. Only correlations with $P < 0.10$ are reported as demonstrating a likely association, although given the small sample size, along with the reduced power of Spearman's rho relative to other correlation tests, this might exclude some real associations (type II error).

RESULTS

Patterns in snow depth.—Snow stations with temperature loggers proved effective tools for measuring snow depth, although a number of stations were damaged by bears during summer months and loggers subsequently had to be replaced. Snowfall varied considerable within and across the 3 winters

included in the study, and among deer home ranges (Fig. 3a). Correcting daily snow maps to a universal 100-m elevation, median snow depth across the study area (i.e., central Prince of Wales Island) was 0.13 m (MAD = 0.13) in 2011, 0.17 m (MAD = 0.10) in 2012, and 0.13 m (MAD = 0) in 2013. Snow depths were far more variable in 2011 and 2012 than in 2013. During the 90-day winter study period, median snow depths at 100-m elevation in the study area exceeded 0.25 m for a cumulative total of 21 days in 2011, 25 days in 2012, and 12 days in 2013. Comparing the winters of the study with the past 20 winters based on data from nearby Annette Island weather station, 2012 represented a moderately severe winter in terms of total snowfall (1.28 m), whereas 2011 and 2013 were relatively mild (0.57 and 0.33 m, respectively; Fig. 3b) compared to the 20-year average ($\bar{x}$ = 0.933, SD = 0.64).

Habitat selection by deer.—Deer had short average step lengths between 2-h relocations (median = 48.21 m, MAD = 51 m), and selection varied across old-growth and 2nd-growth forest classes, and by landscape and forage variables. Interactive effects with snow depth were supported for all models we examined (Table 2). Across all models, deer selected against snow depth.

Measures of forage biomass were highly correlated. Shrub biomass was more predictive of deer selection based on AIC scores for univariate models than other measures (ΔAIC = 0.54 for total biomass model, and ΔAIC = 2.13 for forb biomass model); we therefore included shrub biomass as the forage

Table 2.—Coefficients and *SE*s for top-ranked models of habitat selection by deer (*Odocoileus hemionus sitkensis*) in winter on Prince of Wales Island in Southeast Alaska, 2011–2013. Interactive effects with snow depth are indicated with the "×" symbol. Models for each of the landscape, OG, and SG model groups with $\bar{w}_i > 0.1$ are reported, along with the range of individual variability in the top-ranked model (i.e., random β coefficients). OG = old growth; SG = 2nd growth.

| Model group	Variable	Model 1 β (*SE*)	Model 2 β (*SE*)	Model 3 β (*SE*)
Landscape	Edge density	−0.01 (0.01)		
Landscape	Edge density × Snow depth	0.02 (0.02)		
Landscape	Road density	−0.02 (0.01)		
Landscape	Road density × Snow depth	−0.004 (0.02)		
Landscape	Southing	0.002 (0.001)		
Landscape	Southing × Snow depth	0.01 (0.004)		
Landscape	Shrub biomass	0.15 (0.41)		
Landscape	Shrub biomass × Snow depth	−2.39 (1.27)		
Landscape	Snow depth	−1.29 (1.02)		
	$\bar{w}_i$	0.15		
OG	Low-volume OG	−0.06 (0.30)	−0.06 (0.30)	−0.06 (0.30)
OG	Low-volume OG × Snow depth	0.14 (0.62)		
OG	Medium-volume OG	0.08 (0.36)	0.08 (0.36)	0.08 (0.36)
OG	Medium-volume OG × Snow depth	0.58 (0.76)		
OG	High-volume OG	−0.44 (0.35)	−0.44 (0.35)	−0.44 (0.35)
OG	High-volume OG × Snow depth	1.21 (1.07)		
OG	Snow depth	−2.66 (0.89)	−2.66 (0.90)	
	$\bar{w}_i$	0.16	0.15	0.10
SG	Young SG	0.75 (0.38)	−0.48 (0.54)	−0.50 (0.50)
SG	Young SG × Snow depth	−0.86 (1.03)		
SG	Old SG	−0.21 (0.41)	−0.44 (0.41)	−0.54 (0.41)
SG	Old SG × Snow depth	0.31 (1.02)		
SG	Snow depth	−2.22 (0.97)	−2.22 (0.97)	
	$\bar{w}_i$	0.32	0.24	0.17
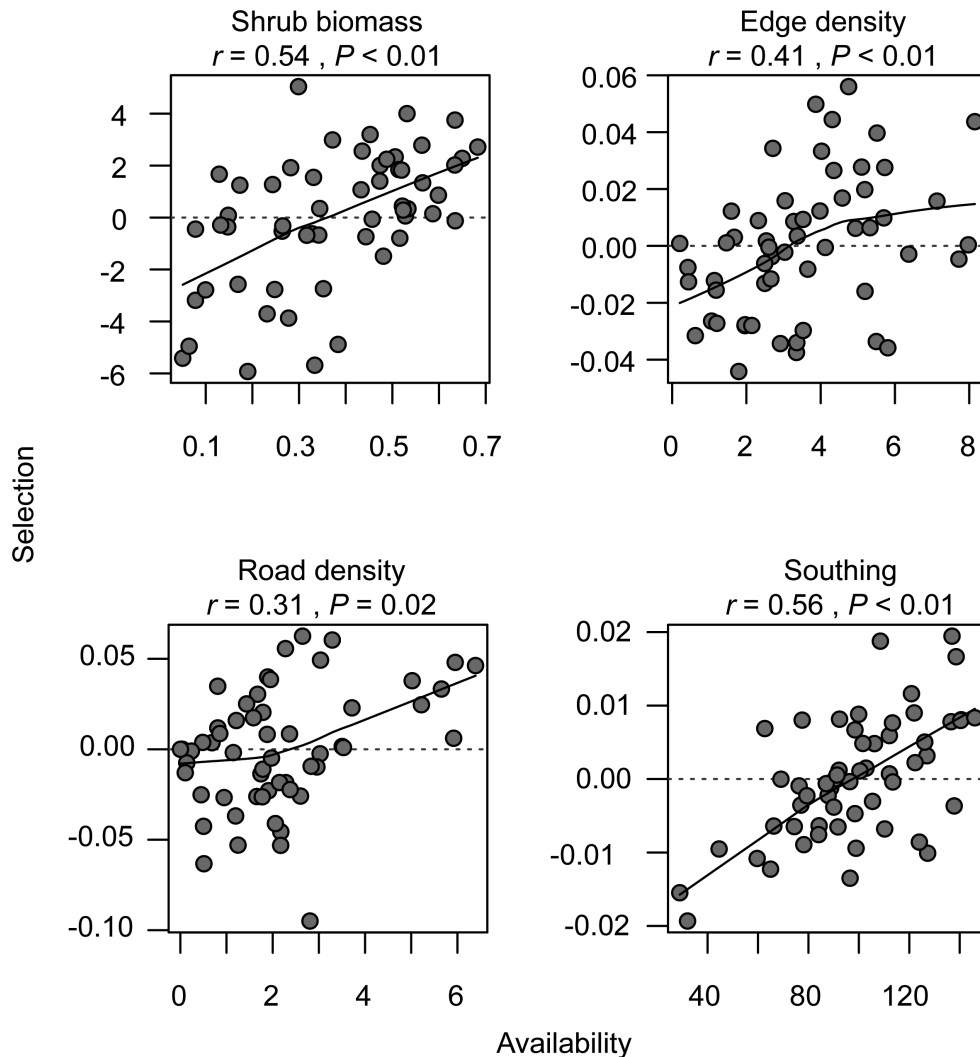
Fig. 4.—Variation among individual deer (*Odocoileus hemionus sitkensis*) in selection (i.e., random effects plus mean population beta coefficient) for each variable versus mean value of the corresponding variable at available locations, with Spearman's rank correlation statistics for each relationship. Smoothed lines (black) were fit with Lowess models. Selection by deer was measured from 1 January to 1 April during 2011, 2012, and 2013 in the study area, located on Prince of Wales Island, Alaska.

variable in landscape models. Among landscape models, the top-ranked model ($\bar{w}_i = 0.15$) included effects of edge density, road density, southing, shrub biomass, and interactive effects of snow depth. In general, deer did not show strong selection patterns for road or edge density at low snow depths, although both main effects were weakly positive (Table 2). As snow depth increased, probability of selection of locations with high road density decreased relative to those with lower road density (Table 2; Supplementary Data SD1). Selection of south-facing slopes was weakly positive at low snow depths, and deer increased selection of south-facing slopes as snow depths increased (Table 2; Supplementary Data SD1). Likewise, selection of locations with high shrub biomass was highly variable at low snow depth but declined relative to those with lower shrub biomass as snow depth increased (Table 2; Supplementary Data SD1). The small magnitudes and large *SE*s of main effects for landscape variables was explained partially by a functional

response in selection, with increased local availability being correlated positively with increased selection (Fig. 4). This positive functional response indicates that as local abundance of a landscape variable increased, deer increased use of that variable disproportionately (i.e., increased selection) at low snow depths. Spearman's rank correlation tests indicated that the positive functional responses were significant, with $r = 0.54$ ($P < 0.01$) for shrub biomass, $r = 0.41$ ($P < 0.01$) for edge density, $r = 0.31$ ($P = 0.02$) for road density, and $r = 0.56$ ($P < 0.01$) for southing.

Deer selection relative to old-growth forest types was also influenced by snow depth (Fig. 5), and the best-supported model ($\bar{w}_i = 0.16$) included all 3 old-growth forest types and snow depth, as well as interactive effects of snow (Table 2). At low snow depths, deer selected variably for high-volume, medium-volume, and low-volume old-growth forest. As snow depth increased, deer selection of locations with more high-volume forest increased. The large *SE*s of the main effects was in part explained
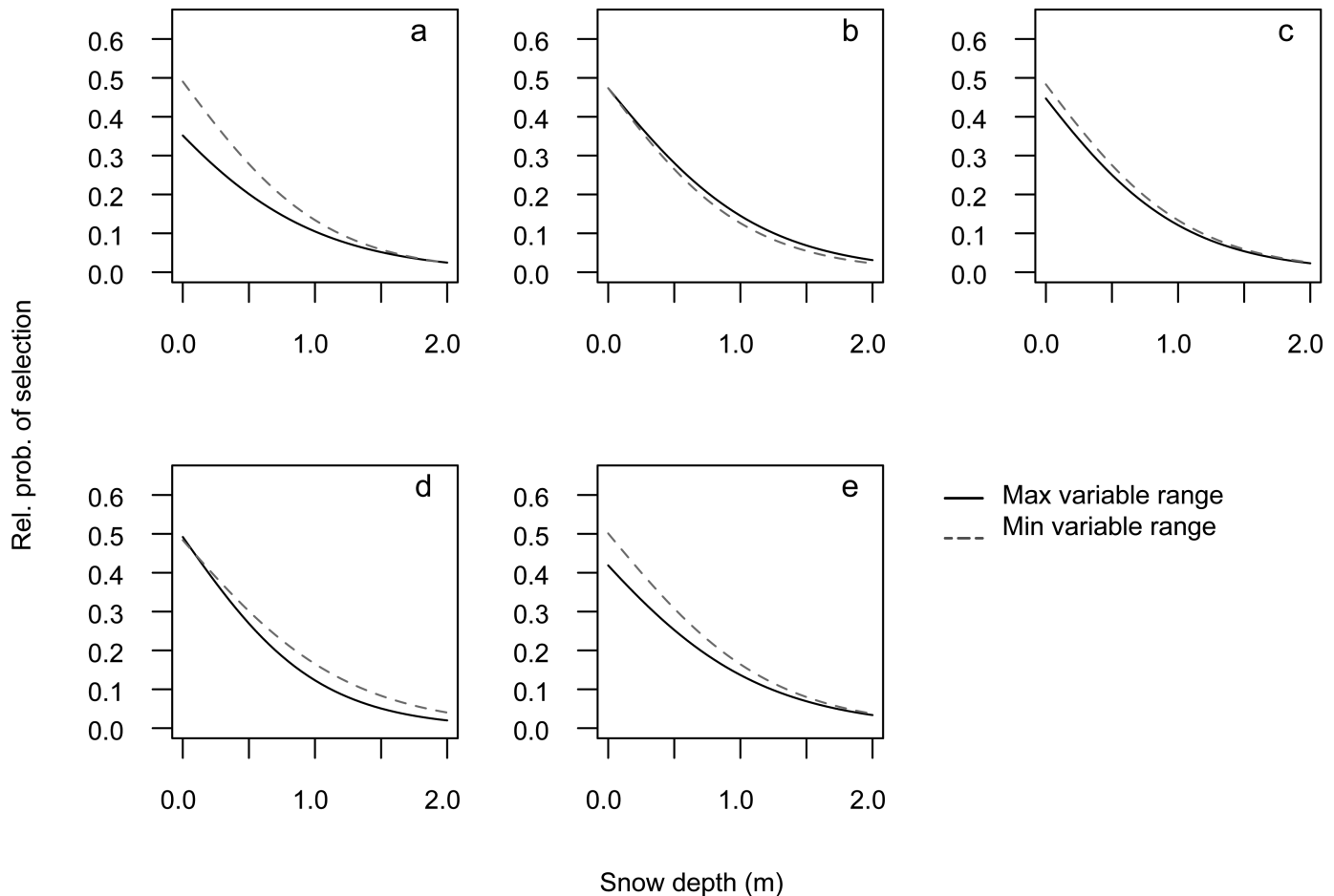
Fig. 5.—Interactive effects of snow depth on selection for old-growth and 2nd-growth forest vegetation classes. Relative probability of selection was calculated by changing snow depth while holding each predictive variable at its maximum value (black line) versus its minimum value (dashed gray line). Probability of selection for a) high-volume old-growth forest, b) medium-volume old-growth forest, c) low-volume old-growth forest, d) young 2nd-growth forest, and e) old 2nd-growth forest. Selection by deer (*Odocoileus hemionus sitkensis*) was measured from 1 January to 1 April during 2011, 2012, and 2013 in the study area, located on Prince of Wales Island, Alaska.

by functional responses to availability of old-growth forest types; when old-growth forest types were common among available locations, deer were more likely to select those old-growth types (i.e., a positive functional response; Fig. 6). Spearman's rank correlation tests indicated that these positive functional responses were significant, with $r = 0.44$ ($P < 0.01$) for low-volume old growth, $r = 0.35$ ($P = 0.02$) for medium-volume old growth, and $r = 0.34$ ($P = 0.03$) for high-volume old growth.

Deer selection of 2nd-growth vegetation classes was highly variable, and the best-supported model ($\overline{w}_i = 0.32$) included effects of young and old 2nd-growth forest, snow depth, and interactive effects with snow depth (Table 2). When snow depth was low, deer selection towards young 2nd growth was highly variable, whereas selection towards old 2nd growth also was variable, but on average slightly negative. As snow depth increased, deer decreased selection of locations with abundant young 2nd growth relative to those with less young 2nd growth and increased selection of locations with abundant old 2nd growth compared to those with less old 2nd growth (Table 2; Fig. 5). In part, the high variability of selection appeared to be

the product of positive, but nonsignificant ($P > 0.10$) functional responses (i.e., random effects; Table 2) between selection and availability of 2nd-growth classes (Fig. 6).

Availability of combined old-growth classes was inversely correlated with availability of young 2nd growth ($r = -0.72$, $P < 0.01$), and with combined old and young 2nd growth ($r = -0.85$, $P < 0.01$), reflecting the reality that timber harvest is often concentrated in specific portions of watersheds, altering the availability of old-growth habitats for deer (Supplementary Data SD2). Correspondingly, across individual deer, the sum of selection coefficients for old-growth classes (i.e., total old-growth selection) was negatively correlated with selection for young 2nd growth ($r = -0.68$, $P = 0.01$), old 2nd growth ($r = -0.55$, $P = 0.05$), and the sum of selection coefficients for 2nd growth ($r = -0.68$, $P = 0.01$; Supplementary Data SD2).

DISCUSSION

Our results add to a growing body of work showing that ecological dynamics, including dynamic weather conditions (van
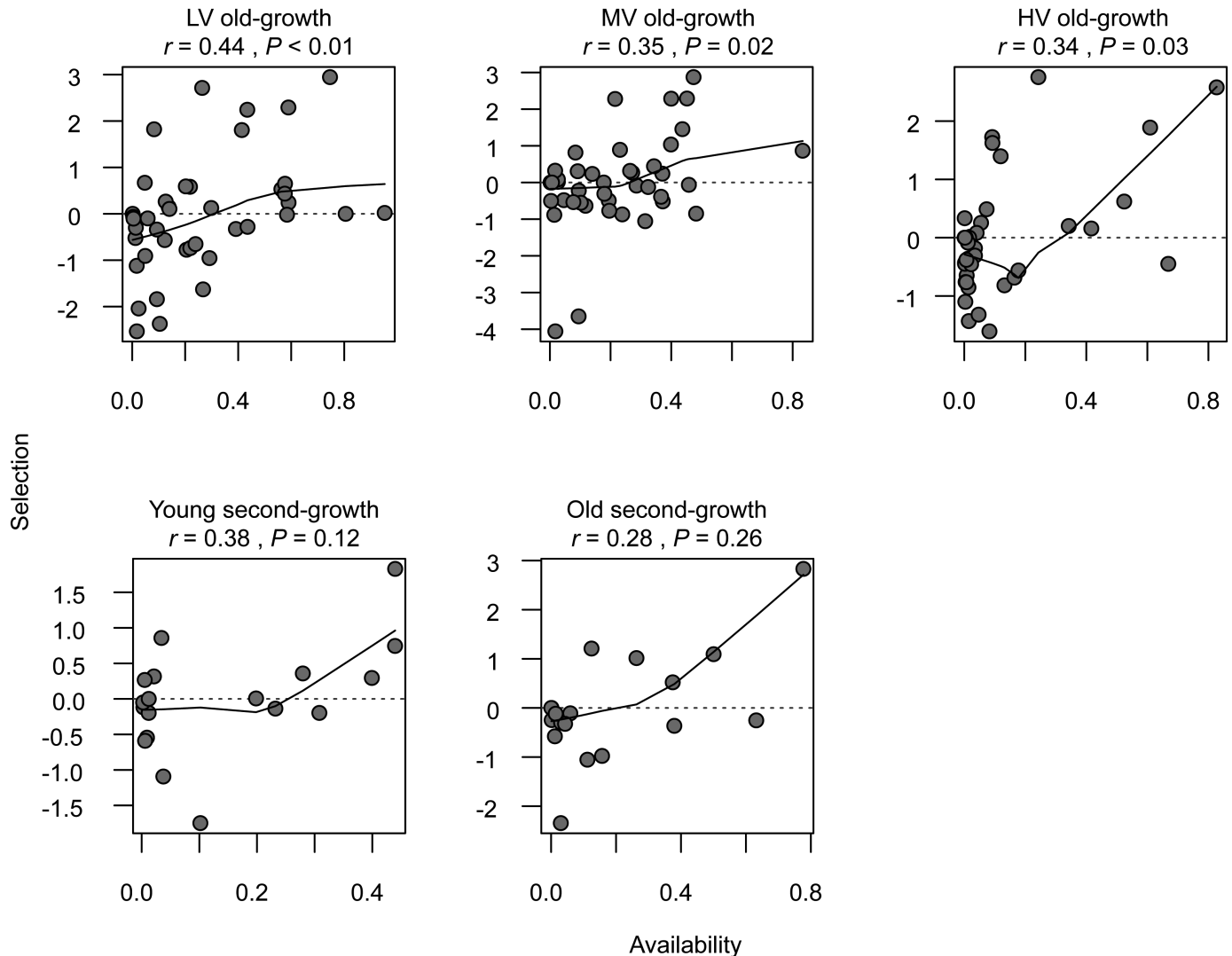
Fig. 6.—Functional responses of deer (*Odocoileus hemionus sitkensis*) to old-growth and 2nd-growth classes of forest indicated by variation among individuals in selection (i.e., random effects plus mean population beta coefficient) for each variable and the mean value of the corresponding variable at available points, with Spearman's rank correlation test statistics for each relationship. Smoothed lines (black) were fit with Lowess models. Selection by deer was measured from 1 January to 1 April during 2011, 2012, and 2013 in the study area, located on Prince of Wales Island, Alaska.

Beest et al. 2012; Long et al. 2014), changing animal density (Mcloughlin et al. 2006; van Beest et al. 2014), and resource availability (as previously discussed), can strongly affect animal selection patterns (Mcloughlin et al. 2010). We found that deer movements in winter were strongly affected by snow depth, and snow depth determined the direction and magnitude of selection for vegetation, forage, and landscape variables. Indeed, snow depth was a far stronger driver than the measures of forage biomass we considered. However, we did not measure forage depletion, which has been shown to cause switching of selection in other temperate herbivores in winter (van Beest et al. 2010), nor did we analyze selection when resting versus foraging (Parker et al. 1999; Frair et al. 2005; Godvik et al. 2009).

Selection was highly variable among individuals and appeared to be largely the consequence of flexible habitat selection, with deer increasingly selecting 2nd-growth forests as availability

increased and availability of old-growth forests correspondingly declined (Supplementary Data SD2). Across predictive variables, selection increased with local availability (Figs. 4 and 6). These functional response patterns, in which selection varies with availability, have recently been demonstrated in several other taxa, including large carnivores (Fortin 2010; Knopff et al. 2014), multiple large herbivore species (e.g., Osko et al. 2004; Godvik et al. 2009; Moreau et al. 2012; Roever et al. 2012), and birds (Gillies and St. Clair 2010). Such behavioral flexibility is presumably adaptive in many situations. For herbivores contending with deep snow, as our deer did, used locations are likely selected from a very restricted set of locally available habitats. This restricted local availability could explain the positive relationship we observed between availability of habitat types and selection of those types, with deer selecting locally abundant types and avoiding isolated patches. In the winter landscape, when cost of movement is potentially high, selection of distant,

isolated patches carries risks, as deer can become stranded by rapid snow accumulation in an old-growth "island" with dwindling forage (Kirchhoff 1994).

The use of time-varying environmental variables to model the response in selection by animals has the potential to unify previously thorny ecological questions if previous, conflicted results were artifacts of static models of the environment. For example, in our study system, the importance of productive old-growth forest to deer in Southeast Alaska compared to other habitat types remains contentious (Schoen and Kirchhoff 1985; Yeo and Peek 1992; Doerr et al. 2005; Person et al. 2009). Here, we resolve these apparently conflicting conclusions using time-varying snow depth, revealing that snow depth is the dominant driver of deer selection in winter. Moreover, deer selection of other habitat variables commonly considered important in this system was weak and contingent on snow depth when snow depth was included in models. Individuals also increased selection of 2nd growth as availability of old growth declined and availability of 2nd growth increased. Thus, previous differences in winter habitat selection by deer across studies likely were because of differences in snow depth and in habitat availability (i.e., landscape configuration and composition).

Our analysis was limited by several factors. First, we analyzed habitat selection at a single spatial scale. Deer likely select at multiple scales (Kie et al. 2002), and selection of seasonal (winter) home ranges at the landscape scale is likely to be important in determining deer survival as well (DeCesare et al. 2013). For example, Farmer et al. (2006) found that landscape variables within 500-m buffers best explained survival patterns in yearling and adult females. Analysis of selection in winter within home ranges is an important next step for modeling habitat suitability for deer under future climate change scenarios (Cherry et al. 2010; Shanley et al. 2015). Secondly, we did not incorporate predation risk as a factor driving habitat selection by deer, but Farmer et al. (2006) documented both positive selection for and increased risk associated with young 2nd-growth forest. Real or perceived predation risk can render otherwise high-quality habitat less preferable to ungulates (Frair et al. 2005; Ford et al. 2014; Kauffman et al. 2014), or alternatively, ungulates may use high-risk winter habitat to minimize energetic costs (Brown and Kotler 2004; Villepique et al. 2015). Similarly, we did not incorporate variability in stand productivity, which should influence successional speed and outcomes, because such data were lacking. Finally, we did not record density of deer during the course of this study, yet high animal density can lead to more generalized selection patterns (Mcloughlin et al. 2006; van Beest et al. 2014). Although deer typically have occurred at lower densities in 2nd-growth habitats compared to old-growth habitats (Brinkman et al. 2011), carrying capacity during winter also is generally lower in 2nd-growth habitat (Suring et al. 1993), and thus the relation between selection and abundance of 2nd growth could be a product of density relative to carrying capacity.

Our results indicate that the timing and distribution of timber harvest matters to deer movement and thus to habitat connectivity in winter. If large proportions of habitat relative to home range size of deer have been clearcut, or if remaining old growth is primarily low-volume, unproductive forest, deer will not be able to move into productive old-growth types as snow depth increases. Additionally, if high-quality, high-volume old growth is preserved but patchily distributed, deer appear less likely to select it. Although deer increased selection of old 2nd growth as snow depth increased, and were more likely to use old 2nd growth as it was increasingly available, old 2nd-growth stands have very low forage available to deer. Deer may use old 2nd growth as a matrix through which to move at high snow depths, but energy budgets of these individuals will likely be negatively affected if productive old growth is not available. Restoration of deer forage within old 2nd growth using small selectively cut patches has been proposed, wherein forage regenerates within and along the edges of clearings and is partially available during winter due to edge effects (Alaback 2010). Currently, there are no data for deer use of such treatments and their value is purely speculative. Further research into the design of such treatments and the preferences of deer across designs is crucial for maintaining deer populations through harsh winters in landscapes dominated by even-aged timber harvest.

Context-dependent selection patterns, such as the snow- and availability-dependent patterns we document here, likely are widespread among many wildlife species, and increased monitoring and incorporation of high-resolution environmental and habitat data into habitat selection studies could improve both ecological inference, and management and conservation outcomes such as designation of suitable habitat. Indeed, direct incorporation of environmental variability into selection studies is critical in the context of widespread environmental changes and increasing alteration and reduction of habitat facing many wildlife populations. Given the strong, context-dependent selection patterns likely for many animals, static models are unlikely to predict habitat suitability in a changing landscape. However, dynamic models may offer a solution to predicting future animal behavior under changing environmental conditions, providing a valuable tool for conservation and ecological inquiry.

Supplementary Data

Supplementary Data SD1.—Interactive effects of snow depth on selection for landscape variables. Relative probability of selection was calculated by changing snow depth while holding each predictive variable at its maximum value (black line) versus its minimum value (dashed gray line). Shown are probability of selection for a) southing, b) edge density, c) road density, and d) shrub biomass. Deer selection was measured from 1 January to 1 April during 2011, 2012, and 2013 in the study area, located on Prince of Wales Island, Alaska.

Supplementary Data SD2.—Covariation between predictive variable availability and selection. Covariation shown between a) availability of sets of spatial variables and b) selection by individual deer for the same sets of variables. Shown with Spearman's rank correlation test statistics for each relationship. Smoothed lines (black) were fit with Lowess models. Deer selection was measured from 1 January to 1 April during 2011,

2012, and 2013 in the study area, located on Prince of Wales Island, Alaska.

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