Long- and short-term temporal variability
in habitat selection of a top predator

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Abstract. Considerable theory explains the importance of understanding temporal variation in ecological processes. Nevertheless, long-term variability in habitat selection is rarely assessed or even acknowledged. We explored temporal variability in the habitat selection of a top-predator, the wolf (*Canis lupus*), at two time scales: interannual and seasonal variability. To do this, we developed resource utilization functions to relate wolf habitat selection to environmental variables in different years and seasons. We used radiotelemetry data collected from a wolf population in Yellowstone National Park during a 10-year period (1998–2007) and added a Year variable in the models to account for interannual variation in the studied processes. We also used a three-year data set (nested within the 10-year data set) to incorporate additional variables in the models and test for differences in short- and long-term patterns of habitat selection. Wolves exhibited seasonal variation in habitat selection with respect to distance from roads, elevation, openness, and habitat type. Habitat selection was considerably more complicated during the winter compared to summer, when wolves only selected habitat based on distance from roads. We detected clear patterns of habitat selection in the three-year data set that could not be detected in the 10-year data set, despite the longer data set had more statistical power for pattern detection. This observation is likely the result of the longer data set being comprised of several shorter-term and countervailing patterns. This explanation is also consistent with having detected significant year effects in the 10-year data set. Insomuch as habitat selection is important to conservation and management, this research is significant for demonstrating the different impressions that can be given by short-term and long-term studies. It may be common for short-term data sets to suggest patterns of habitat selection that do not prevail over longer periods of time.

Key words: *Canis lupus*; interannual variability; long-term series; predator-prey systems; resource selection; seasonal habitat selection; utilization distribution; Yellowstone National Park.

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INTRODUCTION

Animal behaviors are often subject to changes over time which result from, for example, the life stages of the animal, changes in the environment in which it lives, and its relationship with conspecifics or predator/prey. Among other animal behaviors, habitat selection is a well-

studied example of how animals can adapt their behavior to a changing environment or a change in their needs. The literature is filled with examples of how habitat selection varies among seasons (see e.g., Penne and Pierce 2008, Blanchfield et al. 2009, Zweifel-Schielly et al. 2009, Klingbeil and Willig 2010, Rasmussen and Litzgus 2010, Basille et al. 2013) or time of the day (see e.g., Dickson et al. 2005, Godvik et al. 2009). Nevertheless, animal needs and resources availability can also change from one year to the next, thus possibly generating interannual variability in habitat selection (Schooley 1994, May 1999). Analyzing habitat selection over short periods of time may therefore provide a biased understanding of the habitat needed by an animal. However, assessments of how habitat selection varies among years are rare and habitat selection studies are often conducted over short periods of time (but see Szaro et al. 1990, Johnson et al. 2002, Mobaek et al. 2009). We conducted a literature review of papers on habitat-related research from top-ranked ecology journals for the past decade (see Appendix for details). That search resulted in 84 empirical assessments of habitat selection, of which 11.9% had collected data from only a single year. Twenty-one percent had collected data over a time span of between two and seven years. While most (70.5%) of those papers failed to consider possible variations between years, one might not expect to detect such variability with so few years of data. Of the 13 papers that collected data for more than 7 years, only four considered in some way the long-term nature of the data. One analysis treated year as a random effect only to ensure that other portions of the model were appropriate (Loe et al. 2006), two other analyses used models built from one time period to provide statistical validation for models constructed from another time period (Fauchald et al. 2002, Aldridge et al. 2012), while the fourth analysis included year as a covariate in the models (Whittington et al. 2011).

Many species change their selection of habitat based on changing availability of habitat resources or varying environmental pressures both in the long-term (year-to-year variation) and in the short-term (seasonal or daily variation). Mauser et al. (1994) divided the brood period of mallards (*Anas platyrhynchos*) in two seasons to account for differences in water availability and vegetation. Pauley et al. (1993) accounted for changes in snow depth for the habitat selection of white-tailed deer (*Odocoileus virginianus*) dividing the winter season in three shorter periods. Szaro et al. (1990) determined that habitat selection of forest birds changes over the years because of varying climatic conditions and Marks and Marks (1988) found that different habitats are used by Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) in different years in order to adapt to the changing food availability. Human disturbances can also change over time, thus influencing the availability of high-quality habitats. Singh et al. (2010) found that saiga antelopes shifted the location of their calving sites in the last four decades in response to increased human disturbance. Changes in habitat selection can also result from different activities performed by the animal, e.g., mating and young-rearing. Caribou (*Rangifer tarandus*) of the Northwest Territories, Canada avoided high-quality habitats near human infrastructures during the post-calving season, but did not during spring and fall migrations (Johnson et al. 2005).

Wolves (*Canis lupus*) are defined as opportunistic predators and are habitat generalists (Mech and Boitani 2003). Hence, wolves may adapt their habitat selection across years and seasons with variable resource availability. Habitat selection of wolves is known to vary between summer and winter (Mladenoff et al. 1995, Ciucci et al. 2003, Arjo and Pletscher 2004, Oakleaf et al. 2006, Hebblewhite and Merrill 2008, Latham et al. 2011). For example, wolves avoid high elevations in winter, but do not prefer or avoid them during summer (Milakovic et al. 2011, Whittington et al. 2011). Roads are also selected for, avoided, or ignored depending on the season (Latham et al. 2011, Milakovic et al. 2011, Whittington et al. 2011). That seasonal variation is likely attributable, in part, to the summertime rearing of pups, which are less mobile and require protection (Jędrzejewski et al. 2001, Mech and Boitani 2003, Merrill and Mech 2003). Important variation in habitat selection is also likely to occur at finer temporal scales than is typically examined (e.g., Milakovic et al. 2011, Basille et al. 2013). One plausible source of seasonal variation in wolf habitat selection is the seasonal variation in the habitat selection and body condition of wolves'

prey (Mao et al. 2005, Metz et al. 2012). Differences in the physical conditions of wolves' prey between early and late winter may be as important as differences between summer and winter. Prey are in considerably better condition and less vulnerable to predators during early winter than during late winter. Seasonal differences in prey condition certainly affect kill rates (Metz et al. 2012), and are likely to affect habitat selection.

The aim of this study was to determine if changing availability in habitat resources determined an interannual and seasonal change in wolf habitat selection. We examined temporal variability among two periods (a three-year period and a 10-year period) and among three seasons, summer (April–September), early winter (October–December), and late winter (January–March). Data collected from radiocollared wolves in Yellowstone National Park and models of habitat selection were used to assess wolf habitat selection in each year and season, at a territory level (Johnson 1980). We conducted these analyses on data collected throughout a 10-year period (1998–2007), and on a subset of those data, spanning a three-year period (2000–2002). The three-year data set was valuable for two reasons. First, for those three years we had information on the spatial distribution of elk (Cervus elaphus), which are the primary prey for these wolves (Smith et al. 2004). The sites where wolves kill prey seem to be influenced, not so much by the presence of elk, but instead by the presense of habitats that increase the probability of a successful kill (Bergman et al. 2006, Kauffman et al. 2007). Nevertheless, the extent to which wolves' habitat preferences correspond with overall elk distribution remains unclear. Second, the three-year data set gave us the opportunity to compare short- with long-term habitat selection. Comparing results from the three-year period with the 10-year period was extremely valuable because it allowed us to assess interannual variability in habitat selection and verify the applicability of results obtained from short-term studies to longer time periods.

Study Site

The Northern Range of Yellowstone National Park is an area of approximately 1500 km^2,

situated in the northern part of the park and including some land outside the park boundary (Lemke et al. 1998). Elevation ranges between 1500 and 3200 m (80% of the area has an elevation between 1800 and 2500). An average of 25 cm of precipitation falls every year, a third of it falling as snow (Farnes et al. 1999). Valley bottoms in the eastern and north-western part of the Northern Range are characterized by grasslands and shrub steppe. The most common species are big sagebrush (Artemisia tridentata) and Idaho fescue (Festuca idahoensis) (Despain 1990). Forests are predominant in the valley bottoms of the central part of the Northern Range and at higher elevations throughout the area. Lodgepole pine (Pinus contorta) is the predominant species, but some forests also include subalpine fir (Abies lasiocarpa), Engelmann spruce (Picea engelmannii), and whitebark pine (Pinus albicaulis). Aspen (Populus tremuloides) stands are becoming more common in the park, due to the wolf pressure as a predator that keeps elk far from riparian zones (Ripple and Larsen 2000). Primary roads are open to traffic year around and more than 75% of the Northern Range is closer than 7 km to these roads. Moreover, 97% of the Northern Range is closer than 5 km to any main watercourse.

In the Northern Range, elk are the main prey of wolves (Smith et al. 2004). Other ungulates are present, such as bison (Bison bison), moose (Alces alces), and mule deer (Odocoileus hemionus) (Metz et al. 2011).

Data Sources

Wolf location data.—The data were collected between 1998 and 2007 from 289 wolves wearing VHF radiocollars (Telonics, Inc. [Mesa, AZ]) and between 2001 and 2007 from 34 wolves wearing GPS (Global Positioning System) radiocollars (Televilt [Lindesberg, Sweden], Telonics, Inc. [Mesa, AZ], and Lotek [Newmarket, ON, Canada]). GPS radiocollars collected wolf locations automatically every 30 minutes in the summer and every 3 hours in the winter, during both day and night time. GPS locations were also collected from VHF-collared wolves from fixed-wing aircraft that located wolves once every one or two days during winter studies (in March, and between mid-November and mid-December) and

approximately once per week during the rest of the year. Additional details on capture, handling, and location of wolves are available in Metz et al. (2012).

Because locations gathered from VHF-collared wolves were collected during sunlight hours, we sampled locations collected from GPS radio-collars to include only daylight hours. To avoid temporal correlation between locations collected in the same day from different members of the same wolf pack, one location per pack per day was randomly selected for the early winter and late winter seasons. Because wolves can cover their entire territory within 24 hours (Mech 1970), locations collected more than 24 hours apart are unlikely correlated to each other (Otis and White 1999). Because packs are less cohesive during the summer (Metz et al. 2012), and form smaller groups that travel independently within the pack territory (Mech and Boitani 2003), one location per group per day was sampled for the summer data set. These random selections were performed with the extension Hawth's Analysis Tools for ArcGIS (Beyer 2004).

Habitat data.—Habitat characteristics and topographic data were extracted from the Greater Yellowstone Ecosystem GIS coverages of elevation (elev), slope (slope), habitat openness (open), distance from rivers (rivers), distance from primary roads (roads), snow water equivalent (SWE, Farnes and Romme 1993), and vegetation type (veg). All those landscape characteristics are known drivers of wolf habitat selection and their relationship with prey (Mao et al. 2005, Kauffman et al. 2007, Hebblewhite and Merrill 2008, Houle et al. 2010, Latham et al. 2011, Milakovic et al. 2011, Whittington et al. 2011). Vegetation type was represented by a land cover coverage created in 2001 by the Multi-Resolution Land Characteristics Consortium (MRLC, http://www.mrlc.gov/nlcd_multizone_map.php). This coverage has a 30-m cell resolution and 19 vegetation classes, of which 15 are present in the park. We reclassified the vegetation coverage to six categories: herbaceous (including barren land, grassland/herbaceous, sedge/herbaceous, and pasture hay), forest (including deciduous, evergreen, and mixed forest), shrub, wetlands (including woody and emergent herbaceous wetlands), open water, and developed (including all four "developed" categories of the original data set). Habitat openness

was calculated by Mao et al. (2005). This coverage represents the percentage of open-habitat pixels at a distance smaller than 400 m from each grid cell (25-m cell resolution). Elevation (in meters) and slope (in degrees) were obtained from a 30-m Digital Elevation Map (DEM). Distance from roads and rivers (in meters) were calculated as the Euclidean distance between each grid cell (25-m cell resolution) and the nearest primary road or major watercourse (defined as a watercourse longer than 20 km). A 30-m buffer was drawn around each linear feature (road or river) prior to developing distance from roads and rivers maps. The Yellowstone snow model (Wockner et al. 2002) was used to develop a snow map representing SWE in mm for each early winter and each late winter.

In addition to the above described data, maps of the spatial distribution of elk abundance were also developed using resource selection functions presented in Mao et al. (2005), specifically the Post-wolf-W model (following Chetkiewicz and Boyce 2009). The data required to construct these maps were only available for a three-year period (summers 2000–2002, late winter 2001 and 2002, and early winter 2000 and 2001).

ANALYSIS

To assess seasonal and interannual differences in wolf habitat selection, sets of resource utilization functions, RUFs (sensu, Marzluff et al. 2004) were constructed and compared. These RUFs were developed for 10 packs observed over a 10-year period (1998–2007) and for a subset of that sample involving six packs observed over a three-year period (2000–2002). The smaller sample was valuable because that is the period of time during which we had data on the spatial distribution of elk, which is presumed to be an important aspect of wolf habitat selection (Mech 1970, Fritts et al. 1994, Mladenoff et al. 1995).

Resource utilization functions.—Each RUF was a mixed-effect regression model with utilization distribution (UD) values as the response variable and habitat characteristics as candidate predictor variables. A UD is a probability density function ($\hat{f}_{UD}(x, y)$, where x, y represent a location) describing how intensely an animal uses each part of its territory (Seaman and Powell 1996).
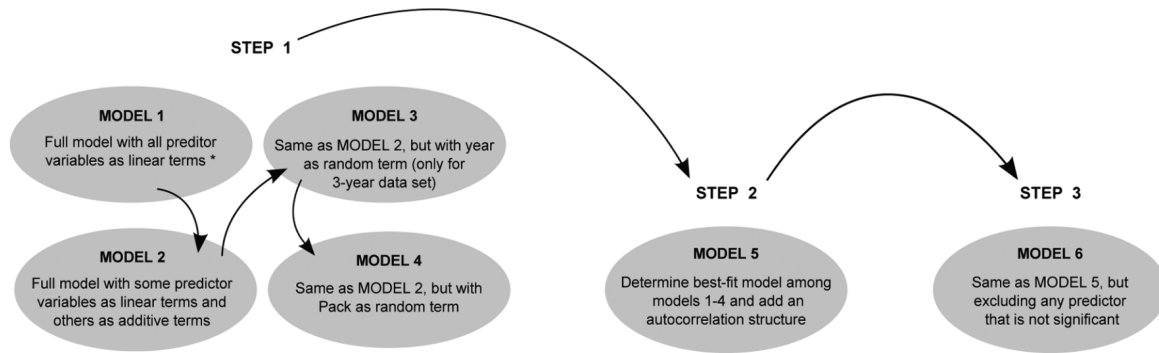
Fig. 1. Flowchart representing the model selection procedure used for each season (summer, early winter, and late winter) and time period (three- and 10-year data set). For a detailed description of the predictor variables see the *Analysis* section. *Because of multicollinearity problems, Snow Water Equivalent was dropped from the winter models (both in the three- and 10-year analyses) and elk from the summer models of the three-year analysis (the elk variable was not available for the 10-year data set). In the 10-year analysis, Year was included from the beginning as a fixed term.

The UDs were estimated using wolf radiotelemetry data and the fixed kernel technique (Seaman and Powell 1996, Kernohan et al. 2001). Radiotelemetry locations representing extraterritorial forays were discarded from the analysis (Messier 1985). The plug-in method for bandwidth selection (Wand and Jones 1995, Gitzen et al. 2006), available in the *ks* package for R 2.15.0 (R Development Core Team 2013) was used. The outer 5% of the UDs was removed in ArcGIS, because the tails of a distribution are typically less reliably estimated (Vanak and Gompper 2010). Following Kertson and Marzluff (2011), the UDs were then changed from density functions to volume, so that the UD values ranged from 0 to 95, where 0 represents no use. Each UD was specific to a particular pack, year, and season (i.e., early winter [E], late winter [L], and summer [S]). Fifteen wolf packs had enough locations (>30) from which to build UDs (Seaman et al. 1999).

Each RUF was computationally complex, including random effect terms, additive terms, spatial autocorrelation functions, and a large sample size. This complexity caused the *mgcv* and *nlme* packages in R 2.15.0 (R Development Core Team 2013) to abort before completing the computations. Consequently, a stratified subsample was drawn from the full sample. In particular, the range of observed UD values was divided into bins (i.e., 6–15, 16–25, . . . , 86–95). UD values between 0 and 5 were discarded (since they represent extremely low use areas). For each pack/year/season, a sample of 200 observations was created from each bin, giving a total of 1800 observations per pack/year/season. Once these data were pooled together by season, the subsample was still too large. Therefore, the same subsampling procedure was applied a second time. The analysis could be computed after reducing the three-year data set to 1800 observations per season, and after reducing the 10-year data set to 3600 observations per season.

Analysis of the three-year data set.—For the three-year data set, which included the spatial distribution of elk, three sets of models were built, one for each season. Each model was evaluated based on *p* values, Akaike Information Criterion (AIC, Burnham and Anderson 2002), and diagnostic tools such as residual plots.

More specifically, several models were built for each season with the purpose of identifying the most parsimonious structure with respect to additive and random-effect terms (Fig. 1). Following Zuur et al. (2009), these assessments were made while including all the candidate predictors. In particular, four of the models for each season were characterized by including: (1) only linear terms (we denote these models as L1, S1, and E1; see for example Table 1), (2) linear terms for most variables and additive terms calculated from cubic regression splines for those variables

Table 1. Performance of resource utilization functions describing wolf habitat selection in the Northern Range of Yellowstone National Park, for a three-year period (2000–2002). Sample sizes were $n = 1800$ from 4 packs for late winter, $n = 1797$ from 5 packs for summer, and $n = 1799$ from two packs for early winter. Each column describes the features of each model. Linear indicates models comprised only of linear terms, and Additive indicates models for which apparently non-linear relationships were described by additive terms. A checkmark in the Correlation function column indicates models that include a term to account for spatial autocorrelation. Cells without a check in the All Predictors column indicate model for which non-significant terms ($p > 0.05$) were removed. Δ_i denotes the difference in AIC (Akaike Information Criterion) compared to the lowest scoring model, and w_i denotes AIC weights.

Model	Season	Model type	Random intercepts	Correlation function	All predictors	Δ_i	w_i
L1	Late winter (Jan–Mar)	Linear	None		✔	3022.16	0.00
L2	Late winter (Jan–Mar)	Additive	None		✔	2840.51	0.00
L3	Late winter (Jan–Mar)	Additive	Year		✔	2831.99	0.00
L4	Late winter (Jan–Mar)	Additive	Pack		✔	2815.58	0.00
L5	Late winter (Jan–Mar)	Additive	Pack	✔	✔	0.00	1.00
L6	Late winter (Jan–Mar)	Additive	Pack	✔		229.23	0.00
S1	Summer (Apr–Sept)	Linear	None		✔	2221.11	0.00
S2	Summer (Apr–Sept)	Additive	None		✔	2102.14	0.00
S3	Summer (Apr–Sept)	Additive	Year		✔	2095.71	0.00
S4	Summer (Apr–Sept)	Additive	Pack		✔	1982.39	0.00
S5	Summer (Apr–Sept)	Additive	Pack	✔	✔	6.14	0.04
S6	Summer (Apr–Sept)	Additive	Pack	✔		0.00	0.96
E1	Early winter (Oct–Dec)	Linear	None		✔	682.45	0.00
E2	Early winter (Oct–Dec)	Additive	None		✔	575.55	0.00
E3	Early winter (Oct–Dec)	Additive	Year		✔	589.90	0.00
E4	Early winter (Oct–Dec)	Additive	Pack		✔	586.98	0.00
E5	Early winter (Oct–Dec)	Additive	Pack	✔	✔	4.50	0.10
E6	Early winter (Oct–Dec)	Additive	Pack	✔		0.00	0.90

that exhibited signs of non-linearity (see page 43 in Zuur et al. 2009; Models L2, S2, and E2), (3) linear terms, additive terms, and a random intercept to account for a year effect (L3, S3, E3), and (4) linear terms, additive terms, and a random intercept to account for a pack effect (L4, S4, E4). For late winter and summer, the fourth model outperformed the other three models (Table 1). Nevertheless, for early winter, model E2 performed best. To make the models comparable and to avoid the computational difficulties that were encountered when applying a spatial autocorrelation function to a fixed-effect additive model, we proceeded with the fourth model (E4) also for early winter. As such, for each season a fifth model was built that included all the terms of the fourth model, plus a spatial autocorrelation structure applied to the model residuals, with Pack as a grouping factor (L5, S5, and E5). The spatial autocorrelation structure was needed because of the potential bias that could result from the spatial nature of our observations, as confirmed by a semivariogram of the residuals. The fifth model outperformed all the others. The last model was characterized by the same basic structure, but excluded any predictor that was not statistically significant (L6, S6, and E6). All generalized additive fixed and mixed-effect models (i.e., all models, except L1, S1, and E1; Table 1) were developed with the *mgcv* package for R (R Development Core Team 2013).

The models were also inspected for outliers and the predictor variables for multicollinearity. Elevation (elev) was collinear with SWE ($r = 0.84$ for late winter; $r = 0.89$ for early winter) and with elk during the summer ($r = 0.81$). For this reason, we dropped SWE from the winter models and elk from the summer models. We retained elev, rather than SWE and elk, to facilitate comparisons among seasons. One observation was identified as outlier in early winter (Bonferroni p-value < 0.05). Omitting this observation reduced the size of the early winter sample to 1799 observations. Using the *corStruct* set of functions available in R to add a spatial autocorrelation structure to the residuals of our top models revealed that the summer data set contained three pairs of observations with the same spatial coordinates. Since the *corStruct* functions do not allow for zero distances between

Table 2. Coefficients (β), standard errors (SE) and p values (p; bold if statistically significant) for the best-performing models of wolf habitat selection (see Tables 1 and 3). This table represents six models, one for each season (based on the three and 10-year data set, respectively). Inconsistencies (in terms of statistical significance) between the two data sets are underscored. The categories of the veg predictor variable are marked with † (the reference category is developed). The reference category for Year is 1999 in late winter and 1998 in summer. Variables marked with ‡ are described by an additive term.

Variable	Data	Late winter β (SE)	p	Summer β (SE)	p	Early winter β (SE)	p
Intercept	10 years	28.62 (4.49)	**$<10^{-4}$**	30.88 (2.21)	**$<10^{-4}$**	23.07 (2.99)	**$<10^{-4}$**
	3 years	−18.19 (14.37)	0.21	5.3 (8.1)	0.51	16.24 (3.2)	**$<10^{-3}$**
Year 1999	10 years			−3.95 (1.19)	**$<10^{-3}$**	…	…
Year 2000	10 years	0.3 (1.45)	0.83	−2.24 (1.19)	0.06	…	…
Year 2001	10 years	5.79 (1.54)	**$<10^{-4}$**	−5.09 (1.21)	**$<10^{-4}$**	…	…
Year 2002	10 years	−10.08 (1.72)	**$<10^{-4}$**	−11.32 (1.26)	**$<10^{-4}$**	…	…
Year 2003	10 years	−4.92 (1.6)	**<0.01**	−12.25 (1.18)	**$<10^{-4}$**	…	…
Year 2004	10 years	−3.26 (1.32)	**0.01**	−7.94 (1.32)	**$<10^{-4}$**	…	…
Year 2005	10 years	−1.51 (1.53)	0.32	−10.09 (1.46)	**$<10^{-4}$**	…	…
Year 2006	10 years	0.65 (1.92)	0.73	−7.92 (1.39)	**$<10^{-4}$**	…	…
Year 2007	10 years	−5.19 (1.39)	**$<10^{-3}$**	−9.71 (1.26)	**$<10^{-4}$**	…	…
forest†	10 years	0.19 (3.66)	0.96	…	…	…	…
	3 years	0.17 (3.54)	0.96			5.39 (3.04)	0.08
herbaceous†	10 years	0.25 (3.7)	0.95	…	…	…	…
	3 years	−0.39 (3.52)	0.91	…	…	53.61 (3.24)	**$<10^{-3}$**
open water†	10 years	0.32(4.84)	0.95	…	…	…	…
	3 years	−2.69 (4.79)	0.57	…	…	0.52 (6.15)	0.93
shrub†	10 years	−0.14 (3.61)	0.97	…	…	…	…
	3 years	−0.8 (3.48)	0.82	…	…	33.73 (3.1)	**$<10^{-3}$**
wetlands†	10 years	0.55 (4.27)	0.90	…	…	…	…
	3 years	−0.62 (3.95)	0.88	…	…	56.78 (3.54)	**$<10^{-3}$**
open	10 years	0.02 (0.01)	0.21	…	…	0.02 (0.01)	0.09
	3 years	0.04 (0.01)	**0.01**	…	…	0.02 (0.01)	**0.05**
slope	10 years	−0.01 (0.03)	0.66	−0.08 (0.03)	**0.01**	…	…
	3 years	−0.08 (0.03)	**0.02**	…	…	…	…
rivers‡	10 years	…	0.08	…	…	…	…
	3 years	…	0.84	…	0.23	…	…
elev‡	10 years	…	**<0.01**	…	…	…	0.11
	3 years	…	0.10	…	0.27	…	**<0.01**
roads‡	10 years	…	**$<10^{-4}$**	…	**0.03**	…	**$<10^{-3}$**
	3 years	…	**$<10^{-3}$**	…	**0.04**	…	**$<10^{-3}$**
elk‡	3 years	…	0.57	…	…	…	…

observations, we randomly deleted one observation from each pair, leading to a reduced sample size of 1797 observations in the summer data set.

To assess seasonal differences in habitat selection, the coefficients of the best model for each season were compared (Table 2). Welch's test was used to compare linear terms and variable coefficient models were used to compare additive terms (Mao et al. 2005, page 60 in Zuur et al. 2009). In our analysis, each variable coefficient model was based on data from all three seasons and included terms only for season and the continuous predictor variable of interest (e.g., roads or elev). With these terms and the *by* option in the *mgcv* R package, we calculated a p-value indicating whether additive terms differed between seasons.

Analysis of the 10-year data set.—This entire regression procedure was repeated for the 10-year data set. Similarly to the models for the three-year data set, SWE was excluded as a candidate predictor because it was collinear with elev ($r = 0.83$ in late winter; $r = 0.84$ in early winter). An observation was identified as outlier in the summer data set (Bonferroni p value < 0.05). The resulting summer data set included 3599 observations. For all the models developed from the 10-year data set, Year was included as a fixed effect rather than a random effect so that we could assess more precisely how each particular

Table 3. Performance of resource utilization functions describing wolf habitat selection in the Northern Range of Yellowstone National Park, for a 10-year period (1998–2007). Sample sizes were $n = 3600$ from nine packs for late winter, $n = 3599$ from nine packs for summer, and $n = 3600$ from three packs for early winter. Other details of this table are as described in Table 1.

Model	Season	Model type	Random intercepts	Correlation function	All predictors	Δ_i	w_i
L7	Late winter (Jan–Mar)	Linear	None		✓	2649.81	0.00
L8	Late winter (Jan–Mar)	Additive	None		✓	2432.57	0.00
L9	Late winter (Jan–Mar)	Additive	Pack		✓	2427.73	0.00
L10	Late winter (Jan–Mar)	Additive	Pack	✓	✓	0.00	1.00
L11	Late winter (Jan–Mar)	Additive	Pack	✓		2521.96	0.00
S7	Summer (Apr–Sept)	Linear	None		✓	3888.01	0.00
S8	Summer (Apr–Sept)	Additive	None		✓	3569.23	0.00
S9	Summer (Apr–Sept)	Additive	Pack		✓	3374.61	0.00
S10	Summer (Apr–Sept)	Additive	Pack	✓	✓	9.34	0.01
S11	Summer (Apr–Sept)	Additive	Pack	✓		0.00	0.99
E7	Early winter (Oct–Dec)	Linear	None		✓	3376.58	0.00
E8	Early winter (Oct–Dec)	Additive	None		✓	2862.97	0.00
E9	Early winter (Oct–Dec)	Additive	Pack		✓	2868.68	0.00
E10	Early winter (Oct–Dec)	Additive	Pack	✓	✓	0.29	0.46
E11	Early winter (Oct–Dec)	Additive	Pack	✓		0.00	0.54

year differed from the others. However, Year effect could not be included in the models that accounted for spatial autocorrelation in the early winter data set (models E10 and E11, Table 3),
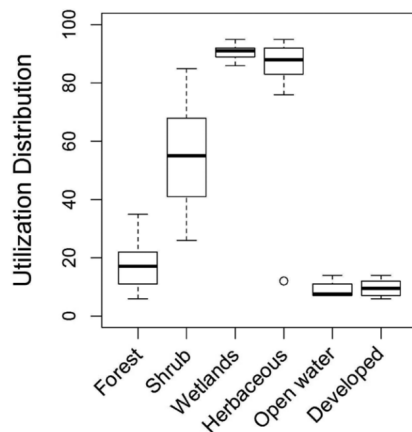

Fig. 2. Selection for different vegetation cover types (x-axis) during early winter. The vegetation categories are ordered from less open (left) to more open habitats (right). Open water and developed areas are fairly rare in the Northern Range of Yellowstone National Park (approximately 0.2% and 0.8% of the study area, respectively). A value of zero on the y-axis represents no use and a value of 95 represents the most intense use. These results represent the three-year data set (see Table 2). Wolves did not select among cover types during the other seasons or for the 10-year data set. Bold bars represent the median, boxes represent the interquartile range, and dotted lines extend to the range of observed data.

because those data included two out of three packs that were observed for only one year. Including Year in those cases would have resulted in division by zero in the variance-covariance matrix that accounts for spatial autocorrelation.

RESULTS

The most parsimonious model, for each season and for each data set required additive terms (for roads, rivers, elk, and elev) and a term to account for random differences among packs (Tables 1 and 3). Details for the best performing model, for each season and data set, are detailed in Table 2. The best models indicate, for example, that wolves did not exhibit preferences for various vegetation cover types during the summer or during late winter, but they did select among cover types during early winter for the three-year data set, but not the 10-year data set. In particular, they selected for wetlands and habitats dominated by herbaceous and shrub cover (Fig. 2).

Wolves also exhibited a preference for shallower slopes, but only during late winter (three-year data set, $p = 0.02$) and summer (10-year data set, $p = 0.01$). They exhibited a preference for open habitats during late winter (three-year data set, $p = 0.01$) and early winter (three-year data set, $p = 0.05$). However, the strength of the preference for open habitats differed significantly between those two seasons ($t = 49.31$; $p < 10^{-3}$) and was greater
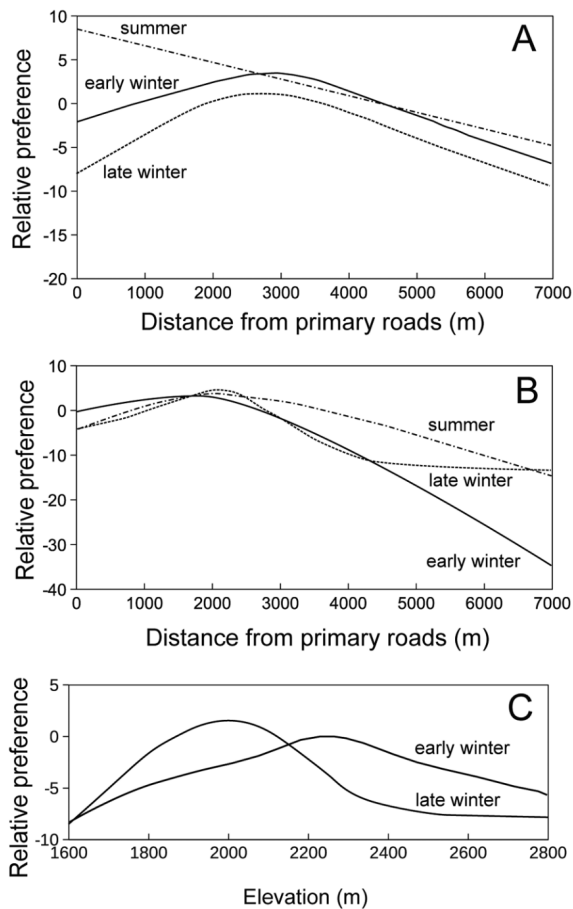
Fig. 3. Relative preferences of Yellowstone wolves for habitats in relationship to their distance from primary roads (A, B) and elevation (C). The curves depict the additive terms (smoothers) computed in R. Larger values on the y-axis depict greater preference. For context, only 25% of the Northern Range area is >7 km from primary roads. Curves in (A), which represent the three-year data set (2000–2002), are significant ($p = 0.04$ for summer, $p < 10^{-3}$ for early and late winter). Curves in (B), which represent the 10-year data set (1998–2007), are also significant ($p = 0.03$ for summer, $p < 10^{-3}$ for early and late winter). In (C), the curve for late winter represents the 10-year data set (1998–2007), and the curve for early winter represents the three-year data set (2000–2002). Both curves are significant (p's < 0.01). Elevation was not a significant variable in any other season or data set.

in late winter (Table 2).

Wolves also selected habitat with respect to its distance from roads, for both data sets and during all seasons (Table 2). During summers between 2000 and 2002, wolves preferred habitats that were closer to the road (Fig. 3A). For all other time periods, however, wolves preferred portions of their territory at intermediate distances (2–3 km) from primary roads (Fig. 3A, B). Moreover, the strength of that preference differed significantly among seasons. That is, the p values for the variable coefficient models were $p < 10^{-3}$ during late and early winter for both data sets, $p = 0.02$ during summer for the three-year data set, and $p = 0.60$ during summer for the 10-year data set. Wolves did not select among habitat on the basis of distance from rivers during any season or time period (Table 2).

The spatial distribution of elk was not a significant driver of wolf habitat selection during late winter ($p = 0.57$, Table 2), or during early winter (omitted during an earlier stage of model development because $p = 0.7$, see Table 1). We omitted elk distribution from the summer model because it was collinear with elevation, which was not significant during the summer for the three-year data set ($p = 0.27$). Nevertheless, wolves did select habitat on the basis of elevation during early winter for the three-year data set and during late winter for the 10-year data set (p's < 0.01; Fig. 3C), but not for any other season or time period. When wolves did select, it was manifest as a preference for habitats at intermediate elevations (Fig. 3C).

For the 10-year data set, year effects were significant during late winter and summer, which are the seasons for which we could assess year effects (Table 2, Fig. 4). In other words, the mean UD value varied among years, which indicates how in some years wolves used some areas of their territory intensively, while using other areas less frequently; and in other years wolves used all (or most) areas inside their territory with the same intensity. Moreover, the summers and late winters between 1999 and 2001 tended to be different from later time periods (Fig. 4). That interval corresponds approximately to the time period covered by the three-year data set. The temporal pattern of year effects also appears autocorrelated. For example, the coefficient for year effect during late winter increased for five continuous years between 2002 and 2006.

Overall there were several instances where wolves' preference differed between the three- and 10-year data sets (Table 2). In particular,
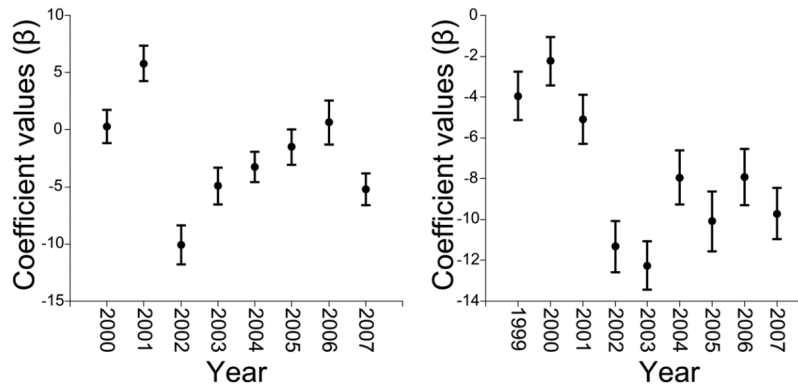
Fig. 4. Coefficients (β) for Year effects for late winter (left panel) and summer (right panel), extracted from the two models in which Year effects were included (see Table 2). These results are derived from the 10-year data set. Each coefficient represents a difference between the reference category (year 1999 for late winter; year 1998 for summer) and the year on the x-axis. Vertical bars represent standard errors.

wolves selected among cover types during early winter for the three-year data set, but not the 10-year data set. Similarly, they showed preference for open habitats during late winter ($p = 0.01$) and early winter ($p = 0.05$) for the three-year data set, but not the 10-year data set (p's = 0.09 and 0.21). Wolves selected habitat with respect to slope during late winter for the three-year data set ($p = 0.02$), but not for the 10-year data set ($p = 0.66$); and selected habitat with respect to slope during summer for the 10-year data set ($p = 0.01$), but not for the three-year data set ($p = 0.64$). Finally, wolves seelcted habitat with respect to elevation during late winter for the 10-year data set ($p < 0.01$), but not for the three-year data set ($p = 0.10$); and selected habitat with respect to elevation during early winter for the three-year data set ($p < 0.01$), but not for the 10-year data set ($p = 0.11$).

DISCUSSION

The discussion is divided into three sections. In the first one, we highlight the significant inter-annual variability that we found in wolf habitat selection and analyze the factors that may cause this variability. In the second one, we suggest that prey distribution may not be a main driver of top-predator habitat selection. In the third one, we address our results on seasonal variability in habitat selection.

Our results indicate that interannual variability

has been an important feature of habitat selection for the studied wolf population (Table 2, Fig. 4). In particular, for the three-year period (2000–2002) wolves avoided steep slopes and preferred open habitats during late winter and they preferred open habitats, habitats at intermediate elevations, and habitats dominated by wetlands, herbaceous vegetation, and shrubs during early winter. However, none of these patterns were observed during the longer time period, 1998–2007 (Table 2). Apparently, the patterns observed during the three-year period were obscured by some countervailing patterns manifest during the longer period of time.

We also observed significant year effects during late winter (Fig. 4). Differences in habitat selection among years could be attributable to interannual differences in any of a variety of factors, such as climate, prey availability, intra-specific competition, and/or various properties of the packs, such as pack size, litter size and individual habits of wolves leading each pack. Uboni et al. (2015) found that wolf space use in late winter is primarily driven by precipitation and pack size. Late winter is the time of year when snow conditions (depth and crustiness) and prey body conditions vary considerably from year to year, more so than in early winter (Mao et al. 2005, Metz et al. 2012). Snow and prey conditions are liable to influence habitat selection as well as space use. Regardless of the causes of this interannual variation, the results of this

study (Table 2, Fig. 4) are of great importance because most habitat research involves data collected over too short a period to assess interannual variability (Appendix). The autocorrelated nature of the coefficients for year effects (Fig. 4) further suggests that data collected from a few consecutive years would not be enough to provide an adequate assessment of interannual variability.

The interannual variation that we observed (especially Table 2) is analogous to an important general lesson from the long-term observations of wolves on Isle Royale, where certain population patterns not only vary over time, but are also apparent over shorter periods of time, but not longer periods of time (e.g., Wilmers et al. 2006, Bump et al. 2009). If the dominant causal factors in a system vary over time, then results based on short-term dynamics would give clear, but misleading impressions of what's happening; and results from longer-term studies would be characterized by less obvious patterns (Vucetich et al. 2010, Nelson et al. 2011).

In agreement with other work on habitat selection, we observed that wolves do not always select habitat on the basis of elk spatial distribution. There are several possible explanations for this result. First, we analysed habitat selection during the day, but wolves tend to hunt between dusk and dawn (Mech and Boitani 2003). Wolves may select daytime habitat on the basis of their interest to perform activities aside from hunting. For example, cougars (*Puma concolor*), which also tend to hunt at night, exhibit diurnal patterns of habitat selection that differ from the nocturnal ones (Dickson et al. 2005). Second, wolves may not be selecting habitat, within their territories, on the basis of elk density, but on the basis of areas where elk are easier to encounter and kill (Bergman et al. 2006, Milakovic et al. 2011). Similarly, Serengeti lions select habitats with good cover that increase their chances to kill their prey more than habitats where prey is more abundant (Hopcraft et al. 2005). In the same region, vultures select habitats where their prey is more likely to die of starvation, rather than habitats with higher prey density (Virani et al. 2014). Wolves did select habitat on the basis of forest cover, elevation, and slope. These are certainly important features to wolf predation (Mao et al. 2005, Bergman et al. 2006, Kauffman et al. 2007,

Gervasi et al. 2013) and it is plausible that wolves' preferences with respect to hunting grounds are captured by those features. We suggest that, with respect to the predator-prey relationship, predator habitat selection at small spatial scale, like the one used in our study, is driven by features of the landscape that enhance hunting success, rather than overall prey distribution.

Wolves selected for intermediate distances (between 2 and 4 km) from roads in all seasons and time periods, except during summer 2000–2002 (three-year data set) when they selected habitats closer to roads (Fig. 3A, B). Nevertheless, the selection of intermediate distances from roads was significantly different among seasons for both data sets. The relatively complex patterns we observed here may account for conflicting results that are found in the literature, with some studies concluding that wolves prefer habitat close to roads (James and Stuart-Smith 2000, Houle et al. 2010, Whittington et al. 2011, Lesmerises et al. 2012) and other studies concluding the opposite (Ciucci et al. 2003, Jędrzejewski et al. 2004, Whittington et al. 2005, Jędrzejewski et al. 2008, Latham et al. 2011). For context, the behavior of Yellowstone wolves near roads within the park and the absence of hunting and poaching along those roads suggest that they would not perceive those roads as a threat. A similar idea was proposed for black bears in Rocky Mountain National Park, where bears chose den sites close to roads despite humans' heavy use of these roads (Baldwin and Bender 2008). Wolf den sites are often located near roads in the Northern Range of the Yellowstone National Park, and this partly explains wolf preference for roads in the summers from 2000 to 2002. Moreover, wolves may use roads to enhance their chances to encounter prey or as travel corridors (Kauffman et al. 2007, Courbin et al. 2013).

Aside from the influence of roads, the most striking observation with respect to seasonal differences in habitat selection was how the complexity of preferences varied among seasons. During early winter, wolves strongly preferred more open landscapes. In addition, they preferred cover types that tend to be open (i.e., wetlands, shrub lands, and grass lands). Open area may provide easier walking (Milakovic et al. 2011) and is where elk tend to be found during winter (Mao et al. 2005). Wolves also preferred

intermediate elevations (see explanation below).

During late winter, wolves continued to prefer more open landscapes, but did not select among cover types that differed in terms of openness, and avoided steeper terrain. Comparing early and late winter gives the impression that wolves begin avoiding the highest elevations that receive snow earliest in the winter, and later in the winter spend more time at lower elevation (Fig. 3C). Avoidance of high elevation during late winter has also been observed in other wolf populations (Ciucci et al. 2003, Whittington et al. 2005, Hebblewhite and Merrill 2008, Milakovic et al. 2011, Whittington et al. 2011, Lesmerises et al. 2012). Presumably, wolves move to lower elevations throughout the winter in response to elevational changes in ungulate habitat selection, as well as to lower the energetic costs of locomotion.

Patterns of habitat selection during summer were least complicated. Aside from the influence of roads, which was important in all seasons, wolves essentially exhibited no habitat preferences during summer, except to avoid habitats with steep slopes. Summer was also characterized by important year effects (Table 2, Fig. 4). The lack of many preferences and interannual variability during summer may indicate that fitness is not much affected by the various decisions a wolf can make about habitat selection. An alternative explanation could involve seasonal variation in wolf sociality. During summer packs are less cohesive, spending much time in smaller groups that often have different interests (raising pups, dispersal, territorial defense, etc.). It is possible that different groups have different preferences. When considered collectively, the preferences of a group could be obscured by different preferences of other groups.

Wolves are certainly habitat generalists in the sense of being able to successfully inhabit a wide range of habitat types (Mech 1970). However, our work clearly shows that wolves do not simply use any habitat that has abundance of prey and low human disturbance, as previous research suggested (Fritts et al. 1994, Mladenoff et al. 1995). Instead, they exhibit specific patterns of preference, patterns that vary considerably from year to year and from season to season (Ciucci et al. 2003, Milakovic et al. 2011). Based on our results, we may hypothesize that temporal variability also acts at higher-order spatial scales

of investigation (for example at the landscape or regional scale; Johnson 1980), scales which are often used during management actions. Further studies are needed to determine the extent of temporal variability at high-order scales.

It may be intuitive to think that data sets spanning longer periods of time are vital for increasing statistical power that is important for detecting patterns in habitat selection. This may be true only in cases where patterns in habitat selection are stationary (i.e., do not vary over time). However, if patterns in habitat selection vary over time, then data sets spanning shorter periods may reveal clear, but short-lived patterns. If so, data sets spanning short periods would not offer an incomplete view of habitat selection so much as a misleading view. Additional support for this idea comes from considering an analogous circumstance in population biology. In one case, for example, a 45-year data set failed to detect the influence of predation on moose population dynamics (Vucetich and Peterson 2004). Subsequent analysis later demonstrated how that moose population had been characterized by a two-decade period of strong top-down control followed by a two-decade period of being influenced primarily by climate (Wilmers et al. 2006). This example is likely the manifestation of what may be common phenomena, i.e., alternative stable states (Beisner 2012) and reddended spectra (Ariño and Pimm 1995). Those potentially common phenomena may also explain why populations seem more likely to exhibit density-dependent patterns over short periods of time, but less likely exhibit that basic pattern over longer periods of time (Ziebarth et al. 2010).

Because of the manner in which population dynamics and habitat selection are linked (Morris 2003), habitat selection is likely to exhibit temporal dynamics similar to those highlighted above for populations. If so, then understanding habitat selection primarily through studies spanning three to five years would be as limited as understanding population dynamics primarily through similarly short periods of study. Surprisingly, the need for conducting long-term research was already pointed out twenty years ago by Schooley (1994), and later by May (1999). We suggest that researchers should be cautious about results obtained from short-term studies and make conclusions depending upon the

question that is asked or the management goals. Analyzing both long-term and short-term data sets may be a useful approach when deriving information on wolf habitat selection to direct conservation and management. Long-term studies may be valuable to detect the most essential resources for the species (i.e., those resources that are selected consistently through time), while short-term studies may indicate which resources are important in exeptional conditions (e.g., how wolves may react to snowy winters or dry summer).

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. We used the Web of Science to search for papers published between 2002 and 2012 in the journals *Ecology, Journal of Animal Ecology, Journal of Applied Ecology, Ecological Applications, Oikos,* or *Journal of Wildlife Management.* We reviewed papers tagged with the topics "habitat selection" or "resource selection" and phrases that represent contemporary methods for analyzing habitat-related behaviors, i.e., "resource selection functions", "resource utilization functions", or "compositional analysis". The results of this review are summarized below.

Years of data analyzed	No. papers published	Papers that analyzed year effect
1	10	0
2	18	7
3	17	4
4	10	3
5	8	2
6	4	1
7	4	1
8	1	0
9	3	3
10	1	1
11	1	0
12	1	0
13	0	0
14	0	0
15	0	0
16	1	0
17	2	0
18	0	0
19	0	0
20	0	0
>20	3	0