

# Identifying ecologically relevant scales of habitat selection: diel habitat selection in elk

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**Abstract.** Although organisms make resource selection decisions at multiple spatiotemporal scales, not all scales are ecologically relevant to any given organism. Ecological patterns and rhythms such as behavioral and climatic patterns may provide a consistent method for identifying ecologically relevant scales of habitat selection. Using elk (*Cervus canadensis*) as an example species, we sought to test the ability of behavioral patterns to empirically partition diel scales for modeling habitat selection. We used model selection to partition diel scales by shifts in dominant behavior and then used resource selection probability functions to model elk habitat selection hierarchically at diel scales within seasons. Model selection distinguished four diel temporal partitions following elk crepuscular behavioral patterns: dawn, midday, dusk, and night. Across seasons, model-averaged coefficients indicated that elk shifted from selecting grassland cover at dawn/dusk, to selecting for greater canopy and forest cover at midday, and then to areas with greater herbaceous biomass at night. Top models changed between diel intervals in spring and fall but stayed the same across diel intervals in winter and summer. In winter, elk selected for southern aspects during midday, for unburned areas at dawn/dusk, and for areas burned within 1–3 yr at dawn/dusk and night. In spring, elk selected for northern aspects and for areas burned within 1–3 yr at midday, for areas farther from roads at dawn/dusk and midday, and for areas farther from water at midday. In summer, elk changed diel preferences for fewer covariates: At dawn/dusk and midday, elk selected for areas farther from water and avoided forest cover, and at night, elk selected for areas burned within 1–3 yr. In fall, elk selected for areas burned the previous year at dawn/dusk and night, for higher elevations at midday, and for areas closer water at night. Using behavioral patterns to identify ecologically relevant scales can help identify overlooked habitat requirements such as diel changes in preference for fire history, forage availability, and cover. We show that the ecological relevancy of a given scale (e.g., a diel temporal scale) can change throughout a given extent (e.g., across seasons).

**Key words:** behavior; *Cervus canadensis*; diel; elk; habitat selection; resource selection probability function; scale; season.

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## INTRODUCTION

How organisms make resource selection decisions varies in magnitude and directionality across multiple hierarchical spatiotemporal scales (Levin

1992, Papastamatiou et al. 2009), but not all scales are ecologically relevant to any given organism, nor are all scales relevant at all periods of a given temporal cycle (Holling 1992, Nash et al. 2014). Organisms might not perceive some scales if they

are too broad (e.g., a mountain range to a beetle) or too fine (e.g., leaf litter structure to a moose [*Alces alces*]; McIntyre and Wiens 1999). Likewise, because resources tend to be distributed discontinuously, organisms make resource selection decisions at discontinuous scales (Allen and Holling 2008). Thus, the broadest and finest limits of an organism's perception curtail multiple, relatively discrete, ecologically relevant scales at which the organism makes resource selection decisions (Morris 1992), and between these relevant scales lie ranges of irrelevant or less relevant scales (Holling 1992). Identifying ecologically relevant scales has been a concern in ecology for decades (Johnson 1980) and is critical for understanding limits of species' perception of resources, the hierarchical nature of habitat selection decision-making by animals, and species' spatiotemporal resource requirements (Allen and Holling 2008, Mayor et al. 2009, van Beest et al. 2011).

Many ecologically relevant scales such as inter-annual climatic changes (Ferguson et al. 1999), daily tidal fluctuations (Luppi et al. 2012), bite sizes (Shipley 2007), and seasonal precipitation changes (Beck et al. 2013) have obvious ecological relevance. For example, herbivore habitat selection can be examined at any spatial scale from the selection of plant parts while foraging, to selection of foraging areas, to landscape selection during transition between seasonal ranges in migratory species (Lee et al. 2002), and at temporal scales from hourly to annually (Schooley 1994, Di Stefano et al. 2009). At larger scales, one can detect broader patterns in home range utilization, migratory routes, and landscape-scale distribution (van Beest et al. 2010), and at finer spatial and temporal scales, one may glean more detailed information, such as forage species consumed, or hourly cover preferences (Shipley et al. 1999, Burks et al. 2002).

But because ecologically relevant scales are not always obvious, many studies simply choose a single scale that appears relevant or exploratorily assess habitat selection at multiple spatial or temporal scales (Johnson 1980, Biggs et al. 2010). These exploratory studies may be necessary in some cases to determine ecologically relevant scales for resource selection, but arbitrary selection of scales for analysis can lead to missed patterns, mistaken patterns, and inefficient analyses (Mayor et al. 2009). Schooley (1994) demonstrated that

solely considering annual habitat selection patterns missed intra-annual variation in habitat selection for black bears (*Ursus americanus*). Beyer and Haufler (1994) and Onorato et al. (2011) reported that although elk (*Cervus canadensis*) and Florida panther (*Puma concolor coryi*) habitat selection studies often binned day and night location data into a single model, partitioning data by diel intervals (e.g., day and night periods) revealed novel habitat selection patterns, implying that intra-diel scales may be more ecologically relevant. Graf et al. (2005) identified multiple grain sizes at which various landscape variables influenced black grouse (*Tetrao urogallus*) habitat selection in the Swiss Alps, but less than half of the grain sizes they chose had biologically relevant support (i.e., home range size), the rest being arbitrarily chosen.

To identify ecologically relevant scales of habitat selection, the scales at which environmental rhythms occur and resources are available must be identified (Munro et al. 2006, Moe et al. 2007, Wilson et al. 2012). Environmental rhythms dictate seasonal patterns in rainfall, food availability, snowfall, and the amplitude in daily shifts in temperature, humidity, and light levels (Boone et al. 2006, Hebblewhite et al. 2008, van Beest et al. 2011). For instance, moose altered habitat selection within diel scales according to hourly changes in temperature (van Beest et al. 2012), and muskoxen (*Ovibos moschatus*) shifted preferences for snow cover between winter and spring (Schaefer and Messier 1995). Resources are often patchily distributed at discontinuous, hierarchical scales in space and time (Holling 1992, Allen and Holling 2008, Nash et al. 2014). To take advantage of these discontinuously distributed resources, species must make selection decisions at the scale of the resource aggregation (Morris 1992, Szabo and Meszena 2006). For example, leopards (*Panthera pardus*) selected patches where catching prey is easier (Balme et al. 2007), and at the patch scale, reef sharks (*Carcharhinus melanopterus*) made clear habitat selection decisions for patch-level characteristics, but at inter-patch scales, they moved randomly (Papastamatiou et al. 2009).

To cope with environmental rhythms and obtain resources, organisms must adjust both how they use habitats and which habitats they use; that is, they must change their behavior (Johnson 1980, Creel et al. 2005, Wilson et al. 2012). Behavioral patterns are associated with

environmental rhythms, resource availability, and organism needs (Burks et al. 2002, Moe et al. 2007, Harju et al. 2013), and animal behavioral patterns are related to habitat use and selection (Di Stefano et al. 2009, Wilson et al. 2012, Middleton et al. 2013). For example, many taxa shift habitat selection patterns throughout the day (Crook et al. 2001, Mukhin et al. 2009). Organisms often divide diel periods between selecting areas for foraging or resting, and these areas can vary greatly in habitat characteristics (Ager et al. 2003, Di Stefano et al. 2009). Prey species modify diel resource use to minimize predation risk, for example, avoiding closed habitats at night (Holomuzki 1986, Jacobsen and Perrow 1998, Creel et al. 2005, Burkepile et al. 2013). Seasonal shifts in behavior can indicate the temporal scale of spawning or parturition periods (Pitman et al. 2014), and diel shifts in behavior can indicate changes between foraging and resting areas with sufficient cover to avoid predators (Holomuzki 1986, Creel et al. 2005, Robinson et al. 2010). Thus, identifying behavioral patterns may enable identification of ecologically relevant scales of habitat selection (Canon et al. 1987, Crook et al. 2001, Munro et al. 2006).

Although no one scale completely describes an organism's habitat selection patterns, ecological patterns and rhythms may provide a consistent method for identifying ecologically relevant scales of habitat selection (Moe et al. 2007, Wilson et al. 2012, Harju et al. 2013). In this study, we use elk to test the ability of an ecological pattern to empirically partition scale for modeling habitat selection. Elk represent a suitable study species because they alter habitat selection at a seasonal temporal scale according to climatic patterns, forage green-up, or heavy snowfall often driving selection across elevational gradients (Hebblewhite et al. 2008, White et al. 2010, Beck et al. 2013), and they are also known to exhibit crepuscular behavioral patterns at a diel scale, typically foraging at dawn and dusk, resting at midday, and intermittently resting and foraging at night (Collins et al. 1978, Green and Bear 1990). However, few studies examine elk habitat selection at diel scales (Toweill and Thomas 2002). Thus, we use diel shifts in elk behavior to investigate a diel scale of elk habitat selection and compare diel and seasonal-scale selection patterns, noting any novel and more detailed selection patterns revealed at the diel scale.

## MATERIALS AND METHODS

### Study site

The study area encompassed approximately 255 km<sup>2</sup> in the Jemez Mountains of north-central New Mexico and included the Valles Caldera National Preserve (VCNP), the Santa Fe National Forest (SFNF), portions of Bandelier National Monument, and the Pueblo of Jemez (Fig. 1). Cattle grazing allotments and outdoor recreation are dominant land uses. Elevation ranges from 1500 to >3000 m, and the climate is semi-arid continental (Western Regional Climate Center [WRCC] 2015). Annual rainfall averages  $43 \pm 25$  (SD) cm and  $58 \pm 25$  cm in the lower and higher elevations, respectively (National Oceanic and Atmospheric Administration [NOAA] 2014a, b). Most rain falls during summer from July through August. Average annual snowfall ranges from  $74 \pm 40$  to  $305 \pm 97$  cm between the lower and higher elevations, respectively (NOAA 2014a, b). From December 2012 to March 2015, annual rainfall and snowfall were both approximately 32% below long-term averages (WRCC 2015).

Vegetation communities include montane grasslands, shrublands, pinyon pine (*Pinus edulis*)–juniper (*Juniperus* spp.) woodlands, ponderosa pine (*Pinus ponderosa*) forests, mixed-conifer forests of Douglas fir (*Pseudotsuga menziesii*), spruce (e.g., *Picea pungens*, *Picea engelmannii*), and firs (*Abies concolor*, *Abies lasiocarpa*), and infrequent stands of aspen (*Populus tremuloides*). Ponderosa pine and pinyon–juniper woodlands dominate elevations <2100 m and are replaced by spruce–fir in the higher elevations. Mule deer (*Odocoileus hemionus*), Rocky Mountain elk (*Cervus canadensis nelsonii*), and domestic cattle (*Bos taurus*) comprise the ungulate community. Common predators include black bear (*Ursus americanus*), mountain lion (*Puma concolor*), and coyote (*Canis latrans*).

Large, severe fires such as the Dome Fire (1996, ~6880 ha), the Cerro Grande (2000, ~17,400 ha), the Las Conchas Fire (2011, ~63,536 ha), and the large mixed-severity Thompson Ridge fire (2013, ~9712 ha) burnt most of the eastern slope of the Jemez Mountains and VCNP, creating a mosaic of burned and unburned swaths in various successional stages (Fig. 1). In 2010, the Southwest Jemez Mountains Collaborative Landscape Restoration Project collaborators began implementing tree thinning and prescribed burning in the SFNF

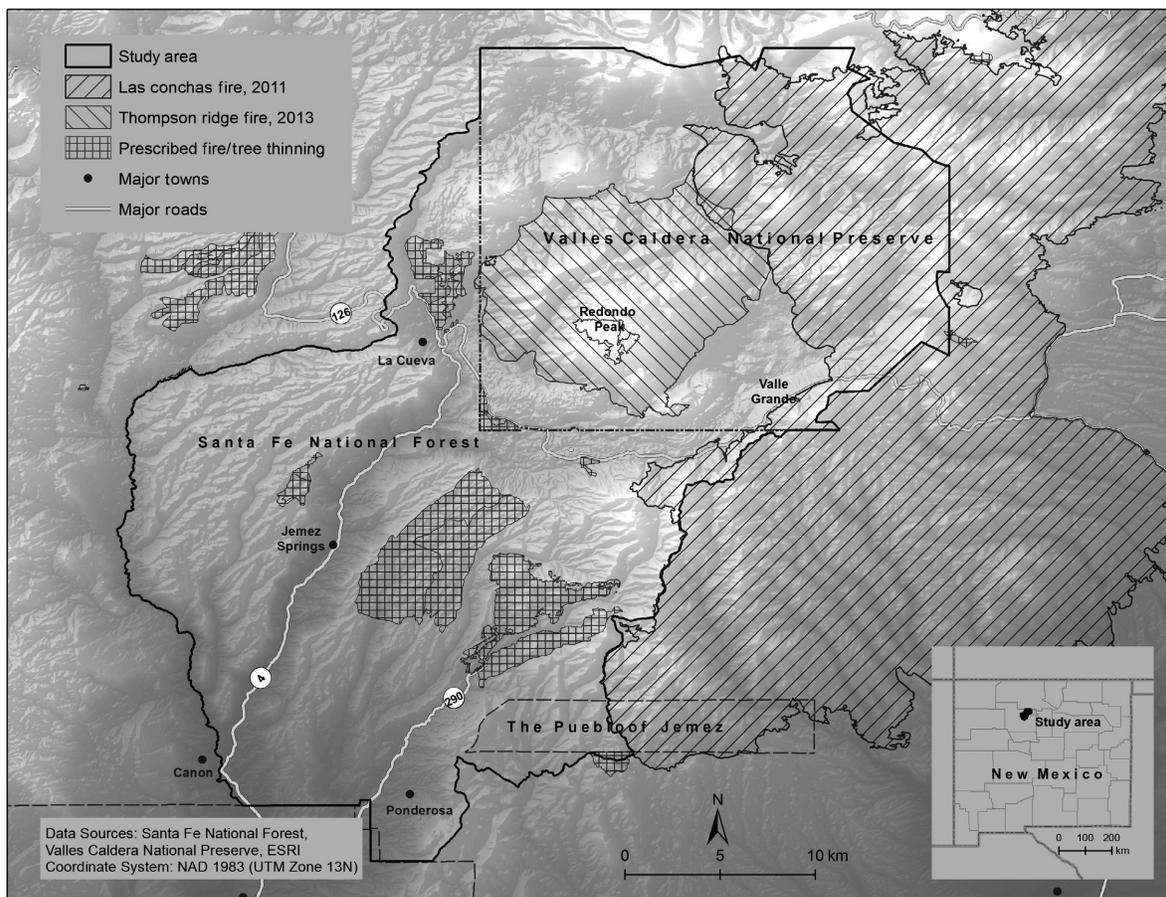


Fig. 1. Study area location in the Jemez Mountains, New Mexico. Polygons with hatched lines indicate estimated perimeters of two recent major wildfires, the Las Conchas (2011) and the Thompson Ridge (2013). Gridded polygons depict perimeters of tree thinning and prescribed fire forestry treatments.

and VCNP, which by the time of this study (May 2013–December 2014) resulted in more than 5233-ha thinned forests and 6826 ha of prescribed burns (Fig. 1).

#### *Elk location data collection*

Adult female elk were captured and collared by net-gunning and darting from helicopter and darting from a vehicle. By replacing animals lost to mortality throughout the study, we fitted 26 adult female elk with global positioning system (GPS) collars. Fifteen store-on-board GPS collars (Advanced Telemetry Systems [ATS], G2110D, Isanti, Minnesota, USA) were deployed in December 2012, six GPS–Iridium (ATS, G2110E Iridium/GPS) collars were deployed in January 2014, and four more GPS–Iridium collars were deployed in March

2014. Store-on-board and ATS Iridium collars were set to take locations at 5- and 6-hourly intervals, respectively, and GPS–Iridium collars transmitted data every three days. All capture and handling procedures followed acceptable methods and were approved by the New Mexico State University Institutional Animal Care and Use Committee (IACUC protocol no. 2011-038; Sikes 2016).

#### *Identifying temporal scales*

*Behavioral observations.*—We conducted behavioral surveys on adult females using focal animal sampling from May to August 2013 and from January to August 2014. Although we did not conduct behavioral surveys in the autumn, because human hunting pressure was low and highly controlled in the majority of the study

area, we do not expect behavioral patterns to differ significantly from other seasons (Green and Bear 1990). To assess behavior throughout diel periods, we sampled all 24 diel hours  $\geq 3$  times over a minimum of 14 d per month (Altmann 1974). For an individual focal survey, the minimum sampling period included in the analyses was 15 min. We selected focal animals opportunistically, focusing on elk with telemetry collars first. If collared elk were absent, we randomly selected any adult female. We considered seven behavioral states: foraging, resting, vigilance, traveling, aggression, nursing, and grooming.

During a focal survey, we recorded the behavioral state of the focal animal every minute. We observed focal animals with a spotting scope or binoculars from vehicles or followed the focal animal at a great enough distance so as not to disturb them. If we visibly disturbed the focal animal, we randomly selected another focal animal that was visibly undisturbed (i.e., not exhibiting prolonged vigilance or rapidly traveling away from the observer). All nocturnal behavioral observations were made from a vehicle with light-amplifying night vision goggles (Morovision, Laguna Hills, California, USA). Focal surveys were conducted in all weather conditions, including heavy rain, snow, and strong winds. However, heavy rain at night prevented nocturnal observations due to the inability of our night vision goggles to see through the rain.

*Temporal partitions.*—To identify relevant scales for habitat selection modeling based on ecological patterns, we used long-term climate data to identify seasonal-scale partitions and behavioral patterns to identify diel-scale partitions. We chose to use climatic patterns to create seasonal partitions because climate is known to drive elk habitat selection at a seasonal scale (Wolf 2003, Beck et al. 2013, Middleton et al. 2013) and because we found that overall diel behavioral patterns were similar among seasons and were thus not useful for seasonal-scale partitioning (Fig. 2). We identified seasons by grouping months with similar mean monthly precipitation and temperature (NOAA 2014a, b). We established winter as December through March, spring as April and May, summer as June through September, and fall as October and November.

We used generalized linear models (GLMs) to assess changes in predominant behavioral patterns

across diel intervals to create diel-scale partitions (Canon et al. 1987, Green and Bear 1990, Ager et al. 2003, Wilson et al. 2012). We compared diel partitioning models with the Akaike information criterion corrected for small sample sizes ( $AIC_c$ ). We developed models for each behavioral category and set percent time spent exhibiting a behavior per hour as the response variable and diel partitions as predictor variables. However, because foraging was the most common behavior and was strongly negatively correlated with the second-most common behavior (resting;  $R = -0.79$ ), and the next two most common behaviors (vigilance and traveling) produced similar partition results, we report only results with foraging as the response variable.

We developed three diel partitioning models: a day–night model, a dawn–midday–dusk–midnight model, and a null model lacking diel partitions (i.e., a seasonal model). For the day–night diel temporal partition, we classified locations recorded from the beginning of civil twilight (when the geometric center of the sun is  $6^\circ$  below the horizon) in the morning to the end of civil twilight in the evening as day and time after civil twilight in evening and before civil twilight in the morning as night. We used the approximate geographic center of the VCNP to estimate civil twilight. To create the dawn–midday–dusk–night diel temporal partition, we examined boxplots of mean time spent foraging for each hour of the day from our data on behavioral patterns of elk and those from the scientific literature. Accordingly, we partitioned dawn from an hour before to two and a half hours after sunrise and dusk from three hours before to two and half hours after sunset (Fig. 2; Collins and Urness 1983, Green and Bear 1990, Toweill and Thomas 2002, Rumble and Gamo 2011). We considered midday and night as the intervals between dawn and dusk and dusk and dawn, respectively. Because dawn and dusk intervals appeared to have similar levels of foraging behavior (Fig. 2), we compared time spent foraging between dawn and dusk with a two-way  $t$  test and via effect size (Cohen's  $D$ ). We detected no difference in time spent foraging ( $P > 0.10$ ;  $D = -0.13$ ), so we pooled all dawn and dusk relocations and analyzed dawn/dusk as a single temporal delineation (Green and Bear 1990, Toweill and Thomas 2002). We used the *maptools* and *lubridate* R packages for temporal data manipulations (Grolemund and

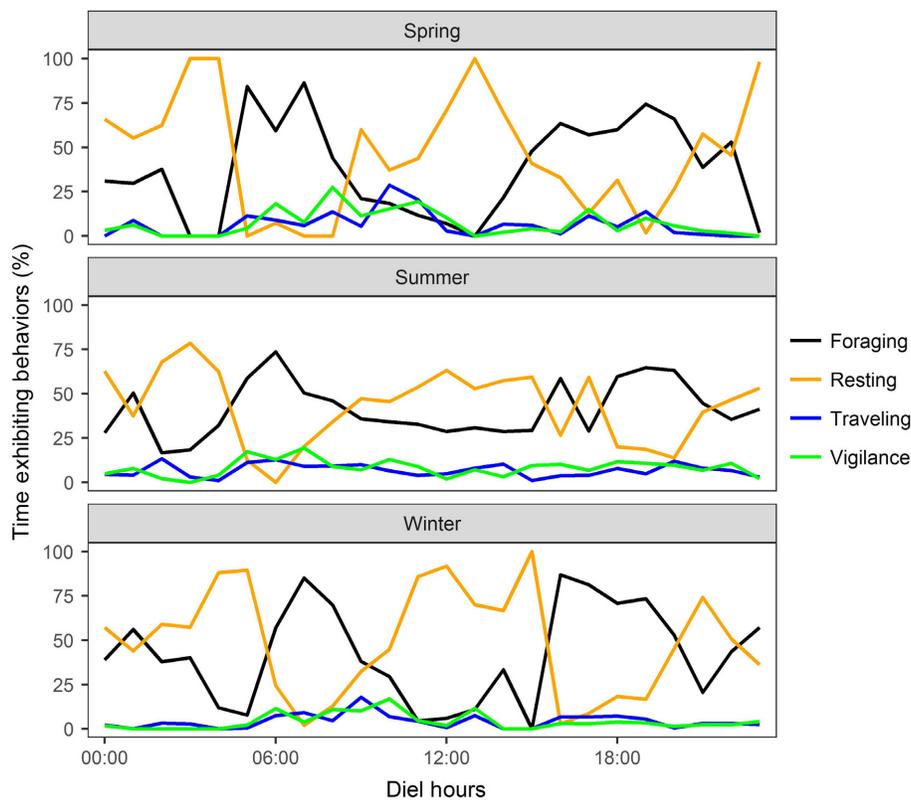


Fig. 2. Mean percentage of time per hour elk spent foraging, resting, traveling, and vigilance behaviors over diel periods during focal behavioral surveys during summer 2013 and winter 2013–2014 to summer 2014, Jemez Mountains, New Mexico.

Wickham 2011, Bivand and Lewin-Koh 2014, R Core Development Team 2014).

#### Habitat modeling

*Sampling units.*—We modeled habitat covariates by systematically distributing circular sampling units across the study area in a grid from a random origin (Nielson and Sawyer 2013). We chose circular sampling units for simplicity in calculations and to leave gaps between sampling units (Sawyer et al. 2009). We determined sample unit size by averaging movement distances (m) between successive GPS locations for each collared elk and then examining histograms of number of relocations per sample unit with various sample unit sizes (e.g., 500, 350, and 250 m radii). We selected a 250 m radius because it was large enough to capture enough animal relocations to produce a histogram approximating a negative binomial distribution, and it was small enough to be sensitive to changes in elk habitat selection and

capture meaningful spatial variability in habitat conditions (Nielson and Sawyer 2013). We then excluded sampling units that fell outside the minimum convex polygons around amalgamated elk locations for each season (Pebesma and Bivand 2005, Sawyer et al. 2009).

*GIS data.*—The respective land management agencies in the study area provided GIS layers for fire history, vegetation type, canopy cover, water source locations, forest restoration treatments (i.e., thinning and prescribed fire), and roads. We obtained a 30 × 30 m resolution digital elevation model from the U.S. Geological Survey to calculate aspect. We considered bearings between 0–67.5° and 292.5–360° as north, 112.5–205.5° as south, 67.5–112.5° as east, and 202.5–292.5° as west. Because east and west aspects were rarely the predominant aspects in sampling units and because north–south aspects were more biologically meaningful in terms of differences in winter snow pack, summer soil moisture, and vegetation

biomass, we only considered north and south aspects for analyses. With ArcGIS 10.2 (Redlands, California, USA), we populated each sampling unit by calculating the percentages of each sampling unit covered by each vegetation type and closed canopy cover (i.e., >30% tree cover), and we determined the most recent fire and treatment that occurred in sampling units, and identified the aspect comprising the majority of each sampling unit (Hebblewhite et al. 2008, Nielson and Sawyer 2013, Environmental Systems Research Institute 2014). We also measured the shortest distance to nearest perennial water source and open road from the center of each sampling unit.

*Forage biomass predictions.*—Because elk primarily select herbaceous plants for forage (Cook 2002), we also estimated herbaceous forage biomass across the study area. We used stratified random sampling with proportional allocation based on vegetation type (i.e., ponderosa, spruce-fir, pinyon-juniper, oak shrubland, aspen, and grassland), canopy cover class (i.e., open canopy  $\leq 29\%$  tree cover, and closed canopy >30% tree cover), aspect, fire history (i.e., burned within past year, burned within past 1–2 yr, burned within past 2–4 yr, burned within past 4–10 yr, and burned >10 yr ago), and restoration treatments (i.e., treated with fire or thinning, not treated) to distribute 224 vegetation monitoring points across the study area. We surveyed vegetation points between May and September in 2013 and 2014. At vegetation monitoring points, we established 200-m transects. We measured biomass of herbaceous forage using a 0.25-m<sup>2</sup> disk pasture meter every 20 m along the transect (Hebblewhite et al. 2008). To calibrate the disk pasture meter height measurements with estimates of herbaceous forage biomass, all herbaceous forage was clipped in 788 plots, separated by growth form (graminoid or forb), dried to a constant mass at 55°C in a drying oven, and then weighed to determine the dry weight. We then determined the relationships between disk height and herbaceous biomass using log–log-transformed linear regression equations. We predicted vegetative biomass for each vegetative biomass plot in each transect using the back-transformed coefficients and then averaged estimated plot biomass for each transect (Newman 1993, Roberts 2015).

Following Hebblewhite et al. (2008), we modeled forage biomass across the study area in

relation to spatial covariates using GLMs. Specifically, we developed predictive GLMs for herbaceous biomass as a function of dominant vegetation type, aspect, slope, treatment type, canopy cover, and fire history as defined above (Hebblewhite et al. 2008). We used a forward and backward stepwise selection to choose the most explanatory and parsimonious predictor variables based on AIC<sub>c</sub> values. Selected spatial covariates were included in GLMs, and we used their coefficients to predict forage biomass across all sampling units (Hebblewhite et al. 2008). We performed all data manipulations and analyses in R (R Core Development Team 2014).

*Resource selection probability functions.*—We modeled habitat selection with a bootstrapped resource selection probability function (RSPF; Sawyer et al. 2006, Sawyer et al. 2009, Nielson and Sawyer 2013) with an information-theoretic approach (Burnham and Anderson 2003). Using negative binomial GLMs, we compared nine a priori candidate models (Table 1). We set habitat covariates within each sampling unit as predictor variables and relocations per sampling unit as the response variable. Total number of animal relocations within the study area per season per diel partition served as the offset terms for the GLMs (Marzluff et al. 2004). To avoid pseudo-replication, we used individual elk as the experimental units (Sawyer et al. 2009).

We developed a five-step algorithm for the bootstrapped RSPF. First, we made a bootstrap sample of the individual elk with replacement (Goldstein et al. 2010, Nielson and Sawyer 2013). Second, we pooled data from all bootstrapped elk by summing all relocations per sampling unit from the temporal partition of interest (Goldstein et al. 2010, Nielson and Sawyer 2013). Pooling data allowed us to collapse differences between individuals (Goldstein et al. 2010, Nielson and Sawyer 2013). For each temporal partition, we totaled the number of locations to calculate the offset term (Nielson and Sawyer 2013). Third, we used the R package MASS to calculate the negative binomial GLM (Venables and Ripley 2002). In each negative binomial GLM, we estimated coefficients and standard deviations for each variable and calculated AIC<sub>c</sub> values for each model. Fourth, we estimated standard errors of the coefficients by averaging the standard deviations from each bootstrap run. Lastly, we

Table 1. A priori model structures used to assess diel-scale habitat selection of elk in the Jemez Mountains, New Mexico, December 2013–November 2014.

Model	Structure
1	Burned 1 yr Ago + Burned 2–3 yr Ago + Burned >10 yr Ago + Canopy Cover
2	Elevation + Canopy Cover + Aspect
3	Herbaceous Biomass + Distance to Water + Elevation
4	Distance to Water + Grassland Cover + Ponderosa Cover + Spruce-Fir Cover + Aspect + Distance to Road
5	Elevation + Burned 1 yr Ago + Burned 2–3 yr Ago + Burned >10 yr Ago
6	Burned 1 yr Ago + Burned 2–3 yr Ago + Burned >10 yr Ago + Aspect
7	Canopy Cover + Herbaceous Biomass + Distance to Water + Aspect
8	Herbaceous Biomass + Ponderosa Cover + Spruce-Fir Cover
9	Elevation + Grassland Cover + Distance to Road

*Note:* Aspect = north and south aspects; Aspen Cover = percent aspen cover; Canopy Cover = percent closed canopy; Grassland Cover = percent grassland cover; Herbaceous Biomass = predicted herbaceous biomass (kg/ha); Ponderosa Cover = percent ponderosa cover; Distance to Road = distance (m) to nearest open road; Spruce-Fir Cover = percent spruce-fir cover; Distance to Water = distance (m) to nearest perennial water source.

averaged  $AIC_c$  values from each bootstrap run. We conducted 999 bootstrap runs (Goldstein et al. 2010, Nielson and Sawyer 2013).

To compare models within each temporal delineation, we ranked the a priori models by  $AIC_c$  weights, which indicate the amount of support for each model (Anderson 2007). With the  $AIC_c$  weights, we calculated model-averaged parameter estimates and 90% confidence intervals for each habitat covariate for each diel partition within each season (Frair et al. 2005, Anderson 2007). We then compared habitat selection patterns between diel partitions by comparing model-averaged parameter estimates for each diel partition and season. We considered habitat selection patterns to differ between diel partitions if either of these conditions were true: (1) model-averaged parameter confidence limits did not overlap (e.g., if the dawn/dusk canopy cover parameter estimate was  $1 \pm 0.1$  and the midday estimate was  $2 \pm 0.1$ ), or (2) a model-averaged parameter's confidence limits did not encompass zero but overlapped with another parameter with confidence limits encompassing zero (e.g., if the dawn/dusk grassland cover parameter estimate was  $1 \pm 0.5$  and the midday estimate was  $1 \pm 1.5$ ).

## RESULTS

### Identifying temporal scales

We collected 668 h of focal observations over 117 d across 10 months. Percent of time per hour spent foraging (mean =  $44.7 \pm 2.81$  95% CI) and

resting (mean =  $40.1 \pm 3.25$  95% CI) dominated focal observations. Vigilance (mean =  $7.66 \pm 1.20$  95% CI) and traveling (mean =  $6.63 \pm 1.00$  95% CI) comprised most of the remainder. We observed grooming, nursing, and aggression only rarely (all <1%). Foraging behavior peaked twice per diel period, corresponding with dawn and dusk, and resting peaked two to three times per diel period directly after foraging bouts during midday and at night (Fig. 2). Traveling and vigilance behaviors increased during or directly after foraging bouts, especially after the dawn foraging. Elk exhibited similar behavioral patterns across seasons, although timing of foraging bouts shifted between seasons with changing dawn and dusk times (Fig. 2).

The dawn–midday–dusk–night diel partitioning model greatly outperformed the day–night ( $\Delta AIC_c = 117.52$ ) and the null models ( $\Delta AIC_c = 118.99$ ). Percent time spent foraging varied by diel partition. Time spent foraging in dawn and dusk partitions did not differ from the overall mean (intercept,  $0.592 \pm 0.062$  95% CI), but midday and night partitions were associated with significantly less time spent foraging ( $-0.298 \pm 0.074$ ,  $-0.248 \pm 0.089$ ; respectively, 95% CI).

### Resource selection probability functions

Top models changed between diel intervals in spring and fall, but in summer and winter, top models stayed the same across diel intervals (Table 2). Delta  $AIC_c$  values between the top- and second-ranked models exceeded 10 in eight out of the twelve model sets, implying strong support for most top models (Table 2). The only

Table 2. The top three models predicting diel habitat selection patterns of elk in the Jemez Mountains, New Mexico, December 2013–November 2014.

Season	Diel period	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>
Winter	Dawn/Dusk	Elev + Can + Aspect	5141.5	0.0
		Elev + Gra + Road Dist	5153.0	11.5
		Water Dist + Gra + Pon + S-F + Aspect + Road Dist	5245.8	104.3
	Midday	Elev + Can + Aspect	3750.3	0.0
		Elev + Gra + Road Dist	3759.8	9.5
		Elev + Fire 1 + Fire 2 + Fire 3	3799.0	48.7
	Night	Elev + Can + Aspect	4720.9	0.0
		Elev + Gra + Road Dist	4764.4	43.5
		Water Dist + Pon + Pon + S-F + Aspect + Road Dist	4846.1	125.2
Spring	Dawn/Dusk	Fire 1 + Fire 2 + Fire 3 + Can	4218.0	0.0
		Elev + Gra + Road Dist	4226.4	8.4
		Water Dist + Gra + Pon + S-F + Aspect + Road Dist	4255.9	37.9
	Midday	Elev + Fire 1 + Fire 2 + Fire 3	3216.7	0
		Elev + Can + Aspect	3310.5	93.8
		Fire 1 + Fire 2 + Fire 3 + Can	3312.5	95.8
	Night	Fire 1 + Fire 2 + Fire 3 + Can	3099.9	0.0
		Water Dist + Gra + Pon + S-F + Aspect + Road Dist	3102.7	2.8
		Elev + Gra + Road Dist	3112.6	12.7
Summer	Dawn/Dusk	Water Dist + Gra + Pon + S-F + Aspect + Road Dist	6513.4	0.0
		Elev + Gra + Road Dist	6612.4	99
		Fire 1 + Fire 2 + Fire 3 + Can	6634.9	121.5
	Midday	Water Dist + Gra + Pon + S-F + Aspect + Road Dist	5138.1	0.0
		Elev + Fire 1 + Fire 2 + Fire 3	5191.1	53
		Herb Bio + Pon + S-F	5248.0	109.9
	Night	Water Dist + Gra + Pon + S-F + Aspect + Road Dist	4933.6	0.0
		Elev + Gra + Road Dist	5025.3	91.7
		Fire 1 + Fire 2 + Fire 3 + Can	5032.2	98.6
Fall	Dawn/Dusk	Elev + Fire 1 + Fire 2 + Fire 3	3886.6	0.0
		Elev + Can + Aspect	3906.8	20.2
		Elev + Gra + Road Dist	3907.5	20.9
	Midday	Elev + Gra + Road Dist	2292.2	0.0
		Elev + Can + Aspect	2293.5	1.3
		Elev + Fire 1 + Fire 2 + Fire 3	2303.3	11.1
	Night	Elev + Can + Aspect	3281.0	0.0
		Elev + Gra + Road Dist	3315.7	34.7
		Herb Bio + Water Dist + Road Dist	3322.7	41.7

Notes: AIC<sub>c</sub>, Akaike information criterion corrected for small sample sizes. Columns indicate year, season, diel periods, model structure, AIC<sub>c</sub> values, and ΔAIC<sub>c</sub> values. Aspect = north and south aspects; Can = percent closed canopy; Elev = elevation; Fire 1 = burned 1 yr ago; Fire 2 = burned 2–3 yr ago; Fire 3 = burned >10 yr ago; Gra = percent grassland cover; Herb Bio = predicted herbaceous biomass (kg/ha); Pon = percent ponderosa cover; Road Dist = distance (m) to nearest open road; S-F = percent spruce-fir cover; Water Dist = distance (m) to nearest perennial water source.

clear model uncertainty occurred in the fall night period, between the top model (containing elevation, grassland cover, and distance to roads) and the second-ranked model (containing elevation, canopy cover, and aspect; Table 2).

Model-averaged habitat covariate coefficients varied across diel intervals in all seasons (Fig. 3; Table 2). Coefficients varied across seasons, and within seasons, coefficients varied most between dawn/dusk–midday and night–midday. Across

winter diel intervals, elk selected for southern aspects during midday, selected for unburned areas at dawn/dusk, selected for areas burned the previous year and within 2–3 yr at dawn/dusk and night, avoided canopy cover less at midday than at dawn/dusk and night, selected for areas farther from roads and water at midday, selected for grassland cover and herbaceous biomass most strongly at dawn/dusk and night, avoided ponderosa cover at dawn/dusk, and selected for

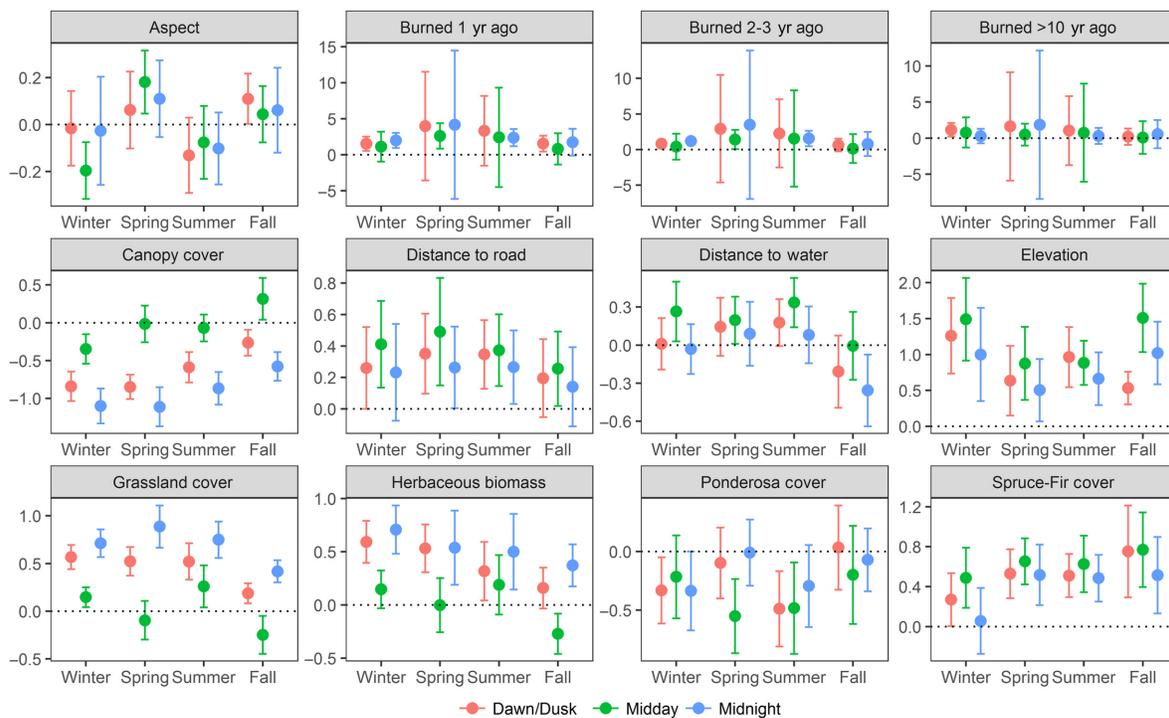


Fig. 3. Model-averaged parameter estimates of elk habitat selection patterns across diel intervals (dawn/dusk, midday, and night) by season in the Jemez Mountains of New Mexico, winter 2013–fall 2014. Error bars indicate 90% model-averaged confidence limits. Diel scales were established according to diel shifts in behavioral patterns, and seasons were delineated based on differences in mean annual temperature and precipitation.

spruce-fir cover at dawn/dusk and midday. Across spring diel intervals, elk selected for northern aspects at midday, selected for areas burned the previous year and areas burned within 2–3 yr at midday, avoided canopy cover at dawn/dusk and night, selected for areas farther from roads at dawn/dusk and midday, and selected for areas farther from water at midday. During spring, elk also selected for grassland cover and herbaceous biomass at dawn/dusk and night and avoided ponderosa cover at midday. In summer, elk changed diel preferences for fewer covariates: They selected for areas burned within the previous year and within 2–3 yr at night, avoided canopy cover at dawn/dusk and night, selected for areas farther from water at midday, selected for grassland cover and herbaceous biomass more strongly at night than at midday, and avoided ponderosa cover at dawn/dusk and midday. In fall, elk shifted between selection and avoidance of covariates more often than other seasons, changing from avoidance of canopy cover at dawn/dusk and

night to positive selection for canopy cover at midday, from selection for grassland cover at dawn/dusk and night to avoidance at midday, and from no preference for herbaceous biomass at dawn/dusk to avoidance at midday and positive selection at night. Fall was also unique in that the only fire history covariate elk showed preference for was positive selection for areas burned the previous year at dawn/dusk and night, they selected for areas closer water at night, and elk showed strong preference for higher elevations at midday compared to dawn/dusk.

We also detected some consistent diel changes in preference across seasons (Fig. 3). Selection for canopy cover, grassland cover, and herbaceous biomass changed the most consistently, whereas aspect, fire history, distance to water, and ponderosa cover showed strong seasonal differences in selection patterns. Elk also shifted preference for areas burned the previous year the most strongly of all fire history covariates across diel intervals in all seasons.

## DISCUSSION

We demonstrate the use of an ecological pattern to empirically partition scale for modeling habitat selection using shifts in elk diel behavioral patterns to model elk habitat selection at an infrequently investigated diel temporal scale. Across diel intervals in every season, elk changed habitat preferences in time with shifts in dominant behaviors. Diel-scale modeling revealed novel and more detailed patterns and variations in elk habitat selection than seasonal-scale studies demonstrate (Boyce et al. 2003, Beck et al. 2013). We detected unique changes in fire history preference across diel intervals, with elk selecting for newer or older fires at different times in the day. Our study agrees with others that found elk select for southern aspects in winter (Skovlin et al. 2002), but we only found selection for southern aspects during winter midday only. Similarly, other studies have reported elk to select for areas nearer water in summer (Beck et al. 2006), but we found that the distance to water was only important in midday models; however, elk selected for areas further from water. Only during the night period in fall did elk select for areas closer to water.

We also show that the ecological relevancy of a given scale (e.g., a diel temporal scale) can change throughout a given extent (e.g., an annual temporal extent). Assuming a given scale is ecologically relevant in all situations may overestimate preference for an individual resource, overestimate the difference in preference between grains (e.g., between seasons), or detect non-existent patterns (Kernohan et al. 1996, Rettie and Messier 2000, Biggs et al. 2010). Because organisms shift selection patterns to exploit changing resource availability (e.g., elk seeking increased forage availability at high elevations as spring turns to summer; Hebblewhite et al. 2008) and to fulfill their shifting resource requirements (e.g., elk selecting birthing sites in the spring; Pitman et al. 2014), greater consistency in resource availability or an increase in fine-scale resource needs at a particular scale may dampen or intensify the relevance of any given scale. For instance in our study, model-averaged coefficients indicated that elk diel preference for individual habitat variables varied seasonally, but model selection indicated that changes in elk diel

preferences were less pronounced in winter and summer than in spring and fall. This suggests that the diel temporal scale may be more ecologically relevant to elk in spring and fall than in winter and summer. Greater consistency across summer and winter months in terms of overall weather patterns (e.g., lower temperature variation across months; WRCC 2015) and forage resource availability (as opposed to spring green-up and increases in forage resources at higher elevations and autumn senescence and reduction of forage at higher elevations; Middleton et al. 2013) may have reduced the need for elk to make major diel-scale shifts in habitat selection patterns. Although the elk during our study were only quasi-migratory (Wolf 2003), the importance of diel temporal scales in spring and fall may indicate that elk make finer-scale resource choices during migration (Hebblewhite and Merrill 2009). Because elk also make reproductive habitat selection decisions in spring (parturition) and fall (rut), the importance of diel temporal scales during spring and fall may also have implications for fine-scale resource choices during reproductive life stages (Wolff and Horn 2003, Pitman et al. 2014).

Because resource preferences and the ecological relevance of scales shift, resources must be accessible at ecologically relevant scales for organisms to utilize a given location (Gehring and Swihart 2003, Onorato et al. 2011, Sawyer et al. 2011). For instance, at the scale of a seasonal migration, mule deer avoided or reduced use of former migration routes where oil and gas development had fragmented landscapes (Sawyer et al. 2005, 2009). Our study found that elk, as a crepuscular species (Canon et al. 1987, Green and Bear 1990), altered their habitat preference in line with their crepuscular rhythm and made novel changes in habitat covariate preference throughout diel intervals in association with activity patterns (e.g., changes in preference for fire history covariates). Thus, when diel temporal scales are ecologically relevant for elk, elk may require landscapes in which resources they need are distributed such that they are accessible within a 24-h interval. Many elk habitat selection studies consider habitat diversity and heterogeneity needs at multiple spatial scales, but most focus on a single temporal scale, usually seasonal (Beyer and Haufler 1994, Skovlin et al. 2002,

Beck et al. 2013). Seasonal climatic patterns make seasonal scales logical and ecologically relevant for understanding broad resource needs, such as summer and winter range requirements (Boyce 1991, Middleton et al. 2013). Indeed, in some situations, such as when landscape-level anthropogenic disturbances or fragmentation via agricultural or urban conversion completely removes resources, fine-scale habitat selection patterns may become less relevant to individual fitness simply because organisms must make broader-scale choices to reach reduced, isolated resources (Rettie and Messier 2000, Boscolo and Metzger 2009). However, the hierarchical scaling nature of habitat selection and the changing needs of organisms make the ecological relevance of any scale relative and mutable, not binary or absolute (Levin 1992, Boyce et al. 2003, Frye et al. 2013).

Attempting to identify ecologically relevant spatiotemporal scales by arbitrarily adjusting extents or grain sizes, although potentially useful for exploratory purposes, will likely miss crucial patterns and processes or even detect patterns where none exist (Wiens 1989, McGarigal et al. 2016). Patterns and processes in ecological systems occur patchily and discontinuously across scales (Szabo and Mesz na 2006). To exploit discontinuously distributed resources, organisms must select habitat at the scale of the resource distribution, making certain scales more ecologically relevant (Nash et al. 2014, McGarigal et al. 2016). Thus, to identify relevant scales of habitat selection, discontinuities in systems, resources, and processes must be identified (Szabo and Mesz na 2006, Allen and Holling 2008). Behavioral patterns can shift discontinuously when searching for resources or switching between types of resources (Collins and Urness 1983, Humphries et al. 2010), and changes in dominant behaviors can indicate changes in habitat selection or usage (Munro et al. 2006, Moe et al. 2007). We found shifts in behavioral patterns identified ecologically relevant scales for elk habitat selection. Thus, shifts in behavior can provide cues to delineate ecologically relevant scales for understanding habitat selection (Ager et al. 2003, Moe et al. 2007). Behavioral shifts may be obvious in some cases (e.g., migratory birds or large ungulates), but other shifts may not be obvious or demand copious effort to

estimate (e.g., elk diel behavioral patterns). But current methods (e.g., GPS collar activity sensors, Brownian movement) can efficiently estimate behavioral patterns at various spatiotemporal scales and aid in identifying discontinuities or major shifts in behavioral patterns (Humphries et al. 2010, Roberts et al. 2016).

Despite the widely acknowledged importance of scaling issues and considering multiple scales when estimating resource selection, empirical identification of ecologically relevant scales for habitat election is uncommon (McGarigal et al. 2016). We demonstrate a method for empirically identifying and partitioning temporal scale by using changes in dominant behaviors over diel intervals to identify diel temporal partitions for modeling elk habitat selection. Species require habitat features to be distributed at specific (i.e., ecologically relevant) scales; therefore, these methods can aid managers and researchers optimize habitat for species of interest or identify overlooked critical habitat for threatened species. Our study also suggests promoting accessibility to necessary habitat features at multiple, ecologically relevant scales is an important management consideration. To assess the availability of habitat requirements across scales, researchers and managers can consider behavior or other cues (e.g., climate, spatiotemporal resource distributions) to identify relevant scales while also ensuring that the scale of interest can be detected, via the grain of monitoring methods (e.g., frequency of behavioral surveys, sensitivity of GPS collar activity sensors, and number of GPS collar location collections per unit time).

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