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Gura, Katherine B., <u>Variation in Habitat Selection, Seasonal Movements, and Reproductive Output of a Facultative Migrant, the Great Gray Owl</u>, Ph.D., Program in Ecology, May 2023.

Identifying key habitat, responses to environmental change, and determinants of fitness are primary goals in ecology. I investigated mechanisms underlying variation in resource selection, movement behavior, and reproductive performance of Great Gray Owls in the Greater Yellowstone Ecosystem in Wyoming and Idaho, USA. In Chapter 1, I quantified resource selection of adult owls (n = 42) and observed different patterns of selection depending on spatiotemporal scale, including between the breeding versus winter seasons. In Chapter 2, I evaluated whether breeding-season resource selection by adult male owls (n = 19) varied across diurnal periods, to improve understanding of foraging and nocturnal habitat. Owls avoided herbaceous wetlands during daytime but strongly selected them at dawn, dusk, and night. They also chose nighttime microhabitat that enabled foraging, such as presence of primary prey and open understories. In Chapter 3, I evaluated whether snow conditions influenced proximate habitat choices and/or migratory movements by Great Gray Owls. Owls proximately avoided deeper snow and more severe wind crusts, whereas probability of migration increased with more severe and persistent ice crusts. Owls appeared to be behaviorally plastic, adopting different strategies depending on the spatial scale and duration of limiting conditions. In Chapter 4, I investigated whether breeding-season prey abundance or prior winter snow conditions influenced reproductive output. Snow conditions during the preceding winter carried over to determine subsequent breeding. Such detailed assessments of factors across scales and contexts contribute to a more thorough understanding of resource requirements, susceptibility to environmental change, and population dynamics.

VARIATION IN HABITAT SELECTION, SEASONAL MOVEMENTS, AND

REPRODUCTIVE OUTPUT OF A FACULTATIVE MIGRANT, THE GREAT GRAY OWL

By

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DEDICATION PAGE

To D. Gura –

"Hope" is the thing with feathers —
That perches in the soul —
And sings the tune without the words —
And never stops — at all —

And sweetest — in the Gale — is heard —
And sore must be the storm —
That could abash the little Bird
That kept so many warm —

I've heard it in the chillest land —
And on the strangest Sea —
Yet, never, in Extremity,
It asked a crumb — of Me.

-Emily Dickinson

ACKNOWLEDGEMENTS

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CHAPTER ONE

Seasonal and spatial variation in habitat selection by Great Gray Owls

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Abstract:

Animals balance multiple selective pressures via habitat choices, and therefore they can rely on habitats that are heterogeneously distributed through space and time to meet varying resource requirements. Habitat selection studies that explicitly incorporate multiple relevant scales, including the full annual cycle, therefore strengthen understanding of important resources for a species. We quantified the resource selection of adult Great Gray Owls (n = 42) in the Greater Yellowstone Ecosystem, considering multiple spatial (home range and within-home-range) and temporal (breeding and non-breeding seasons) scales of selection. We analyzed location data and created Resource Selection Functions using Generalized Linear Mixed Models, scale optimization, and remotely-sensed habitat data. We observed different patterns of resource selection depending both on season and spatial scale, indicating how environmental conditions, limiting factors, and therefore key habitat can change over space and time. For example, during the breeding season owls placed home ranges within northerly aspects that were predominantly forested, whereas they avoided development. During the non-breeding season, owls switched in favor of low elevation, developed areas and southerly aspects. Our comprehensive assessment of resource selection advances knowledge of Great Gray Owl breeding-season habitat and fills in critical information gaps regarding non-breeding-season resource requirements. Habitat selection studies that incorporate scale dependence can result in a more holistic understanding of key resources and therefore facilitate more effective habitat conservation.

Key Words: Full annual cycle, Great Gray Owl, Greater Yellowstone Ecosystem, habitat selection, optimal neighborhood, resource requirements, scale

Introduction:

Knowledge of an organism's habitat requirements is central to ecology and conservation (Wiens 1989, Boyce and McDonald 1999, Manly et al. 2002). Habitat dictates a species' distribution, abundance, and persistence (Kearney 2006, Gaillard et al. 2010, Hall et al. 1997), primarily via habitat selection, a dynamic process by which individuals select or avoid resources to maximize fitness (Orians and Wittenberger 1991, Gaillard et al. 2010). Because animals balance multiple selective pressures via habitat choices, they can rely on habitats that are heterogeneously distributed through space and time to meet varying resource requirements. Therefore, key habitat can be context-dependent, and thorough evaluations of habitat selection are needed for a holistic understanding of an organism's resource requirements (Rosenzweig 1991, Gaillard et al. 2010).

Biological and ecological processes operate at different scales, and consideration of scale in habitat selection inquiries is long-standing (Johnson 1980, Hutto 1985, Wiens 1989, Levin 1992, Chave 2013, Cushman and Huettmann 2010). Resource selection can differ across spatiotemporal scales when selective pressures, limiting factors, and the environment change across space and time (Johnson 1980, Fahrig 1992, Rettie and Messier 2000, Mayor et al. 2009, Filla et al. 2017). Thus, habitat selection at one level cannot necessarily be used to make inferences about habitat preferences at another level (McLoughlin et al. 2002, 2004). Accordingly, although research has shifted from single- to multi-level habitat selection analyses and many taxa showcase scale-dependent resource selection (Mayor et al. 2009, Timm et al. 2016), cross-scale habitat associations for many species are lacking.

The scale of analysis can influence observed patterns of habitat selection (Boyce et al. 2003, Anderson et al. 2005, Boyce 2006), thereby underscoring the importance of empirically

testing the scales at which habitat selection occurs (Holland et al. 2004, Fisher et al. 2011). For example, habitat selection may depend on the scale at which selective processes are operating, and the composition and heterogeneity of the landscapes in which individuals reside (Mayor et al. 2007, Schaeffer and Mayor 2007, LaForge 2015). Scale-optimization analysis explicitly evaluates the neighborhood size (or optimal grain) at which individuals respond to environmental variables (Holland et al. 2004, Fisher et al. 2011, McGarigal et al. 2016, Klassen and Broekhuis 2018, Zeller et al. 2017). Likewise, scale optimization considers how surrounding habitat influences resource selection decisions (LaForge 2022). Incorporating ecologically-relevant, optimal grains in resource selection analysis can lead to greater ecological inference by specifically considering spatial scale of selection from the perspective of the study organism (Mayor et al. 2009).

Whereas scale-optimization empirically tests how spatial characteristics determine patterns of habitat selection, temporal scale also is critical to consider for a comprehensive understanding of resource requirements. For example, there is growing emphasis on the importance of the full annual cycle in ecology (Marra et al. 2015), particularly for understanding species distribution (Kéry et al. 2010, Fink et al. 2019) and population trends (Horns et al. 2018, Fink et al. 2019, Meehan et al. 2019). Similar attention to seasonal variation in resource selection is warranted, as resource requirements can change across time (Zweifel-Schielly et al. 2009), and the environmental conditions that an individual experiences throughout the annual cycle can influence fitness (Levin 1992, Marra et al. 2015).

Multi-scale, scale-optimized habitat selection analyses that consider the full annual cycle are needed particularly for rare, declining, or even understudied wildlife. The Great Gray Owl (*Strix nebulosa*) is an example of such a species, ranking as one of the rarest and least-studied

raptors in North America. Knowledge of Great Gray Owl habitat selection is limited, particularly during the non-breeding season. Furthermore, much of the boreal, montane, and sub-alpine forest habitat with which the Great Gray Owl is associated is characterized as restricted and vulnerable (BirdLife International 2016). Simultaneously, the Great Gray Owl has been characterized as at extreme risk because of threats related to anthropogenic environmental change (Siegel et al. 2014, Wilsey et al. 2019). Effective conservation of this iconic forest raptor and its habitat therefore requires improved understanding of its resource requirements and how they potentially vary across scales.

We evaluated the habitat selection of Great Gray Owls across the full annual cycle within the Greater Yellowstone Ecosystem (GYE) using scale-optimization techniques and multiple spatial (home-range selection and within-home-range) and temporal (breeding and non-breeding season) levels. We expected Great Gray Owl habitat selection to vary across scales in accordance with shifting environmental conditions and selective pressures. During the breeding season, we hypothesized that owls would place home ranges in areas including suitable nesting habitat, such as older-aged forest with high canopy cover (Bryan and Forsman 1987, Bull et al. 1988a, Franklin 1988, Whitfield and Gaffney 1997, Fetz et al. 2003, Wu et al. 2015). In contrast, snow conditions may limit the Great Gray Owl's ability to forage for primary prey (small mammals) and thus influence home-range selection during the non-breeding season (Bull et al. 1988a, Franklin 1988, Bull and Henjum 1990, Duncan 1992, Beck and Winter 2000, van Riper and van Wagtendonk 2006). We therefore predicted that the winter ranges of owls would include areas that facilitate easier access to subnivean prey including lower elevations, south-facing aspects, increased canopy cover, and roads/development that are cleared of snow or situated in areas of less deep snow.

We expected within-home-range selection to reflect foraging opportunities and refugia from predators and stressful thermal conditions. We therefore predicted that owls would select areas with increased primary prey and foraging opportunity (open meadows and wetlands, proximity to wetlands, and south-facing aspects) year-round. Because thermoregulatory risk changes during the breeding versus non-breeding seasons, however, we further predicted that more open, sun-exposed south-facing aspects also may allow owls to stay warm during the winter (Winter 1986, Duncan and Hayward 1994, Bull and Duncan 1993). However, areas of increased cover likely are important for protection from predators year-round (Bull and Henjum 1990, Duncan and Hayward 1994, Whitfield and Gaffney 1997), and minimize heat exposure during the breeding season (Beck and Smith 1987, Winter 1986, Franklin 1988, Sears 2006, van Riper et al. 2013).

Methods:

Study Area:

We conducted our research in the GYE primarily in Teton County, Wyoming, USA, between Hoback, Wyoming (43.3001º N, 110.8878º W), north along the Snake River riparian corridor and surrounding foothills of the Teton Range to Moran, Wyoming (43.8417º, 110.5081º W) (Figure 1). Data were collected within the Bridger-Teton National Forest, Grand Teton National Park, and on private lands. During the winter, Great Gray Owls also migrated to Targhee National Forest, Yellowstone National Park, and Lincoln and Sublette counties in Wyoming and Bonneville, Madison, and Teton counties in Idaho. The study area included riparian cottonwood (*Populus angustifolia*) and spruce (*Picea pungens*), aspen (*Populus tremuloides*), and conifer (*Pinus contorta*, *Pseudotsuga menziesii*, *Abies lasiocarpa*, *Picea*

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engelmannii) forest, wet and mesic meadows, sagebrush (*Artemisia tridentata*) steppe, ranchlands, agriculture, high-alpine forest (*Pinus albicaulis*) and meadow, and scree. The elevation at the valley floor averaged 1900 m, and housing subdivisions were located throughout portions of the study area but rarely above 2100 m. The study area was characterized by high seasonality including extensive winters with deep snow and relatively dry, warm summers.

Capture, Tagging, and Location Data:

We opportunistically located adult Great Gray Owls at known territories for capture between 2017–2021. Capture techniques primarily involved the use of bal-chatri, bow-net, and pan traps, and capture, banding, and tagging methods adhered to standard raptor handling protocols (Bloom et al. 2007). We determined sex of captured owls using genetic tests (Animal Genetics, Inc.) and morphological measurements. Based on comparisons between genetic tests and morphometric data, we previously determined that measurements of toe-pad length can be used to sex individuals in the field within our study population (toe-pad ≥70 mm = female, <70 mm = male). We determined age of owls based on molt (Suopajarvi and Suopajarvi 1994).

We tagged owls with Global Positioning System (GPS) remote-download transmitters (Lotek Swift-Fix), outfitted as either tail-mount or back-pack attachments (Bloom et al. 2007). Transmitters (20g and 30g units) weighed ≤ 3% of the owl's body weight (males = ~1050 g, females = ~1300 g). Transmitters collected year-round locations ranging from one location/24 hr to one location/hr, and the units had a typical lifespan of 1–3 yrs depending on the model. GPS location data were collected from transmitters using Very High Frequency homing techniques and a wireless downloader. We excluded GPS locations with high Dilution of Precision (DOP) values from our analysis (DOP > 5) due to their lower probability of accuracy (Lotek Wireless

Inc. 2021).

Habitat Covariates and Scale Optimization:

We used remotely-sensed GIS data to quantify environmental covariates, extracting raster

values to used and available points for resource selection analyses (see *Statistical Analysis*

section). We incorporated covariates we deemed as potentially biologically-relevant

determinants of habitat selection at each spatiotemporal scale. We included land cover type,

forest stand age, canopy cover, elevation, slope, aspect, Topographic Position Index (TPI) (a

measure of terrain ruggedness), Integrated Moisture Index (IMI) (a measure of soil moisture)

(Evans et al. 2014), distance-to-development, distance-to-road, and distance-to-wetland habitat.

We used 2019 National Land Cover Database data (Dewitz and USGS 2021), specifically

incorporating pasture/cultivation; deciduous, evergreen, and mixed forest; shrub/scrub; woody

and emergent herbaceous wetlands; grassland/herbaceous; and development (based on

reclassification of open space, and low, medium, and high intensity development categories).

Additionally, we reclassified all wetland types into a "wetland" classification. For all distance

rasters, we calculated the distance from each cell center to the nearest cell with that covariate

value (land cover raster data) or feature (roads). The distance-to-road layer was created using the

United States Geological Survey (USGS) road layers for Idaho and Wyoming (USGS 2022a,b).

We used 2020 Landfire Existing Vegetation Cover (EVC) and Existing Vegetation Height

(EVH) data for forest stand age and canopy cover (Landfire 2020a,b). We also included

elevation and derived slope and aspect from a 30 m Digital Elevation Model (DEM) (USGS

2021). Aspect was transformed into a circular transformation of aspect (TRASP) index, in which

a value of zero equates to north/northeast slopes and a value of 1 equates to southerly slopes

(Roberts and Cooper 1989). All raster covariates had an analytical grain of 30 m $\times$ 30 m and we projected them in Universal Transverse Mercator Zone 12N North American Datum 83.

Statistical Analysis:

We scale-optimized each environmental covariate (separately, for the home-range and within-home-range models, and within the breeding and non-breeding seasons, respectively) to determine the optimal neighborhood size for each variable at that given order of selection (Fattebert et al. 2018). We scaled each covariate at increasing intervals (of 60 m, corresponding to an increase of 30 m $\times$ 30 m (30 meters squared) in each direction from the focal cell) from 90 meters squared up to 3 kilometers squared. We increased covariate neighborhoods >3 kilometers squared by 500 m intervals up to 15 kilometers squared for the breeding season and 20 kilometers squared for the non-breeding season. We determined maximum neighborhood sizes based on mean Kernel Density Estimates (KDE) of overall range areas. Specifically, we calculated core area (50% contour), home range area (95% contour), and overall area (99% contour) using an *h* value (or bandwidth) of 200 because this value appeared to fit the data best without over-smoothing the areas (Silverman 1986, Wand and Jones 1995). The maximum neighborhood sizes (15 kilometers squared and 20 kilometers squared) approximately corresponded to the mean overall breeding and winter range areas for Great Gray Owls (see *Results* section). We identified the optimal neighborhood size for each covariate for a given level of habitat selection by fitting singular linear regressions of use versus availability as a function of each scaled variable and selecting the optimal size based on the model with the lowest Akaike's Information Criterion value corrected for small sample size (AIC$_c$) for that given variable. We incorporated top scale-optimized variables into global Resource Selection Function (RSF)

models. To illustrate this scale-optimization process, rather than simply incorporating a binary raster with 30 meters squared pixels indicating "forest" and "non-forest" at used and available sites in the RSF models, we iteratively tested the degree to which proportion of forested cells within x number of neighborhood cells (x = 2 cells (90 meters squared), 4 cells (150 meters squared)…665 cells (19,980 meters squared)) best explained selection of forest.

We delineated between breeding (April–September) and non-breeding seasons (October–March) for analysis. For each season, we used Generalized Linear Mixed Models (GLMMs) with binomial error distributions to create RSFs based on a used versus available design (Manly et al. 2002). For each season, we created RSFs for home-range (where on the landscape owls place their home ranges) and within-home-range (sites owls select within their home ranges) selection. In order to assess home range selection, we defined availability via a MCP (buffered by 20 km, based on maximum mean overall range size) drawn around all of the combined study animal locations, delineating the overall study area. We randomly selected available points from this population-level MCP. We selected "used" points by randomly selecting available points from within 95% KDE home-range areas for each owl, assuming that the entire home-range area was "used" at this spatial scale (DeCesare et al. 2012). For the RSF analysis, we estimated KDEs using "href" as the h value to define availability broadly. At the within-home-range scale, we randomly selected available points from within 95% KDE areas, and used points were the actual GPS locations. For each scale, we iteratively tested ratios of used-to-available points (1:1, 1:2…1:20). We used a ratio of 1:5, as model coefficients reached an asymptote and changed minimally when the ratio was increased beyond 1:5.

We scaled covariates to a mean of 0 and a standard deviation of 1 so we could compare effect size between each variable. To account for potential collinearity between covariates, we

tested for correlation using Spearman's rho ($|r| > 0.7$). When we encountered correlation between variables, we removed the covariate that we expected to be less biologically relevant. We did not include evergreen forest or canopy cover in global RSF models because they were positively correlated with canopy height ($|r| = 0.92, 0.96; 0.881, 0.974; 0.846, 0.915, 0.856, 0.916$ for the breeding home-range and within-home-range models and the winter home-range and within-home-range models, respectively), which we expected was most biologically relevant for owls. We checked for outliers in our data using Cook's Distance, confirming that Cook's Distance values were less than 1. We checked for non-linearity in our data and incorporated a quadratic effect for elevation. We included individual-by-year as a random effect, to account for any variation in our models explained by individual owls (Gillies et al. 2006). We fitted GLMMs using the R package 'lme4' (Bates et al. 2015).

We used a backward step-wise selection approach to identify the most parsimonious model based on AIC_c value (Hosmer et al. 2013, Burnham and Anderson 2002) for each scale of resource selection. We removed the most insignificant variables ($P > 0.05$) one-by-one, with the GLMM re-run after each removal, until only significant variables remained (Hosmer et al. 2013).

R-squared values, which are metrics that can indicate how well a model fits the data, are not well-suited to use-availability data because inherent contamination occurs between used and available locations (Boyce et al. 2002). Instead, to evaluate model validity, we used a *k*-fold cross-validation approach to determine each model's ability to predict use versus availability accurately based on Spearman-rank correlation (Boyce et al. 2002). All statistical analyses were performed in R (R Core Team 2017).

Results:

Capture, Tagging, and Location Data:

We outfitted 42 adult GGOWs with remote-download GPS transmitters between 15 November 2017 and 01 September 2021. We collected 135,087 total locations for 22 male and 20 female owls, including locations for some individuals across multiple years (69 individuals-by-year). For the breeding season, we amassed 113,974 total locations (individual-year mean: 1600; range: 20–3,341). We collected 21,113 non-breeding-season locations (individual-year mean: 398; range: 11–1,288). Mean breeding overall range area was 13.92 km^2 ($\pm$ 1.77 km^2), mean home-range area was 8.39 km^2 ($\pm$ 0.99 km^2) and mean core area was 1.31km^2 ($\pm$ 0.10 km^2). Mean non-breeding overall range area, home range area, and core area were 19.50 km^2 ($\pm$ 1.22 km^2), 13.37 km^2 ($\pm$ 0.84 km^2), and 2.54 km^2 ($\pm$ 0.16 km^2), respectively.

Scale Optimization:

We observed different optimal neighborhood sizes for environmental covariates depending on both spatial and temporal scale of habitat selection (Table 1). Optimal neighborhood sizes generally were larger for home-range habitat selection, particularly during the non-breeding season. During the breeding season, optimal neighborhood sizes for home-range selection ranged from 0.87 kilometers squared to 15 kilometers squared and sizes for within-home-range selection ranged from 0.15 kilometers squared to 15 kilometers squared. During the non-breeding season, optimal neighborhood size ranged from 2.43 kilometers squared to 20 kilometers squared and 0.09 kilometers squared to 12.5 kilometers squared for home-range and within-home-range selection, respectively.

Breeding-Season Resource Selection:

Breeding-season habitat selection varied between the home-range and within-home-range scales. Great Gray Owls selected mature forests (increased canopy height) for breeding home ranges, including wooded wetland, deciduous and mixed forests (Table 2, Figure 2). They also chose steeper slopes, northerly aspects, valleys, increased soil moisture, higher elevation (Figure 3), and closer proximity to development, roads, and wetlands. Breeding home range selection was negatively related to pasture/cultivated, herbaceous, herbaceous wetlands, and developed habitat. Within breeding home ranges, owls similarly selected increased canopy height, wooded wetlands, ridges, northerly aspects, and proximity to roads and wetland areas. Likewise, owls were less likely to use increased proportion of pasture/cultivated, developed, and herbaceous habitat (Table 3, Figure 4). However, in contrast to the home-range scale, owls selected herbaceous wetlands, shallower slopes, and decreased soil moisture.

Non-Breeding-Season Resource Selection:

In contrast to the breeding season, during the winter Great Gray Owls placed home ranges in developed areas, south-facing aspects, lower elevations, and valleys (Table 4, Figures 3,5). They also selected wooded wetlands and mixed forest in particular, whereas they were less likely to use deciduous forest and shrub habitat. Similar to the breeding season, they also chose winter home ranges with steeper slopes, increased canopy height, proximity to roads and development, and soil moisture, and were less likely to use herbaceous land cover. Within non-breeding home ranges, owls were less likely to use development and chose to be farther from development (Table 5, Figure 6). They also selected increased canopy height, wooded wetlands, north-facing aspects, shallow slopes, valleys, proximity to wetlands, and decreased soil moisture, whereas they were less likely to use pasture/cultivated, shrub, herbaceous wetland, and

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herbaceous habitats.

Model Validation:

Each of the four top models predicted habitat use well for the given spatiotemporal scale, based on cross-validation results. Mean Spearman's rank coefficients for folds k1-k5 were 0.97 ($\pm$ 0.06) and 0.93 ($\pm$ 0.12) for the breeding-season home-range and within-home-range models, and 0.98 ($\pm$ 0.02), and 0.99 ($\pm$ 0.01) for the non-breeding-season home-range and within-home-range models, respectively.

Discussion:

We evaluated the extent to which habitat selection varied across multiple spatiotemporal scales for the Great Gray Owl in the GYE. We observed different patterns of resource selection depending both on season and spatial scale, suggesting that abiotic conditions, limiting factors, and therefore key habitat can change over space and time. Great Gray Owls also selected habitat features at larger optimal neighborhood sizes at the home range versus the within-home-range scales. Optimal grain was therefore consistent with the implicit difference in spatial scale between broad placement of a home range on the landscape and site selection within that home range (McGarigal et al. 2016, Fattebert et al. 2018). Patterns of resource selection can be combined with observations of optimal grains to identify not only key habitat attributes but also the neighborhood sizes at which these features are selected. In turn, conservation and management efforts can target important resources at ecologically-relevant resolutions and considering the composition of surrounding habitat.

Resource selection differed across the annual cycle, suggesting that selective pressures

and limiting factors change across seasons, resulting in different habitat requirements. In the case of several habitat covariates, Great Gray Owls exhibited opposite patterns of resource selection during the breeding versus non-breeding. For example, owls selected deciduous forest during the breeding season but exhibited a strong negative relationship with this habitat during the winter. Abscission of leaves may result in deciduous forest no longer providing suitable cover during the non-breeding season. Likewise, habitat selection potentially shifted during the winter due to changing access to prey. Great Gray Owls hunt small mammals, which are primarily subnivean during the wintertime, and owls likely selected habitat that provided better access to prey beneath the snow during the winter. For example, although owls selected relatively forested, north-facing aspects during the breeding season, they placed their winter ranges within lower-elevations and open, south-facing aspects, which can be snow-free or have shallower snow cover that allows for easier foraging. During the winter in other regions or study periods in the GYE, Great Gray Owls moved to lower-elevation and snow-free areas (Winter 1986, Bull et al. 1988a, Franklin 1988, Duncan 1992, Beck and Winter 2000, van Riper and van Wagtendonk 2006, Jepsen et al. 2011). We did not evaluate winter habitat selection explicitly in relation to snow, and further research on Great Gray Owl winter movements and snow conditions is warranted.

Placement of a home range may not be sufficient if the area does not contain resources needed for functional processes that operate at finer spatial scales. Great Gray Owls require a "juxtaposition" of habitat for breeding: older-aged forest and meadows (Winter 1986, Greene 1995, Whitfield and Gaffney 1997, Quintana-Coyer 2004, van Riper and van Wagtendonk 2006, Keane et al. 2011, Wu et al. 2015). Our multi-scale habitat selection analysis illuminates how this juxtaposition manifests; Great Gray Owls selected breeding home-range areas dominated by relatively undisturbed mature forest, but these areas also contained herbaceous

wetlands, which owls used intensively relative to their availability within home range areas. Evaluating habitat selection across spatial scales can illuminate the nested, hierarchical nature of resource selection (Johnson 1980, Mayor et al. 2009, Meyer and Thuiller 2006). Although broad-scale habitat selection may reflect primary limiting factors (Rettie and Messier 2000), multi-scale assessments of habitat selection can reveal how animals use heterogeneous landscapes to meet such varying, spatiotemporally explicit resource requirements.

Several habitat attributes emerged as important for Great Gray Owls, including across multiple spatiotemporal scales. Throughout the annual cycle, Great Gray Owls consistently selected older-aged forests and wooded wetlands. Mature forests and riparian woodlands likely provide sufficient cover, which may be important for thermoregulation during the breeding season and for protection from predators year-round. Other studies corroborate that Great Gray Owls can occupy a diversity of forest types (Bull et al. 1988b, Bull and Henjum 1990, Wu et al. 2015, Polasik et al. 2016), as long as stands are sufficiently mature with dense overstory cover (Greene 1995, Whitfield and Gaffney 1997, Fetz et al. 2003, Wu et al. 2015). Older-aged forests provide suitable nesting structures (Nero 1980, Bryan and Forsman 1987, Franklin 1988, Whitfield and Gaffney 1997, Wu et al. 2015), cover (Bull and Henjum 1990, Greene 1995, Wu et al. 2015), and even foraging opportunities (Bryan and Forsman 1987, Bull and Henjum 1990). Additionally, riparian forests and herbaceous wetlands likely function as primary foraging areas. Both habitats are characterized by loose, moist soils (Faber-Langendoen et al. 2019) and contain *Thomomys* and *Microtus* species (Mattson 2004, Bedrosian et al. 2015), the primary prey of Great Gray Owls in our study system (Bedrosian et al. 2015, Franklin 1988). Likewise, riparian forests tend to occur at lower elevations and can contain shallower snow depths, which may facilitate foraging during the winter in particular. Our observation that Great Gray Owls were

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less likely to use pasture/cultivated, xeric meadows, or shrub habitats year-round indicates that these areas are less suitable for owls.

Evaluating resource selection across scales also can reveal the complexity of species-habitat associations, which vary as limiting factors and environmental conditions change across space and time. For example, the relationship between Great Gray Owl distribution and human activity varied depending on spatiotemporal scale and anthropogenic variable. Selection for proximity to roads across spatiotemporal scales may be an artifact of our sampling design for capturing owls, which prioritized more accessible territories. At the same time, roads are often routed through lower elevation areas and riparian corridors, so disproportionate use of roads may be a function of their location in optimal owl habitat (van Riper et al. 2013). Finally, owls may select roadsides to predate small mammals that cross or congregate around roads. Owls had a negative response to development during the breeding season and at the within-home-range scale during the winter. Similarly, in the Sierra Nevada, owls preferred lower levels of human activity (van Riper et al. 2013) and avoided human disturbance within breeding territories (Wildman 1992), and during the winter (Jepsen et al. 2011). However, we found owls placed winter home ranges in developed areas, potentially because otherwise suitable wintering areas were altered by anthropogenic activity (Hansen and Rotella 2000, Smith and Wachob 2006, Storm et al. 2007, Jepsen et al. 2011, Lendrum et al. 2012). Further research on patterns of distribution prior to and after development, and across a gradient of development (but see Jepsen et al. 2011, van Riper et al. 2013) can clarify understanding of natural habitat associations and the impact of anthropogenic activity on resource selection.

Inference from thorough assessments of habitat preferences clarify the vulnerability of wildlife to particular factors. For example, increased drought and reduced snowpack associated

with a changing climate threaten wetland systems that function as year-round Great Gray Owl

habitat. Likewise, increasing and intensifying wildfire events, disease and insect outbreaks, and

drought related to climate change as well as logging, resource extraction, and development

threaten the mature forest habitat on which this species relies year-round (Bull and Henjum

1990, Romme and Turner 2015, Allen et al. 2010). Already, Great Gray Owl population declines

are presumed in several regions of the western United States due to the loss of mature forest

(Winter 1986, Bryan and Forsman 1987), and any further reduction in this habitat likely will be

consequential for this species. Great Gray Owl winter habitat may be limited, as riparian habitat

makes up a relatively small portion of the landscape in western North America (Knopf et al.

1988) and is disproportionately altered by development (Hansen and Rotella 1999, Jepsen et al.

2011) and dams (Kozlowski 2002). Finally, increasing overlap between owls and anthropogenic

activity can result in increased risk for this species, for example due to vehicle collisions (Wu et

al. 2016).

We conducted a comprehensive assessment of Great Gray Owl resource selection that

advances knowledge of breeding-season habitat and fills in critical information gaps regarding

non-breeding-season resource requirements. Our findings demonstrate that single-scale analyses

of habitat selection may not identify intra-annual variation in resource requirements (Schooley

1994). Likewise, management of breeding-season habitat does not necessarily address

conservation needs across the full annual cycle. Using the Great Gray Owl as a model species,

we demonstrate how a multi-level, scale-optimized analytical framework can broaden ecological

understanding and strengthen hierarchical conservation recommendations. For example,

knowledge of key habitat can improve the protection of resources surrounding a breeding site,

the identification of suitable patches of potential habitat for survey efforts, or the maintenance of

landscape connectivity between breeding and winter ranges. Such a holistic approach can be

applied to any species of conservation concern or research interest for which understanding of

comprehensive habitat associations are lacking.

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Tables:

Table 1. Optimal neighborhood sizes (in kilometers squared) of environmental covariates included in global Resource Selection Functions used to assess habitat selection at the home-range (HR) and within-home-range (WHR) scales by adult Great Gray Owls (n = 42) in the Greater Yellowstone Ecosystem between 2017–2022.

Covariate	Breeding		Non-breeding	
	HR	WHR	HR	WHR
Aspect	1.53	0.57	20	0.51
Canopy Height	0.93	0.15	7.5	0.09
Developed	12.5	0.27	10	1.29
Herbaceous	5	5	7.5	3.5
IMI	12.5	0.57	20	5
Slope	15	0.21	20	12.5
TPI	5	2.13	15	0.09
Woody Wetland	15	15	17.5	0.09
Herbaceous Wetland	15	15		0.09
Pasture/Cultivated	15	1.89		0.21
Deciduous	2.5		20	
Elevation	3.5		20	
Mixed Forest	5		10	
Shrub			2.43	0.09

Table 2. Scaled and centered fixed-effect beta coefficients (β), standard errors (SE), p-values, and confidence intervals (CI) of the top generalized linear mixed-model (based on Akaike's Information Criterion adjusted for small sample size) for resource selection functions used to assess breeding-season (April–September) home range selection by adult Great Gray Owls (n =42) between 2017–2022 in the Greater Yellowstone Ecosystem.

Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	-3.120	0.059	<0.001	-3.236	-3.004
Aspect	0.261	0.005	<0.001	0.251	0.270
Canopy Height	0.659	0.006	<0.001	0.648	0.671
Deciduous	0.597	0.006	<0.001	0.585	0.608
Developed	-0.183	0.010	<0.001	-0.203	-0.163
Distance to Developed	-0.699	0.008	<0.001	-0.714	-0.684
Distance to Road	-0.505	0.011	<0.001	-0.526	-0.484
Distance to Wetland	-0.064	0.006	<0.001	-0.075	-0.053
Elevation	-0.192	0.010	<0.001	-0.212	-0.173
Elevation^2	0.166	0.008	<0.001	0.151	0.181
Herbaceous	-1.101	0.017	<0.001	-1.134	-1.069
Herbaceous Wetland	-0.081	0.008	<0.001	-0.096	-0.066
IMI	0.333	0.005	<0.001	0.322	0.344
Mixed Forest	0.139	0.005	<0.001	0.130	0.149
Pasture/Cultivated	-2.614	0.029	<0.001	-2.671	-2.557
Slope	0.495	0.008	<0.001	0.480	0.511
Woody Wetland	0.691	0.010	<0.001	0.671	0.712

Table 3. Scaled and centered fixed-effect beta coefficients (β), standard errors (SE), p-values, and confidence intervals (CI) of the top generalized linear mixed-model (based on Akaike's Information Criterion adjusted for small sample size) for resource selection functions used to assess within-home-range habitat selection during the breeding season (October–March) by adult Great Gray Owls (n =42) during 2017–2022 in the Greater Yellowstone Ecosystem.

Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	-2.985	0.058	<0.001	-3.098	-2.872
Aspect	0.123	0.005	<0.001	0.113	0.132
Canopy Height	0.627	0.005	<0.001	0.617	0.637
Developed	-0.232	0.006	<0.001	-0.244	-0.220
Distance to Roads	-0.048	0.005	<0.001	-0.058	-0.037
Distance to Wetlands	-0.159	0.005	<0.001	-0.168	-0.150
Herbaceous	-0.213	0.008	<0.001	-0.229	-0.197
Herbaceous Wetland	0.142	0.010	<0.001	0.123	0.161
IMI	-0.256	0.006	<0.001	-0.268	-0.245
Pasture/Cultivated	-0.315	0.016	<0.001	-0.347	-0.283
Slope	-0.422	0.005	<0.001	-0.432	-0.412
TPI	0.167	0.004	<0.001	0.160	0.174
Woody Wetland	0.184	0.009	<0.001	0.165	0.202

Table 4. Scaled and centered fixed-effect beta coefficients (β), standard errors (SE), p-values, and confidence intervals (CI) of the top generalized linear mixed-model (based on Akaike's Information Criterion adjusted for small sample size) for resource selection functions used to assess non-breeding-season (October–March) home range selection by adult Great Gray Owls (n =42) during 2017–2022 in the Greater Yellowstone Ecosystem.

Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	-2.852	0.047	<0.001	-2.945	-2.760
Aspect	-0.052	0.014	<0.001	-0.079	-0.025
Canopy Height	0.287	0.023	<0.001	0.243	0.332
Deciduous	-1.758	0.026	<0.001	-1.808	-1.708
Developed	0.132	0.017	<0.001	0.098	0.165
Distance to Developed	-0.304	0.014	<0.001	-0.331	-0.277
Distance to Roads	-0.578	0.023	<0.001	-0.624	-0.532
Elevation	-0.260	0.024	<0.001	-0.306	-0.213
Elevation^2	-0.168	0.018	<0.001	-0.204	-0.133
Herbaceous	-0.810	0.024	<0.001	-0.856	-0.763
IMI	0.267	0.009	<0.001	0.249	0.285
Mixed Forest	0.640	0.011	<0.001	0.618	0.661
Shrub	-0.206	0.016	<0.001	-0.238	-0.175
Slope	1.664	0.021	<0.001	1.623	1.705
TPI	-0.026	0.009	<0.001	-0.045	-0.008
Woody Wetland	0.924	0.014	<0.001	0.897	0.950

Table 5. Scaled and centered fixed-effect beta coefficients (β), standard errors (SE), p-values, and confidence intervals (CI) of the top generalized linear mixed-model (based on Akaike's Information Criterion adjusted for small sample size) for resource selection functions used to assess non-breeding-season (October–March) within-home-range selection by adult Great Gray Owls (n = 42) during 2017–2022 in the Greater Yellowstone Ecosystem.

Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	-3.245	0.047	<0.001	-3.338	-3.153
Aspect	0.087	0.010	<0.001	0.067	0.107
Canopy Height	0.577	0.016	<0.001	0.545	0.608
Developed	-0.204	0.015	<0.001	-0.234	-0.175
Distance to Developed	0.090	0.012	<0.001	0.067	0.112
Distance to Roads	-0.081	0.013	<0.001	-0.106	-0.056
Distance to Wetland	-0.032	0.011	0.003	-0.053	-0.011
Herbaceous	-0.206	0.015	<0.001	-0.235	-0.176
Herbaceous Wetland	-0.278	0.019	<0.001	-0.316	-0.240
IMI	-0.102	0.009	<0.001	-0.120	-0.085
Pasture/Cultivated	-0.996	0.051	<0.001	-1.095	-0.896
Shrub	-0.424	0.017	<0.001	-0.458	-0.391
Slope	-0.524	0.017	<0.001	-0.556	-0.491
TPI	-0.201	0.008	<0.001	-0.217	-0.185
Woody Wetland	0.123	0.009	<0.001	0.104	0.141

Figures:
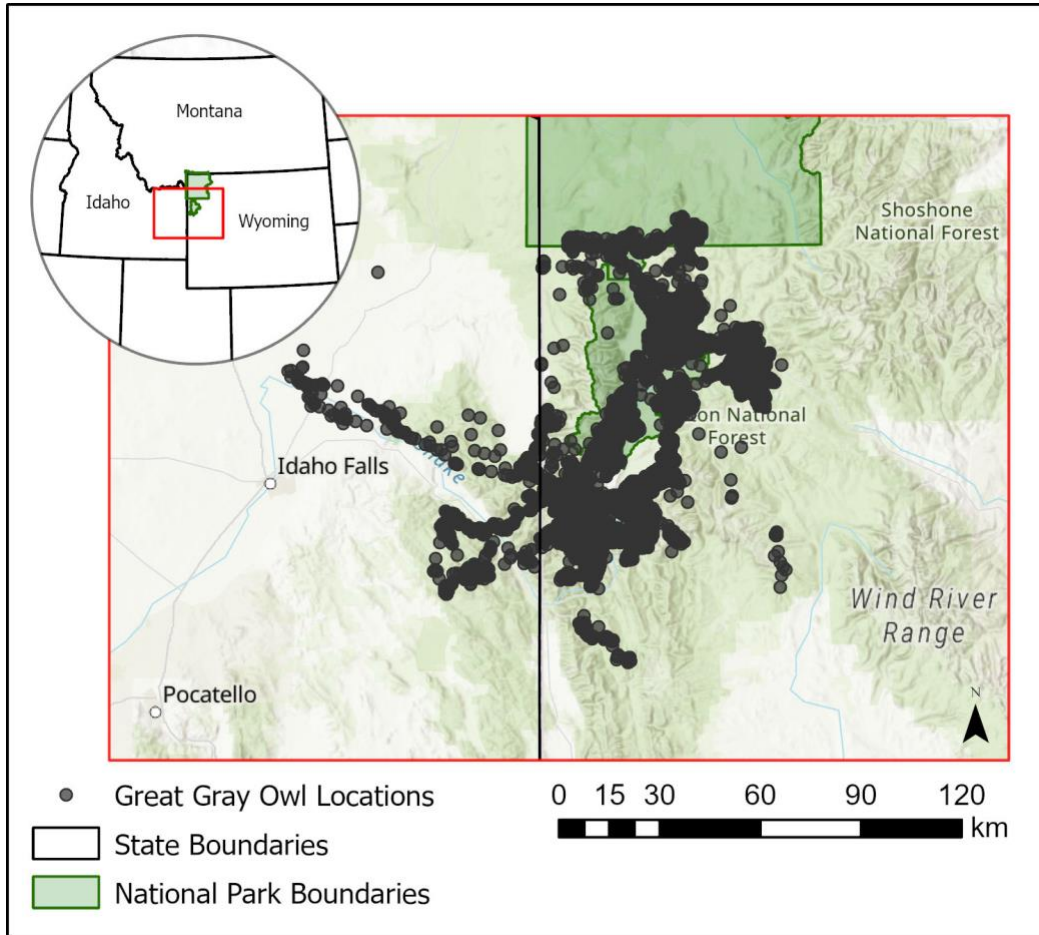
Figure 1. Study area within the Greater Yellowstone Ecosystem in northwestern Wyoming and eastern Idaho. Great Gray Owl locations (n = 135,087) collected from Global Positioning System (GPS) transmitters (n = 42) during 2017–2022 are shown with gray circles.
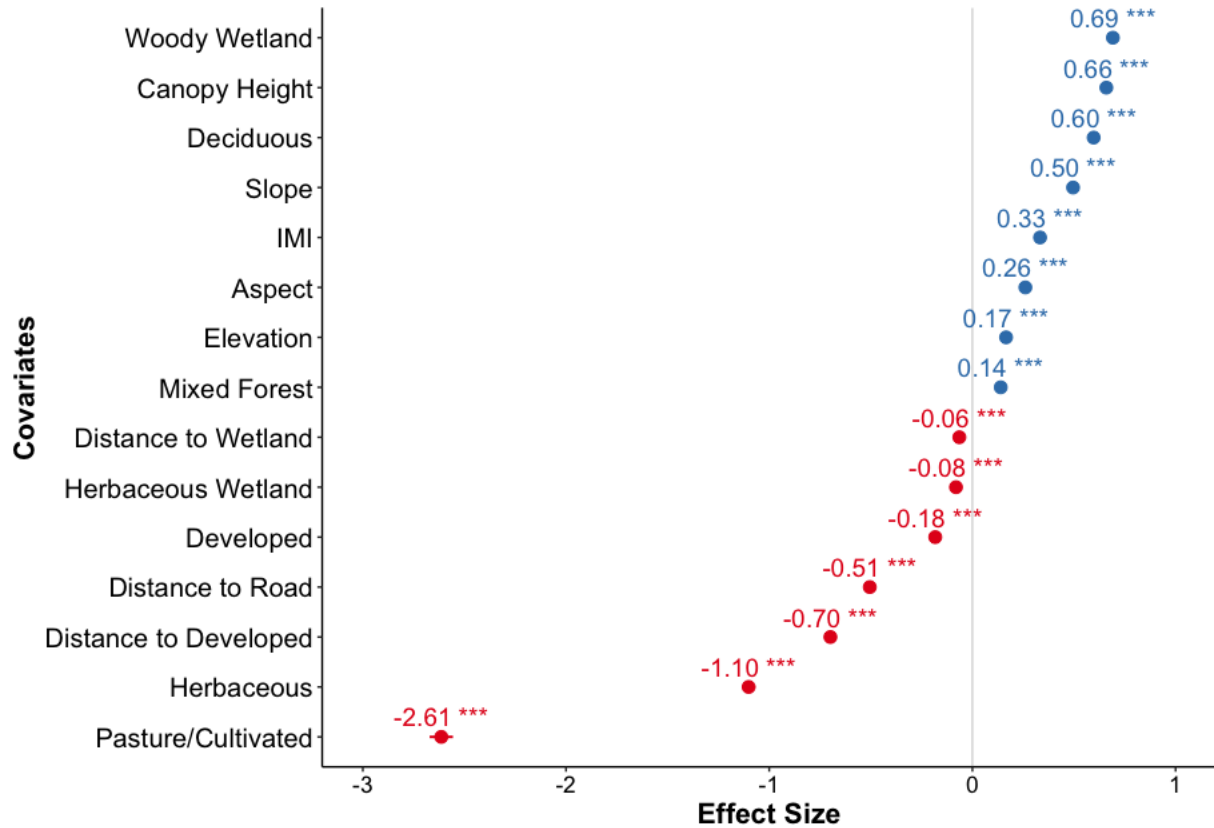
Figure 2. Breeding-season (April–September) home-range habitat selection by adult Great Gray Owls (n = 42) from 2017–2022 in the Greater Yellowstone Ecosystem. Summary results are based on resource selection functions relating the relative selection strength of scaled and centered environmental covariates. Results are derived from top, model-averaged Generalized Linear Mixed-Models based on values of Akaike's Information Criterion adjusted for small sample size. Values indicate estimated model coefficients (mean ± 95% confidence interval), and asterisks indicate statistical significance values ('***' = $P \leq .001$, '**' = $P \leq .01$, '*' = $P \leq$ .05). Positive values indicate increased probability of use relative to availability and negative values indicate decreased probability of use.

Figure 3. Probability of use of elevation during the breeding season (April–September) (A) versus non-breeding season (B) by adult Great Gray Owls (n = 42) from 2017–2022 in the Greater Yellowstone Ecosystem. Results are derived from top, model-averaged Generalized Linear Mixed-Models used to assess resource selection at the home-range spatial scale. Gray indicates 95% confidence intervals.
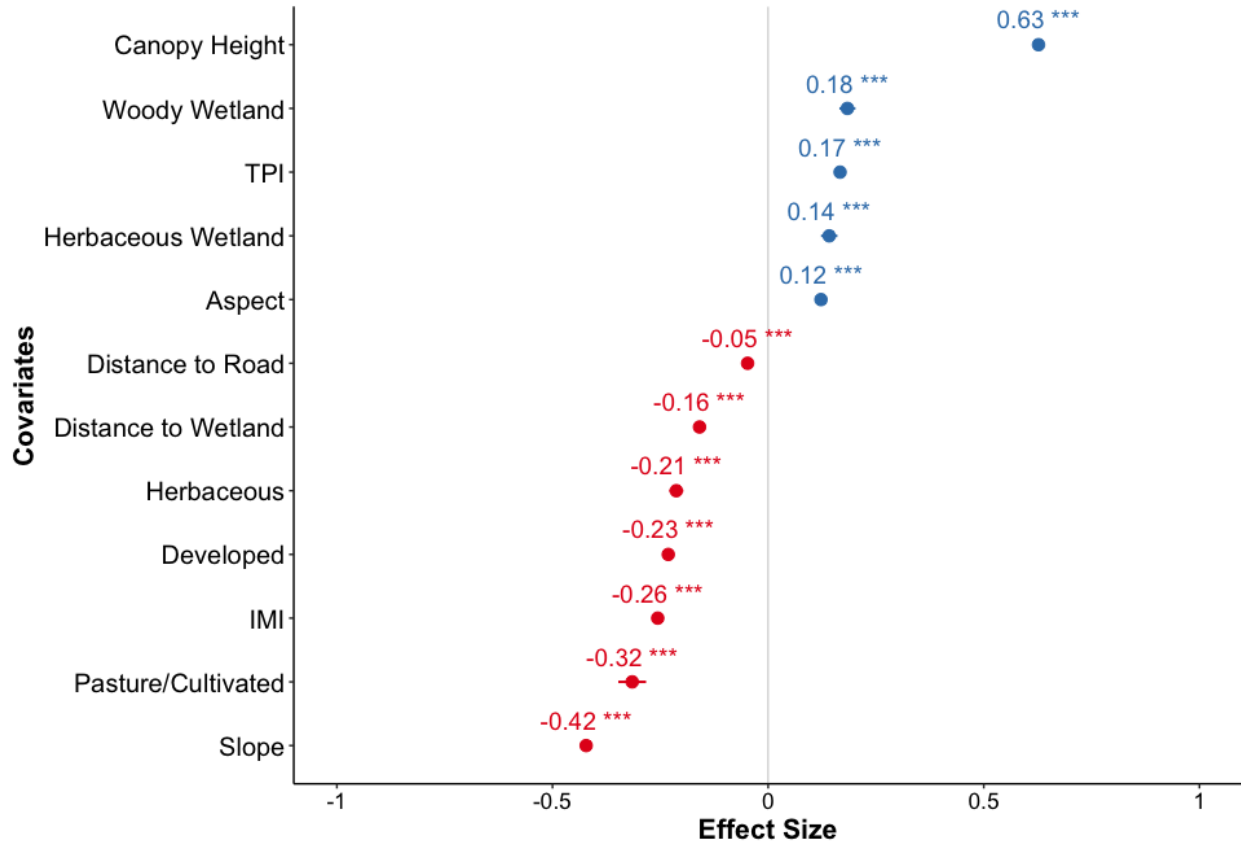
Figure 4. Within-home-range habitat selection by adult Great Gray Owls (n = 42) during the breeding-season (October–March) from 2017–2022 in the Greater Yellowstone Ecosystem. Summary results are based on resource selection functions relating the relative selection strength of scaled and centered environmental covariates. Results are derived from top, model-averaged Generalized Linear Mixed-Models based on values of Akaike's Information Criterion adjusted for small sample size. Values indicate estimated model coefficients (mean ± 95% confidence interval), and asterisks indicate statistical significance values ('***' = $P \leq .001$, '**' = $P \leq .01$, '*' = $P \leq .05$). Positive values indicate increased probability of use relative to availability and negative values indicate decreased probability of use.

Figure 5. Non-breeding-season (October–March) home-range habitat selection by adult Great Gray Owls (n = 42) from 2017–2022 in the Greater Yellowstone Ecosystem. Summary results are based on resource selection functions relating the relative selection strength of scaled and centered environmental covariates. Results are derived from top, model-averaged Generalized Linear Mixed-Models based on values of Akaike's Information Criterion adjusted for small sample size. Values indicate estimated model coefficients (mean ± 95% confidence interval), and asterisks indicate statistical significance values ('***' = $P \leq .001$, '**' = $P \leq .01$, '*' = $P \leq$ .05). Positive values indicate increased probability of use relative to availability and negative values indicate decreased probability of use.

Figure 6. Within-home-range habitat selection by adult Great Gray Owls (n = 42) during the non-breeding season (October-March) from 2017–2022 in the Greater Yellowstone Ecosystem. Summary results are based on resource selection functions relating the relative selection strength of scaled and centered environmental covariates. Results are derived from top, model-averaged Generalized Linear Mixed-Models based on values of Akaike's Information Criterion adjusted for small sample size. Values indicate estimated model coefficients (mean ± 95% confidence interval), and asterisks indicate statistical significance values ('***' = $P \leq .001$, '**' = $P \leq .01$, '*' = $P \leq .05$). Positive values indicate increased probability of use relative to availability and negative values indicate decreased probability of use.

CHAPTER TWO

Time-varying habitat selection by male Great Gray Owls

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Abstract:

Increased consideration of specific contexts and scales in habitat selection studies can reveal novel, ecologically important associations that otherwise may be masked by more general evaluations. For example, organisms can exhibit sex-specific habitat selection, or habitat choices can vary temporally as conditions and limiting factors change over time. We evaluated whether breeding-season habitat selection by adult male Great Gray Owls (n = 19) varied across diurnal periods. We focused specifically on male owls because their breeding habitat selection remains largely unknown despite the critical role they play as food provisioners. To address knowledge gaps related to nocturnal habitat, we also evaluated microhabitat selection by male owls at night. Owls avoided herbaceous wetlands during the day but strongly selected them at night, indicating context-dependent habitat selection and that open wetlands potentially comprise important foraging areas. Owls also chose nighttime microhabitat that enabled foraging, such as areas containing presence of primary prey and open understories dominated by graminoids and forbs. During the day owls selected higher canopy cover and areas of increased soil moisture, which likely provided suitable roosting habitat. Across taxa, knowledge of key habitat across behavioral roles, activity periods, and other contexts can improve the identification and conservation of critical habitat for wildlife. This work contributes to understanding of how animals balance resources related to food provisioning versus safety, both of which are critical for individual fitness and population persistence.

Key Words: Behavioral role, diel cycle, diurnal period, foraging, habitat selection, Great Gray Owl, sex-specific behavior, temporal scale

Introduction:

Understanding how and why animals use particular resources is a primary goal in ecology. Habitat selection can be context- and scale-dependent, as behavioral roles, selective pressures and the environment vary across space and time (Johnson 1980, Mayor et al. 2009, McLoughlin et al. 2010). Therefore, increased consideration of specific contexts and scales in habitat selection studies can reveal novel, ecologically important associations that otherwise may be masked by more general evaluations (Boyce et al. 2003, Northrup et al. 2021). Understanding such variation in how organisms select habitat is essential to identify key resources, as habitat choices have direct fitness implications, for example for reproductive success, food acquisition, and survival (Hutto 1985, Wiens 1989, Jones 2001).

Many organisms demonstrate sex-specific behavior, including habitat selection (Hillen et al. 2011, Marchand et al. 2015, Delaney and Warner 2016). Biological roles, physiological states, and risk factors can be unique to or more pronounced for a particular sex, which can result in specific habitat requirements. In many avian species, for example, females incubate eggs and brood chicks at the nest during the breeding season whereas males primarily are responsible for providing food to the female and young (Royle et al. 2012). Thus, males and females can experience different selective pressures during the reproductive period, as females are restricted to the nest site and males utilize a broader area for foraging and roosting. Although nest sites are a key resource for avian species because of their fitness implications for offspring (Millsap et al. 2015, van der Hoek et al. 2017, Jiménez-Franco et al. 2018), resources related to other ecological requirements, such as areas used by the food-provisioning parent for foraging (Naef-Daenzer et al. 2000, Pearce-Higgins and Yalden 2004) and suitable cover (Lack 1968, Sunde et al. 2003, Beck et al. 2013), also are important for successful reproduction. Considering sex-specific roles

in evaluations of habitat selection therefore can reveal critical resources that are unique to, or highly utilized by, a particular sex.

Habitat choices also can vary temporally because environmental conditions and selective pressures change over time. Individuals can modify habitat use according to changing levels of foraging availability (Godvik et al. 2009, Zweifel-Schielly et al. 2009, Tutterow 2021), risk (Laundré et al. 2001, Kohl et al. 2018, Smith et al. 2019, Gallo et al. 2022) or exposure (van Beest 2012). Indeed, many animals select habitat to maximize safety during times of increased risk, whereas they forage during windows of diminished risk, and these periods often coincide with diel intervals (Northrup et al. 2012, Filla et al. 2017, Kohl et al. 2018). Given sufficient habitat heterogeneity, organisms can balance this forage-safety trade-off by selecting habitat differently across time of day (Northrup et al. 2012, Richter et al. 2020). Despite the long-standing recognition that animals partition diel time (Park and Sejba 1935), however, understanding of how habitat selection varies across different diel periods remains limited for most species (Gaston 2019).

Accurately quantifying the context-dependent habitat selection and activity patterns of species that are difficult to observe can be particularly challenging. Much of the animal kingdom, for example, is nocturnally active (Hölker et al. 2010), yet studies that characterize nocturnal behavior remain rare (Gaston 2019). However, recent technological advances, including enhanced Global Positioning System (GPS) tracking technology, now enable the collection of data across the 24-hour cycle for many species (Lambert et al. 2009, Cozzi et al. 2012, Donati et al. 2012, Tan et al. 2013). Particularly for difficult-to-observe and/or nocturnal species, capitalizing on advanced monitoring technology to collect more comprehensive location data can improve understanding of behavior and habitat used across contexts and scales.

The Great Gray Owl *(Strix nebulosa)* is a secretive forest raptor that potentially exhibits sex-specific and time-dependent habitat selection during the breeding season. Females remain on or directly adjacent to the nest site to incubate eggs and brood young, whereas males provide food to nesting females and young during the nestling and post-fledging periods (April–September) (pers. obs., Beck and Smith 1987, Bull et al. 1988a, Bull and Henjum 1990, Duncan 1992). Furthermore, Great Gray Owls are relatively unique among *Strigiformes* in that they are thought to be somewhat crepuscular (active at dawn and dusk) (Reid 1989, Quintana-Coyer et al. 2004) and even can forage during the daytime (pers. obs., Reid 1989). Nighttime habitat and activity patterns are essentially unknown, however, which precludes a holistic understanding of Great Gray Owl habitat requirements and whether they change over time.

Here we used Great Gray Owls to evaluate whether habitat selection varies temporally, within the contexts of sex-specific behavior and differing selective pressures. Specifically, we quantified the habitat selection of adult males within their breeding home ranges, across different diurnal windows. We focused specifically on male owls because their breeding habitat selection remains largely unknown despite the critical role they play as food provisioners to mates and offspring. Moreover, to address knowledge gaps related to nocturnal habitat, we also evaluated microhabitat selection by male owls at night.

We expected that breeding-season habitat selection by male Great Gray Owls would be associated primarily with optimal foraging opportunities while also balancing risks that may vary diurnally. Great Gray Owls hunt small mammals primarily by sound and rely on perches from which they locate prey out in the open (Nero 1980, Bull and Henjum 1990, Bull and Duncan 1993) including in meadows, wetlands, and bogs (Nero 1980, Goggans and Platt 1992, Greene 1995, Sears 2006, Keane et al. 2011). Additionally, the species is associated with northern-

latitude boreal forests (Nero 1980, Mikkola 1983) and is well-adapted for cold conditions, but it can be susceptible to heat stress during the day. Finally, the Great Gray Owl is a secretive raptor that tends to avoid anthropogenic disturbance (van Riper et al. 2013, Jepsen et al. 2011, Gura et al. *in prep.*). However, perceived risk may vary depending on time of day in accordance with varying levels of human activity. Hence, we specifically predicted that owls would select areas of increased prey (wooded wetlands, open meadows and wetlands, and increased soil moisture) and foraging opportunity (proximity to woody and herbaceous wetlands) during dawn, dusk, and night, whereas they would select areas of increased cover (increased canopy cover) for thermoregulation at roosts during the day. Likewise, we hypothesized that nighttime site selection would be comprised of microhabitat characteristics that primarily facilitate foraging success. Specifically, we predicted that at night, owls would select microhabitats that contain primary prey (Northern Pocket Gophers (*Thomomys talpoides*) (Bedrosian et al. 2015, Franklin 1988)), coarse woody debris, and forested areas with open understory, and decreased basal area and canopy cover. Finally, we predicted that owls would avoid development and roads specifically during the day when human activity is highest.

Methods:

Study Area:

We conducted our study in Teton County, Wyoming, USA, within the Greater Yellowstone Ecosystem (GYE). The area was characterized by the rugged Teton mountain range as well as the Absaroka and Gros Ventre ranges, between which were extensive valleys primarily comprised of sagebrush steppe (*Artemisia tridentata*), and interspersed grasslands, riparian

corridors and ranch lands. The study area included the Snake River corridor and associated mixed cottonwood (*Populus angustifolia*)-spruce (*Picea pungens*) forest. The surrounding foothills were comprised of montane and subalpine forest primarily dominated by Lodgepole Pine (*Pinus contorta*), with patches of aspen (*Populus tremuloides*), Douglas Fir (*Pseudotsuga*), Engelman Spruce (*Picea engelmannii*), and Sub-alpine Fir (*Abies lasiocarpa*). Forests were interspersed with more open areas including sagebrush, willow, herbaceous meadow, montane meadow, and riparian habitats. The study area neared the southern-most extent of the contiguous species range for Great Gray Owls in North America.

Animal Capture and Movement Data:

Between March–May of 2018–2021, we targeted adult male Great Gray Owls for capture at known breeding territories within the study area. We identified adult male owls via behavioral observations in the field, toe-pad length measurements (toe-pad ≥70 mm = female, <70 mm = male (Gura, unpublished data)), and assessments of molt (Suopajarvi and Suopajarvi 1994) to confirm age and sex. We captured owls primarily using mouse lures in combination with pan, bal-chatri, and dho gazza traps (Bloom et al. 2007). We outfitted owls with GPS remote-download transmitters (Lotek SwiftFix) fitted as a backpack-style attachment using tubular Teflon ribbon (Bloom et al. 2007). We programmed transmitters to collect hourly GPS locations throughout the breeding season (15 March–30 September). We located tagged owls via Very High Frequency radio telemetry and downloaded GPS data from tags using a hand-held, wireless downloader (Lotek Wireless Inc. 2021).

Within-Home-Range Habitat Selection:

We incorporated remotely-sensed habitat data within a geographic information system (GIS) to evaluate habitat selection within breeding home ranges. We included only habitat variables with potential a priori biological relevance (Table 1). Specifically, we incorporated land cover type data (Dewitz and USGS 2021), including herbaceous, herbaceous wetland, woody wetland and developed habitat (reclassified from open space, low development, medium development, and high development land cover into one 'developed' classification); a distance-to-wetland raster (created by reclassifying herbaceous wetland and woody wetland classifications as a 'wetland' classification and calculating the nearest distance to a pixel with that classification); a distance-to-road raster (derived from USGS road layer for Wyoming (USGS 2023)); canopy cover data (Landfire 2020); and Integrated Moisture Index (IMI) data (Evans et al. 2014). We extracted remotely-sensed raster values to used and available owl locations (see *Statistical Analysis*).

Nocturnal Microhabitat Selection:

We evaluated microhabitat characteristics at a subset of locations used nocturnally by male owls during July–September 2018 and 2019 compared with paired available sites. We conducted surveys at approximately 30 used and 30 available locations for each owl. We selected used sites via a stratified random sampling design in which we selected no more than one used location per night per individual. This approach minimized spatiotemporal autocorrelation by ensuring that used sites were distributed across the breeding season rather than being clustered across a few nights. We randomly selected 30 available locations within the home ranges of each individual. We surveyed the sites within the same breeding season in which they were used. We primarily evaluated forest structure characteristics (Table 1), which likely

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did not change considerably over the course of the breeding season. Surveys were completed

prior to the abscission of leaves in autumn so that canopy cover measurements reflected

conditions during the breeding season.

We conducted habitat surveys using 0.04 ha fixed radius (12 m) plots (Solis and

Gutiérrez 1990, Bias and Gutiérrez 1992, Moen and Gutiérrez 1997). We first recorded the plot's

general habitat class (aspen, Douglas fir, lodgepole pine, marsh, meadow, mixed conifer, mixed

deciduous-conifer, sagebrush, subalpine fir, wet meadow, willow), dominant understory type,

and any special features (residential area, road, water feature, burned area, etc.). We measured

habitat characteristics that we predicted would facilitate access to prey and foraging success at

night (Table 1). From the plot center, we assessed the number of tree stories, and we measured

the distance to the nearest edge and meadow (if visible) using a range-finder. We defined 'edge'

as a change in primary habitat type from the plot habitat class. We defined a 'meadow' as a 5 m

$\times$ 5 m (or larger) opening containing grass, forbs, but no trees (based on field observations of

meadow openings utilized by Great Gray Owls for foraging). We collected four canopy closure

measurements (one in each cardinal direction) at five points within the plot (plot center and half

the plot radius in each cardinal direction) using a convex spherical densiometer. We calculated

the mean canopy closure for the plot based on these 20 measurements. We measured basal area

for live trees (within variable-radius plots using a 10-factor edge prism at plot center), noting the

tree species for each measurement of diameter at breast height. We tallied all coarse woody

debris (CWD) (1 m long and $\geq$ 12.5 cm in diameter) within the plot. We also tallied all snags

(dead trees standing or leaning between 0-45 degrees from vertical that are over 3 m high and

>12.5 cm diameter) within the plot. Finally, we recorded presence versus absence of primary

prey within each plot by surveying the area of the plot for Northern Pocket Gopher sign (soil

mounds in the form of eskers or tailings).

Statistical Analysis:

To evaluate both within-home-range habitat selection during different times of day and nocturnal microhabitat selection, we used Generalized Linear Mixed Models (GLMMs) with binomial error distributions to create Resource Selection Functions (RSFs) based on a used versus available design (Manly et al. 2002). We considered actual GPS locations of owls as used points, and calculated 95% Kernel Density Estimate (KDE) areas (using "href" as the *h* value to define availability broadly), from which we randomly selected available points. To provide core area and home range size estimates (Powell 2000) for male Great Gray Owls, we also calculated 50% and 95% KDE areas using an *h* value of 200, which we determined fit the data well based on visual inspection. Habitat attributes were extracted from rasters (for site-selection analyses) or collected via on the-the-ground surveys (nighttime microhabitat selection). We calculated variance inflation factors (VIF) within variables and removed variables with VIF > 3. We also tested for collinearity between covariates using Pearson's correlation, and ensured that all model covariates had a pairwise correlation r such that $-0.5 \leq r \leq 0.5$. If two variables were correlated ($-0.5 \geq r \geq 0.5$), we retained the variable that we expected may be a more important determinant of habitat selection.

For the within-home-range analysis, we began with a used-available ratio of 1:1 and iteratively re-ran the GLMMs with an increased ratio of available points (1:2, 1:3…1:20). However, increasing the ratio did not considerably alter the beta coefficients of the variables, so we selected the most parsimonious 1:1 ratio. Because we expected that resource selection may differ depending on the time of day, we delineated between dawn, day, dusk and night locations

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using the package 'suncalc' in R (Thieurmel and Achraf 2019). Specifically, we characterized

'dawn' locations as any locations that occurred at or after the start of morning astronomical

twilight and/or at or prior to the end of morning golden hour, 'day' locations as any locations that

occurred after the end of morning golden hour and prior to the start of evening golden hour,

'dusk' locations as any locations that occurred at or after the start of evening golden hour and

prior to the start of night, and 'night' locations as any locations that occurred at or after the start

of night and prior to the start of morning astronomical twilight. We included interaction terms

between time of day and covariates incorporated into the global RSF model. For the nighttime

microhabitat selection analysis, the ratio of used to available points was approximately 1:1 (we

were unable to access survey sites in limited cases). Microhabitat model covariates consisted of

the aforementioned habitat metrics collected via field surveys.

We included individual-by-year as a random effect in GLMMs to account for variation

attributable to individual owls (Gillies et al. 2006). For both within-home-range habitat selection

and nighttime microhabitat selection analyses, we began with a global model containing all

covariates and used a manual, backwards step-wise approach, removing variables that were not

statistically significant ($P > 0.05$). We compared model iterations and selected the most

parsimonious model based on the Akaike Information Criterion value corrected for small sample

size (AIC$_c$) (Hosmer et al. 2013, Burnham and Anderson 2002). If additional models were within

two AIC$_c$ values of the top model, we used model averaging to account for uncertainty between

the top candidates (Johnson and Omland 2004). To evaluate model performance, we used a *k*-

folds cross-validation approach that compared expected versus observed outcomes to determine

predictive ability (Boyce et al. 2002). We performed all statistical analyses in the program R (R

Core Team 2017), and fitted GLMMs using the R package 'lme4' (Bates et al. 2015).

Results:

We collected 73,299 breeding-season GPS locations for 19 adult male Great Gray Owls (per owl minimum = 241, maximum = 8,017, mean = 3,857, SD = 2,232) between 2018–2022. Overall, these data resulted in locations for 35 individuals-by-year (minimum = 241, maximum = 3,329, mean = 2,094, SD = 955). The data included 9,208 dawn, 36,385 daytime, 8,749 dusk, and 18,957 nighttime locations. Mean core area size was 1.75 km^2 (SE = 0.18) and mean home range size was 11.8 km^2 (SE = 2.14) (based on 50% and 95% KDEs). We conducted 618 microhabitat habitat surveys within breeding home ranges of eleven adult male owls during 2018–2019.

The habitat selection of male Great Gray Owls within their home ranges varied by temporal period (day, night, dawn, dusk) (Table 2). Owls selected areas with a higher proportion of herbaceous wetland during dawn, dusk, and nighttime, whereas probability of use of such wet and mesic meadows decreased during the day (Figure 2A). Across diurnal periods, though particularly during the day, owls selected areas with increased canopy cover and were less likely to use herbaceous meadows (drier meadows) and development (Figure 2B-D). Owls selected areas closer to roads, particularly during the day (Figure 2E), and closer to wetlands, particularly during dusk and at night (Figure 2F). We observed weak evidence that owls chose areas with increased soil moisture during the day whereas probability of use decreased during dawn, dusk, and at night (Tables 2,3). Finally, owls selected wooded wetlands to a similar extent across diurnal periods (Table 2). Cross validation results indicated that the within-home-range model predicted habitat use well, as mean Spearman's rank coefficient for folds k1-k5 was 0.792 (SD =

0.013).

Male Great Gray Owls selected nighttime microhabitats based upon dominant understory type, presence of primary prey, and dominant tree species (Table 4, Figure 2). Four different models at this scale, however, had comparable support (within 2 AIC_c values of the top model) (Table 5). Model-averaged results indicated that owls selected understories containing grass, forbs, and shrubs (as opposed to sagebrush, willow, or saplings). Owls also tended to select nighttime microhabitats with presence of Northern Pocket Gopher sign and were less likely to use areas with a dominant habitat class of Douglas Fir and Lodgepole Pine forest (Table 4, Figure 2).

Discussion:

We evaluated habitat selection in the context of a sex-specific behavioral role and time-dependent activity patterns, specifically for adult male Great Gray Owls during the breeding season. Resource selection by adult males revealed critical foraging habitat and roosting areas for this species, such as herbaceous wetlands and areas of high canopy cover. Additionally, consideration of how habitat selection differed across diel periods suggests how functional processes and resultant resource requirements vary according to temporal periods. For example, owls selected herbaceous wetlands specifically at dawn, dusk, and night, indicating they do not forage in open wetlands during the day. Such assessments of context- and time-dependent habitat selection not only help identify key habitat but also strengthen inference regarding how and why resources are utilized by animals.

Consideration of context-dependence in assessments of habitat selection can reveal key

resources for wildlife that otherwise may be overlooked (Northrup et al. 2021). For example, male Great Gray Owls exhibited temporal variation in habitat selection of herbaceous wetlands, with increased probability of use at dawn, dusk, and night compared with decreased use during the daytime. If we evaluated habitat selection solely based upon day-time observations of owls, we likely would fail to recognize that herbaceous wetlands were highly utilized during the breeding season. Similarly, the relative importance of open wetlands may not have been apparent had we assessed resource selection of females, as they tend to be localized at nest sites during the breeding period. Finally, such nuanced, scale-dependent patterns could be washed out or masked by more general assessments of habitat selection (i.e., an evaluation based on male and female locations combined).

Detailed analyses of context-dependent habitat selection can reveal resource requirements specific to behavioral roles. For example, our work contributes to knowledge of Great Gray Owl foraging habitat, as adult male owls act as food provisioners for nesting females and young during the breeding season. Herbaceous wetlands likely serve as primary foraging areas for Great Gray Owls during the breeding season. Herbaceous wetlands tend to have perennial graminoid or forb cover and fine-textured, moist soil (Faber-Langendoen et al. 2019) that is home to Northern Pocket Gophers (*Thomomys talpoides*) and *Microtus* species (Findley 1951, Clark 1973, Streubel 1989, Mattson 2004), both of which are primary prey for Great Gray Owls in the Rocky Mountains (Franklin 1988, Gura et al. *in prep.*). Owls were less likely to use more xeric herbaceous habitat, indicating that drier meadows may be less important for foraging. Great Gray Owls in the Sierra Nevada similarly were associated with wetter herbaceous habitats including montane meadows at higher elevations and riparian meadows at lower elevations (Winter 1986, Reid 1989, van Riper and van Wagtendonk 2006, Wu et al. 2015).

Fine-scale analysis of microhabitat selection can add further detail on key resources related to specific functional processes. For example, owls chose nighttime microhabitat that facilitated foraging, such as areas containing presence of primary prey and dominated by graminoids and forbs, which simultaneously provide suitable *Thomomys* and *Microtus* habitat and open understories for easier hunting. Owls did not select nighttime microhabitats with sagebrush, willow, or saplings, which indicates that these understory types do not enable foraging. Although retainment of suitable perches is key to facilitate Great Gray Owl hunting (Winter 1986), preventing encroachment by woody vegetation may be important to maintain suitable foraging habitat for owls (Bryan and Forsman 1987, Williams et al. 2012, Wu et al. 2016). Indeed, within wetland meadows, fine, loose soil as well as snow accumulation and windy conditions naturally prevent the establishment of woody vegetation (Faber-Langendoen et al. 2019). Instead, proximity to forest edge, which provides perches from which owls can forage, is likely an important factor for how open wetland meadows are utilized for hunting (Winter 1986, Bull and Henjum 1990, Beck and Craig 1991, Greene 1995).

Differential patterns of habitat selection according to time of day can reflect how animals conduct different activities across diurnal periods. For example, both within-home-range and microhabitat selection indicate that owls chose areas conducive to foraging success specifically at dawn, dusk, and night. Likewise, during the day male Great Gray Owls selected higher canopy cover, which likely provided suitable roosting habitat. We hypothesized that areas of increased soil moisture would serve as foraging areas, similar to open wetlands. However, we found weak evidence that male owls selected areas of increased soil moisture during the day whereas probability of use decreased during the rest of the diurnal period. Because areas of increased soil moisture tend to have less direct solar radiation and occur at the base of slopes and

in depressions (Iverson et al. 1997), these areas may provide thermoregulation for roosting owls during the day. Although conducting behavioral observations to determine activity patterns of owls was beyond the scope of this study, Great Gray Owls typically roost during the day (Winter 1986, Bull and Henjum 1990) and forage at dawn and dusk (Bull and Henjum 1990). Few observational data exist on nocturnal activity patterns by Great Gray Owls, but we observed that nocturnal habitat was similar to areas used during dawn and dusk, most likely for foraging.

Changing levels of opportunity and risk can result in differential patterns of resource selection across time, as animals balance trade-offs via habitat choices. For example, during the day Great Gray Owls did not select open wetlands and instead strongly selected increased canopy cover, most likely to reduce daytime heat stress (Winter 1986, Beck and Smith 1987, Duncan and Hayward 1994). Probability of use of developed areas was lowest during the day, which we predicted because anthropogenic activity is highest during this time. However, Great Gray Owls were less likely to use development across diurnal periods, corroborating that this species has a negative behavioral response to anthropogenic activity in general (Wildman 1992, Jepsen et al. 2011, van Riper et al. 2013). On the other hand, owls selected to be closer to roads at all times of the day, even though collision with vehicles is a primary cause of injury and mortality for this species (pers. obs., Wu et al. 2016). Selection of proximity to roads may be an artifact of roads occurring in areas of suitable foraging habitat, such as riparian corridors and meadows. In this case, foraging opportunities for male owls may outweigh the risk associated with roads.

Certain habitats may facilitate multiple functional processes, enabling animals to utilize them across contexts. For example, wooded wetlands likely provide both roosting and foraging habitat, as owls selected them across the diurnal periods. In our study area, wooded wetlands

primarily consist of riparian forests (including *Populus angustifolia* and *Picea pungens*) with high canopy cover and densely vegetated perches that can serve as suitable roosts (Winter 1986). Riparian forests also are characterized by seasonal flooding and loose, moist soils that contain graminoids or forbs, limited woody shrubs (Faber-Langendoen et al. 2019), and *Thomomys* and *Microtus* populations (pers. obs.), all of which are characteristic of foraging habitat. Owls also selected increased percent canopy cover at all times of the day, indicating densely forested habitat likely facilitates other functional processes besides thermoregulation, such as protection from predators (Whitfield and Gaffney 1997) or foraging opportunities (Forsman and Bryan 1987, Bull et al. 1988b). Male owls also chose to be in close proximity to wetlands across the diurnal period. Great Gray Owls are more active during the day compared to most *Strigiformes*, and proximity to wetland habitats may allow for opportunistic foraging throughout the day (Winter 1986).

Quantifying sex-specific and time-dependent habitat selection is an important step towards a more holistic understanding of key resources for a species. Here, we advance knowledge of Great Gray Owl breeding-season habitat by focusing specifically on the resources chosen by adult males. We also provide greatly-needed information on nocturnal habitat (including microhabitat characteristics), which generally is poorly understood for this species. Finally, this work contributes to understanding of how owls balance resources, for example for food provisioning and safety, which are critical for individual fitness and population persistence. We did not explicitly evaluate the fitness implications of habitat selection by adult male Great Gray Owls, and future avenues of research include investigations of how choice of habitat determines proxies for fitness or actual fitness metrics, including foraging success, prey delivery rates, reproductive performance, and survival. Likewise, comparative studies between

populations would clarify the extent to which patterns of habitat selection in the GYE reflect the resource requirements of other Great Gray Owl populations.

Considering that organisms can select habitat differently depending on scale and context, management strategies that incorporate the diversity of resources required by a species can result in more effective conservation. Likewise, maintaining relevant habitat heterogeneity can ensure that adequate resources are available for different functional processes and activities. For example, conservation of Great Gray Owl breeding habitat may be strengthened by targeting not only suitable nest sites but also areas required by adult male owls for foraging during crepuscular and nocturnal periods, such as adjacent wet and mesic meadows. Furthermore, many species including the Great Gray Owl are at high risk to threats related to habitat change (Bateman et al. 2020a, Bateman et al. 2020b). Knowledge of key resources across behavioral roles, activity periods, and other contexts can improve the identification and conservation of critical habitat in the face of environmental change.

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Tables:

Table 1. Habitat attributes used to asses within-home-range and nighttime microhabitat selection by adult male Great Gray Owls (n = 19) during the breeding season between 2018–2022 in the Greater Yellowstone Ecosystem, Wyoming, USA. Within-home-range attributes were based on remotely-sensed habitat data (30 m × 30 m resolution). Microhabitat attributes were collected *in situ* using 12 m-radius plots.

Habitat Attributes	
Within-home-range	**Microhabitat**
% Canopy Cover	Basal Area
Developed	Basal Area Coniferous
Distance-to-Road	Basal Area Deciduous
Distance-to-Wetland	% Canopy Closure
Herbaceous	# Coarse Woody Debris
Herbaceous Wetland	Distance-to-Edge
Integrated Moisture Index	Distance-to-Meadow
Woody Wetland	Dominant Understory
	Habitat Class
	Presence of Pocket Gophers
	# Tree Stories
	# Snags

Table 2. Model-averaged fixed-effect beta coefficients (β), standard errors, and p-values of the top generalized linear mixed-model (based on Akaike's Information Criterion adjusted for small sample size) for resource selection functions used to assess habitat selection within breeding home ranges by adult male Great Gray Owls (n = 19) during 2018–2022 in the Greater Yellowstone Ecosystem, Wyoming, USA. The model included an interaction term of time-of-day based on periods of the diurnal window (dawn, day, dusk, night).

Explanatory Variable	β	Standard Error	p-value
Intercept	-0.083	0.044	0.056
Canopy	0.004	0.001	< 0.001
Developed	-1.789	0.288	< 0.001
Distance to Roads	> -0.001	< 0.001	< 0.001
Distance to Wetlands	> -0.001	< 0.001	0.005
Herbaceous	-1.453	0.320	< 0.001
Herbaceous Wetland	0.582	0.123	< 0.001
Integrated Moisture Index	> -0.001	0.000	0.460
Woody Wetland	0.409	0.044	< 0.001
PeriodDay	-0.731	0.045	< 0.001
PeriodDusk	-0.068	0.055	0.218
PeriodNight	-0.006	0.047	0.901
Canopy:PeriodDay	< 0.001	0.001	< 0.001
Canopy:PeriodDusk	0.003	0.001	0.004
Canopy:PeriodNight	0.002	0.001	0.014
Developed:PeriodDay	< 0.001	0.361	0.040
Developed:PeriodDusk	0.420	0.399	0.292
Developed:PeriodNight	0.153	0.348	0.661
Distance to Roads:PeriodDay	> -0.001	< 0.001	< 0.001
Distance to Roads:PeriodDusk	> -0.001	< 0.001	0.154
Distance to Roads:PeriodNight	> -0.001	< 0.001	0.202
Distance to Wetland:PeriodDay	> -0.001	< 0.001	0.762
Distance to Wetland:PeriodDusk	> -0.001	< 0.001	0.247
Distance to Wetland:PeriodNight	> -0.001	< 0.001	0.050
Herbaceous:PeriodDay	-0.989	0.447	0.027
Herbaceous:PeriodDusk	0.833	0.442	0.059
Herbaceous:PeriodNight	0.908	0.371	< 0.001
Herbaceous Wetland:PeriodDay	-0.587	0.149	< 0.001
Herbaceous Wetland:PeriodDusk	0.334	0.174	0.055
Herbaceous Wetland:PeriodNight	0.209	0.145	0.149
Integrated Moisture Index:PeriodDay	< 0.001	< 0.001	0.181
Integrated Moisture Index:PeriodDusk	> -0.001	< 0.001	0.676
Integrated Moisture Index:PeriodNight	> -0.001	< 0.001	0.087

Table 3. Summary of top models from resource selection functions to assess habitat selection of adult male Great Gray Owls (n = 19) within home ranges during the breeding season from 2018–2022 in the Greater Yellowstone Ecosystem, Wyoming, USA. K indicates number of parameters in the model, logLik indicates log of the likelihood function of the model, and AIC_c indicates Akaike's Information Criterion values adjusted for small sample size. Model covariates include canopy cover (CC); land cover types including developed (Dvlpd), herbaceous (Herb), herbaceous wetland (HW), and woody wetland (WW); distance to roads (Dist2Rds); distance to wetland (Dist2Wetland); and Integrated Moisture Index (IMI). The models also included an interaction term of time-of-day (Pd) based on diurnal periods (dawn, day, dusk, night).

Model	K	logLik	AICc	Δ AICc
CC + Dvlpd + Dist2Rds + Dist2Wetland + Herb + HW + IMI + WW + CC*Pd + Dvlpd*Pd + Dist2Rds*Pd + Dist2Wetland*Pd + Herb + HW*Pd + IMI*Pd	34	-99158.591	198385.198	0
CC + Dvlpd + Dist2Rds + Dist2Wetland + Herb + HW + WW + CC*Pd + Dvlpd*Pd + Dist2Rds*Pd + Dist2Wetland*Pd + Herb + HW*Pd	30	-99168.706	198397.425	12.228
CC + Dvlpd + Dist2Rds + Herb + HW + WW + CC*Pd + Dvlpd*Pd + Dist2Rds*Pd + Herb + HW*Pd	26	-99205.805	198463.619	78.422
CC + Dvlpd + Dist2Rds + Herb + HW + CC*Pd + Dvlpd*Pd + Dist2Rds*Pd + Herb + HW*Pd	25	-99260.328	198570.665	185.467
CC + Dvlpd + Dist2Rds + HW + CC*Pd + Dvlpd*Pd + Dist2Rds*Pd + HW*Pd	21	-99335.836	198713.678	328.480
CC + Dvlpd + Dist2Rds + CC*Pd + Dvlpd*Pd + Dist2Rds*Pd	17	-99432.581	198899.166	513.968
CC + Dvlpd + CC*Pd + Dvlpd*Pd	13	-99569.442	199164.887	779.690
CC + CC*Pd	9	-99743.460	199504.922	1119.724
Null	2	-101613.990	203231.981	4846.783

Table 4. Model-averaged fixed-effect beta coefficients (β), standard errors, confidence intervals (CI) , and p-values of the top generalized linear mixed-models from resource selection functions to assess the nighttime microhabitat (0.04 ha plot) selection of adult male Great Gray Owls (n = 19) within breeding home ranges during 2018–2022 in the Greater Yellowstone Ecosystem, Wyoming, USA.

Explanatory Variable	β	Standard Error	2.5% CI	97.5% CI	p-value
Intercept	-2.208	0.548	-3.284	-1.132	< 0.001
Presence of Pocket Gopher Sign	0.245	0.197	-0.036	0.645	0.214
Grass	2.369	0.542	1.304	3.434	< 0.001
Shrub	1.395	0.600	0.216	2.574	0.020
Forbs	2.110	0.565	1.001	3.219	< 0.001
Douglas Fir	-0.564	0.988	-3.507	0.971	0.568
Lodgepole Pine	-0.130	0.413	-2.166	0.664	0.753

Table 5. Top models and Akaike's Information Criterion adjusted for small sample size (AIC$_c$) values from resource selection functions to assess nighttime microhabitat (0.04 ha plot) selection of adult male Great Gray Owls (n = 19) during the breeding season from 2018–2022 in the Greater Yellowstone Ecosystem, Wyoming, USA. *K* indicates number of parameters in the model and logLik indicates log of the likelihood function of the model.

Model	K	logLik	AIC$_c$	Δ AIC$_c$
Forb + Grass + Shrub + Pocket Gopher Presence	6	-394.657	801.456	0
Douglas Fir + Forb + Grass + Shrub + Pocket Gopher Presence	7	-393.914	802.017	0.561
Forb + Grass + Shrub	5	-396.292	802.684	1.228
Douglas Fir + Lodgepole Pine + Forb + Grass + Shrub + Pocket Gopher Presence	8	-393.338	802.919	1.463
Douglas Fir + Lodgepole Pine + Mixed Forest + Forb + Grass + Shrub + Pocket Gopher Presence	9	-392.814	803.933	2.477
Aspen + Douglas Fir + Lodgepole Pine + Mixed Forest + Forb + Grass + Shrub + Pocket Gopher Presence	10	-392.464	805.302	3.847

Figures:
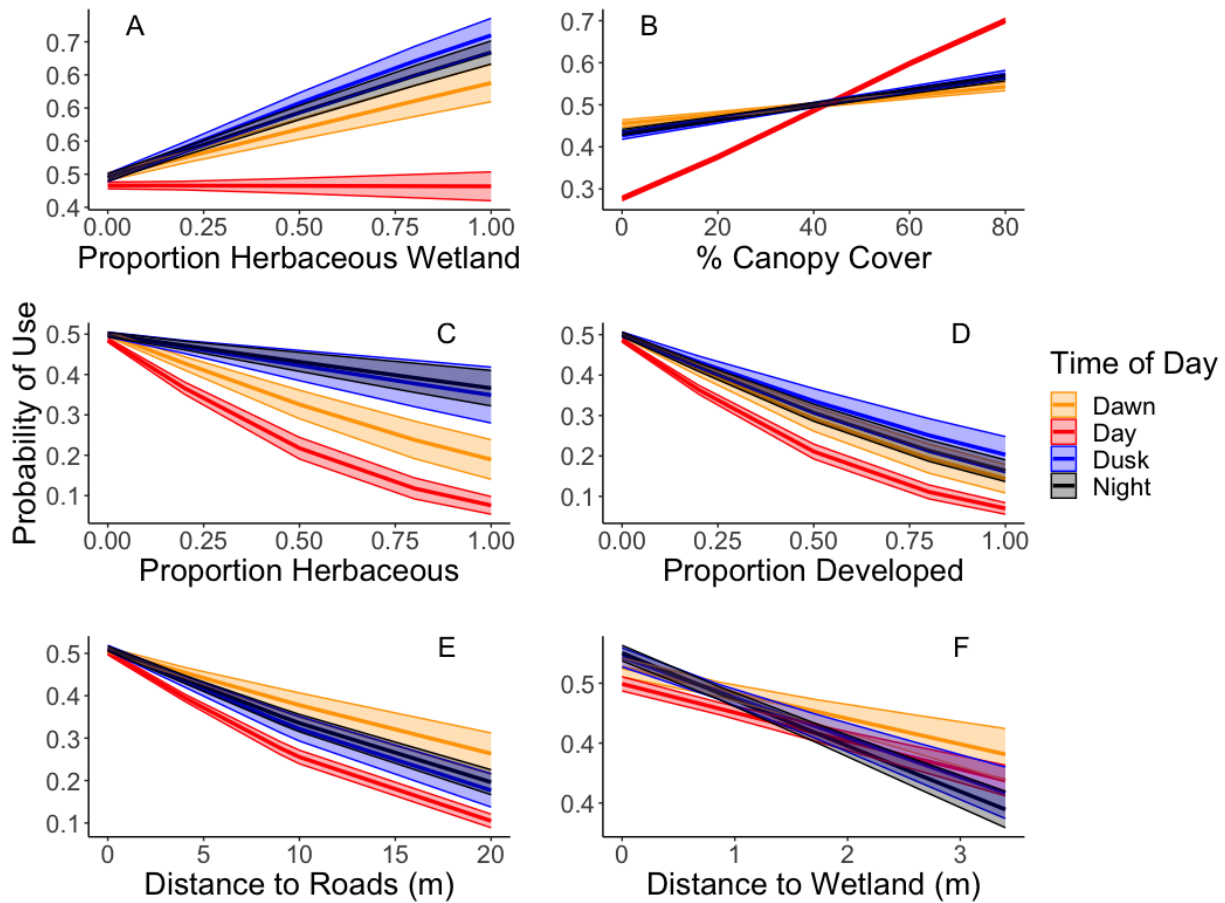
Figure 1. Probability of use of environmental covariates during the breeding season by adult male Great Gray Owls (n = 19) from 2018–2022 in the Greater Yellowstone Ecosystem, Wyoming, USA. Probability of use was determined via the top model (based on values of Akaike's Information Criterion adjusted for small sample size) from resource selection functions at the within-home-range level, which included interaction terms between time of day (dawn, day, dusk, night) and environmental covariates. Proportion of herbaceous wetlands (A), percent canopy cover (B), proportion of herbaceous (C), proportion of development (D), distance to roads (E), and distance to wetlands (F) each were statistically significant when interacting with time of day.
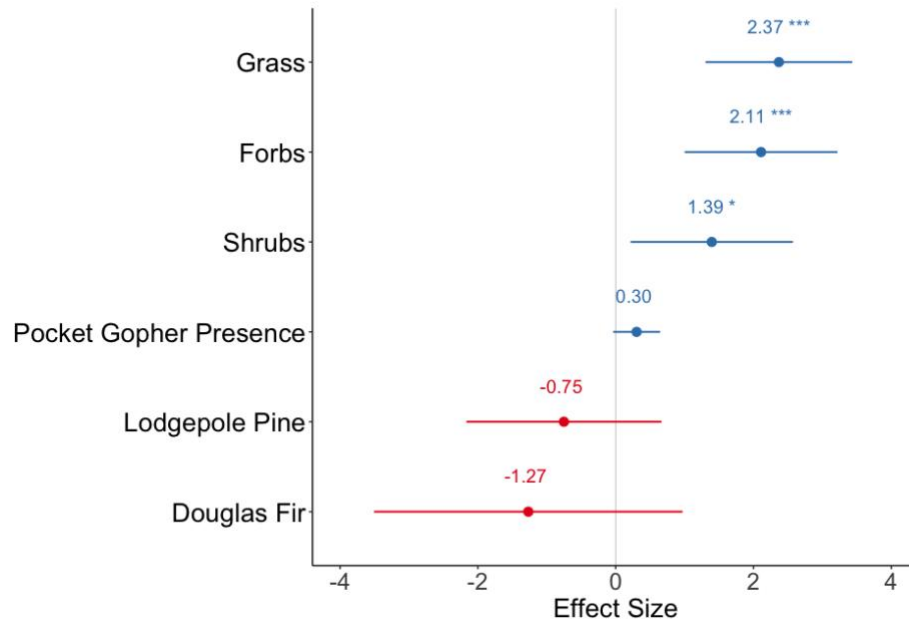
Figure 2. Nighttime microhabitat selection by adult male Great Gray Owls (n = 19) during the breeding season from 2018–2022 in the Greater Yellowstone Ecosystem, Wyoming, USA. Results are based on resource selection functions relating the relative selection strength of environmental covariates. Results are derived from top, model-averaged Generalized Linear Mixed-Models based on values of Akaike's Information Criterion adjusted for small sample size. Values indicate estimated model coefficients (mean ± 95% confidence interval), and asterisks indicate statistical significance values ('***' = $P \leq .001$, '*' = $P \leq .05$).

CHAPTER THREE

Variable snow conditions modulate movement behavior by a facultative migrant

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Abstract:

Movement and habitat selection are key mechanisms by which animals respond adaptively to environmental change. However, knowledge gaps persist related to the context-dependence of behavioral responses to climatic stressors. In particular, how spatiotemporally variable snow conditions affect wildlife remains poorly understood, despite the key role that snow plays in ecological processes. We evaluated whether limiting snow conditions influence proximate habitat choices and/or long-distance movements by a facultative migrant species, the Great Gray Owl. We hypothesized that snow conditions that restrict owls' access to subnivean prey prompt movement responses. We used SnowModel, a data-model fusion snow evolution modeling system, to estimate fine-scale, spatiotemporally explicit snow depth and snow crust conditions within the Greater Yellowstone Ecosystem (GYE) during 2017–2022. We evaluated habitat selection and migratory movements in response to snow depth and snow crusts using Step-Selection Functions and Cox proportional hazards analysis, respectively. Owls proximately avoided deeper snow and more severe wind crusts. Probability of long-distance movement increased with more severe and persistent ice crusts (caused by rain-on-cold-snow and melt-freeze events). In the GYE, wind crusts are locally spatially heterogeneous, whereas ice crusts can affect broader areas. Owls therefore appear to be behaviorally plastic, adopting different strategies depending on the spatial scale and duration of limiting conditions. Our findings have implications for understanding species' vulnerability to environmental change. Even relatively plastic animals, however, may have limited capacity to offset the effects of climate change, which is occurring at unprecedented rates and scales.

Introduction:

The global climate system is changing at an unprecedented rate and scale (IPCC 2022), and understanding the effects of climatic change has emerged as a primary goal in the field of ecology (Sih et al. 2011, Watson 2018, Bateman et al. 2020). Some of the most profound manifestations of climate-associated changes are occurring in regions characterized by seasonal or long-term snow. Increasing global temperatures are disrupting snow regimes (Lemke et al. 2007), resulting, for example, in reduced snowpack (Kunkel et al. 2016), earlier snowmelt (Brown et al. 2017), shorter core snow periods (Dye et al. 2002), and increased precipitation in the form of rain rather than snow (Mote et al. 2005, Solomon et al. 2007, Kapnick and Hall 2012). Snow is a primary determinant of community structure and ecosystem function, particularly in high-elevation and arctic systems where snow persists for a majority of the annual cycle (Bokhorst 2016). Considering the susceptibility of snow regimes to climatic change, and the key role that snow plays in ecological processes, knowledge of the effects of changing snow conditions on co-occurring organisms is critical.

Behavioral plasticity is a primary mechanism by which individual organisms can proximately mediate environmental stressors (Hadfield and Strathmann 1996, Snell-Rood 2013, Snell-Rood et al. 2018, Hollander et al. 2015). Behavioral responses can occur relatively rapidly and are more readily observable compared to other adaptive changes, such as shifts in gene frequencies associated with natural selection or population-level responses such as range shifts (Beever et al. 2017). The extent to which individuals exhibit behavioral flexibility, therefore, can be an important indicator of the susceptibility of populations to climate change (Berger-Tal et al. 2011). Although knowledge of behavioral responses to climatic change is increasing, critical information gaps persist related to the context-dependence of such responses. For example, some

animals adjust behavior in response to changes in phenology of food resources (i.e., Tøttrup et al. 2008) and temperature (i.e., Hall and Chalfoun 2018), yet the efficacy of behavioral plasticity in mediating other climatic stressors, such as changing snow regimes, is less understood (Beever et al. 2017). Research also tends to focus on directional, chronic changes (Beever et al. 2017), whereas the effects of climatic variability and acute or extreme stressors remain unclear. Finally, a better understanding of the responses of organisms in the wild to multiple climatic stressors will clarify which are most limiting.

Animal movement evolved as a behavioral response to environmental change (Dingle et al. 1996, Alerstam and Hedenström 1998, Newton 2008, Robinson et al. 2009), and degree of plasticity in movement behavior likely comprises a key factor influencing how animals respond to changing climatic conditions (i.e., Tøttrup et al. 2008). In contrast to obligate migrants, facultative migrants are thought to be more plastic, moving proximately in direct response to the conditions encountered (Newton 2008). However, movement can be risky and energetically costly (Hebblewhite and Merril 2007, Shaw 2016), and a facultative movement only is beneficial if the constraints and costs associated with staying outweigh the risks associated with leaving. Although facultative strategies are thought to function well in systems with lower spatiotemporal predictability (Newton 2006, 2012), the specific contexts under which facultative strategies occur warrant further examination (Newton 2006, 2012; Therrien 2014; Robillard 2016), particularly in relation to changing climatic conditions with important fitness consequences (Shaw 2016).

Understanding facultative responses to environmental changes requires consideration of the interaction between movement strategy and habitat selection (Newton 2010, Van Moorter et al. 2016, Bastille-Rousseau et al. 2017). Variation in the spatiotemporal structure and availability

of resources, such as spatial distribution, seasonality, and interannual predictability, governs

habitat selection and therefore movement strategies of animals (Morris et al. 1992, Harel et al.

2016, Bastille-Rousseau et al. 2017). Facultative responses to changing conditions can range

from proximate shifts in habitat selection (Shipley et al. 2019, Wolff et al. 2020, Riddell et al.

2021, Hebblewhite and Merril 2009) to broader-scale migrations (Curk et al. 2020), each of

which can be advantageous, depending in part on the degree and extent of environmental

heterogeneity. Resident individuals that adjust proximate habitat selection at a finer scale can

capitalize on knowledge of local conditions and forgo an energetically-costly migration.

Conversely, a lack of sufficient local habitat heterogeneity may necessitate larger-scale

movement responses to offset limiting conditions. However, how animals use proximate habitat

selection versus broad-scale movements to buffer changing conditions, and the extent to which

the spatiotemporal structure of limiting conditions influences movement responses, remains

unclear.

The phenomenon of "locked pastures" (Hansen et al. 2013) in which food resources

become unavailable due to snow conditions (Helle 1984, Forchhammer and Boertmann 1993) is

a highly constraining stressor that occurs in response to changing climatic conditions (Hansen et

al. 2014, Serreze et al. 2021). The largely negative fitness effects of ice-locked forage due to

rain-on-snow events, for example, have been documented in arctic herbivore populations (Berger

et al. 2018, Langlois 2017, Stien et al. 2012, Hansen et al. 2013, Gilg et al. 2009, Ims et al. 2008,

Kausrud et al. 2008, Kohler and Aanes 2004). The potential impacts of locked pastures on other

taxa that acquire food resources beneath the snow, however, remain unknown. Furthermore,

although locked pastures are associated with severe rain-on-snow icing events, other geophysical

mechanisms also can potentially limit subnivean foraging, including melt-freeze icing events,

wind crusts, and increased snow depths (Mysterud 2016). Behavioral responses to locked pastures, and the relevance of the spatiotemporal scales at which these snow conditions change, remain poorly understood. Although some organisms appear limited in their capacity to cope with locked pastures (Hansen 2013, Riseth et al. 2016), the ability to respond adaptively may be context-dependent (Mysterud 2016, Hansen et al. 2019).

We evaluated the contexts under which variable environmental conditions influence proximate habitat choices versus broader, long-distance movements, using a facultative migrant population of Great Gray Owls (*Strix nebulosa*) as a model system. The Great Gray Owl is a holarctic raptor that preys upon subnivean small mammals during the winter (Figure 1) (Nero 1980, Franklin 1988, Bull and Henjum 1990), and therefore they may be increasingly susceptible to locked-pasture snow conditions given recent climatic changes (Mysterud 2016). Great Gray Owls in the southern part of their range are partially migratory, exhibiting high inter- and intra-individual variation in the timing, direction, and distance of winter movements (pers. obs., Bull et al. 1988, Franklin 1988, Williams et al. 2012). Observed movement patterns include residency, altitudinal migrations, long-distance migrations to discrete winter ranges, and nomadic movements. The proximate mechanisms underlying such variation in movement behavior remain unknown, although snow conditions that preclude owls from accessing subnivean prey may be an important factor. Moreover, the study population is situated within a highly seasonal, mountainous environment that is spatiotemporally heterogenous, which may modulate snow conditions and resultant behavioral responses by owls. Although the hypothesis that limiting snow conditions determine Great Gray Owl winter movements is long-standing (Bull et al. 1988, Franklin 1988, Bull and Henjum 1990, Beck and Winter 2000), we are unaware of any previous study that explicitly evaluated the influence of snow on winter habitat selection

and/or movement behavior (Mysterud 2016), in large part due to the difficulty of quantifying the specific snow characteristics needed to test this relationship (Reinking et al. 2022).

We hypothesized that limiting environmental conditions prompt facultative movements by wildlife, and that increasing spatiotemporal scales of limiting conditions warrant longer-distance movements. Specifically, we expected that snow conditions that restrict owls' access to subnivean prey elicit facultative movement responses. We predicted that owls would avoid more severe and persistent snow crusts (due to rain-on-snow, melt-freeze, and wind events) and increased snow depths, and that owls would migrate as the spatiotemporal scales of limiting snow conditions increased.

Methods:

Study Area:

We conducted our research within the Greater Yellowstone Ecosystem (GYE) in Wyoming, USA, which nears the southern extent of the Great Gray Owl's contiguous range in North America. The study area was topographically variable and contained the rugged Teton mountain range that extended up to ~4,100 m as well as surrounding foothills, riparian corridors, and lower-elevation valleys (~1,450-1,950 m). The study area also hosted a diversity of habitats including forests, sagebrush steppe, montane meadows, wetlands, agricultural zones, and residential areas. Lodgepole pine (*Pinus contorta*) was the primary forest type, and the area also included aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), sub-alpine fir (*Abies lasiocarpa*), cottonwood (*Populus angustifolia*), Engelmann spruce (*Picea engelmannii*), blue spruce (*Picea pungens*), and white-bark pine forests (*Pinus albicaulis*). The study area was highly seasonal and characterized by extensive, snowy winters.

Animal Capture and Movement Data:

We captured adult male and female Great Gray Owls during 2017–2021. We located owls on both breeding and winter ranges, and we used molt to identify adults (Suopajarvi and Suopajarvi 1994). We primarily used pan, bal-chatri, and dho gazza traps that included mouse lures (Bloom et al. 2007). We outfitted owls with Global Positioning System (GPS) remote-download transmitters (Lotek SwiftFix) using either a backpack-style attachment with tubular Teflon ribbon or a tail-mount attachment (Bloom et al. 2007). Transmitters collected GPS locations throughout the annual cycle, with number of locations per day ranging from 1 to 24 loc/day depending on the unit. We tracked tagged owls using Very High Frequency (VHF) radio telemetry and downloaded GPS location data using a wireless downloader (Lotek PinPoint Beacon and PinPoint VHF GPS Tags User Manual 2021).

Snow Data:

To evaluate snow conditions in relation to Great Gray Owl movement data, we estimated snow characteristics across the study area for 01 September 2017–31 August 2022. We used SnowModel, a spatiotemporally distributed snow-evolution modeling system that utilizes land cover, topography, meteorology, and *in situ* observations of snow characteristics to simulate snowpack evolution across space and time (Figure 2) (Liston and Elder 2006a, Liston et al. 2020). SnowModel simulates the geophysical processes that influence snow/water mass and energy balances, and it includes four sub-models that each resolve different processes: EnBal calculates exchanges of surface energy (Liston 1995, Liston et al. 1999), MicroMet provides meteorological forcings (weather data) to drive simulations (Liston and Elder 2006b),

SnowPack calculates evolution of snow depth and snow-water equivalent (SWE)) (Liston and Hall 1995, Liston and Mernild 2012), and SnowTran-3D calculates snow redistribution due to wind (Liston and Sturm 1998, Liston and Elder 2006a, Liston et al. 2007). We modeled the evolution of snow conditions within our study area at two spatiotemporal resolutions to address each of our study objectives. First, we modeled snow evolution at a three-hourly time step and 500 m spatial resolution to assess probability of long-distance movement relative to broad snow conditions. Second, we simulated snow characteristics at a three-hourly time step and 30 m spatial resolution to assess fine-scale habitat selection in response to snow conditions.

Inclusion of meteorological, topographical, and land cover data enables SnowModel to account for primary, synoptic controls of snow conditions such as weather and storm cycles, temperature, wind, presence of forest versus non-forest habitat, elevation, ridges versus gullies, windward versus leeward aspects, and sun-exposed versus shaded areas. We used the 2015 North American Land Change Monitoring System landcover dataset, which was produced from Landsat satellite imagery and consisted of 30 m × 30 m spatial data (Commission for Environmental Cooperation 2015). To calculate topography, we used the United States Geological Survey (USGS) Digital Elevation Model (DEM), which was a 1 arc-second tiled dataset from the 3D Elevation Program (3DEP) (USGS 2020). We used the National Land Data Assimilation System, Version 2 (NLDAS-2) meteorological data, which consisted of hourly weather data with a 1/8th-degree spatial resolution (NLDAS 2022, Mitchell et al. 2004, Xia et al. 2012).

SnowModel allows users to produce unique model outputs tailored to address specific research applications (Reinking et al. 2022), such as estimating snow crust conditions. For each spatiotemporal scale, we modeled the amount of run-off from the base of the snowpack, amount

of liquid precipitation, amount of snow precipitation, SWE depth, SWE melt, snow density, snow depth, air temperature, snow surface temperature, temperature at each layer of the snowpack, and windspeed (Liston et al. 2020). To help ensure our estimated snow conditions represented reality, we assimilated *in situ* SWE and snow depth observations from 77 Natural Resources Conservation Service (NRCS) snow telemetry (Snotel) Snow course sites within our study domain (Stuefer et al. 2007, Liston and Hiemstra 2008, Reinking et al. 2022) (Figures 3–4).

Using the aforementioned snow variables, we modeled the spatiotemporal evolution of snow crusts associated with the three main phenomena that produce them: rain-on-snow, melt-freeze, and wind events. Rain-on-snow ice crusts form when rain precipitation falls on cold snow and the liquid freezes into an ice layer. We identified events when rain fell on a cold snowpack (snowpack layer with a temperature < -0.01°C) and the liquid did not run off. Snow crusts also form when snow melt occurs within the snowpack and any liquid water that does not run-off instead is retained in the snowpack and freezes. We calculated snow crusts formed during a melt-freeze cycle by identifying when snow melt occurred within a cold snowpack (< -0.01°C). To account for subsequent freeze events after melting, we also identified when snow melt occurred followed by a snowpack layer temperature < -0.01°C within the next 12 hr. The index of severity for both rain-on-snow and melt-freeze crusts was based on the amount of liquid water (either in the form of rain precipitation or snow melt) that reached a < -0.01°C snowpack layer, minus the amount of run-off, which equated to the amount of liquid water retained within the snowpack as a frozen crust. Rain-on-snow and melt-freeze crust indices were therefore comparable in scale, so we combined rain-on-snow and melt-freeze events into a single variable: ice crust events.

Wind crust formation occurs when high-speed winds combine either with falling or blowing snow, resulting in the mechanical breakage or tumbling of snow into round crystals that can set and form strong, grain-to-grain bonds when they stop moving. To model wind crust events, we calculated the change in snow density due to blowing snow based on the windspeed 2 m above the land surface. The severity index of a wind crust event was calculated based on the relative increase in snow density due to wind speed and amount of blowing snow (Liston et al. 2007). The severity indices for ice versus wind crusts are not directly comparable due to the inherent differences in how these crusts form, and we therefore did not combine them into a single index. It is important to note that our estimates of snow crust severity are indices, and they do not equate to measurements of snow crust hardness or snow density.

Once formed, both wind and ice crusts can persist even as new snow falls and buries them below the surface. Therefore, we calculated the formation and initial severity index of crusts (crust event), and their cumulative severity index (summed event severity index over time) and persistence (consecutive number of days the crust persisted within the snowpack). Snow crusts disappear from a snowpack when it becomes isothermal (i.e., reaches 0.0°C) and liquid water reaches the ground. Once run-off occurred, we reset cumulative variables (cumulative severity index, persistence) to simulate this process. See Equations section for additional snow crust modeling details.

Habitat Selection:

We used integrated step-selection analysis (iSSA) (Avgar et al. 2016) to evaluate whether snow conditions influenced proximate habitat selection by Great Gray Owls during the winter. In contrast to traditional Resource Selection Functions (RSFs), in which use versus availability are

compared at a designated spatial scale (i.e., the home range), iSSA evaluates habitat selection at the spatiotemporal scale of the movement step. A step consists of both a starting and ending location between a set time interval. This analysis assumes that for each observed step, there exist alternate available steps that the animal could have selected. These steps are drawn from theoretical distributions of average step length and turning angles for that specific individual (Fortin et al. 2005, Avgar et al. 2016). ISSA accounts for inherent autocorrelation that exists in movement data and therefore is a suitable modeling approach to evaluate fine-scale, step-level habitat selection decisions (Avgar et al. 2016).

We subsampled Great Gray Owl GPS location data to include the core snow period (15 September–15 April) and one location per day such that successive locations were 24 hr apart. We rounded times of GPS locations to the nearest hour (00:00) because a constant time step between successive steps was required for iSSA. However, we deemed it unnecessary to correct an owl's position to account for this rounding because the majority of subsampled GPS locations occurred at 00:00 (n = 38,259 (99.8%) observed locations) except several locations that occurred within 2 min of 00:00 (n = 56), and a relatively small subset that occurred <00:30 min from 00:00 (n = 10). We generated five corresponding random steps for each observed step, using a Weibull distribution (Forester et al. 2009) and Von Mises distribution (Marsh and Jones 1988) for step-length and turning angle, respectively. At the end point of each step, we extracted values of snow depth; wind crust severity, cumulative severity, and persistence; and ice crust severity, cumulative severity, and persistence. We used Pearson's correlation coefficients to test for collinearity between environmental covariates (we considered $|r| > 0.7$ significantly correlated). If two variables were correlated, we retained the one we deemed most biologically relevant. We centered and scaled the extracted values of environmental covariates to allow for comparison of

effect sizes, or relative selection strength (RSS), between variables (Avgar et al. 2017). We used conditional logistic regression to analyze selection of step end points (Fortin et al. 2005), presenting results as the natural logarithm of RSS (log-RSS), and we selected top models based on AIC value. We conducted analyses in program R, and we prepared data for the iSSA using the MoveTools package.

Timing of Long-Distance Movement:

To evaluate whether snow conditions influenced the probability of broad migratory movement, we identified long-distance movement events by Great Gray Owls during the core snow period (15 September – 15 April). To identify migratory movements, we used Net Squared Displacement analysis (NSD) (Turchin 1998, Nouvellet 2009, Bunnefeld et al. 2011), which characterizes movement trajectories by calculating the squared Euclidean distance between a starting location and subsequent locations. We also manually inspected GPS location data to confirm that long-distance movement events met specific criteria. We identified a migratory movement event as a significant movement away from a) a discrete breeding range, or b) a discrete winter range. A significant movement was defined as a movement of 8 km or farther (based on twice the diameter of the mean overall winter range area (19.5 km^2, based on 99% Kernel Density Estimates (KDE)). A breeding home range area was defined based on 95% KDE using locations between April–September. A discrete winter home range was defined as an area <3.7 km in diameter (based on mean winter home range size (13.4 km^2; 95% KDE)) in which an owl settled for a minimum of 1 week (between 1 October–30 March). We excluded movements away from discrete winter ranges in which owls returned to their breeding range, as we could not ascertain whether an innate instinct to defend the breeding territory or begin breeding determined

this movement decision as opposed to snow conditions. We subsampled all GPS locations to one location per day per individual, and we excluded movement sequences with >5 days of missing location data and/or <6 months of GPS location data.

For each long-distance movement event, we identified the onset of risk as the point at which the owl first settled in either a discrete breeding or winter range (settlement decision), and we included all locations in which the owl remained settled (settlement) up until the point at which the owl departed the settled range to undertake a long-distance movement (departure event). For all locations beginning with the settlement decision through the departure event, we extracted values of snow depth and crust severity, cumulative crust severity, and crust persistence for ice and wind crusts. We used Cox proportional hazards (CPH) analysis (Cox 1972, Anderson and Gill 1982) to evaluate whether snow conditions influenced probability of departure by Great Gray Owls. CPH is a type of hazards model that analyzes time-to-event data, disregards data following the event, and assumes independence between recurrent events (Cox 1972). We calculated the baseline hazard function of time-to-departure (Dossman et al. 2016) using hazard regression to determine the probability of a migratory movement occurring at a given point in time, using time-dependent snow conditions as explanatory variables. We included strata for year and sex to account for any additional variation in probability of departure due to annual variation and sex of owls. We tested for correlation among predictor covariates using Pearson's correlation ($|r| \leq 0.5$) and confirmed that variance inflation factors were < 4. We used a bootstrap, stepwise model-selection approach based on AIC value (Austin and Tu 2004, Hosmer et al. 2008). We confirmed that model covariates exhibited a linear relationship with the hazards ratio by using a Generalized Additive Model to evaluate effective degrees of freedom (EDF) of the covariates, and we ensured that covariates and the top model met the assumption of

proportionality using Schoenfeld residuals (Schoenfeld 1982, Grambsch and Therneau 1994, Hosmer et al. 2008). We conducted CPH analysis in program R using the Survival package.

Results:

Animal Movement Data:

We captured and deployed GPS transmitters on 42 adult Great Gray Owls between 15 November 2017–01 September 2021. We collected 135,087 total GPS locations for 22 male and 20 female owls between 15 November 2017–31 September 2022. These data amounted to locations for 69 individuals-by-year and included 21,113 winter locations.

Snow Data:

The spatiotemporal distribution of snow characteristics varied across the study domain. Specifically, wind crusts exhibited high spatial heterogeneity (Figure 5A-D), snow depths were moderately spatially variable, and ice crusts were relatively homogenously distributed across broad areas (Figure 5E-H). Wind events occurred throughout the core snow periods (Figure 6A). Ice crust events primarily occurred during the early winter and early spring periods when temperatures tended to be relatively warmer (resulting in increased rain-on-snow and melt-freeze events) (Figure 6B), although ice crust events did occur mid-winter. Both wind and ice crusts persisted for extensive periods of time, although we observed periodic mid-winter run-off events that dissolved wind and ice crusts (Figure 6D-E). Snow depths steadily increased from late fall until mid-spring (Figure 6C). There was inter-annual variation in snow conditions in the GYE over the course of the study period and during the past several decades, including yearly

variation in average maximum severity of wind and ice crusts and average maximum snow depth (Figure 7).

Habitat Selection:

We evaluated 2,940 observed Great Gray Owl steps across years, which we compared to 14,700 associated available step locations. Average daily step-length was 1,321.50 m ($\pm$ 2001.42; range: 1.96–23,607.07). Cumulative wind crust severity and wind crust persistence were highly correlated ($|r| = 0.81$), so we retained only cumulative wind crust severity in the modeling process, as we expected that more severe crusts would be more limiting to foraging.

Wind crust conditions and snow depth best explained fine-scale habitat choices. Relative selection strength decreased in response to increased severity of wind crust events, increased cumulative wind crust severity, and increased snow depth (Table 1, Figure 7). In contrast to wind crust severity, we did not observe a statistically significant relationship between Great Gray Owl step-selection and ice crust event severity, cumulative severity, or persistence.

Timing of Long-Distance Movement:

We analyzed long-distance movement behavior of 36 individual owls following sub-sampling of data. Five owls did not depart during the winter and remained on their breeding range throughout the entire annual cycle. We identified 139 long-distance movement events for 15 male and 16 female owls across years (109 individuals-by-year). The farthest observed movement was 112 km. Long-distance movements occurred as early as 28 September and as late as 10 April. Mean date of first departure was 5 November ($\pm$ 31.62 days), and mean number of departure events per individual-by-year was 3.09 ($\pm$ 1.73; range: 1-8). Average day of first

departure was 25 October (± 21.74 days) and 14 November (± 35.90 days) for female and male owls, respectively. All environmental covariates included in the global model met the Cox model assumptions of linearity (EDF = 1.097-1.54) and proportionality (P = 0.16-0.91). We observed correlation between snow depth and ice crust persistence (|r| = 0.733), so we retained ice crust persistence in the model, as we expected ice crusts to be more limiting than deep snow for Great Gray Owl foraging.

The probability of long-distance movement increased with increased ice crust event severity (HR = 1.016, CI = 0.001–0.030) and increased persistence of ice crusts (HR = 1.01, CI = 0.005–0.017) (Table 2). Although ice crust severity was calculated simply as an index (based on amount of liquid water incorporated into the crust), each increasing increment of the crust severity index during icing events was associated with a 2% increase in probability of departure. We observed a 1% increase in probability of departure for every additional day that an ice crust persisted.

Discussion:

Great Gray Owls within the GYE exhibit facultative movement behavior and rely on subnivean prey during the winter. Therefore, this population served as an excellent model system to assess how animals respond to highly variable, changing climatic conditions via proximate habitat selection and/or broad-scale, migratory movements. We used novel snow data, produced through the integration of observations and models, to estimate the evolution of snow crusts and snow depths across space and time, which we linked to owl movement data to ascertain wildlife responses to variable, limiting winter conditions. On a daily basis, Great Gray Owls proximately avoided areas of deeper snow and more wind-compacted snow. However, individuals were more

likely to undergo long-distance movements in response to more severe and persistent ice crusts. Although different climatic factors underlie the evolution of snow depths, wind crusts, and ice crusts, each of these mechanisms can result in a locked pasture scenario that precludes species such as the Great Gray Owl from accessing subnivean prey. However, the spatial scale and duration of limiting snow conditions likely determined whether owls employed proximate shifts in habitat selection or long-distance movements to facilitate foraging success and therefore survival.

The environments constituting key winter habitat for owls were dynamic and highly dependent on changing snow conditions. Several individuals remained on breeding ranges year-round and most migrating owls repeatedly returned to breeding ranges over the course of the winter, suggesting that maintaining residency is beneficial (Duncan 1987, Winter 1986). The Great Gray Owl is the largest owl in North America, and its body size may better enable it to remain a year-round resident compared to smaller facultative migrant owls, which are less able to withstand food shortages, have higher critical body temperatures, and have more difficulty capturing prey beneath the snow (Mikkola 1983, Korpimäki 1986). However, when faced with locked-pasture snow conditions, Great Gray Owls responded negatively (avoidance or long-distance movement) regardless of whether these conditions were associated with increased snow depths, wind crusts, or ice crusts. The proximate cues for each locked-pasture mechanism likely were impenetrable snow and inaccessible prey.

There are inherent mechanistic and spatiotemporal differences in how wind crusts, ice crusts, and snow depths evolve. Areas susceptible to wind crusts include higher elevations, windward aspects, ridges, and open habitats, whereas wind crusts generally do not form within forested habitat that is buffered by trees (Liston et al. 2007). Wind crusts were relatively

heterogeneously distributed within the GYE, a region that varies in terms of elevation, topography, and land cover type. In contrast to wind crust formation, the rain-on-snow and melt-freeze events that create ice crusts are influenced by broad-scale weather and storm cycles as well as temperature regimes (Rennert et al. 2009). Although ice crusts can vary spatially, for example based on amount of solar radiation, canopy cover, or elevation, our modeling approach accounted for these environmental characteristics (Liston et al. 2020), and ice crust events generally occurred across broad swathes of the GYE. Snow depths occupied a middle-ground, steadily increasing across the study domain over the course of a winter due to broad, synoptic-scale weather and storm cycles, although depths varied spatially according to local aspect, elevation, and land cover type.

Differences in the spatial scales and durations of limiting conditions likely elicit specific behavioral responses by wildlife. In the case of heterogenous wind crusts, for example, Great Gray Owls were able to find refuges from wind-compacted areas at the daily step level. However, refuges from more severe and persistent ice crusts rarely existed at the step level, which prompted more extensive, long-distance movements. This finding reinforces the notion that broad-scale environmental structuring determines migratory movements (Mueller et al. 2011, Teitelbaum et al. 2015, Bastille-Rousseau et al. 2017). However, our results also demonstrate that movement behavior is context-dependent, with proximate habitat selection and migratory movement both serving as viable responses to limiting conditions, depending on the degree of environmental heterogeneity and presence of local refugia. Therefore, in the context of understanding effects of environmental change on wildlife, explicit consideration of the spatiotemporal scales of limiting factors is critical.

The extent to which other populations or species can use movement behavior to respond

adaptively to environmental change can depend on a variety of factors. Proximate cues that are reliably coupled with environmental conditions are necessary for adaptive phenotypic expression (Ghalambor et al. 2007). Shifts in habitat selection and regional migrations may be less adaptive for organisms that reside in relatively homogenous systems, such as arctic tundra or extensive boreal forest. Indeed, a lack of environmental heterogeneity may contribute to the continental-scale irruptions by large numbers of Great Gray Owls from boreal forests (Collins 1980, Cramp 1985, Nero 1969). Great Gray Owls in more heterogeneous regions do not exhibit irruptive behavior or extreme long-distance migrations (pers. obs., Winter 1986), potentially because sufficient local or regional heterogeneity exists to escape limiting conditions (Winter 1986, Franklin 1988, van Riper and van Wagtendonk 2006, Bull and Henjum 1990). Range-edge populations, such as Great Gray Owls in the GYE, also may be better adapted to respond to climatic variation and extremes compared with core populations (Rehm et al. 2015). Individuals with better body condition (Hansen et al. 2019) or dispersal ability and/or propensity (Steyn 2016, Claramunt 2021) may be well-equipped to use movement to offset changing conditions, although this evaluation was not within the scope of our study. Finally, the range of behaviors across which an organism is plastic may influence responses. Because movement can be energetically costly, it can be more adaptive to employ alternative behavioral responses to environment change. For example, prey-switching may explain how some Great Gray Owls remain in areas of deep snow (Bull and Henjum 1990).

Great Gray Owls in the GYE appeared to be relatively flexible in their ability to respond to locked pastures, which suggests this population is robust in its ability to cope with variable and acute climatic stressors. Indeed, long-term trends for wind and ice crusts and snow depths in the GYE are highly variable, and Great Gray Owls appear well-adapted to cope with these

changing snow conditions. However, behavioral plasticity in response to certain conditions does not necessarily imply that individuals can accommodate other limiting or changing factors. Furthermore, organisms can incur fitness trade-offs even as they cope with changing conditions (van Buskirk 2012, Snell-Rood 2013). We found that owls were restricted to particular habitats at the daily step level, endured periods of limited foraging accessibility, and ultimately initiated energetically costly long-distance movements, all in response to locked pasture conditions. Although evaluating direct fitness consequences was beyond the scope of this study, snow conditions and resultant behavioral responses potentially negatively impacted Great Gray Owl fitness (i.e., body condition, timing of arrival on breeding territory, ability to defend a breeding territory, reproductive performance, and/or survival). Furthermore, even for behaviorally plastic organisms, physiological thresholds likely exist beyond which individuals no longer are able to modulate the effects of limiting conditions (i.e., exceptionally long periods of inaccessible prey, particularly severe and extensive crust conditions, or limits to dispersal distances). Long-term studies that evaluate the range of climatic conditions across which an organism is behaviorally flexible, physiological limits, and fitness trade-offs can clarify the extent to which responses are adaptive (Beever et al. 2017).

A lack of synthesis between spatiotemporally-relevant snow and wildlife data can preclude researchers from adequately addressing research questions related to wildlife-snow interactions (Reinking et al. 2022, Boelman et al. 2019). Our research objectives specifically required spatiotemporally-continuous snow crust data, which, to our knowledge, did not exist prior to our modeling approach described herein. Our use of SnowModel to characterize snow crust conditions exemplifies how researchers can integrate biologically-relevant, scale-specific snow data into wildlife research (Reinking et al. 2022). We used a mechanistic understanding of

rain-on-snow, freeze-thaw, and wind events to model the evolution of snow crusts across space and time. We also explicitly matched the spatiotemporal scales and resolutions of modeled snow data with our wildlife data and research questions, allowing for direct, ecologically-relevant comparisons. There are limitations to the modeling approach (i.e., SnowModel assumes uniformity across a grid cell), and certain fine-scale sub-processes that influence snow conditions were not taken into account by SnowModel (e.g., the accumulation of snow in tree canopies, which can result in deeper snow when it sluffs to the ground). However, by integrating meteorological, topographical, and land cover data and assimilating on-the-ground snow measurements, SnowModel captures the primary physical conditions that determine snow characteristics and connects estimates to reality (Liston et al. 2020). As we demonstrate, SnowModel is a flexible tool that can be used for specific applications and research objectives, including an improved understanding of wildlife-snow dynamics.

Our findings contribute to understanding of behavioral responses to environmental change, and address particular gaps in knowledge related to the effects of variable, acute climatic stressors and changing snow regimes. In particular, we demonstrate how animals can use both proximate habitat selection and broader-scale movements to mediate variable, limiting conditions, depending on their spatiotemporal scales. Management practices that maintain local habitat refugia and migratory corridors can help ensure that facultative wildlife can employ multiple key strategies and use diverse areas in response to changing conditions. Likewise, improved knowledge of effects of variable conditions on wildlife can inform vulnerability assessments related to environmental change.

Even behaviorally plastic organisms such as the Great Gray Owl, however, may have limited capacity to accommodate anthropogenic environmental change (Snell-Rood et al. 2018),

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which is occurring at unprecedented rates and spatial scales, far beyond what organisms have experienced in their evolutionary history (Palumbi 2001, Sih et al. 2011). Although certain systems such as the GYE evolved amidst high spatiotemporal variability and seasonality, the potential remains for variable and extreme stressors due to climate change to upend individual fitness strategies, population dynamics, and ecosystem function (Melillo et al. 2018). Climate change is altering the timing, frequency and intensity of storm cycles (Lawrimore et al. 2014, Danco et al. 2016, Janoski et al. 2018) and rain-on-snow events (McCabe et al. 2007, Musselman 2018, Pan et al. 2018), amount of precipitation that falls as rain versus snow (Solomon et al. 2007, Kapnick and Hall 2012, O'Gorman 2014), means and extremes of daily precipitation including snowfall (Kunkel et al. 2013, Janoski et al. 2018), formation and persistence of snowpacks (Mote et al. 2005, Kapnick and Hall 2012, Kunkel et al. 2016, Mussellman et al. 2021), timing and degree of snow melt (Hamlet et al. 2005, Mote et al. 2005, Barnett et al. 2008), and the dynamics of wind regimes (Cheng et al. 2014, Pryor and Barthelmie 2010, Seneviratne et al. 2012). As we demonstrated, multiple, changing climatic factors can impact wildlife, potentially with cumulative or interactive effects. However, understanding the extent to which organisms can keep pace and cope with the complex and unprecedented changes associated with climate change remains a critical priority in the field of ecology (Wilcove 2008, Malhi et al. 2020).

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Tables:

Table 1. Relative selection strength of environmental variables at the daily step level by adult Great Gray Owls (n = 42) in the Greater Yellowstone Ecosystem during the winters of 2017–2022. Relative selection strength is based on population-level averages of integrated step selection analysis coefficient estimates for snow depth, wind crust event severity, and cumulative wind crust severity at the endpoint of daily steps.

Explanatory Variable	Estimate	SE	p-value	95% CI	
Snow Depth	-0.008	0.002	<0.001	0.989	0.995
Wind Crust Event Severity	-0.641	0.370	0.083	0.255	1.087
Cumulative Wind Crust Severity	-0.004	0.000	<0.001	0.995	0.997

Table 2. Environmental covariates influencing probability of winter long-distance movements by adult Great Gray Owls (n = 42) in the Greater Yellowstone Ecosystem during the winters of 2017–2022. To evaluate the possible effect of snow conditions on owl migrations, we performed Cox proportional hazards analysis. Here, we show Cox proportional hazards coefficients, hazard ratios (HR), standard errors (SE), p-values, and 95% confidence intervals (CI) for covariates in the top model (Wald test = 19.09, degrees of freedom = 2, P = <0.001, n_{events} = 139).

Explanatory Variable	Estimate	HR	SE	p-value	95% CI	
Ice Crust Event Severity	0.015	1.016	0.007	0.034	0.001	0.03
Ice Crust Persistence	0.011	1.011	0.003	<0.001	0.005	0.017

Figures:

Figure 1. Great Gray Owls hunting for subnivean small mammals, and an owl print with blood, indicating a successful foraging attempt. (Photos: Steve Mattheis)
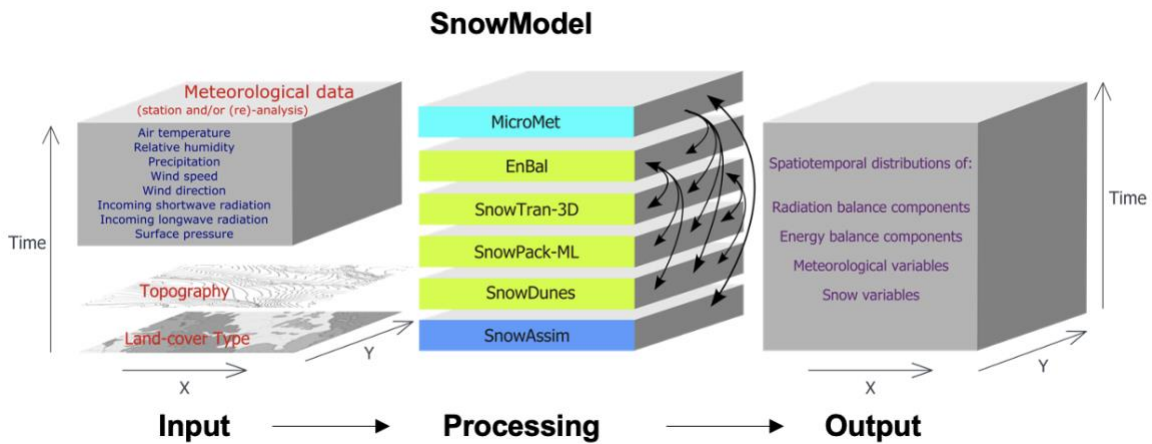
Figure 2. SnowModel schematic showing model inputs, processing modules, and outputs (from Liston et al. 2018, modified from Pedersen 2017).
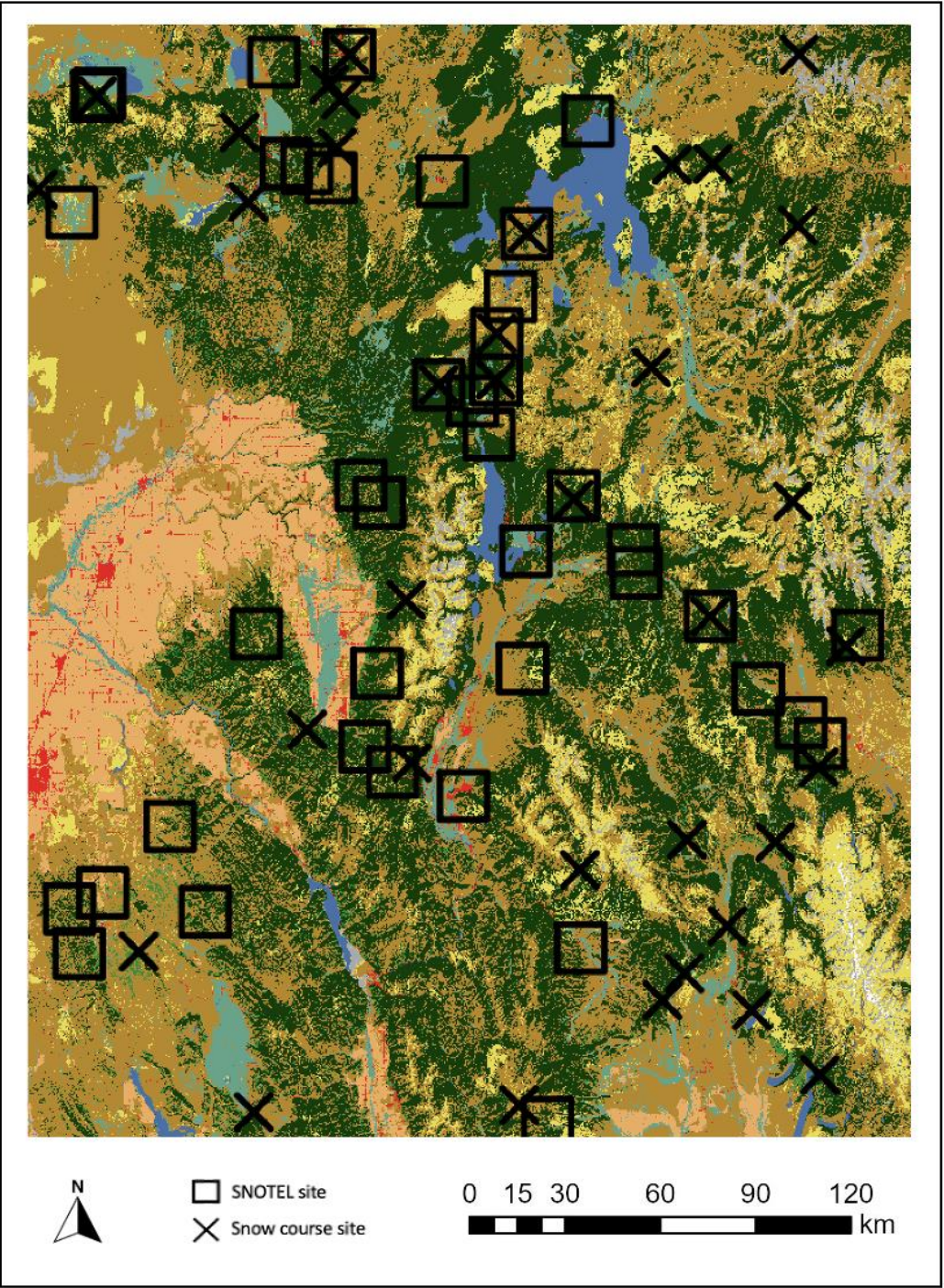
Figure 3. Locations of Snotel and Snow course sites within the study domain. Observations from sites (n = 77) were used for SnowModel assimilation. Modeled snow depth and snow-water equivalent values were assimilated based on observed measurements from Snotel and Snow course sites using a correction factor of 0.5.
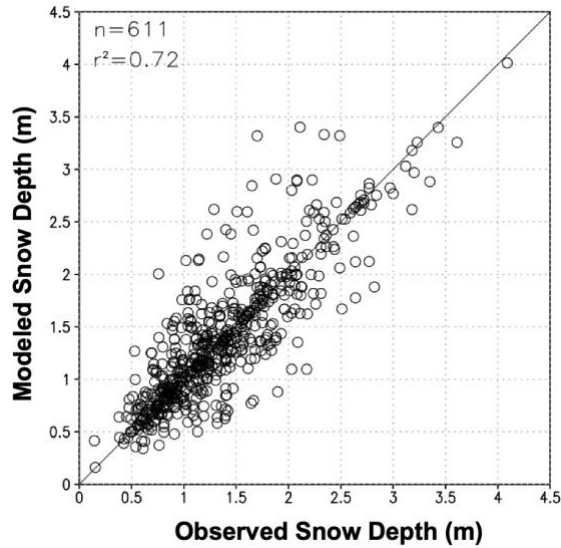
Figure 4. Modeled snow depth measurements versus *in situ* observed snow depth measurements (n = 611) from Snotel and Snow course sites during 2014–2022 in the Greater Yellowstone Ecosystem. Modeled snow depth data were assimilated based on observed measurements from Snotel and Snow course sites using a correction factor of 0.5.
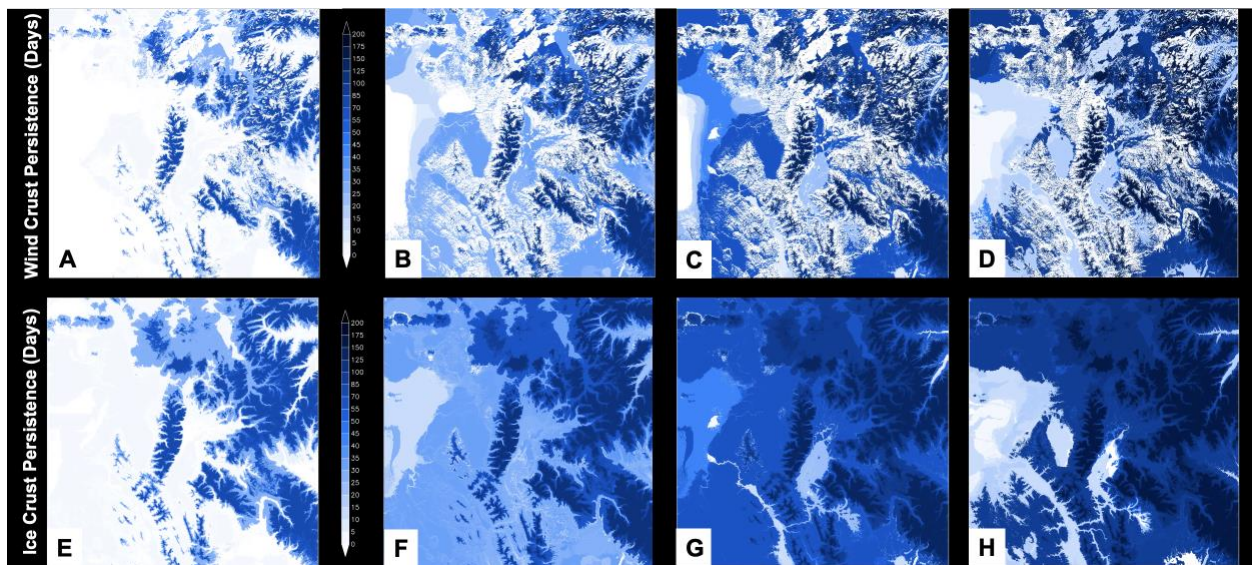
Figure 5. Spatiotemporal evolution of wind crust persistence (A-D) and ice crust persistence (E-H) across the Greater Yellowstone Ecosystem on 1 December 2017 (A,E), 1 January 2018 (B,F), 1 February 2018 (C,G), 1 March 2018 (D,H). Snow crust persistence was derived from estimated indices of snow crust severity, modeled at a 3-hrly time step and 30 m spatial resolution using SnowModel.
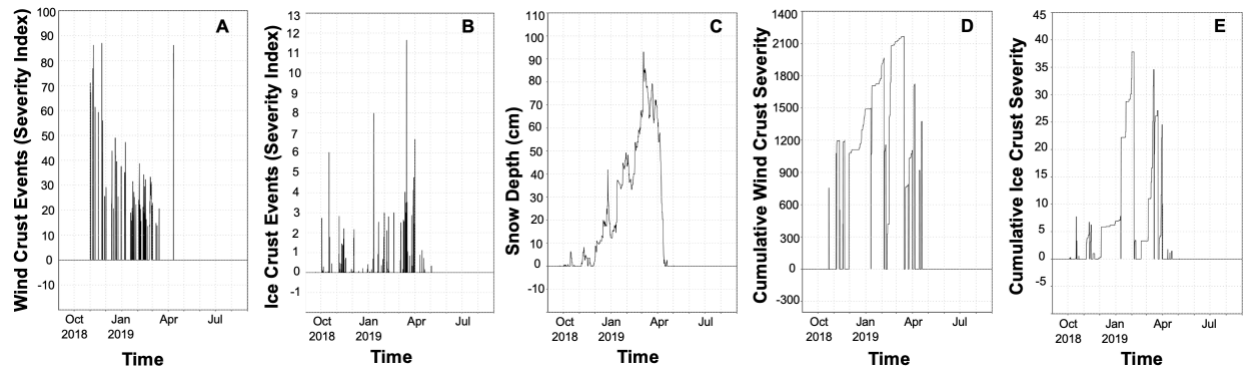
Figure 6. Example time series of wind crust events (A), ice crust events (B), snow depths (C), cumulative wind crust severity (D), and cumulative ice crust severity (E) at one point in space in the Greater Yellowstone Ecosystem between 1 September 2017–31 August 2018. Snow conditions were modeled at a 3-hrly time step and 30 m spatial resolution using SnowModel.

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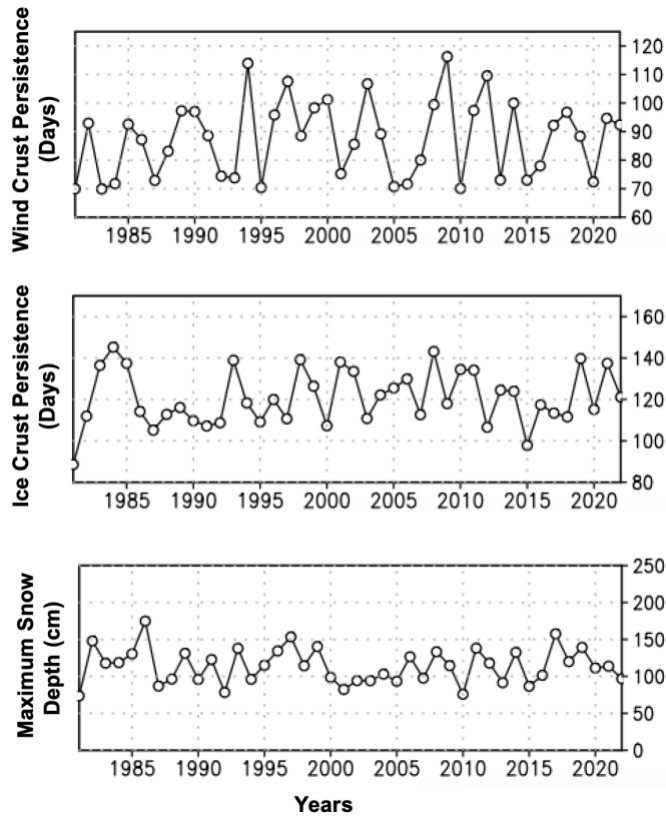
Figure 7. Annual variation in average maximum wind crust severity (A), average maximum ice crust severity (B), and average maximum snow depth (C) in the Greater Yellowstone Ecosystem during 1 September 1980–31 August 2022. Snow conditions were modeled at a 3-hrly time step and 30 m spatial resolution using SnowModel.
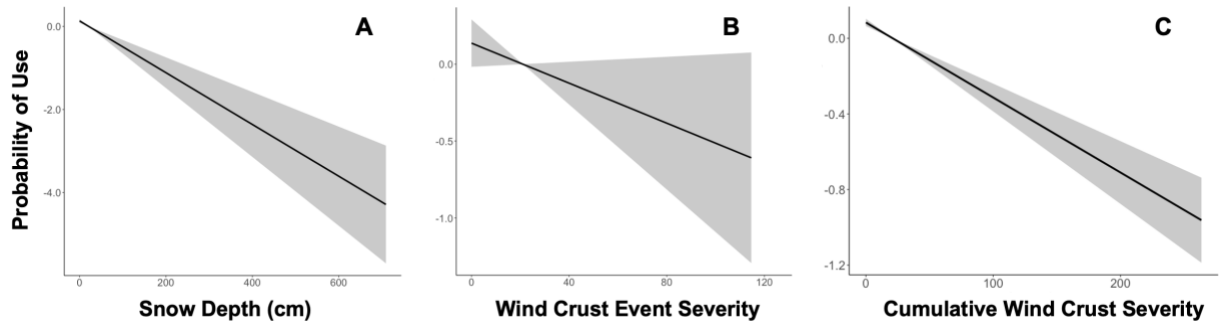
Figure 8. Probability of use of varying snow depths (A), wind crust event severity (B), and cumulative wind crust severity (C) by Great Gray Owls (n = 42) in the Greater Yellowstone Ecosystem during the winters of 2017–2022. Estimates are based on integrated step selection analysis (iSSA) at the daily step level. Gray shading indicates 95% confidence intervals, and probabilities are based on mean coefficients of iSSA.

Equations:

Melt Crust:

A melt-crust event quantity, M_e (m), at time, t (s), was defined to equal the snowmelt produced by SnowModel during that time step, $M(t)$ (m), for any case where the snowpack had a snow-layer temperature, $T_s(t)$ (°C), below the snow temperature threshold, $T_{s\_threshold}$ (= -0.01 °C),

$$M_e(t) = \begin{cases} M(t) & ; & T_s(t) < T_{s\_threshold} \\ 0.0 & ; & T_s(t) \geq T_{s\_threshold} \end{cases} \tag{1}$$

The snow layer temperature was defined to be the lowest snow temperature in any of SnowModel's snowpack layers at the current time, t. The threshold temperature identifies whether the snowpack is cold enough to freeze liquid water (i.e., the snowpack requires a cold content, so this threshold must be below 0.0 °C).

A non-zero melt-crust event indicated that a melt crust of that magnitude, formed at that time step. In addition, the crust sub-model assumed that crust-formation events are cumulative throughout the winter. For example, each subsequent winter crust formation event produced a thicker crust representation. This crust measure was assumed to persist in the snowpack until the entire snowpack was isothermal (0.0 °C), melting, and water was running out the bottom of the snowpack. This condition occurs when SnowModel's snowmelt runoff variable, R (m), is non-zero. Thus, the melt-crust persistence, M_p (m), is given by,

$$M_p(t) = \sum_{t=1}^{t=t_{max}} \begin{cases} M_e(t) + M_p(t-1) & ; & R(t) = 0.0 \\ 0.0 & ; & R(t) > 0.0 \end{cases}$$ (2)

where t_{max} is the number of time steps in an annual SnowModel simulation.

The melt-crust sub-model also counts the number of consecutive time steps, M_c (m), that had a non-zero melt crust. This is given by,

$$M_c(t) = \sum_{t=1}^{t=t_{max}} \begin{cases} M_c(t-1) + 1.0 & ; & M_p(t) > 0.0 \\ 0.0 & ; & M_p(t) = 0.0 \end{cases}$$ (3)

Rain on Snow Crust:

A rain-on-snow (ROS) crust was simulated in a similar fashion to the melt crust formulation. The ROS-crust event quantity, ROS_e (m), at time, t (s), was defined to equal the rain precipitation produced by SnowModel during that time step, $P(t)$ (m), for any case where the snowpack had a snow-layer temperature, $T_s(t)$ (°C), below the snow temperature threshold, $T_{s\_threshold}$ (= -0.01 °C),

$$ROS_e(t) = \begin{cases} P(t) & ; & T_s(t) < T_{s\_threshold} \\ 0.0 & ; & T_s(t) \geq T_{s\_threshold} \end{cases}$$ (4)

A non-zero ROS-crust event indicated that a melt crust of that magnitude, formed at that time step. The ROS-crust sub-model assumed that crust-formation events were cumulative throughout

the winter. This ROS-crust measure was assumed to persist in the snowpack until the entire snowpack was isothermal (0.0 °C), melting, and water was running out the bottom of the snowpack. This condition occurs when SnowModel's snowmelt runoff variable, R (m), is non-zero. Thus, the ROS-crust persistence, ROS_p (m), is given by,

$$ROS_p(t) = \sum_{t=1}^{t=t_{max}} \begin{cases} ROS_e(t) + ROS_p(t-1) & ; \quad R(t) = 0.0 \\ 0.0 & ; \quad R(t) > 0.0 \end{cases} \tag{5}$$

The ROS-crust sub-model also counts the number of consecutive time steps, ROS_c (m), that had a non-zero ROS crust. This is given by,

$$ROS_c(t) = \sum_{t=1}^{t=t_{max}} \begin{cases} ROS_c(t-1) + 1.0 & ; \quad ROS_p(t) > 0.0 \\ 0.0 & ; \quad ROS_p(t) = 0.0 \end{cases} \tag{6}$$

Ice Crust:

For the purposes of our analyses, we merged the melt-crust and ROS-crust variables described above into a single liquid-freeze (ice) crust event variable, L_e (m). Our reasoning for adopting this approach was that the wildlife do not care about the physical processes and mechanisms that created the crusts, they only care about the presence and magnitude of the crusts. Thus, we deemed it appropriate to combine the melt-crust and ROS-crust variables in the following way,

$$L_e(t) = M_e(t) + ROS_e(t) \tag{7}$$

Then the persistence and counts were created following Eqns. 5 and 6, but for L_e.

Wind Crust:

Our wind crust formulation closely follows the wind-related snow density evolution formulation of Liston et al. (2007, 2020). Creation of the wind crust variable first requires converting the SnowModel wind field, U_{obs} (m s^{-1}), at height, z_{obs} (m), to a common height (z_{2m} = 2.0 m). This is done using,

$$U_{2m} = U_{obs} \frac{\ln\left(z_{2m}/z_0\right)}{\ln\left(z_{obs}/z_0\right)} \tag{8}$$

where U_{2m} (m s^{-1}) is the wind speed at 2 m height, and z_0 (m) is the snow surface roughness (assumed to = 0.001 m). The wind crust can then form under two different conditions: new snowfall under blowing-snow conditions, W_{bs1} (kg m^{-3}), and snow blowing without new snow falling, W_{bs2} (kg m^{-3}).

During snowfall, a wind crust forms in the newly created top snow layer through the influence of blowing and drifting snow. For wind speeds ≥ 5 m s^{-1}, the new-snow wind crust contribution from blowing-snow, W_{bs1} (kg m^{-3}), is given by,

$$W_{bs1} = C_1 + C_2 \left\{ 1.0 - \exp\left[-C_3 \left(U_{2m} - 5.0 \right) \right] \right\} \tag{9}$$

where C_1, C_2, and C_3 are constants set equal to 25.0 kg m^{-3}, 250.0 kg m^{-3}, and 0.2 s m^{-1}, respectively; C_1 defines the density offset for a 5.0 m s^{-1} wind, C_2 defines the maximum density increase due to wind, and C_3 controls the progression from low to high wind speeds (Liston et al. 2007, 2020).

If the new-snow wind crust, at the current SnowModel time step, has a higher value than the final wind crust value at the previous time step, then the wind crust metric is updated following,

$$W_{bs2}(t) = W_{bs1}(t) \quad ; \quad if \ W_{bs1}(t) > W_{bs2}(t-1) \tag{10}$$

Wind speed at the current time step also contributes to wind crust formation during periods of no precipitation, W_{bs2} (kg m^{-3}). In this case, the top snow layer wind crust evolves similar to snow density evolution defined by Anderson (1976), but with a wind-speed contribution, U. This temporal change in snow crust from blowing snow is updated using,

$$\frac{dW_{bs2}}{dt} = m_1 \, m_2 \, U \, W_{bs2} \, \exp\left(-m_3 \, W_{bs2}\right) \tag{11}$$

which is discretized as follows,

$$W_{bs2}(t) = W_{bs2}(t-1) + m_1 \, m_2 \, \Delta t \, U \, W_{bs2}(t-1) \exp\left(-m_3 \, W_{bs2}(t-1)\right) \tag{12}$$

where $m_1 = 0.0005$ is a non-dimensional constant that controls the simulated snow crust change

rate, and $m_2 = 0.0013$ and $m_3 = 0.021$ following Anderson (1976).

For wind speeds ≥ 5 m s^{-1}, U is given by,

$$U = E_1 + E_2 \left\{ 1.0 - \exp\left[-E_3 \left(U_{2m} - 5.0 \right) \right] \right\} \tag{13}$$

with E_1, E_2, and E_3 defined to be 5.0 m s^{-1}, 15.0 m s^{-1}, and 0.2 s m^{-1}, respectively; E_1 defines the U offset for a 5.0 m s^{-1} wind, E_2 defines the maximum U increase due to wind, and E_3 controls the progression of U from low to high wind speeds (Liston et al., 2007, 2020). For wind speeds $<$ 5 m s^{-1}, U is defined to equal 0.0 m s^{-1}. This approach limits the crust value increase resulting from wind transport to winds capable of moving snow (assumed to be winds ≥ 5 m s^{-1}).

The above wind crust formulation is similar to the melt crust persistence variable; it keeps evolving in time and is set to zero when snowmelt water is running out of the snowpack. Therefore, we define the wind crust persistence, W_p (kg m^{-3}), to be,

$$W_p(t) = \sum_{t=1}^{t=t_{max}} \begin{cases} W_{bs2}(t) & ; & R(t) = 0.0 \\ 0.0 & ; & R(t) > 0.0 \end{cases} \tag{14}$$

This can be used to extract the time evolution of wind crust events, W_e (kg m^{-3}), using the formula,

$$W_e(t) = \begin{cases} W_p(t) - W_p(t-1) & ; \quad W_p(t) - W_p(t-1) > 0.0 \\ 0.0 & ; \quad W_p(t) - W_p(t-1) \le 0.0 \end{cases} \tag{15}$$

The wind-crust sub-model also counts the number of consecutive time steps, W_c (kg m^{-3}), that had a non-zero wind crust. This is given by,

$$W_c(t) = \sum_{t=1}^{t=t_{max}} \begin{cases} W_c(t-1) + 1.0 & ; \quad W_p(t) > 0.0 \\ 0.0 & ; \quad W_p(t) = 0.0 \end{cases} \tag{16}$$

CHAPTER FOUR

Within-season versus carry-over effects on breeding by a facultative migrant

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Abstract:

The environmental conditions that an individual experiences throughout its life history can influence key fitness metrics. Thus, consideration of the full annual cycle, including both within-season and carry-over effects, is essential for identifying primary factors that determine population dynamics. We analyzed potential mechanisms influencing variation in reproductive performance by Great Gray Owls in the Greater Yellowstone Ecosystem between 2014–2022. Specifically, we evaluated how territory occupancy, nest initiation, timing of nesting, nest success, and nesting productivity (number of young fledged per nest) related to prey abundance and/or winter snow conditions that influence foraging success. Owl reproduction was inversely related to relative abundance of primary prey during the breeding season. Snow conditions during the preceding winter carried over to influence subsequent breeding, although the directionality of fitness responses differed with specific snow characteristics. For example, more severe wind crusts negatively affected occupancy, nest initiation, and productivity, whereas more severe ice crusts were associated with increased nest initiation and productivity. Owl behavioral responses to wind versus ice crusts varied, which potentially explains differences in fitness outcomes. Our findings emphasize that carryover effects from previous periods can influence subsequent fitness, and potentially more powerfully than proximate, within-season factors. The reproductive consequences of snow conditions leading into the breeding season, moreover, have implications for sensitive species amidst on-going climatic changes in the temperate zone.

Key words: Carry-over effect, facultative migrant, foraging, Great Gray Owl, prey abundance, snow conditions, snow crust

Introduction:

Identifying determinants of individual fitness and consequent population demographics is a central goal in ecology and conservation. Many factors influence population dynamics, making it challenging to identify which are most limiting (Szostek and Becker 2015). Indeed, the environmental conditions that an individual experiences throughout its life history can influence key fitness metrics (Sherry and Holmes 1996, Newton 2004, Norris 2005), warranting increased consideration of factors across the annual cycle and their relative importance for demographics (Norris et al. 2004, Harrison et al. 2011, Marra et al. 2015).

Conditions, events, or processes during one point in time can have consequences for individual fitness during a subsequent period, in a phenomenon known as a carry-over effect (Marra et al. 1998, Norris and Marra 2007, Harrison et al. 2011). Although examples of carry-over effects are well-established, the specific contexts under which they occur can vary and are poorly understood (O'Connor et al. 2014, Akresh et al. 2019). In some systems, the relative influence of carry-over effects is minimal compared to more immediate, within-season effects (Ockendon et al. 2013). In other cases, conditions from a prior phase can be more important than proximate, within-season conditions (Finch et al. 2014). Condition- and time-mediated effects are two mechanisms by which prior circumstances can influence subsequent vital rates (Piersma 1987, Lepage et al. 2000, Drake et al. 2013). For example, previous conditions can cause an individual to arrive on its breeding grounds in poor body condition, which can reduce reproductive output (Ebbinge and Spaans 1995, Prop and Black 1998, Drent et al. 2003, Smith and Moore 2003). Likewise, an individual might arrive to its breeding grounds late, which can delay pair formation and nest initiation, create a phenological mismatch between breeding and key resource availability, and ultimately decrease reproductive performance (Verhulst and

Tinbergen 1991, Lozano et al. 1996, Siikamaki 1998, Lepage et al. 2000, Norris et al. 2004, Smith and Moore 2005). Given the potential ramifications of carry-over effects on population dynamics (Sæther and Bakke 2000, Vickery et al. 2014), consideration of the full annual cycle, including both within-season and carry-over effects, is essential for determining primary factors that influence population dynamics (Norris et al. 2004, Marra and Holmes 2001).

The majority of research on carry-over effects focuses on long-distance migrants (Harrison et al. 2011). Carry-over effects are thought to be particularly important in such systems because phases of the annual cycle are extremely spatiotemporally disparate (Sherry and Holmes 1996, Harrison et al. 2011, Szostek and Becker 2015, Rushing et al. 2016). However, even year-round resident animals experience distinct phases that can be characterized by environmental variation and temporal constraints, for example in highly seasonal systems (Harrison et al. 2011, O'Connor et al. 2011). Likewise, the potential for carry-over effects may be high for facultative migrants for which movement behavior varies in direct response to unpredictable, constraining environmental conditions (such as extreme weather or food abundance) (Newton 2008). Determining the extent to which carry-over effects operate in facultative migrant populations is critical for understanding population dynamics, limiting factors, and vulnerability to environmental change.

In cold regions dominated by snow, such as high-elevation environments, snow is a key determinant of ecological processes (Bokhorst 2016). For example, snow conditions can influence wildlife population dynamics (Forchhammer and Boertmann 1993, Ims et al. 2008, Bhattacharyya et al. 2014, Hansen et al. 2019), resource availability and foraging opportunities (Skogland 1978, Laperrierre and Lent 1977, Collins and Smith 1991), habitat selection (Gilbert et al. 2017, Mahoney et al. 2018, Berman et al 2019, Pedersen et al. 2021), movement behavior

(Droghini and Boutin 2018, Pedersen et al. 2021), and predator-prey dynamics (Gese et al. 1996, Nelson and Mech 1986, Horne et al. 2019, Peers et al. 2020). Despite growing understanding of the ecological importance of snow regimes, however, the effects of changing snow conditions on wildlife remain relatively unknown, in part because of a lack of integration of available snow data and wildlife responses (Boelman et al. 2019, Reinking et al. 2022). As a result, the effects of snow conditions on individual fitness and population dynamics remain poorly understood. Such understanding is particularly critical and timely considering the extent to which snow regimes are changing rapidly (IPCC 2022).

In northwestern Wyoming, the Greater Yellowstone Ecosystem (GYE) is home to one of the world's most iconic facultative migrant species, the Great Gray Owl (*Strix nebulosa*). The reproductive performance of Great Gray Owls can fluctuate dramatically from year to year (Bull and Henjum 1990, Hipkiss et al. 2008). Prey abundance strongly affects breeding in many boreal species including some raptors (Mikkola 1983, Korpimäki and Hakkarainen 1991, Newton 1998, Lehikoinen et al. 2011, Schmidt et al. 2012). Indeed, in boreal Great Gray Owl populations that primarily prey upon *Microtus* species, reproductive output often co-varies numerically with highly cyclical prey densities (Bull and Henjum 1990, Hipkiss et al. 2008). In the GYE, however, Great Gray Owls primarily feed on Northern Pocket Gophers (*Thomomys talpoides*) (unpub. data, Franklin 1988), which may exhibit more stable population dynamics compared with voles. Therefore, the extent to which within-season or carry-over effects of primary prey abundance determine reproductive performance by Great Gray Owls in the GYE remains unclear.

Changing snow conditions can influence animals that rely on food resources beneath the snow (Kausurd et al. 2008, Kohler and Aanes 2004, Ims et al. 2008, Gilg et al. 2009, Hansen et

al. 2013, Langlois 2017, Berger et al. 2018). During the winter, Great Gray Owls primarily hunt subnivean small mammals, and snow conditions such as increased snow depth and snow crusts can limit foraging success (Mysterud 2016). In the GYE, Great Gray Owls avoided and/or migrated in response to increased snow depths and more severe and persistent snow crust conditions, most likely due to associated restricted foraging opportunities (Gura et al. *in prep*). Such limiting snow conditions not only determine habitat selection and movement behavior but also likely influence fitness, potentially via carry-over effects. Restrictive foraging conditions during the winter may result in poor body condition (condition-mediated effect) and/or delay reproduction (time-mediated effect), thereby influencing reproductive performance (Meltofte et al. 2008, Liebezeit et al. 2014). However, the effects of snow conditions on subsequent reproductive output by facultative breeders such as the Great Gray Owl are poorly understood (Mysterud 2016, but see Domine et al. 2018).

Here, we evaluated the relative influence of within-season versus carry-over effects related to foraging opportunity on reproductive performance by Great Gray Owls in the GYE. We hypothesized that environmental conditions that limit foraging success within the breeding season may determine Great Gray Owl reproductive output. Specifically, we predicted that decreased primary prey abundance during the breeding season would result in decreased nest initiation, nest success, and productivity rates for owls. Alternately, we hypothesized that environmental conditions that limit foraging success during the winter would carry over to determine subsequent breeding performance and timing of reproduction. Specifically, we predicted that decreased primary prey during the prior breeding season, and increased severity and persistence of snow crusts, increased snow depths, and increased length of the core snow

period would result in delayed breeding, and decreased nest initiation, nest success, and number of young fledged during the subsequent breeding season.

Methods:

Study Area:

We conducted our study in the GYE in northwestern Wyoming and eastern Idaho. Great Gray Owl breeding territories were located in Teton County, Wyoming in the foothills of the Teton Range between Hoback and Moran, Wyoming. Breeding areas were dominated by lodgepole pine (*Pinus contorta*) forest and also contained quaking aspen (*Populus tremuloides*), blue spruce (*Picea pungens*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and mixed cottonwood-spruce riparian forest (*Populus angustifolia*, *Picea pungens*). Breeding areas also contained patches of montane and xeric meadows, sagebrush steppe, and wetlands. The study domain included wintering locations of owls in Teton, Lincoln, and Sublette counties in Wyoming and Bonneville, Madison, and Teton counties in Idaho. Wintering areas overlapped with breeding habitat but also included south-facing aspects and lower-elevation valleys, riparian corridors, and developed areas. The climate was highly seasonal, with extensive, snowy winters. Across the study domain and study period, mean annual snow onset day occurred on 10 November and mean snow-free day was 30 April.

Reproductive Performance:

We monitored Great Gray Owl reproduction within known breeding territories in the GYE between 2014–2022. We originally located territories using a combination of nighttime

call-back surveys during the courtship period (March–April), nest-searching, and tracking owls tagged with transmitters. Each year during the study period, we assessed territory occupancy, nest initiation, nest success, and productivity by surveying territories once/week between March–July. We defined a territory as occupied if a territorial Great Gray Owl was detected during nighttime call-back surveys and/or on automated recording units during the courtship period. We deemed a territory active (i.e., successful nest initiation) if we observed direct evidence of nesting (i.e., nest initiation by an incubating female owl, presence of chicks and/or fledglings). The nesting effort was considered successful if the pair successfully fledged young. We calculated productivity as the number of young fledged from a nest. If nest sites were unknown, we searched the territory for nests and owls by walking 25m transects throughout the area, checking suitable nest structures and perches for owls and playing call-back broadcasts to initiate a vocal response from nesting females. If we did not observe direct evidence of a nesting attempt, we classified the territory as inactive, although we acknowledge the potential for survey error due to nest failure and/or the discreet, secretive nesting behavior of Great Gray Owls. When an active nest was located, we monitored its status once/week to determine nest success, fledge dates, and productivity.

Breeding-season Prey Abundance:

We monitored Great Gray Owl primary prey, the Northern Pocket Gopher, annually during the breeding season at 18 owl territories between 2014–2022 following van Riper et al. (2013). We surveyed the same territories once per year between late April–early September. We selected this subsample based on accessibility and also included territories from across our entire study domain that spanned a gradient of elevational zones. For each territory, we digitized all

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meadows within 500 m of known nests and randomly selected three meadows in which we conducted prey surveys across years. We started at the head of each meadow and walked 45-degree diagonal transects until we reached the end of the meadow. We tallied new pocket gopher mounds (tailings) and old pocket gopher mounds (eskers) visible within 10 m of the transect. We calculated total survey length for each territory/year and divided by the number of pocket gopher sign to quantify relative abundance (separately for new, old, and combined new and old sign). We combined data across territories to determine annual relative pocket gopher abundance.

Snow Conditions:

We estimated snow characteristics across the GYE from 01 September 2013–31 August 2022 to evaluate whether annual variation in snow conditions influenced reproductive performance by Great Gray Owls. We used SnowModel, which is a data-model fusion system that incorporates land cover, topography, and meteorological data and available snow observations to estimate the evolution of snow conditions across space and time (Liston and Elder 2006a, Liston et al. 2020). Specifically, we incorporated 30 m spatial resolution 2015 North American Land Change Monitoring System landcover dataset (Commission for Environmental Cooperation 2015), the United States Geological Survey's (USGS) 1 arc-second Digital Elevation Model (DEM) (USGS 2020), and the National Land Data Assimilation System's (NLDAS-2) meteorological data, which consisted of hourly weather data with a 1/8th-degree spatial resolution (NLDAS 2022, Mitchell et al. 2004, Xia et al. 2012). We assimilated *in situ* SWE and snow depth measurements (n = 611) from Natural Resources Conservation Service (NRCS) snow telemetry (Snotel) and/or snow course sites within our study domain to ensure model results were tied to observations (Stuefer et al. 2007, Liston and Hiemstra 2008, Liston et

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al. 2008, Reinking et al. 2022).

We modeled snow conditions likely to limit Great Gray Owl winter foraging, and subsequently, influence reproductive performance. Specifically, we calculated snow depth, length of the core snow period, wind crust, and ice crust conditions. We identified wind crust events by calculating the change in snow density associated with blowing snow 2 m above the land surface. We estimated indices of wind crust severity based on the relative increase in snow density due to wind speed and amount of blowing snow (Liston et al. 2007). We modeled indices of ice crust severity by identifying rain-on-snow events or melt-freeze events. Specifically, we calculated the amount of liquid water that reached a cold snowpack (snowpack layer temperature $< -0.01°C$) and did not run off but instead froze within the snowpack. The severity indices for wind crusts versus ice crusts are not directly comparable due to the inherent differences in how these crusts form and were calculated. When a crust forms within a snowpack, it can persist even as new snow falls and buries the crust below the surface. Therefore, for wind and ice crusts, we calculated not only their formation and initial severity (crust event) but also their cumulative severity (summed indices of event severity over time) and persistence (consecutive number of days the crust persisted within the snowpack). Snow crusts disappear from snowpacks when liquid water reaches the ground, so we reset cumulative variables (cumulative severity index, persistence) when the snowpack became isothermal (i.e., temperature throughout $= 0.0°C$) and run-off occurred. We modeled snow conditions at a 500 m $\times$ 500 m spatial resolution and three-hourly time-step. See Chapter 3 Equations for additional details on modeling of snow crust conditions.

We summarized annual (1 September–31 August) winter snow conditions by calculating domain-wide values based on the aforementioned fine-scale snow characteristics. Specifically,

for each winter at the domain level, we calculated average maximum snow depth; average total number of days in the core snow period; average cumulative crust severity index, maximum crust severity index, maximum crust persistence, and total number of days with a crust for both wind and ice crusts.

Statistical Analysis:

We used Generalized Linear Mixed Models (Zuur et al. 2009) with negative binomial or poisson distributions to evaluate within-season versus carry-over effects on Great Gray Owl reproductive performance. Specifically, we tested whether the relative abundance of pocket gopher sign within breeding territories, both within the breeding season or during the prior breeding season, explained owl territory occupancy, nest initiation, nest success, productivity, and/or nest initiation date. We also assessed whether reproductive metrics were explained by prior winter snow conditions, including maximum snow depth, total number of days in the core snow period, cumulative and maximum crust severity, maximum crust persistence, and total number of days with a crust for wind and ice crusts, respectively.

We tested for collinearity between environmental covariates using Spearman's rho ($|r| >$ 0.7). We used a tiered model-selection process whereby we created univariate models when two covariates were correlated and selected the variable from the model with the lowest Akaike's Information Criterion value (AIC_c) to include in global models. Then, we compared models considering all combinations of variables from the top univariate models using AIC_c (Doherty et al. 2012). We included year as a random effect in all global models to account for any annual variation in reproductive performance not explained by our covariate dataset. We also modeled

the relationships between nest initiation day of the year and nest success and productivity. We selected top models based on the lowest AIC$_c$ value (Burnham and Anderson 2002).

Results:

Reproductive Performance:

We observed breeding attempts at 32 Great Gray Owl territories during 2014–2022. Overall, we monitored 246 territories-by-year, 190 of which were occupied, 96 of which attempted breeding, and 65 of which successfully fledged young. We observed relatively high and consistent annual occupancy rates within monitored owl territories (mean = 0.79, SD = 0.15) (Figure 1A). The proportion of occupied territories that initiated nesting each year, however, was variable (mean = 0.50, SD = 0.35, range = 0.06–1.0) (Figure 1B), and number of active nests ranged from 1 (in 2017)–24 (in 2015). The proportion of active nests that successfully fledged young also varied (mean = 0.52, SD = 0.29, range = 0–0.81) (Figure 1C), and number of successful nests ranged from 0 (in 2017)–19 (in 2015). Number of young fledged per nest ranged from 1–4 and varied across years (Figure 1D). We also observed annual variation in mean nest initiation date (Figure 1E), with an average nest initiation date across years of 22 April (SD = 13.4; range = 26 February–18 May). The earliest observed nest initiated (which failed) occurred on 26 February; this initiation was abnormally early so we excluded it from analysis as an outlier. The next earliest observed initiation date was 5 April. Earlier nest initiation was associated with increased nest success (Table 1, Figure 2A) and increased productivity (Table 1 Figure 2B).

Primary Prey Abundance:

Relative abundance of Northern Pocket Gophers within owl territories during the breeding season varied annually (Figure 1F). Across years, mean number of new gopher mounds per meter surveyed was 0.16 (SD = 0.06, min = 0.07, max = 0.23). Mean number of total pocket gopher sign (old eskers and new mounds) per meter was 0.06 (SD = 0.03, min = 0.13, max = 0.09).

Snow Conditions:

Maximum snow depth averaged across the study domain fluctuated annually (mean = 0.70cm, SD = 0.05) (Figure 3A), and the average number of days in the core snow period followed a similar pattern, varying between 101 and 109 days (mean = 104.82, SD = 2.20) (Figure 3B). Maximum wind crust severity and cumulative wind crust severity also fluctuated across years (mean = 60.65, SD = 2.04; mean = 30.01, SD = 27.86), as did maximum and cumulative ice crust severities (mean = 0.14, SD = 0.01; mean = 0.49, SD = 0.05) (Figure 3C-F).

Within-season Effects on Breeding:

Within-season prey abundance was related to the reproductive performance by Great Gray Owls, but not as predicted. The best-supported models explaining Great Gray Owl breeding territory occupancy, nest initiation, and nest success included relative primary prey abundance during the breeding season (Table 2). Specifically, with greater abundance of fresh pocket gopher mounds, the likelihoods of territory occupancy and nest initiation declined (Figures 4A, 5A). Increased abundance of combined old and new pocket gopher mounds also was associated with later nest initiation dates (Figure 7A). We found a weak negative relationship between the relative abundance of fresh pocket gopher mounds and the probability that a nest was successful

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(Table 2). Primary prey during the breeding season was not included in the top model for Great Gray Owl productivity.

Carry-over Effects on Breeding:

Snow conditions during the preceding winter influenced Great Gray Owl breeding territory occupancy, nest initiation, timing of nesting, and productivity (Table 2). Maximum wind crust severity was inversely related to territory occupancy (Figure 4B), meaning that more severe wind crusts were associated with lower likelihood of occupancy. A similar trend was seen between cumulative wind crust severity and the probability of a territory being active (5B), with likelihood of nest initiation decreasing with increased total wind crust severity. Cumulative wind crust severity also was negatively associated with the number of young fledged from active nests (Figure 6A). Additionally, increased cumulative wind crust severity resulted in later nest initiation dates (Figure 7B).

In contrast to wind crust severity metrics, greater maximum ice crust severity resulted in earlier nest initiation (Figure 5C) and increased number of young fledged (Figure 6B). Snow depth, length of the core snow period, and prior breeding-season prey abundance were not statistically significant in explaining timing of breeding or reproductive performance and were not included in top models.

Discussion:

We evaluated the influence of within-season versus carry-over effects on reproductive performance in a facultative migrant population, Great Gray Owls in the GYE. Contrary to our expectations, within-season prey abundance was inversely related to Great Gray Owl

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reproductive output and timing of nesting. We found strong support, however, for the presence

of carry-over effects, including both positive and negative relationships between prior winter

snow conditions and breeding. Considering that owls employed different movement strategies

during the winter in response to varying snow conditions (Gura et al. *in prep*), such patterns may

shed light on the efficacy and fitness implications of specific facultative movement behaviors

used to modulate the effects of limiting conditions. Furthermore, our findings suggest that prior

conditions potentially can be more important determinants of fitness than current conditions.

Carry-over effects of snow conditions that can influence foraging success during winter

in turn affected subsequent breeding. Therefore, fluctuating snow regimes, and behavioral

responses to such changes, have implications for populations and community dynamics

(Mysterud 2016). Although many predators exhibit numerical responses to fluctuating prey

populations (Mikkola 1983, Korpimäki and Hakkarainen 1991, Newton 1998, Lehikoinen et al.

2011, Schmidt et al. 2012), conditions that influence foraging success also can be an important

factor determining population dynamics. Indeed, there is potential for interactions between prey

abundance and foraging conditions, whereby predators may not be able to capitalize on increased

prey populations if conditions are not conducive to foraging. Likewise, low prey abundance and

poor foraging conditions may compound one another, with potentially detrimental effects on

predators. Finally, particular behavioral strategies can be used to alleviate limiting conditions,

thereby modulating the effects of poor foraging conditions and low prey abundance on fitness.

We found that these dynamics can carry-over to effect subsequent fitness, underscoring the

importance of considering past conditions and contexts when evaluating factors that are most

limiting for populations (Gaillard et al. 2010).

Consideration of behavioral responses to limiting conditions can strengthen inference regarding determinants of fitness and the effects of environmental conditions. In the case of Great Gray Owls in the GYE, severe wind crusts were associated with reduced reproductive performance, despite owls' avoidance of these conditions at the proximate scale during the winter (Gura et al. *in prep*). Increased severity of wind crusts consequently restricted where owls could forage, and proximate refugia potentially were not sufficient to offset the negative effects of wind crusts on foraging success and ultimately, body condition leading into breeding. On the other hand, more severe ice crust conditions were associated with earlier nest initiation and number of young fledged by Great Gray Owls. Ice crusts generally were spatially homogenous in the GYE due to their broad-scale, synoptic systems that control their formation such as weather patterns and temperature regimes (Rennert et al. 2009), and as a result, Great Gray Owls typically migrated in response to severe and persistent ice crusts (Gura et al. *in prep*). Therefore, a possible explanation for different fitness responses to wind versus ice crusts is variation in the adaptiveness of specific behavioral tactics used in response to each condition (Losier et al. 2015). For example, long-distance movements after initial exposure to severe and persistent ice crusts (Gura et al. *in prep*) may be effective for offsetting the fitness consequences of such limiting snow conditions; these results align with the general theory that most broad-scale migrations are adaptive and maximize fitness in the face of environmental seasonality or variability (Alerstram 2003). However, evaluating fitness consequences of specific behavioral strategies, such as long-distance migration, was beyond the scope of this study and warrants further attention.

Prior conditions also influenced subsequent fitness via a time-mediated carry-over effect. Timing of breeding can affect reproductive output and therefore should be optimized to maximize individual fitness (Drent and Daan 1980). In many species, variation in individual

body condition explains differences in timing of breeding (Öberg et al. 2014), and reproductive performance generally decreases as the breeding season advances (Perrins 1970, Korpimäki 1987, Hochachka 1990, Brinkhof et al. 1993). We found evidence for this pattern, as Great Gray Owl nests that were initiated earlier were more likely to be successful and produce more fledglings. Winters with increased cumulative wind crust severity resulted in decreased territory occupancy and nest initiation, later nest initiation dates, and decreased productivity. The negative effects of more severe wind crusts on Great Gray Owls potentially included decreased body condition leading into breeding and resultant delays in nest initiation, both of which decreased reproductive performance. We observed no effect of ice crust conditions on timing of reproduction or breeding performance, suggesting that migratory movements that typically occurred in response to rain-on-snow and melt-freeze events the preceding winter may not delay owls returning to breeding territories to initiate nesting, or result in decreased body condition to the extent that they negatively impacted subsequent reproductive output. Likewise, although snow cover is suggested as a factor influencing timing of breeding for Great Gray Owls (Franklin 1988, Voous 1988, Bull et al. 1989) and increased snow depth delayed breeding by Ural Owls (Lehikoinen et al. 2011), maximum snow depth and length of the core snow period did not explain timing of nesting nor reproductive output in our study. Finally, prey abundance during the prior year can influence timing of breeding and reproductive output of owls (Lehikoinen et al. 2011), but we did not observe a statistically significant relationship between pocket gopher abundance during the prior breeding season and subsequent Great Gray Owl reproduction.

Many predators demonstrate positive numerical responses to prey populations (e.g., Korpimäki and Norrdahl 1989, Durant et al. 2003, Seress et al. 2018, Mougeot et al. 2019, Fayet et

al. 2021), yet we observed a negative relationship between Great Gray Owl reproductive output and relative prey abundance during the breeding season. Several factors may explain this pattern of decreased reproduction in relation to increased prey. First, specific timing of primary prey surveys varied across years, although we typically surveyed Northern Pocket Gophers during the Great Gray Owl fledging period (late June – mid-July), which also coincided with the timing of pocket gopher juvenile dispersal (Clark and Stromberg 1987, Verts and Carraway 1999). We therefore may have surveyed primary prey too late in the breeding season to accurately assess the influence of prey availability on reproduction. Instead, increased abundance of pocket gophers during poor reproductive years for Great Gray Owls may reflect a positive response in the prey population to decreased predation pressure (Nilsson 2001). Additionally, prey can exhibit breeding suppression in response to increased risk of predation (Ylönen 1989, Lima and Dill 1990, Ylonen 1994, Kokko and Ruxton 2000). Pocket gophers may produce fewer young and therefore be less abundant during years of increased reproductive output (and likely greater predation) by Great Gray Owls. Finally, there may be a time lag or offset in the predator-prey cycles of Great Gray Owls and pocket gophers in the GYE (Macdonald 1976, Poulin et al. 2001, Avotins et al. 2023), although pocket gopher abundance during the prior breeding season did not explain subsequent owl reproduction in our system.

The extent to which Great Gray Owls in the GYE rely upon alternate prey is poorly understood but may be a factor influencing facultative breeding (Murdoch and Oaten 1975). Our previous analyses of owl pellets opportunistically collected near nests between 2013–2015 indicated that Great Gray Owls primarily fed on Northern Pocket Gophers numerically (53%) and in terms of biomass (64%), followed by voles (37% and 26% based on frequency and biomass, respectively) (Gura et al., unpublished data), which corroborated findings in previous

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years in the GYE (Franklin 1988) and in other regions of the western United States (Winter 1986, Bull and Henjum 1990). Based on pellet analyses, we therefore focused on Northern Pocket Gophers for primary prey surveys in the current study. However, pocket gophers are larger than voles, and central place foraging theory predicts that larger prey items preferentially will be brought to the nest, particularly when foraging occurs at increasing distances from the nest (Orians and Pearson 1979). Although voles were found less frequently in pellets adjacent to nests, they may be a critical food resource for owls in the GYE, potentially influencing body condition of adults entering the reproductive season and/or condition of foraging adult males during breeding. In the Sierra Nevada, Great Gray Owl reliance on *Microtus* and *Thomomys* species changed depending on prey availability (Williams et al. 2012), and Great Gray Owls in the western United States are thought to forgo breeding during years of low vole abundance, even if pocket gophers are prevalent (Williams et al. 2012). Improved understanding of the potential interactions between *Microtus* and *Thomomys* populations and their influence on Great Gray Owl breeding in the GYE warrants further investigation.

The consideration of more explicit metrics of prior winter foraging conditions and breeding-season prey abundance also would benefit future inquiry. For example, we quantified annual variation in average snow conditions across the study domain, which was an area containing all winter locations of owls across years. However, we did not explicitly link the snow conditions individual owls directly experienced with subsequent reproduction. Likewise, we estimated annual relative primary prey abundance by surveying a sub-sample of Great Gray Owl territories each year. However, prey abundance potentially differed between owl territories, and linking territory-specific prey metrics with territory-specific reproductive performance could strengthen inference. More direct measures of proxies for fitness, such as foraging success and

prey delivery rates, also can improve understanding of the fitness implications of winter snow conditions and primary prey abundance. Snow conditions in the GYE persist into the early breeding season for Great Gray Owls, but we did not explicitly test the effect of spring snow crust and snow depth conditions or timing of snow melt on reproduction. Weather conditions during the breeding season can influence timing of reproduction and fitness metrics such as egg hatching success, nestling growth, and fledging success (i.e., James and Whitford 1994, Bangerter et al. 2021, Zwaan et al. 2020). The extent to which early breeding-season snow conditions influence reproductive performance by Great Gray Owls remains an important avenue of study. Finally, directly evaluating the fitness effects of behavioral strategies can improve inference regarding the effects of limiting conditions on wildlife.

We demonstrate that both within-season and carry-over effects should be considered when evaluating determinants of individual fitness and population dynamics, including for facultative migrants and breeders. The lack of a positive numerical response between owl reproduction and within-season primary prey underscores our finding that prior conditions can influence subsequent fitness, potentially even more so than proximate conditions. In particular, we found evidence that "locked pastures" (Hansen et al. 2013), in which food resources are rendered inaccessible due to snow conditions, influenced subsequent breeding by Great Gray Owls in the GYE. However, fitness responses to locked pastures differed depending on the characteristics of snow conditions, and potentially according to the behavioral tactics used to modulate their effects. Understanding proximate and carryover effects on sensitive species induced by limiting conditions such as the snowpack properties is critically important in light of the expanding extent and increasing rapidity of climate changes (Palumbi 2001, Sih et al. 2011).

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Tables:

Table 1. Modeled relationship between Great Gray Owl nest success (at least one young fledged) and number of young fledged (productivity) as a function of nest initiation date. Results include beta coefficients (β), standard errors (SE), p-values, and 95% confidence intervals calculated using Generalized Linear Mixed Models and data from nest-monitoring of Great Gray Owl territories within the Greater Yellowstone Ecosystem during 2014–2022.

Nest Success					
Explanatory Variable	**β**	**SE**	**p-value**	**95% CI**	
(Intercept)	2.938	1.227	0.017	0.532	5.343
Nest Initiation Date	-1.920	0.910	0.035	-3.703	-0.137

Productivity					
Explanatory Variable	**β**	**SE**	**p-value**	**95% CI**	
(Intercept)	1.203	0.188	<0.001	0.834	1.572
Nest Initiation Date	-1.598	0.464	0.001	-2.508	-0.688

Table 2. Top models of Great Gray Owl territory occupancy, nest initiation, nest success (at least one young fledged), number of young fledged (productivity), and nest initiation date in relation to primary prey abundance during the breeding season and/or prior winter snow conditions. Results include beta coefficients (β), standard errors (SE), p-values, and 95% confidence intervals calculated using Generalized Linear Mixed Models and data from nest-monitoring of Great Gray Owl territories within the Greater Yellowstone Ecosystem during 2014–2022. Top models were selected based on lowest Akaike Information Criterion (AIC$_c$) value.

Territory Occupancy

Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	3.878	1.038	<0.001	1.845	5.912
Relative Prey Abundance	-2.944	1.231	0.017	-5.356	-0.532
Maximum Wind Crust Severity	-2.510	0.935	0.007	-4.342	-0.678

Nest Initiation

Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	-0.448	0.188	0.017	-0.816	-0.080
Relative Prey Abundance	-0.775	0.191	<0.001	-1.148	-0.401
Cumulative Wind Crust Severity	-1.186	0.211	<0.001	-1.599	-0.773
Maximum Ice Crust Severity	0.502	0.206	0.015	0.099	0.905

Nest Success

Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	0.838	0.274	0.00218	0.302	1.374
PGNew	-0.348	0.221	0.11622	-0.781	0.086

Productivity

Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	-0.595	0.383	0.120	-1.347	0.156
Cumulative Wind Crust Severity	-0.912	0.362	0.012	-1.621	-0.202
Maximum Ice Crust Severity	2.402	0.655	<0.001	1.118	3.685

Nest Initiation Date

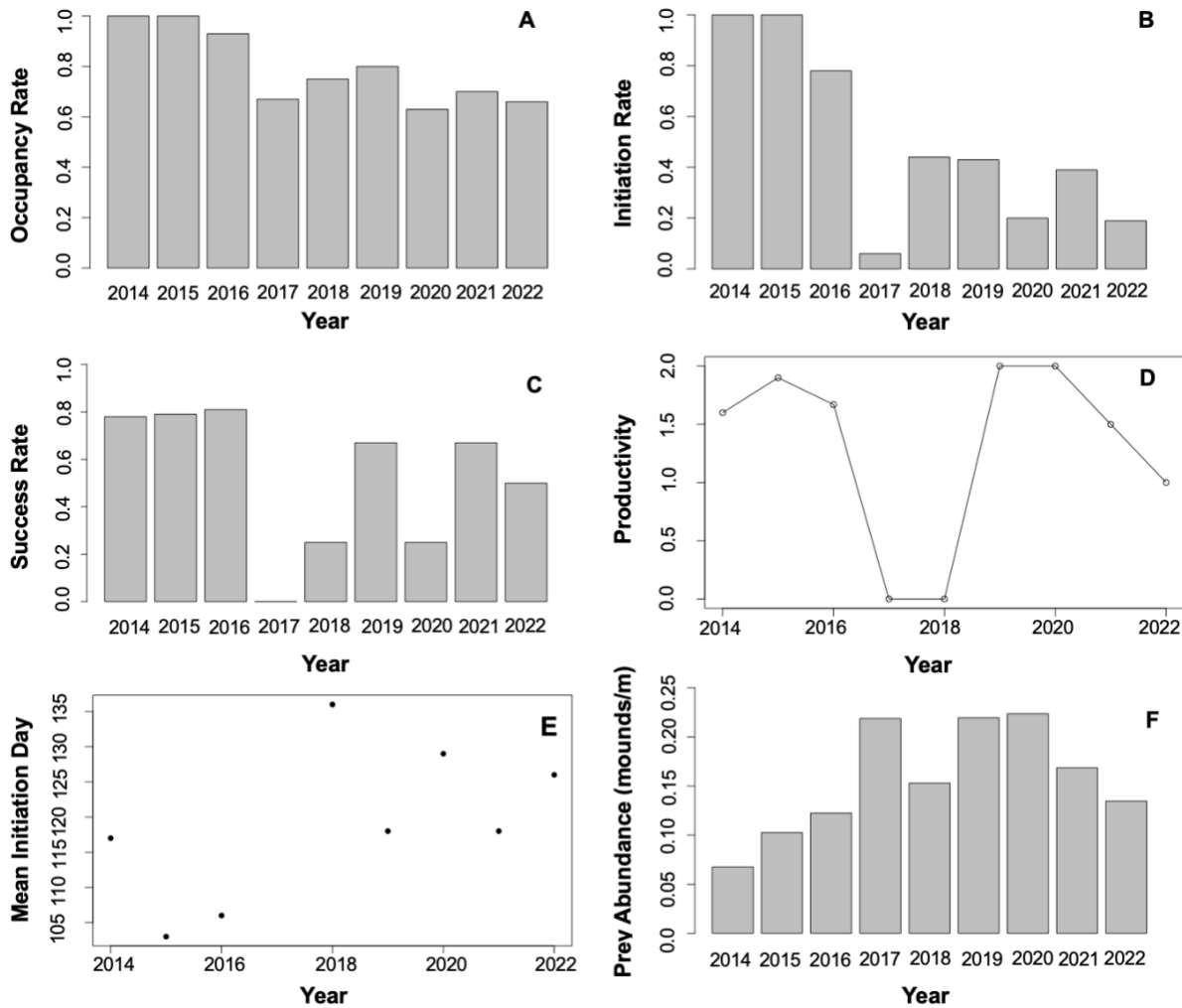| Explanatory Variable	β	SE	p-value	95% CI	
(Intercept)	4.618	0.026	<0.001	4.567	4.668
Cumulative Wind Crust Severity	0.150	0.038	<0.001	0.075	0.225
Relative Prey Abundance	0.165	0.039	<0.001	0.088	0.242

Figures:

Figure 1. Annual variation in territory occupancy rates (n = 246) (A), nest initiation rates (n = 190) (B), nest success (n = 96) (C), number of young fledged per nest (D), nest initiation Julian day of the year (E), and relative abundance of primary prey (F) for Great Gray Owls in the Greater Yellowstone Ecosystem during 2014–2022. Relative primary prey abundance was based on number of fresh Northern Pocket Gopher mounds observed per meter surveyed within 18 known owl territories.
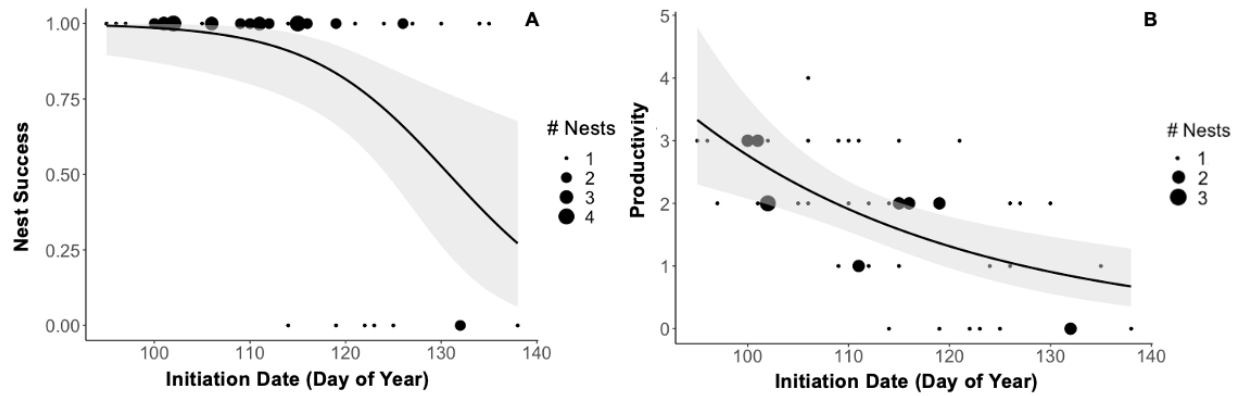
Figure 2. Observed and modeled nest success (at least one young fledged) ($P = 0.035$) (A) and productivity (number of young fledged per nest) ($P = 0.001$) (B) for Great Gray Owls within the Greater Yellowstone Ecosystem during 2014–2022. Modeled nest success and productivity were calculated using Generalized Linear Mixed Models and nest initiation day of the year as an explanatory variable. Black circles indicate observed territory occupancy, black lines indicate linear regression lines and gray shading indicates 95% confidence intervals for regression lines.
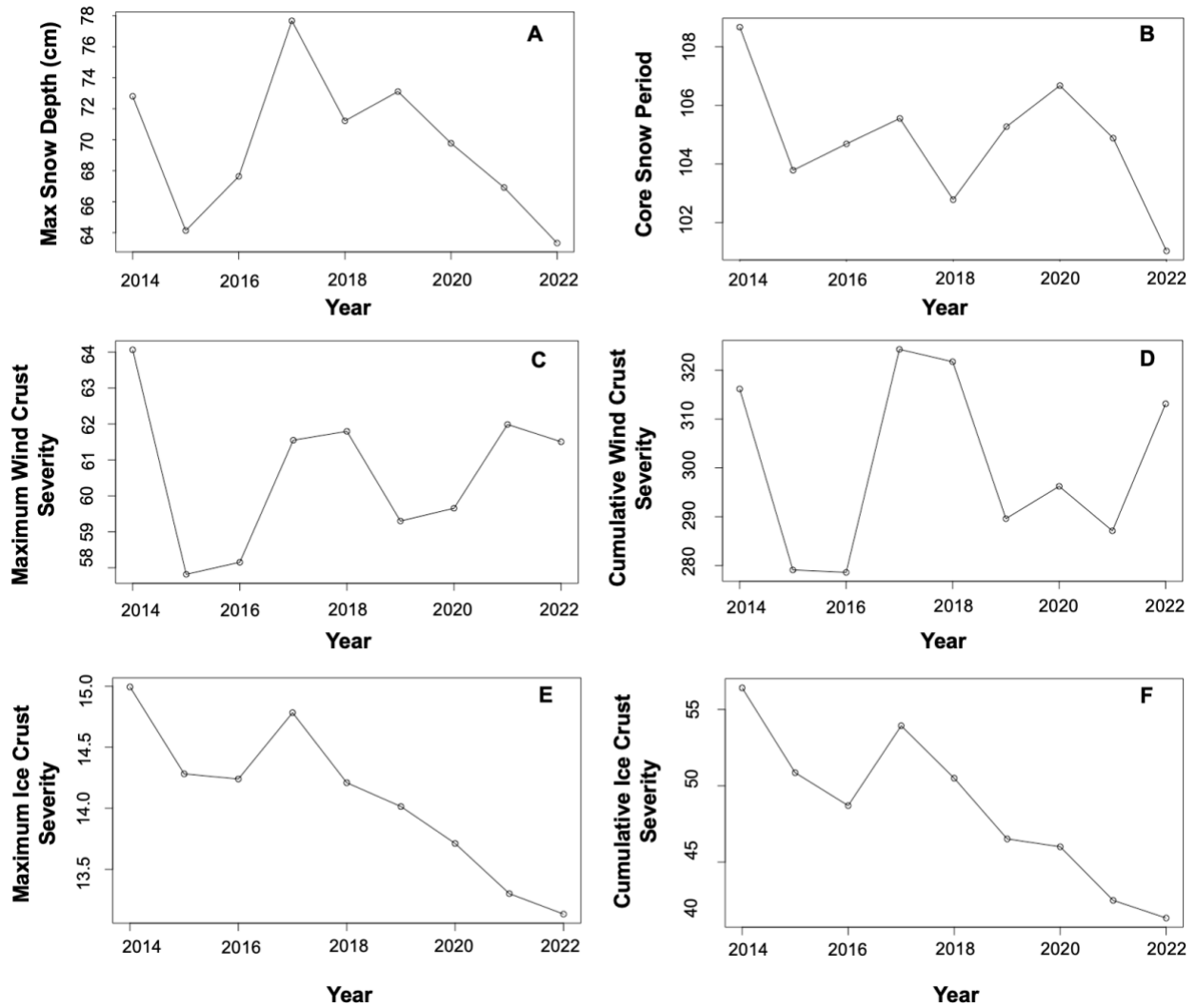
Figure 3. Annual variation in snow conditions across the study domain within the Greater Yellowstone Ecosystem during 2014–2022. Estimated snow conditions included maximum snow depth (A), length of the core snow period (B), maximum wind crust severity (C), cumulative wind crust severity (D), maximum ice crust severity (E), and cumulative ice crust severity (F).
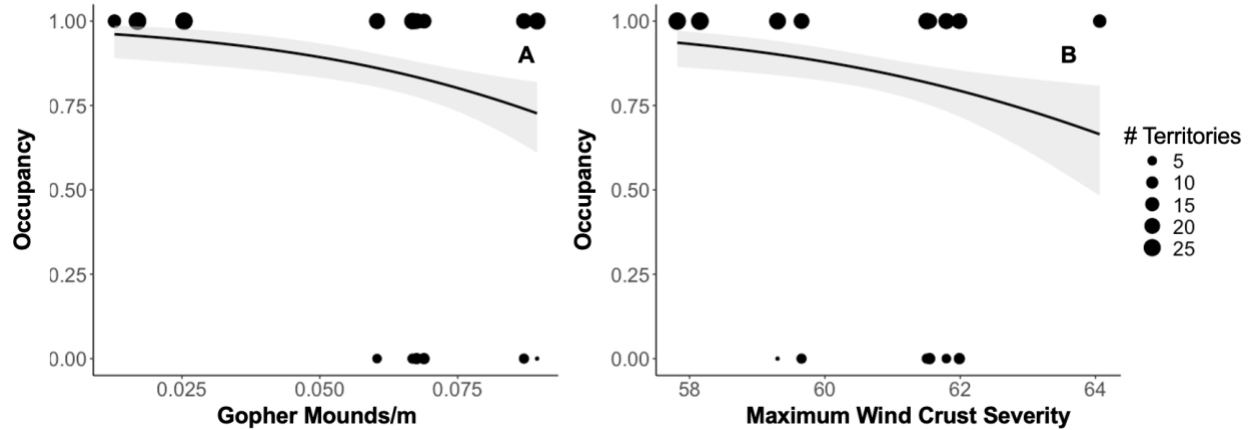
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Figure 4. Observed and modeled territory occupancy metrics for Great Gray Owls within the Greater Yellowstone Ecosystem during 2014–2022. Modeled territory occupancy was calculated using Generalized Linear Mixed Models and was based on the best-supported model that included relative primary prey abundance during the breeding season ($P = 0.17$) (A) and average maximum wind crust severity during the prior winter ($P = 0.007$) (B). Black circles indicate observed territory occupancy, black lines indicate linear regression lines and gray shading indicates 95% confidence intervals for regression lines.
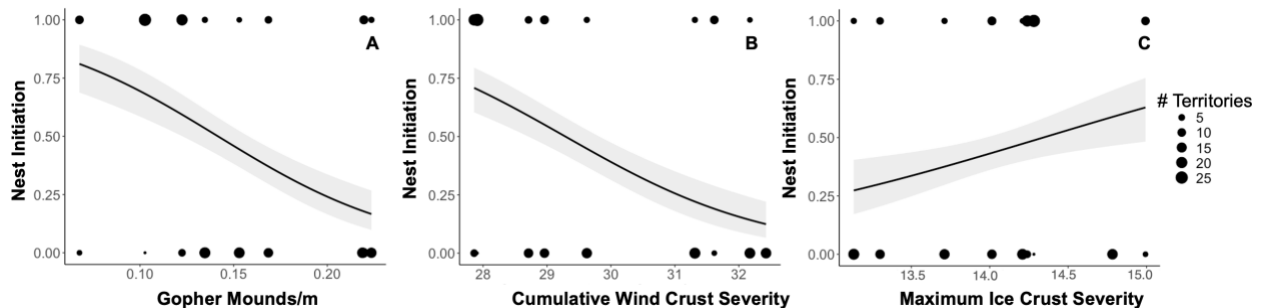

Figure 5. Observed and modeled nest initiation metrics for Great Gray Owls within the Greater Yellowstone Ecosystem between 2014–2022. Modeled nest initiation was calculated using Generalized Linear Mixed Models and was based on the best-supported model that included relative primary prey abundance during the breeding season ($P < 0.001$) (A), average cumulative wind crust severity during the prior winter ($P < 0.001$) (B), and average maximum ice crust severity during the prior winter ($P = 0.015$) (C). Black circles indicate observed territory occupancy, black lines indicate linear regression lines and gray shading indicates 95% confidence intervals for regression lines.
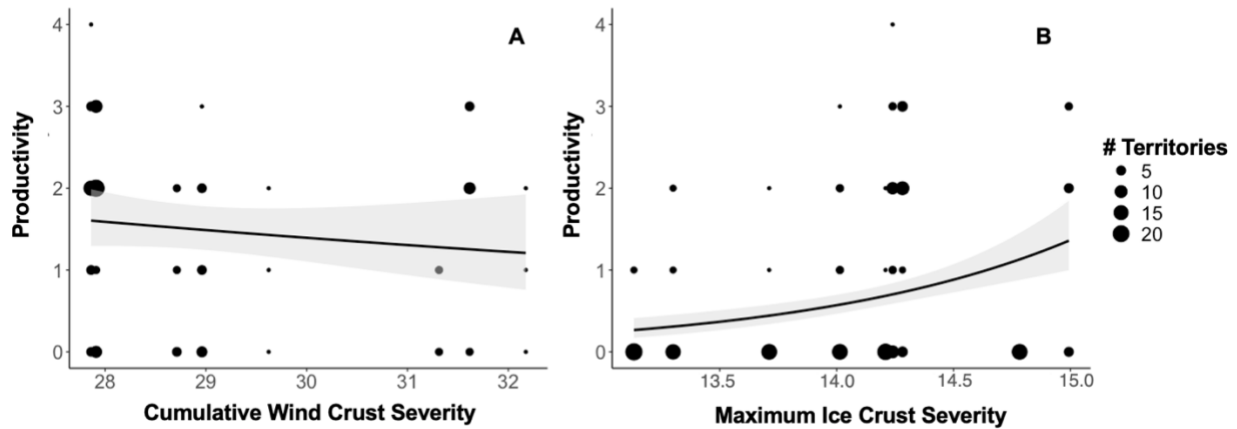
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Figure 6. Observed and modeled productivity metrics for Great Gray Owls within the Greater Yellowstone Ecosystem between 2014–2022. Modeled productivity was calculated using Generalized Linear Mixed Models and was based on the best-supported model that included cumulative wind crust severity ($P = 0.012$) (A) and maximum ice crust severity ($P < 0.001$) (B) during the prior winter. Black circles indicate observed territory occupancy, black lines indicate linear regression lines and gray shading indicates 95% confidence intervals for regression lines.
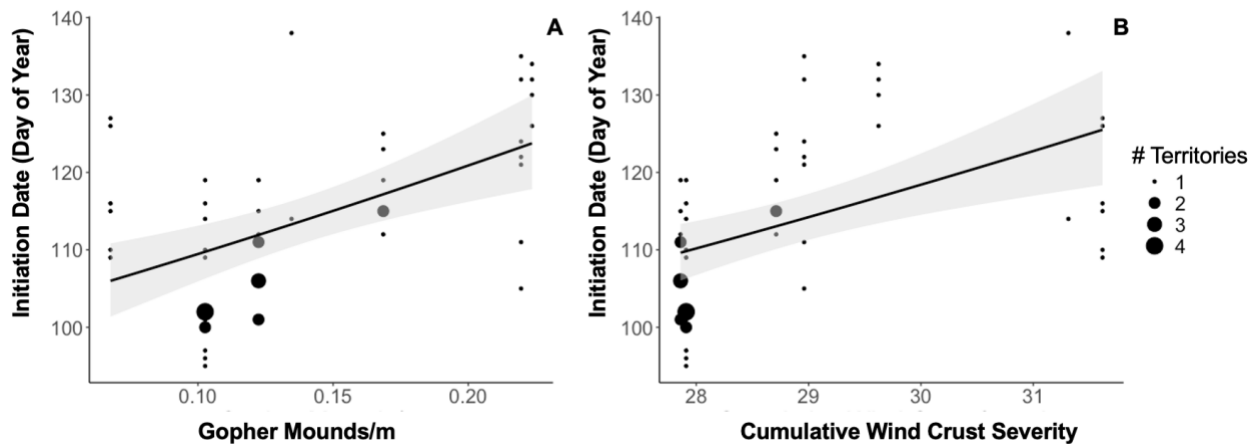

Figure 7. Observed and modeled nest initiation date for Great Gray Owls within the Greater Yellowstone Ecosystem between 2014–2022. Modeled initiation date was calculated using Generalized Linear Mixed Models and was based on the best-supported model that included relative primary prey abundance during the breeding season ($P < 0.001$) (A) and cumulative wind crust severity ($P < 0.001$) (B) during the prior winter. Black circles indicate observed territory occupancy, black lines indicate linear regression lines and gray shading indicates 95% confidence intervals for regression lines.

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