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THERE'S SNOW(SHOE) PLACE LIKE HOME: INTEGRATING FIELD MEASUREMENTS AND REMOTELY SENSED DATA TO ASSESS AND MODEL SNOWSHOE HARE HABITAT

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Thesis

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ABSTRACT The Southern Rocky Mountains are at the southern range of snowshoe hares (*Lepus americanus*) and their iconic predator, the Canada lynx (*Lynx canadensis*). In this region recreational uses, backcountry roads and trails, and other human developments have been identified as risk factors affecting lynx productivity through altering the snowshoe hare prey base. Beginning in 2013, Crested Butte Mountain Resort in western Colorado began proposals, and was conditionally approved in 2019 to construct ski trails and infrastructure in an undeveloped section of the Gunnison National Forest that currently supports snowshoe hare. In continuation of a 2016 pilot study, we carried out fecal pellet counts in the summer-fall of 2020 to assess whether this area contains adequate hare density (~0.5 hares/hectare) to support the imperiled Canada lynx. Pellet counts were significantly higher at a site dominated by old-growth spruce-fir forest, which has been cited as an important determinant of snowshoe hare and Canada lynx presence. Mean and median pellets counted varied by year; nonetheless, in neither year nor study site did values reach the threshold of 0.5 hares/hectare. We also estimated dense horizontal cover, considered an important component of winter hare habitat, as a rough assessment of habitat quality. Alongside this data, we utilized forest structural variables derived from satellite and LiDAR imagery to develop candidate models for predicting snowshoe hare population density. Our aim was to determine whether remotely sensed data could serve as a supplement or alternative to the traditional, resource-intensive field methods for assessing snowshoe hare population density and habitat quality for lynx management purposes. We conclude that open-access, remotely sensed data is valuable for land managers, but may not yet be collected at the scales suitable to assess habitat for species that rely on both stand-level variables (i.e., forest type) and fine-scale forest structural variables including dense horizontal cover.

As human populations expand, so too does the use of public lands by recreationists and the potential for human-wildlife conflict. Throughout the western United States, public lands are increasingly used for winter recreation as technological advances have expanded recreationists' access to previously undeveloped and undisturbed areas (Olson et al. 2017). Mountain and alpine ecosystems are vulnerable to winter tourism and recreation due to their natural fragility, and increases in the number of people using a recreation area or in the spatial extent of recreation have negative consequences including impacts to wildlife (Patthey et al. 2008, Olson et al. 2017). Wildlife within alpine and subalpine habitats, which possess physiological adaptations for dealing with harsh winter conditions, may additionally need to contend with disturbances resulting from winter recreational activities and associated development (Patthey et al. 2008, Marchand 1996, Arlettaz et al. 2007). For example, ski lift density was determined to be a principal determinant of reduced abundance for black grouse (*Tetrao tetrix*), a key indicator species of timberline ecosystems (Patthey et al. 2008). Understanding how development and human use associated with recreation affects wildlife promotes implementation of mitigation strategies designed to reduce negative effects and supports coexistence. For example, Patthey et al. (2008) recommend that vegetation patchiness be maintained along ski runs and that wintering preserves where human access is banned or strictly limited should be promoted within ski resorts to protect black grouse populations.

The snowshoe hare (*Lepus americanus*) is a subalpine species with the potential to be affected by increased winter recreation. Hares can be considered chionophiles or “snow-lovers," possessing large feet with low foot loading and other adaptations that enable them to thrive in deep snow conditions. The same is true for the Canada lynx (*Lynx americanus*) whose diet consists primarily of snowshoe hare and is active throughout the winter, traveling in deep snow. As specialists, Canada lynx are dependent on snowshoe hare population density and habitat. In the western United States, most snowshoe hare populations occur in conifer forests at elevations ranging from 645 to 3,415 meters (ILBT 2013). Snowshoe hares are reliant on vegetation cover for both food and defense; in the western United States, this cover is provided by species including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), aspen (*Populus tremuloides*) mixed with spruce-fir, and lodgepole pine (*Pinus contorta*) mixed with spruce-fir (ILBT 2013). Within such forests, dense understories serve as important food sources and cover from predators for snowshoe hares (Fekety et al. 2019, Berg et al. 2012, Ivan et al. 2014). In central Colorado, hare density has been found to be positively associated with horizontal cover, stem density, canopy cover, and area of willows in the surrounding landscape (Ivan et al. 2014). Dense horizontal cover and abundant coarse woody debris are also qualities important for Canada lynx denning in Colorado (IBLT 2013).

In the Rocky Mountains, more than 75% of critical Canada lynx habitat is on land managed by the U.S. Forest Service (USFS). The Canada lynx was federally listed as Threatened under the Endangered Species Act in 2000 due to concerns that existing regulatory mechanisms did not provide sufficient guidance for the conservation of lynx habitats and populations or snowshoe hare habitat in consideration of potential threats (USFWS 2017). As such, the USFS and other federal agencies are obligated to monitor this species and potential impacts to its habitat (USFS 2008). While the habitat requirements of the Canada lynx are well-studied, only recently have the potential impacts of recreation and associated development on this species been examined. Studies have found that winter recreation may impact snowshoe hares and Canada lynx by increasing snow compaction. Specifically, researchers have hypothesized that such compaction could make it easier for other carnivores such as coyotes to travel through deep snow, increasing direct competition with Canada lynx and/or increasing stress rates and thereby lowering reproductive rates among snowshoe hares (Kolbe et al. 2007, Ripple et al. 2011). Studies have begun to examine these hypotheses through quantifying snow compaction caused by snowmobiles and examining predator movements and kill sites, although the degree to which other carnivores influence lynx hunting success is unclear. Impacts may be significant in developed resorts as well as backcountry areas that are heavily used for winter recreation which increases snow compaction and physical disturbance to the species (Olson et al. 2018).

Studies regarding the potential impacts of winter recreation also shed light on how these species could be affected by changing environmental characteristics associated with climate change. Authors including Ivan and Shenk (2016) suggest that environmental conditions in the Rocky Mountains may be altered to a lesser degree than other ecosystems, although potentially drastic changes to mountain snowpack may be difficult to predict. A camera-trapping study found that Canada lynx were more likely to be found at camera sites when snowshoe hare abundance and elevation were high and slopes were gentle, corresponding with colder temperatures, moisture retention, and deeper snow (Scully et al. 2018). Furthermore, lynx were less likely to be found at these same sites when bobcats were present. Bobcats and lynx overlapped more when there was no snow, demonstrating that increasing temperatures could lead to more interaction between these two species (Scully et al. 2018). As Canada lynx are adapted to deep snow, decreased snow depth and increased snow compaction caused by recreational activities and/or warming temperatures could decrease the advantages this species possesses over other predators in the winter. Indeed, predation of snowshoe hare by lynx was largely unaffected by snow conditions, but predation by coyote increased where snow was shallower (Peers et al. 2020). Studies have also found evidence for increased camouflage mismatch for snowshoe hares (Mills et al. 2013, Wilson et al. 2019, Zimova et al. 2016) due to declines in snow duration (Sultaire et al. 2016) and increased temperatures (Burt et al. 2016). Particularly along the southern range periphery, habitat may not be a strong enough buffer against resulting snowshoe hare mortality (Wilson et al. 2019, Wilson et al. 2020), so that snowshoe hares may face declines and extirpation due to climatic changes with consequences for Canada lynx.

The most recent 5-year review conducted by the U.S. Fish and Wildlife Service (USFWS 2017) concluded that lynx populations are very likely to persist in all five units that currently support them (including Unit 6, which encompasses the state of Colorado) in the near term (2025) and are likely to persist at mid-century (2050). However, the USFWS had low confidence in assessing the risk to these populations beyond the year 2050, suggesting the need for more research and gathering of relevant data. Furthermore, they state that lynx populations in each of these units are expected to become smaller and more patchily distributed in the future due to projected climate-losses in habitat quantity and quality and related factors (USFWS 2017). Smaller, more isolated populations like those within western Colorado would be less resilient and at a higher risk of extirpation (USFWS 2017). To ensure the conservation of Canada lynx, it is important to assess factors that could be managed to reduce human-wildlife conflicts during an era in which climate change is likely to add additional pressures on the species' persistence.

In light of expected increases in recreation and changing environmental conditions relevant to snowshoe hare and Canada lynx, it is important to monitor population density along with habitat quality and presence for these species. This is particularly important in Colorado, which comprises the southernmost range for Canada lynx. Canada lynx were considered extirpated from Colorado in the 1970's, and only reached current numbers following a 1999-2006 reintroduction program which is considered the largest mammal reintroduction effort in the

United States (Devineau et al. 2010, USFWS 2017). A resident population has persisted since the release of these 218 individuals in the San Juan Mountains, and it is important to continue monitoring this reintroduced population along with its prey base and available, high-quality habitat (USFWS 2017). The species, and particularly the Colorado population, will likely face increasing challenges in the near future. Indeed, it has been proposed that cold-adapted species in the Northern Hemisphere may be particularly vulnerable to climate change at their southernmost ranges (Scully et al. 2018). Increases in winter recreation may additionally impact this species through changes to predator behavior, as noted above, but also through the development associated with establishing and expanding recreational operations and subsequent loss and degradation of suitable habitat.

Within the Gunnison National Forest, located in Gunnison County, CO, an area known as Teo Park and Teo Drainage has been identified as potential habitat for Canada lynx (Stern 2017). This area, while not developed, is utilized by winter recreationists including skiers and snowboarders. Crested Butte Mountain Resort has therefore proposed to expand into this area as outlined in their most recent Master Development Plan. This expansion would expand the resort’s Special Use Permit (SUP) boundary area permitted by the USFS by over 400 acres, and would bring new infrastructure into the area including 2 chairlifts, 69 acres of developed ski terrain and 29 acres of expert glades, 32 acres of snowmaking, and 15 miles of mountain biking and multi-use trails (CBMR 2013). This expansion was approved contingent on the original plan being updated to reflect project design criteria and best management practices outlined in the Environmental Impact Statement Record of Decision (USFS 2019). In a unique partnership, Crested Butte Mountain Resort and the U.S. Forest Service aim to evaluate and promote snowshoe habitat while maintaining and expanding winter recreation opportunities in a subalpine forest.

A pilot study was established in 2016 to improve understanding of the snowshoe hare population (i.e., the prey base for Canada lynx). This research aimed to establish study plots and grids for future monitoring, assess fecal pellet count methodology in the study area, and develop a baseline understanding of snowshoe hare density in the study area prior to proposed development. In 2020, we revisited the study sites established in the pilot, re-counting fecal pellets at a subset of plots as well as adding an assessment of snowshoe hare density. Our primary aim was to assess whether the approved ski resort expansion area contains sufficient prey to support Canada lynx and whether this expansion area differs in snowshoe hare utilization from a nearby site that is excluded from development. Such knowledge will inform the development of best management practices for Canada lynx consistent with the Forest Service's responsibilities under Section 7A1 of the Endangered Species Act and future project design of this public land by the recreation industry. Through our research, it became clear that the field methodologies used were time-intensive, and therefore restricted us to collecting data in a small area within the overall landscape. We therefore expanded our aims to acquire additional data from remote sensing products, potentially allowing us to model, predict, and map snowshoe hare population density across the Gunnison National Forest. In doing so, we focused on open-access data sources utilizing imagery captured on broad scales, as such sources would be more accessible and feasible for natural resource managers and agencies to utilize in similar studies. Snowshoe hare and Canada lynx habitat requirements vary by geographical location, so our intent was to develop an approach that could be replicated (albeit incorporating different data sources) at no or low cost. Through this goal, we aimed to make recommendations to improve monitoring efforts and thereby support continued, informed management of these iconic species.

STUDY AREA

This study took place within the Gunnison National Forest in southwestern Colorado, approximately 200-250 kilometers north of the Canada lynx reintroduction area in the San Juan Mountains (Figure 1; Devineau et al. 2010). The Gunnison National Forest is part of a group known as the Grand Mesa, Uncompahgre, and Gunnison National Forests (GMUG). The GMUG maintains a government-to-government relationship with three federally recognized Ute tribes, who have maintained deep cultural ties to the area despite their removal in the 1870s (GMUG 2018). Despite increasing recognition of the intersection between cultural and natural resources, due to their removal it is likely that information possessed by these tribes about wildlife populations in this area prior to European settlement has been lost or obscured.

Our study sites were located on Crested Butte and Gothic Mountain, prominences to the south and west of the East River. Both mountains are part of the Elk Mountain Range, a series of high, rugged mountains in western Colorado that is part of the larger Southern Rockies. Snowfall and snowpack have been recorded daily in the town of Gothic, CO, since 1975 (Inouye et al. 2000). Here, permanent snowpack began on average on November 4 (with a range of October 15-November 24), and lasted until May 24 (with a range of April 26-June 19) (Inouye et al. 2000). In Crested Butte, monthly snowfall totals have been recorded at the Crested Butte Weather Station since at least 1962, when the Crested Butte Ski Area opened (Crested Butte 2016). Throughout this time, snowfall was on average higher in Gothic compared to the lower elevation town of Crested Butte (Figure 2). The Crested Butte Mountain Resort is located between these two sites.

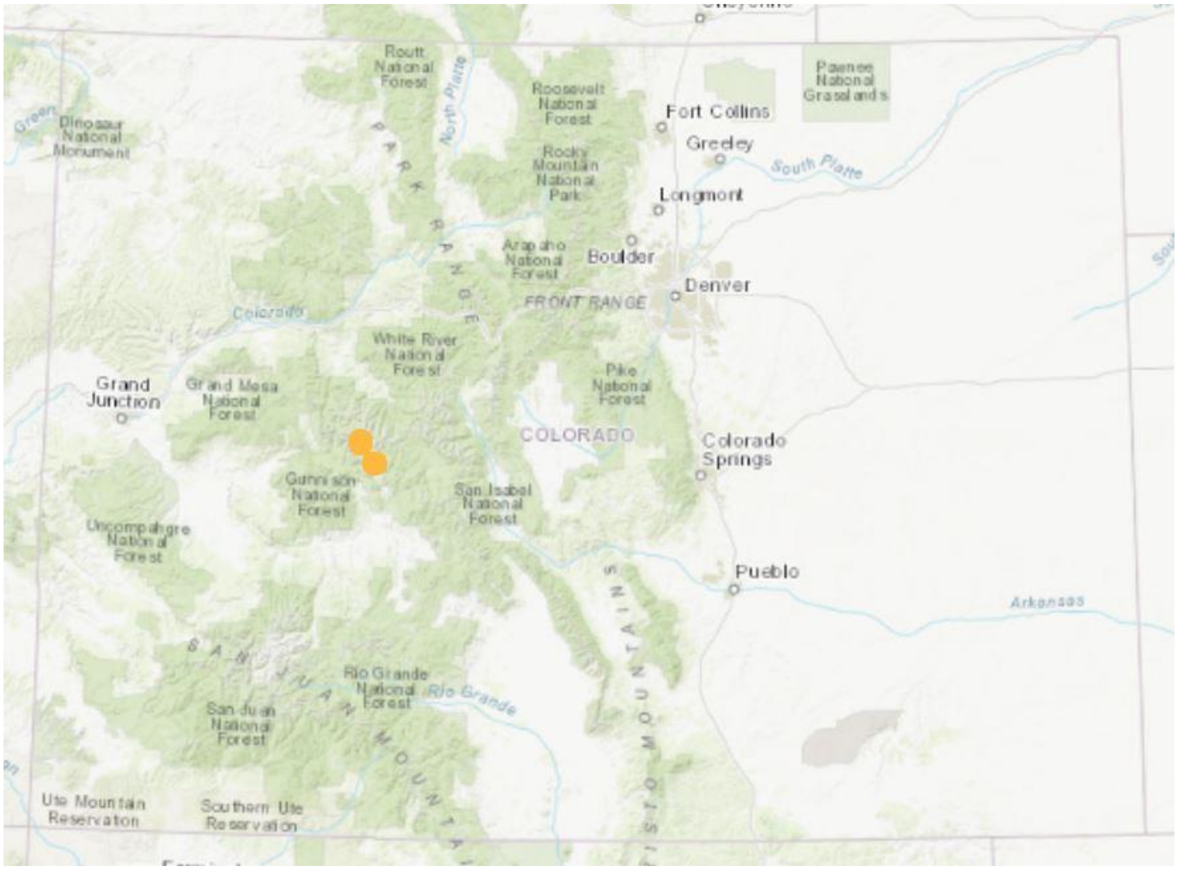

Figure 1: Study area in the Gunnison National Forest, Colorado.

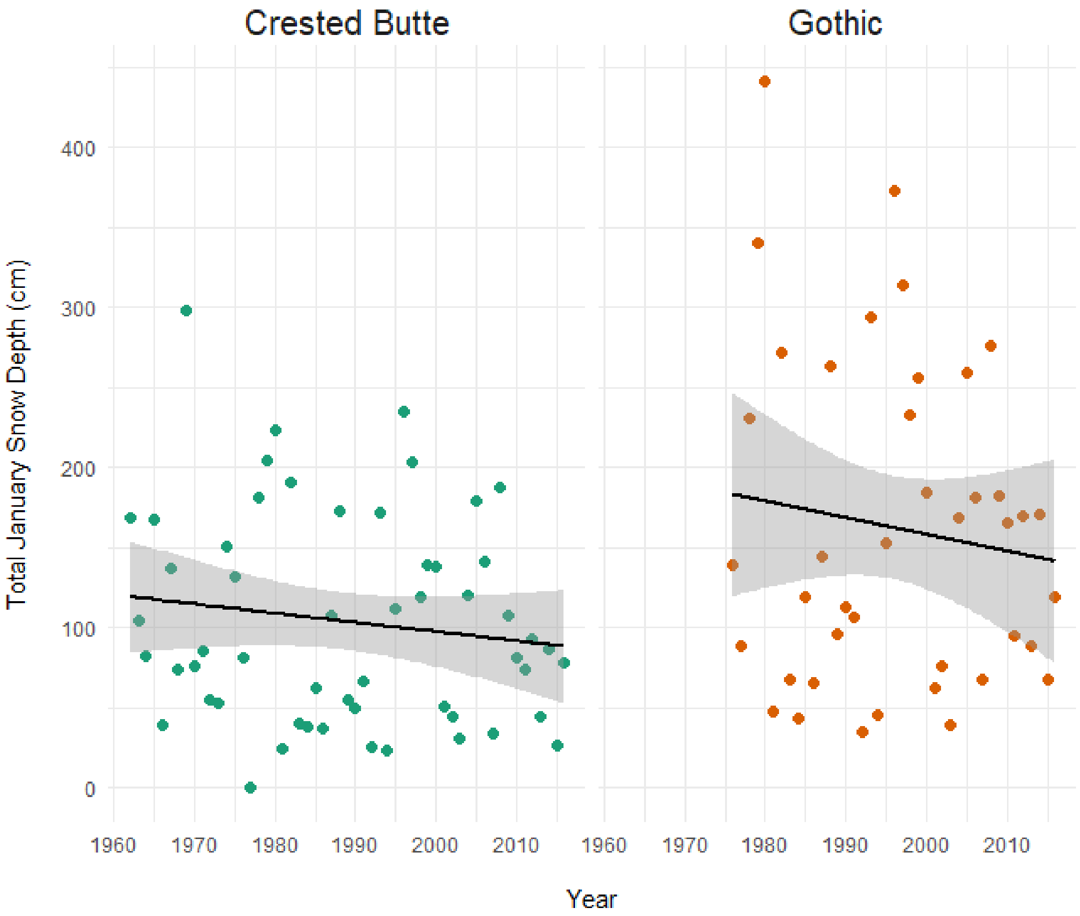

Figure 2: Cumulative January snow depth (cm) observed at the Crested Butte Weather Station in Crested Butte, CO (left) and the Rocky Mountain Biological Laboratory in Gothic, CO (right) from 1962-2016. Linear regression lines and 95% confidence intervals are displayed.

We collected data at two sites, the Teo Park/Teo Drainage ski resort expansion area and the Gothic Research National Area (RNA), both established as part of the 2016 pilot study (Figure 3, Stern 2017). These sites are located at high elevations and possess stands of subalpine fir (*Abies labioscarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and some quaking aspen (*Populus tremuloides*). The Gothic RNA is restricted from development and timber harvest, and was included for the sake of comparison ahead of proposed development in the Teo Park/Teo Drainage area. The Gothic RNA is at ~3,350 m elevation, has mostly northeast facing slopes with lower gradients, is moister, contains dense spruce-fir forest, and has a denser, more diverse understory that includes grasses, forbs, and shrubs (Stern 2017). On the contrary, the ski resort expansion site is at a lower elevation (~2,865 m), has mostly southeast facing slopes with higher gradients, is drier, contains more lodgepole pine stands as well as some patches of open canopy and rocky slopes, and has less understory diversity (Stern 2017). Although these differences preclude the Gothic RNA from being considered as a true control, the heterogeneity captured between the two sites proved valuable for our modeling attempts and understanding of variation in snowshoe hare use within and between the sites.

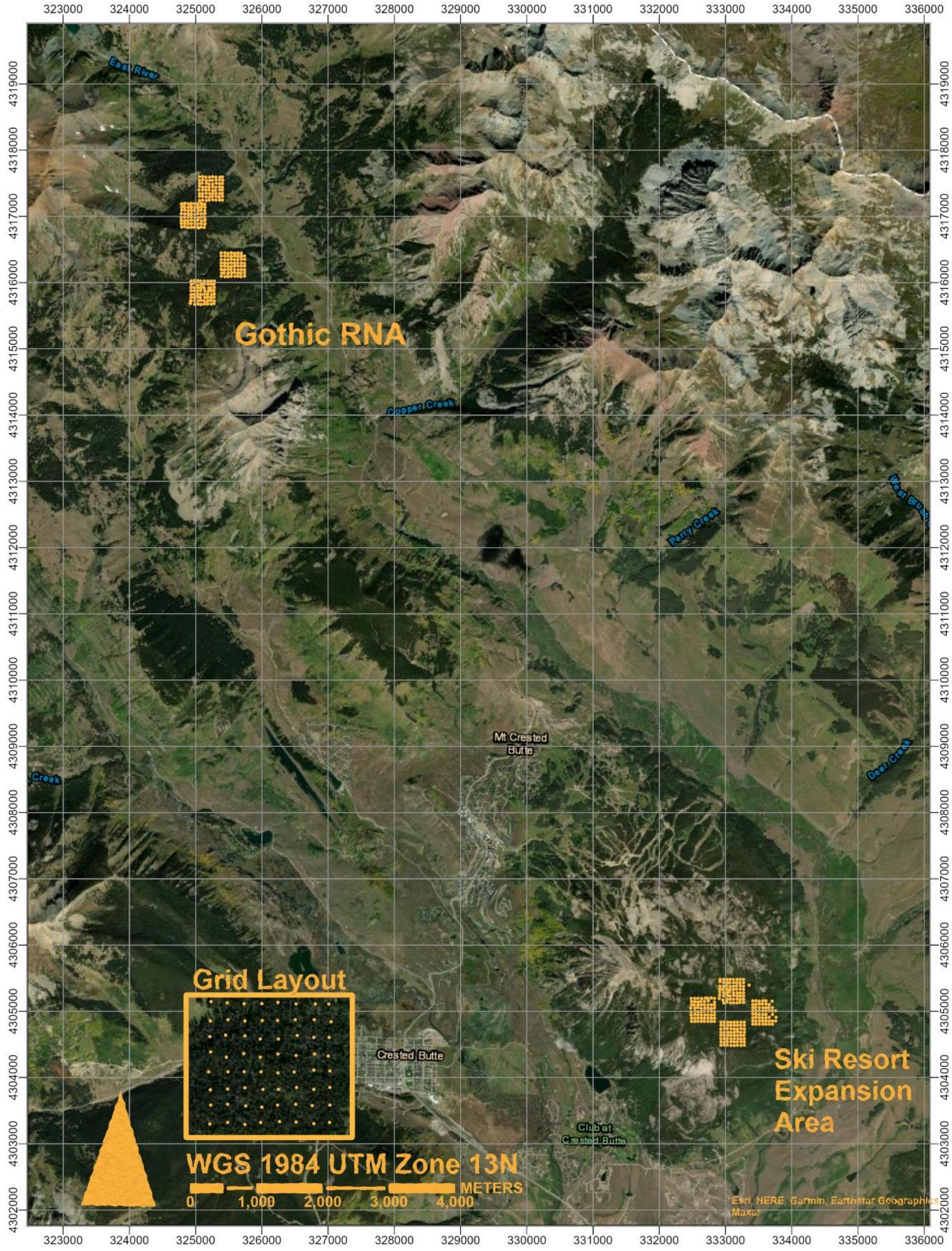

Figure 3. Field survey grids in the Gothic RNA and ski resort expansion area study sites (grid in UTM meters).

METHODS

As established in the pilot study, each study site contained 4, 16-ha grids, and each grid contained 64 plots located 50-m apart in an 8x8 arrangement (Figure 3). Any plots deemed inaccessible in the field were excluded from analysis. A large nail was hammered into the ground at the center of each plot. At the ski resort expansion area site, about 4 in. of each nail were kept aboveground and marked with orange paint to be more easily relocated during future survey years. In contrast, at the Gothic RNA site nails were required to be hammered flush to the ground to minimize disturbance to wildlife and other research being conducted, so a metal detector was used to aid in locating plots (Stern 2017). We recorded plot localities using a Trimble Juno GPS unit accurate to ~20-30m at the ski resort expansion area and a Trimble GeoXT unit with submeter accuracy at the Gothic RNA. During the pilot study, pictures were taken of each plot stand which will aid in future monitoring of these sites.

Hare Population Density

We conducted snowshoe hare fecal pellet count surveys to estimate prey density and determine whether each site can support Canada lynx. This method for estimating snowshoe hare population density from pellet plots was pioneered by Krebs et al. (1987; 2000) and is a commonly used practice by natural resource management agencies including the USFS. Berg and Gese (2010) examined whether fecal pellet counts were an effective estimate of snowshoe hare density within the Greater Yellowstone Ecosystem, which like our study area does not appear to support a persistent lynx population. They found that correlations between pellet counts and hare density do hold true, so long as the equations used to estimate density are modified and tested for each geographic region in which they are applied (Berg and Gese 2010).

Authors have similarly examined whether the plot type and sample size used impact the application and effectiveness of fecal pellet counts (Hodges and Mills 2008). Hodges and Mills

(2008) found that small sample sizes performed worse than large sample sizes at estimating the actual number of pellets in plots, and rectangular plots took longer to sample than circular plots. Overall, thin rectangles and large circles were found to be the most effective plot types. They also recommend small rectangles over 1-m circular plots, but do not recommend switching plot types if circular plots were already established, as is the case for this study (Hodges and Mills 2008). Other researchers including McCann et al. (2008) and Murray et al. (2002) have similarly utilized and evaluated the fecal pellet count method for estimating snowshoe hare density, including where densities are presumed to be low. Our study design, including the formula used to estimate snowshoe hare population density, was based on the results of this earlier research as well as consultations with experts (Stern 2017). All plots that could be accessed were sampled during the pilot study, and a subset of these plots were re-sampled in 2020. Surveys were carried out during the snow-off season, from early July through early November. At each plot sampled, we rotated a 0.5-m string around the nail to create a 0.785 m^2 circular plot, and counted the number of intact snowshoe hare pellets inside (Murray et al. 2002). To avoid bias, we did not count pellets that were incomplete or had been incorporated in the forest floor (Stern 2017).

Habitat Assessment

As snowshoe hares use dense understories as a food source and for cover from predators, degree of dense horizontal cover is an important determinant of their presence and abundance (Fekety et al. 2019, Berg et al. 2012, Ivan et al. 2014), and therefore in assessing where Canada lynx could be supported. A standard protocol for assessing snowshoe hare and Canada lynx habitat in the Rocky Mountains is to estimate dense horizontal cover using a cover board (Fekety et al. 2019). We used a cover board measuring 0.5-m x 2.0-m that was placed 5-m from an observer. An individual standing at the plot center held the cover board, which consists of red and white squares each measuring 0.25-m x 0.25-m, and turned to face each cardinal direction. From each direction, the observer took a photograph of the board which was later visually assessed (Figure 4). We determined the proportion of the cover board that was obscured and averaged the horizontal cover from all four directions across each plot. As with fecal pellet count surveys, although horizontal cover assessments are used to determine whether forest stands support wintering snowshoe hares, it is not necessary that stands be measured in the winter. Therefore, we took these measurements in the summer-fall, when survey sites located in avalanche terrain are accessible and not heavily utilized by recreationists. Dense horizontal cover estimates were not made in the 2016 pilot study.

Figure 4: Example photograph of a cover board used to estimate dense horizontal cover (left) and fecal pellet counting methodology (right).

Remote-sensing techniques such as airborne LiDAR (Light Detection and Ranging) may allow estimates of dense horizontal cover to be extended across areas larger than can be feasibly assessed in the field (Fekety et al. 2019). Therefore, in our analyses we included airborne LiDAR data previously collected across the Gunnison Basin. LiDAR units, which are utilized on aircraft, function by emitting a laser pulse toward the ground that is returned to a sensor on the aircraft. Based on the time-of-flight of this pulse and information provided by a global navigation satellite system (GNSS) and an inertial unit measuring aircraft orientation, the position of the object causing the laser reflection can be accurately located (Fekety et al. 2019). LiDAR returns can be classified to determine what caused the reflection, and are therefore used to produce maps that indicate features of a forest including topography and vegetation. According to Fekety et al. (2019), LiDAR data can be appropriately applied to modeling horizontal cover because both LiDAR and cover boards permit measurement of obstructions. These authors developed an approach to predict understory habitat for Canada lynx in the Northern Rocky Mountains using LiDAR data, which they ground-truthed through in-field cover board measurements (Fekety et al. 2019).

In our study, we attempted to determine whether LiDAR imagery combined with dense horizontal cover could be used to predict and map understory habitat in the Southern Rocky Mountains. Rather than model dense horizontal cover using LiDAR imagery, however, we set out to model snowshoe hare fecal pellets counts (as a proxy for population density) using dense horizontal cover estimates, LiDAR imagery, and environmental variables thought to be important for snowshoe hare habitat. Fekety et al. (2019) based their analyses on LiDAR flights planned in consideration of dense horizontal cover. In contrast, we acquired open-access LiDAR and other remotely sensed data through the Rocky Mountain Biological Laboratory Spatial Data

Platform (SDP) (RMBL 2020). Such open-access data, from sources including the SDP and the U.S. Forest Service's FSVeg database, could be considered more available and accessible to natural resource managers and agencies.

Statistical and Spatial Analysis

We carried out all hypothesis testing and modeling using the software R version 4.0.3 (R Core Team 2014). From our fecal pellet counts, we estimated snowshoe hare density for each plot using a version of Krebs' (1987, 2001) formula tailored to our study area (Stern 2017). The log-log regression outlined by Krebs et al. (2001) was based on a plot area of 0.155 m^2 as opposed to our plots of 0.785 m^2. Mean pellet counts must be divided by a conversion factor of 5.0645 to obtain an estimate of population density in hares/hectare. Our formula would have included this and another conversion factor from Krebs' updated formula, so we used these factors and the original formula to derive the following equation:

$$Population\ density\ = 0.1097\ x\ (mean\ number\ of\ pellets)^{0.889}$$

To include vegetation data in our models, we utilized data contained in the Field Sampled Vegetation (FSVeg) database. FSVeg stores data about trees, fuels, down woody material, surface cover, and understory vegetation, storing such data from sources including common stand exam, fuels data collection, permanent grid inventories, and other vegetation inventory collection processes. (USFS 2020). As possible explanatory variables we chose to explore percent and species of the top three dominant life forms, percent of combined *Picea engelmannii* and *Abies lasiocarpa* (PIEN-ABLA) cover, and layering (whether a stand was multistoried or single storied, under the assumption that stands that have experienced disturbance but retain a multi-storied character could remain as suitable habitat). We derived a value from each of these variables (with the exception of the top third dominant life form, which was not present in all areas) for each plot.

Alongside vegetation data, we acquired and utilized a 10-m resolution Digital Elevation Model (DEM) which covered the extent of Gunnison County. From the DEM, we used tools included within the ArcGIS Surface Tools Toolbox to calculate the explanatory variables elevation, slope, and aspect. We also imported and utilized the Geomorphometric and Gradient Metrics Toolbox to calculate topographic roughness, heat load index, and topographic position index (TPI) for each plot (Evans et al. 2014). Heat load index represented hot-dry to cool-moist areas and the TPI represented relative concavity or complexity; it was assumed that snowshoe hares and therefore pellets would be found at higher numbers in cool-moist areas and that water accumulation would be higher in basins. All these variables were included in our model along with our estimates of dense horizontal cover, with the assumption that greater pellet numbers would be associated with greater percent cover. We carried out all geostatistical analyses using ArcGIS Pro version 2.6.0.

Following *a priori* hypotheses and literature on snowshoe hare and Canada lynx habitat features, we built a variety of candidate linear mixed-effects models with different combinations of fixed and random effects. Count data often follow a Poisson distribution; however, our data did not fit the assumption that the mean of a variable (i.e., pellet number) must equal the variance. Furthermore, models in the Poisson class may not be well-suited for data consisting mostly of small counts with substantial spatial correlation (De Oliveira 2013). We created generalized linear mixed models with the same covariates following Poisson distribution, negative binomial distribution, and zero-inflated negative binomial distribution. Implementing models under a Bayesian approach allowed us to include random effects; this was particularly important as effects from the variables site, grid, or year could result from environmental factors that had not been measured. We compared the fit of these models using the leave-one-out (LOO) cross-validation procedure, finding that non-zero-inflated models following negative binomial distribution fit our data better than other structures (Vehtari, Gelman, & Gabry 2017). The LOO Information Criterion (LOOIC) is similar to the Akaike Information Criterion (AIC) in that it can be used to estimate the expected log predictive density (ELPD) for a dataset, however LOO does not assume a normal posterior distribution. Models are ranked with the largest ELPD (smallest LOOIC), and the lowest ELPD difference and standard error of the difference, are prioritized. The "top-performing model" is that with an ELPD difference and standard error of the difference of zero, meaning that there is no difference between this model and itself.

In terms of model creation and selection, we began by considering variables in the categories; vegetation data (that acquired from the FSVeg database), topographic data (that derived from a DEM), field data (estimated dense horizontal cover), and remotely sensed data (models derived from LiDAR imagery). For each of these categories, we used the pairs function in R to create a matrix of scatterplots displaying the correlation between each log-transformed variable and to log-transformed fecal pellet counts. Through this approach, we determined which (if any) of the variables from each category to include in candidate models. As noted above, candidate models were compared using LOO cross-validation. When warnings about Pareto *k* estimates indicated observations with problematic approximations, we set the k threshold to 0.07, below which increased errors in the LOO approximation tend to be negligible. After identifying top candidate models with combinations of fixed effects, we added in random effects to account for spatial autocorrelation (site, year, and interaction between site and year).

RESULTS

As pellet numbers are discrete, count data, we assumed they were non-parametric and utilized the non-parametric Wilcoxon signed rank test for statistical analysis. As expected, the number of pellets counted at the Gothic RNA, at higher elevation and dominated by old-growth spruce-fir forest, was significantly higher than the number counted at the ski resort expansion area site (Figure 5; W = 61361, $p < 0.05$). This same relationship was seen when results from the 2016 pilot study and 2020 study were analyzed separately. The mean number of pellets at Gothic RNA was 6.427 in 2016 (0.581 hares/ha) and 4.988 in 2020 (0.458 hares/ha). For the ski resort expansion area, the mean was 4.580 in 2016 (0.430 hares/ha) and 2.708 in 2020 (0.266 hares/ha). Although non-significant (W = 74295, p-value = 0.6991) and possessing the same median of 2, mean pellet counts combined between the two sites were higher in 2016 than they were in 2020. In terms of dense horizontal cover, we assumed that habitat had not changed a great deal in a period of less than 5 years, so where possible we assigned plots sampled in the pilot study the same average values estimated at those plots in 2020. Contrary to expectations, average dense horizontal cover was significantly higher at the ski resort expansion area site compared to the Gothic RNA site (W = 5082.5, $p < 0.05$).

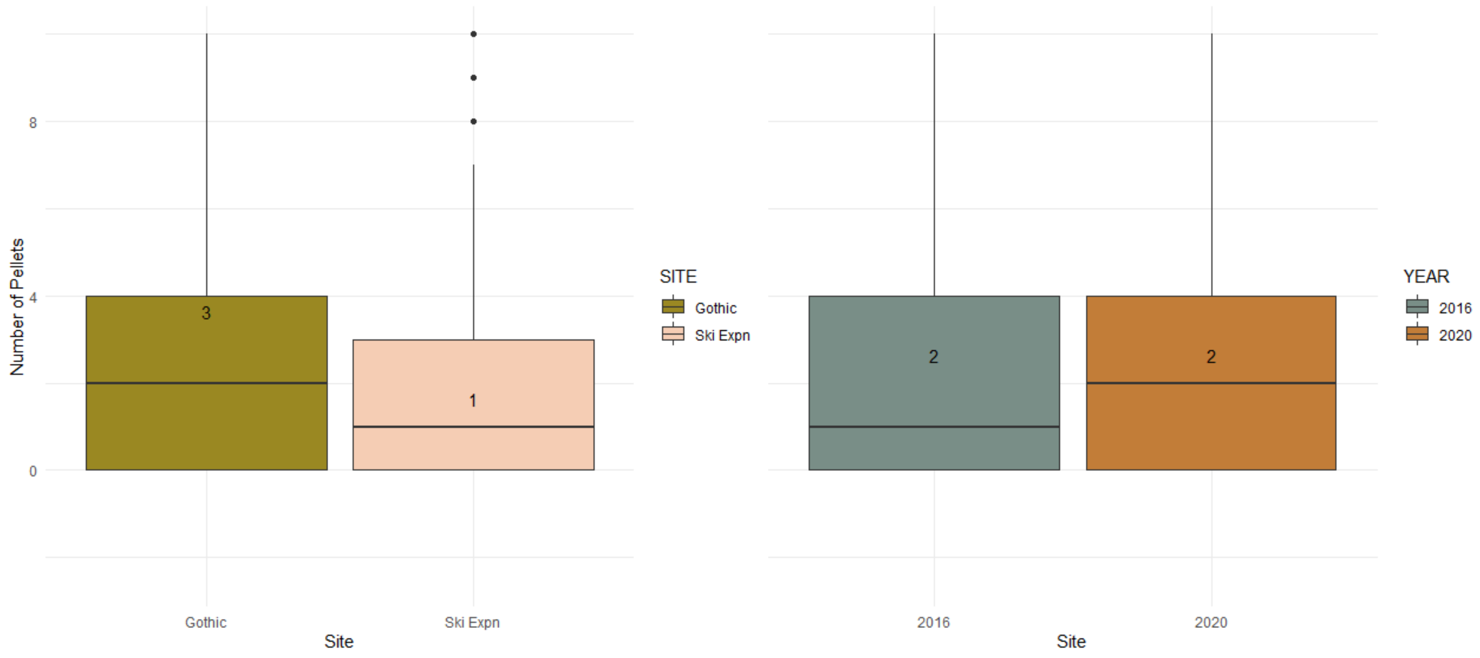

Figure 5. Boxplots indicating interquartile range of number of pellets per plot by study area (left) and year (right). The number of pellets counted at the Gothic RNA was significantly higher than the number counted at the ski resort expansion area site ($p < 0.05$), whereas there was no significant difference in the number of pellets counted by study year ($p = 0.6991$). The average number of pellets across both years was 3.855 at the ski resort expansion area and 5.870 at the Gothic RNA, and across both sites was 5.498 in 2016 and 3.911 in 2020. Based on the formula derived for our study area, the threshold of 0.5 hares/hectare is equivalent to approximately 6 pellets/plot.

Our best-performing model included study site (Gothic RNA vs. ski resort expansion area) and year as random effects, and the following variables as fixed effects: site, proportion canopy from 3-m LiDAR imagery, year, percent combined spruce-fir cover, and topographic roughness (Table 1). Pellet numbers were lower where topographic roughness was higher (Table 2). Posterior credible intervals were positive for the variable proportion canopy, suggesting that pellet numbers were higher where proportion canopy was higher, as could be expected. However, intervals were negative for combined spruce-fir cover. This finding was contrary to the array of literature citing spruce-fir cover as an important determinant of snowshoe hare presence and abundance. The best-performing model did not perform as well when the variables proportion canopy, percent combined spruce-fir cover, or topographic roughness were removed, or when the term representing average estimated dense horizontal cover was added. Regardless of whether dense horizontal cover was included, or whether the term site was included as a fixed effect, the signs, magnitudes, and coefficients of other covariates remained consistent. To examine the fit of this model, we generated posterior predictive checks as illustrated in Figure 6 (Gabry et al. 2019).

Candidate Model	**ELPD Difference**	**SE Difference**	**ELPD Estimate**	**ELPD SE**	**LOOIC Estimate**	**LOOIC SE**
Pellets ~ Topographic Roughness + Spruce-Fir Percentage + 3m Proportion Canopy + Year + Site + (1 | Grid:Year)*	0.0	0.0	-2024.8	46.2	4049.6	92.3
Pellets ~ Topographic Roughness + Spruce-Fir Percentage + 3m Proportion Canopy + Year + (1 | Grid:Year)	-3.5	3.2	-2028.3	46.2	4056.6	92.4
Pellets ~ Topographic Roughness + Spruce-Fir Percentage + 3m Proportion Canopy + (1 | Grid:Year)	-3.6	3.2	-2028.4	46.6	4056.9	93.2
Pellets ~ Topographic Roughness + Spruce-Fir Percentage + 3m Proportion Canopy + Year + (1 + 3m Proportion Canopy | Grid:Year)	-3.7	3.2	-2028.5	46.0	4056.9	92.1
Pellets ~ Topographic Roughness + Spruce-Fir Percentage + 3m Proportion Canopy + (1 + 3m Proportion Canopy | Grid:Year)	-4.3	3.3	-2029.1	46.6	4058.2	93.2
Pellets ~ Topographic Roughness + Spruce-Fir Percentage + Year + Site + (1 | Grid:Year)	-4.8	7.1	-2029.6	44.7	4059.2	89.3
Pellets ~ Topographic Roughness + Spruce-Fir Percentage + (1 + 3m Proportion Canopy | Grid:Year)	-6.8	4.6	-2031.6	45.5	4063.2	91.0

* Top-performing model.

Table 1: Summary table of candidate models showing estimates and standard error (SE) for expected log predictive density (ELPD) and LOO Information Criterion (LOOIC). Models are ranked by the largest ELPD (smallest LOOIC) and smallest difference in ELPD and SE.

Variable	**N_eff**	**R-hat**	**Mean**	**MCSE**	**SD**	**2.50%**	**97.50%**
(Intercept)	1973	1.000627	210.314542	2.624606	116.5886	-10.8463	452.2892
Topographic Roughness	2583	1.000501	-0.000066	0.000001	0.000036	-0.00014	0.000004
Spruce-Fir Combined Percentage	2312	0.99996	-0.02678	0.000137	0.006579	-0.03972	-0.0136
3-m Canopy Height Model	5494	0.99945	0.853923	0.002949	0.218606	0.411004	1.273411
Year	1974	1.000626	-0.102735	0.0013	0.057772	-0.22269	0.007018
Site (Ski Expansion Area)	2657	1.001309	-1.195039	0.008263	0.425938	-2.02155	-0.36688
b[(Intercept) Grid:Year:1:2016]	2439	0.999765	-0.090684	0.00419	0.206937	-0.55345	0.27724
b[(Intercept) Grid:Year:1:2020]	3044	1.000096	-0.127591	0.00399	0.220122	-0.64059	0.251496
b[(Intercept) Grid:Year:2:2016]	2159	1.000087	-0.078409	0.003696	0.171703	-0.45715	0.239292
b[(Intercept) Grid:Year:2:2020]	2835	0.999501	-0.121638	0.00354	0.188468	-0.51838	0.223312
b[(Intercept) Grid:Year:3:2016]	1724	1.000128	0.265814	0.00453	0.188093	-0.04256	0.659092
b[(Intercept) Grid:Year:3:2020]	1666	0.999616	0.298518	0.005449	0.222415	-0.05046	0.811098
b[(Intercept) Grid:Year:4:2016]	3112	1.000955	-0.039011	0.003326	0.185546	-0.41145	0.336189
b[(Intercept) Grid:Year:4:2020]	3086	0.999334	-0.050932	0.003688	0.204848	-0.47242	0.401532
b[(Intercept) Grid:Year:5:2016]	2400	1.001631	-0.064368	0.00352	0.172451	-0.41552	0.278521
Reciprocal Dispersion	4995	1.000251	0.484293	0.000431	0.030464	0.427773	0.546939
σ[Grid:Year:(Intercept),(Intercept)]	1169	1.000654	0.082892	0.002647	0.090492	0.002656	0.317677
Mean Posterior Predictive Distribution	4130	1.000576	4.973007	0.006398	0.41117	4.216958	5.827993
Log-posterior	851	1.000035	-2037.12597	0.131466	3.834825	-2045.51	-2030.78

Table 2: Summary table for the top-performing model including number of effective samples (N_eff), R-hat statistic, mean, Monte Carlo simulation estimate (MCSE), standard deviation (SD), 2.50% and 97.50% confidence intervals.

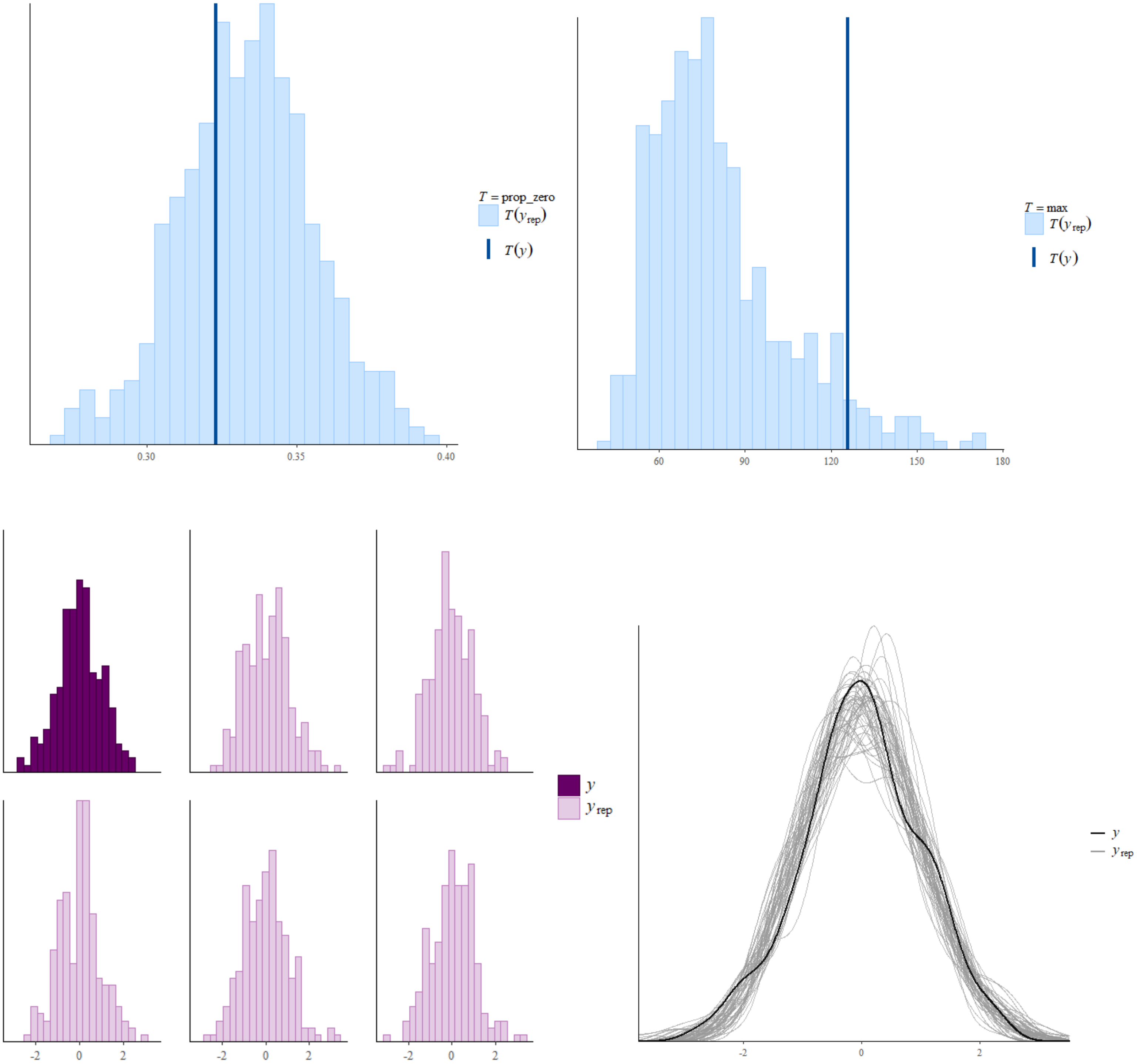

Figure 6: Posterior predictive checks of our top performing model including the distribution of the proportion of zeros over the replicated datasets from the posterior predictive distribution (A), distribution of the maximum value in the replications (B), and plotted posterior predictive check in histogram (C) and line (D) diagrams.

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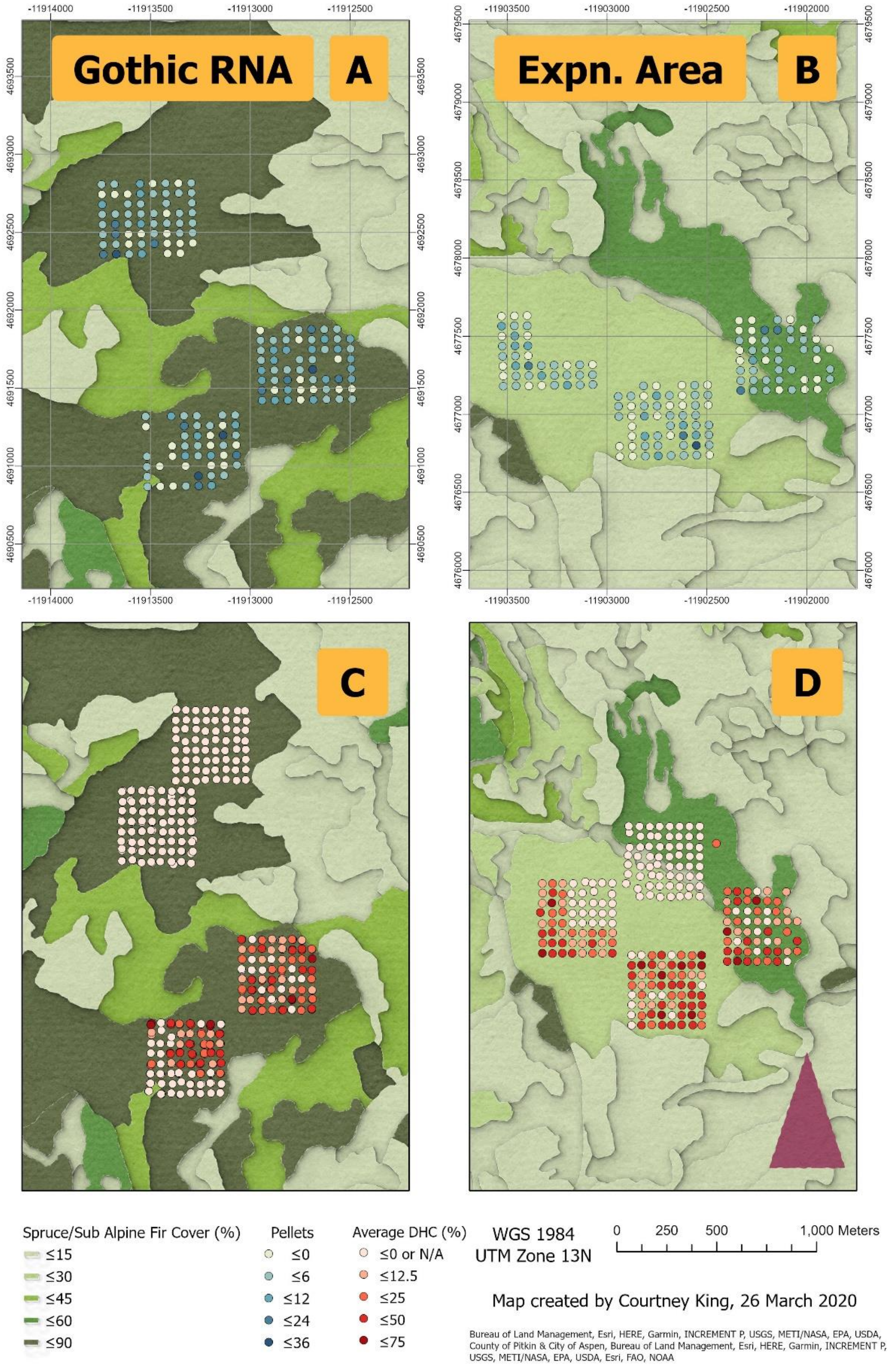
DISCUSSION

Hare Population Density

As previously noted, research suggests that a minimum prey density of 0.5 hares/ha is necessary to sustain a lynx population within a lynx home range (Mowat and Slough 2003). Therefore, based on our analyses, our study area may not have adequate prey density to support resident Canada lynx. Nonetheless, the area may serve as a corridor for Canada lynx traveling between home ranges, and such habitat connectivity has been deemed particularly important in the Southern Rocky Mountains (Shenk 2009, USFS 2008). We were surprised to find that average fecal pellet counts were lower in 2020 as compared to the 2016 pilot study, although this difference was not significant. This could be due to sampling errors, but could also be attributed to other factors including outliers or the lower sampling size in the 2020 study. The maximum number of pellets counted at a plot was 33 during the 2020 study and over 100 during the 2016 pilot study, which likely contributed to these years possessing different mean but equal median pellet numbers.

Fecal pellet counts may also have been overestimated during the initial pilot study. Fecal pellet counts are intended to represent the pellets accumulated throughout a single year to avoid overestimating snowshoe hare density, and it is therefore advisable to clear lots before the first year of fecal pellet count surveying and after each sampling year (Stern 2017). Indeed, the relationship between fecal pellet counts and snowshoe hare density estimates is stronger when plots are cleared the year prior to surveying, and inaccurate measurements are especially likely when hare density is expected to be low as in our study (Berg and Gese 2010). Due to time constraints, however, plots were not cleared prior to our 2016 pilot study, and only a subset of plots were recounted and therefore cleared prior to the 2020 field season. Although this is an important consideration, un-cleared plots remain a useful index of habitat used by snowshoe hare, and counts from cleared and uncleared plots are, on average, highly correlated (Berg and Gese 2010; Hodges and Mills 2008). Apart from these possible complications, Rabbit Hemorrhagic Disease Virus (RHDV) spread through the state of Colorado in the summer of 2020 and may have affected hares in our study area, although there were no direct signs of such including deceased hares.

The differences in pellet counts between 2016 and 2020 could also be attributed to our capturing different periods in the snowshoe hare population cycle. Lynx observations have peaked every 10 years in Minnesota and surrounding states (Moen et al. 2008). However, while northern snowshoe hare and Canada lynx populations are known to undergo a 10-year population cycle, this may not be the case in southern populations (Roberts and Potter 2019). The lack of this strong dynamic in southern populations has been attributed to forest fragmentation and predation of snowshoe hares by generalist species, such as the coyote (Ripple et al. 2011). Nonetheless, while perhaps not as strong as in northern populations, a population cycle with highs and lows likely exists to some degree in our study area. As the Colorado lynx population was established through translocations of individuals from northern populations, and southern lynx populations in general may require immigration from northern populations to persist, both lynx and snowshoe hare populations are likely influenced by cycles in the north. Ultimately, long-term monitoring of snowshoe hares in our study area would be required to conclusively determine whether population cycles or other factors led to the lower-than-expected number of fecal pellets counted during this study.



Map created by Courtney King, 26 March 2020

Bureau of Land Management, Esri, HERE, Garmin, INCREMENT P, USGS, METI/NASA, EPA, USDA, County of Pitkin & City of Aspen, Bureau of Land Management, Esri, HERE, Garmin, INCREMENT P, USGS, METI/NASA, EPA, USDA, Esri, FAO, NOAA

Figure 7: Map indicating pellets counted by plot at the Gothic RNA (A), pellets counted by plot at the ski resort expansion area site (B), and dense horizontal cover (DHC) estimated at these sites, respectively (C,D) during the 2020 field season.

Habitat Assessment

Forest stands where the horizontal cover is greater than or equal to 48% when measured in summer surveys or 35% if measured in winter surveys are considered winter hare foraging habitat (Fekety et al. 2019). In studies using this factor, however, photographs are typically taken and dense horizontal cover estimated from 10-m or 11.2-m from the cover board. In our study, due to factors including extremely difficult terrain, observers instead stood 5-m from the cover board. This may have led us to underestimate dense horizontal cover, so we did not attempt to compare our results to those from other studies or determine where estimates of cover exceeded 35%. Instead, we simply compared plots within our study. Prior to our analyses, we expected measures of dense horizontal cover to be higher in the Gothic RNA as compared to the ski resort expansion area. Olson et al. (2018) found that canopy cover was low within highly developed ski areas, such as that adjacent to the ski resort expansion area. Average dense horizontal cover was significantly higher at the ski resort expansion area, which as of the time of this study has not yet been developed. The Gothic RNA is mostly dominated by older-growth forest, and our study grids within this larger area could possess lower understory density. Also, we were unable to estimate dense horizontal cover at all the plots in the Gothic RNA at which we counted fecal pellets during the 2020 field study.

Apart from our study design, dense horizontal cover estimates may be inadequate to characterize snowshoe hare and Canada lynx habitat in the absence of other data. For example, although we recorded percent slope at each direction while taking photographs of the cover board, researchers have not yet determined whether correction factors based on slope should be applied to results. This may be an important consideration, particularly in areas like our ski resort expansion site where terrain is quite steep. Dense horizontal cover estimates are a simple assessment of snowshoe hare habitat that do not typically include identification of vegetation to the species level, although they are likely carried out in forest types already expected or known to support hares. Recent research suggests that in some geographical areas, the amount of dense cover of any vegetation type is more important than forest type (Sultaire et al. 2016). Future studies may attempt to model dense horizontal cover using LiDAR imagery, as did Fekety et al. (2019). This approach, however, would require high-accuracy (submeter) geolocations of all plots, and equipment to collect such data was not available throughout our study.

Interpretation of Models and Covariates

As previously noted, there was a positive relationship between log-transformed pellet numbers and proportion canopy (as derived from 3-m LiDAR imagery) in our candidate models. This was anticipated as cover is cited as an important predictor of hare presence and abundance in the literature, although snowshoe hare habitat assessments are typically focused on dense horizontal cover near the understory. There was not a strong relationship between log-transformed pellet numbers and proportion understory as derived from the same imagery, although this could be attributed to limitations in the LiDAR technology ability to assess cover obscured by vegetation at higher forest strata. However, there was also not a strong relationship between pellet numbers and our field estimates of dense horizontal cover. This may indicate that dense horizontal cover estimates by themselves are not adequate for assessing and predicting habitat used by snowshoe hares in our study area.

Our candidate and top models also showed a negative relationship between log-transformed pellet numbers and percent combined spruce-fir cover, regardless of whether the term site (Gothic RNA or ski resort expansion area) was included as a covariate. As noted previously, this relationship disagrees with the literature citing spruce-fir cover as an important determinant of snowshoe hare presence and abundance. There is also a conflict between this result and the fact that the Gothic RNA, noticeably dominated spruce-fir, had more pellets counted at plots during both the 2016 and 2020 studies. It could be the case that in our study area, hares select for greater dense horizontal cover and/or unmeasured variables such as snow cover more-so than they select for forest type, as in Sultaire et al. 2016. It may be more likely, however, that this relationship in our models can be attributed to the spatial scale at which FSVeg data were summarized. The polygons across which these data were averaged were quite large in comparison to our study sites, in many cases extending beyond one or two of our 16-hectare study grids (Figure 7). That is, the data may be averaged across polygons too large to capture the fine-scale spatial heterogeneity in forest-related variables including percentage of dominant life forms and of combined spruce-fir cover. This suggests that while databases like FSVeg are useful, containing both field-collected and remotely sensed data, such data may be collected at and/or extrapolated across areas too large to be sufficient (in the absence of additional data) for monitoring efforts meant to predict habitat occupancy at a finer scale.

Finally, of the topographic variables we examined, topographic roughness had the strongest relationship with log-transformed pellet numbers. This index expresses the amount of elevation difference between adjacent cells in a digital elevation model, thereby quantifying topographic heterogeneity. In our candidate and top models, higher topographic roughness was associated with lower pellet numbers. This could suggest that snowshoe hares do not prefer or require high topographic heterogeneity on a small scale, but could also be related to the fact that areas with extreme topographic heterogeneity could be difficult to access and/or prevent pellets from collecting in plots. Through LOO cross-validation, we found that any models excluding one of the explanatory variables included in our top-performing model or with a different random effects structure did not perform as well. Simpler models including less covariates, however, could serve as useful alternatives when certain types of data are not available.

Integrating Field-Based Measurements, Remote Sensing Imagery, and Other Data

The question remains: how can snowshoe hare habitat be assessed without intensive field studies, and how can such results be extrapolated on a larger scale to inform management decisions? We recommend that natural resource managers follow a similar approach as this study, bringing together both field and remotely collected data available in their study areas. Greater information about the spatial scales at which wildlife make decisions will inform future monitoring efforts so that they are carried out more efficiently and effectively; for example, if sample sizes or study areas can be decreased while retaining statistical power.

Efforts to include remotely sensed data in wildlife studies and monitoring efforts are also likely to improve as such data becomes more affordable, accessible, and applicable to habitat-related questions. Indeed, data like that collected by the Sentinel satellite missions can be considered “gateways” for natural resource managers interested in utilizing remotely sensed data for a variety of applications. Organizations like the Rocky Mountain Biological Laboratory offer training in how to utilize such data, and are increasingly making both raw imagery and models derived from such imagery open access. As these data become more available, researchers and natural resource managers can develop models and otherwise utilize previously collected data in ways suitable to their needs. As remote sensing technologies become more affordable and as technologies are improved, flights of aircraft or unmanned aerial vehicles can be fitted with an array of multispectral sensors to address specific research questions not addressable with previous-collected data. While all this technology is exciting for the future of addressing management questions, it is equally important to incorporate other ways of understanding ecological patterns and predications.

The importance of integrating Traditional Ecological Knowledge (TEK) with “western” science in wildlife management is increasingly recognized, especially where funding, time, and other resource limitations preclude animal-based field studies from being carried out (Polfus et al. 2013). For certain taxa, TEK can be used in developing habitat models and for reliably revealing and estimating population trends, including and especially where population densities are low and traditional sampling methods resource-intensive (Polfus et al. 2013, Timko et al. 2015, Anadón et al. 2009). In Canada’s Yukon territory, for example, community members have indicated concerning numbers (compared to previous observations) of species including snowshoe hares (Timko et al. 2015). TEK may be particularly difficult for natural resource managers to include in areas where indigenous communities have been excluded from their traditional lands and/or resources for long periods of time. Concerns also exist among some Indigenous communities about data being made open access; in these cases, managers working with those communities should identify and protect sensitive Indigenous data. Local Ecological Knowledge (LEK), with a greater focus on direct experiences as opposed to knowledge based through generations, may similarly be available to natural resource managers through knowledge exchanges. In our study area, for example, extensive weather observations have informed local studies as well as provided evidence of global climate change over the past ~50 years (Inouye et al. 2000).

Future Modeling and Projections

Although the lynx reintroduced to Colorado were originally trapped from northern populations (Alaska and Canada), the “dogma” of what is considered quality habitat based on these northern populations may not necessarily hold true for this southern population. In the northern Rocky Mountains, Squires et al. (2010) found that during the winter, Canada lynx selected mature forests with large-diameter trees, high horizontal cover, more abundant snowshoe hares (estimated through fecal pellet counts), and deeper snow compared to random availability. On the contrary, in central Colorado lynx were found to have greatest hunting success in areas that supported less-than-peak hare density (Ivan and Shenk 2016). Furthermore, while Canada lynx here primarily consumed snowshoe hare, their diet also contained a significant amount of red squirrel (Ivan and Shenk 2016). As Canada lynx in this region consume prey other than snowshoe hare, they could be more resilient to changes in snowshoe hare density associated with recreational development and/or climate change. Other studies have similarly found that high snowshoe hare density does not necessarily identify high-quality hare habitat (Ivan et al. 2014). While a habitat may be thought of as high-quality because it supports a high species density, it could also function as a population sink in which survival and/or recruitment decrease over time (Ivan et al. 2014). On the contrary, habitats consisting of multi-storied, old-growth spruce-fir forest may possess snowshoe hare densities which are low-moderate but remain stable over time (Vasquez 2021). Therefore, when evaluating the suitability of a site for Canada lynx it is important to consider both snowshoe hare density and habitat qualities such as vegetation cover, and to acknowledge that Canada lynx may be supported even in areas thought to have low snowshoe hare density.

Although our pilot study suggests that snowshoe hare density may be too low to support Canada lynx in the ski resort expansion area, it is important to continue this pilot study and collect data across a longer time period. This is especially true as it is unclear whether snowshoe hare populations within our study site are undergoing a high or low in their population cycle (Roberts and Potter 2019). Canada lynx may also be able to use lower-quality habitat as corridors between core habitat patches even in cases of fragmentation and disturbance (Vanbianchi et al. 2017). Maintaining habitat connectivity is particularly important for the long-term conservation of populations at the periphery of a species' range, where populations can be especially vulnerable if they experience large amounts of anthropogenic disturbance (Squires et al. 2013). Furthermore, Olson et al. (2018) found that habitat alone was a poor predictor of lynx use of highly developed ski areas, as the rate and tortuosity of lynx movements was dependent on a combination of environmental (e.g., proportion forest) and recreational variables (e.g., recreation intensity). A remaining challenge that we hope to address in future studies is better understanding the appropriate scale(s) at which environmental characteristics such as horizontal cover should be summarized given the scale(s) at which hares utilize habitat features (Holbrook et al. 2016, Lewis et al. 2011). Continued monitoring of our study area will allow us to gain better understanding of the habitat qualities selected for by snowshoe hares along with population trends, allowing us to better understand whether Canada lynx could be supported and to tailor management decisions in advance of and response to changes in recreational development.

As previously discussed, snowshoe hare and Canada lynx are likely impacted by changes in snowpack related to both winter recreation and climate change. Top-ranking models of snowshoe hare site occupancy have included such variables, with higher maximum temperature and lower number of days with snow on the ground increasing the likelihood of a site becoming unoccupied (Burt et al. 2016). Ideally, therefore, habitat models would include snow and climate-related variables. As with other habitat qualities, there is a need for snow data at scales relevant to wildlife including snowshoe hares (Wilson et al. 2020). Although significant snow records exist for our study area, we were unable to incorporate these in our models or analyses as we lacked corresponding data about snowshoe hare density. That is, we could not understand how changes in snow and/or climate impacted hares without knowledge of how hare populations have changed along the same time period. As this study has allowed us to collect such baseline data, future studies will be able to determine how human-caused disturbances ranging from local-scale recreational increases to regional-scale climate changes influence snowshoe hare populations in our study area.

MANAGEMENT IMPLICATIONS

A better understanding of prey density and habitat quality within our study area will aid us in suggesting voluntary mitigation strategies to be implemented during or after the time the proposed ski resort expansion area is developed. Squires et al. (2018) suggest that while low or moderate levels of winter recreation may not produce enough disturbance to impact Canada lynx, the development and intensity of human use associated with ski resorts may be significant enough so that lynx avoid these areas. However, mitigation strategies such as the maintenance of undisturbed “islands” could be utilized to retain or promote lynx presence within and movement through ski resorts (Roberts & Potter 2019). The Record of Decision (USFS 2019) for this ski resort expansion project includes guidelines related to the conservation of Canada lynx and other wildlife, as does the more general Southern Rockies Lynx Management Direction (USFS 2008), which could be updated for the final record of decision based on the knowledge gained through this study and review of recent literature presented in this thesis. We hope to utilize this research to develop mitigation and other strategies so that development can be carried out by the recreation industry while promoting the conservation of a threatened species.

Through the process and analysis outlined here, we conclude that neither non-invasive field techniques such as fecal pellet counts nor remotely sensed data can sufficiently predict snowshoe hare habitat. On the other hand, data collected exclusively through remote sensing may not be suitable for assessing and predicting wildlife habitat, particularly where there is high spatial heterogeneity in environmental characteristics and wildlife decision-making. Other non-invasive techniques such as tracking prints or camera trapping, as well as techniques including live trapping and tracking, likely provide more conclusive evidence about the scales at which snowshoe hares select for various habitat features and the degree to which lynx are present in the habitat. Our ability to connect remote sensing technologies to field data is limited, so that such an approach may not yet be sufficient to answer questions about wildlife exclusive of traditional, field-based methodologies, particularly concerning species dependent on both fine- and broad-scale landscape features present at or near the understory and in densely forested locations. These data are, however, useful in concert with other data, and we expect they will become even more useful as technologies are improved and new applications are developed. As such, we recommend bringing field and remotely sensed data together, as many studies have already done. Such co-joining of data techniques is vital as subalpine and alpine wildlife. Subalpine and alpine habitats are expected to face local- and broad-scale fragmentation and decline along with other challenges associated with increased recreation within forests, the combined impacts of wildfires and beetle outbreaks, and climatic changes currently happening and on the horizon; these potential impacts highlight the importance of continued and improved monitoring in support of informed management.

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