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# Variation in seasonal movements, habitat selection, and demographics of an irruptive, facultative migrant

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**Abstract** Understanding how organisms respond to environmental variation is a primary goal in ecology, especially considering the rate and magnitude of anthropogenic change occurring worldwide. The extent to which facultative movements function in response to constraining conditions is unclear, and empirical examination of the proximate cues eliciting facultative behavior is limited. This study tests whether winter facultative movements by Great Gray Owls (GGOWs) in the GYE occur in response to constraining snow conditions, and how these conditions impact fitness. We outfitted GGOWs (n=40) with GPS transmitters, monitored reproductive output, and surveyed breeding-season prey abundance between 2014-2021. We will analyze movements and habitat selection using Net Square Displacement models, Resource Selection Functions, and analyses will incorporate remotely-sensed weather, geophysical, and landscape covariates. We will assess fitness metrics in relation to within-season prey abundance versus carry-over effects from the prior winter using Generalized Linear Mixed Models. Evaluation of facultative systems can indicate how animals use plasticity in movement behavior to cope with environmental change. This work also will identify determinants of fitness for a facultative migrant species, which is critical for understanding population dynamics in such systems.

## Introduction

Understanding how organisms respond to environmental variation is a primary goal in ecology, especially considering the rate and magnitude of anthropogenic change occurring worldwide (Shaw, 2016; Griswold et al., 2011). Movement has evolved across taxa as an adaptive response to environmental conditions (Newton, 2008; Alerstam and Hedenström, 1998; Dingle, 1996) and animals exhibit varying degrees of plasticity in movement behavior. For example, obligate migrants have consistent seasonal movement patterns, whereas facultative migrants exhibit considerable variation in when, where, and whether they migrate (Newton, 2008). The extent to which facultative movements function in response to constraining environmental conditions is unclear, however, and empirical examination of the proximate cues eliciting facultative behavior is limited (Newton, 2012; Therrien et al., 2014; Robillard et al., 2016). Facultative systems can indicate how animals use plasticity in movement behavior to cope with environmental change. Individuals may shift proximate habitat selection or rely on broad-scale movements such as dispersal to buffer limiting conditions, but the contexts under which different movement strategies are employed are poorly understood.

Linking behavior to fitness is critical for understanding the consequences of ecologically-limiting conditions, and the strategies employed to offset them. In general, studies rarely link facultative movement behavior to fitness metrics. Because facultative movements may occur in response to unpredictable, constraining conditions (such as extreme weather or food abundance; Newton, 2008), there is potential for this behavior to incur carry-over effects, in which factors during one phase of the annual cycle have downstream consequences for fitness in a subsequent period (Marra et al., 1998; Ryan Norris and Marra, 2007; Harrison et al., 2011). The majority of research on carry-over effects focuses on long-distance migrants (Harrison et al., 2011). The extent to which carry-over effects operate in facultative migrant populations, by contrast, remains relatively unclear. Information on determinants of fitness in facultative systems is critical for understanding population dynamics and limiting factors.

In Wyoming, the Greater Yellowstone Ecosystem (GYE) is home to one of the world's most iconic facultative migrant species, the Great Gray Owl (GGOW), and provides an ideal system for studying the contexts and consequences of facultative movement behavior, and the extent to which carry-over effects operate. In the GYE, GGOWs are partially migratory, exhibiting high inter- and intra-individual variation in the timing, direction, and distance of non-breeding-season movements (Bedrosian et al., 2015). Likewise, GGOW productivity fluctuates dramatically from year to year (Bedrosian et al., 2015). The proximate mechanisms driving this variation in movement behavior and reproductive output are unknown. However, during the winter GGOWs predate subnivean small mammals, thus snow conditions that preclude owls from accessing prey may be an important factor. Snow conditions may prompt owls to shift proximate habitat selection and/or disperse in order to acquire sufficient forage. Likewise, these winter conditions, or the movements required to modulate them, may carry over to impact subsequent reproductive performance.

We are testing whether winter facultative movements by GGOWs in the GYE occur in response to constraining snow conditions, and whether certain habitat attributes modulate these conditions. Additionally, we will evaluate the influence of within-season versus

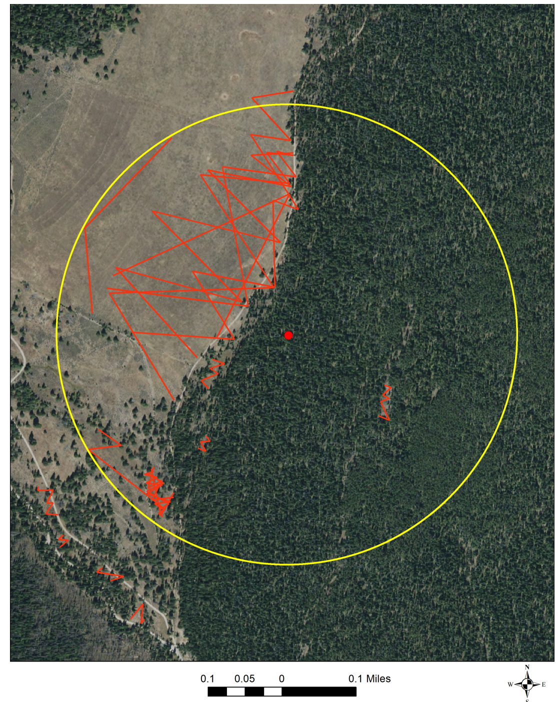


**Figure 1.** Transects for surveying for Northern Pocket Gophers.

carry-over effects from the prior winter on reproductive performance.

Objectives:

1. Identify the proximate cues prompting dispersal from breeding ranges by GGOWs during the non-breeding season.
2. Compare habitat attributes between seasonal ranges from which GGOWs disperse during the non-breeding season versus ones in which owls remain and/or settle.
3. Compare the relative influence of within-breeding-season effects versus carry-over effects from the prior winter on GGOW reproductive performance and apparent survival.

## Methods

### Study area

This research was conducted in Teton County, Wyoming, between Hoback, WY, north through the Snake River riparian corridor and surrounding

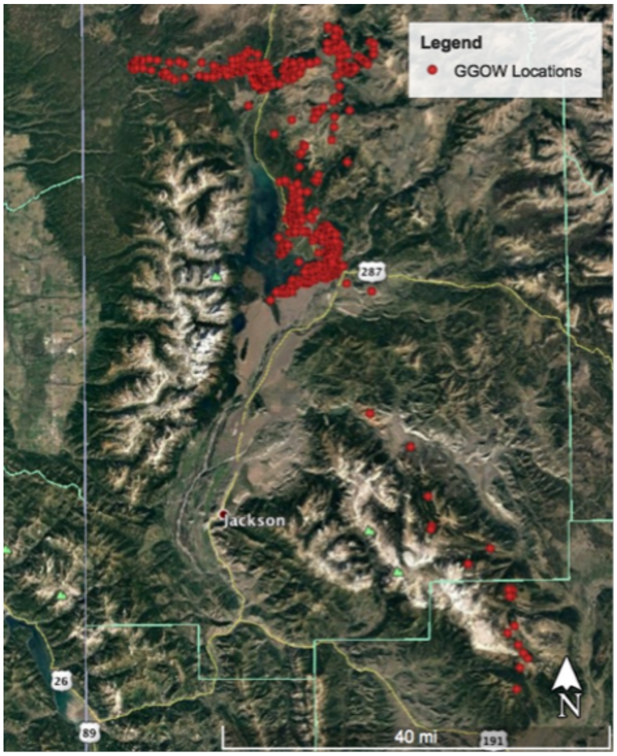


**Figure 2.** Locations for an adult male GGOW between summer 2018-spring 2020. This individual dispersed from its breeding range in Yellowstone National Park southeast to the Upper Green River basin during the winter.

foothills of the Teton Range, to the Pacific Creek area. Owl territories ranged from riparian forest zones to areas dominated by aspen forest or conifer forest. Owls were located within Bridger-Teton National Forest, Grand Teton National Park, and on private lands.

## Location data

We outfitted 40 adult Great Gray Owls with remote-download GPS transmitters (manufactured by Lotek) between 2018-2021. Capture techniques included the use of bal-chatri traps and bow nets, and capture, banding, and tagging methods adhered to standard protocols (including IACUC requirements). GPS transmitter technology provided the opportunity to remotely monitor Great Gray Owl movements and habitat selection. The transmitters collected year-round locations for ∼2 years per unit.

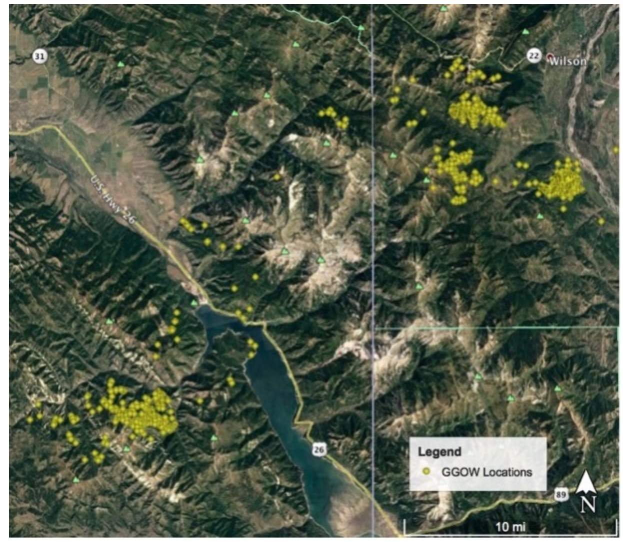


**Figure 3.** Locations for an adult female GGOW from summer 2019 – spring 2020. The cluster in the bottom left is her discreet winter home range west of Palisades Reservoir.

## Nest monitoring

This study leverages productivity data from >30 known GGOW territories in the study area from 2014-2021. We determined reproductive success by monitoring nests throughout the breeding season. If the nest site was unknown, we searched the territory by walking 25-50m transects throughout the area. Once active nests were located, we checked nesting status at least once each week to determine nest success and fledge dates. We documented whether a female was observed initiating, incubating, and brooding, and recorded number of chicks as well as young fledged. We considered a territory active if we found direct evidence of breeding, such as an incubating female or fledglings. Nests that fledged at least one young were considered successful. Additionally, beginning in 2016, We monitored territory occupancy using audio recorders placed adjacent to known nest sites or in an array (300m apart) in known territories.

## Prey abundance sampling

Between 2014-2021, we assessed primary prey (Northern pocket gopher, *Thomomys talpoides*) abundance during the breeding season at 18 territories. For these 18 territories, we digitized all mead-

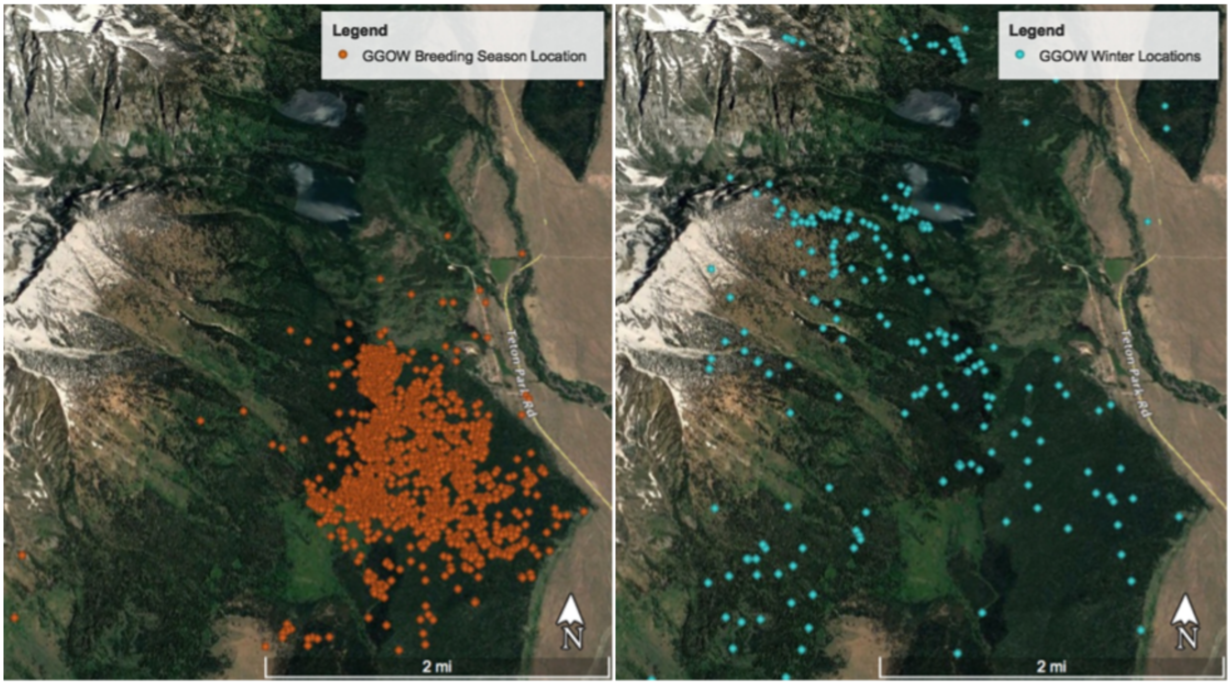


**Figure 4.** Breeding-season (left image, orange points) and winter (right image, blue points) locations for the same adult male GGOW in the Greater Yellowstone Ecosystem from spring 2019 - spring 2020. During the winter the owl repeatedly moved upslope into the Teton Range, as high as 2,750m (>9,000ft) in elevation.

| Year | Occupancy | Nest Initiation |
|---|---|---|
| 2016 | 100% | 100% |
| 2017 | 67% | 0% |
| 2018 | 78% | 11% |
| 2019 | 81% | 35% |

**Table 1.** GGOW territory occupancy and nest initiation rates from 2016-2019 in the Greater Yellowstone Ecosystem.

| Year | Mean Fledglings |
|---|---|
| 2013 | 1.5 |
| 2014 | 1.56 |
| 2015 | 1.75 |
| 2016 | 1.3 |
| 2017 | 0 |
| 2018 | 0.11 |
| 2019 | 0.34 |

**Table 2.** GGOW mean number of young fledged across years in the Greater Yellowstone Ecosystem.

ows within 500m of known nests and randomly selected three meadows (when available) for prey surveys. We started at the head of each meadow and walked 45-degree diagonal transects back and forth until reaching the end of the meadow, tallying fresh and old gopher mounds visible within 10m of the transect (Figure 1). Because we were interested in relative abundance between years and among territories, we annually tallied total survey length for each territory and divided by the number of fresh mounds to create an index of gopher abundance.

### Apparent survival

We deployed audio recorders at known GGOW territories between 2017-2021 primarily to determine territory occupancy rates. However, we also will evaluate multiple years of audio data using automated sound analyses to distinguish individual GGOWs via vocalizations (i.e., "vocal fingerprints"; Rognan et al., 2009). By identifying individuals by calls within and across seasons, we will determine territory turn-over

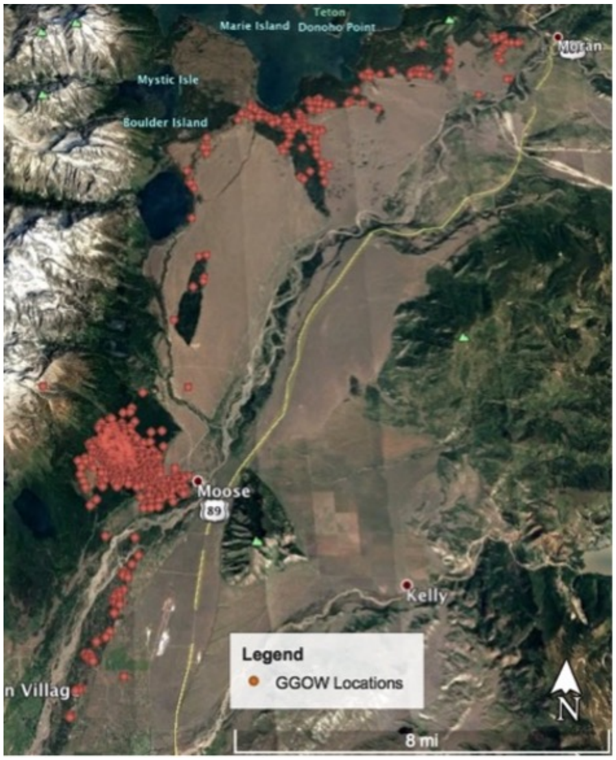


**Figure 5.** Locations for an adult male GGOW in the GYE from summer 2018 – spring 2019. This individual bred near Moose, WY, then dispersed into the Snake River basin to the south, as well as north through Grand Teton National Park to Moran, WY during the winter.

and annual survival rates (Williams et al., 2002). We will use these metrics along with reproductive performance to evaluate the influence of within-season versus carry-over effects on demographic patterns for GGOWs in Wyoming.

### Statistical analyses

Upcoming analyses will incorporate Net-Square Displacement and Time-to-Event analyses to identify and evaluate dispersal events, and we will use Resource and Step Selection Functions and Generalized Linear Mixed Models to assess habitat selection between seasonal ranges. Analyses of dispersal movements and winter habitat selection will incorporate weather and geophysical covariates related to snow conditions as well as habitat variables we hypothesize may modulate snow conditions. We will include multiple spatiotemporal scales, as well as non-linear decay functions and coefficients of variation to identify threshold levels and individual variation in behavioral responses to environmental conditions.

We will analyze annual reproductive metrics (including initiation date, apparent nest success, and number of young fledged) and apparent survival in relation to within-season prey abundance and environmental conditions and prior non-breeding-season environmental conditions (including weather and geophysical conditions). We also will evaluate winter dispersal distance in relation to timing of arrival on breeding ranges and subsequent reproductive performance metrics, as well as on apparent survival rates. Analyses will include Generalized Linear Mixed Models with territory-by-year and territory as random effects.

## Preliminary results

As of February 2021, we collected non-breeding-season locations for 33 adult GGOWs (18 males and 15 females). We deployed seven additional transmitters during the summer of 2021, and these units will collect locations through the winter of 2021-2022. One owl dispersed 120km from its breeding home range, which was the farthest dispersal observed (Figure 2). We also observed owls remaining on breeding ranges throughout the non-breeding season, migrating to discrete winter ranges (Figure 3), repeating back-and-forth movements from breeding to discrete winter ranges multiple times over the course of a winter, altitudinal migrations (Figure 4), as well as nomadic movements both north and south of breeding ranges (ie. Figure 5). In general, GGOWs appear to be faithful to breeding territories, as we observed all individuals return to their breeding territories except one female that settled on a new breeding territory 5km from her original one.

Across years, preliminary data indicate GGOW breeding-range occupancy remained relatively high across years compared to nest initiation (Table 1), apparent nest success (Figure 6), and productivity rates (Table 2), which exhibited high annual variation. Annual apparent nest success rates did not appear to correspond to primary prey abundance (Figure 7), al-

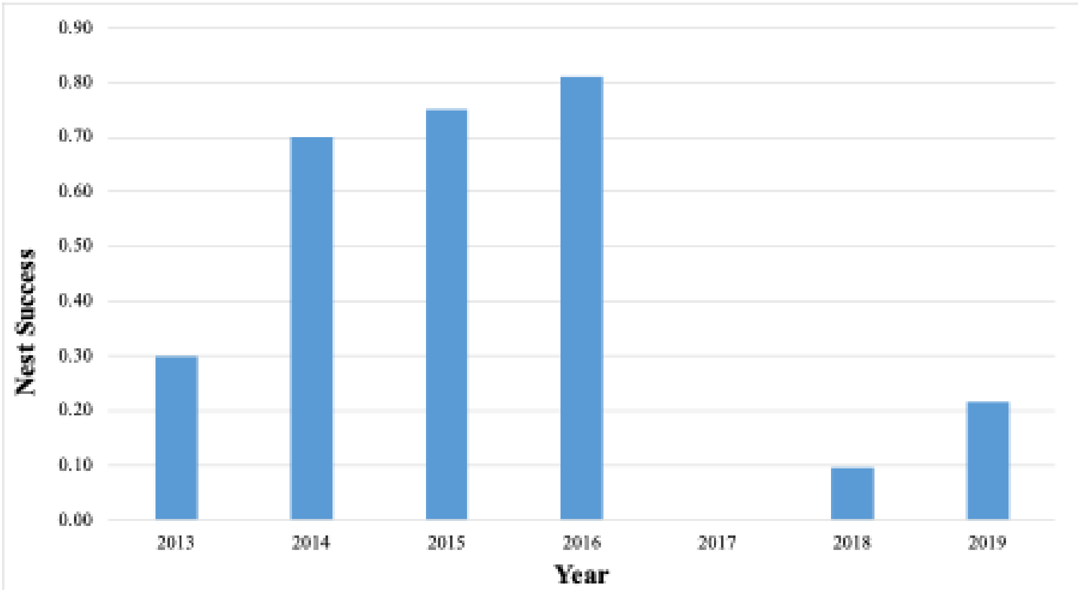


**Figure 6.** GGOW apparent nest success (number of successful nests/known occupied territories) from 2013-2019 in the Greater Yellowstone Ecosystem.

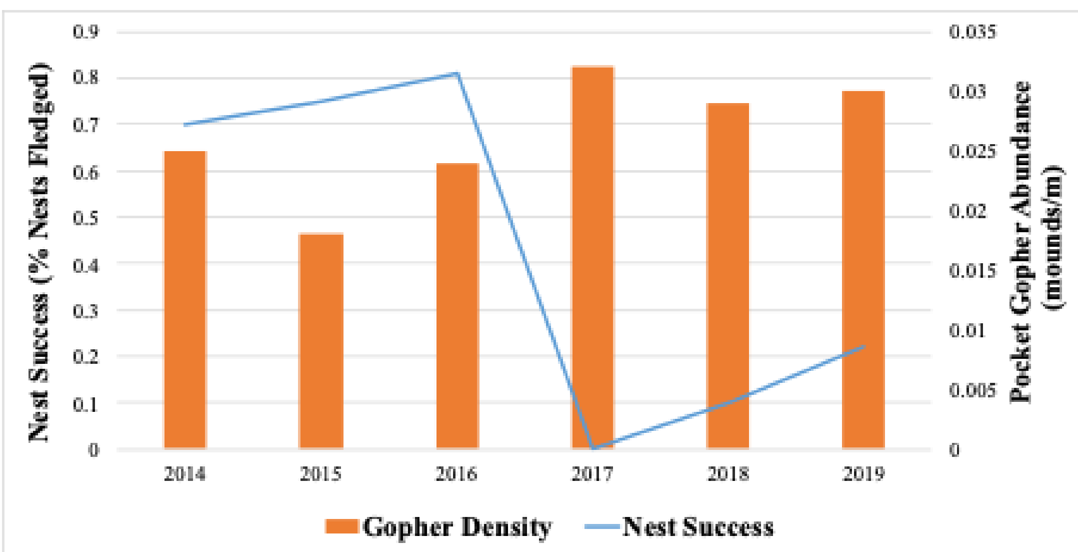


**Figure 7.** GGOW mean annual productivity (number nests that successfully fledge/number of territories) in relation to primary prey abundance (number of Northern Pocket Gopher mounds/m) between 2014-2019 in the Greater Yellowstone Ecosystem.

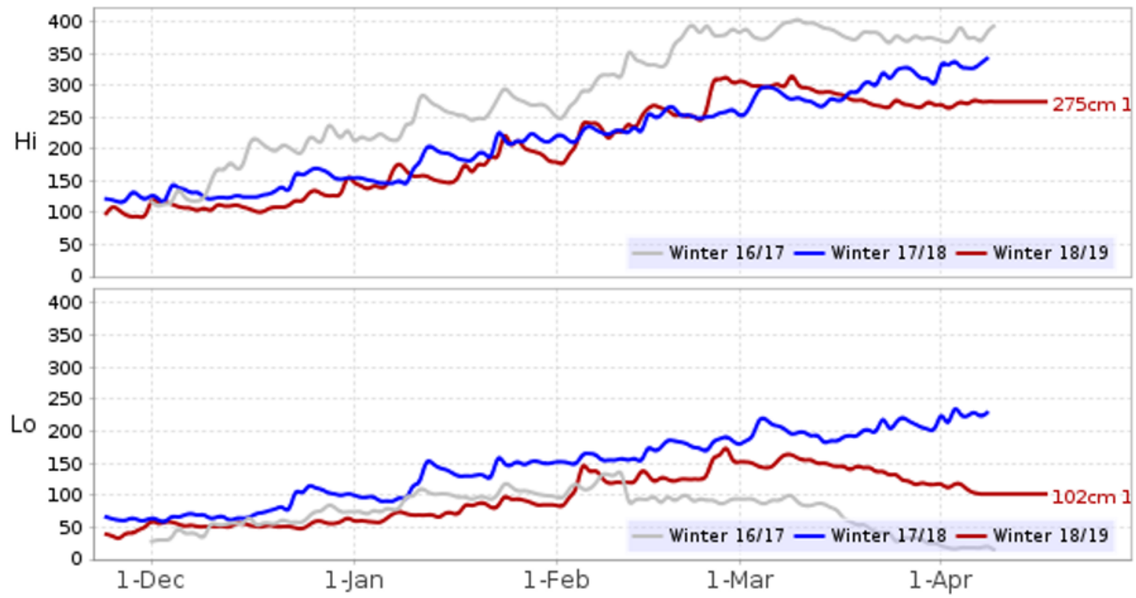


**Figure 8.** Total snow depth at high (top graph) and low (bottom graph) elevations between late November through early April across a three-year period in Jackson, Wyoming (J2Ski2019).

though additional years of data will be incorporated into final analyses. Snow depth and timing of snow melt can vary considerably from year to year within the study area (Figure 8).

Following collection of winter 2021-2022 location data and spring 2022 breeding and apparent survival data, we will conduct final analyses of movement behavior, habitat selection, reproductive performance and apparent survival.

## Conclusions

Knowledge of environmental stressors and how they influence behavior and fitness is essential if we aim to predict how species will respond to future environmental change (Wilcove, 2008). Many migratory populations are declining (Griswold et al., 2011), making this research particularly pressing. Research on climate change vulnerability tends to focus on physiological constraints due to thermoregulatory risks (Wilcove, 2008), as well as shifts in phenology (Rickbeil et al., 2019). My work will broaden understanding of climate change risks by testing a novel stressor, foraging constraints that fluctuate with changes in precipitation and temperature, both of which are expected to be more variable and extreme with climate change (Meehl and Tebaldi, 2004). When carry-over effects occur, stressors can accumulate, with potentially detrimental implications for population persistence (Sæther and Bakke, 2000; Gunnarsson et al., 2005). Assessing how carry-over effects impact facultative migrants is key for understanding determinants of fitness in these systems.

This research has specific implications for avian conservation, including in the GYE. The GGOW is a species of Greatest Conservation Need in Wyoming (WGFD, 2017) in large part because its habitat associations and population status remain unknown. Like many boreal forest species, the GGOW is at extreme risk to threats related to anthropogenic environmental change (Siegel et al., 2014; Wilsey et al., 2019) that are expected to reduce its range considerably in North America, effectively extirpating this raptor from the Lower 48 during the breeding season by 2080. I will identify key breeding, migratory, and winter habitat in the GYE. Productivity is declining in the region (Bedrosian et al., 2015), and I will evaluate whether within-season or carry-over effects limit reproduction, which can inform population management. Evaluating the effects of weather on movement and fitness will shed light on how this raptor may respond to changing climate regimes. Although the GYE evolved amidst high spatiotemporal variability, the potential for extreme weather related to climate change to upend population dynamics and ecosystem function remains (Melillo et al., 2014).

## Future work

We will conduct final analyses following the upcoming winter season of data collection. Following analyses, a written dissertation will summarize results of this study. Additionally, findings will be consolidated and submitted for publication in peer-reviewed journals. Continuing long-term data collection will be valuable to understand variation in GGOW fitness, population dynamics, and habitat selection over time. Explicitly evaluating how habitat alteration influences habitat selection and demographics is an important future direction for our research on GGOWs in Wyoming. Additionally, juvenile dispersal behavior is a key gap in our understanding of GGOW movement ecology in the GYE.

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