OCCUPANCY, NEST SUCCESS AND HABITAT USE OF GREAT GRAY OWLS IN WESTERN WYOMING

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ABSTRACT

The Great Gray Owl (*Strix nebulosa*) is designated a Species of Greatest Conservation Need in Wyoming due to limited and vulnerable habitat. In 2013, we initiated a multi-year study on Great Gray Owls in western Wyoming to understand seasonal habitat use, determine prey use, and develop habitat selection models for predicting seasonal habitats in western Wyoming. From 2013-2015, we conducted nighttime call-back detection surveys for forest owls and estimated a total of 40 territories across 207 km^2 of effectively surveyed habitat. We documented 36 nesting attempts across years, with an average nesting density of one nest/2.7km^2. Productivity has declined from previous estimates for this population to 1.7 fledglings/nest. Nests are typically located in old stick nests or snags. Nest success was lower in snag nests and in territories with fewer pocket gophers. Characteristics of habitat at nest sites and within breeding home ranges of marked owls compared to random plots included older-aged forests with higher canopy cover, further from roads and on lower slopes. Owls moved towards riparian habitats during the winter months and winter range was concentrated in the southern half of the Jackson Hole valley. We suggest that productivity may be limited by a combination of decreasing winter range and changing snow characteristics in western Wyoming. Further research is warranted on territory habitat use by breeding males to determine the importance of meadow habitats and relationship of productivity to long-term prey fluctuations. Understanding female condition prior to egg laying in relationship to prey populations, habitat conditions, and weather are necessary to better understand observed decreases in productivity. It appears that Great Gray Owls are regularly spaced within suitable habitat. Long-term studies are needed to investigate population trends and potential impacts of

climate change. Potential decreases in productivity and limited critical winter range over time also

warrant concern.

INTRODUCTION

The Great Gray Owl (*Strix nebulosa*) is classified as a Species of Greatest Conservation Need with a Native Species Status Unknown (Tier I) in Wyoming. Population status and trends for the Great Gray Owl are unknown but suspected to be stable, while habitat is restricted and vulnerable (WGFD 2010). Overall, there are little population and habitat data from western Wyoming. Franklin (1988) studied Great Gray Owl breeding ecology in eastern Idaho and western Wyoming in the early 1980s and a follow-up nesting habitat study was conducted in the mid-1990s (Whitfield and Gaffney 1997). Anecdotal nesting data exist from other studies in Wyoming (e.g., Craighead and Craighead (1969), the US Forest Service, and public reports), but no data exist on owl densities or movements in the Rocky Mountain region. Wyoming is the southernmost extent of this species' breeding range in the Rocky Mountains (Bull and Duncan 1993) though recent reports of Great Gray Owls have been documented during the summer months in Utah (US Forest Service, pers. comm.). The older-aged, boreal forest habitats associated with Great Gray Owls may be at risk from both natural and anthropogenic disturbances such as wildfire, disease outbreak, drought, climate change, logging and development.

Boreal forest owls, such as the Great Gray Owl, are often difficult to study due to relatively low occurrence rates, difficult-to-access habitats, and secretive nesting behaviors. They remain one of the least-researched raptor species in the USA. The majority of studies employ passive methods of monitoring owls such as occurrence and call-back surveys. Previous studies in the USA include a large demographic and movement study in northeastern Oregon from 1982-1988 (Bull and Henjum 1990), a three-year study on breeding and nesting habitat in eastern Idaho and western

Wyoming from 1980-1983 (Franklin 1988), a follow-up of the Franklin (1988) study from 1994-1996 (Whitfield and Gaffney 1997), and several projects on the isolated sub-species of Great Gray Owl in the Sierra Mountains of California. Two additional studies on Great Gray Owl movements from Canada incorporate small mammal abundance influences on movements and dispersal (Nero 1980, Duncan 1992). With the exception of one study that correlated owl population trends with clear-cut logging and forest thinning (Whitfield and Gaffney 1997), no published studies have investigated changes in populations based on changing forest dynamics.

A distinct subspecies of the Great Gray Owl occurs in the Sierra Mountains of California (Hull et al. 2010). Many studies have been conducted on that discrete population. Sears (2006) modeled habitat suitability based on occurrence surveys of meadow complexes. Van Ripper et al (2013) investigated the influence of prey availability, forest structure, and anthropogenic disturbance, again based on occurrence sampling. Wu et al. (2015) conducted a retrospective study of nest site characteristics. Rognan et al. (2009) began utilizing automated recorders as a census method. Van Ripper and Wagtendonk (2006) used radio-tagged locations from 12 owls in 1986-1990 to assess home range characteristics.

Great Gray Owls typically occupy older-aged Douglas-fir (*Psuedotsuga menziesii*) forest stands in the northwestern U.S., where neighboring owl nests can be located as close as 430 m (Bull et al. 1988a). Great Gray Owls in Idaho and Wyoming have also been associated with lodgepole pine (*Pinus contorta*) forests due to presence of raptor stick nests (Franklin 1988). During the breeding season Great Gray Owls depend on forests with high canopy cover that are suspected to increase fledgling survival (Whitefield and Gaffney 1997). During the winter months, some populations move to areas of lower elevation and snow cover (Bull et al. 1988, van Ripper and Wagtendonk

2006). Since Great Gray Owls do not built nests, they rely on existing structures for nesting, such as mistletoe (*Arceuthobium* spp.), broken snags, and stick nests constructed by other raptors and corvids (Bull and Henjum 1990, Duncan and Hayward 1994). In Wyoming during the early 1980s, Franklin (1988) found 60% of Great Gray Owl nests on broken snags, and 40% in old stick nests, typically built by Northern Goshawks (*Accipiter gentilis*). Subsequent studies within that area suggested decreased snag nest-use and an increased reliance on raptor nests (Whitfield and Gaffney 1997). A six-year study of nesting Northern Goshawks on the Caribou-Targhee National Forest in the 1990s reported Great Gray Owls nesting in eight of 27 goshawk territories; 17 of these alternate goshawk nests used by the owls were in Douglas fir and one was in an Englemann spruce (*Picea engelmannii*; Patla 1997). Great Gray Owls consistently avoided clear-cuts for nesting (Bull et al. 1988, Whitfield and Gaffney 1997, Fetz et al. 2003), but such areas may be important for foraging (Franklin 1988).

Prey abundance and availability drives movements (Duncan 1992) and occurrence (van Ripper et al. 2013) of owls and likely influences nesting demographics (Franklin 1988). Several analyses of Great Gray Owl pellets found a reliance on *Microtus* vole species (Oregon; Bull et al. 1989, Manitoba; Duncan 1992) and pocket gophers (Franklin 1987, California; Winter 1986). The proportion of voles to pocket gophers in the diet is likely a function of relative density.

In 2013, we initiated a large-scale ecological study on Great Gray Owls in western Wyoming. The study area partially overlaps the previous studies of Franklin (1987) and Whitfield and Gaffney (1997), both of which included both sides of the Teton Mountain range, allowing for direct comparisons. Several groups collaborated on this study, including the Teton Raptor Center, Wyoming Game and Fish Department, Bridger-Teton National Forest, Grand Teton National

Park, and Craighead Beringia South. We designed the placement of the main study area to correspond with planned forest treatments in the interest of using these data for future inquiries into the effects of thinning and burning on owl movement and nesting ecology.

The main objectives of this study were:

1. Understand nesting habitat for Great Gray Owls in northwest Wyoming

2. Determine nesting density for Great Gray Owls

3. Determine seasonal home ranges of adult and sub-adult Great Gray Owls

4. Create a long-term framework for surveying small mammal populations

5. Begin investigating how fluctuations in small mammal abundance relates to occupancy and productivity

6. Create and validate a breeding season habitat suitability model

7. Create a long-term monitoring framework for Great Gray Owl populations

We supplemented the above with secondary concurrent objectives (as sample sizes of known territories allowed):

1. Determine if nest site availability limits the Great Gray Owl population

2. Investigate the use of nest cameras for prey assessment

3. Examine prey use through regurgitated pellets

METHODS

Study Area

The primary study area for 2013-2015 included the base of the Teton Range and the Snake River riparian corridor from the areas around Moose, WY in southern Grand Teton National Park south to the Snake River Canyon. We expanded the study area in 2015 to include northern areas within Grand Teton National Park (e.g., Emma-Matilda/Two Oceans area) and Bridger-Teton National Forest (e.g., Rosie's Ridge and Blackrock areas). The typical forest habitats consisted of Douglas fir, lodgepole pine, sub-alpine fir (*Abies lasiocarpa*), and aspen (*Populus tremuloides*) surrounding the valley and mixed cottonwood (*Populus* spp.) spruce (*Picea* spp.) forests within riparian areas. Both mesic and sagebrush (*Artemesia* spp.) meadows occurred throughout the study area. Housing subdivisions are common throughout the study area but rarely extend beyond 1.5 km from the valley floor.

Nesting Surveys

From 2013-2015, we conducted call-back surveys across our study area to record the presence of Great Gray Owls during their courtship period (mid-February-April). We followed the USFS-BLM protocol (Quintana-Coyer et al. 2004) with slight modifications described below.

To determine call-back survey locations, we used the existing Bridger-Teton National Forest (BTNF) habitat layer to delineate any forest stand (regardless of species) with an average diameter at breast height (DBH) of 25 cm or greater because the average DBH of Great Gray Owl nest trees was 52.7 cm in previous studies (Franklin 1988). Within that layer, we placed survey points to completely cover the applicable habitat. Although Cramp (1985) asserts that Great Gray Owl calls

are audible at distances up to 800 m, we conservatively adjusted our detection radius to 200 m. Therefore, survey locations were ca. 400 m apart. We began surveys no earlier than one half hour after sunset and typically completed before 02:00 hours. Using a FOXPRO caller near maximum volume, we played calls for Great Gray Owls and Boreal Owls (*Aegolius funereus*). Each calling period consisted of a 2-min listening period, followed by the Boreal Owl territorial call, a 1-min listening period, the Great Gray Owl male territorial call, a 1-min listening period, the Great Gray Owl male territorial call again, and a final 2-min listening period. We also re-surveyed a proportion of the calling locations to help determine detectability. In 2015, we only re-surveyed within known Great Gray Owl nesting territories and at locations with Great Gray Owl detections in the first round. All known territories were surveyed at least twice during the call period.

We conducted backcountry surveys in pairs, typically on skis or snowshoes. We surveyed areas surrounding neighborhoods and roads singly, using vehicles. We also used snow machines on designated routes when possible and in teams of two for safety. All vehicles were turned off and surveyors did not move or talk during the survey period to maximize detectability.

When a Great Gray Owl was detected at a survey location, we did not survey neighboring locations to help ensure the owl(s) did not follow us. When Great Horned Owls were detected during the initial listening period at a survey location, we omitted the Boreal Owl call (this prevented eliciting a response from a Boreal Owl that could potentially increase predation risk by the Great Horned Owls). Similarly, if we detected a Boreal Owl, we omitted the Boreal Owl call at neighboring locations, but we still played the Great Gray Owl call.

In 2015, we created a preliminary resource selection model using re-locations from marked owls in 2013-2014 and used the model to help predict valuable survey locations in 2015. We also

reduced total call locations by focusing on the interior of forest patches, which maximized survey areas.

We recorded all owl species detected and estimated distance to and direction of each owl. To help with distance estimates, we played owl calls at typical volumes for each species at known distances during training sessions. We also recorded type of call for all Great Gray Owls (e.g., male territorial, female contact, female agitated, exclamatory, etc.) and for other species when possible. We noted the predominant tree species within the immediate area surrounding the survey location and average DBH of the stand. We did not conduct surveys when wind speeds exceeded 16 km/hr or during significant precipitation events.

We examined call-back data for patterns in owl responses and removed all suspected records of the same owl (e.g., an owl was heard at successive survey points in the same general direction or followed the surveyors). We then categorized detections by species in 7 bins based on hour from 19:00-01:00 hr. Surveys rarely occurred prior to 19:00 hr or after 01:00 hr. We then calculated expected detections based on total surveys conducted in each bin. We used Chi-square tests to determine if detections differed from expected.

Nest Searching & Monitoring

Following the night call-back survey period, we searched for nests in all areas where Great Gray Owls were detected. We exhaustively searched suitable habitat for old stick nests, abnormal tree growths (hereafter witches brooms), and broken snags large enough for an owl nest. Any potential nesting structure was recorded and searched for signs of occupancy (e.g., an incubating bird, feathers, whitewash, or pellets). We also used the male contact call or begging call to

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regularly solicit calls from nesting owls, nestlings, and/or fledglings while nest-searching. To record search effort, we recorded all of our tracks every 10 m using a Garmin etrex20 or extrex10 GPS unit. This also helped us determine if particular areas were not adequately searched.

In all areas where we detected Great Gray Owls during the night call-back surveys but did not locate an active nest, we also conducted fledgling call-back surveys during July and August. For fledgling surveys, we covered the entirety of suitable nesting habitat, playing a mixture of contact and begging calls 400 m apart or less to solicit responses from fledgling owls. We also opportunistically used call-backs while traversing the study area conducting other tasks (i.e., nest platform set-up, small mammal trapping, etc.).

We considered a territory "active" only if we found direct evidence of breeding, such as an incubating female or fledglings. We considered a territory "occupied" if we documented multiple night detections or saw at least one adult owl multiple times but no active nest or fledglings were located. Once active nests were located, we checked on nesting status at least once every week to determine success and fledge dates. We considered fledged nests as successful but could not dependably monitor post-fledging mortality since chicks were not radio-marked.

To estimate density of Great Gray Owls, we omitted the northern areas (Emma Matilda/Two Ocean Lakes, Blackrock, and Rosie's Ridge) because these areas were first searched in 2015 and are not yet adequately surveyed for density estimates. After analyzing call-back detections, we regularly detected Great Gray Owls up to 300 m, so we used 300 m as our detection radius for the density estimates. We buffered all nighttime call locations by 300 m to determine the total effective area surveyed. We then used the 30 m GAP vegetation layer to delineate only forested habitat within our effective calling perimeter, since Great Gray Owl nests occur within

this habitat. We then clipped the total area surveyed to only forested habitat, thereby removing all habitats where owls could not nest (i.e., sagebrush, meadows, water, etc.) to estimate how much nesting habitat was surveyed. We used this effective call area to calculate territory density of Great Gray Owls. To determine the number of territories within the study area, we used all confirmed nests sites and locations of fledglings. We also estimated active, non-nesting territories using our night survey results when we detected a female and/or at least three male detections within 500 m of each other.

We could not effectively search all of the areas surveyed with call-backs for nests so we estimated our effective search areas across all years to calculate nesting density. First, we combined all of our track data and reduced the dataset to 1 May – 31 August to correspond with the nesting season. We then buffered all track data by 100 m. We used a conservative estimate of 100 m for effective search area because we could generally see nests up to 50 m and hear females and juveniles up to 300 m away while nest searching. Because detectability of nests and juveniles was not 100%, we felt that the conservative estimate of 100 m best-reflected the cumulative effective search proximity. We then clipped this total area to only forested habitats in which owls could nest and used that to determine our effective search area. We used this effective search area estimate divided by the total active nests (and fledgling locations) within the search area to determine nesting density.

Nesting Habitat

We measured habitat variables at nest sites on two scales: on-the-ground at the nest level and at a 30 m scale using remote sensing layers and a GIS. To directly measure variables, we

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followed Wu et al. (2015) and measured canopy cover, nest height, nest tree height, nest tree

DBH, slope, aspect, and the deterioration of the nest tree. The type of nest fell into three

categories: broken snag, stick nest (built by another bird species), or mistletoe. We assigned a

number from 1-5 for deterioration (Wu et al. 2015), which scaled from a live intact tree (1) to a

broken-top rotting tree with most of the bark and branches gone (5). We measured tree height

and nest height with a laser rangefinder, standing on the same level as the tree with a clear view,

and calculated later, accounting for the eye level of the observer. For the habitat characteristics

immediately surrounding the nest, we measured the degree and aspect of the slope (if applicable)

with a protractor and compass and the tree's position on the slope (top, middle or bottom). We

binned aspect measurements based on cardinal directions to assess general aspect of nest sites.

Standing under the nest tree, we used a convex spherical densiometer for canopy cover assessment

in the four cardinal directions and calculated the mean for the nest location. From the nest

location, we also determined the distance to the nearest meadow available for owls to hunt using

the rangefinder, and if a meadow was not readily visible we located it using aerial photographs in a

GIS. A meadow was defined as any opening with a minimum of ca. 25 m radius.

We further characterized the nest plot based on a 50 m radius around the nest (Wu et al.

2015). In the plot we visually determined the dominant tree species, followed by the second most

abundant tree species. We assessed the canopy cover at four random azimuths 25 m from the nest

tree and also at the nearest tree in each cardinal direction from the nest using a convex spherical

densiometer.

We also assessed the slope, aspect, canopy cover, and distance-to-meadow for all nests using

the 30 m 2011 NLCD in a GIS.

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Nesting Platforms

To assess whether nesting structures are limiting the breeding population of Great Gray

Owls, we began installing nesting platforms in the study area in the fall of 2013 with support from

1% for the Tetons. Wooden nesting platforms were made following Bull and Henjum (1990) with

the aid of local Boy Scout and Girl Scout troops as part of our community outreach and education

program. We used a random design to assign locations to install the structures. First, we

delineated the area in which we adequately surveyed for nesting owls both by call-back surveys and

fledgling surveys and could thereby accurately describe nesting density in 2013. We divided this

area into two sections: a control area and a treatment area. The control area was defined so

natural fluctuations in owl density could be compared with any changes in density as a result of

increasing nesting substrate options in the treatment area. In the treatment area, we used a GAP

habitat layer to identify any forest patch with >25 cm DBH to define potentially available nesting

habitat. We then randomly projected points within this layer that were a ≥100 m from the nearest

edge and ≥400 m from the nearest neighboring point. We projected 40, 60, and 100 points in this

manner. We determined that 40 locations was inadequate, as several large forest tracts did not

have any points, and the 100 location layer placed too many locations near the forest edge to abide

by the 400 m inter-point distance rule. So, we chose 60 random points, which adequately covered

the treatment area without missing any large forest tracts. When placing platforms, we chose a

tree of the species representative of that forest tract, with ≥40 cm DBH, and with an adjacent tree

in which we could place a motion/thermal-triggered trail camera to monitor the platform for use.

We chose the tree nearest to the random location that met this criterion. When tree height permitted, we installed all platforms 10.6 m above ground level. We also placed one remote camera near each of the platforms. Test cameras were deployed at our offices to monitor battery life of the units, and batteries were replaced as necessary.

Remote Nest Monitoring

Beginning in 2014, we placed remote still-cameras at known nest sites to determine if they could be used to determine prey delivery rates and prey composition between nests and years. Cameras were typically situated in an adjacent tree with one exception where the camera was placed above the nest due to a lack of nearby trees. We continued camera placement in 2015 on the same nests monitored in 2014.

Prey Surveys

We opportunistically located regurgitated pellets while conducting all surveys. Each pellet was collected, labeled with date and location, and stored for later analysis. If no Great Gray Owls were detected in the immediate vicinity of a pellet location during the study, we did not assign a species to the pellet. However, if Great Gray Owls were regularly within the area where a pellet was found or if the pellet was within 150 m of a known nest, we assigned that species to it for later analysis. We searched areas below and directly surrounding nest sites and associated roosting locations to collect pellets from nesting pairs and nestlings. Female owls typically leave the nest to regurgitate pellets and sometimes use the same location, often within 100 m of a nest site.

Prey items were identified using skeletal remains in the pellets. We separated skulls and mandibles from pellet matter using forceps, dissecting needle, and water (Marti et al. 2007). We identified prey to species when possible, including northern pocket gopher (*Thomomys talpoides*), red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*) and long-tailed weasel (*Mustela frenata*). We combined species from the genera *Myodes*, *Microtus* and *Phenacomys* combined into a "vole" category, *Peromyscus* and *Zapus* combined into a "mice" category, and *Tamius* species into a "chipmunk" category. We used tooth type and mandibular tooth-row length for the majority of identification to genera (Chomko 1990). For intact specimens of rodents, shrews, and weasels, we measured greatest skull length and mandible length (Elbroch 2006) to help identify species. We calculated total number of prey items identified, percentage of the diet by frequency, and percentage of diet by biomass. To estimate biomass, we used average species weights from Franklin (1989).

We conducted mark-recapture small mammal trapping at a sub-sample of known and suspected nesting territories during August and September each year. We selected one meadow site as close to the nest as possible and one forest site that was representative of the forest type near the nest. We used a 50 m square grid, placing 25 traps at a 10 m interval in each site. Over a 72 hr period we checked traps at dawn and dusk. We made an effort to identify captured animals to species, noted sex and weight, and individually color marked using non-toxic markers (Pauli et al. 2004). We calculated populations for different groups (chipmunks, mice, and voles) with Lincoln-Peterson estimates using the Chapman's modification of the estimation of animal abundance and related parameters (Seber 1982).

We surveyed for pocket gopher abundance following van Ripper et al. (2013). We digitized all meadows within 500 m of known nests and randomly selected three (when available) for 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 mound visible within 10 m of the transect. 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.

Tagging & Tracking

We captured Great Gray Owls and outfitted them with either a VHF transmitter, a store-on-board GPS transmitter, or a remote-downloadable GPS data-logger with affixed VHF transmitter. We mainly used backpack-style attachments (GPS and VHF) and one tail mount attachment (VHF). We originally designed this project to utilize solar-powered satellite GPS transmitters but did not pursue that option after speaking with the manufacturers and other researchers utilizing solar-powered transmitters on owls, because feathers cover the solar panels. We custom-made store-on-board and remote-download data-loggers for this study that were pre-set to gather GPS locations once or twice daily for ca. six months. VHF transmitters (Advanced Telemetry Systems and Holohil Systems, Ltd) had a typical lifespan of ca. two years. Backpack-style transmitters weighed less than 3% of the owl's body mass (18-22 g) and the tail mount transmitter weighed 6 g. We fit GPS units on females only due to the greater mass of both the transmitters (30 g) and the females (range 1210-1550 g).

We used bal-chatri traps, bow-nets (Bloom et al. 2007), hand nets, pan traps, and mist nets with mice, sparrows, gerbils, or a raven decoy to capture owls. Trapping with prey-baited traps occurred year-round and the raven decoy was only used for difficult recaptures post-fledging (Bull and Henjum 1988). Fledglings captures took place in 2015 within one week of fledging using a net on an extendable pole and were leg tagged only (no transmitters) because of their small size at fledging. We banded owls with a USGS and custom-made blue, yellow, or orange plastic alphanumeric leg flags. We used blue bands on all adults, yellow leg bands on the 2014 cohort, and orange on the 2015 cohort.

For all marked owls, we took standard ornithological measurements of each individual and collected a blood sample for later genetic analysis. Sex was determined using a small portion of the blood sample (Zoogen DNA Services, Davis, California) and age was determined based on molt (Suopajarvi and Suopajarvi 1994).

We attempted to relocate each marked owl ≥1 weekly throughout the study. We recorded relocations obtained via homing techniques within 30 m of the owl without disturbing it. GPS data were gathered from transmitters either remotely via a wireless connection with a laptop or by recapturing the owl and removing the transmitter. We did not replace any removed GPS transmitter due to the difficulty of recaptures. If marked owls could not be located, we searched the entire study area on foot, by vehicles, and via fixed-winged aircraft when possible.

Habitat Use

We created both minimum convex polygons (MCP) and kernel density estimates (KDE) for each owl using ArcMap 10.3 (ESRI, Redlands, CA) and geospatial modeling environment (GME,

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Beyer 2004). We calculated MCPs and KDEs for annual ranges, summer ranges (1 May – 31 Aug), and winter ranges (1 Dec – 31 Jan) for individuals. We removed all locations from incubating females when they were on the nest prior to analysis. If individuals had the same nesting status in consecutive years, we pooled the data. We used 1 Dec – 31 Jan to represent winter range because we were interested in owl movements during the period of deepest snow depths across the study area. We compared age, gender and breeding status for differences in MCPs and KDEs.

We used the National Land Cover Datasets (NLCD) 2011 land cover product accessed from www.mrlc.gov to extract land cover use within the KDEs to estimate land use by breeding owls and for owl winter range. We created 50%, 75%, 90%, and 95% KDE estimates for all owls during the summer as well as winter. Using mean inter-nest distance and general knowledge of regular owl movements, we determined that 75% KDEs were the most appropriate measure of territory size of actively breeding owls. We re-classified the NLCD into seven categories of land cover; conifer forest, deciduous forest, riparian forest, meadows, developed, agriculture, and water/ice/rock and extracted the percentage of land cover types within the 75% KDE for actively breeding owls during the summer to estimate land cover within active territories.

We extracted the same reclassified land cover types within the 75% KDEs for owls with GPS transmitters during the winter. Low sample sizes from VHF marked birds in the winter because of the restricted time period precluded the creation of individual KDEs for VHF marked owls. Therefore, we created a population-level winter KDE using VHF marked owls and extracted land cover percentages within that KDE for comparison.

Habitat Modeling

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Habitat modeling was completed with the help of Matt Hayes from Lone Pine Analytics, LLC. We investigated several covariates to include in a resource selection model to predict breeding and winter habitat, including land cover type, elevation, slope, aspect, distance to roads, distance to meadows, total vegetation height (as a proxy for stand age), and canopy cover. All raster covariates were resampled to thirty meters and projected in UTM zone 12N NAD 83. Elevation was measured and slope and aspect were calculated from a 30 m digital elevation model created by USGS and accessed from the NRCS Data Gateway web service (https://gdg.sc.egov.usda.gov/). Aspect was transformed into a TRASP (transformation of aspect) index, which is a circular transformation where a value of zero is an area on north/northeast slopes (coolest and wettest orientation in northern latitudes) and a value of 1 is an area on southerly slopes (Roberts & Cooper 1989). A distance-to-road layer was created from a statewide Wyoming Department of Transportation road shapefile, which included numbered Forest Service roads. This layer shows the distance to the nearest road for the center of each 30 m cell. Land cover was reclassified, several ways, using the NLCD layer. Distance to meadow was created by reclassifying the NLCD land cover data into a meadow/no meadow classification and calculating the shortest distance for each cell to a cell of the reclassified meadow. We reclassified the NLCD on two scales based on biological relevance to owls. First, we reclassified the NLCD into seven categories as described above and second, we created a forest/no forest layer. Vegetation height and percent of tree canopy cover were both taken from the Landfire data products accessed at http://landfire.cr.usgs.gov/. These metrics provide a measure of the height of vegetation in a pixel as well as the percent of the canopy, which is from trees.

We created breeding habitat models using the actual used relocations from all ≥2 yr old

owls from 1 May – August 31, excluding any relocations of incubating females (all points were

combined, forming a population-level model). We created a set of "available" points to compare

with owl relocation points (i.e., "used" points). To create the available points, we randomly

selected 5x the number of used points in a 25 km buffer outside of the 75% KDE created from the

known used points. This insured that we were not sampling available points within our KDE.

After running the global model, we ran all possible combinations of that model because it is

realistic that any subset of that model would be biologically relevant and meaningful. We ranked

the models using AICc and used the top model as our best model. We calculated odds ratios and

coefficients from this final model.

We also created models of winter habitat. Because we were interested in assessing winter

habitat during peak snow depths, we reduced the total relocation dataset to 15 December – 31

January, which resulted in a relatively small sample size. Because we had too few "Used" locations

during this time period, we created 90% KDE home ranges for winter range using all owls to

create a population level model. Used points were sampled randomly within this KDE and

available points were, again, sampled within a 25 km buffer around the KDE at a ratio of 1:5 for

used:available. We ran all possible model permutations because it is realistic that any subset of

that model would be biologically relevant and meaningful. We ranked the models using AICc and

used the top model as our best model. We calculated odds ratios and coefficients from this final

model.

For all models we ran a 10-fold cross validation and reported the cross validation error.

Final models for both seasons were predicted spatially at a resolution of 30 m for use in

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subsequent work and publications. All data were processed in Program R (R Core Team 2015) utilizing various packages. All models were binomial logistic regressions.

Great Gray Owls typically need large stands of contiguous, suitable habitat. Modeling habitats creates an index of habitat "value" for each 30 m cell, but unless there is sufficient habitat surrounding that cell, then the habitat is not actually available for nesting. We created a measure to help account for this. We created a layer using, conservatively, the top 10% of the predictive breeding model and eliminated any areas not within the top predicted 10%. We then calculated the number of cells within a 500 m radius that also occurred within the top 10% of the model. Each cell then had a value of all the cells within a typical owl territory size with predicted habitat with a maximum of 901 cells. We binned the resulting layer into quartiles, removed any cells with less than 25% suitable habitat within 500 m and created a predictive layer incorporating patch size.

RESULTS

Call-back Surveys

We surveyed 558 individual locations in 2013 for nighttime call-back detections, re-surveyed 158 of those locations once and resurveyed eight twice, for a total of 724 surveys. In 2014, we surveyed 557 unique locations and re-surveyed 186 of those once and 31 twice. In 2015, we surveyed 337 locations and resurveyed 72 of those once. It appeared that Great Gray Owls reduced calling towards the last few days of the survey period in 2013 (13 March – 26 April), so we altered the calling period to 18 February - 14 April in 2014. However, we did not detect the first calling Great Gray Owl until 3 March 2014, so we again altered the calling period to begin 3 March and ceased surveys 9 April in 2015 due to a sharp decline in detections that week.

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Because there were multiple survey crews out each night, we had a total of 101 survey

nights in 2013, 77 survey nights in 2014, and 53 survey nights in 2015. Total time spent surveying

was 272 hr 1 min in 2013, 286 hr 12 min in 2014, and 183 hr 57 min in 2015. Using a 300 m

detection radius, we surveyed a total of 120.8, 112.6, and 77.8 km^2 in each year from 2013-2015.

Combined, we surveyed a total of 207 km^2 of forested habitat (Figure 1).

To tally total number of detections, we first removed all possible duplicate detections of the

same individual from the data by examining both field notes and mapped calling locations. After

removal of those data, we tallied a total of 288, 129, and 263 individual owl detections from seven

species in 2013-2015, respectively (Figure 2). By year, we encountered an average of 2.96, 2.43,

and 4.96 owls/survey night from 2013-2015, respectively. By time, we encountered 1 owl every

56.7, 133.1, and 42.0 min in 2013-2015, respectively. The owl species encountered most

frequently across years was Great Horned Owl (n = 217), followed by Great Gray Owl (n = 159),

Boreal Owl (*Aegolius funereus*, n = 124), Northern Saw-whet Owl (*Aegolius acadicus*, n = 121),

Northern Pygmy Owl (*Glaucidium gnoma*, n = 24), Long-eared Owl (*Asio otis*, n = 13) and Barred
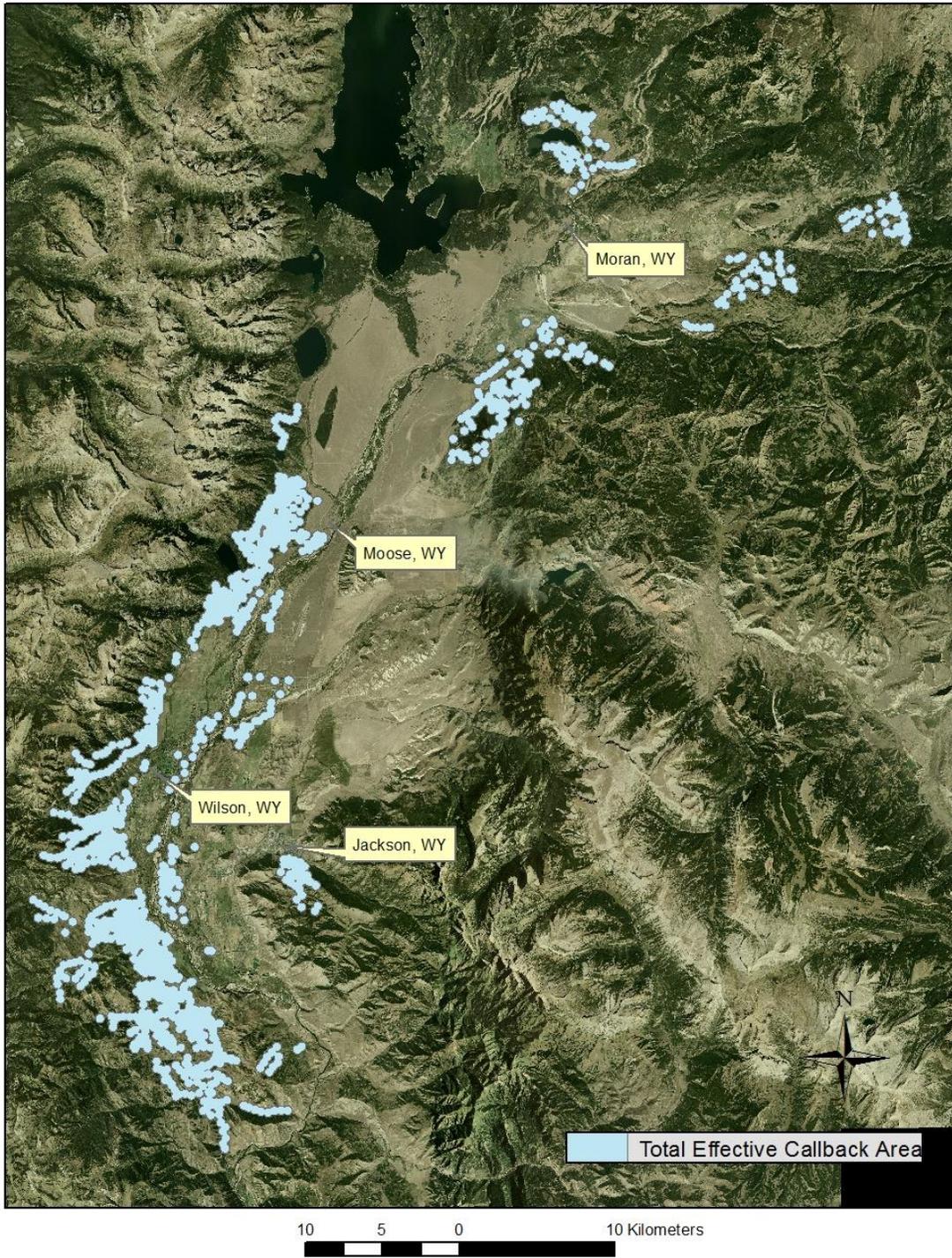
Owl (*Strix varia*, n = 2).

Figure 1. Total area effectively surveyed for forest owls in Jackson Hole, Wyoming (2013-2015) using nighttime call-back technique and a 300 m detection radius.
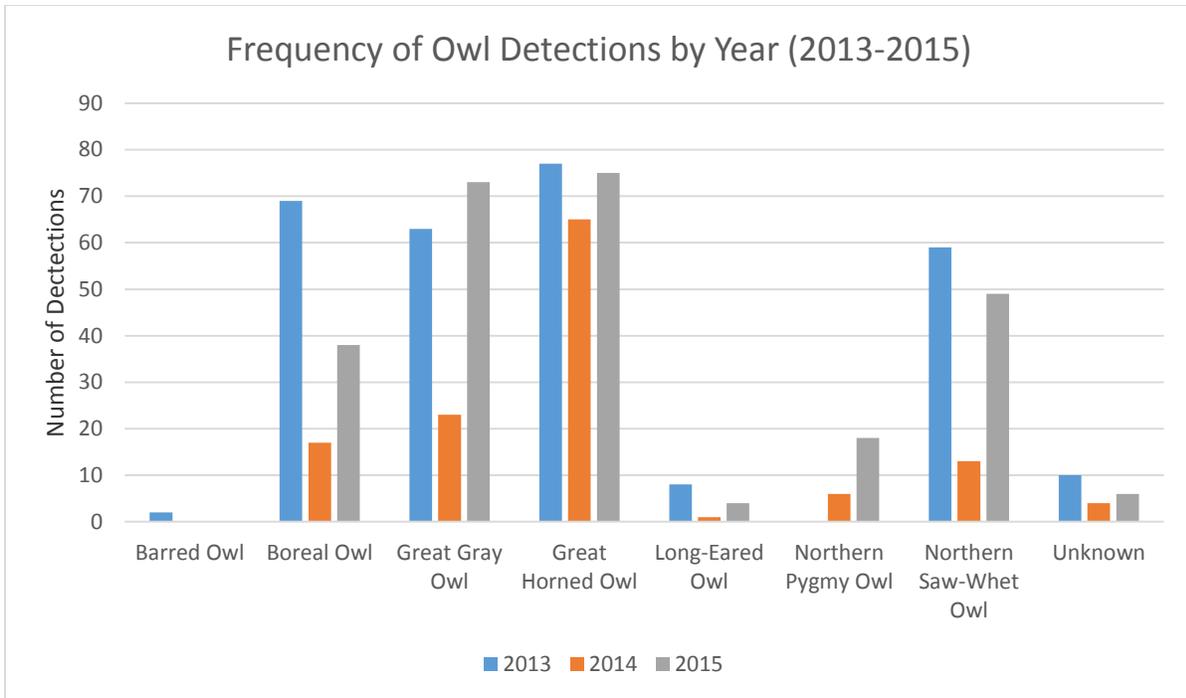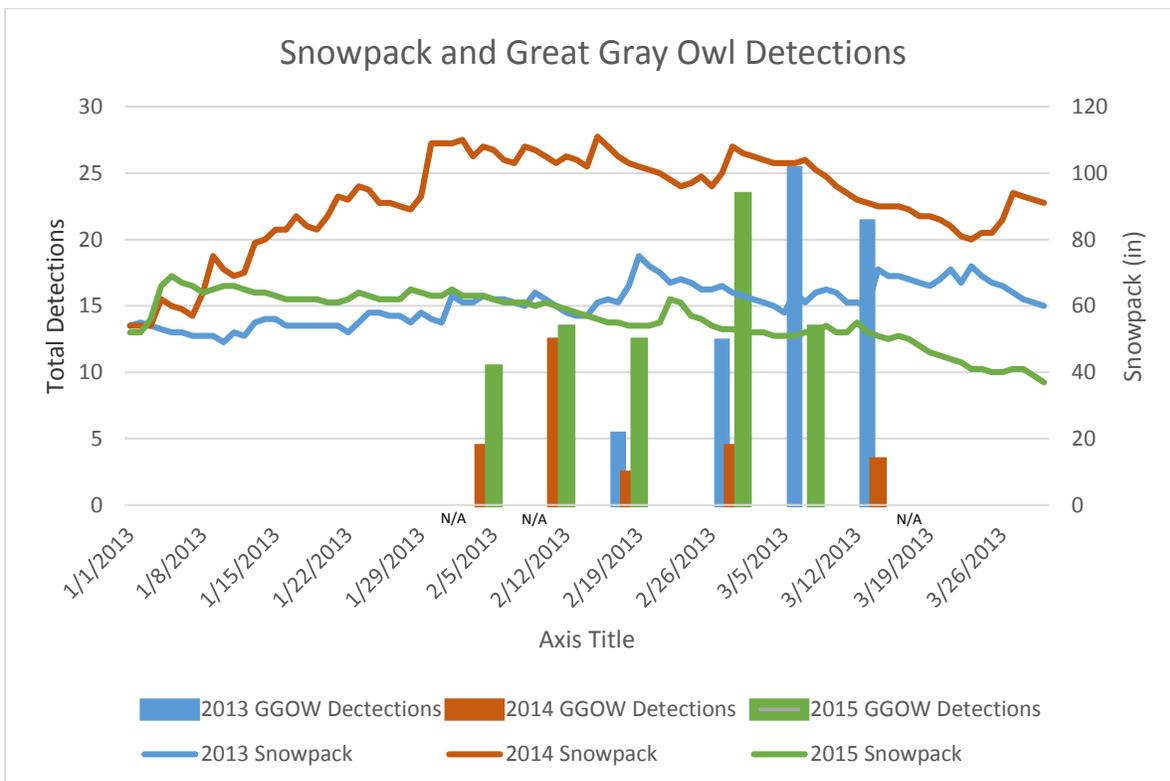
Figure 2. Frequency of owl detections in Jackson Hole, WY by year and species.

Figure 3. Frequency of Great Gray Owl detections by week and daily snowpack levels within the study area.

We had significantly fewer Great Gray Owl detections in 2014 (avg. = 4.2 detections/week) compared to both 2013 and 2015 (15.8 and 14.2 detections/wk, respectively, p = 0.017). Snowpack in 2014 was also significantly greater in 2014 than 2013 or 2015 (Figure 3, p < 0.001). During the survey period, average snowpack at the Phillips Ridge Snotel site was 1.61 m in 2013, 2.59 m in 2014, and 1.41 m in 2015 (USDA 2015). We detected 35 Great Gray Owl territories across years using a minimum of three male detections and/or one female detection within 500 m of each other.

Call-back Timing

We found that Great Gray Owl and Northern Saw Whet Owl detections did not differ from expected over the course of the evening (measured between 19:00 and 02:00 h). Boreal Owls, however, called more than expected during the early evening (p = 0.019) and Great Horned Owls had higher call rates earlier and later in the evening with a lull from 21:00-23:00h (p = 0.032; Figure 4). There was large variation in number and timing of detections among years for Great Gray Owls (Figure 2, 3). We detected many more Great Gray Owls in 2013 (n = 63) and 2015 (n = 73) when compared with 2014 (n = 25). Detections peaked in early April in 2013, mid-March in 2014 and were fairly constant from March-mid-April in 2015. In all years, there were few detections prior to March or after mid-April.

Detectability

To begin estimating Great Gray Owl call-back detectability, we examined how often owls were detected within known and estimated territories (based on call-back criterion). Within all

territories, we detected owls on the first survey round in 73, 20, and 50% of known territories in 2013-2015, respectively. Within territories that were surveyed twice, we increased detection rates to 91, 31, and 82%, respectively. Restricting the analysis to only active territories (those with confirmed nests), we detected owls in 67, 22, and 47% of territories during our first survey and 67, 44, and 80% using multiple surveys, respectively across years.
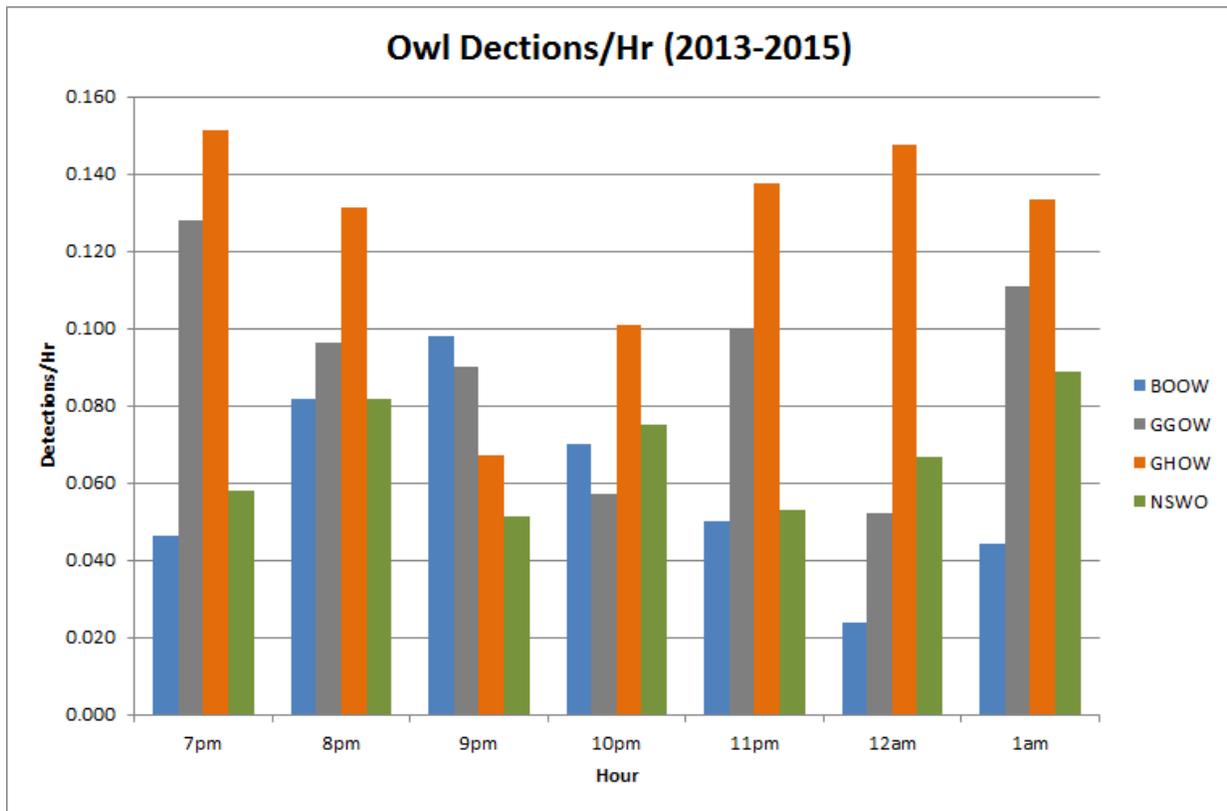

Figure 4. Hourly detection frequency of forest owls in Jackson Hole, 2013-2015.

Nesting Demographics

To calculate nesting density, the effective search areas must be known. For raptor species, standardized nest search efforts are not cost-effective and are not typically used. Therefore, we used our best efforts to record all of our tracks while in the field to determine the effective search

area. We first reduced all track data to the nesting season (May 1 – August 31) when we were actively searching for nests and fledglings. We then buffered each track location by 100 m. We dissolved the buffer boundaries and calculated the effective search areas by year, similar to the effective calling areas for nighttime detections. We effectively searched a total of 30.2, 63.9, and 30.6 km^2 in 2013-2015, respectively. Cumulatively, we searched a total of 88.1 km^2 over the three-year study period.

We found a total of 36 confirmed nests across three years. We also had four instances (2013 = 1, 2014 = 1, 2015 = 2) where we found fledgling Great Gray Owls but did not locate the nest. Including the instances when fledglings were located, we found four active territories in 2013, nine in 2014, and 24 in 2015. Nest success was 75%, 78%, and 83% in 2013-2015, respectively. Average fledging success was 1.5, 1.6, and 1.9 fledglings/nest across years, respectively. Incubation was initiated as early as April 7 and the latest we observed females incubating was June 11. Average fledge dates were June 18, June 27, and June 13 for 2013-2015, respectively.

Nesting Habitat

We found the majority of nests in lodgepole pine (n = 8), followed by Douglas fir (n = 5), subalpine fir (n = 5), aspen (n = 3), spruce spp (n = 2), and narrow-leaf cottonwood (n = 1). Ten nest sites were located in old stick nests, ten in broken trees (snags), three in growths caused by mistletoe, and one in an artificial nesting platform. All nests but three were located in the low-mid elevation coniferous forests surrounding the valley floor. The exceptions were three nests located within the Snake River riparian area.

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We measured nesting habitat both on-the-ground and via remote sensing. Using direct measurements at 17 of our 23 active nest sites, nest heights ranged from ca. 1.5 – 18 m, and nests in snags were significantly lower in than other nests (p <0.001). Mean slope of nests was 9.7 degrees (range 4-22) and most were located on a north-northwest aspect. Average canopy cover at the nest was 72.9% and did not vary between snag and stick/mistletoe nests. Average DBH of snag nest trees (74 cm) was greater than the average DBH of stick/mistletoe nest trees (36 cm; p = 0.017). We also measured the level of deterioration of nest trees on a scale of 1-5 (Wu et al. 2015), and found that snags had an average level of 4.2 while stick/mistletoe trees had an average level of 1.3. We found no difference between the canopy cover at nests sites than the average canopy cover within 50 m of the nest. Based on meadow criterion as defined by Wu (2015), we measured a mean distance from nest to meadow of 49 m (range 0-148).

We used the 2011 30 m NLCD to measure canopy cover and distance-to-edge for all nests. Because riparian habitat differs from the mixed coniferous forests surrounding the valley, we investigated those nests separately. For non-riparian nests, the mean canopy cover at nest sites was 67% (SD = 9.8, range = 45-81). Mean distance from the nest to meadow was 218 m (SD = 133, range 77-600 m). While sample size was limited (n = 3), nests within the Snake River bottom had a mean canopy cover of 40% (SD = 18, range = 24-61) and a mean distance to meadow of 75 m (SD = 66, range = 0-121). Forest nests had significantly more canopy cover (t = 3.96, p < 0.001) and were farther from the forest edge (t = 1.80, p = 0.043) than riparian nests. The mean elevation for nests was 2052 m (range = 1850-2404) and mean slope was 8.2% (range = 0.2 – 27.5). We found that the majority of nests were situated on north aspects (50%), followed by east (33%), south (12.5%), and west (0.5%).

Using the remote sensing data, we investigated habitat variable influence on nesting success only for 2015 because most nesting data existed for that year. Nests in snags had lower success compared with stick nests and mistletoe (F = 4.49, p = 0.025). We found no difference between successful and failed nests for canopy cover or distance-to-edge. We did find that nest site elevation was positively-correlated with fledge date in 2015 (P = 0.031). Likewise, fledge date was also correlated to latitude (p = 0.028) because of a strong correlation between latitude and elevation (p = 0.003). However, these results were strongly influenced by one high altitude nest (2404 m) in the northern portion of the study area (Rosie's Ridge). After removing this outlier, fledge dates were correlated to latitude (p = 0.007) but not elevation (P = 0.085).

Nesting Density

We identified territories when multiple detections of males and/or a female detection was recorded within a 500 m radius. In known, active territories, Great Gray Owls were rarely detected at the nest. More typically detections occurred within a 500 m radius of the nest and most often near the territorial boundary. Retrospectively investigating call detections and known, active territories, we found five nest sites at which night call detections did not identify a territory (i.e., no calling or fewer than three male detections). Combining all known territories and estimated territories from detections, we found a total of 40 occupied Great Gray Owl territories within the areas we surveyed and searched.

We surveyed a total of 114.2 km^2 of forested habitat among years for calling owls using the nighttime call-back technique. Using the known and estimated territories, we found a territory density for Great Gray Owls of one occupied territory/3.57 km^2. We effectively searched 54.0 km^2

of forested habitat for nests within the southern portion of our study area. Within that area, we located 20 known, active nest sites, giving a nesting density of one nest/2.7 km². We found an average nearest neighbor distance of 914 m. We tested for a clumped distribution of active territories using Ripley's K-function in ArcMap (Fisher et al. 2007) with 99 permutations for a confidence interval and found no evidence of clustering within our study area.

Using our breeding season habitat models, we calculated the percentage of cells ≥ the top 10% surrounding each cell that is ≥ the top 10% predicted area within a 500 m radius surrounding that cell (see below). So, we effectively reduced our model to only include cells that had at least 50% of the surrounding cells within 500 m that were also in the top predicted habitat to define areas that are available for breeding. This measure took into account that some cells of predicted habitat did not have much habitat surrounding them, and were therefore not likely available to owls for breeding. Using this measure, we estimated a total are of 279.43 km² within and directly surrounding the Jackson Hole Valley (excluding the east side of the Tetons and south of the Snake and Hoback Rivers) as potentially available for Great Gray nesting.

Nesting Platforms

We set up 24 nesting platforms during fall 2013 and an additional 18 in 2014. We found that Duracell UltraLithium batteries generally lasted up to one year. By the winter of 2014/15, three nesting platforms erected in 2013 had been discovered by Great Gray Owls. One of these nesting platforms was used by a Great Gray Owl pair in the 2015 breeding season. That pair successfully fledged three chicks. We saw no other species nesting in platforms but did detect red squirrels, pine martens and a variety of songbirds at platforms throughout the years.

Tagging & Tracking

Between 2013 and July of 2015, we captured a total of 71 individual Great Gray Owls, all of which we banded. We outfitted 33 Great Gray Owls with transmitters, deploying 19 VHF transmitters on juvenile, sub-adult and adult owls, and 13 GPS transmitters on adult owls (Table 1). We used blue color bands on owls captured as sub-adults or adults, yellow on 2014 fledglings, and orange on 2015 fledglings. Of the 33 transmitters we put out on Great Gray Owls, 14 are still transmitting. Eight of the units stopped transmitting (battery died), two of the transmitters fell off the birds, and we removed three of the GPS transmitters by recapturing the owls. We deployed four store-on-board GPS units in 2013, but we were unable to re-locate three of these owls to recover their units. Subsequently, we deployed only remote-download GPS so we would not have to recapture individuals. However, the expected lifespan of the transmitters was greater than the observed lifespan, so we had to recapture several owls in 2015 to recover the final data from the units. We were unable to recapture one owl with a dead transmitter and could not relocate another. Two owls with VHF transmitters are missing but it is assumed their transmitters are still functioning. During the course of our study, we gathered a total of 702 relocations from VHF marked birds and an additional 1,731 relocations from GPS marked owls.

Table 1. Transmitter deployment records for Great Gray Owls in Jackson Hole, WY from 2013-2015.

	Fledgling			Sub-Adult			Adult			TOTAL
	Band	VHF	GPS	Band	VHF	GPS	Band	VHF	GPS	
2013				1	2	2		3	2	10
2014		7			2			4	8*	21
2015	39							1	1	41
Total	39	7	0	1	4	2	0	8	11	72*

* includes one recapture and deployment on previously marked owl

We estimated breeding season home ranges for all sub-adult and adult owls for which we had sufficient data. We restricted the breeding season to 1 May – 31 August and separated owls by breeding status. For owls with multiple years of data, we combined movement data if the breeding status was the same among years, and separated years if the breeding status changed. We found that the average MCP estimate for breeding owls (n = 7 females, 3 males) was 1.53 km^2 (range = 0.18-4.47, SD = 1.39) and non-breeding owls (n = 7) was 14.41 km^2 (range = 1.22-76.69, SD = 27.60). However, one non-breeding adult female exhibited a very atypical home range, inflating the average. Her MCP was 76.69 km^2, while the next largest MCP was 8.4 km^2. Excluding her MCP, the average was 4.03 km^2 (SD = 2.48 km^2). We found (both with and without the atypical female), that MCPs for non-breeding owls was larger than breeders (p = 0.0084, W = 88.0). However, we found no difference in MCP size between breeding males (n = 3) and breeding females (n = 7; p = 0.58).

We also estimated KDEs for the owls during the breeding season. We used 50, 75, and 95% KDEs. Visual inspection of the data, confirmed by our field observations, nighttime call-back locations and re-locations, suggested that 75% KDEs (0.83 km^2, range = 0.18-1.96, SD = 0.59) are the most appropriate for estimating home range of owls in our study area. Based on a circular home range surrounding the nest, the average 75% KDE for breeding owls equals a 514 m radius around the nest, which corresponds to the typical call distance of territorial owls encountered during nighttime surveys, corroborating that using a 75% KDE is appropriate for this population. We found that the 75% KDEs for non-breeding owls (mean = 6.60 km^2, range = 2.43-60.87, SD = 20.78) was larger than breeding owls (p = 0.002, W = 93.0). Excluding the atypical non-breeding owl did not affect the difference. Using a 50% KDE to estimate core area for breeding owls, we

found a mean 50% KDE of 0.35 km^2 (range = 0.05-0.87, SD = 0.26). This equates to a core area within a 334 m circular area centered on the nest site.

Because we restricted the dates for wintering areas to the core winter times (Dec 15 – Jan 31), we had limited samples sizes of relocations and we could not create KDEs for individuals with VHF transmitters. Therefore, we created a population-level KDE of critical winter range using VHF marked owls in addition to individual KDEs for GPS marked owls. We found that the entire winter range (75% KDE) for Great Grays within our study area was 111.3 km^2 (95% KDE = 148.2 km^2). The individual 75% KDE estimates for the three wintering GPS-marked owls was 0.89, 2.0, and 5.7 km^2.

We measured the distance from the center of winter and summer ranges for all owls that we had multiple season data from (n = 15). The total mean distance for all owls moved between ranges was 12.2 km (range = 0.00 - 52.50). The mean distance moved for juvenile owls (n = 7) was 9.21 km, while adults (n = 8) moved an average of 14.8 km between winter and summer ranges. All but one owl had discrete winter and summer ranges, with winter ranges typically within the Snake River corridor. We found no differences in mean movements between adults and juveniles (p = 0.39). We did not re-locate two owls (a mated male and female) from the southern extent of our study area during the winter months. GPS relocations from the female in the fall suggest that they may have wintered further south (closer to Alpine, WY) than other owls in this study. We also marked several individuals during the winter months that could not be relocated in the summer, suggesting some owls are dispersing more widely.

Habitat Use

We measured habitat use of breeding owls and wintering owls by extracting habitat remote covariate data from within each owl's home range. We used the 75% KDE because we were not interested in assessing habitat use at the fringe (or infrequently used portions) of the territories. We used our reclassified 2011 NLCD layer to estimate percentages of habitat type with the home ranges. We found the highest percentage of habitat used within the breeding season was conifer forest, followed by meadow (Table 2). In the winter, owls used a much greater proportion of riparian forest and meadows. We did find that the average habitat percentages were different when comparing the population level winter KDE to individuals. However, the individual level is likely more representative of how owls are using the habitat on a fine scale.

Habitat Modeling

We found that reducing the categories within the land cover dataset to forest/non-forest significantly improved model fit of the breeding season models compared to the more inclusive land cover raster. Using forest/non-forest as our land cover covariate, the top model showed selection for treed habitat with greater height and canopy cover that was further from roads and had lower slope and elevation (Table 2, 3, Figure 5, 6, 7, 8).

Table 2. Percentage of land cover classes within the 75% KDE for Great Gray Owls during the breeding season in western Wyoming.

Land Cover	A3	A5	A7	A8	C3	C5	E4	E6	E7	Mean
water/Ice/Rock	0.0	0.0	0.0	0.0	0.0	11.4	0.0	0.0	0.0	1.3
Developed	0.0	0.0	0.0	0.0	3.2	1.5	0.0	0.0	0.0	0.5
Deciduous (Aspen) Forest	16.3	6.4	0.4	6.0	0.1	0.0	0.6	5.2	0.0	3.9
Conifer Forest	74.0	76.6	90.7	89.8	72.0	53.7	63.0	93.5	82.2	77.3
Mixed (Riparian) Forest	3.5	0.6	0.0	0.3	3.1	8.4	0.0	0.0	3.5	2.1
Meadow	6.2	16.4	9.0	4.0	21.6	25.1	36.4	1.3	14.3	14.9
Pasture/Crops	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 3. Percentage of land cover classes within the 75% KDE for Great Gray Owls during the winter in western Wyoming

Land Cover	E3	E4	E7	Mean GPS	Mean VHF
water/Ice/Rock	0.0	0.0	5.0	1.7	3.4
Developed	0.0	1.2	1.5	0.9	2.5
Deciduous (Aspen) Forest	0.0	0.0	0.1	0.0	2.5
Conifer Forest	0.0	1.4	9.8	3.7	34.6
Mixed (Riparian) Forest	50.9	68.2	27.9	49.0	18.7
Meadow	49.1	29.2	33.5	37.3	37.6
Pasture/Crops	0.0	0.0	22.1	7.4	0.8

Table 4. Top nine breeding habitat models and selection criteria.

Intercept	Aspect	Distance to Road	Elevation	Vegetation Height	Distance to Meadow	% Canopy Cover	Slope	df	logLik	AICc	delta	weight
-3.254			-0.814	0.203		0.524	-0.906	6	-1938.13	3888.3	0	0.322
-3.252	0.033		-0.813	0.202		0.526	-0.906	7	-1937.80	3889.6	1.33	0.165
-3.259			-0.819	0.190	-0.034	0.545	-0.907	7	-1937.91	3889.8	1.55	0.148
-3.256		-0.013	-0.810	0.202		0.523	-0.903	7	-1938.10	3890.2	1.95	0.122
-3.257	0.032		-0.818	0.190	-0.033	0.546	-0.908	8	-1937.59	3891.2	2.93	0.075
-3.254	0.033	-0.012	-0.810	0.201		0.525	-0.903	8	-1937.77	3891.6	3.29	0.062
-3.261		-0.012	-0.815	0.190	-0.034	0.544	-0.905	8	-1937.88	3891.8	3.51	0.056
-3.259	0.032	-0.011	-0.814	0.189	-0.032	0.545	-0.905	9	-1937.57	3893.2	4.89	0.028
-3.315			-0.819		-0.078	0.586	-0.902	6	-1942.06	3896.1	7.86	0.006

Table 5. Top breeding season model coefficient estimates.

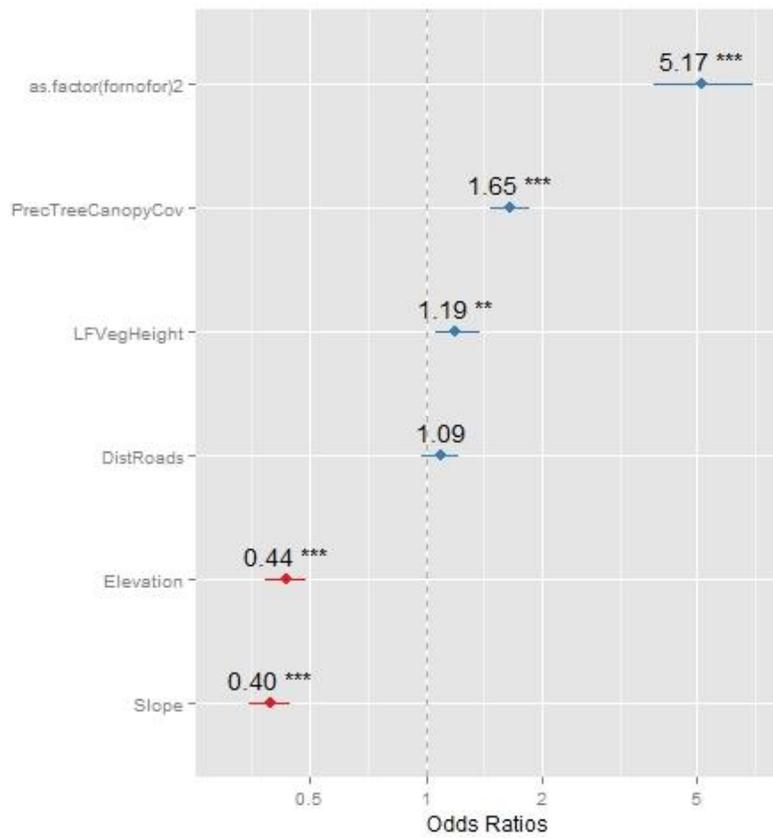|	Estimate	Std. Error	z value	Pr(>|z|)	Significance Level α
Intercept	-3.25376	0.11889	-27.367	< 2e-16	0.001
Forest	1.63329	0.14667	11.136	< 2e-16	0.001
Elevation	-0.81355	0.05704	-14.262	< 2e-16	0.001
Veg Height	0.20263	0.06915	2.93	0.00339	0.01
% Canopy Cover	0.52354	0.05751	9.103	< 2e-16	0.001
Slope	-0.90548	0.06065	-14.93	< 2e-16	0.001

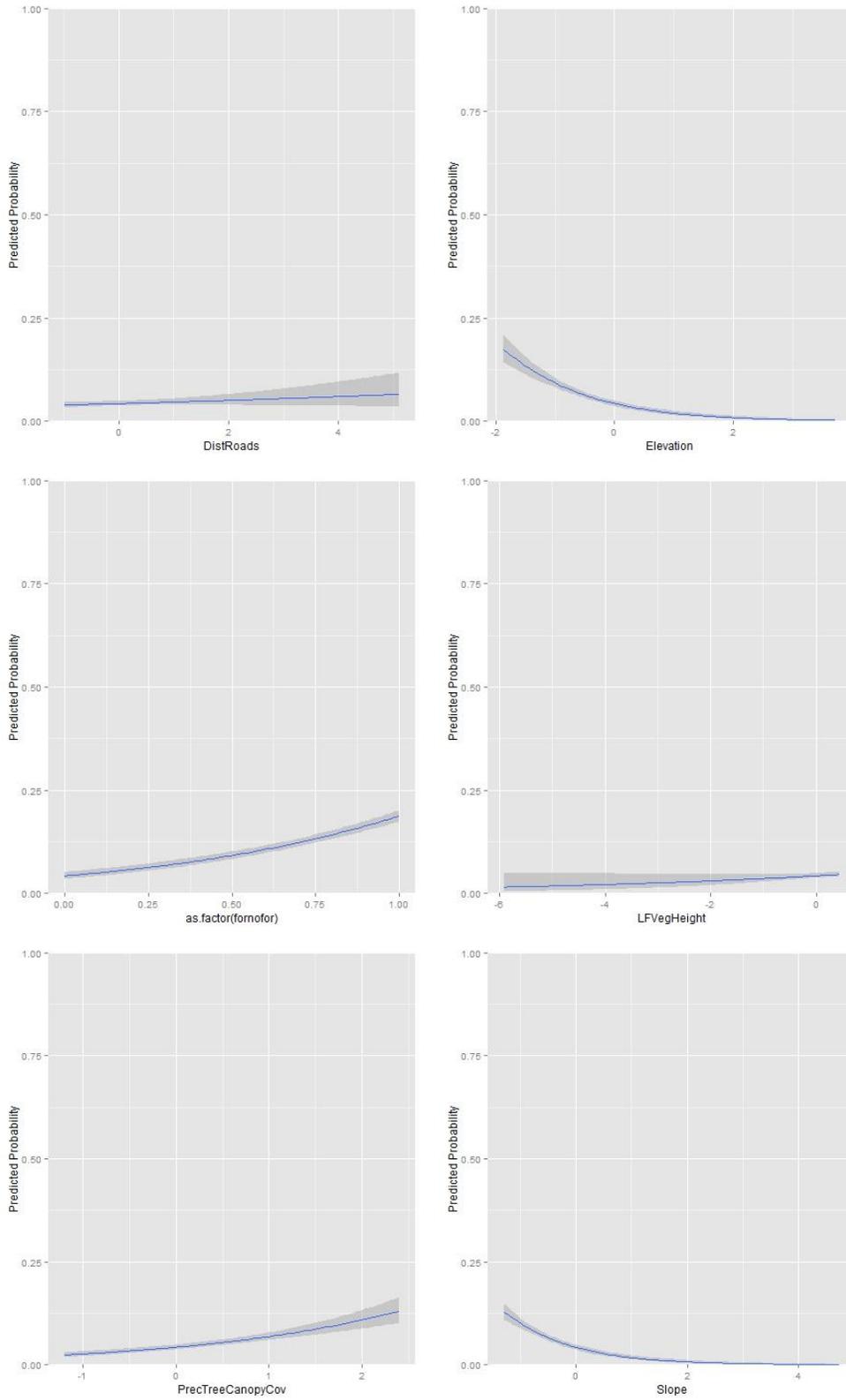*Figure 5. Breeding season model coefficient selection ratios.*

Figure 6. Breeding season model coefficient predicted probabilities.
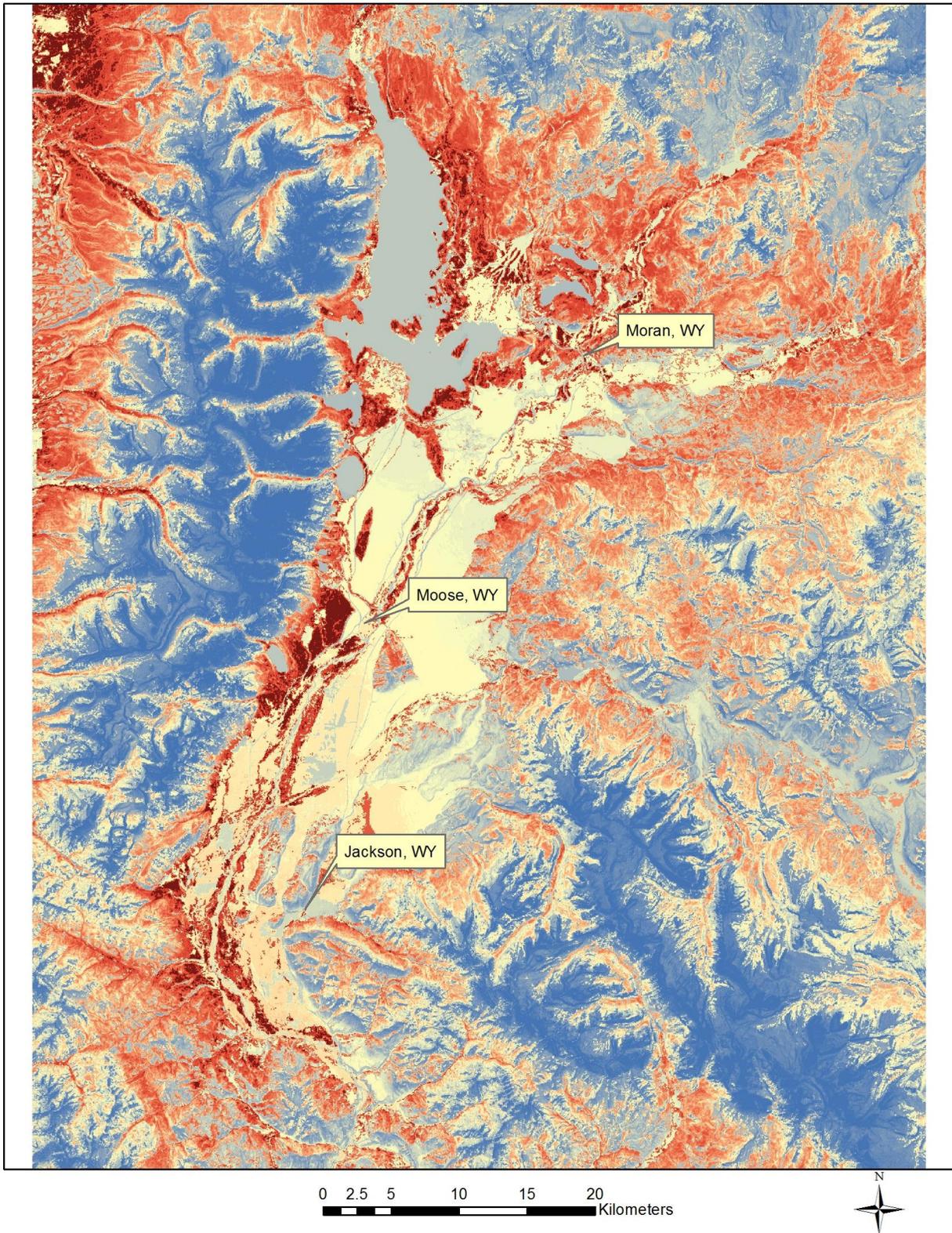
Figure 7. Great Gray Owl breeding resource selection model. Blue indicates areas with low probability of use and red indicates high probability of use. Darkest red corresponds to the top 5% of the model.
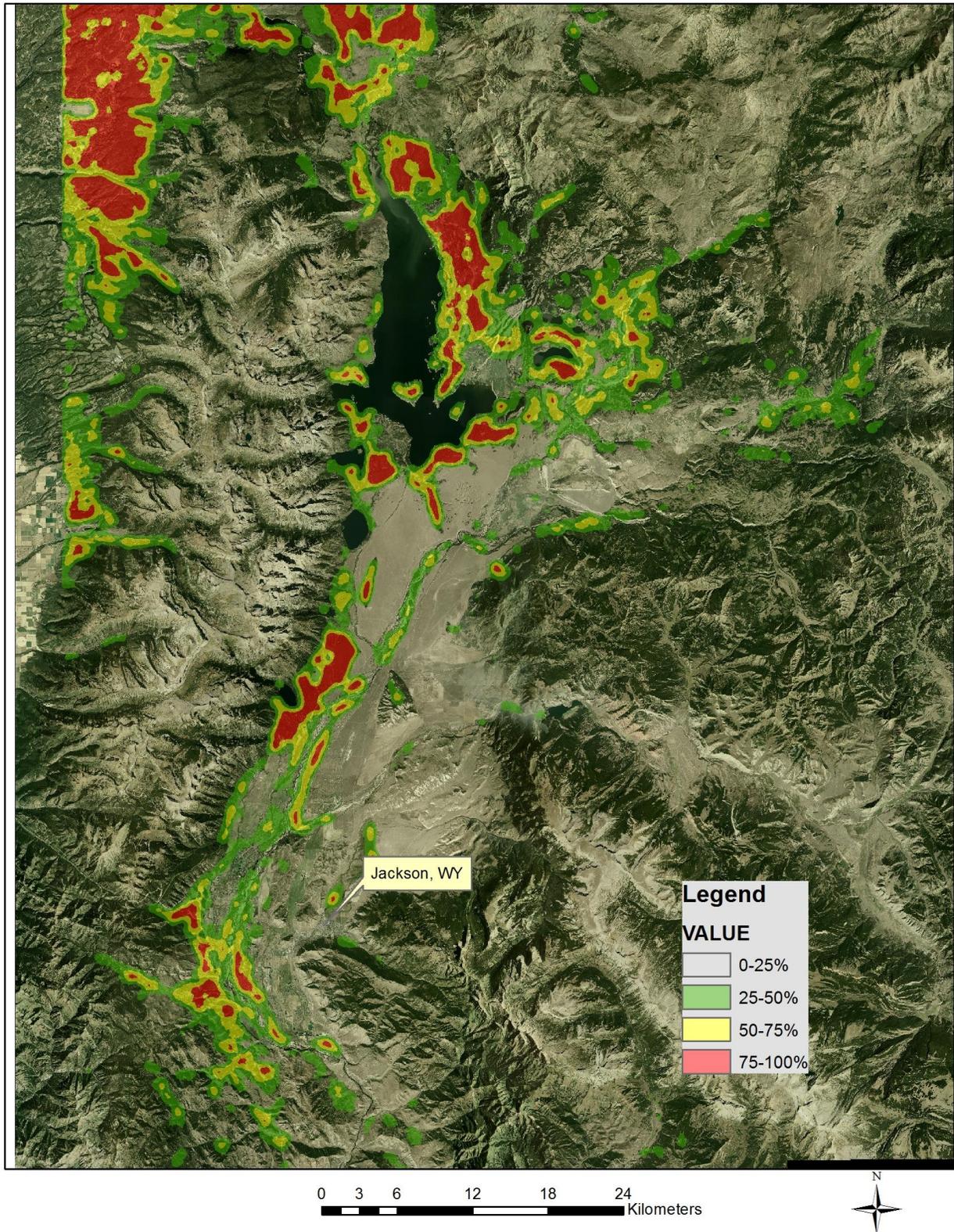
Figure 8. Areas within the top 10% of the breeding season RSF models with the percentage of neighboring cells within 500 m that also are within the top 10% of predicted habitat.

We also created a model of critical winter habitat for Great Gray Owls within Jackson Hole. For this model, we used our second-order level land cover ranking, which separated different forest types and meadows. We chose this level because our field observations of winter movements suggested a differentiation between conifer and riparian forests may be an important factor for winter range. Contrary to the breeding habitat models, the critical winter resource selection model predicted that owls had an affinity for nearer proximity to roads, lower elevation, and areas closer to meadows (Tables 6, 7, Figure 9). There was essentially no critical winter habitat predicted in Jackson Hole north of the map extent in Figure 9.

Table 6. Top nine critical winter habitat models and selection criteria for Great Gray Owls in western Wyoming.

Intercept	Aspect	Distance to Road	Elevation	Veg Height	Distance to Meadow	% Canopy Cover	Slope	df	logLik	AICc	delta	weight
-1.833		-1.208	-2.64		0.140		-0.180	9	-775.267	1568.6	0	0.152
-1.641		-1.194	-2.64	0.093	0.162		-0.185	10	-774.74	1569.6	0.97	0.094
-1.785		-1.216	-2.782		0.148			8	-777.036	1570.1	1.52	0.071
-1.785		-1.205	-2.643		0.129	0.064	-0.192	10	-775.136	1570.4	1.76	0.063
-1.832	0.0060	-1.207	-2.64		0.140		-0.180	10	-775.263	1570.6	2.01	0.056
-1.731		-1.137	-2.611				-0.189	8	-777.377	1570.8	2.2	0.05
-1.874		-1.188	-2.656		0.171	0.239	-0.221	6	-779.625	1571.3	2.67	0.04
-1.614		-1.205	-2.786	0.083	0.168			9	-776.617	1571.3	2.7	0.039
-1.619		-1.193	-2.642	0.088	0.153	0.045	-0.194	11	-774.679	1571.5	2.86	0.036
-1.65		-1.146	-2.621			0.135	-0.214	9	-776.727	1571.5	2.92	0.035
-1.64	0.0059	-1.194	-2.64	0.093	0.162		-0.185	11	-774.736	1571.6	2.98	0.034

Table 7. Winter model coefficient estimates.

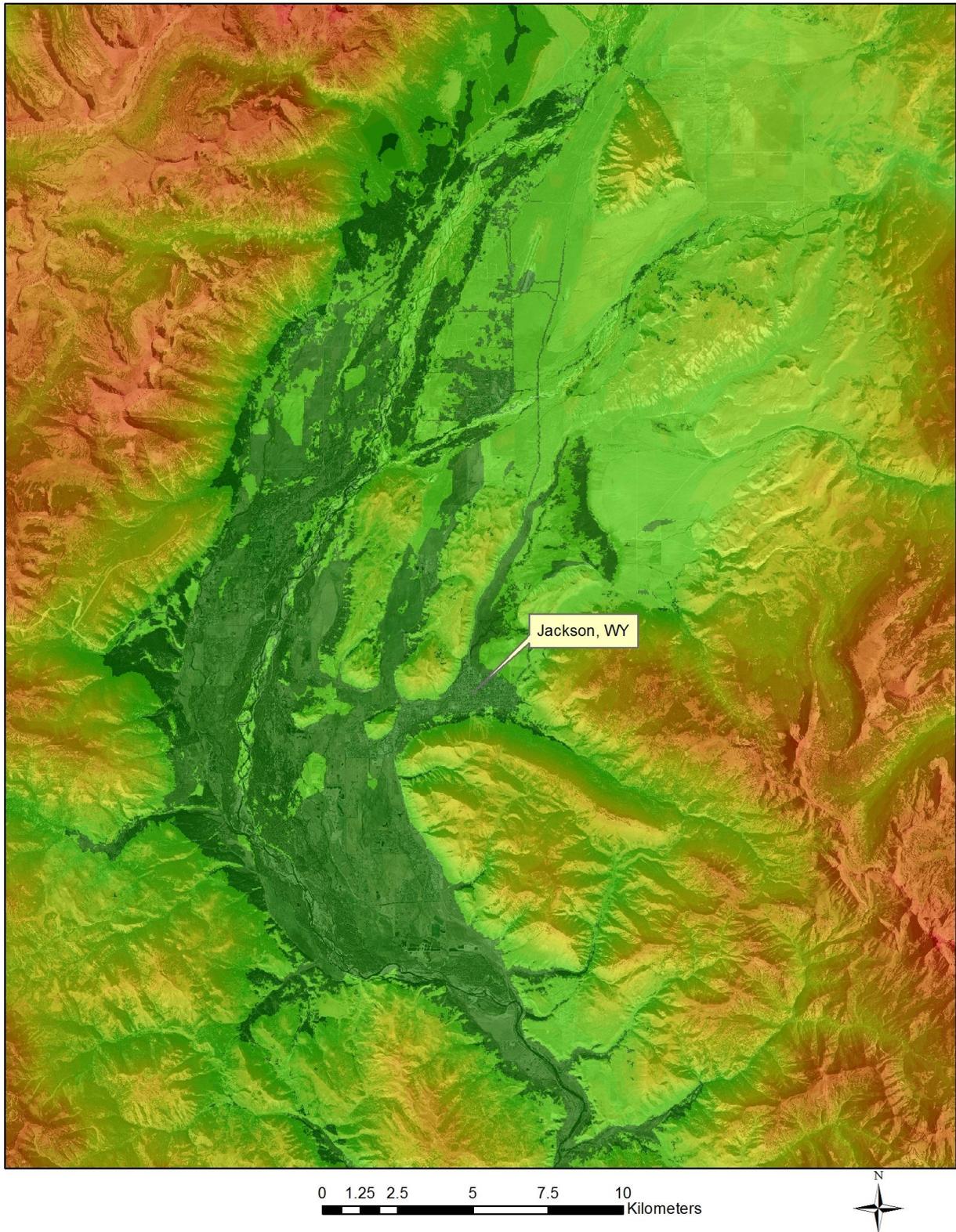|	Estimate	Std. Error	z value	Pr(>|z|)	α level
(Intercept)	-1.833	0.238	-7.690	1.47E-14	0.001
Conifer Forest	0.330	0.236	1.395	0.163	
Deciduous Forest	0.198	0.296	0.669	0.5038	
Riparian Forest	1.848	2.071	0.892	0.3722	
Meadow	-0.353	0.211	-1.674	0.0941	0.1
DistRoads	-1.208	0.188	-6.432	1.26E-10	0.001
Elevation	-2.640	0.209	-12.611	< 2e-16	0.001
MeadDis	0.140	0.068	2.055	0.0399	0.05
Slope	-0.180	0.095	-1.884	0.0595	0.1

Figure 9. Great Gray Owl critical winter resource selection model. Red indicates areas with low probability of use and green indicates high probability of use. Darkest green corresponds to the top 7.5% of the model.
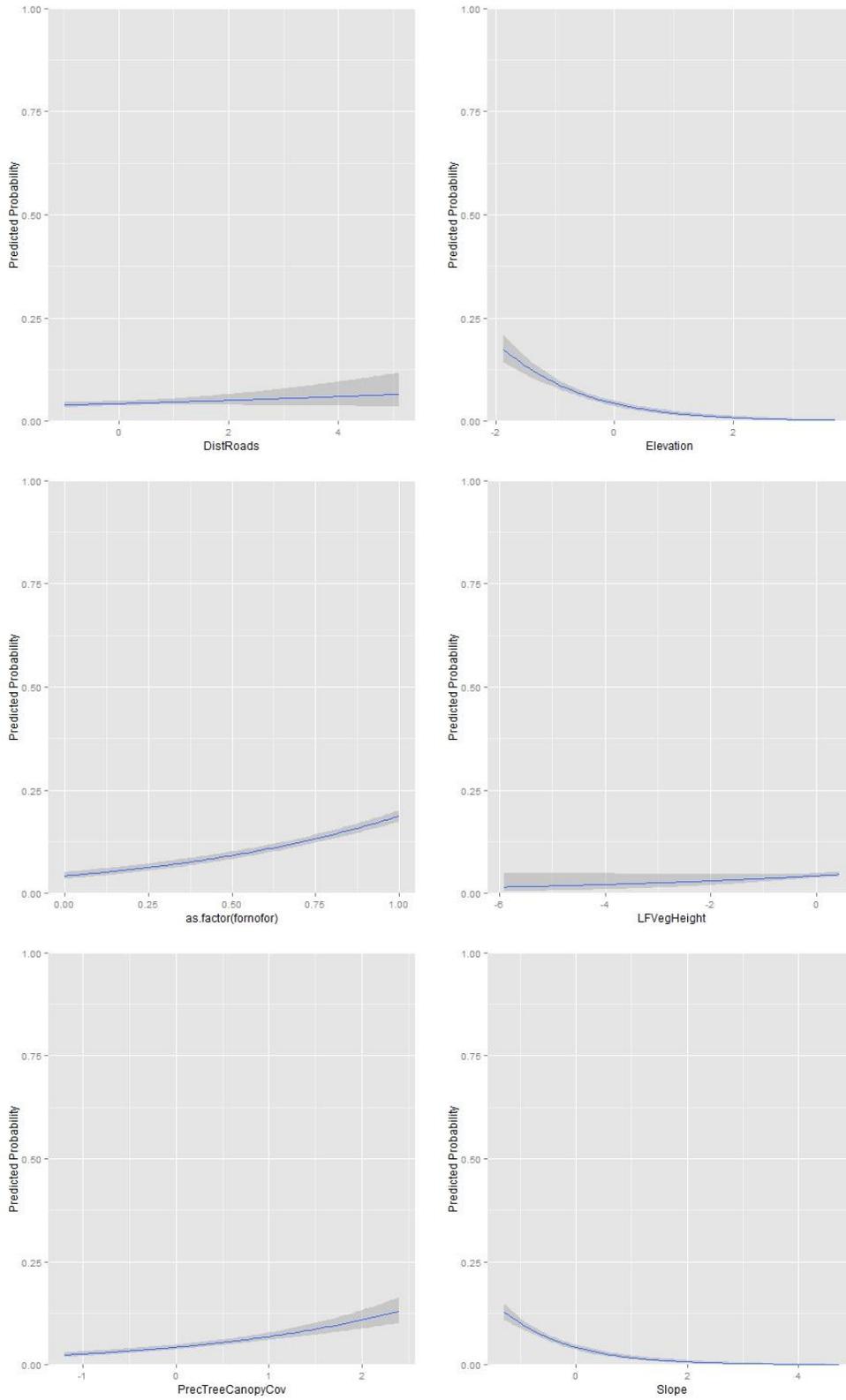
Figure 10. Winter model coefficient selection ratios and predicted probabilities.

Prey Sampling

POCKET GOPHER SURVEYS

We completed pocket gopher surveys in 2014 and 2015 at all known nesting territories. We estimated gopher abundance in ten territories in 2014 and 21 territories in 2015. We surveyed an average of 4974 m^2/territory (249 m survey length) in 2014 and 3548 m^2/territory (177 m length) in 2015. Using only fresh mounds to estimate abundance, we found significantly fewer gophers (mean = 0.00000230 mounds/m^2) in 2014 than 2015 (mean = 0.00000442 mounds/m^2; t = 1.76, p = 0.044). Based on linear transect distance and not area (see van Ripper et al. 2013), we found 0.013 and 0.028 mounds/m in 2014 and 2015, respectively. Failed territories had fewer pocket gophers than successful territories (t = -3.02, p = 0.003), but we did not detect a relationship between gopher abundance and number of fledglings at successful nests (F = 1.03, p = 0.400).

SMALL MAMMAL TRAPPING

We conducted small mammal trapping at 14 different territories and suspected territories from 2013-2015. We trapped at nine territories for at least two years and five of those all three years. We encountered several instances in which suspected territories were not confirmed or the territory was first located in 2015. Each site was sampled at both a forest and meadow location for three consecutive morning and evening sessions.

The most abundant species encountered were chipmunks (*Neotamias* spp), followed by deer mice (*Peromyscus maniculatus*), southern red-backed vole (*Clethrionomys gapperi*), dwarf shrew (*Sorex nanus*), long-tailed vole (*Microtus longicaudus*), western jumping mouse (*Zapus princeps*), northern

flying squirrel (*Glaucomys sabrinus*), and pocket gopher (*Geomys bursarius)*. We used the data from all territories sampled with multiple years to investigate annual differences in abundance of each group by forest or meadow site. We combined small mammals into a vole, chipmunk, and mice categories and excluded other species encountered due to low sample sizes.

We found no significant differences among years for any small mammal group in either forest or meadow sites (all p > 0.05). There is some evidence to suggest there were more chipmunks in meadows during 2015 than the previous years (p = 0.096). We also investigated the total territorial small mammal abundance with productivity by combining all small mammal estimates for a given territory, testing for influence on productivity for that year using an ANOVA test, and we found that total small mammal abundance did not differ by the number of fledglings produced (p = 0.324). Nor could successful or failed nests be predicted by the total small mammal abundance using a binary logistic regression (p = 0.277).

PELLETS

We collected 86 Great Gray Owl pellets in 20 territories throughout the study area from May 2013 to July 2015. Those pellets contained 157 prey items with a mean of 1.8 prey items (defined by at least one skull or mandible) per pellet. The number of skulls/mandibles that indicated a separate individual ranged from zero to five per pellet. Since skull or lower jaw bones had to be present for identification, decapitated prey items were not accounted for.

We found that Great Gray Owl diet consisted entirely of rodents except for two shrews and one mustelid. The species identified were *Thomomys talpoides* (Northern pocket gopher), *Myodes gapperi* (Southern red-backed vole), voles of the genera *Microtus* and *Phenacomys* (Montane vole,

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Meadow vole, Long-tailed vole and Western heather vole), *Peromyscus maniculatus* (Deer mouse),

Zapus princeps (Western jumping mouse), *Tamiasciurus hudsonicus* (Red squirrel), *Tamius amoenus*

(Yellow-pine chipmunk), *Glaucomys sabrinus* (Northern flying squirrel), shrews in the genus *Sorex*

(Masked shrew and Vagrant shrew) and *Mustela frenata* (Long-tailed weasel). Two unknown

mandibles with teeth missing appeared to be mice or chipmunks. Great Gray Owls primarily fed

on pocket gophers (both by frequency and biomass) and voles (Table 2).

Table 8. Species, frequency, and biomass estimates of small mammal biomass found in Great Gray Owl pellets in Jackson Hole 2013-2015.

Prey	N	Frequency (%)	Biomass (g)	Biomass (%)
Pocket Gophers	82	53	5,666	64
Voles	58	37	2320	26
Mice	7	5	154	2
Chipmunks	1	1	200	2
Red Squirrels	1	1	213	2
Flying Squirrels	3	2	110	1
Shrews	2	1	20	0
Weasels	1	1	150	2

NEST CAMERAS

In the fall of 2013, we placed three still-cameras at nest sites to monitor nests in 2014.

Two cameras were situated laterally from the nest in an adjacent tree and one was situated in the

nest tree directly above the nest. We also had an additional camera on a used platform in 2015.

After reviewing the still images captured, we could not accurately assess prey items, prey delivery

rates or breeding behaviors of the females. The cameras did not regularly capture images, probably

a result of distance from the nest or low sensitivity settings on the motion trigger. Often, prey

exchanges would take place outside the view of the camera and/or the adult would be blocking the

view of the prey item. Future camera placements should be closer to the nest and multiple

cameras from different angles may help refine this technique.

Survivorship

Over the course of our study, four of our tagged owls died. One sub-adult owl and one juvenile owl died of injuries caused by vehicle collisions, one sub-adult mortality was due to a suspected predation, and one breeding adult owl died of Trichomoniasis. Trichomoniasis (*Trichomonas gallinae)* is a protozoan parasitic infection that causes lesions in a bird's throat, restricting its ability to swallow and has been documented in two Great Gray Owls in California (Rogers 2014). The disease is primarily carried by Rock Pigeons (*Columbia livia*) and doves. Pigeons are very rare within Jackson Hole, but there is a relatively small population of Mourning Doves (*Streptopelia decipiens*) and an increasing population of Eurasian Collared Doves (*Streptopelia decaocto*). The owl that died of Trichomoniasis was a breeding female with fledglings that was nesting in the Snake River bottom among low-density housing. It is likely that this Great Gray Owl preyed upon doves to contract Trichomoniasis. We searched for the fledglings following the mortality of the female but were unable to locate them, suggesting they may have also succumbed to Trichomoniasis.

Tail Molt

We studied the molt patterns of sub-adult and adult Great Gray Owls throughout the study. Replacement of rectrices occurred in what is known as a "simultaneous" or rapid, complete molt over the course of several days, rendering the owls temporarily "tail-less." Rectrices were lost either in unison or centrifugally (from the innermost to outermost), but molt always occurred rapidly, usually within a couple of days and at the most within two weeks. No disjunct, or gradual, tail molt was observed, whereas the simultaneous molt pattern was seen in adult breeding, adult

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non-breeding and sub-adult owls. In all, we observed 18 occurrences from 16 individual Great Gray Owls undergoing rapid, complete tail molt. We did not observe any owls that did not exhibit this type of simultaneous tail molt.

We only observed one sub-adult in 2013 that we know exhibited simultaneous tail molt, and we increased observation efforts in 2014 and 2015 to determine average dates of tail molt and if this was a universal phenomenon in Great Gray Owls. In 2014, we observed eight breeding owls, one non-breeder and one owl with unknown breeding status that molted their tails simultaneously. The average molt date was 17 July 2014 (range = 24 June – 14 August). In 2015, we compiled simultaneous molt observations from five breeding adults and two sub-adults, with an average molt date of 4 July 2015 (range = 10 June – 25 July).

Little documentation exists regarding the molt patterns of Great Gray Owls and information surrounding the tail molt sequence in particular is limited. We observed sixteen sub-adult and adult Great Gray Owls molting their tails completely and rapidly. Mayr and Mayr (1954) believed tail molt was gradual in large owl species but simultaneous in small owls. However, rapid, complete tail molt has since been documented in both Spotted Owls (*Strix occidentalis*) and Barred Owls (*Strix varia*) (Forsman 1981). We found no record of simultaneous tail molt in Great Gray Owls previous to our study. The advantages and implications of this molt pattern are not well understood. We observed no flight impairment due to tail loss and no connection between simultaneous tail molt and survivorship or nest success was apparent. More research investigating the benefits and impacts of owls undergoing a rapid, complete tail molt is warranted.

DISCUSSION

 Most studies of forest owl abundance and distribution rely on nighttime surveys. Nighttime playbacks proved to be an effective but labor-intensive method for surveying boreal forest owls, particularly Great Gray Owls. However, several key ecological and behavioral factors play important roles on how detectability rates and how detections can be interpreted. Duncan (1987) and Bull and Henjum (1990) suggested that Great Gray Owls defend the nest itself and not the territory. Contrary to these studies, we generally documented Great Gray Owls calling closer to the perimeter of the territory, suggesting that Great Gray Owls in Wyoming are defending the territory boundary, which has been also been reported for California populations (Reid 1989).

 Seasonal and annual fluctuations in the number and timing of boreal forest owl species responding to playback recordings indicate that there are limitations to call-back surveys and interpretation of the survey results. Call-back detections and timing of forest owls can vary widely (Francis and Bradstreet 1997) depending on factors such as moon phase (Ibarra et al. 2014) and weather (Wintle et al. 2005). Winter (1986) found that Great Gray Owl call response in California peaked at 2200 and 0100 hrs, but we found relatively consistent detections for Great Gray Owls throughout our survey periods. However, we rarely continued surveys after 0130 hr, so detectability in the early-morning hours still remains unknown in this region. Furthermore, estimated owl population abundance is likely influenced by other factors such as prey availability and snowpack (Francis and Bradstreet 1997, Palmer 1987, Duncan and Duncan 1997). High prey availability possibly can lead to inflated population estimates due to sub-adults or floaters trying to establish territories. Conversely, in years of low prey abundance, estimates may be deflated

because breeders may temporarily migrate or be occupying territories but choose not to breed and therefore reduce territorial calling (Lane et al. 1997).

We estimated our night survey detectability based on how often we heard Great Gray Owls within known territories. We found that detectability always increased in territories that were resurveyed, and multiple surveys (>2) are likely needed to accurately assess occupancy. Further, seasonal timing of Great Gray Owl response can fluctuate from year to year. Our low detection rates during a year of high snowpack suggests more studies are necessary to understand detectability of Great Gray Owls and influences on detectability. In years with increased snowpack, we suggest lengthening call-back periods to account for delayed nesting. Future studies using automated recorders are planned to better assess calling detectability.

Factors such as snowpack not only effect Great Gray Owl detectability but also nesting demographics. We detected fewer Great Gray Owls in 2014 and fewer nesting attempts, likely resulting from increased snowpack that year. High snow loads with hard crust layers may preclude owls from successfully hunting within higher-elevation territories. Mean annual fledge dates were later in 2014, suggesting that the owls delayed reproduction in 2014 until snowpack decreased. We also found that later nest initiation dates were also correlated to latitude within the study area, which is consistent with higher spring snowpack at these more northern sites. This corroborates previous studies where great grays initiated incubation later in years of higher snowpack (Franklin 1988, Bull et al. 1989).

Great Gray Owls rely on small mammals for prey, feeding primarily on northern pocket gophers and/or voles in Idaho and Wyoming, northeast Oregon, and Yosemite National Park (Franklin 1988, Bull and Henjum 1990, Winter 1986, Whitfield and Gaffney 1997, Fetz et al.

2003). Our data are consistent with previous studies in this region, indicating that Great Gray

Owls are primarily relying on pocket gophers as prey (Table 8, Franklin 1988). Gophers typically

do not exhibit large population fluctuations the way vole species do and can offer a more

consistent prey base, though small changes in gopher population densities do occur. Changes in

primary prey populations dictate owl dispersal, survivorship, and breeding (Duncan 1987, Hilden

and Helo 1981, Nero 1980, Pulliainen and Loisa 1977, Bull and Henjum 1990).   Bull and

Henjum (1990) noted that most Great Gray Owls nested every year between 1982 and 1988 except

1987, which corresponded with a crash in prey populations.

We noted fewer northern pocket gophers in 2014 than 2015, suggesting that a decline in

prey populations, combined with a harsher winter, may have limited Great Gray Owl detectability

and nesting attempts in 2014. We not only detected fewer Great Gray Owls during call-back

surveys, but we also observed fewer nest attempts that year. We documented several occupied

territories in 2014 but did not find active nests sites at locations that were active the next year in

2015, suggesting that a decline in prey availability restricted owl breeding that year. Furthermore,

failed nest sites had fewer pocket gophers than successful territories, suggesting that prey

populations most likely impact nesting success.

Over the course of the study, we documented 36 Great Gray Owl nest attempts. We

observed relatively high nest success that was comparable to that found in other studies (Bull et al.

1989, Franklin 1988, Whitfield and Gaffney 1997). However, while nest success was high, we

found that productivity has been steadily decreasing in western Wyoming over the past 30 years.

In previous studies adjacent and overlapping ours, mean productivity was 3.0 fledglings/nest in

1980-1984 (Franklin 1988), 2.3 fledglings/nest in the mid-90s (Whitfield and Gaffery 1997), while

we found an average of 1.7 fledglings/nest during this study. While territories with fewer pocket gophers had lower nest success, gopher counts did not appear to impact the number of young fledged, although this may be a product of low sample size and few years sampled. Franklin (1988) found that fledgling success was higher at nests where pocket gophers comprised a higher percentage of the owls' diet. More extensive, long-term analysis of prey abundance, diet, and productivity is warranted to better understand why Great Gray Owl productivity has apparently decreased in productivity over the past thirty years in western Wyoming.

We observed Great Gray Owls nesting in relatively close proximity (less than 500 m) to one another, but our estimate of density (1 pair/3.6 km^2) is lower than other reported densities for this species. Bull and Henjum (1990) recorded 1 pair/1.34 km^2 and 1 pair/0.58 km^2 in two different study areas in Oregon, Duncan (1987) observed 1pair/0.53 km^2 in Manitoba, Winter (1986) found 1 pair/1.51 km^2 in California, and Spreyer (1987) found 1 pair/6.66 km^2 in Minnesota. Duncan (1997) suggested that Great Gray Owls may be "loose colonial nesters." However, we found that Great Gray Owls do not exhibit a clustered nesting distribution within our study area. Fisher et al. (2007) found that definition of study areas as they relate to the spatial distribution of nests can greatly influence estimates of nesting density. Differences in study area calculations based on how searched areas are defined may account for variability in observed densities.

Regular spacing coupled with our observations of calling locations suggests that Great Gray Owls are defending territories. Defense of territory boundaries instead of actual nest sites further suggests that the resources (i.e., prey) within the territory are limited. Limited prey resources may also explain lower densities and decreases in productivity over time. Further work should explore

nest spacing in Great Gray Owls and how/if nest density and spacing relates to prey densities, productivity, and nest defense.

The reasons nesting density is relatively low and productivity has decreased across time are not completely clear. It is likely that studies areas for Great Gray Owls are chosen based on a perceived high density of owls (Duncan 1997) and lower density areas may not be surveyed often. If this is the case, then comparing densities across studies may not be that revealing. Rather, long-term monitoring to document changes in density within our study area would better inform managers about population health.

In addition to weather and prey influences on nesting demographics, habitat quality and availability within the territory and foraging areas is a clear factor in nesting demographics and also influences prey populations (Duncan 1997). Several studies have quantified habitat use across the species' range, including Whitfield and Gaffney (1997) who quantified habitat use within the Greater Yellowstone Ecosystem. Previous studies have found that Great Gray Owls prefer to nest in larger patches of mature forest stands with high canopy cover (e.g., Bull and Henjum 1988, Stepnisky 1997, Fetz et al. 2003). No other study has quantified habitat use of Great Gray Owls utilizing radio telemetry.

According to Duncan (1997), nest site availability may limit Great Gray Owl nesting abundance in some areas. We tested this hypothesis in western Wyoming through the use of nesting platforms. Great Gray Owls have readily nested on man-made platforms in timber-harvest areas (Bohm 1985, Bull et al. 1987, Nero 1982), and platforms have been used to indicate if there is a shortage of adequate natural nesting sites (Sulkava and Huhtala 1997). Beginning in 2013, we installed nesting platforms in a portion of the study area to investigate if increasing nest sites

would increase nesting density compared to our control area. By the end of 2014, three of 42 platforms had been visited by Great Gray Owls, although one of these encounters was only by fledgling owls. Only one of these platforms was used for nesting, and that pair successfully fledged three chicks. It took two years for these three platforms to be discovered so it may be too early to determine whether the number of nesting Great Gray Owls are limited by nest availability since some of the platforms were only erected in 2014.

In general, we observed Great Gray Owls nesting in diverse tree and structure types. The majority of our stick nests were in lodgepole pines and snag nests were in Douglas firs, which is consistent with previous observations of Great Gray Owl nests in the Greater Yellowstone Ecosystem (Franklin 1988, Whitfield and Gaffney 1997). Great Gray Owls preferred old stick nests and broken off snags for nesting sites, although they used other structures including mistletoe and man-made nesting platforms. Whitfield and Gaffney (1997) suggested Great Gray Owls were shifting to a reliance on stick nests (91% of nests) because of fewer available old-growth snags due to age and firewood production. We documented more nests in stick nests than both previous studies, indicating the results of Whitfield and Gaffney (1997) may have been a product of small samples size. We observed nest success was lower in snags versus stick nests, perhaps indicating that broods are more vulnerable in these more-exposed nesting structures. Future studies using remote monitoring of nest sites could help determine causes of nest failures and differences in success between nesting substrates. Furthermore, trees containing snag nests were generally atypical of the forest stands where they were situated. Snags were typically much older than the forest stands and availability of these structures may decrease over time.

We measured nest-site habitat characteristics in two different ways: with on-the ground measurements and using remote sensing and a GIS. Both techniques resulted in similar results for canopy cover at nest sites but were significantly different for measurements of distance to meadow. Several studies emphasize the importance of meadows proximal to nest sites for foraging and thereby nest success (e.g., Winter 1986). However, Wu et al. (2015) noted that 10 out of 47 nest sites were farther than 750 m from the nearest meadow.

Using a 30 m GIS land cover layer, we measured mean distance to meadow for non-riparian nest sites at 218 m, while the mean was 49 m for on-the-ground measurements. Most meadows measured at the nest site were smaller than 30 m x 30 m and would not be classified as meadows by remote layers. Also, we regularly observed owls foraging within forest patches and distance to meadow did not come out as a significant variable in our predictive models of breeding season habitat. The scale at which meadows are measured obviously affects the significance of this variable. More detailed studies of microhabitat use within a territory using high-frequency relocations of breeding male Great Gray Owls are needed to assess the size and type of meadow habitat that may be most important for foraging and nest site selection.

The mean elevation of Great Gray Owl nests was 2052 m (range 1850-2404 m), indicating that owl nests generally occurred at low-to-mid-elevation coniferous forest habitat. Franklin (1988) observed a similar mean elevation of 2,078 m for nesting Great Gray Owls in Idaho and Wyoming. However, we also located a few nests in lower elevations in the Snake River corridor in our study area. Wu et al. (2015) also recently noted Great Gray Owls nesting in lower elevation hardwood habitats in California. Future studies should survey "atypical" breeding habitats such as riparian area because of the nesting plasticity exhibited across studies.

The models we created to predict breeding habitat within Jackson Hole corroborated our measurements of nest site characteristics, indicating that owls are selecting for older-aged forests (using vegetation height as a proxy for age) with higher canopy cover that are farther from roads in areas with lower elevation and slope. While habitat characteristics at the nest are important, foraging habitat and habitat composition within a territory may play a more important role in nesting density and demographics (Duncan 1997). Researchers using 95% MCPs to estimate territory size have inferred that Great Gray Owls do not defend territories (e.g., Bull and Henjum 1988). However, we found no overlapping of adjacent territorial owls at the 75% KDE level, suggesting that owls are defending their territories at this level (75% KDE for breeding owls corresponds to a 514 m radius surrounding the nest site). KDEs from non-breeding adults also indicated direct avoidance of neighboring nesting territories.

Models of nesting habitat are useful for predicting nesting areas but may be limited without incorporation of some measure of patch size (Laberson et al. 1994). For example, our models predicted many areas of good habitat that occurred at spatial scales not suitable for raptor nesting (i.e., too small patch size). We incorporated a measure of patch size by refining the model to assess the percentage of all cells within a 500 m radius of each cell that also fell within the top 10% of predicted habitat ("good habitat"). We then eliminated cells that had less than 50% of the surrounding cells as "good habitat." This gave a conservative estimate of areas that were predicted as "good habitat" in a patch size large enough to host a territory (based on our 75% KDE from breeding owls). However, there may be finer-scale habitat variables that drive owl nest site selection that we did not measure or attempt to model.

All but one Great Gray Owl tracked during our study moved to areas of lower elevation in the winter months, which also has been noted in other radio-tracking studies (Bull et. al 1988). This shift in seasonal habitat use and selection can be seen in in both KDEs (Tables 2, 3) and the habitat models. Owls are selecting areas in riparian habitats with meadows that are closer to roads at lower elevations during the winter. Our models did not predict any winter habitat surrounding or within the northern half of the Jackson Hole region, including the Gros Ventre drainage. The highest proportion of winter habitat measured occurred within the Snake River Drainage south of Moose, Wyoming. This finding is corroborated by the fact that all but one marked owl in this study moved to discrete winter ranges within predicted winter habitat. This was consistent for the two marked owls who have summer ranges in the northern part of the valley and in the Gros Ventre drainage, traveling 52.5 and 25.0 km to winter range, respectively. However, our winter habitat models are largely based on one year with a limited sample size of locations and should be viewed as a preliminary model for this population. More work is needed to validate and refine models of winter habitat in Wyoming.

Great Gray Owls dispersed to lower elevations in winter, presumably because these areas had less snow and greater prey availability, which was also reported by van Ripper and van Wagtendonk (2006) and Franklin (1987). Selection for areas of lower snowpack means that owls tended to occupy areas nearer to roads. This can become a mortality hazard, as we attributed 50% of documented mortalities to vehicle strikes in the winter months. Because of limited available winter habitat, most owls wintered in one of three locations within the Snake River drainage. There are other reports of Great Gray Owls grouping up in the winter (Patla, pers. comm.), and we observed as many as 15 individual owls in one day within a 3-km stretch of river bottom.

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In the late fall and winter, several groups of hatch-year Great Gray Owls from different broods were regularly observed together, employing a semi-colonial wintering strategy. We did not observe Great Gray Owl pairs wintering together. In general, individuals returned to the same nesting territories each year. However, we recorded one instance when a breeding female died and no birds nested at that site the following year. We also observed one nest where the same breeding male returned to nest with a new female (we do not know the fate of the previous breeding female). We also observed several breeding males visiting other known Great Gray Owl territories in the early spring (February) before settling on their territory from the previous year. A few weeks after fledglings left the nest, males assumed sole responsibility for feeding the chicks as females dispersed from territories. Females were then observed visiting neighboring Great Gray Owl territories on numerous occasions. Once fledglings dispersed in late September and early October, several breeding pairs returned to their territories, visiting nest sites and displaying courtship behaviors before separating again for the winter. We propose that owls may be strengthening pair bonds and selecting nest sites in the fall for the following spring.

The majority of our winter movement data are based on observations during one winter. However, our findings indicate that studying a larger sample size of radio-tagged Great Gray Owls over more years is important to further understand the family group dynamics, social interactions, and crucial winter habitat requirements of Great Gray Owls. More tracking data are also needed from fledgling owls to determine natal dispersal, winter range associations, mortality, and movement dynamics during the sub-adult phase.

Our modeling results highlight several aspects of Great Gray Owl biology with significant management implications. First, Great Gray Owls are selecting summer habitat of older-aged

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forests with higher canopy cover. We also believe that patch size plays an important role in nest placement but further studies on the scale of patch selection is needed. Counter to general assertions in the literature, we did not find that owls were selecting for meadows. However, most previous studies are not based on detailed investigations of habitat use and selection from radio-marked owls. We regularly observed owls foraging within closed canopy forests but we also generally located owls during the day. Also, the majority of nests were located in sticks nests, presumably mostly constructed by Northern Goshawks, based on size and characteristics. Further work is needed to understand the relationship and reliance on species such as Northern Goshawks for owl nest sites. Though our results indicate nests are not limiting this population, a significant reduction in Northern Goshawks or snag availability may impact future populations of Great Gray Owls.

Based on our preliminary models of winter habitat, we found winter habitat is greatly limited within our study area. The majority of owls were funneled into habitat within the Snake River corridor. Human populations also are attracted to these habitats which can significantly impact future Great Gray Owl winter habitat. While we did find Great Gray Owls inhabiting low density housing areas, the effects of occupying these areas are unknown. Future studies should investigate potential differences in survival rates and breeding success of owls from wintering areas with varying levels of anthropogenic disturbance.

Long-term changes to habitat may also be affecting the reproductive success of Great Gray Owls in western Wyoming. Changes in prey availability can significantly reduce overall body condition in owls, which has been shown to affect clutch size (e.g., Korpimaki and Hakkarainen 1990, Durant et al. 2010). Increasing development within the modeled winter range may have

reduced overall prey populations or adversely changed small mammal community assemblages already. Attraction to areas with available, abundant primary prey species (pockets gophers and voles) may explain why we observed concentrations of Great Gray Owls during the winter months. Studies on survival and dispersal of young owls are needed in light of the low observed productivity rates in this study.

Because the Great Gray Owl is a long-lived species that specializes on fluctuating prey species such as voles, long-term monitoring is essential to truly assess population health. This study has created models of habitat selection by breeding owls, and although our study investigated habitat selection at a landscape level using course scale satellite imagery, more data are needed on fine-scale habitat use within territories. Understanding how habitat selection and habitat/prey interactions within a territory may be limiting density and productivity is critical to understanding apparent declines in fledging success.

This study provides the basis for long-term research and management for Great Gray Owls in Wyoming. The magnitude of territories and nest sites located during this study provides a base for long-term monitoring, and our models provide a clear direction for locating additional nest sites. Furthermore, the summer habitat model can be used by managers to estimate the effects of wildfire, future forest treatments, and changes to forest structure because of disease and insect outbreaks.

In addition to potential anthropogenic impacts during the winter, climate change likely also has and will affect Great Gray Owls in this region. Snow cover has been melting earlier in recent years due to climate change and increasing spring temperatures in western Wyoming (Hall et al. 2015) which may increase foraging habitat in the pre-nesting period. However, changing

temperatures may also cause an increase in crust hardness during the late spring months (Kausrud et al. 2008). Great Gray Owls typically hunt by plunging into snow to capture prey and increased crust hardness may lead to decreased prey capture rates (Kausrud et al. 2008), thereby reducing female body condition and clutch size. Furthermore, increased temperatures can advance the timing of avian nesting, but nest productivity can decrease if nesting does not coincide with the timing of peak prey availability (Lehikoinen 2010). Longer duration studies are needed on winter habitat use and the potential influence of spring snow conditions on female condition and productivity. Understanding how long-term climate trends may affect the timing of nest initiation, foraging in the pre-nesting period, prey abundance and availability, seasonal movements, and persistence of nesting habitat for Great Gray Owls is essential to manage for the long-term viability of Great Gray populations in Wyoming.

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