DIET, BREEDING SUCCESS, DETECTABILITY, AND DENSITY OF THE GREAT HORNED OWL (*Bubo virginianus*) AT ITS NORTHERN RANGE LIMIT

By

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Abstract

I studied the diet, breeding success, detectability, and density of great horned owls (*Bubo virginianus*) in the Middle Fork of the Koyukuk Valley in Arctic Alaska. The study extended from the southern slopes of the Brooks Range to latitudinal tree line, the northern breeding limit of the species, and included what are likely to be the northernmost great horned owl nests on record (up to 68.0113 degrees north). I completed the study during the 2017 and 2018 breeding seasons, during years of high snowshoe hare (*Lepus americanus*) abundance. The focus of this study was to gain an understanding of how high snowshoe hare abundance influences the recruitment, diet, and distribution of this apex generalist predator, and to determine best methods of detecting great horned owls for similar studies in the future. I used motion sensor cameras on nests as well as pellet analysis for diet and breeding studies, and call surveys for information on detectability and density. Great horned owl diet consisted mostly of snowshoe hares by mass (mean 80%, range 65–99%), with an average prey size of 714 g (95% CI ± 34.26). Nestlings received an average of 459 g (95% CI ± 75) of prey per chick per day, and the proportion of hares in their diet positively correlated with fledging success (*P* = 0.01). During call surveys, length of playback was the most important factor in detecting great horned owls throughout 12 minute surveys, reaching 23% (95% CI = ± 6.4) at 3 minutes, and up to 80% (95% CI = ± 6.1) at 9 minutes. Inclusion of silent listening periods may lessen the chance of detecting great horned owls during playback surveys, though a larger sample size is needed (*P* = 0.18). There was no correlation between cloud cover and probability of detection (*P* = 0.60) or wind speed and probability of detection (*P* = 0.28). However, there was a positive correlation between temperature and probability of detection (*P* = 0.02). Call surveys gave an estimate of 4.1 great horned owls per square kilometer (*z* = 4.302, 95% CI = ± 2.63). This was the northernmost study of North America’s most widespread year-round bird of prey, and the first density estimate at their northern breeding limit.
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I am grateful for the cooperation of Alyeska Pipeline Service Company for allowing us to access the Trans-Alaska Pipeline System to install cameras on owl nests, and for their help in identifying possible territories. The people of Wiseman and Coldfoot were very helpful in sharing their local observations to help find nests, especially Jack Reakoff and Todd Strong. Additionally, I would like to thank my family and friends for all of their encouragement and support throughout my time in grad school.
General Introduction

Understanding the causes and consequences of ecosystem resilience is vital to biological conservation. With the complexity of ecosystems, we can often identify and use different taxa as indicators of this resilience (Hilty & Merenlender, 2000; Medellin, Equihau, & Amin, 2000). Because the health of predator populations relies on the health of prey populations, which relies on the productivity of primary producers in an ecosystem, we can use top predators as indicators of overall ecosystem resilience (Barraquand et al., 2014; Hilty & Merenlender, 2000). Indicator species must be abundant, occupy a significant functional role in the ecosystem, occupy a wide geographic distribution, have cost-effective sampling, and respond to environmental change quantitatively and predictably (Mooney, Lubchenco, Dirzo, & Sala, 1995; Noss, 1990). I argue that the great horned owl (Bubo virginianus) may act as an indicator of prey populations as well as stability and disorder in an ecosystem (Errington, 1938).

The great horned owl is the most widespread year-round raptor in North America (Powell, 2010; Sibley, 2014). Despite being nearly ubiquitous and often used as a charismatic symbol of wildlife, little current research examines the diet and distribution of this relatively inexpensive- and easy-to-sample bird of prey. Because this species occupies virtually every ecosystem across North America, and many ecosystems in Central and South America, great horned owls can be used as a consistent monitor of ecosystem health in ecosystems across the continent once a baseline for diet and density is established across its range (Bent, 1961; Mikkola, 2012; Weidensaul, 2015).

Great horned owls are important to ecosystem processes through top-down control of prey populations (Ims & Fuglei, 2005). How this species responds to changing prey abundances has been previously examined in ecosystems of the Midwest, northeastern United States, and boreal forests and plains of Canada (Bent, 1961; Errington, 1937, 1938; C. Rohner, Doyle, & Smith, 2001; Rusch, Meslow, Doer, & Keith, 1972). I aimed to provide a baseline study for diet and distribution of the great horned owl at its northern range limit in Arctic Alaska. I used traditional techniques as
well as new technology to provide a more detailed and complete assessment of diet necessary to predict how future changes in prey populations may impact productivity of this apex predator in the Arctic (Robinson, 2016).

In order to inhabit ecosystems from Arctic Alaska to the desert southwest and the Amazon jungles, the great horned owl must be highly adaptable to different habitat types and food sources (Bent, 1961; Donázar, Hiraldo, Delibes, & Estrella, 1989; Mikkola, 2012). Though these great horned owls display a generalist diet, they depend more on certain prey items in different parts of their range. In Minnesota and Wisconsin, great horned owls consumed more ruffed grouse (*Bonasa umbellus*) at times of ruffed grouse abundance (Errington, 1937); in Iowa they consumed more ring-necked pheasants (*Phasianus colchicus*) during times of pheasant abundance (Errington, 1938); and in Alberta (Rusch et al., 1972) and the Yukon Territory (C. Rohner et al., 2001) the breeding success of these great horned owls increased with increasing snowshoe hare (*Lepus americanus*) abundance. In this study, I sought to estimate the composition and quantity of great horned owl diets in relation to breeding success at their northern range limit during years of high hare abundance (3-5 hares/ha) (Montgomerie & Kielland, 2018). In addition, I investigated abundance and detectability of great horned owls across the ~200 km² study area.

Because this is the northernmost study of North America’s most widespread owl (Houston, Smith, & Rohner, 2013; Mikkola, 2012; Weidensaul, 2015), I encountered many challenges in undertaking this project, most notably a low sample size of nests over the course of the two field seasons (n=14, with n=7 in 2017, and n=7 in 2018). Nests proved to be much more difficult to find in the boreal forests than they are in the mixed and deciduous forests of lower latitudes (Little & Little, 2018; Christoph Rohner & Doyle, 1992). Despite the low sample size of nests, I detected abundant great horned owls during call surveys, and I was able to gather important information on the nesting habits, diet, and breeding ecology of these great horned owls, described in Chapter 1.
The challenges of this project produced other novel opportunities such as building upon the limited knowledge of how to find great horned owl nests in the boreal forest, and bolstering the knowledge of how to detect the presence of owls using call surveys. The latter can also be used to estimate density of the species, and became the second chapter of this thesis. In both of these chapters, I aimed to establish a baseline for great horned owl diet and density in Arctic Alaska, as well as test methods for sampling these variables to establish protocols that can be used in sampling this possible indicator species across its range.
References


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Chapter 1 – Diet and Reproductive Success of the Great Horned Owl at its Northern Breeding Limit in Arctic Alaska

1.1 Abstract

I studied the diet and reproductive success of the great horned owl (Bubo virginianus) at its northern range limit during a high in the snowshoe hare (Lepus americanus) population. I performed diet analyses using motion sensor cameras and pellet collections at nests, and gathered data on breeding success through cameras and visual observations. Pellet data at 14 nests produced 1,277 prey observations, where the great horned owl diet consisted of 65-99% snowshoe hare mass. Great horned owls ate a total of 18 different prey types, with overall biomass consisting of 93% mammal, 7% bird, and less than 1% insects, frogs, and fish. The mean prey mass of 714 g (95% CI ± 34.26) was between 2 and 25 times the mean prey mass of studies at more southerly latitudes. Camera observations showed that great horned owls delivered an average of 459 g (95% CI ± 75) of food per chick per day throughout nesting. This was significantly (P=0.005) higher than observations in similar studies in Alberta, at 328–411 g per chick per day. Pellet data showed a correlation between the proportion of hares in the diet to breeding success, where great horned owls delivering a higher proportion of hares to their nestlings successfully raised more chicks (P = 0.01), testifying to the importance of this prey in the population dynamics of the great horned owl.
1.2 Introduction

Through predation pressures, predators enable evolution of life history traits in prey (Doligez & Colbert, 2003; Moller, Fiedler, Berthold, & editors, 2010). In the midst of changing ecosystems, a lot of emphasis is placed on interpreting the productivity and diversity of an ecosystem to predict impacts of change, and manage our resources for the future (Heller & Zavaleta, 2009). To completely assess impacts of changes to an ecosystem, predator-prey interactions fundamental to ecosystem function must be understood (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010). In the Arctic, avian predators can be important in maintaining the health of the ecosystem via acting as top-down ecosystem controls (Ims & Fuglei, 2005; Krebs, 2001). Despite this importance, avian predators are little studied at these latitudes. I aimed to help fill this gap by using new technologies and traditional methods to provide baseline data for the largest year-round avian predator of Arctic boreal forests, the great horned owl. Hence, this study examined the relationship between diet and breeding success of the great horned owl at its northern range limit in Arctic Alaska during a snowshoe hare high, examining the amount of snowshoe hares in the owl’s diet, identifying other species in their diet, and comparing the proportion of hares in the diet to breeding success. Given the abundance of hares, I predicted a positive relationship between fledging success and proportion of hares in the diet, while recognizing that the amount of food procured for the chicks may be more important than the composition per se.

Nests

Since great horned owls are not nest builders, they typically usurp nests built by other raptors such as red-tailed hawks (*Buteo jamaicensis*) or large Passerines such as common ravens (*Corvus corax*) (Bent, 1961; Sibley, Elphick, & Dunning, 2001). In the boreal forests near the latitudinal treeline, however, raptor diversity and density is relatively low (Marti, Korpimaki, &
Jaksic, 1993) and avian-built stick nests in trees large enough to host a great horned owl are scarce. Therefore, tree-nesting great horned owls in the boreal forest tend to nest in witch's broom (Chrysomyxa arctostaphyi) growths in lieu of old raptor nests (C. Rohner, Doyle, & Smith, 2001).

Witch's brooms, also known as spruce broom rust, are the result of a fungal infection affecting mainly Picea and Arctostaphylos spp. throughout North America (Nienstaedt & Zasada, 1990). The infection causes black spruce (Picea mariana) and white spruce (Picea glauca) throughout the boreal forests to produce branches that proliferate wildly, often in large clumps. These clumps can grow large enough to host a family of growing owls. Where cliffs, human structures, and other raptor nests are absent, they present the most probable nest location for a great horned owl in much of the northern boreal forests.

1.3 Methods

Study Area

The study took place along the Middle Fork of the Koyukuk River in Arctic Alaska roughly between latitudes 67 and 68 degrees North. The study site was bounded to the north by latitudinal treeline and it extended south approximately 100 kilometers along the Dalton Highway, where the highway exits the southern reaches of the Middle Fork Valley.

Flowing south out of the Brooks Range, the Middle Fork of the Koyukuk River creates a well-defined nesting habitat for great horned owls, where trees large enough for roosting and nesting are generally confined to drainages at low elevation. The area is accessible by the Dalton Highway, which parallels the river and runs through much of the preferable great horned owl habitat on its way from Fairbanks to Deadhorse, Alaska. This highway was built in 1974 as a supply road to support the Trans-Alaska Pipeline System, which also runs the length of the Middle Fork Koyukuk Valley through the study area. The area lays adjacent to the southeastern border of Gates
of the Arctic National Park, and includes the small communities of Coldfoot and Wiseman.

Scientific permits for this study were obtained through the Alaska Department of Fish and Game and the Institutional Animal Care and Use Committee under the name of Principal Investigator Knut Kielland, PhD (Appendix A).

**Nest Searching**

I located nests using a combination of methods from Shook (2002) and Rohner and Doyle (1992) who performed similar work in Interior Alaska and in the southeastern Yukon Territory respectively. In addition, my study included Local Ecological Knowledge (Gilchrist, Mallory, & Merkel, 2005), nest surveys of the pipeline and cliffs, and call surveys (Chapter 2).

I used playback experiments and silent observation to locate great horned owl territories in February and March, before owls initiated nesting in 2017 and 2018, and by listening for territorial owls at night (Christoph Rohner & Doyle, 1992). After nesting began at the beginning of April, I continued to use call playback to elicit responses throughout the day and night following Christoph Rohner and Doyle (1992).

When great horned owls responded to playback, I identified their sex using differences in pitch and cadence described by Powell (2010), where females often use more syllables in their call and have a higher pitch than males. I used ArcGIS (ESRI, 2017) to triangulate the location of the great horned owl’s territory as done by Christoph Rohner and Doyle (1992). After identifying territories, systematic daytime searching on foot was used to locate nests within a 200 meter radius of the triangulated calling location (Christoph Rohner & Doyle, 1992).

During these daytime nest searches, I searched all potentially useable nesting platforms, looking for signs indicating that a platform was occupied. These signs included the presence of bone fragments, feathers, and hare feet in and under trees; pellets or prey remains in branches or under trees; and owl feathers stuck to nearby roost trees. The best indication of an occupied nest,
even when an incubating owl was not visible, was the presence of down feathers stuck to the outside of a nest (e.g. a witch's broom).

*Nest Monitoring*

I monitored nests by checking them visually every two weeks, noting whether the nest was occupied, which adults were present, and how many chicks were present. I also deployed motion sensor cameras to monitor hatch dates, dates when chicks left the nest, chick survival, and diet. Like many owls, great horned owls often start the branching phase (leave the nest before they are capable of flight) at 45-49 days after hatch (Hoffmeister & Setzer, 1947; Houston, Smith, & Rohner, 2013). Hereafter “fledging date” refers to the date when chicks start branching, regardless of their ability to fly. I accumulated diet information through collections of pellets, prey remains and motion sensor cameras on nests.

*Cameras*

Initially I intended to deploy Reonyx Hyperfire PC900 motion sensor cameras (hereafter “nest cameras”) at all nests to capture diet information. In practice, nest camera placement was not always feasible, so nest cameras were placed on as many nests as possible (n=7; n=4 in 2017, and n=3 in 2018). All cameras contained AA lithium batteries and SD cards of 16 or 32GB capacity. I set all nest cameras to take 3 rapid-fire pictures with each trigger on medium/high sensitivity. To save battery as chicks became continually active in the nest, I set a quiet period of 30 seconds between triggers. This typically allowed cameras to last from hatch until fledge without continued maintenance, capturing between 50,000 to 60,000 photos before running out of memory or batteries. Nest cameras used an infrared illuminator to take pictures at night, using the balanced night mode setting. I attached nest cameras to the pipeline and trees using bungee cords rated for -40°C. Where possible I set a back-up camera on nests that took 2 pictures per trigger. This
allowed me to identify prey items from a different angle when they were not clearly visible on the main camera, and helped ensure that if the main camera ran out of battery or memory, I would have a back up camera whose battery and memory would last longer (through taking less pictures per trigger) from which I could gather information without causing additional nest disturbances to change batteries.

Generally, I followed Robinson's (2016) recommendations for consistent nest camera placement, placing cameras 1-2 meters laterally, and 1 meter above nest. While gyrfalcons (*Falco rusticolus*) in Robinson's study uniformly nested on cliffs, allowing for consistent camera placement, great horned owls in the Middle Fork Koyukuk Valley nested on more varied structures such as the Trans-Alaska Pipeline System, trees, and cliffs, leading to less consistency in nest camera placement. I was able to place cameras on all pipeline nests (n=5, with n=3 in 2017, and n=2 in 2018) according to Robinson's standards for maximal trigger distance and focus range. On the single cliff nest (n=1 in 2018) I was unable to place a camera due to a hazardous and unstable cliff face. On tree nests (n=8, with n=4 in 2017, and n=4 in 2018), I was able to place 3 cameras in 2017, and 1 camera in 2018. I placed cameras on the closest neighboring tree to maximize trigger and focus distance. However, in 2017 I discovered that cameras placed on trees over 10 meters from the nest did not trigger reliably. Thus, some tree nests had no neighboring trees close enough for camera placement.

Out of 14 total nests (n=7 in 2017, and n=7 in 2018), I was able to place functional nest cameras on a total of 7 nests (n=4 in 2017, and n=3 in 2018), 4 of which survived to hatch (n=2 in 2017, n=2 in 2018). Cameras were removed after nestlings fledged by the end of June each year, and I used methods described by Robinson (2016) to analyze photos for diet information.
Pellets

I collected pellets and prey remains, hereafter referred to as pellets, at all nests in order to 1) supplement diet information gathered by the nest cameras, 2) compare the accuracy of pellets and nest cameras in capturing the most complete picture of great horned owl diet, and 3) gather standardized diet information on nests despite not being able to equip all nests with a camera.

Upon finding a nest, I scoured the surrounding area to collect all pellets. This way, I could ensure that future pellets collected were deposited between known pellet collection dates (Shook, 2002). I collected pellets upon nest discovery, and whenever the nests were visited thereafter. Methods of one- or two-time pellet collection were used in many previous studies of raptor diet in the Arctic (Eisaguirre, 2015; Longland, 1989; Robinson, 2016), where researchers found that pellets accumulated under nest and roost sites. I analyzed pellets using the methods of Nielsen (1999).

For both nest camera and pellet analysis, I identified prey to the lowest possible taxonomic level. I assigned average mass values of species for biomass calculations based on the literature for birds (Sibley, 2014), mammals (Kays & Wilson, 2009), amphibians (Stebbins, 2003), fish (Wootton, 1998), and insects (Collet, 2010). Because dentition is key in distinguishing many small rodent species in this area, if I was not able to identify a small rodent to species due to missing teeth or inability to see teeth in photographs, I assigned its biomass to be the average weight of the study’s most commonly identified small rodent species, the northern red-backed vole (*Myodes rutilus*). In the analysis, I clumped all rodents weighing less than 100 grams into the category “Microtine.” To assign biomass of immature prey, I visually estimated the prey’s size as a proportion of adult size, then applied this proportion to the average biomass value of the species (Robinson, 2016).
1.4 Results

Composition of Diet

Cameras at 7 nests in the 2017 and 2018 nesting seasons revealed 258 prey items and 12 different prey types with an estimated total of 171 kg of prey consumed. Pellets from these same 7 nests revealed 138 prey items and 11 different prey types with an estimated 94 kg of prey consumed. Since it was possible to collect pellets at 7 additional nests not suitable for camera deployment, pellets were collected at a total of 14 nests. In the 14 total nests with pellet collections in the 2017 and 2018 seasons, 215 prey items were identified from 14 different prey types, with an estimated total mass of 170 kg of prey consumed. Altogether, cameras and pellets revealed a total of 18 different prey types. Table 1.1 shows a list of prey types detected, the means of detection, the total estimated mass of each prey type, and proportion of total biomass for each prey type.

Both nest cameras and pellets identified snowshoe hares as the largest component in the diet with an average of 93% and 91% percent of total diet biomass, respectively. Of this hare biomass, cameras showed 85% from adult hares and 8% from juveniles, while pellets showed 88% from adults and 3% from juveniles. Pellets were collected at all nests, and showed no difference in the proportion of hares in the diet between 2017 and 2018, at 90% (95% CI ± 8%) and 91% (95% CI ± 7%) respectively.

The next most important prey items as identified by mass from camera data were muskrats (2.5%), microtine rodents (1.0%), bird species (1.5%), and other (1.6%) (Figure 1.1). Bird species seen in cameras were mallard (Anas platyrhynchos), green-winged teal (Anas carolinensis), spruce grouse (Falcipennis canadensis), gray jay (Perisoreus canadensis), small Passerine species such as dark-eyed junco (Junco hyemalis), and sandpiper species (Calidris sp.). Prey items comprising the “other” category were red squirrel (Tamiasciurus hudsonicus), wood frog (Lithobates sylvaticus), dragonfly (Odonata sp.), and 6 small (<350g) unknown prey items that were likely either leverets or squirrels.
From the pellet data, the next most important items in the diet after hares were birds (7.2%), microtine rodents (1.1%), and other (0.6%) (Figure 1.1). Bird species seen in pellets were mallard (3.2%), spruce grouse (1.9%), and willow ptarmigan (*Lagopus lagopus*) (1.3%), with northern hawk owl (*Surnia ulula*), green-winged teal, gray jay, and small Passerine species making up the remaining 0.84 percent. The “other” category was comprised of red squirrel, ermine (*Mustela erminea*), Carabid beetles, a small fish, and small chunks of moose (*Alces alces*) fur indicative of scavenging.

**Provision Rates per Chick**

Since cameras recorded daily food events, while pellet collections showed roughly biweekly food events, I used camera data to calculate the amount of food brought back to the nest daily. Of the 7 nests equipped with cameras, only 4 survived to hatch (n = 2 in 2017, and n = 2 in 2018). From these four nests, the average amount of food brought back to the nest each day after hatch was 1,304 g (± 208.79 g), and the average food per chick per day was 459 g (± 75.69 g). The minimum amount of food brought back to a nest in a 24-hour period was zero, whereas the maximum was 4,920 g for three chicks, delivered four days before the chicks left the nest. The maximum food per chick per day was a 2,750 g brought back for one chick, also four days before it left the nest.

The amount of food brought back to the nest each day remained constant or increased throughout the season in all but Nest 1, which decreased slightly (Figure 1.2). The most dramatic increase in total food per nest per day was seen in Nest 2, about 3.5 weeks after hatch. The amount of food per chick per day increased over time in three of the four nests (Figure 1.3).
Diet and Nesting Success

Of the 14 nests monitored throughout the study, four failed before hatch (n = 2 in 2017, n = 2 in 2018). The 10 nests that hatched each fledged between one and three chicks. Since chicks often start branching out of the nest up to one month before being able to fly (Houston et al., 2013), I am using “fledge” to refer to the time when the chicks leave the nest on their own volition, as I did not monitor survival rates beyond this point. Nests fledged an average of 1.4 chicks per nest (95% CI ± 0.53) in both 2017 and 2018.

I used pellet information to compare the diet at each nest to fledging success because pellet information was collected at all 14 nests. The average proportion of hares in the diet was 85% percent (95% CI ± 6.36), which did not differ significantly between 2017 and 2018. Four nests had a diet consisting of 95% hares or greater; 1 nest had a diet of 85-95% percent hares; 5 nests had a diet of 75-85% hares; and three nests had a diet of 65-75% hares. One nest failed before I could gather adequate diet information. Figure 1.4 shows the number of chicks fledged per nest and the proportion of hares in the diet at each nest.

Using a Poisson regression, I found a significant, positive relationship (P = 0.01) between fledging success and the proportion of hares in the diet at all nests (Figure 1.4), demonstrating the importance of hares in the diet of great horned owls during the study.

1.5 Discussion

Pellets versus Cameras

In this study, data from pellets and cameras resulted in similar overall inference, however, camera data captured much more detail. Cameras recorded events by the second, minute, or hour as they occurred, while pellets captured biweekly events when they were collected. Pellets captured six types of prey that cameras did not capture, while cameras captured four types of prey
not seen in pellets. Because camera placement was only possible at half of the nests where pellets were collected, it is possible that the six prey types not captured by cameras could have been captured if all nests were equipped with cameras. Cameras also captured richer behavioral data, including exact dates of hatch, fledge, nest failure, and even successful and attempted nest predation events by common ravens.

Although the nest cameras captured many more details than pellets, they clearly required very specific conditions for successful deployment. Similar to observations of gyrfalcon nests by Robinson (2016), cameras in this study did not trigger reliably unless they were positioned 1-2 meters from the nest. There was nowhere to attach cameras within this maximal trigger and focus distance for most nests in witch’s brooms, making pellets the best option for diet estimation at the majority of tree nests.

I discovered an additional bias in using pellets when hares are abundant. Unlike previous studies of raptor diet in the Arctic (Eisaguirre, 2015; Longland, 1989; Robinson, 2016; Shook, 2002), pellets in this study did not accumulate under nests at expected rates. The majority of pellets deposited below nests quickly disappeared, leaving mainly large prey remains, along with fragmentary remains of pellets, if any. To investigate, I deployed motion sensor cameras underneath nests and roosts ("pellet cameras"). I deployed cameras on the trunk of the closest tree, ~5-10m away from the nest tree, facing its trunk. I observed that the majority of pellets were being removed or consumed by snowshoe hares and red squirrels (Tamiasciurus hudsonicus), often shortly after they were deposited. Based on meal to pellet intervals (Duke, Ciganek, & Evanson, 1973; Marti, 1969), I assumed that each great horned owl over 7 days old casts at least one pellet per day (Houston et al., 2013). Therefore, a nest with three chicks should produce about 21 pellets per week. At only one nest did I collect that expected number of accumulated pellets; a cliff nest where pellets fell onto a lower outcropping unreachable by squirrels or hares. On several occasions at other nests, I found a little less than half the expected number of pellets. However, during most
pellet collections, I found fewer than a quarter of the expected number, and sometimes only scattered prey remains and a few pellet fragments.

Poor winter nutrition may be driving hares and squirrels to supplement their diet with the undigested bone, feathers, fur, and carbohydrate residues found in owl pellets. The carbohydrate residues from pellets may contain seeds, cellulose, and chitin from stomachs of prey items (Houston et al., 2013), and osteophagy was observed in several other herbivores to acquire adequate phosphorus and calcium in the diet (Denton, Blair West, McKinley, & Nelson, 1986). Owl pellets may be a significant nutritional supplement for hares and squirrels in the boreal forests; further study is needed to quantify this impact on prey nutrition.

In summary, where it was possible to use nest cameras, they provided a better view of diet, nesting ecology and success and detected prey species not seen in pellets. Where perfect conditions for camera placement did not exist, pellets and personal observations provided a good representation of diet make-up, detected prey species not seen by cameras but yielded less resolved information on behavior or chick provisioning rates.

*Landscape of Fear*

Pellet cameras under three nests recorded hares visiting the ground below great horned owl nests an average of 8.25 times per day, with a maximum of 97 hare-visits in one day. The average length of these visits could not be determined with the camera settings used. Hares visited the ground below nests on 148 of 170 observation days. Although hares visited the ground underneath nests at all hours of the day, they made the most visits between 20:00 and 04:00, coinciding with the nocturnal activity of owls (Figure 1.5), but avoiding much of the diurnal activity of several other predators (northern goshawk, golden eagle, red-fox, lynx, wolf, bear).

Red squirrels also frequented this area, with an average of 0.94 visits per day, and a maximum of 9 visits per day. Red squirrels visited this area on 81 out of 170 observation days. Other rare
visitors to the ground below nests included Passerine birds such as gray jay and varied thrush (*Ixoreus naevius*), arctic ground squirrels (*Spermophilus parryii*), wolves (*Canis lupus*), lynx (*Lynx Canadensis*), and one black bear (*Ursus americanus*).

Great horned owls also visited the ground below their nests. One sequence of photographs shows a great horned owl fly to the ground below the nest, and reappears with a severed hare head in its bill. This demonstrates that great horned owls may be killing prey directly below their nests. Because the ground underneath spruce trees became snow-free more than a week before the surrounding ground, hares in winter pelage often risked camouflage mismatch when frequenting the area under nests, likely putting them at even higher risk of predation (Mills, Zimova, Running, Abatzoglou, & Lukacs, 2012; Zimova, Mills, & Nowak, 2016).

These observations of the great horned owl’s main prey species spending time directly underneath nests where they are at considerable risk of predation could add a new level of complexity to the landscape of fear model. This model categorizes habitats within the prey’s home range as relatively risky or safe, and uses the landscape of fear to partly explain controls of prey abundance (Laundre et al., 2014; Sih, 2005). The model suggests that prey may concentrate in safe patches, but diminished food resources could drive them into riskier patches (Lima, 1998). However, the model does not account for the possibility that prey could be attracted to riskier landscapes due to possible resources provided by predators. Studies of the landscape of fear also suggest that hares frequenting riskier areas should display reduced fitness due to the increased glucocorticoid concentrations brought about by physiological stress (Sheriff, Krebs, & Boonstra, 2009). Photographs from pellet cameras in this study showed that hares visiting the ground underneath owl nests may be killed by owls, or be rewarded with carbohydrate residues and bones of owl pellets.

Images from pellet cameras also showed hares grooming themselves directly underneath nests on a camouflage-mismatched background, perhaps suggesting that spending time in higher risk
areas does not always indicate higher stress in prey. These observations warrant additional study to further our understanding of the controls of prey abundance and the landscape of fear.

*Diet and Breeding Success*

The average amount of food brought back to the nests daily based on camera observations (1,304 g) was slightly less than the average mass of one hare per day. On average, adults delivered between 459 grams per chick per day (95% CI ± 76), which is significantly higher (P = 0.005) than observed in Alberta, where McInvaille and Keith (1974) found that chicks received between 328 and 411 grams per day during high hare abundance. Because the study in Alberta used pellet observations instead of cameras, the increase in grams per chick per day may be due to a difference in methods, where cameras gather more complete data. Cameras recorded the adult females eating from these same rations sporadically, which could slightly exaggerate the calculations for grams per chick per day. In a low hare year, McInvaille and Keith (1974) recorded chicks receiving much smaller amounts of food, between 166 and 190 grams per chick per day. Assessing these numbers for the northernmost population would be critical to understanding their ecology throughout the hare cycle.

Though great horned owls often display a generalist diet, other studies highlight their increased dependence on particular prey items during times of prey abundance. For example, in Minnesota and Wisconsin, great horned owls consumed more ruffed grouse (*Bonasa umbellus*) at times of high ruffed grouse abundance (Errington, 1937); in Iowa they consumed more ring-necked pheasants (*Phasianus colchicus*) during times of pheasant abundance (Errington, 1938); and in Alberta and the Yukon Territory the breeding success of these owls increased with increasing snowshoe hare abundance (C. Rohner et al., 2001; Rusch, Meslow, Doer, & Keith, 1972). Results of this study underscore the direct link between the abundance of great horned owls and hares (C.
Rohner et al., 2001; Shook, 2002), where owls consuming a greater proportion of hares fledged more chicks. During hare peaks in Alberta and the Yukon Territory, hares composed 90-98%, and 75-97% of the great horned owl’s winter biomass, respectively (Adamcik, Todd, & Keith, 1978; C. Rohner, 1995). Hares composed a similar proportion of the great horned owl’s biomass in this study, at 65-99% of the owl’s winter biomass. My study also showed a positive correlation between the proportion of hares in the diet and breeding success, an important effect of this key predator’s vital role in the boreal forest. Bringing a hare back to the nest may be more energetically efficient than bringing back multiple smaller prey items that total to an equivalent energetic value. First, hares may represent more digestible food compared to the equivalent mass of voles due to the difference in their surface area to volume ratio (indigestible hide and fur versus muscle and organ tissue). Second, when hares are abundant and easy to catch, bringing back a hare to the nest is more efficient per time unit of hunting and travelling.

Adamcik et al. (1978) and C. Rohner (1995) also studied Alberta and Yukon populations during troughs in the local hare populations, and observed that in low hare years, hares composed only 16 and 12.7% of the great horned owl’s biomass respectively. The northernmost breeding population studied here should also be studied during years of hare scarcity to better quantify the importance of hares in the great horned owl’s breeding ecology throughout the hare population cycle.

The proportion of mammal biomass in the great horned owl diet was consistent with study and literature review by Cromrich, Holt, and Leasure (2002). The authors noted that in pellet studies across North America, at least 93% of the biomass in the great horned owl’s diet consisted of mammals. In this study, pellets revealed 93% of the biomass did in fact consist of mammals. Mean prey size in this study, however, differed greatly from previous studies, and was between 2 and 25 times greater than that of other studies. Mean prey sizes recorded in other studies ranged from 28 to 266 grams in northern and central California, southwest Idaho, central Washington, and Chile (Fitch, 1947; Jaksic & Yañez, 1980; Marti & Kochert, 1996; Rudolph, 1978). Mean prey size in
this study was 616 grams for cameras and 714 grams for pellets. This may be an example of known pellet bias, where detection in pellets was bias toward larger prey items (Simmons, Avery, & Avery, 1991), or an effect of local environment.

Studies from across North America show great horned owls nesting earlier at more southerly latitudes (Houston et al., 2013). Great horned owls nested as early as December in the Carolinas (Sprunt, 1970), January in Ohio (Holt, 1996), February in New England (Bent, 1961), March in Alberta (Priestley, 2005), and April in arctic Alaska during this study. While other studies cite chicks beginning to leave the nest 6 weeks after hatch (Houston et al., 2013), chicks in this study branched out as early as 28 days after hatch. Chicks stayed in the nest for 42 days in only one of the 6 nests where exact hatch dates are known. The average time between hatch and chicks leaving the nest in this study was 35.5 days (95% CI ± 4.2). Greater mean prey size and g/chick/d compared to other studies might explain why chicks developed faster and were able to leave the nest earlier in this study compared to populations studied elsewhere.

Conclusions

This study highlighted the differences in two methods of diet analysis. Pellets provided good overall diet composition data, but did not provide the level of detail that could be gathered from the use of nest cameras. However, pellet collection was possible at all nests, while camera deployment required specific conditions that were only available at only half of the nest sites in this study. Pellet collections also allowed data collected in this study to be directly compared with studies of the last one hundred years of owl research, despite their known biases (Dodson & Wexler, 1979; Simmons et al., 1991).

During this study, I found that pellets were often quickly removed or consumed by red squirrels and snowshoe hares, which may add a previously unstudied bias to using pellet data. It also opened the door for future studies on the possible role of owl pellets in boreal small mammal
nutrition, or how a top predator may influence the spatial distribution of prey contrary to the landscape of fear models proposed by Laundre et al. (2014). Using methods of both nest cameras and pellet collections, where possible, allowed for the most detailed and accurate assessments of raptor ecology.

Between 65-99% of biomass in this generalist predator’s diet at the northern breeding limit consisted of snowshoe hares during high hare abundance. The proportion of hares in the diet strongly correlated with the number of chicks successfully fledged from each nest (R-squared = 0.673, p = 0.0006). This population showed an unusually large mean prey size compared to studies at lower latitudes (Houston et al., 2013). However it was consistent with the proportion of hares in the diet observed in other northern studies (Adamcik et al., 1978; McInvaille & Keith, 1974; C. Rohner, 1995).

While this study showed the importance of snowshoe hares in the diet during years of hare abundance, it would be equally important to assess this population in years of hare scarcity in order to gain a more complete picture of great horned owl breeding ecology and diet at this latitude. Future studies during hare scarcity are important to determine the dependence of this generalist predator on hares, assess influences of other prey types in diet and breeding success, and monitor changes in average prey size and grams per chick per day.

This study required searching for and monitoring nests in witch’s brooms. Throughout this time, I observed four other species nesting in witch’s brooms in the study site including common raven, northern goshawk, merlin (Falco columbarius), and American kestrel (Falco sparverius); and 8 additional species visiting witch’s brooms frequently including yellow-rumped warbler (Setophaga coconata), spruce grouse, boreal chickadee, white-crowned sparrow, varied thrush (Ixoreus naevius), gray-cheeked thrush (Catharus minimus), American marten (Martes americana), and red squirrel. Additionally, Shook (2002) found a northern hawk owl nesting in a witch’s broom within the limits of this study site, and several more throughout Interior Alaska. Very little
information exists on the ecology of witch's brooms, yet they appear attractive to many species in the boreal forests. Future studies of witch's brooms could reveal possible symbiotic relationships between *Chrysomyxa arctophyti* and the many species that use their manifestations. This fungus may play an important role in boreal ecosystems.
1.1 Percent biomass of each prey item identified in the great horned owl diet through pellet analysis and the use of motion sensor cameras in the Middle Fork Koyukuk River Valley, Alaska, in 2017 and 2018.
Figure 1.2 Daily food provisioning (grams/nest/day) to great horned owl nests in the Middle Fork Koyukuk River valley between hatch and fledging (2017 & 2018). Lowess curves show general trends in data. Date is given in Julian days. Nest 1 fledged 2 chicks in 2017. Nest 2 fledged 3 chicks in 2018. Nest 3 fledged 2 chicks in 2017. Nest 4 fledged 3 chicks in 2018.
Figure 1.3 Specific food provisioning rates (grams/chick/day) to great horned owl chicks between hatch and fledging in the Middle Fork Koyukuk River valley (2017 & 2018). Lowess curves show general trends in data. Nest 1 and 4 are from 2018; Nest 2 and 3 are from 2017. Dates are in Julian Days. Nest 1 fledged 2 chicks in 2017. Nest 2 fledged 3 chicks in 2018. Nest 3 fledged 2 chicks in 2017. Nest 4 fledged 3 chicks in 2018.
Figure 1.4 Plot showing the relationship between fledging success and the amount of hares in the diet of great horned owls at their northern breeding limit in the Middle Fork Koyukuk Valley in 2017 & 2018 ($P = 0.01$).
Figure 1.5 Frequency of hare visits to the ground directly underneath 3 active great-horned owl nests on a total of 170 observation days, recorded by motion sensor cameras in the Middle Fork Koyukuk Valley in 2017 & 2018.
Table 1.1 Prey types and minimum number of prey items detected, the means of detection, the total estimated mass of each prey type, and proportion of total diet for each prey type. MALL is mallard. GWTE is green-winged teal. SPGR is spruce grouse. WIPT is willow ptarmigan. GRJA is gray jay. NHOW is northern hawk owl.

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January 11, 2017

To: Knut Kielland, Ph.D.
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [1010807-1] Ecology of Great Horned Owls

The IACUC reviewed and approved the New Project referenced above by Designated Member Review.

Received: January 10, 2017
Approval Date: January 11, 2017
Initial Approval Date: January 11, 2017
Expiration Date: January 11, 2018

This action is included on the January 12, 2017 IACUC Agenda.

This protocol is approved with a caveat that any sign of nest abandonment following camera placement will result in discontinuation of all camera placement until the researchers determine how to preclude abandonment.

PI responsibilities:
• Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.
• Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)
• Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.
• Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.
• Ensure animal research personnel are aware of the reporting procedures on the following page.
December 12, 2017

To: Knut Kielland, Ph.D. Principal Investigator
From: University of Alaska Fairbanks
IACUC Re: [1010807-3] Ecology of Great Horned Owls

The IACUC has reviewed the Progress Report by Administrative Review and the Protocol has been approved for an additional year.

Received: December 12, 2017
Initial Approval Date: January 11, 2017
Effective Date: December 12, 2017
Expiration Date: January 11, 2019

This action is included on the December 14, 2017 IACUC Agenda.

PI responsibilities:
• Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.
• Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)
• Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.
• Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.
• Ensure animal research personnel are aware of the reporting procedures detailed in the form 005 "Reporting Concerns".

STATE OF ALASKA
DEPARTMENT OF FISH AND GAME
P.O. Box 115526
Juneau, AK 99811-5526
Permit no. 18-114 Expires 12/31/2018
1.6 References


Robinson, B. (2016). *Gryfalcon Diet During the Brood Rearing Period on the Seward Peninsula, Alaska, in the Context of a Changing World.* (Master of Science in Raptor Biology), Boise State University, Boise State University. Retrieved from https://scholarworks.boisestate.edu/td/1144 (1144)


Shook, J. (2002). *Breeding biology, nesting habitat, dietary analysis and breeding behaviors of Northern Hawk Owls (Surnia ulula) in Interior Alaska.* (Master of Science in Raptor Biology), Boise State University.


2.1 Abstract

Audio playback of vocalizations by conspecifics is commonly used to elicit calls when surveying birds, including birds of prey. Methods for these call surveys vary widely in their use of silent listening periods, and range from 3 to 15 minutes in length. I aimed to refine this approach to determine the most accurate means of detecting great horned owls in Arctic Alaska by comparing various playback protocols. Protocol 1 entailed uninterrupted playback, whereas Protocol 2 interspersed silent listening periods with playback during 12 minute surveys. In playback surveys consisting of 166 point counts during the 2017 and 2018 breeding seasons, I observed a higher probability of detection using continuous playback than when incorporating silent listening periods, though these results were not statistically significant (P = 0.18). The probability of detection rose with the length of the playback, reaching 23 percent at 3 minutes (95% CI = ± 6.4), 52 percent at 6 minutes (95% CI = ± 7.6), and 80 percent at 9 minutes (95% CI = ± 6.1). Results showed that including silent listening periods was not necessary in detecting great horned owls during call surveys. There was no correlation between cloud cover and probability of detection (P = 0.60) or wind speed and probability of detection (P = 0.28). However, there was a positive correlation between temperature and probability of detection (P = 0.02). These surveys allowed me to calculate the density of great horned owls in the Middle Fork Koyukuk Valley to be 4.15 owls per square kilometer (z = 4.302, 95% CI = ± 2.63), the first estimate of density at the northern nesting limit of the species.

2 To be submitted to the Journal of Raptor Research for publication by Madison McConnell, Knut Kielland, Greg Breed, and John Shook
2.2 Introduction

Many different survey methods exist to detect the presence of owls across North America (Anderson, 2007; Fuller & Mosher, 1987; Takats et al., 2001). These methods can be used to estimate abundance and density, and locate territories and nests (Anderson, 2007). Using an audio playback greatly increases the detectability of forest owl species, yet response varies depending on many factors such as time of year, weather, habitat characteristics, and observer attributes (Anderson, 2007; Debus, 1995; Loyn, McNabb, Volodina, & Willig, 2001). While the only other published study of nesting great horned owls in high latitudes mentioned using audio playbacks in order to identify nesting territories, it included no description of playback methods (Christoph Rohner & Doyle, 1992). My aim for this study was two-fold: 1) to test the effectiveness of different methods in detecting the presence of great horned owls, and 2) calculate the density and abundance of great horned owls in the Middle Fork Koyukuk Valley in Arctic Alaska.

Call surveys using playback may include a long broadcast of vocalization imitating the usual rate and number of calls that are characteristic to the target owl species without separate periods of silent listening (Martinez, Zuberogoitia, Colas, & Macia, 2002; Morrell, Yahner, & Harkness, 1991). However most protocols for surveying owls using playbacks alternate broadcasting the playback with periods of silent listening (Francis & Bradstreet, 1997; Hausleitner, 2006; Piorecky & Prescott, 2004; Takats et al., 2001). Protocols for these alternating patterns of playback and silent listening vary in survey length from 3-15 minutes, as well as in playback length from 20 seconds to 3 minutes.

Perhaps the most widely used method in detecting owls is through the Bird Studies Canada’s Guidelines for Nocturnal Owl Monitoring in North America. This protocol suggests a 20 second playback followed by a 3 minute listening period to detect great horned owls (Takats et al., 2001). At the onset of this research, I applied this method of detection with the intention of quickly finding territorial great horned owls in the Middle Fork Koyukuk Valley, but detected far fewer owls
than expected. However, when playback was broadcasted for several minutes, I noticed an increase in response. This study was designed to address the following questions: 1) How does the rate of detection change with survey length? 2) Does alternating silent listening periods with playback increase detection over simply letting a playback play? In addition to answering these questions, I was able to calculate the density of great horned owls in the Middle Fork Koyukuk Valley.

2.3 Methods

Study Area

The study took place along the Middle Fork of the Koyukuk River in Arctic Alaska roughly between latitudes 67 and 68 degrees North. The study site was bounded to the north by latitudinal treeline around 68 degrees north. It extended south 106 kilometers along the Dalton Highway, where the highway exits from the Middle Fork Koyukuk Valley.

Flowing south out of the Brooks Range, the Middle Fork of the Koyukuk River creates a well-defined nesting habitat for great horned owls, where trees large enough for roosting and nesting are generally confined to drainages at low elevation. The site is accessible by the Dalton Highway, which parallels the river and runs through much of the preferable great horned owl habitat on its way from Fairbanks to Prudhoe Bay, Alaska. This highway was built in 1974 as a supply road to support the Trans-Alaska Pipeline System, which also runs the length of the Middle Fork Koyukuk Valley through the study site. The site lays adjacent to the southeastern border of Gates of the Arctic National Park, and includes the small communities of Coldfoot and Wiseman.

Scientific permits for this study were obtained through the Alaska Department of Fish and Game and the Institutional Animal Care and Use Committee under the name of Principal Investigator Knut Kielland, PhD (Appendix B).
Transect:

Using the Dalton Highway as a transect, survey locations were spaced at approximately 1.6 km intervals \cite{Morrell1991, Takats2001}, where pullouts were available to safely avoid the heavy truck traffic servicing Prudhoe Bay on the Trans-Alaska Pipeline System. I extended the transect from milepost 168 to 234, stretching approximately 106 kilometers with the northernmost survey location at latitudinal treeline. Because the radius of each call survey was 600 meters (the farthest detection distance for great horned owls in this study), the transect width measured 1.2 kilometers, for an overall area of 127 km$^2$ for the study site. Sections of road considered dangerous or under construction left the transect containing 56 stops, each with an observable area of 1.13 km$^2$, for a total area surveyed of 63.6 km$^2$. I used the statistical programs Distance \cite{Thomas2010} and R \cite{RStudioTeam2015} to estimate population size and density using the equations:

\[
N = \frac{nA}{aP} \quad \text{and} \quad D = \frac{N}{A}
\]

where $N$ is the population estimate, \(n\) is the number of individuals observed, $A$ is the total area of the study site, $a$ is the area surveyed, $P$ is the probability of detection, and $D$ is density. I calculated probability of detection $P$ by creating a histogram of the frequency of detection distances, and dividing the area under the curve of best fit by the overall area of the histogram (Figure 2.1).

Call surveys began at least 30 minutes after sunset, and ended at least 30 minutes before sunrise. I conducted call surveys using the playback at all locations 3 times over the course of two winters. In 2017, I conducted call surveys in late January when great horned owls in the area might be most vocal, and in late February before great horned owls begin nesting \cite{C.Rohner2001}. Because the amount of exposures to a playback in a given season can affect response rate, I waited until the winter of 2018 to conduct a call survey during the nesting period in early April \cite{Morrell1991}. This waiting period was intended to minimize the effects of owls becoming habituated to the playback, hence altering their response.
Playback:

I obtained the playback recording from the Xeno-canto archives (Xeno-canto, 2005-2018). I chose a recording of a male and female subspecies *Bubo virginianus lagophonus* (Mikkola, 2012) calling back and forth. Each calls two times at a natural pace before the recording repeats at a cadence typical for the species. I broadcast the playback using a FoxPro Predator Call megaphone, between 90 to 110 decibels (Fuller & Mosher, 1987). At each stop, I observed 30-60 seconds of silent listening while setting up the speaker system. If I heard an great horned owl during this time, it was considered “unsolicited” calling at time zero, before the playback survey began. Each survey took 12 minutes once the first broadcast began, and I alternated the playback protocol at each stop as described below. I discontinued the playback with the response of the first great horned owl, and spent the remaining time listening for any additional individuals. Responses included either a vocal response, or a visual observation. Visual or aural, I recorded my estimated distance from the first observation.

Protocol 1:

Playback is broadcast for 12 minutes without pauses.

Protocol 2:

Playback is broadcast for 3 minutes, paused for 2 minutes, broadcast for 3 minutes, paused for 2 minutes, and broadcast for 2 minutes, for a total survey length of 12 minutes. I used a generalized linear model to test for a difference in response between the two protocols.

At each stop, I recorded the number of great horned owls present, time of first response, and sex of the individuals. Because most birds reduce their calling rates and are more difficult to hear during wind or precipitation events, I did not conduct surveys in the presence of sustained
precipitation or if wind speeds were greater than 19 km/hr (>3 on the Beaufort scale) (Morrell et al., 1991; Palmer, 1987; Richards, 1981).

Cloud Cover, Wind Speed, and Temperature

I used a general linear model to test for a relationship between the likelihood of detection and environmental factors: wind speed, cloud cover, and temperature. Cloud cover was ranked on a scale of 1 to 4 where 1 signified skies with 0-25% cloud cover, 2 was 26-50% cloud cover, 3 was 51-75% cloud cover, and 4 was 76-100% cloud cover. I used the Beaufort Scale to record wind speed (1970), and a thermometer to record ambient temperature in Fahrenheit.

2.4 Results

Detection of Great horned owls

I conducted a total of 166 point counts through the three survey sessions (n = 56 in January 2017, n = 55 in February 2017, n = 55 in April 2018). I detected great horned owls in 70 out of 166 point counts for a response rate of 42.17 percent (95% CI ±7.67). In all point counts, a total of 121 great horned owls were detected. Of point counts where great horned owls were detected, an average of 1.73 owls responded (95% CI ± 1.92), where 37 percent were female, 39 percent were male, and 23 percent were unknown. I detected a maximum of 6 individuals in one January point count. Of all point counts, an average of 0.73 great horned owls (95% CI ± 2.12) were detected at each stop. Of the point counts where I detected great horned owls, the average response time was ~7 minutes after the start of the point count (95% CI = ± 0.81).

Protocol 1 vs. Protocol 2

The probability of detecting a great horned owl using Protocol 1 (without pauses) and
Protocol 2 (with pauses) was 0.46 and 0.35 respectively. A binomial regression fit as a generalized linear model indicated this large difference in the probability of detection between the two protocols was not significant (P = 0.18). However, given the large effect size, I interpret this significance level to be most likely a sample size issue, rather than equivalence between the two protocols.

Detection Rate

I used a Bartlett’s Test to test for equal variance among months for time of first detection and the number of great horned owls detected each month. A Bartlett’s Test for equal variance among survey months showed equal variance in the time of first detection, indicating the use of a One-Way ANOVA (K² = 1.99, df = 2, p = 0.3697). A Bartlett’s Test showed unequal variance in number of great horned owls detected each month, indicating the use of a Kruskal-Wallis Rank Sum Test (K² = 14.49, df = 2, p = 0.001).

I used a One-Way ANOVA to test for a difference in time of first detection in great horned owls in January, February, and April. Results indicated no significant difference in the time of first detection (F = 1.42, df = 2, p = 0.25). A Kruskal-Wallis test likewise showed no significant difference in the number of great horned owls detected throughout the three different survey months (chi² = 3.47, df = 2, p = 0.18).

The number of great horned owls detected increased with the length of the survey. Assuming the total number of great horned owls detected in all surveys represents 100 percent of the owls available for detection, Figure 2.2 shows the likelihood of detection as the point count progresses. Fourteen percent (95% CI = ± 5.3) of great horned owls were detected at time zero, calling before the start of the point count. Setting the total number of great horned owls detected throughout the 12-minute point count as 100%, 23% of owls responded in the first three minutes (95% CI = ± 6.4), 52% in the first 6 minutes (95% CI = ± 7.6), and 80% in the first 9 minutes (95%...
CI = ± 6.1). Both protocols and all months are included in this data since the results show no statistical difference between these survey parameters.

Cloud Cover, Wind Speed, and Temperature

There was no correlation between cloud cover and probability of detection \( (P = 0.60) \) or wind speed and probability of detection \( (P = 0.28) \). However, there was a positive correlation between temperature and probability of detection \( (P = 0.02) \).

Density and Abundance

Using the detection-distance relationship (Figure 2.2), I calculated the probability of detection \( P \) to be 0.15. These data include only February and April surveys since distances were not taken in all January surveys. In January, I detected a total of 52 individuals in 56 point counts for an overall abundance estimate of 655 great horned owls in the study area \( (95\% \, CI = ± 176) \). February and April surveys revealed 32 and 37 individuals respectively in 55 point counts, for abundance estimates of 436 \( (95\% \, CI = ± 283) \) and 490 \( (95\% \, CI = ± 166) \) total great horned owls respectively. Density estimates for January, February, and April revealed an estimated 5.1 \( (95\% \, CI = ± 1.39) \), 3.4 \( (95\% \, CI = ± 2.22) \), and 3.8 \( (95\% \, CI = ± 1.31) \) great horned owls per km\(^2\) respectively. The average density across all survey months was 4.1 great horned owls per km\(^2\) \( (z = 4.302, 95\% \, CI = ± 2.63) \) (Table 2.1).

2.5 Discussion

There was a large difference in response between the two protocols, although it was not statistically significant \( (P = 0.18) \). While the P-value of 0.18 shows equivocal evidence that continuous playback may be more effective in detecting great horned owls than surveys using silent
listening periods, the lack of significance may be due to a small sample size, as evidenced by the large standard error. I would recommend using continuous playback (Protocol 1) to detect great horned owls, not only to increase chances of detection, but also to help standardize protocols across different studies.

In a study of forest owl detectability in Southeast Alaska focused on the western screech owl (*Megascops kennicottii*), northern saw-whet owl (*Aegolius acadicus*), and barred owl (*Strix varia*), Kissling, Lewis, and Pendleton (2010) noted that 48% of these forest owls responded during one minute silent listening periods, whereas 52% responded during 30 second periods of playback. Though the authors did not discuss this result in depth, it may suggest that these forest owls have a higher likelihood of responding if the playback continues without pause. Likewise the great horned owls in this study had a higher rate of detection during Protocol 1 (46% detection rate with continuous playback) than during Protocol 2 (35% detection rate when incorporating silent listening periods), although this difference was not statistically significant. With the plethora of protocols that alternate silence and playback (Debus, 1995; Francis & Bradstreet, 1997; Hausleitner, 2006; Ibarra, Martin, Altamirano, Vargas, & Bonacic, 2014; Kissling et al., 2010; Morrell et al., 1991; Takats et al., 2001), I suggest standardizing methods for great horned owl detection by eliminating silent listening periods. This study showed a marked increase in detection as survey playback lengthened. Without the variable introduced with silent listening periods, one could use point counts without silent listening periods to estimate how many great horned owls went undetected during point counts of shorter lengths.

I used a survey length of 12 minutes, considering this to be the maximum amount of time I could allot to each point count and still complete survey transects within one week. Point counts of longer lengths could help determine the time at which detection rates saturate, and researchers can be more confident that they have detected a better estimate of the population.
Morrell et al. (1991) observed that great horned owl detections in Pennsylvania significantly changed with wind speed, cloud cover, and temperature. They noted that no great horned owls were detected when wind speed exceeded 5 m/s. For that reason, I only conducted surveys when wind speed was less than 5 m/s; and within this constraint throughout my study, wind speed did not correlate with probability of response. Morrell et al. (1991) detected the greatest number of great horned owls when cloud cover was between 0-25 percent. I did not see a correlation between detection and cloud cover in this study, which could partially be explained by nearly all surveys falling on nights where cloud cover was less than 24 percent.

Morrell et al. (1991) noticed an increase in detection when temperatures were below freezing, and a decrease in detection when temperatures were above freezing. However, temperature ranges in their study did not drop below -20 degrees Celsius. In this study, the highest survey temperature was -4°C, with a low of -39°C. No opportunity existed to perform surveys in above freezing temperatures during this study. Within these below freezing temperatures, warmer temperatures strongly increased the probability of detection.

Although there was no statistical difference in the detection rate between the three survey months, some notable differences existed. In February surveys, I detected great horned owls as far as 600 meters from the survey point. In the February surveys alone, 13 of the 32 great horned owls detected were first observed at a distance of over 200 meters. During the April surveys however, all 37 great horned owls detected were first observed within 200 meters of the survey point. This suggests that during the April surveys, great horned owls tended to fly closer to the caller before being detected. Due to the nocturnal nature of these surveys, I often could not see whether or not great horned owls flew towards me before announcing their presence. However, on several point counts, I noted great horned owls silently flying towards the caller before beginning to call.

Because the probability of detection, and hence both the abundance and density estimates assume that surveys do not influence the spatial distribution of great horned owls across the
landscape, the abundance and density estimates produced in this study are likely over-estimates of the great horned owl population in the Middle Fork Koyukuk Valley. This spatial bias should be taken into account in all future abundance and density estimates for this species. The use of audio recording boxes such as Song Meters could be an expensive solution in eliminating this bias by recording unsolicited calls, and not altering spatial distribution. The month of the survey could help decrease this bias as well. Great horned owls in February were detected at the maximum detectable distance, making the bias notable only in the April survey after nests were initiated.

January recorded the highest density of great horned owls at 5.4 owls/km², whereas February and April showed densities of 3.4 and 4.0 owls/km², respectively. Differences in density estimates could be due to several factors. First, based on the findings of the Kluane Project (C. Rohner et al., 2001) I expected great horned owls at this latitude to be most vocal and territorial in late January, just before nesting. January was also the first period of call surveys in the study, and Morrell et al. (1991) noted that response rate can decrease with subsequent exposures to a playback. The higher density in January surveys could also be influenced by the presence of non-territorial floaters in the population (Christoph Rohner, 1997). Rohner (1997) estimated that through immigration, non-territorial floaters can compose up to 50 percent of the population during peak densities of prey. The population of snowshoe hares (Lepus americanus), the great horned owl’s primary prey at this latitude, was indeed high during this study (3-5 hares/ha) (Montgomerie & Kielland, 2018), and possibly led to an increased presence of floaters. Presence of these floaters can delay detection of population declines due to temporarily increased numbers, and could be another factor in possibly over-estimating abundance and density in this study (Christoph Rohner, 1997).

The Breeding Bird Survey is a common passive call survey used nationwide, meaning this survey does not include broadcast of conspecific species, and are through three minutes of silent listening at each survey stop. Review of Breeding Bird Survey data from the contiguous states
indicated a 33% decline in great horned owls between 1966 and 2015 (Sauer et al., 2017). Although great horned owls are considered a species of least concern, this alarming trend calls for accurate and streamlined sampling methods to detect population changes of this top predator across its continental range. I recommend standardizing call survey methods to remove periods of silent listening, and recording the time of first response to estimate the percent of great horned owls detected. I also recommend further research on the vocal response of non-territorial floaters in the population to gain the best estimates of density and abundance.
Figure 2.1 The number of initial great horned owl detections at each distance throughout February 2017 and April 2018 call surveys.
Figure 2.2. Rate of great horned owl detection throughout all 166 call surveys, each lasting a total of 12 minutes.
Table 2.1 Detection of great horned owls (GHOW) in call surveys during different months. This table shows the number of owls detected during each month, the proportion of point counts where owls were detected, the average number of owls detected per count, the average number of owls per count only in sites where owls were detected, the average time of first detection, the estimated abundance and density, and the percent of each sex detected during counts.

<table>
<thead>
<tr>
<th></th>
<th>Total Point Counts</th>
<th>Surveys where GHOW were Detected</th>
<th>% Surveys where GHOW Detected (%)</th>
<th>Ave. GHOW per Survey</th>
<th>Ave. GHOW/ Survey where Detected</th>
<th>Ave. Time of First Response (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
<td>56</td>
<td>27</td>
<td>48</td>
<td>0.93</td>
<td>1.96</td>
<td>6.0</td>
</tr>
<tr>
<td>Feb</td>
<td>55</td>
<td>19</td>
<td>35</td>
<td>0.58</td>
<td>1.74</td>
<td>7.4</td>
</tr>
<tr>
<td>Apr</td>
<td>55</td>
<td>24</td>
<td>44</td>
<td>0.67</td>
<td>1.50</td>
<td>7.5</td>
</tr>
<tr>
<td>Total</td>
<td>166</td>
<td>70</td>
<td>42</td>
<td>0.73</td>
<td>1.73</td>
<td>6.9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Total GHOW Observed</th>
<th>Percent Females Observed (%)</th>
<th>Percent Males Observed (%)</th>
<th>Percent Unknown Observed (%)</th>
<th>Est. Pop. ± 95% CI</th>
<th>Est. Density (GHOW/km²) ± 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
<td>52</td>
<td>44</td>
<td>35</td>
<td>21</td>
<td>655 ± 176</td>
<td>5.16 ± 1.39</td>
</tr>
<tr>
<td>Feb</td>
<td>32</td>
<td>28</td>
<td>25</td>
<td>47</td>
<td>436 ± 283</td>
<td>3.42 ± 2.22</td>
</tr>
<tr>
<td>Apr</td>
<td>37</td>
<td>35</td>
<td>59</td>
<td>5</td>
<td>490 ± 166</td>
<td>3.86 ± 1.13</td>
</tr>
<tr>
<td>Total</td>
<td>121</td>
<td>37</td>
<td>40</td>
<td>23</td>
<td>527 ± 129</td>
<td>4.15 ± 2.63</td>
</tr>
</tbody>
</table>
January 11, 2017

To: Knut Kielland, Ph.D.
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [1010807-1] Ecology of Great Horned Owls

The IACUC reviewed and approved the New Project referenced above by Designated Member Review.

Received: January 10, 2017
Approval Date: January 11, 2017
Initial Approval Date: January 11, 2017
Expiration Date: January 11, 2018

This action is included on the January 12, 2017 IACUC Agenda.

This protocol is approved with a caveat that any sign of nest abandonment following camera placement will result in discontinuation of all camera placement until the researchers determine how to preclude abandonment.

PI responsibilities:
• Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol.
  Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.
• Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)
• Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.
• Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.
• Ensure animal research personnel are aware of the reporting procedures on the following page.
December 12, 2017

To: Knut Kielland, Ph.D. Principal Investigator
From: University of Alaska Fairbanks
IACUC Re: [1010807-3] Ecology of Great Horned Owls

The IACUC has reviewed the Progress Report by Administrative Review and the Protocol has been approved for an additional year.

Received: December 12, 2017
Initial Approval Date: January 11, 2017
Effective Date: December 12, 2017
Expiration Date: January 11, 2019

This action is included on the December 14, 2017 IACUC Agenda.

PI responsibilities:
• Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.
• Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)
• Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.
• Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.
• Ensure animal research personnel are aware of the reporting procedures detailed in the form 005 "Reporting Concerns".
2.6 References


General Conclusions

Through monitoring populations facing known environmental change, we can improve management and decision-making in the ecosystem (Kremen, 1992; Medellin, Equihau, & Amin, 2000). Through establishing improved and standardized monitoring techniques for a relatively easy-to-monitor, widespread, apex predator, we can improve management and decision-making in ecosystems throughout the continent. Although avian predators are crucial in maintaining the health of arctic and boreal ecosystems through top-down controls, little is known about the role of the most widespread year-round bird of prey at the northern reaches of the boreal forests (Ims & Fuglei, 2005). To address these topics, I gathered data on the density, detection, diet, and breeding success of this widespread bird of prey, the great horned owl, at its northern breeding limit.

Because prey abundance influenced great horned owl diet in former studies across North America, I performed this study during a high in snowshoe hare population cycle to assess the importance of hares in the diet and breeding success of great horned owls, and to estimate maximum population density at their northern range limit (Errington, 1937, 1938; C. Rohner, Doyle, & Smith, 2001; Rusch, Meslow, Doer, & Keith, 1972). Nesting great horned owls in the Middle Fork Koyukuk Valley during the snowshoe hare highs of 2017 and 2018 consumed 65-99% snowshoe hare biomass during nesting periods. Out of 14 nests, four failed before hatch and 10 nests raised between one and three chicks until chicks were able to leave the nest. The number of chicks that survived until leaving the nest correlated strongly with the proportion of snowshoe hares in the diet. Nestlings that consumed a greater proportion of hares had a higher rate of fledging success ($P = 0.01$).

Through using playback in call surveys, I estimated the density of great horned owls during the snowshoe hare high to be 3.42 - 5.47 owls/km$^2$, with an average of 4.15 owls/km$^2$ ($z=4.302, 95\% CI = \pm 2.63$). This is the first estimate of great horned owl density in Arctic Alaska. This density may be explained by the abundance of non-territorial floaters that may accompany high
hare abundance, though it is also possible that this represents somewhat of an overestimate due to playback surveys influencing the spatial distribution of owls before the first detection. Through immigration, non-territorial floaters can compose up to 50 percent of the local great horned owl population during peak prey densities, inflating the density estimate (Christoph Rohner, 1997). Thus, the presence of floaters may add complications in determining population trends of great horned owls both locally, and across the species’ range.

I used playback surveys for density estimates, to identify nesting territories for diet and breeding data, and also to test detectability of great horned owls using two different protocols. Most studies involving call surveys embedded periods of silent listening between playback periods, yet there is very little standardization in length of playback or silence (Francis & Bradstreet, 1997; Hausleitner, 2006; Piorecky & Prescott, 2004; Takats et al., 2001). I found equivocal evidence that great horned owls are more likely to be detected in surveys that do not incorporate silent listening periods, though these results were not statistically significant (P = 0.18). A larger sample size will be needed to determine if this difference is indeed significant. Because this evidence slightly favors the use of continuous playback, I recommend not incorporating silent listening periods into surveys to increase chances of owl detection, and to help standardize protocols across different study sites.

The length of survey was the most important factor in detecting great horned owls during the 12-minute call surveys, with 23% of great horned owls detected in the first 3 minutes (95% CI = ± 6.4), 52 percent in the first 6 minutes (95% CI = ± 7.6), and 80 percent in the first 9 minutes (95% CI = ± 6.1). By standardizing protocols through elimination of silent listening periods, we can use these rates of detection to estimate the proportion of great horned owls detected in playback surveys of various lengths.

Close observations of great horned owls in this study through the use of pellets and nest cameras led to insights on using traditional pellet analysis versus new camera technology in assessing raptor diet. Cameras captured diet in much greater detail than pellets, and gathered
minimally invasive data in real-time. Aside from the known biases of pellet analysis, pellets only provided biweekly data, when pellet collections occurred (Simmons, Avery, & Avery, 1991). However, camera deployment required very specific conditions, and was possible at only half of the locations where pellet collection was possible.

Pellet collections motivated new observations warranting additional research. Red squirrels and snowshoe hares frequently removed or consumed pellets falling to the ground under roosts and nests. This new observation may indicate additional unstudied bias to using pellet data in ecosystems where pellet theft occurs. This observation also calls for future research in the role of pellets in prey nutrition in the Arctic, and how an apex predator may influence the spatial distribution of prey contrary to the landscape of fear model (Laundre et al., 2014; Sheriff, Krebs, & Boonstra, 2009). In future studies, I recommend using both cameras and pellet collections where possible in order to garner the most accurate diet information.
References


