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Diet and reproductive success of Great Horned Owl (*Bubo virginianus*) at its northern breeding limit

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Abstract

We studied the diet and reproductive success of Great Horned Owl (*Bubo virginianus*) at its northern range limit during an apparent high in the Snowshoe Hare (*Lepus americanus*) population. We performed diet analyses using images from fixed motion sensor cameras and pellet and prey remains collected at active nests, and gathered data on breeding success through camera and visual observations. Pellet data at 14 nests produced 1277 prey records consisting of 65–95% Snowshoe Hare biomass. Great Horned Owls ate 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 (± 34 SE) was 2–25 times the mean prey mass of studies of this species at more southerly latitudes. Camera observations showed that Great Horned Owls delivered an average of 459 g/chick/d (± 75) throughout nesting. This was significantly ($P = 0.005$) higher than observations from Alberta, at 328–411 g/chick/d. Pellet/prey remains data showed that Great Horned Owls delivering a higher proportion of hares to their nestlings successfully raised more chicks ($\chi^2_1 = 6.3$, $P = 0.012$), highlighting the importance of this prey in the population dynamics of Great Horned Owl. In addition, we observed Snowshoe Hare removing pellets beneath nest sites, revealing an apparently undocumented bias to the use of pellet analysis.

Key words: Great Horned Owl; *Bubo virginianus*; diet; Snowshoe Hare; direct observation; pellet analysis; nest camera; Arctic; Alaska boreal forest

Introduction

Predator–prey interactions are key structuring features to many ecosystems (Gilman *et al.* 2010). In Arctic ecosystems, which are generally less productive and have strong seasonal pulses, avian predators are important in maintaining ecosystem stability via top-down controls (Ims and Fugelei 2005). However, little is known about the role of Great Horned Owl (*Bubo virginianus*) in these controls, despite it being an apex avian predator in the Arctic (Rohner *et al.* 2001).

Great Horned Owl is the most widespread year-round raptor in North America (Sibley 2014). In order to inhabit ecosystems from Arctic Alaska to Amazon jungles, Great Horned Owl must be highly adaptable to different habitat types and food sources (Bent 1961; Donázar *et al*. 1989). Although this owl typically has a generalist diet (Bent 1961), it specializes in different prey items across its range during periods of prey abundance. For example, in Minnesota and Wisconsin, Great Horned Owls consumed more Ruffed Grouse (*Bonasa umbellus*) at times of high grouse abundance (Errington 1937), while in Iowa they consumed more Ring-necked Pheasant (*Phasianus colchicus*) when pheasants were abundant (Errington 1938). In Alberta and Yukon Territory, its breeding success increased when Snowshoe Hare (*Lepus americanus*) was more abundant (Rusch *et al.* 1972; Rohner *et al.* 2001). To gain a better understanding of the interactions between this apex avian predator and abundant prey in the Arctic, we sought to estimate the composition and quantity of Great Horned Owl's diet in relation to breeding success during years of high hare abundance (3–5 hares/ha; C. Montgomerie and K.K. unpubl. data). We used a combination of traditional pellet analysis techniques (despite its known biases; Dodson and Wexler 1979) and more modern nest camera technology. Nest camera technology was recently tested in studies of raptor diet to help reduce biases in pellet analysis (Robinson *et al.* 2015) and nest cameras proved an effective tool to study the diet and breeding success of Gyrfalcon (*Falco rusticolus*) nesting on cliffs in the Arctic (Robinson 2016).

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Methods

Study area

We studied Great Horned Owl diet during the spring breeding seasons of 2017–2018 along the Middle Fork Koyukuk River in Arctic Alaska roughly between latitudes 67–68°N and longitudes 149–150°W. The low elevations of the river valley are surrounded by mountainous topography of the Brooks Range. At this latitude, the boreal forest is confined to lower elevations and consists largely of Black Spruce (*Picea mariana* Miller) and White Spruce (*Picea glauca* Moench). Trees large enough to support nests tend to concentrate in drainages, creating a well-defined nesting habitat for Great Horned Owl. The area is accessible by the Dalton Highway, which parallels both the river and the Trans-Alaska Pipeline System (hereafter "the pipeline"). The study site was bounded to the north by latitudinal tree line north of Nutirwik Creek and extended ~100 km south along the Dalton Highway to Cathedral Mountain. The area lies adjacent to the southeastern border of Gates of the Arctic National Park, and includes the small communities of Coldfoot and Wiseman, Alaska.

Nest searching

Great Horned Owls do not build their own nests but typically use nests built by other raptors such as Red-tailed Hawk (*Buteo jamaicensis*) or large passerines such as Common Raven (*Corvus corax*; Bent 1961). However, in boreal forests near the latitudinal tree line, raptor diversity and density are relatively low (Marti *et al.* 1993) and tree-nesting Great Horned Owls in these northerly boreal forests often use witch's broom growths in lieu of old nests (Rohner *et al.* 2001). Witch's brooms, also known as spruce broom rust, result from infections of the fungus *Chrysomyxa arctostaphyli* affecting mainly *Picea* and *Arctostaphylos* spp. throughout North America (Nienstaedt and Zasada 1990). The infection causes Black Spruce and White Spruce throughout the boreal forest to produce branches that proliferate in clumps that can grow large enough to support an owl nest (Figure 1). All tree nests we observed in the Middle Fork Koyukuk Valley were in witch's brooms. We observed owls laying eggs directly into depressions in the witch's brooms without any apparent structure, as well as in crushed nest-like structures that could have been old raven nests.

FIGURE 1. Great Horned Owl (*Bubo virginianus*) adult and chicks nesting on a large witch's broom along the Middle Fork Koyukuk Valley, Alaska (67.8442°N, 149.8326°W), June 2017. Only pellets were collected from this nest because it could not be monitored by cameras. Photo: M. Reynolds.

We located nests using a combination of methods from Shook (2002) and Rohner and Doyle (1992). We used call surveys to locate Great Horned Owls in January and February, before owls initiated nesting (Ronher and Doyle 1992; Reynolds *et al.* 2021). After nesting began in late March–early April, we continued to use call surveys and conspecific broadcasts to elicit responses during the day and night following Rohner and Doyle (1992). When Great Horned Owls responded to playback, we used ArcGIS (ESRI 2017) to triangulate their location (Rohner and Doyle 1992). We used systematic daytime searching on foot to locate nests within ~200 m radius of the triangulated location (Rohner and Doyle 1992; Shook 2002). During these daytime nest searches, we examined all potential nest platforms for signs of occupation such as bone fragments, feathers, Snowshoe Hare feet, pellets, prey remains, and owl feathers stuck to branches. The best indication of occupation was the presence of down feathers on the outside of a nest.

Nest monitoring

We visited nests every two weeks, noting occupation, which adults were present, and number of chicks. Motion sensor cameras were deployed to monitor diet, hatch, and fledging dates between our visits at half the nests we monitored (see below). Great Horned Owls typically start "branching" (leaving the nest before capable of flight) 45–49 d after hatch (Hoffmeister and Setzer 1947). Thus, we define fledging date as the date when chicks start branching, regardless of their ability to fly.

Where possible, we deployed motion sensor cameras (Reconyx Hyperfire PC900, Holmen, Wisconsin, USA) at nests to collect diet information ($n = 7$). We set all nest cameras to take three rapid-fire pictures with each trigger on medium/high sensitivity. To conserve battery power as chicks became continually active in the nest from hatch until fledge, we set a quiet period of 30 s between triggers. Nest cameras used an infrared illuminator to take pictures at night with the balanced night mode setting. We attached nest cameras to the pipeline and trees using bungee cords rated for –40°C. We set a back-up camera on each nest that took two pictures per trigger and allowed us to identify prey items from different angles.

We followed Robinson's (2016) recommendations of placing cameras 1–2 m laterally and 1 m above the nest. Unlike Gyrfalcon in Robinson's (2016) study that nested on cliffs, Great Horned Owl in the Middle Fork Koyukuk Valley nested on a variety of structures (e.g., pipeline supports, trees, and cliffs). We were able to place cameras on all five pipeline nests (Photos S1, S2, S3, S4), two of eight tree nests, but not on the single cliff nest due to an unstable cliff face. We were not able to place cameras on tree nests when the

nest tree and surrounding trees were unable to support a climber. Thus, out of the 14 nests we monitored ($n = 7$ in 2017, $n = 7$ in 2018), we placed cameras on seven ($n = 4$ in 2017, and $n = 3$ in 2018), four of which hatched ($n = 2$ in 2017, $n = 2$ in 2018). Three of the nests observed were occupied both years of the study. Cameras were removed after nestlings fledged by the end of June.

Collection of pellets and prey remains

We collected pellets and prey remains at all 14 nests to compare the accuracy of pellets and nest cameras in providing the most complete picture of diets and to gather standardized diet information on nests not equipped with a camera. Upon finding a nest, we collected all pellets and prey remains in the surrounding area to ensure that future pellets collected were deposited between known collection dates (Shook 2002), and biweekly thereafter.

Prey identification

We analyzed the prey composition and biomass using both pellet/prey remains and nest cameras. We used nest camera photos to identify prey consumed at nests to the lowest possible taxonomic level (Nielsen 1999), then assigned average mass values of species based on references for birds (Sibley 2014), mammals (Kays and Wilson 2009), amphibians (Stebbins 2003), fish (Wootton 1998), and insects (Collet 2010). Because small rodents can be difficult to identify using photographs, we combined all rodents weighing less than 100 g into the category "microtine".

Pellets and prey remains were grouped by collection date and nest site, wrapped in heavy duty aluminum foil, and dried/sanitized in a standard oven at 165°C for 45 min. We counted the most frequently occurring bone of each species per collection to avoid double-counting prey (Nielsen 1999). Again, we identified prey to the lowest possible taxonomic level and combined all rodents weighing less than 100 g into the category "microtine" to be consistent with nest camera methods and assigned average mass values of species using references listed above. We also used MacDonald (2003) and Scott and McFarland (2010) to identify remains of small mammals and birds from pellets. To assign biomass of immature prey in analyses of both nest cameras and pellets/prey remains, we 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).

We used a Poisson regression to examine the relationship between fledging success and the proportion of hare biomass in the diet at all nests. Values reported are means ± SE. Alpha levels for significance testing was set to 0.05 and computed using R statistical software (R Core Team 2013).

Results

Diet composition

Nest cameras on seven nests captured up to 40 000 photos each, documenting 258 prey items and 12 different prey types, with an estimated total of 171 kg of prey consumed. Pellets and prey remains from these same seven nests revealed 138 prey items and 11 different prey types with an estimated 94 kg of prey consumed. Pellets and prey remains collected from a total of 14 nests, including the seven nests without cameras, yielded 215 prey items from 14 different prey types, with an estimated total mass of 170 kg of prey consumed. Altogether, cameras and pellets/prey remains revealed a total of 18 different prey types.

Both nest cameras (Photo S3) and pellets/prey remains identified Snowshoe Hare as the largest component in the diet with an average of 93% and 91% of total biomass, respectively (Figure 2). Of this hare biomass, 85% and 88% came from adult hares for cameras and pellets/prey remains, respectively. Pellets were collected at all nests and showed little difference in the proportion of hare biomass in the diet between 2017 (90 ± 8%) and 2018 (91 ± 7%).

Based on camera data, the items that contributed most biomass to the diet after hares were Muskrat (*Ondatra zibethicus*; 2.5%), microtine rodents (2.0%), birds (1.5%), and other (1.6%). Birds identified in images were Mallard (*Anas platyrhynchos*), Green-winged Teal (*Anas crecca*), Spruce Grouse (*Canachites canadensis*), Canada Jay (*Perisoreus canadensis*), Dark-eyed Junco (*Junco hyemalis*), and a sandpiper (*Calidris* sp.). Prey items in the camera data comprising the "other" category were Red Squirrel (*Tamiasciurus hudsonicus*), Wood Frog (*Lithobates sylvaticus*), dragonfly (Odonata), and six small (<350 g) unidentified mammalian prey (Table 1).

From the pellet/prey remains data, the items that contributed most biomass to the diet after hares were birds (7.3%), microtine rodents (1.1%), and other (0.6%). Birds identified in pellets/prey remains were Mallard (3.2%), Spruce Grouse (1.9%), and Willow Ptarmigan (*Lagopus lagopus*; 1.3%), with Northern Hawk Owl (*Surnia ulula*), Green-winged Teal, Canada Jay, and small passerines making up the remaining 0.8%. The "other" category was comprised of Red Squirrel, Ermine (*Mustela erminea*), carabid beetles, a small fish, and small pieces of Moose (*Alces americanus*) fur indicative of scavenging (Table 1).

Provisioning rates

We used camera data to calculate the daily provisioning rate. Of the seven nests equipped with cameras, only four hatched (*n* = 2 in 2017, *n* = 2 in 2018). From these four nests, the average post hatch provisioning rate was 1304 g/d (± 209), or 459 g/chick/d (± 76). Provisioning rates increased over time in all but Nest 2, where it decreased slightly (Figure 3). Dramatic increases in g/chick/d corresponded with chick mortalities in Nests 1 and 3, when nest occupancy decreased from three to two chicks (Figure 3).

Diet and nesting success

Of the 14 nests monitored during the study, four failed to hatch. Of the four failed nests, two succumbed to predation by Common Raven (Photo S5) and two failed for unknown reasons, where intact eggs were found on the snow below the nest. Of the 10 nests that hatched, each fledged 1–3 chicks (average 1.4 ± 0.5 chicks/nest) in both 2017 and 2018. We used pellet/prey remains information collected at all 14 nests to compare the diet at each nest to fledging success. The average proportion of hare biomass in the diet was 85% (± 6) across both years. Hare biomass in the diet varied among nests. Four nests had ≥95% hare biomass, one nest had 85–95% hare biomass, five nests had 75–85% hare biomass, and three nests had 65–75% hare biomass. One nest failed before we could gather adequate diet information. A likelihood ratio test showed a significant positive relationship (χ^2_1 = 6.3, *P* = 0.012) between fledging success and the proportion of hare biomass in the diet at all nests, where nestlings consuming a greater proportion of hares were more likely to fledge (Figure 4).
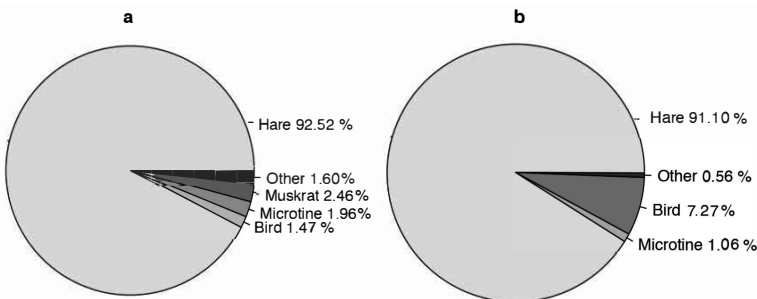

FIGURE 2. Composition of the diet of nesting Great Horned Owl (*Bubo virginianus*) as captured through the use of fixed motion sensor cameras (a) and pellet/prey remains analysis (b) in the Middle Fork Koyukuk Valley, Alaska, USA in 2017–2018.

TABLE 1. Number of each prey type observed, the method of observation (nest camera or pellet/prey remains collection), the total estimated mass of each prey type, and proportion of the total diet consisting of each prey type in the diet of nesting Great Horned Owl (*Bubo virginianus*) in the Middle Fork Koyukuk Valley, Alaska, during the breeding seasons of 2017–2018.

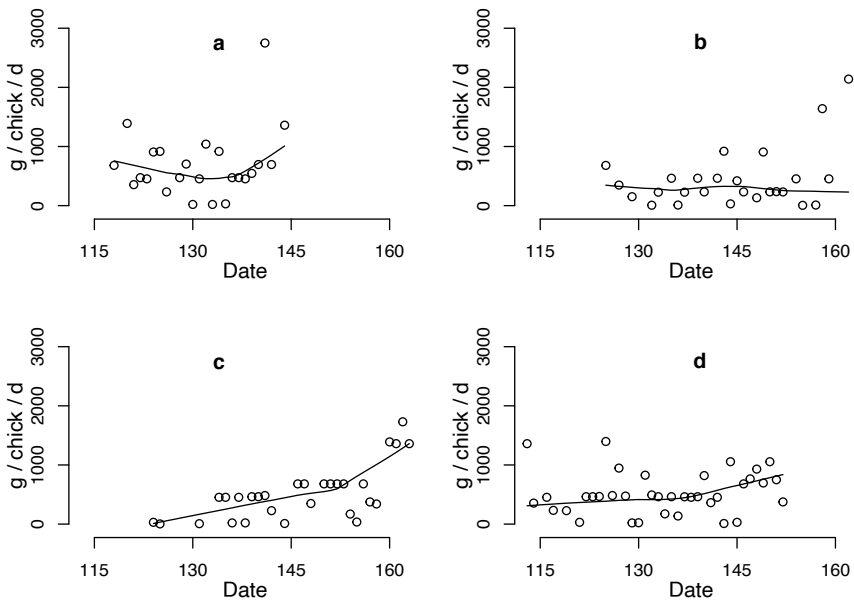| Prey type		Method of observation					
		Camera (*n* = 7 nests)			Pellets (*n* = 14 nests)		
Prey Type	Avg. weight (g)	Min. no. of items	Total weight (g)	% Total mass (g)	Min. no. of items	Total weight (g)	% Total mass (g)
Hare	750–1360	124	158 270	93	116	154 710	91
Microtine	30	112	3360	2	60	1800	1
Muskrat	1400	3	4200	2	0	0	0
Squirrel	340	2	680	<1	2	680	<1
Unknown	340	6	2040	1	0	0	0
Ermine	588	0	0	0	1	258	<1
Birds	27–1100	8	2507	1	31	12 350	7
Frog	8	2	16	<1	0	0	0
Dragonfly	1	1	1	<1	0	0	0
Beetle	1	0	0	0	3	3	<1
Fish	20	0	0	0	1	20	<1
Moose	270 000–600 000	0	0	0	1	1	0

FIGURE 3. Specific food provisioning rates (g/chick/d) to Great Horned Owl (*Bubo virginianus*) chicks between hatch and fledge, based on nest cameras in the Middle Fork Koyukuk Valley, Alaska, USA (2017–2018). Lowess curves show general trends in data. Dates are in day of year. Nest 1 (a) fledged two chicks in 2017. Nest 2 (b) fledged three chicks in 2018. Nest 3 (c) fledged two chicks in 2017. Nest 4 (d) fledged three chicks in 2018.

Discussion

Nests proved to be more difficult to find in Arctic boreal forests than the mixed and deciduous forests at lower latitudes (Rohner and Doyle 1992; Little and Little 2018), leading to a small sample size of nests (*n* = 14). Half of these nests were also monitored using cameras. Using two methods allowed us to compare diets identified by each; supplementary cameras also showed a previously undocumented potential bias in pellet analysis in the boreal forest when Snowshoe Hares are present.

Unlike previous studies of raptor diet in the Arctic (Longland 1989; Shook 2002; Eisaguirre 2015; Robinson 2016), pellets in our study accumulated under
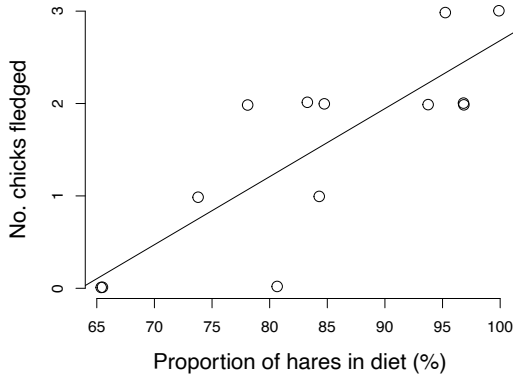
FIGURE 4. Relationship ($\chi^2_1 = 6.3$, $P = 0.012$) between fledging success and Snowshoe Hare (*Lepus americanus*) biomass in diet of Great Horned Owl (*Bubo virginianus*) based on pellet/prey remains at their northern breeding limit in the Middle Fork Koyukuk Valley, Alaska, USA, 2017–2018.

nests at lower than expected rates. Most pellets deposited below nests disappeared quickly, leaving mainly large prey remains. To investigate this observation, we deployed motion sensor cameras ~5–10 m away from nest trees, facing the trunk and observed that most pellets were removed or consumed by Snowshoe Hare (Photo S6) and Red Squirrel. We observed hares below owl nests on 148/170 observation days (average of ~8 times per day) while Red Squirrels were observed on 81 of the same observation days (average one visit per day). Based on meal to pellet intervals (Marti 1969), we assumed that each Great Horned Owl older than seven days old casts about one pellet per day (Houston *et al.* 2013). At only one nest, a cliff nest where pellets fell onto a lower outcropping unreachable by squirrels or hares, did we collect the expected number of accumulated pellets. However, during most pellet collections, we found less than a quarter of the expected pellets.

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 prey stomachs (Houston *et al.* 2013), and osteophagy was observed in several other herbivores for dietary phosphorus and calcium (Denton *et al.* 1986). Further study is needed to determine if owl pellets are a significant nutritional supplement for hares and squirrels in boreal forests.

Pellets versus cameras for estimating diet
Data from pellets/prey remains and cameras showed similar results, however camera data captured greater detail. Cameras recorded events as they occurred, while cameras acted as biweekly summaries. Pellets/

prey remains revealed six types of prey that cameras did not, while cameras captured four types of prey not seen in pellets. Because cameras were placed only at half of the nests where pellets were collected, it is possible that the six prey types not captured by cameras could have been observed if all nests had been equipped with cameras. Nest cameras also captured behavioural data, including dates of hatch, fledge, and failure, as well as successful and attempted nest predation by Common Ravens.

Although nest cameras provided more diet detail than pellets/prey remains, they were logistically feasible at fewer nests. All cameras positioned 1–2 m from the nest as recommended by Robinson (2016) successfully captured photos throughout the nesting period. However, cameras positioned farther from the nest did not trigger reliably and were not included in our analysis. In most cases, we were unable to use cameras for nests in witch's brooms, making pellets the only feasible option for analyzing diet of most tree nesting pairs. Another potential difference exists if Great Horned Owl pairs that nest on pipeline structures have a different diet than natural tree nesters.

Diet and breeding success
We estimated that adults delivered an average of 459 g/chick/d (± 76) from nest camera data. Previous studies in Alberta showed a lower average of 328–411 g/d during high hare abundance (McInvaille and Keith 1974). Because the study in Alberta collected pellet/prey remains every other day, the larger daily provisioning of prey we observed could be due to the different dietary analysis methods. The unexpected disappearance of pellets around nests and our bi-weekly as opposed to every other day pellet collections precludes a direct comparison using pellet analyses.

Although Great Horned Owls often display a generalist diet, other studies highlight their increased dependence on particular prey species during times that species is abundant. Results of our study confirm the direct link between the abundance of Great Horned Owl and Snowshoe Hare (Rohner *et al.* 2001), where we found that owls consuming a greater proportion of hare biomass fledged significantly more chicks. During hare peaks in Alberta and Yukon, hares composed 90–98% and 75–97% of the Great Horned Owl's winter diet biomass, respectively (Adamcik *et al.* 1978; Rohner 1995). Hares composed a similar proportion of the Great Horned Owl's biomass in our study: 65–99%.

Adamcik *et al.* (1978) and Rohner (1995) also studied Alberta and Yukon owl populations during lows in the local hare populations and observed that in low hare years, hares composed only 16% and 13% of the Great Horned Owl's diet biomass, respectively. The northernmost breeding population we studied

should also be examined 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 other studies across North America (93%; Cromrich *et al.* 2002). However, mean prey size in our study was 2–25 times greater than previous studies. Mean prey sizes recorded by others in California, Idaho, Washington, and Chile ranged from 28 to 266 g (Fitch 1947; Rudolph 1978; Jaksic and Yañez 1980; Marti and Kochert 1996). Mean prey size in our study was 616 g for cameras and 714 g for pellets/prey remains.

Although a literature review by Houston *et al.* (2013) showed that chicks leave the nest 42 d after hatch, we found that chicks branched out as early as 28 d after hatch. Chicks stayed in the nest for 42 d in only one nest where exact hatch dates were known. The average time between hatch and branching in our study was 36 d (± 4). The greater mean prey size (616–714 g) and daily provisioning (459 g/chick/d) compared to other studies might explain why chicks developed faster and were able to leave the nest earlier in our study.

Witch's brooms

Little information on the ecology of witch's brooms has been published, yet they appear attractive to many species in boreal forests. We observed four other species nesting in witch's brooms including Common Raven, Northern Goshawk, Merlin (*Falco columbarius*), and American Kestrel (*Falco sparverius*). We saw eight species visiting witch's brooms frequently including Yellow-rumped Warbler (*Setophaga coronata*), Spruce Grouse, Boreal Chickadee (*Poecile hudsonicus*), White-crowned Sparrow (*Zonotrichia leucophrys*), Varied Thrush (*Ixoreus naevius*), Grey-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 in our study area, and several more throughout interior Alaska. Future studies of witch's brooms could reveal possible symbiotic relationships between *C. arctostaphyli* and the many species that use their manifestations. This fungus may play an unsung role in boreal ecosystems that may prove important in future conservation efforts.

Author Contributions

Original Draft: M.R.; Writing – Review and Editing: M.R., K.K., G.B., and J.S.; Conceptualization: M.R. and K.K.; Investigation: M.R., K.K., and J.S.; Methodology: M.R., J.S., and K.K.; Formal Analysis: M.R. and G.B.; Funding Acquisition: K.K.

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Supplementary Materials:

Photo S1. Adult Great Horned Owl (*Bubo virginianus*) triggers nest camera placed on Trans-Alaska Pipeline nest near Coldfoot, Alaska, while three chicks watch from the nest, June 2018.

Photo S2. Adult Great Horned Owl (*Bubo virginianus*) broods three chicks in a nest along the Trans-Alaska Pipeline near Coldfoot, Alaska, May 2018.

Photo S3. An adult Great Horned Owl (*Bubo virginianus*) delivers a Snowshoe Hare (*Lepus americanus*) to chicks in a nest on the Trans-Alaska Pipeline near Coldfoot, Alaska, May 2018.

Photo S4. Common Raven (*Corvus corax*) visits Great Horned Owl (*Bubo virginianus*) nest on the Trans-Alaska Pipeline near Coldfoot, Alaska.

Photo S5. Common Raven (*Corvus corax*) steals an egg from Great Horned Owl (*Bubo virginianus*) nest in witch's broom, May 2018, likely the northernmost Great Horned Owl nest on record at 68.0113°N, 149.7345°W.

Photo S6. A camera placed on the ground beneath Great Horned Owl (*Bubo virginianus*) nest shows Snowshoe Hare (*Lepus americanus*) removing an owl pellet shortly after it was cast, June 2018, at 67.8442°N, 149.8326°W.