National Park Service
U.S. Department of the Interior

Science Report NPS/SR—2024/214
https://doi.org/10.36967/2306544

Snowshoe Hare Population Trends at Mineral and Non-mineral Sites in the Central Brooks Range, Alaska

Final Report on the Snowshoe Hare Ecology Project, 1997–2023



A snowshoe hare visits a mineral lick near the Hammond River in the central Brooks Range, Alaska.
NPS / DONNA DIFOLCO

Snowshoe hare population trends at mineral and non-mineral sites in the central Brooks Range, Alaska: Final report on the snowshoe hare ecology project, 1997–2023

Science Report NPS/SR—2024/214

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Please cite this publication as:

DiFolco, D. L., and J. A. K. Maier. 2024. Snowshoe hare population trends at mineral and non-mineral sites in the central Brooks Range, Alaska: Final report on the snowshoe hare ecology project, 1997–2023. Science Report NPS/SR—2024/214. National Park Service, Fort Collins, Colorado. https://doi.org/10.36967/2306544

NPS 185/195270, November 2024

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Abstract

This report presents data we have compiled while monitoring localized snowshoe hare populations in the central Brooks Range near Wiseman, Alaska, using track and pellet counts. In addition, we documented snowshoe hare geophagy—the practice of consuming soil—via trail cameras, thus confirming the use of mineral licks by snowshoe hares in this area.

Evidence of geophagy by snowshoe hares (*Lepus americanus*) was observed during track count surveys in Gates of the Arctic National Park and Preserve west of Wiseman, Alaska, in 1997–2001 when the hare population reached an exceptionally high peak. Long-time residents claimed that hares with winter access to mineral licks reached higher densities than hares without year-round access to licks.

In 2007 we initiated pellet plot counts to monitor hare populations in four areas where hares had year-round access to a mineral lick ("mineral" sites) and three areas where hares did not have minerals available year-round ("non-mineral" sites). Hare densities in non-mineral areas peaked around 2009, albeit moderately, 10 years after the extreme peak in 1997–2001 documented by the track count. By contrast, hares at mineral sites exhibited no apparent increase in population densities at this time. Local knowledge predicted that there would not be another large increase in hare densities in mineral areas until approximately 2018. Pellet count data later supported this prediction when, in 2019, peaks of hare populations at mineral sites surpassed those at non-mineral sites.

Acknowledgments

Many thanks go to Dr. Knut Kielland of the University of Alaska Fairbanks for his subject area expertise and use of his laboratory and equipment. We greatly appreciate former UAF graduate students Suzanne Worker, Claire Montgomerie, and Laura Knutsen for assisting with this project and especially for delving into additional aspects of snowshoe hare ecology to expand our knowledge of this fascinating subject. Thank you to Glenn Stout and the Alaska Department of Fish and Game for providing the lynx pelt sealing records. We are grateful to the hundreds of volunteers who have helped with the annual pellet count, especially Eric DiFolco, who participated in the count for 14 years consecutively and helped to train new recruits. Thank you, Bureau of Land Management, for accommodating us at the Marion Creek Campground, and all the agencies at the Arctic Interagency Visitor Center for supplying us with additional volunteers when we needed them most. We also thank Patty Christian and Nancy Birkholz for helping with logistics in the pellet grid setup, and the National Park Service Fairbanks Administrative Center for its administrative support. Also, the authors are grateful to Terry Bowyer, Melanie Flamme, Jenna DiFolco, Knut Kielland, and the anonymous reviewer for their helpful comments and edits, which greatly improved this report. And perhaps most importantly, thank you Jack Reakoff, for encouraging the initiation of this project, and all the residents of Wiseman, especially Jack, Bernie and Uta Hicker, and Scott and Heidi Schoppenhorst, for offering your perspectives on the amazing natural history of this beautiful country.



The Middle Fork Koyukuk River valley in the central Brooks Range near Wiseman, Alaska, where the snowshoe hare ecology project study area is located. NPS / DONNA DIFOLCO



Snowshoe hare pellets accumulate on dried leaves during a snowshoe hare high in the central Brooks Range, Alaska. NPS / DONNA DIFOLCO

Introduction

The National Park Service (NPS) at Gates of the Arctic National Park and Preserve (GAAR) initiated a snowshoe hare (*Lepus americanus*) monitoring program in 1997 just as hares in that area were building to peak densities. The project was developed in response to a 5-year furbearer study that discovered unusual sex and age ratios in the lynx (*Lynx canadensis*) population in the eastern region of the park. While male lynx and juveniles are generally more prone to capture, during the winters between 1988 and 1993, trappers caught more female lynx than males and a lower proportion of juveniles to adults (Swanson 1994). The relatively low number of juveniles caught may have been an indication of lower juvenile survival. As lynx populations have been shown to cycle closely behind that of snowshoe hares (Elton and Nicholson 1942, Alaska Department of Fish and Game 2024), biologists recommended that NPS initiate a snowshoe hare monitoring program.



Tracks and freshly browsed willows indicate the presence of snowshoe hares in Gates of the Arctic National Park and Preserve west of Wiseman, Alaska. NPS / DONNA DIFOLCO

In the early years of this study, we witnessed drastic changes in the vegetation during an extreme peak in hare densities: willows (*Salix* spp.) were severely browsed, completely stripped of bark, and many spruce (*Picea* spp.) saplings were killed after being denuded of needles, bark, and branches by browsing hares. While young spruce trees may die if too severely browsed, willows are able to recover from severe browsing by regrowing adventitious shoots, or "stump spouts," over the next several years. These stump sprouts contain high levels of phytochemicals that are unpalatable to hares (Bryant 1981; Bryant et. al. 1985). We also observed signs of hares visiting exposed soil banks, apparently using them as mineral licks. Locals from the village of Wiseman informed us that hares in this area reached these extreme densities about once every 20 years and that the utilization of mineral licks coincided with peak densities. They also told us that hare populations to the south of Wiseman did not reach such high densities or utilize mineral licks.

Locals from the village of Wiseman informed us that hares in this area reached these extreme densities about once every 20 years and that the utilization of mineral licks coincided with peak densities.

With our curiosity roused by our own observations of hare activity and their impact on the vegetation while conducting track counts, and with the encouragement of long-time residents who had witnessed fluctuations in the hare cycle over several decades, we decided to investigate this question of snowshoe hare geophagy and its possible influence on population densities. We expanded the scope of the study to compare hare populations in "mineral" vs. "non-mineral" areas. Due to the difficulty of counting tracks at high hare densities, we instead chose to use pellet counts to monitor hare densities in the expanded study. For each site, we collected data on tree, shrub, and winter cover densities, vegetation strata, browse measurements, along with tannin and nitrogen concentrations, and heavy metal and mineral salt concentrations of soils at each site. This data is summarized in an earlier report (DiFolco & Maier 2015). This report focuses on the track and pellet count data since the inception of each of these studies in 1997 and 2007, respectively. We compare our results with the observations of Wiseman residents and lynx pelt sealing records from this area collected by the Alaska Department of Fish and Game (ADF&G). We also report on the photographic documentation we collected of snowshoe hare geophagy and look at the mineral content of hare pellets from each study site during a low hare population year and a high hare population year.

Background

In Alaska, hare populations exhibit substantial cyclical variance (Kielland et al. 2010). Factors that control the frequency and amplitude of the snowshoe hare cycle have been investigated for decades (Krebs et al. 2001). Snowshoe hare populations are known to cycle through a low phase, increase phase, peak, and then an abrupt decline, or "crash," back to the low phase. While the fact that this nine- to ten-year cycle occurs in hare populations at northern latitudes is not a point of contention, what causes the crash has yet to be fully understood. The two most prevalent hypotheses speculate that either predator density (Krebs et al. 2018) or food quantity and/or quality (e.g., Keith & Windberg 1978, Fox & Bryant 1984) lead to crashes in the snowshoe hare populations. The predator hypothesis suggests that increasing predation pressure is the primary cause of the rapid decline. Alternatively, plant species respond to increased browsing by producing plant secondary metabolites (PSMs) which either inhibit digestion or are toxic to hares, thereby effectively starving or poisoning them (Fox & Bryant 1984).

Long-time residents of the village of Wiseman, Alaska, have witnessed trends in local snowshoe hare populations over the decades and observed how the largest peaks occur in areas where mineral licks are present and how the amplitude of the cycle varies from one region to another. This appears to be related to the presence or absence of mineral licks, as licks are not distributed evenly throughout the landscape. This suggests that mineral licks may be yet another factor influencing snowshoe hare population densities.

Hares consume a variety of herbaceous and woody vegetation, but during winter, their diet is restricted to the twigs and buds of shrubs and trees (Wolff 1978). All these forages contain PSMs,

such as tannins in willows (*Salix* spp.), which inhibit digestion (Bryant 1987, Worker et al. 2015), or papyriferic acid in birch (*Betula* spp.), which is toxic to hares (Forbey et al. 2011). Geophagy (soil consumption) has been reported in a variety of herbivorous mammals and birds (Johns 1990), presumably to acquire nutrients insufficient in the diet or to counter the effects of PSMs (Krishnamani & Mahaney 2000, Slamova et al. 2011, Young et al. 2011). Soil collected from our study area in feeding trials of captive snowshoe hares suggested that geophagy may provide essential minerals that are otherwise deficient in their diet (Worker 2013). In addition to supplying essential nutrients (Rea et al. 2013), geophagy may also counteract the effects of PSMs (Gilardi et al. 1999) in hares. By consuming these soils, hares living in lick areas may be able to maintain better overall health.

Study Area

The study area lies in the boreal forest on the flanks of the southern slopes of the Brooks Range in northcentral Alaska. The composition of this forest is black spruce (*Picea mariana*), white spruce (*P. glauca*), paper birch (*Betula papyrifera*), shrub birch (*B. glandulosa*), aspen (*Populus tremuloides*), and balsam poplar (*P. balsamifera*). Willow (*Salix* spp.) and alder (*Alnus* spp.) thickets up to 3.5 m in height occur along stream channels and gravel bars. Lower elevation temperatures fluctuate from an average July maximum of 21°C and an average January minimum of −30°C (PRISM 2023). The average annual snowfall total in the nearby (70 km) village of Bettles is 232 cm and is a sufficient proxy for our study area.

Our study area is comprised of seven sites, roughly centered around the village of Wiseman (67° 24' 34" N, 150° 6' 35" W, elevation 360 m). Six of the seven sites were chosen for ease of access and lie in the Middle Fork Koyukuk River valley near the Dalton Highway (Figure 1). A pellet plot grid is located at each of these sites. The seventh site is the original track count study site, which lies just inside GAAR's eastern border along Wiseman Creek, a tributary of the Koyukuk, and is approximately 500 feet higher in elevation than the sites in the Koyukuk valley. In addition to the track count transect, we also established a pellet grid at this site. The region containing mineral licks is generally the northern half of the study area with the village of Wiseman at its southern edge.

Over 25 years have passed since this study began. Following an extremely high peak in the hare population 1997–2001, we observed high mortality among young spruce trees and wide swathes of denuded willow shrubs above the snowline along the track count transect in the park. After this period of extreme hare densities when we expanded the study to include additional sites, we found similar levels of spruce sapling mortality at Jennie, also a mineral site. Such severe browsing was not observed in the non-mineral areas. In recent years, we have noticed a regrowth of young spruce saplings along the track count transect that had been dominated by willow and alder during the "super peak" of 1997–2001. These young spruce trees do not yet dominate the landscape and the area is still only lightly vegetated, but it is possible that spruce could become more dominant in the future. We address this issue further in the Discussion.

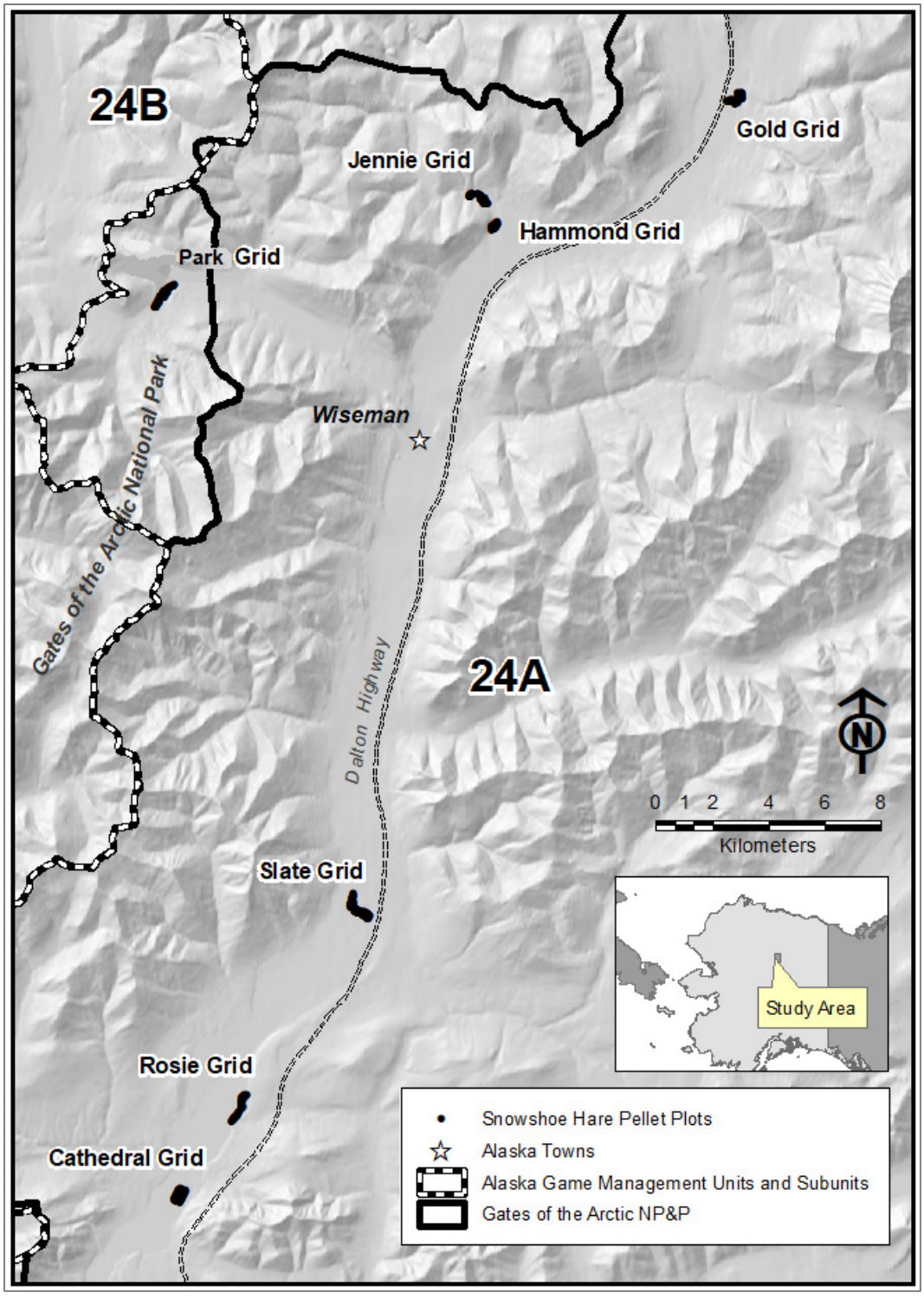


Figure 1. Map of the snowshoe hare study area and the seven sites where pellet plot grids are located in the central Brooks Range near Wiseman, Alaska. The annual track count is conducted at the Park site, which is located inside Gates of the Arctic National Park and Preserve (GAAR). Mineral sites are in the northern half of the study area (Park, Jennie, Hammond, and Gold); non-mineral sites lie in the southern portion of the study area (Cathedral, Rosie, Slate). NPS / DONNA DIFOLCO

Methods

Annual Track Count

Before initiating the track count, aerial photos of the study area (at the time, the area just inside the eastern GAAR boundary) were taken on February 24, 1997, from the back seat of the NPS Super Cub, flying 70 mph at 800 ft above ground level, using a 35 mm camera with 52 mm lens and 400 ASA color print film. We used the photos to divide the study area into winter vegetative cover and composition (VCC) classes (Golden 1994). Our survey area is comprised of three cover classes: light = 10–24% vegetation cover; moderate = 25–59% cover; and dense = 60–100% cover. (Scarce = 0–9% cover, was not found on the study route.) We further described each cover class by listing, in order of dominance, the major tree or tall shrub species. The survey route passes through six VCCs: L-SB = light cover dominated by spruce and shrub birch; L-WA = light cover dominated by willow and alder; M-SW = moderate cover dominated by spruce and willow; M-SPW = moderate cover dominated by spruce, poplar, and willow; D-WS = dense cover dominated by willow and spruce; and D-WPS = dense cover dominated by willow, poplar, and spruce.

The annual survey usually takes place in mid-March but has occasionally occurred as early as late February or as late as early April. We typically access the park boundary by snowmobile (occasionally by ski or snowshoe) and conduct the survey on snowshoe or ski. We conduct the count approximately 24 hours following either fresh snowfall of at least 1 cm, or after we have erased all existing tracks along the transect route using the backside of leaf rakes. The route follows a 3,480 m transect (Figure 2), most of which is on a winter trail that may or may not be broken in by local subsistence users from Wiseman on snowmobiles or dog sleds. The first 1,500 m of the transect follows the winter trail through lightly vegetated areas (L-SB and L-WA). The transect then diverts off the winter trail and goes 300 m through a densely vegetated area (D-WS) closer to the creek. Following the winter trail again, the vegetation then becomes moderately vegetated for another 1,500 m (M-SW and M-SPW). At the end of the route, the path once again diverts from the winter trail to go a final 180 m through dense vegetation (D-WPS).



Figure 2. Satellite image of the snowshoe hare track count transect in Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska. The transect generally follows the winter trail—except where we divert off the trail into more densely vegetated areas—and is divided into vegetation cover and composition (VCC) zones, each depicted as a different color. VCC codes are as follows: the first letter stands for vegetative cover (D = dense, M = moderate, L = light); the letters following the hyphen stand for the dominant vegetation (W = willow, P = balsam poplar, S = spruce, B = shrub birch, A = alder). NPS / DONNA DIFOLCO

Beginning in 1998, due to the abundance of hares, tracks had become so numerous that we divided the transect route into 100 m subsections and randomly selected 11 to count tracks on: four 100 m subsections in lightly vegetated areas, four in moderately vegetated areas, and three in densely vegetated areas. We counted tracks within these eleven 100 m subsections through 2002. The number of tracks becomes difficult to distinguish after two or three passes over the same place. During 1998–2001, we were sometimes unable to decipher the number of tracks due to overlap. In those cases, we would record it as a trail. For calculation purposes, we arbitrarily decided that 1 trail = 4 tracks. Since 2003, we have conducted the count along the entire transect line. We converted data from the years when the entire transect was counted to number of tracks per 100 m using the formula:

(#tracks counted in VCC/length of VCC in m) × 100 = #tracks/100 m

This conversion to tracks/100 m allowed us to better compare with the counts from 1998–2002 when data were recorded from only the eleven 100 m subsections.



A volunteer brushes out snowshoe hare tracks using a leaf rake the day prior to the annual snowshoe hare track count in eastern Gates of the Arctic National Park and Preserve near Wiseman, Alaska. NPS / DONNA DIFOLCO

Annual Pellet Count

When the scope of the study expanded to monitor hares in mineral and non-mineral areas, we selected five sites in addition to the original study area in GAAR, for a total of six study sites. We relied on the decades of personal experience and observations by Wiseman resident J. Reakoff of the natural history in this area for guidance in selecting three study sites in areas where we believe hares do not have access to desired mineral soils during the winter months (non-mineral sites), and three sites (including the original study area in the park) where hares have access to mineral soils during winter (mineral sites). While it's difficult to ascertain whether hares access mineral licks of some sort during the snow-free season, determining use during winter is relatively easy since they leave evidence of their activities behind in the snow in the form of tracks and trails leading to exposed soil, which can only be found in certain places. There are very few places in the non-mineral sites where hares could possibly access a potential lick since most of the area is blanketed in snow. Walk-through site visits have been performed during 15 of the past 17 winters, and no evidence of hares visiting licks in non-mineral areas has ever been detected. Criteria for choosing a site was based on its history

of supporting hare populations, whether its vegetation and topography were similar to other sites (i.e., valley bottoms with a mix of boreal forest species), and relative ease of access.

In June and July 2006, we established snowshoe hare pellet plots at six study sites following the procedure outlined in Kluane Ecological Monitoring Project Monitoring Protocols (2004 Edition) for setting up snowshoe hare pellet transects. A seventh site (fourth mineral site—Hammond) was added in 2013 when we became concerned that one of our mineral sites (Jennie) might be destroyed by mining activities. Each study site has one "grid" of pellet plots. As the size and shape of each site varies due to differences in topography and vegetation patterns, so do the sizes and shapes of the grid patterns at each site (Figure 3). Each grid is comprised of transects spaced 75 m apart. Individual pellet plots are spaced 25 m apart within each transect. The plots are 5.1 × 305 cm (2 in × 10 ft), cover an area of 0.155 m^2 oriented north-south, and marked at each end by plastic survey stakes.

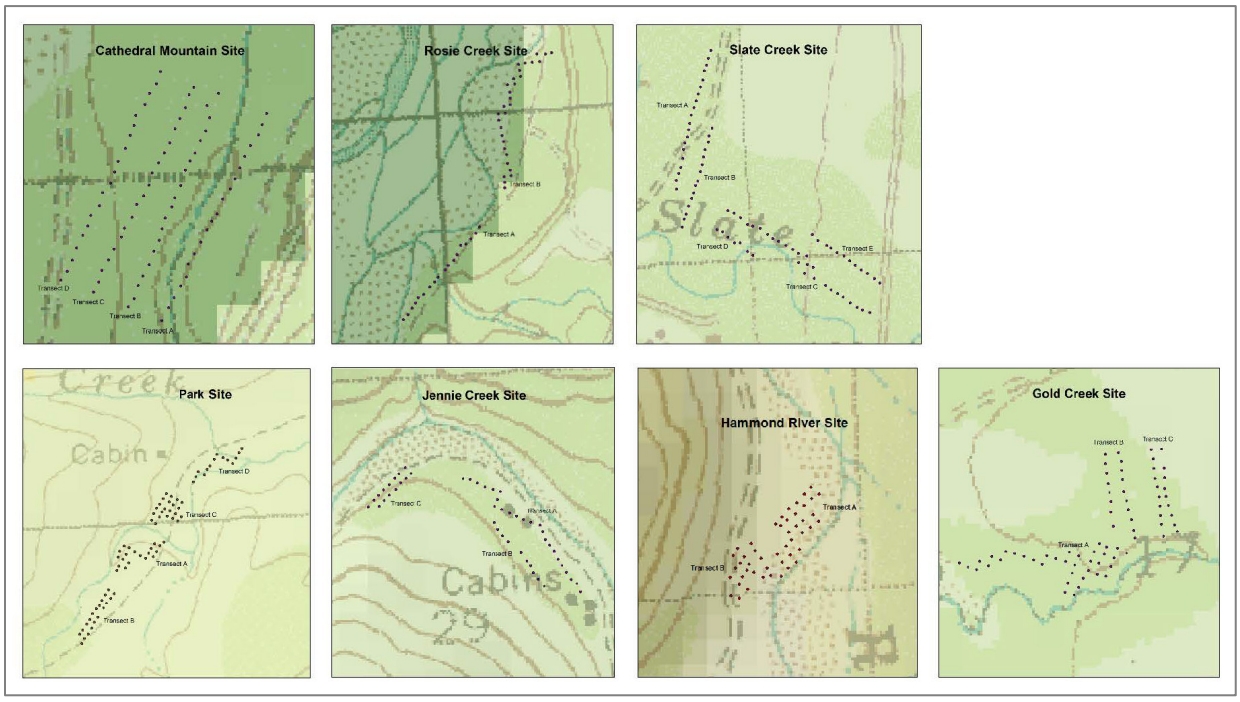


Figure 3. The original plot layout at three non-mineral pellet grids (Cathedral, Rosie and Slate, top row) and four mineral pellet grids (Park, Jennie, Hammond, and Gold) in the snowshoe hare study area near Wiseman, Alaska, in the central Brooks Range. The dots represent individual plots. Each plot is 2" wide by 10' long; plots are spaced 25 m apart. Some plots have since been lost due to human disturbance, but all grids are still being monitored. NPS / DONNA DIFOLCO

The first pellet count took place in 2007 at six study sites (Cathedral, Rosie, Slate, Park, Jennie, and Gold) at the end of a low phase/beginning of a build phase in the snowshoe hare population. The first pellet count at the seventh site, Hammond (a mineral site), was in 2014. Since the grids were originally established, some individual plots have been destroyed by human disturbance. In certain cases, we were able to re-establish plots in nearby locations. The total number of pellet plots

currently at each site is Cathedral = 80 plots; Rosie = 48 plots; Slate = 80 plots; Jennie = 48 plots; Hammond = 48 plots; Gold = 58 plots; and Park = 76 plots.



A volunteer checks a plot for snowshoe hare pellets in the central Brooks Range near Wiseman, Alaska. NPS / DONNA DIFOLCO

Every year in June we count the annual accumulation of hare pellets. A pellet is counted "in" if it is at least half inside the plot. All pellets in the plot are collected. Pellets nearby the plot (but not in it) are tossed farther away so that they cannot be mistakenly counted the following year. Since the number of plots per site varies, counts are standardized by calculating the number of pellets per plot at each site. The standardized number of pellets per plot per site is then used to derive the estimated densities of hares per site using the following formula derived from Krebs et al. (1987):

$$\#\text{hares/ha} = 0.4704(\text{mean pellets/site})^{0.889}$$

Trail Cameras

We began deploying motion-sensing trail cameras (Bushnell HD Model 119537) throughout the study area in both mineral and non-mineral areas in 2015 during the low phase of the snowshoe hare cycle. At that time, as local knowledge had told us, we could not find evidence of snowshoe hares visiting mineral licks, and cameras recorded typical hare activity (e.g., grooming, feeding, and resting) and the pattern of pelage molt rather than geophagy.



A trail camera positioned at a mineral lick near the Hammond River in the central Brooks Range, Alaska. This lick became very popular with snowshoe hares as hare densities in the area increased and peaked. NPS / DONNA DIFOLCO

We began seeing evidence of geophagy in 2017 and repositioned cameras to document potential lick sites. Most cameras were programed to collect one photo plus a 5–10 sec video at each motion trigger with 1–5 sec between triggers. Creek and slough banks and other places where exposed soils might provide a mineral source for hares were chosen in mineral and non-mineral areas to place cameras. When we established (after at least one year) that hares were not using a site as a lick, the camera was moved to a different location. Licks where we collected photographic data of hare geophagy are described in the Appendix. Cameras were examined twice a year to exchange batteries and memory cards, although we still found dead batteries sometimes after winter months.

Pellet Ash Content

If snowshoe hares consume mineral soil, their pellets should contain whatever amount they ate that is indigestible. Although mineral salts such as sodium or calcium can be absorbed from mineral soil, most of what is consumed from a mineral lick is insoluble and will eventually be expelled from the body. We assumed that the mineral content of a hare pellet is directly proportional to the amount of mineral consumed, and that all undigestible mineral consumed is expelled in the pellets, with only the dissolvable salts being absorbed. We also assumed that hares that do not visit mineral licks will have relatively little mineral content in their pellets. (However, they may inadvertently ingest soil along with their forage.) Conversely, hares that regularly visit licks may produce pellets with high mineral content.

Pellets collected from plots during the annual pellet counts were sampled to determine what percentage of the diet was composed of mineral soil from each study site. We collected pellet samples from all sites from 2015, a “low hare density” year, and 2019, a “high hare density” year. We also collected pellet samples in 2019 from the Wiseman Road Lick and the Gold Creek Lick (see Appendix for descriptions). Samples were dried, ground, weighed, and then incinerated in a muffle furnace at 550°C for four hrs to remove all organic material. All the pellets collected from a single site (or lick) in a single year were combined before grinding and incinerating. The ash remains were reweighed to obtain percent mineral content.

Results

Annual Track Count

Snowshoe hare track counts were conducted annually in the park along Wiseman Creek from 1997–2023, except 2013 and 2020, when administrative restrictions were placed on travel. The results indicate wide variations in hare densities (Figure 4). In the early years of the track count, primarily 1998–2001, we witnessed drastic changes in the vegetation during the extreme peak in hare densities: willows were severely browsed, completely stripped of bark, and many spruce (*Picea* spp.) saplings were killed after being denuded of needles, bark, and branches by browsing hares. This period also proved to be an extremely challenging one for obtaining accurate track counts, with the abundance of overlapping tracks combined with a general lack of fresh snowfall most years during the count period. These factors resulted in the snow becoming very compacted in areas where hares were most abundant. During these times, we counted tracks as best as we could, but we felt our counts likely underrepresented the actual number of hares in the area. This was the primary reason we chose to use pellet counts when we expanded the study.

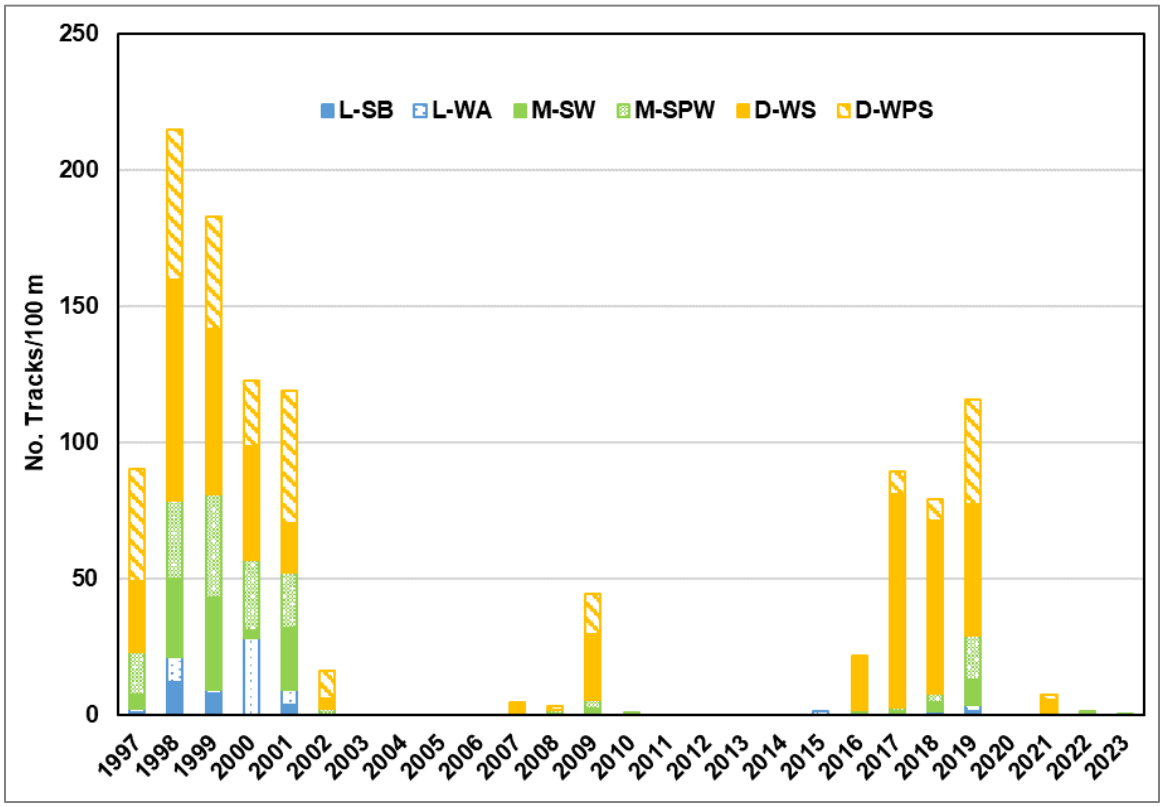


Figure 4. Results of the annual snowshoe hare track count, 1997–2023, through six vegetation cover and composition zones (VCCs) in eastern Gates of the Arctic National Park and Preserve near Wiseman, Alaska, in the central Brooks Range, expressed in number of tracks per 100 m. For VCC codes, the letter before the hyphen symbolizes relative vegetative cover; letters following hyphen are main vegetation types in order of dominance. L = lightly vegetated, M = moderately vegetated, D = densely vegetated, S = spruce, B = shrub birch, W = willow, A = alder, P = poplar. (Note: Counts were not conducted in 2013 or 2020.) NPS / DONNA DIFOLCO

From 1997–2001, the period which we have since referred to as the earlier super-peak, the proportion of tracks counted in moderate to lightly vegetated areas combined accounted for 26–47% of all tracks, with greater proportions of these less densely vegetated areas used in successive years as the hare population high persisted (Table 1).

Table 1. The proportions (in percentages) of snowshoe hare tracks counted within areas of light, moderate, and dense vegetative cover during two periods of peak hare densities, 1997–2001 and 2017–2019, in eastern Gates of the Arctic National Park and Preserve, central Brooks Range, Alaska.

Percentage of Tracks Counted in Each Cover Class	1997–2001 Super-Peak					2017–2019 Super-Peak		
	1997	1998	1999	2000	2001	2017	2018	2019
Percent of tracks in light veg cover	2.4	9.8	4.9	22.9	7.6	0.1	1.4	3.2
Percent of tracks in moderate veg cover	23.1	26.9	39.2	23.7	36.1	2.8	8.4	21.8
Percent of tracks in dense veg cover	74.0	63.3	55.8	53.5	56.3	97.1	90.2	75.0

By 2002, the hare population had noticeably declined from the previous four years of peak densities. In 2003, we recorded only a few tracks, and in 2004–2006, no hare tracks were observed. We began seeing signs of hares in 2007, and by 2009, hare tracks had become more common in the densely vegetated VCCs. By March 2011, however, we again counted no tracks along the entire survey line. The cancellation of the survey in 2013 was likely of little consequence as snowshoe hare densities had been and were expected to continue at extremely low levels.

We did not see another track until a few appeared on the survey line in 2015. The 2016 track count indicated that hares were increasing, with tracks counted predominantly in more densely vegetated areas. Track count results continued to exhibit an increase through 2019, with the proportion of tracks counted in moderately vegetated areas increasing from only 3% of tracks counted in 2017 to 25% of tracks counted in 2019, but not to the levels we saw in these VCCs in 1998–2001. Unfortunately, we were unable to conduct the track count in 2020. Results from 2021 and 2022 indicate a marked decline in hare densities.

A notable difference between the first super-peak (1997–2001) and the second (2017–2019) is the distribution of hares within the different VCCs. During both peaks, the numbers of hares in densely vegetated areas reached roughly equal numbers (Figure 5). However, in the earlier peak, in addition to utilizing the more densely vegetated areas, which are dominated primarily by willows that can provide both browse and some cover, hares also moved into more open habitats, where willow and other tall shrubs are more scattered, and which hares generally tend to avoid. This contrasts with the more recent peak when hares remained restricted mostly to more densely vegetated areas.

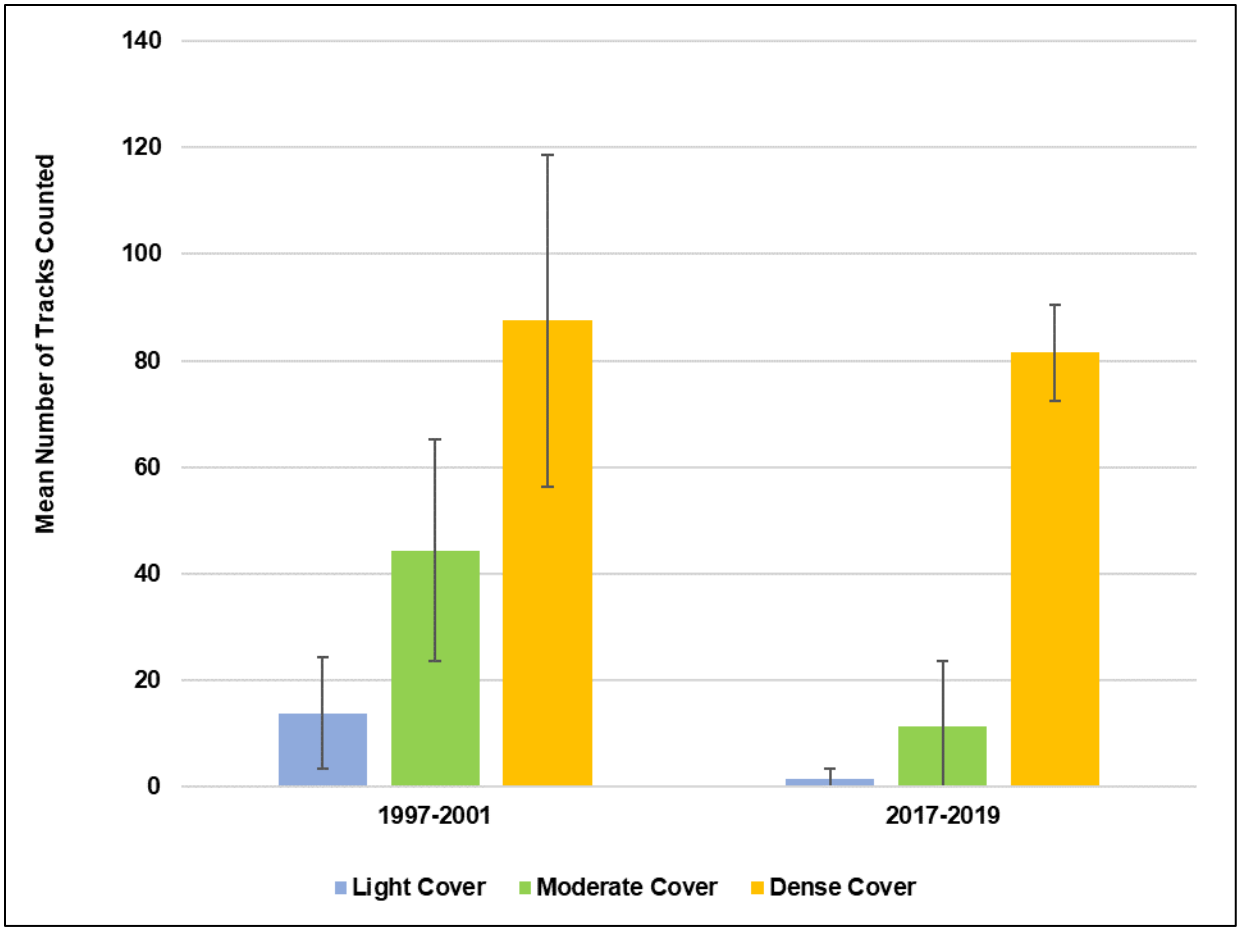


Figure 5. Comparison of the mean number of tracks counted in areas of light (10–24%), moderate (25–59%), and dense (60–100%) vegetation cover (± standard deviation of the mean) in the 1997–2001 and 2017–2019 peaks in the snowshoe hare population in eastern Gates of the Arctic National Park and Preserve near Wiseman, Alaska, in the central Brooks Range. NPS / DONNA DIFOLCO

Annual Pellet Count

Pellet counts revealed a wide range of population densities among the localized hare populations within our study area during the first few years. A summary of the raw data (in average number of pellets/plot) is shown in Figure 6. The data indicate a moderate peak in hare densities between 2007 and 2012 at the non-mineral sites of Rosie and Cathedral. Data from the third non-mineral site, Slate, suggest only a minimal increase in hare densities during this period. At the mineral sites, hares remained at very low densities, with only a one-year bump in hare densities at Jennie in 2010. From 2012–2015, pellet counts indicated low hare densities at all sites. Beginning in 2016, we began to count more pellets per plot at all sites, indicating that hares throughout the entire study area were increasing. In the non-mineral areas, hare numbers reached a peak in 2017–2018. At the mineral sites, however, hares continued to increase after populations in non-mineral areas began to decline, peaking in 2019. From 2019–2023, hare populations at all sites have declined.

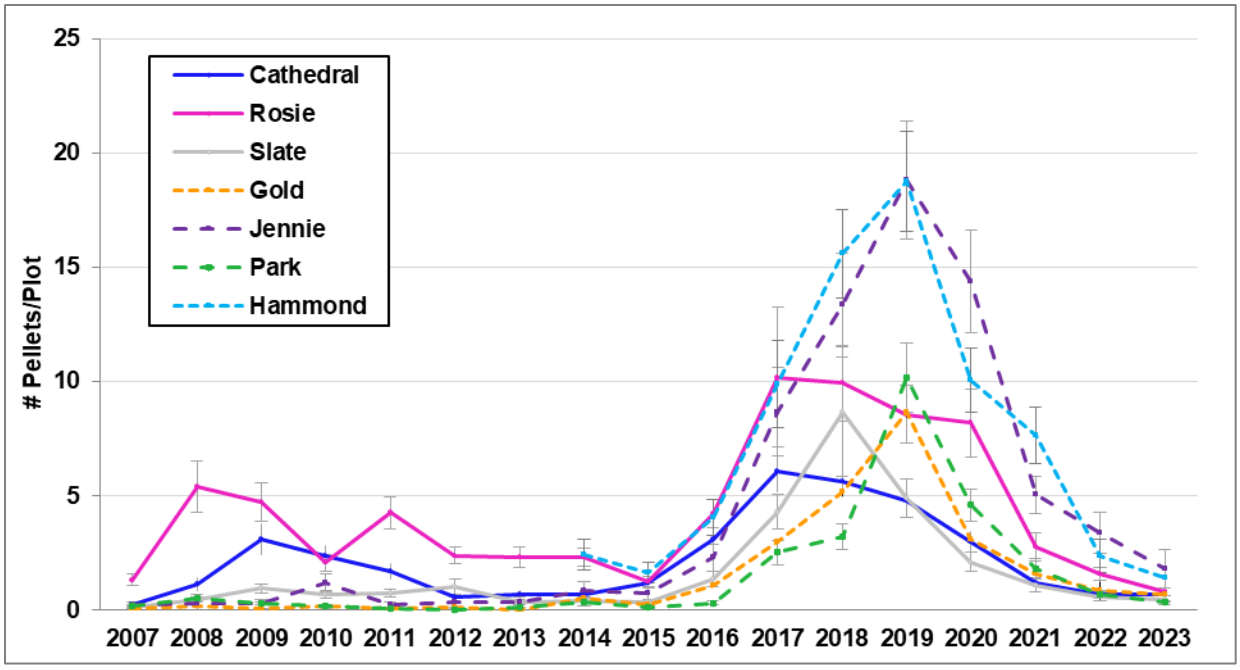


Figure 6. Trends in snowshoe hare populations at seven sites, 2007–2023 (± standard error), as indicated by pellet counts in the Middle Fork Koyukuk River valley (six sites) and Gates of the Arctic National Park and Preserve (Park site). Non-mineral sites (solid lines) are Cathedral, Rosie, and Slate; mineral sites (dashed lines) are Park, Jennie, Hammond, and Gold. Data collection at the Hammond site began in 2014. NPS / DONNA DIFOLCO

The general trends in the hare populations (converted to hares/ha) at mineral and non-mineral sites are compared in Figure 7. This simplification makes it easier to see the differences between the two types of sites more easily and supports the idea, as suggested by local knowledge, that hare populations in mineral areas follow a different pattern than hare populations in non-mineral areas.

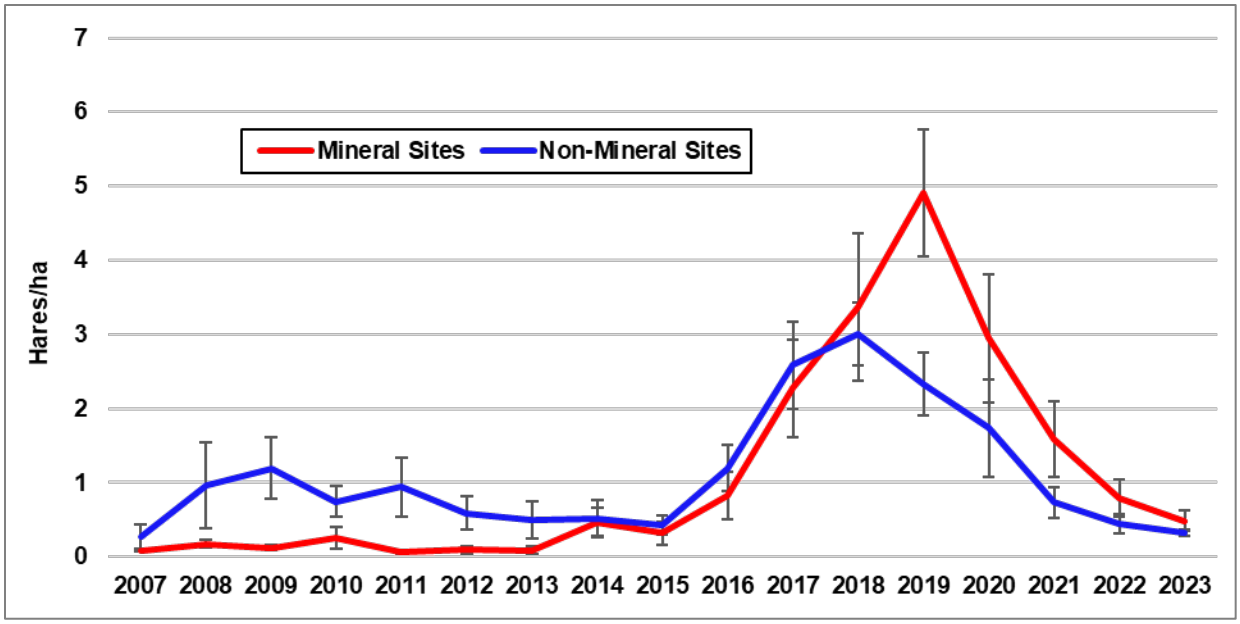


Figure 7. Comparison of trends in snowshoe hare densities as derived from pellet data, converted to hares/ha (± standard error), at four sites where hares have year-round access to mineral licks (Mineral Sites, red line) vs. three sites without year-round access to licks (Non-Mineral Sites, blue line) within the snowshoe hare study area in the central Brooks Range near Wiseman, Alaska, 2007–2023.
NPS / DONNA DIFOLCO

Trail Cameras

The use of mineral licks by snowshoe hares was confirmed by trail cameras at seven locations throughout the study area in and near our mineral grids, although minimal use was recorded at a couple of these locations (Table 2). Naturally formed licks were found primarily along creeks or riverbanks, river terrace edges, sloughs, and man-made road cuts or mining deposits. All these places had some sort of overhang where snow did not accumulate, leaving them exposed throughout the winter or at least until snowfall reached a depth that buried them (or they were overtaken by overflow). The first photos of snowshoe hares engaging in geophagy were captured in the fall of 2017 at the edge of a river terrace in the Hammond pellet grid as hare populations were increasing throughout the region. Extensive use of this lick has been recorded, although use varied greatly among the licks that we monitored.

Table 2. Numbers of photos of snowshoe hares visiting mineral licks (2017–2020) and estimated number of individual visits by hares (multiple photos were usually recorded of each visit) in the snowshoe hare study area in the central Brooks Range near Wiseman, Alaska.

Lick	Number of Photos	Number of Visits
Track Count Transect	3	3
Nolan Flats	718	154
Wiseman Road	1,405	638
Hammond Grid	7,475	1,981
Union Creek	525	125
Confederate Creek	41	35
Gold Creek	23	13

Most activity at the licks occurred in 2018 and 2019 when hare populations were increasing and peaking, supporting the prediction by Wiseman resident J. Reakoff of the timing of geophagic activity in the hare cycle. Some licks saw visitation at all hours of the day; others were visited only at night/dark hours. The Appendix describes each lick and the level of activity each received. Since the drop in hare densities in 2020, observations of geophagy have correspondingly declined.

Potential Licks at Non-mineral Sites

Cameras in non-mineral areas—at three locations at Rosie Creek and one location at Cathedral—did not record any geophagic activity. While this alone does not preclude the possibility of licks in the area, annual site visits to non-mineral areas during winter months verified the lack of geophagy. Had hares been visiting a lick, however small, we would have seen their tracks leading to and from a lick. We observed no use of snow-free creek banks or other areas that could potentially be licks at any of the non-mineral sites. However, during one of the June pellet counts, we did find one pellet at Rosie that looked like it was composed almost entirely of minerals (it was not analyzed however). This suggests that there may be places at non-mineral sites where hares can access minerals during the snow-free season, e.g., on forest floors where seasonal flooding may deposit silt (see Discussion).

Pellet Ash Content

Ash concentrations of hare pellets at mineral sites Gold, Hammond, and Jennie were greater in 2019, when hare densities were at their peak, than when hare densities were at their low in 2015. The opposite was found for pellets from Park, also a mineral site, and Rosie and Cathedral, non-mineral sites, which had lower concentrations of ash in their pellets in 2019 than in 2015. There was virtually no difference in the ash content of pellets from Slate, a non-mineral site, in 2015 and 2019 (Figure 8).

The ash content of pellets collected in 2019 directly from licks along Wiseman Road (16.3%) and at Gold Creek (17.8%) contained a greater proportion of ash than any of the samples from the pellet grids, mineral and non-mineral.

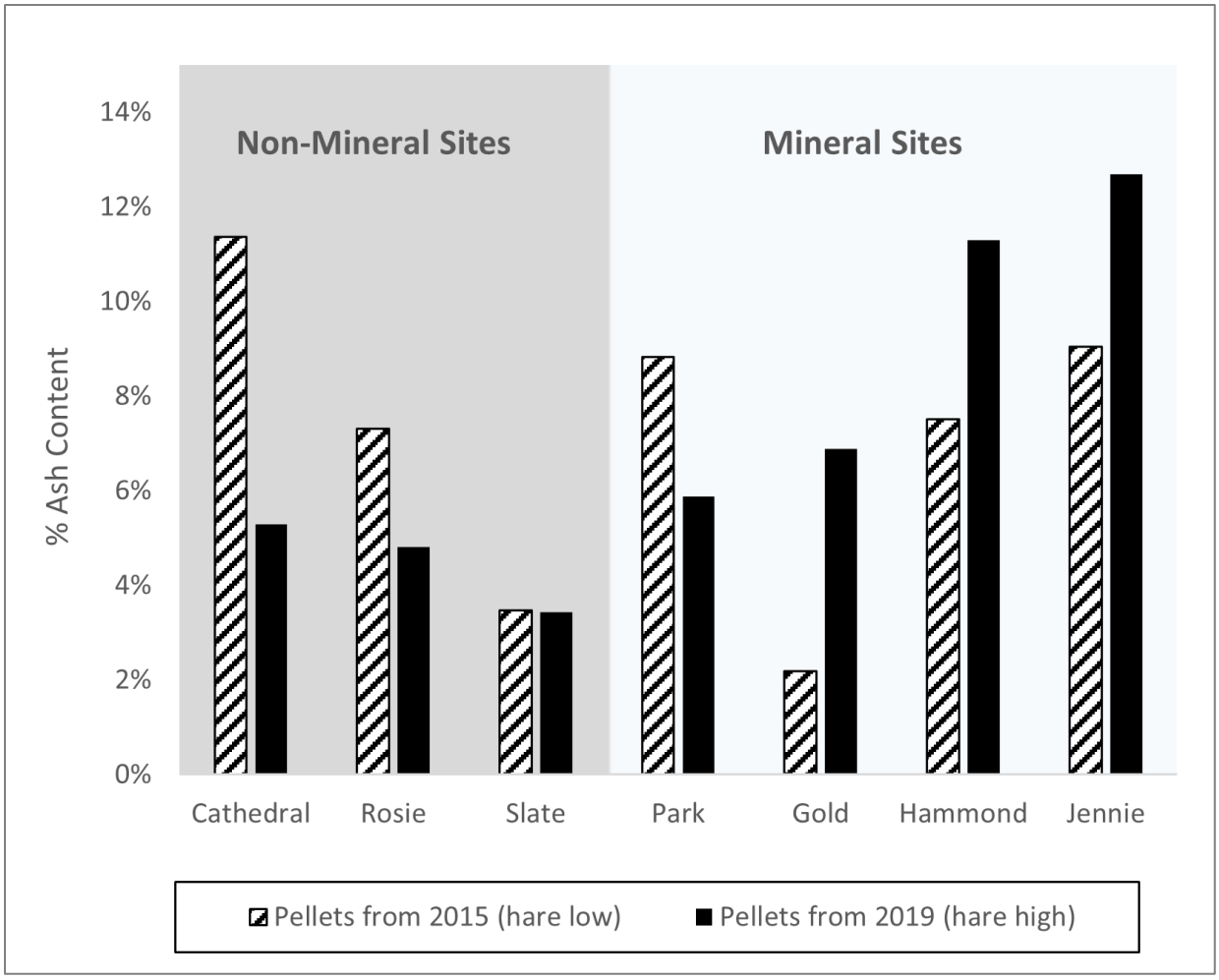


Figure 8. Percentage of ash content in snowshoe hare pellets collected from pellet plots in 2015 (a low hare population year) and 2019 (a high hare population year) in non-mineral sites (shaded area) and mineral sites in the snowshoe hare study area in the Koyukuk River drainage near Wiseman in the central Brooks Range, Alaska. NPS / DONNA DIFOLCO

Discussion

The evolution of this study from its start as a simple track count to monitor the snowshoe hare population in the park to an investigation of hare geophagy and population trends in mineral and non-mineral areas has provided interesting insights into snowshoe hare ecology as well as a more practical understanding of methodology. We began the track count during the increase phase of what became a super-peak in the snowshoe hare population in our study area. We quickly learned that track counts, while simple to set up, and effective when hare densities are low, become increasingly difficult as track densities increase. At peak densities, severe overlapping of tracks created compacted snow conditions such that hares left little imprint. During many of our surveys, this was exacerbated by the lack of fresh snow, as well as by overcast skies causing flat light conditions, the combination of which made discernment of individual tracks extremely difficult. When the area received no fresh snow, we brushed out the old tracks before the count. Even though we used the back of the leaf rake to "fluff" the snow, we unwittingly created more compact snow by "working" it, just as snow "turns to cement" following an avalanche, especially since temperatures often fell to well below 0°F at night. Since most of our counts were conducted under these conditions, we felt that our counts during those early years—particularly in the densely vegetated areas where hares were most abundant—became less accurate as hare densities increased, and that our counts underrepresented actual numbers.

Even with less than perfect conditions during the first few years of the survey, our track count data show that hare densities during the super-peak of 1997–2001 were greater than during the 2017–2019 peak. The distribution of tracks within the VCCs illustrate how the peaks were different by the varying utilization of VCCs during these two periods. As indicated by the track count data, hares do not immediately venture into less densely vegetated areas but remain in more densely vegetated areas until circumstances push them beyond those borders. In 1997, the first year of our track count, 26% of tracks counted were already in light to moderately vegetated areas. As the hare population continued to increase over the next few years, the proportion of tracks counted in less densely vegetated areas expanded to as much as 47% of all tracks counted. By comparison, far fewer tracks were counted in light to moderately vegetated areas during the 2017–2019 peak, with a maximum of 25% of tracks counted in more open areas by 2019. While data for the light and moderately vegetated areas may be inflated relative to densely vegetated areas due to possible undercounting of tracks in densely vegetated areas, the relative differences in habitat use between the 1999 and 2019 peaks are distinctly apparent. This trend of moving into less densely vegetated habitat as high hare population densities persist suggests that the favored, densely vegetated habitat reaches an upper limit for hare densities, thereby forcing hares into less-favored, more-open habitat in search of food.

Snow depth, which can vary greatly from year to year, is one factor that may influence where hares choose to forage. While deep snow may make taller browse more available to hares by giving them a "step up," it may also reduce opportunities for browsing low shrubs, while simultaneously increasing hares' vulnerability to predation as brush cover is buried. At peak hare population densities, browsing intensity increases particularly in densely vegetated areas where hares are most abundant.

The winters of the first super peak (1996–1997, 1997–1998, and 1998–1999) had relatively little snowfall compared to the winters of the second peak (2017–2018, 2018–2019, and 2019–2020) (Western Regional Climate Center 2023; J. Reakoff, unpublished data; D. DiFolco, unpublished data). During the earlier super-peak, due to less snow depth, hares could have expanded into less densely vegetated areas and still found forage and at least minimal cover. In March of 2018, and especially in March 2019, we observed particularly deep snowpacks. There were places where some hares were able to find excellent cover under bowed over alders that been buried by snow. Hares could rest and forage on alder twigs within these caverns. However, for the most part, low vegetation was buried and inaccessible, presenting wide swaths of relatively barren landscape mostly devoid of cover or forage.



Alders buried under deep snow can form caverns that hares may spend time in, as evidenced by abundant pellets, while they forage on alder twigs, also visible in this photo taken in 2018 in Gates of the Arctic National Park and Preserve near Wiseman, Alaska. However, deep snow years can be a double-edged sword, as many forage plants become buried and inaccessible to hares while exposing them to more predation as shrub cover disappears. NPS / DONNA DIFOLCO

Following the super-peak of 1997–2001, we observed considerable mortality of young spruce saplings that were completely girdled and denuded of needles by hares. We have also observed “double trees” sprouting from spruce whose tops were removed by hares, resulting in (usually) two branches taking over the role as the apical stem. There are several fully mature spruce trees in this area that are growing close together that appear to be growing from a single truck at their base, suggesting that this type of regrowth following severe snowshoe hare browsing has occurred in the past.



Spruce trees browsed by snowshoe hares. The young spruce tree in the left photo likely recovered from the girdling by snowshoe hares in 2000, since the top half of the tree was out of reach of hares. However, many small spruce trees were so severely browsed during the hare super-peak of 1997–2001 in the central Brooks Range near Wiseman, Alaska, that they were killed (center photo). In 2008, we observed regrowth occurring on some of the young survivors (right photo), commonly with two former branches becoming the start of a "double tree." There are several fully mature spruce trees in this area that are growing close together, with a single trunk at their base, suggesting that this type of regrowth following severe snowshoe hare browsing has occurred in the past. NPS / DONNA DIFOLCO

Over the course of the last two decades, young spruce trees that survived the early super-peak have grown into larger, more mature trees, and a new crop of spruce saplings is now tall enough to not get buried under snow in a "normal" winter. The increase in the size and distribution of spruce trees has been observed mainly in the more open, lightly vegetated areas along the track count transect. The larger spruce trees can offer hares some cover from predators; however, this relatively recent growth has not yet resulted in any changes in the track count vegetation cover classifications.

Both track and pellet data point to a very long recovery of hare populations following a super-peak in mineral areas. During 1997–2001, in addition to high mortality among young spruce trees, we also observed wide swathes of denuded willow shrubs above the snowline within the study area in the park. Later, when we expanded the study area, we discovered similar levels of spruce sapling mortality at the Jennie mineral site along with the dead stems of willows. Hare populations in non-mineral areas increased to relatively high densities during 2008–2009; however, there was no population boom in mineral areas, where hare densities increased only minimally. Rejected browse stems collected from Park, a mineral site, in 2009 were shown to have elevated levels of tannins relative to browse collected in 2006 when no rejected stems were observed (DiFolco and Maier 2015). This may have been a factor in the low densities and early decline in hare populations in mineral areas. There was no evidence of hare geophagy at that time. Also, as hare populations in non-mineral areas increased, predators also became more abundant throughout the region. Hare populations in mineral areas, still at relatively low levels, may not have been able to overcome the

increased predation pressure and were again depressed to very low levels. Only after predation again became less intense following the decline in hare populations in non-mineral areas did hares in both non-mineral and mineral areas begin rebuilding in 2016 towards another population peak.



Browse rejected by snowshoe hares indicates that the portion of the stem discarded contains antiherbivory compounds that either disrupt or inhibit digestion or are toxic to hares. Hares in Gates of the Arctic National Park and Preserve near Wiseman, Alaska, rejected the stem tips of this willow (left photo) in 2009 as the hare population struggled to recover from extremely low densities. The same year, hares near the Hammond River avoided shrub birch stem tips that were covered in granules of papyrific acid, which is toxic to hares, and can readily be seen in the photo at right. Farther south, local hare populations increased to much higher densities. NPS / DONNA DIFOLCO

As hare populations throughout the study area increased, the numbers of predators also increased. Figure 9 compares our track count data to lynx pelt sealing records from ADF&G for Game Management Unit 24A, the region which includes the upper Middle Fork Koyukuk and Dietrich River valley and its tributaries, and the few records from the Wiseman resident harvest in 24B. The pattern follows the typical one seen in snowshoe hare and lynx populations that have been documented over the past century (Elton and Nicholson 1942, Alaska Department of Fish and Game 2024) and also suggests an alternating pattern of high peaks and low peaks for the lynx population similar to what we have found in the hare population in this area.

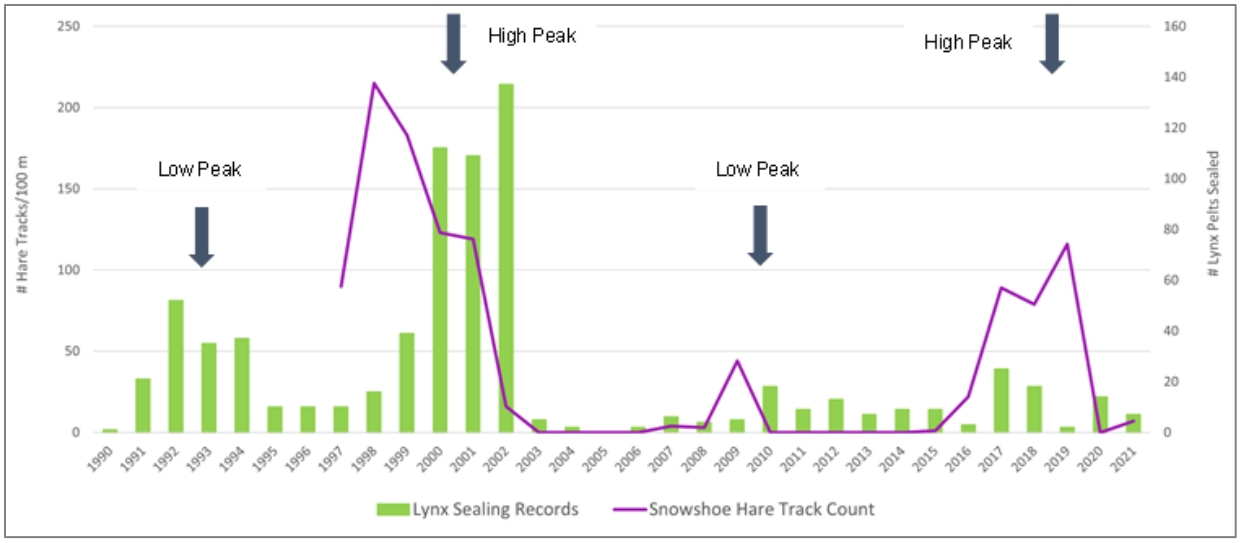


Figure 9. Decadal pattern of lynx (bars) and snowshoe hare (line) populations, depicting large and small peaks for both species, and the time lag for lynx relative to hares, in the upper Middle Fork Koyukuk River drainage, central Brooks Range, Alaska. Data are from Alaska Department of Fish and Game lynx sealing records from GMU 24A, 1990–2021, and snowshoe hare track count records from 1997–2021. NPS / DONNA DIFOLCO

Avian predators also were more abundant when the snowshoe hare population peaked. Reynolds et al. (2021), in a study of great-horned owls in the Brooks Range during the increase phase of the hare population in 2017–2018, discovered that over 90% of their diet was comprised of snowshoe hare. Montgomerie (2020) analyzed blood biomarker and fecal cortisol metabolite levels in snowshoe hare during this same period in the same area. Fecal cortisol, which is associated with stress, did not vary markedly throughout the year other than in August, when it increased by about 105%. At this time of year, lynx kittens are mobile and on a solid-food diet moving about with their mother. This suggests that stress in snowshoe hares may not be associated with nutrition as much as with increased predator activity. Krebs et al. (2018) found that the fecundity of female hares declined, presumably, due to chronic stress from being chased by predators even when supplemental food was available. At the cycle's climax, a tipping point is reached when the stress of predation outweighs the benefits of a dietary supplement/antidote to PSMs, and decreased hare productivity, compounded by increased predation, causes the hare population to plummet.

Along with observations reported by locals of evidence of hare geophagy, we observed signs of geophagic activity during the first few years of the track count (1997–2001) in the form of heavily used trails leading to a lick located along the transect line from the surrounding forest. We observed far less activity at this spot during the peak of 2017–2019, with camera data recording only a few visits in 2017. The ash content of pellets showed fluctuations in mineral content in the diet. Whereas the higher percentages of ash content found in most mineral sites from 2019 were expected, the opposite result from Park is counterintuitive. This may be due to the relatively few pellets found there in 2015—only 7—which were scattered among three of the four transects. Being a mineral site, it is possible that the hare refugia, where hares retreat to during periods of low population densities,

provide not only cover and forage, but access to a mineral source during at least part of the year. During years of higher hare densities, hares are distributed across a broader spectrum of habitats, including areas where minerals may not be as easily accessible. Thus, pellets collected in areas where hares were not consuming (as much) mineral may have diluted the pool of pellets sampled for analysis.



During the snow-free season, mineral “licks” may spring up on bare ground. A bare patch of silt on the forest floor in the Rosie Creek pellet grid, a non-mineral site, appeared as if hares had been using it as a lick due to the presence of pellets and a compacted surface. However, we did not have a camera at this location to confirm this. NPS / DONNA DIFOLCO

In non-mineral areas, where hares may not have year ‘round access to minerals, they may opportunistically take advantage of ephemeral “licks” that appear following seasonal flooding. Silt that was most likely deposited by seasonal flooding in the non-mineral site at Rosie Creek showed evidence that snowshoe hares had visited this spot, possibly using it as a lick. However, since it was directly on the forest floor, it would only be available to hares during snow-free months. Given that camera data suggest that hares visit licks the most during the summer months (Knutsen 2024), perhaps winter access is not as important a factor as we had thought. However, given the differences in the peaks of 1997–2001 and 2017–2019, it’s possible that hares in the earlier peak, which reached

greater densities than during the latter peak, were more compelled to seek additional minerals in their diet. We observed far more winter use of mineral licks in the park during the first several years of the track count than we did later on.

Seasonally available licks at Rosie and Cathedral may help explain why these sites support greater densities of hares than Slate, where we have not observed such ephemeral "licks." Apparently, the geology of the mineral and non-mineral areas—the mineral sites to the north, and the non-mineral sites to the south—is different, inviting further investigation into this question. The minerals originating along the Hammond River and its tributaries, as well as the tributaries of the Middle Fork Koyukuk River north of Wiseman, may be washed downstream and eventually deposited on the floodplain in the Rosie and Cathedral area (but not at Slate, which does not neighbor the Koyukuk River like the other two non-mineral sites do), thereby making the forest floor there rich in the sought after nutrients, but available only during snow-free (and flood-free) seasons.



A soft gray substrate can be found on bluffs used as mineral licks in the central Brooks Range. Snowshoe hare pellets found at the base of this lick were the same pale gray color. NPS / DONNA DIFOLCO

Unsurprisingly, the ash content of pellets collected directly from lick sites was higher than the ash content of pellets collected from the study site pellet grids, which were from much larger and more

heterogeneous areas. While working on another project north of our study area we discovered a lick where we found hare pellets that were a light gray color, the same color as the soft, pale substrate of the lick. When combined with pellets nearby that had more of a "normal" appearance, the ash content at that location was found to be nearly 40%.

The method we used to determine ash content—with a small sample size and combining all pellets collected from a site in a single year—could be improved, and additional research would be useful to determine the variability of the ash content in pellets not only among sites, but within sites.

Feeding trials of snowshoe hares in Alaska have found that hares with access to mineral soil readily consumed it, and thus maintained their weight better than hares that did not have access to mineral supplements (Worker et al. 2015). Local observations suggest that hares do not visit mineral licks regularly throughout the population cycle but utilize licks primarily during the increase and peak phases. On a seasonal basis, preliminary camera data analysis shows that lick visitation rates vary throughout the year, generally seeing the highest rates of visitation during summer (June–August) (Knutsen 2024) corresponding with the annual recruitment by reproduction in the hare population. While hares may choose not to visit licks as much during winter, it is possible that access to some licks may become restricted or blocked, usually during late winter due to heavy snowfall or overflow, thereby prohibiting use of the lick by hares who otherwise may have utilized it. On the other hand, camera batteries were often dead by the time we would replace them during the spring track count visit, so it is possible we were unable to record visits during the latter part of the winter (although these "data gaps" were accounted for in the camera data analyses, L. Knutsen, personal communication). On an individual basis, data from GPS collared hares revealed that, as the hare population was increasing, collared individuals centered their activities around local mineral licks, visiting approximately once every 24 hrs (Kielland et al. 2018). While the specific proportions of elements necessary to meet hares' needs may not all be present in a lick, it appears that geophagic hares seek out and benefit from the nutrients that are available. Worker et al. (2015) found that lick soil (obtained from the lick at Jennie) provided Na, Ca, Mg, K and N, but not P, and suggested that these supplements could alter hares' foraging behavior and consumption of available browse.

An example may illustrate the importance hares place on having access to minerals. As we mentioned earlier, predator populations increase in response to the increase in the snowshoe hare population. Reynolds et al. (2021) described how, when great-horned owl pellets mysteriously disappeared from beneath their nests, they deployed cameras and discovered that the main culprits were snowshoe hares. This seemingly suicidal behavior, given that snowshoe hares comprised 90% of the owls' diets at that time, suggest a craving for minerals that can be satisfied by the consumption of owl pellets. This source of minerals, as opposed to mineral licks, may have ratios of minerals—Ca and P in particular—favorable for hares, as they are likely composed primarily of snowshoe hare bones and fur. Owl pellets would be a restricted mineral source both in time and space, as owl populations rise and fall in response to the snowshoe hare cycle, and active nests would be limited spatially to a breeding pair within each pair's territory. However, since according to our observations and local knowledge, hares seek minerals mainly when their population is increasing and peaking, the timing of owl "mineral deposits" may occur just when needed most by hares.

We have documented three peaks in localized snowshoe hare populations in the central Brooks Range. The data suggest that hare populations in these localized areas follow different patterns, which seem to coincide with the presence or absence of year-round-accessible mineral soils.

Starting in 1997 with the track counts, and initiating pellet counts in 2007, we have documented three peaks in localized snowshoe hare populations in the central Brooks Range. The data suggest that hare populations in these localized areas follow different patterns, which seem to coincide with the presence or absence of year-round-accessible mineral soils. The population trends corroborate with what residents originally told us about the snowshoe hares in this area before we began the study, namely, that hare populations in mineral areas reach super-peaks roughly every 20 years, the intervening 10-year peak being of minor amplitude, while hares in non-mineral areas follow the well-known cycle of more regular 10-year peaks. However, continued monitoring of these cycles is needed to get a more detailed picture of the frequencies and amplitudes of hare populations in this area.

Recommendations for future study

After 27 years of conducting this study, the National Park Service is currently in the process of handing over the snowshoe hare track and pellet counts to the Bureau of Land Management, which, other than the Park site, oversees the land on which the study takes place. The seven sites where the pellet counts are conducted, while selected to be as closely similar as practical, represent a range of hare habitat, some seeming to be more suitable than others. We suspect that areas of poor hare habitat will support hares only when areas of more favorable hare habitat have reached capacity during a population super-peak. Like the hares who ventured into less favorable, more open habitat during the 1997–2001 super-peak in the park, this remarkable occurrence of hares being "everywhere" could be documented in what thus far has appeared to be poor hare habitat at many of our pellet plots at some sites, notably, Slate in the non-mineral area, and Wiseman and Gold in the mineral area. The reason for establishing plots in these areas was the presence of former hare sign in these areas, presumably left there during the super-peak of 1997–2001.

Possible foci of additional study could include a closer look at changes over time in browse species' plant secondary metabolites, the relationship between snow depth and hares' access to browse and cover, and additional data and analysis of mineral content of hare pellets throughout the study area. If time and personnel resources become an issue such that monitoring all seven study sites is prohibitive, then we would recommend trimming the study area down to the four most productive sites: Rosie and Cathedral in the non-mineral area, and Jennie and Hammond in the mineral area. Each pair of sites is geographically close to each other and relatively easy to access. If desired, 100 m transects could be set up in each of these sites for winter track counts. This would be a new start for the track count, but accessibility would be simpler, and the track counts could be directly associated with each site's pellet count. At a minimum, it is our hope that the monitoring of snowshoe hare populations at the local level be continued in some capacity for as long as the agency involved is willing to support this project.

Literature Cited

Bryant, J. P. 1981. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. Science 213:889–890.

Bryant, J. P., G. D. Wieland, T. Clausen, and P. Kuropat. 1985. Interactions of snowshoe hare and feltleaf willow in Alaska. Ecology 66:1564–1573.

DiFolco, D. L. and J. A. K. Maier. 2015. Snowshoe hare (*Lepus americanus*) ecology monitoring in Gates of the Arctic National Park and surrounding areas. Natural Resource Data Series. NPS/GAAR/NRDS—2015/783. National Park Service. Fort Collins, CO.

Elton, C. and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. Journal of Animal Ecology 11:215–244.

Golden, H. 1994. Furbearer track count index testing and development. Alaska Department of Fish and Game, Division of Wildlife Conservation Grant W-24-2, Study 7.17.

Kielland, K., K. Olson, and E. Euskirchen. 2010. Demography of snowshoe hares in relation to regional climate variability during a 10-year population cycle in interior Alaska. Can. J. For. Res. 40:1265–1272.

Kielland, K., D. DiFolco, and C. Montgomerie. 2018. Dining dangerously: geophagy by snowshoe hares. Ecology 0:1–3.

Kluane Ecological Monitoring Project: Monitoring protocols. 2004 edition. Available online at field_manual_2016-long.pdf (ubc.ca) (Accessed 26 June 2023).

Knutsen, L. 2024. Controls over visitation rates to mineral licks by snowshoe hares (*Lepus americanus*) in northern Alaska. MS thesis, University of Alaska Fairbanks.

Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair. 2001. What drives the 10-year cycle of snowshoe hares? BioScience 51:25–35.

Krebs, C. J., R. Boonstra, and S. Boutin. 2018. Using experimentation to understand the 10-year snowshoe hare cycle in the boreal forest of North America. Journal of Animal Ecology 87:87–100.

Krebs, C. J., B. S. Gilbert, S. Boutin, and R. Boonstra. 1987. Estimation of snowshoe hare population density from turd transects. Can. J. Zool. 65:565–567.

Lynx (*Lynx canadensis*) species profile. Alaska Department of Fish and Game. Available online at Lynx Species Profile, Alaska Department of Fish and Game (Accessed 12 August 2024).

Montgomerie, C. K. 2020. Seasonal variation in nutritional biomarkers and fecal cortisol concentrations in a northern population of snowshoe hares. MS thesis, University of Alaska Fairbanks.

PRISM Climate Group, Oregon State University. Data available online at PRISM Climate Group at Oregon State University (Accessed 26 June 2023).

Reynolds, M., J. Shook, G. Breed, and K. Kielland. 2021. Diet and reproductive success of Great Horned Owl (*Bubo virginianus*) at its northern breeding limit. The Canadian Field-Naturalist 135:337–345.

Swanson, S. A. 1994. Furbearer harvest study, Gates of the Arctic National Park and Preserve, Alaska. National Park Service Technical Report NPS/ARRNR/NRTR-94/21.

Western Regional Climate Center. 2023. Total snowfall (inches) for Wiseman, Alaska—monthly totals. WRCC, Reno, NV. Data available online at WISEMAN, ALASKA - Climate Summary (dri.edu) (accessed 15 August 2023).

Worker, S. B., K. Kielland, and P. Barboza. 2015. Effects of geophagy on food intake, body mass, and nutrient dynamics of snowshoe hares (*Lepus americanus*). Canadian Journal of Zoology 93:323–329.

Appendix: Camera placements and descriptions of licks

Track Count Transect Lick

This is a large cavity, likely cut by seasonal flooding, adjacent to Wiseman Creek in Gates of the Arctic National Park and Preserve where the winter trail crosses the creek (Figure 10). We recorded only minimal activity here in October 2017. The lick was flooded with overflow and frozen by December. Numerous challenges were faced with the camera setup at this location and very little activity was either observed via winter tracks or recorded. However, abundant use of this lick was observed during the super-peak of 1997–2001 when numerous hare tracks and well-maintained hare trails led to/from the area. These trails were dirty from the hares being at the lick, which at that time was in the form of a shallow cave and therefore could be used throughout the winter. Currently, much, though not all, of the "roof" of the cave has collapsed and now the area becomes filled with snow or overflow by mid-winter, often preventing hare access later in the season.



Figure 10. A trail camera captures a visit to the Track Count Transect Lick adjacent to Wiseman Creek by a snowshoe hare in Gates of the Arctic National Park and Preserve in the central Brooks Range, Alaska. NPS

Nolan Flats Lick

This lick is a mound of earth that is a relic of historic mining activity in this area (Figure 11). It has since been mostly overgrown with vegetation with bare spots on the side that hares use as a lick. Willows and other shrubs surround the lick, but trees are sparse. Hares used this lick only at night. We began recording activity in early October 2017. As snow accumulated, hares were able to continue using the lick by kicking it out of the way. Hares used this lick regularly until a snowfall of several inches in late January 2018 buried it too deep for them to access.



Figure 11. A snowshoe hare ventures to a lick at nighttime in the Nolan Flats just east of Gates of the Arctic National Park and Preserve in the central Brooks Range, Alaska. NPS

Wiseman Road Lick

This lick is in a steep bank of a slough of the Middle Fork Koyukuk River, between the river and the Wiseman Road (Figure 12). The bank is used heavily by ground squirrels, but a couple spots are favored by hares as lick sites. In winter, hares will completely disappear into these small caves to access the mineral soil as videos from the trail cam at this location show. Visits by hares to this lick were recorded periodically between October 2017 until June 2019.



Figure 12. A snowshoe hare visits a mineral lick along a slough of the Middle Fork Koyukuk River near Wiseman, Alaska. NPS

Hammond Grid Lick

This lick is a roughly 2-ft high terrace of the Hammond River, from which hares access minerals along an approximately 15-ft stretch (Figure 13). The lick is bordered by mature spruce on its upper edge and alders on the lower, river bar side, which provide reasonable cover for hares, who have been recorded visiting the lick at all times of the day and night. This is the first site where we recorded photographs of snowshoe hare geophagy in the study area in August 2017 and is where we have recorded the greatest amount of geophagic activity, logging visits to the lick by hares through January 2022. While usually only a single hare is seen at the lick, during June 2018, we recorded up to three hares using the lick simultaneously. Lynx also have been captured on camera walking along the edge of this lick. For the past couple winters, the Hammond Grid Lick has been flooded with overflow, effectively terminating use of the lick until after spring melt.



Figure 13. A snowshoe hare consumes mineral soil along a low terrace of the Hammond River in the central Brooks Range, Alaska. NPS

Union Creek Lick

This camera was set up in early October 2017 at a culvert along the Hammond Road near Union Creek (Figure 14). We recorded multiple instances of hare geophagy over a 10-day period before the batteries died in mid-October and were not changed until February 2018.



Figure 14. A snowshoe hare visits the Union Creek lick along the Hammond Road north of Wiseman, Alaska, in the central Brooks Range. UNIVERSITY OF ALASKA FAIRBANKS

Confederate Creek Lick

This lick is a cutbank along the Hammond Road near the mouth of Confederate Creek (Figure 15). Two cameras on separate occasions recorded activity from Oct 5–Nov 14, 2017, and Mar 23–28, 2018. Like the Hammond Grid lick, multiple hares were recorded simultaneously visiting this lick.



Figure 15. A snowshoe hare visits the Confederate Creek lick along the Hammond Road north of Wiseman, Alaska, in the central Brooks Range. UNIVERSITY OF ALASKA FAIRBANKS

Gold Creek Lick

Camera placement at Gold Creek required some trial and error before eventually finding an adequate location to record lick activity, an inconspicuous cut bank along the creek bed (Figure 16). Hare geophagy here was documented in March 2018 and April–June 2019.



Figure 16. A snowshoe hare visits the Gold Creek lick in the Middle Fork Koyukuk River valley in the central Brooks Range, Alaska. NPS



A midday sun dog glows over the Koyukuk River valley near the mouth of the Hammond River, near a mineral lick frequented by snowshoe hares, in February 2019. NPS / DONNA DIFOLCO

National Park Service
U.S. Department of the Interior

Science Report NPS/SR—2024/214
https://doi.org/10.36967/2306544



Natural Resource Stewardship and Science
1201 Oakridge Drive, Suite 150
Fort Collins, CO 80525

NPS 185/195270, November 2024