

Review

# A Worldwide Review of Snowy Owl Feeding Ecology: The Importance of Lemmings and Voles in a Changing Climate

Denver W. Holt <sup>\*</sup>, Matthew D. Larson <sup>†</sup>, Mathew T. Seidensticker <sup>‡</sup> and Stephen P. Hiro <sup>§</sup>

Owl Research Institute, Charlo, MT 59824, USA; mattdlarson@hotmail.com (M.D.L.); mat\_seidensticker@yahoo.com (M.T.S.); stevehiromd@gmail.com (S.P.H.)

<sup>\*</sup> Correspondence: owlmontana@blackfoot.net; Tel.: +1-406-644-3412

<sup>†</sup> Present address: Independent Researcher, 2000 Raymond Ave., Missoula, MT 59802, USA.

<sup>‡</sup> Present address: Independent Researcher, 136 Luby Lane, Florence, MT 59833, USA.

<sup>§</sup> Present address: Independent Researcher, 3026 Old Pond Road, Missoula, MT 59802, USA.

**Simple Summary:** It is common knowledge that Snowy Owls eat lemmings during the nesting season, and it is believed that lemming populations fluctuate dramatically over several years, often termed a cycle. When lemming populations reach high densities, Snowy Owls have a highly successful breeding season, producing numerous young per nest. This successful nesting results in large numbers of young Snowy Owls migrating south during their first winter. This movement, generally called an irruption migration, has been known for over a century, and stirs the admiration of the public. Indeed, each time an irruption migration happens, it is among the most popular wildlife viewing events in North America. Given this predator–prey relationship between Snowy Owls and lemmings, we were interested in quantifying how important lemmings were to Snowy Owls throughout their worldwide breeding range. Of the 15 studies we reviewed, 59,923 prey items were recorded. Lemmings were clearly the most important food source for breeding Snowy Owls, but voles were sometimes also important. Given the near obligate dependency on lemmings for breeding, one wonders how a changing climate will affect lemming populations and distribution, and consequently Snowy Owl breeding. And, will this affect the Snowy Owl breeding population, resulting in fewer young Snowy Owls migrating south during an irruption migration.



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**Abstract:** We compared Snowy Owl feeding ecology from 15 breeding season studies throughout Nearctic and Palearctic circumpolar regions. We used raw data and information theory to assess the owls' feeding niche. Combined studies yielded 59,923 prey items, of which 59,585 were used for calculations. Overall, mean food niche breadth (FNB) was narrow:  $H' = 1.95$ ;  $R = 1.60$ ,  $D = 0.526$ . In 10 of 15 studies, lemmings were > 71.8% of the owls' diet. In four studies, *Lemmus* was > 90% of the diet, and in three studies *Dicrostonyx* was >90% of the diet. In three other studies, *Lemmus* represented 71.8%, 73.8%, and 84.0% of the diet. In one study, *Lemmus* and *Dicrostonyx* were about equal: 49.1% and 47.5%. In the four remaining studies, *Microtus* and *Clethrionomys* voles were important. In contrast, of 5888 winter prey items from seven North American studies, the mean FNB ( $H' = 4.61$ ) was twice that of 15 breeding season scores, FNB ( $H' = 1.95$ ). The Snowy Owl is primarily an obligate lemming predator for breeding. Changes to population ecology and distribution of lemmings due to climate change will have direct affects and effects on the Snowy Owls' reproductive output. The conservation of Snowy Owls is the conservation of lemmings.

**Keywords:** snowy owl; *Bubo scandiacus*; breeding; feeding ecology; lemmings; voles; conservation; climate

## 1. Introduction

The Snowy Owl (*Bubo scandiacus*) is a large ground-nesting species that breeds in the circumpolar region of the northern hemisphere (Holt et al., 1999 [1], Holt, 2006 [2], König and

Weick, 2008 [3], Holt et al., 2020 [4], Holt et al., 2024 in press [5]). It has the most northern breeding and non-breeding distribution of any owl species in the world. The Snowy Owls' circumpolar distribution has led previous researchers to suggest that it is a monotypic species (Parmelee, 1992 [6]). Results from one mtDNA (mitochondrial DNA) study suggested a single global panmictic population (Marthinsen et al., 2008 [7]), and later buttressed by SNP (single-nucleotide polymorphism) analysis (Gousy-LeBlanc et al., 2023 [8]).

Several studies have reported the breeding ecology of this species in Canada (Watson, 1957 [9], Parmelee, 1972 [10], Taylor, 1973 [11], Parker, 1974 [12], Therrien et al., 2015 [13]); Great Britain (Tulloch, 1968 [14], Robinson and Becker, 1986 [15]; Greenland (Gilg et al., 2006 [16]); Russia (Dorogoy, 1987 [17], Menyushina, 1994 a, b, c [18–20], 1997 [21], 2007 [22], Wiklund and Stigh, 1983 [23], 1986 [24], Wiklund et al., 1998 [25], Potapov and Sale, 2012 [26], Morozov et al., 2013 [27]); Scandinavia (Løenskoid, 1947 [28], Hagen, 1960 [29], Andersson and Persson, 1971 [30], Hakala et al., 2006 [31]); and the United States (Murie, 1929 [32], Pitelka et al., 1955 a, b [33,34], Holt et al., 2008 [35], Seidensticker et al., 2011 [36], Holt et al., 2015 [37], Holt, 2020 [4], and Holt et al., 2024 in press [5]).

With the exception of Menyushina (1994 a, b, c [18–20], 1997 [21], 2007 [22]) from Vrangal Island, Russia (1982–2014), and this study from Utqiagvik (formerly Barrow), Alaska (1990–2024), most breeding season studies were intermittent or lasted only 1 to 4 seasons.

Nonetheless, it has been common knowledge for >100 years, that Snowy Owls are dependent on high densities of lemmings for successful breeding (Holt et al., 2020 [4], Holt et al., 2024 in press [5]). But surprisingly few studies have quantified this common knowledge with large sample sizes from the entire Snowy Owl breeding range (Holt et al., 2020 [4], Holt et al., 2024 in press [5]). And, given the importance of lemmings to Snowy Owl breeding, there has been no overall review of the owls' feeding ecology and relationship with lemmings in a changing climate.

Lemmings, are small Arvicoline rodents and have the most northern distribution of any rodent species in the world (Stenseth and Ims, 1993 a, b [38,39], Ehrich et al., 2020 [40]). Lemming's live much of their life under the snow, and are known to have dramatic population fluctuations where amplitude and density vary annually through space and time—often called “cycles” (Stenseth and Ims 1993 a, b, [38,39], Pitelka and Batzli, 2007 [41], 2018 [42], Krebs, 1993 [43], 2013 [44], Ehrich et al., 2020 [40]). Whether lemmings cycle in a predictable mathematical fashion is unlikely, yet patterns do emerge.

However, clear answers to population fluctuations of lemmings remain complicated, despite an enormous amount of research (Stenseth and Ims, 1993a [38], Krebs, 1993 [43], 2013 [44], Pitelka and Batzli, 2007 [41], Pitelka and Batzli, 2018 [42], Ehrich et al., 2020 [40]). Most researchers would agree, however, that multifactorial events, both intrinsic and extrinsic, such as food, predators, social behavior, genetics, and climate play a role (see Krebs, 2013 [44]).

Herein, we provide an assessment of the Snowy Owl breeding season feeding ecology throughout its circumpolar breeding range. We emphasize the importance of lemmings for the successful breeding of Snowy Owls. We also suggest how a changing climate might affect, and have an effect on, lemmings, with related consequences to Snowy Owls. To emphasize our assessment, we also compare breeding season feeding ecology with non-breeding season/winter feeding ecology.

Our objectives were as follows: (1) compare the Snowy Owl breeding season feeding niche throughout the Arctic; (2) compare the breeding season feeding niche with the winter feeding niche; (3) discuss the importance of lemmings to Snowy Owl breeding success and conservation; (4) discuss the potential affects and effect of lemmings being replaced by voles in Arctic regions as the climate warms, and (5) suggest future research directions.

## 2. Materials and Methods

We reviewed breeding season food habits of 15 studies throughout the Snowy Owls' worldwide breeding range. These areas include Canada, Finland, Greenland, Norway, Russia, Sweden, and the United States (Figure 1). We only included studies with >200 prey

items to ensure we had reasonable sample sizes of prey, and a reasonable sample of studies. For some studies, we back-calculated prey reported as percentages to numbers.



**Figure 1.** Approximate locations of Snowy Owl food habits studies cited in this manuscript. Note there are 16 red pins for the 15 studies. The Wrangel Island site is included in the Wiklund et al. (1998) [25].

We summarized and discussed the percent of total prey that were small mammals (i.e., lemmings, voles) for the combined studies. To describe the owls' feeding ecology, and make comparisons among studies, we calculated Food Niche Breadth (FNB) and Dietary Evenness (DIEV), see below. We also compared breeding season feeding ecology from these 15 studies, with seven winter season feeding ecology studies, reviewed by Detienne et al. (2008) [45]. We did this to show the dietary diversity and flexibility of Snowy Owls during winter, but the obligatory narrowness during breeding.

To explore Snowy Owl feeding ecology (e.g., Food Niche Breadth (FNB) and Dietary Evenness (DIEV)), we used information theory equations to examine the structure of the owls' feeding niche. Also known as diversity indices, we chose the Shannon–Weaver and Simpson equations to examine species richness, and Hill's equation to examine evenness (see Marti et al., 2007, [46]). Ultimately, these equations allow large data, such as those presented here, to be weighted in order of "importance" and expressed as single values. For example, although several species of birds or small mammals could be in the diet, they are such a low percentage that they are not important, while others are. In turn, values can be compared from different studies, provided that the same or similar methods are used. There are strengths and weaknesses to each equation, with some reviewers favoring one equation over another, and some reviewers see little or no value (see Zar, 1999 [47], Marti et al., 2007 [46], Collier and Schertner, 2012 [48] for reviews). For example, the antilog of Shannon–Weaver's diversity index is linearly related to the number of prey categories in the sample. Some statisticians believe  $H'$  can underestimate diversity unless samples are large (Zar, 1999 [47] (p. 41), whereas others believe  $H'$  can be biased if many species are represented (Collier and Schertner, 2012 [48] (p. 62). For Simpson's equation, we used the reciprocal ( $1/D$ ) because it is believed to yield a more meaningful number (Marti et al., 2007 [46]). Some statisticians prefer Simpson's  $D$  over Shannon–Weaver  $H'$ , as it is simple to calculate and understand, robust, and meaningful (Collier and Schertner, 2012 [48] (p. 62). Due to differing opinions, we provide both values for comparisons.

We defined the annual feeding niche as the relationship between the owls and their prey, and followed Holt, 1993 [49], Cromrich et al., 2002 [50], Detienne et al., 2008 [45] in describing FNB and DIEV. Because FNB and DIEV are influenced by levels of resolution, we attempted to identify all prey to species. However, that was not always easy, because of different methods used to identify prey by different researchers, and characteristics of prey were not always identifiable.

We used a Mann–Whitney non-parametric medians test because samples from cached prey at nests could also show up in pellets, thus violating the assumptions of independence of the parametric test for means. Furthermore, non-parametric tests are appropriate for comparing indices, such as diversity and evenness scores (Fowler and Cohen, 1990 [51], Zar, 1999 [47]). Alpha levels were set at 0.05.

We defined a broad FNB as a high number of prey species, relatively equally distributed in the owls' diet (i.e., heterogeneous); and a narrow FNB as a low number of prey species, relatively unequal distribution in the owls' diet (i.e., homogeneous). Because DIEV scores range from zero to one, we considered a score of one or approximating one, a uniform representation of prey proportions in the diet. And, scores  $< 0.50$  represent non-uniform or shared distribution of prey in the diet (see Detienne et al., 2008 [45]).

#### *Information Theory*

Food niche breadth (FNB) was calculated using the antilog of the Shannon–Weaver index, where

$$H' = -\sum p_i \log p_i$$

and  $p_i$  represents the proportion of each species in the sample.

Food niche breadth FNB using Simpson's equation was calculated, where

$$D = \sum p_i^2$$

where  $p^i$  is the proportion of each member of the assemblage being investigated. Hill’s dietary evenness (DIEV) scores were calculated, where

$$F = (N_2 - 1)/(N_1 - 1)$$

and  $N_1$  is the antilog of the Shannon–Weaver index ( $H'$ ) and  $N_2$  is the reciprocal of Simpson’s index, where  $(1/D)$ . We used Spearman Rank Correlation to examine if FNB and DIEV scores were influenced by sample size.

We then discuss our findings on the predator–prey relationship between Snowy Owls and small mammals, particularly lemmings. Finally, we suggest future research directions.

### 3. Results

#### 3.1. Comparison with Other Breeding Season Studies

The combined 15 studies yielded 59,923 prey (Table 1). Although various methods were used to tally prey among studies, we tried to standardize these data with our methods. Thus, 59,585 prey were used for these calculations.

**Table 1.** Food niche breadth (FNB) and dietary evenness (DIEV) of breeding Snowy Owls from 15 studies worldwide. Total prey items were 59,923. However, because we used only prey identified to species for niche calculations, the total number was 59,585.  $H'$  = Shannon’s Diversity Index;  $R$  = Simpson’s Diversity Index;  $D$  = Hill’s Dietary Evenness Index. Table Code: Location = country of study; # prey = total number reported from study; # prey used = total number of prey items identified to species at least once; # species = total number of species identified from each study; % L = *Lemmus* lemmings; % D = *Dicrostonyx* lemmings; % M = *Microtus* voles; C = *Clethrionomys* voles; % O = Other prey species.

Location	# Prey Total	# Prey Used	# Species ID	% L	% D	% M	% C	% O	$H'$	R	D
Alaska <sup>1</sup> USA pellets	43,689	43,689	23	94.6	3.1	0.0	0.0	1.3	1.38	1.19	0.423
Canada <sup>2</sup>	2263	2263	7	49.1	47.5	0.0	0.0	3.4	2.30	2.14	0.873
Canada <sup>3</sup>	964	964	2	98.1	1.9	0.0	0.0	0.0	1.09	1.03	0.391
Canada <sup>4</sup>	425	423	3	97.4	9.0	0.0	0.0	<1	1.12	1.04	0.381
Canada <sup>5</sup>	358	358	5	2.8	96.0	0.0	0.0	1.2	1.22	1.08	0.370
Canada <sup>6</sup>	265	265	5	0.0	94.7	0.0	0.0	5.3	1.30	1.11	0.368
Finland <sup>7</sup>	1301	1062	13	41.8	0.0	20.5	35.7	1.5	4.01	3.24	0.744
Finland <sup>8</sup>	811	739	17	58.1	0.0	13.5	23.3	5.0	3.37	2.44	0.610
Greenland <sup>9</sup>	4024	4003	10	0.0	99.1	0.0	0.0	<1	1.07	1.01	0.266
Norway <sup>10</sup>	1395	1395	8	14.7	0.0	80.5	0.0	4.5	1.89	1.52	0.583
Norway <sup>11</sup>	288	285	11	84.0	0.0	11.0	0.0	0.0	1.92	1.37	0.400
Russia <sup>12</sup>	2730	2730	3	53.0	9.1	37.8	0.0	0.0	2.51	2.30	0.864
Russia <sup>13</sup>	994	994	9	71.8	26.8	<1	0.0	<1	1.96	1.70	0.730
Russia <sup>14</sup>	210	209	8	73.8	0.0	17.6	0.0	8.6	2.61	1.75	0.471
Sweden <sup>15</sup>	206	206	6	90.3	0.0	7.3	0.0	1.5	1.51	1.21	0.424
Total	59,923	59,585									
Mean									1.95	1.60	0.526
Range									107–4.01	1.01–3.24	0.266–0.873
SD									0.878	0.659	0.194

SUPERSCRIPT CODES: <sup>1</sup> Holt et al. (this study 1992–2016)—Barrow, Alaska; <sup>2</sup> Therrien et al. (2015)—Bylot Island Canada [13]; <sup>3</sup> Watson (1956)—Baffin Island, Canada [52]; <sup>4</sup> Watson (1957)—Baffin Island, Canada [9]; <sup>5</sup> Parker (1974)—South Hampton Island, Northwest Territories, Canada [12]; <sup>6</sup> Kennedy (1981)—Prince of Wales Island, Northwest Territories, Canada [53]; <sup>7</sup> Hakala et al. (2006) \*—Finland [31]; <sup>8</sup> Hakala et al. (2006) \*—Finland [31]; <sup>9</sup> Gilg et al. (2006)—Greenland [16]; <sup>10</sup> Løenskoid (1947)—Norway [28]; <sup>11</sup> Hagen (1960)—Norway [29]; <sup>12</sup> Potapov and Sale (2012)—Russia [26]; <sup>13</sup> Wiklund et al. (1998)—Russia [25]; <sup>14</sup> Morozov et al. (2013)—Russia [27]; <sup>15</sup> Andersson and Persson (1971)—Sweden [30]. \* Two studies included in this citation; 1975/1975 and 1988/1989.

Overall, the mean feeding niche calculated from the 15 breeding season studies was narrow:  $H' = 1.95$ ;  $R = 1.60$ ,  $D = 0.526$ . The lowest values were  $H' = 1.07$ ;  $R = 1.01$ ;  $D = 0.266$ , from Greenland, and the highest:  $H' = 4.01$ ;  $R = 3.24$ ; from Finland, while  $D = 0.873$  from Canada (Table 1). In 10 of the 15 studies, lemmings (*Lemmus* and/or *Dicrostonyx*) were >71.8% of the owls’ diet. Lemmings dominated the diet in most studies (Table 1). In four studies, *Lemmus* was >90% of the diet, and in three studies *Dicrostonyx* was >90% of the diet. In three other studies, *Lemmus* represented 71.8%, 73.8%, and 84.0% of the diet. In one study, *Lemmus* and *Dicrostonyx* were about equally represented: 49.1% and 47.5%, respectively. In

the remaining four studies, *Microtus* and *Clethrionomys* voles were important. For example, in one study from Norway, *Microtus* made up 80.5% of the diet, while in two other studies from Finland, prey was more evenly distributed among three species, with *Lemmus* (41.8%), *Clethrionomys* (35.7%), and *Microtus* (20.5%) having higher proportions in one study, and *Lemmus* 58.1%, *Clethrionomys* 23.3%, and *Microtus* 13.5% in the other study. In the final study from Russia, *Lemmus* and *Microtus* were 53.0% and 37.8% of the diet (Table 1).

### 3.2. Comparison with Other Non-Breeding Season Studies

Feeding ecology of wintering Snowy Owls in North America was conducted and reviewed by Detienne et al. (2008) [45]. They only calculated Shannon–Weaver  $H'$ , and Hill's Dietary Evenness  $D$ , for their study. Of 5888 prey items reported from 7 studies, the mean winter FNB ( $H' = 4.61$ ) was more than twice that of the 15 breeding seasons reported herein, FNB ( $H' = 1.95$ ). Interestingly, however, DIEV between winter;  $D = 0.531$  ( $n = 7$  studies) and breeding DIEV,  $D = 0.526$  ( $n = 15$  studies) were similar (Table 2).

**Table 2.** Food niche breadth (FNB) and dietary evenness (DIEV) of Snowy Owls from seven non-breeding/winter studies from North America, representing 5888 prey items. Prey were identified as species for comparison. Table Code: Location = USA state and/or country of study; total prey = # total number reported from the study;  $H'$  = Shannon's Diversity Index;  $D$  = Hill's Dietary Evenness Index.

Non-Breeding/Winter			
Location	Prey Total	$H'$	$D$
Canada <sup>1</sup>	240	3.26	0.647
Canada <sup>2</sup>	212	7.73	0.584
Michigan <sup>3</sup>	185	1.65	0.509
Michigan <sup>4</sup>	121	2.99	0.552
Montana <sup>5</sup>	4680	1.28	0.428
New England <sup>6</sup>	136	13.85	0.559
Canada <sup>7</sup>	314	1.49	0.441
Total	5888		
Mean		4.61	0.531
Range		1.28–13.85	0.428–0.647
SD		4.64	0.078

SUPERSCRIPIT CODES NON-BREEDING/WINTER (citations in Detienne et al., 2008 [44]). <sup>1</sup> Boxall and Lein 1982—Alberta [54]; <sup>2</sup> Campbell and MacColl 1978—British Columbia [55]; <sup>3</sup> Chamberlin 1980—U.S.A. [56]; <sup>4</sup> Allan 1977—U.S.A. [57]; <sup>5</sup> Detienne et al. (2008)—U.S.A [45]; <sup>6</sup> Gross 1944—U.S.A [58]; <sup>7</sup> Catling 1973—Ontario [59].

## 4. Discussion

Our comparisons of studies from Nearctic and Palearctic regions buttress a consensus that Snowy Owls are primarily obligate lemming predators for successful breeding. In fact, lemmings are the primary prey from most areas, although northern species of voles can be important in certain years, and regions. Overall, however, lemmings constitute the majority of prey in all but one study. And, only in unusual circumstances do breeding Snowy Owls deviate from this predator–prey relationship. Thus, environmental perturbations that affect, and have an effect on, populations of lemmings could have direct effects on Snowy Owl breeding populations—whether negative or positive.

The fact is, lemmings drive the ecology of the tundra wherever they occur, and influence the reproductive output of numerous species of birds and mammals (see Behavior; Social and Interspecific Behavior; Unique Snowy Owl interactions with other species/Association with Non-predators: in Holt et al., 2024, in press [5]).

Nonetheless, why has natural selection favored such a narrow feeding niche for breeding Snowy Owls? Foremost, the most reasonable explanation is the narrow diversity of prey species, particularly small rodents, throughout the Snowy Owls' Arctic breeding range. Next, the Snowy Owl is one of the largest and heaviest owls in the world (Holt et al., 1999 [1], Holt et al., 2024, in press [5]). Thus, its individual food requirements are likely high. And, feeding a family—female and brood probably require an enormous

amount of food. Consequently, preying on the sparsely distributed stable population of small tundra nesting birds apparently does not fulfill these energetic requirements. However, preying upon abundant small rodents such as lemmings, during population highs, do. Indeed, lemmings and voles can exhibit dramatic population fluctuations, where intervals between population highs, amplitude, and density, vary annually. For example, during times of high populations, lemmings can increase by factors of 25, 50, 200, or more (see Krebs, 1964 [60], Krebs, 1993 [43], Pitelka and Batzli, 1993 [61]; Pitelka and Batzli, 2007 [41], Krebs, 2013 [44], Ehrich et al., 2020 [40], D. Holt, unpubl. data, this study 1992–2021).

Each Snowy Owl and lemming annual population fluctuations have their own signature, and numerous factors—abiotic and biotic—are believed to influence those fluctuations. So how do Snowy Owls find, and assess, regional populations of lemmings, and decide to stay and breed, move on, or forego breeding for that season? It has long been suggested Snowy Owls wander the Arctic in search of high lemming densities in order to breed. This hypothesis remains to be verified annually on a large geographic scale. Nonetheless, what cues/mechanisms do Snowy Owls use to search and discover high densities of lemmings or voles for breeding? Currently, this is unknown, but at our study site in Utqiagvik, Alaska, Snowy Owls never miss a high lemming population, and immediately respond to annual spring numbers (D. Holt, unpubl. data, this study 1992–2021). The owls appear to have the ability to assess lemming density quickly—perhaps a day or a few days—and stay or move on, as suggested by Holt et al. (2015) [37], Holt et al., 2024 [5], in press).

#### 4.1. Climate Change

Will climate change affect future lemming populations? In one of the first reports implicating the effects of snow conditions, Shelford (1943) [62] recorded a decline in collared lemmings associated with the absence or reduced amounts of snow cover at Churchill, Manitoba, Canada. And, approximately 40–45 years ago, researchers at Utqiagvik, Alaska, cautioned that climate change could affect snow quality, which is important for winter breeding in lemmings. Thus, any climate change-related effects on winter snow quantity and quality could affect lemming populations (Fuller, 1967 [63], MacLean et al., 1974 [64], Batzli, 1981 [65]).

More recently, fluctuating snow conditions related to climate change are believed to have affected collared lemmings, European lemming (*Lemmus lemmus*), and gray-sided vole (*Myodes rufocanus*) population cycles (Kausrud et al., 2008 [66], Gilg et al., 2006 [16], Karell et al., 2008 [67], Ims et al., 2011 [68], Schmidt et al., 2012 [69]). And, Gilg et al. (2006) [16] provided convincing data that when regional lemming populations decline due to climate change, obligate lemming predators such as Snowy Owls also decline in that area. Additionally, in response to declining lemmings, declines in Arctic fox and Snowy Owls numbers in Norway, and declines and disappearance of Arctic fox, Long-tailed Jaeger, stoat/short-tailed weasel, and Snowy Owls in Greenland were attributed to changes and declines in lemming populations cycles due to climate change (Gilg et al., 2006 [16], Kausrud et al., 2008 [66], Schmidt et al., 2012 [69]).

However, Ehrich et al. (2020) [40] suggested that the lemming population worldwide shows no indications of population declines due to climate change (Ehrich et al., 2020) [40]. If true, then what explains the results of Gilg et al. (2006) [16], Kausrud et al. (2008) [66], and Schmidt et al. (2012) [69]? And, why are nesting Snowy Owl numbers trending downward at our study site at Utqiagvik, Alaska? Are other measures of lemming population health not detected by standardized sampling methods that could be used? And, as concluded by Krebs (2013, pp. 190–208) [44], multifactorial events likely drive lemming and vole population fluctuations.

In an interesting inferential study using SNP methods, Gousy-LeBlance et al. (2023) [8] suggested Snowy Owls have been declining for about 200 years. If true, then have lemmings been declining since then too? Given the conflicting results from papers cited within this section, we suggest a need for another worldwide lemming population assessment. And,

if possible, we also suggest a SNP study be conducted on lemmings to assess if their populations have declined in step with the purported Snowy Owl decline.

#### 4.2. Nutrition

Does the nutritional value of lemming food fluctuate, and thus affect lemming population fluctuations, as suggested by Pitelka and Batzli (2007, 2018) [41,42]? If the nutrition of lemming forage is changing, will this affect lemming growth and body mass? In turn, could this affect successful Snowy Owl breeding?

Of the several multifactorial events driving lemming population fluctuations suggested by Krebs (2013, pp. 190–208) [44], Pitelka and Batzli (2018) [42] stressed that nutrition—the nutrient recovery hypothesis—likely plays the “most important role” in seasonal changes, with predation playing a “smaller role”, and social strife having “little effect”. Whether the nutrient-recovery hypothesis, predation, or social strife in lemming population dynamics has a hierarchical order is not clear. In a thorough review of predation on small mammal population structure in rodents, Krebs (2013, pp. 160–161) [44] emphasized that predation can play a major and a minor role in influencing population structures.

#### 4.3. Vole Incursions

What about northern latitude species of voles? Are they declining or stable in response to climate change? Voles in some latitudes appear to be expanding north. In fact, three studies have suggested vole species are moving northward with a warming climate, and infiltrating lemming habitats (Golovnyuk, 2017 [70], Dudenhoeffer et al., 2021 [71], Sokolova et al., 2023 [72]). If this is a continuing trend, how will vole range expansion affect, and have an effect on, lemmings and Snowy Owls? Will voles eventually replace lemmings in some Arctic regions as the Arctic warms? Will vole population fluctuations (“cycles”) be similar to lemming population fluctuations? Will voles be an adequate food source in terms of numbers/density, and body mass, to maintain breeding Snowy Owls, and other obligate lemming predators? Will voles be as easy to catch as lemmings are believed to be? In a few studies cited herein, voles were important to Snowy Owls’ breeding; however, lemmings are clearly the driving force behind Snowy Owl breeding worldwide (Holt et al., 2024, in press [5]).

### 5. Conclusions

Snowy Owl and lemmings appear to have a long evolutionary predator–prey history. We recommend long-term studies that monitor lemming population fluctuations while simultaneously monitoring Snowy Owl population fluctuations, and nesting production. This is the only way to assess factors that might influence the predator–prey dynamics between these species. These studies should cover multiple lemming population fluctuations, perhaps 20 or more years at a minimum. Any environmental perturbations that affect, and have an effect on, lemming and vole populations throughout the Arctic, whether negative, neutral, or positive, will have direct effects on Snowy Owl breeding populations.

The Snowy Owl is the avian icon of the Arctic. However, it is lemmings that drive Snowy Owl breeding success. Unfortunately, lemmings are rodents, and have rodent stigma. Indeed, they do not fit the charismatic social appeal that other animals do. However, given Snowy Owls’ enormous popularity and good looks, it renders them the poster animal to help galvanize Arctic conservation. By using Snowy Owl population fluctuations as an indicator of lemming population fluctuations, Snowy Owls could be the harbinger/indicator of a healthy Arctic environment, both locally and wide-ranging. Finally, one must conclude—how lemmings go—so do Snowy Owls.

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