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EDITED BY
Aurelio F. Malo,
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REVIEWED BY
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Eastern Washington University, United States
Lech Stempniewicz,
University of Gdańsk, Poland

*CORRESPONDENCE
Anders Angerbjörn
anders.angerbjorn@zoologi.su.se

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The triangulation between Arctic birds, Arctic foxes and Arctic lemmings

Anders Angerbjörn[1]*, Magnus Tannerfeldt[1] and Sören Svensson[2]

[1]Department of Zoology, Stockholm University, Stockholm, Sweden, [2]Department of Ecology, Lund University, Lund, Sweden

Many studies have suggested that Arctic predators preying on lemmings, especially the Arctic fox, take advantage of the high prey densities during peak years, but have to switch to alternative prey during years of low lemming density, thereby forcing other prey species into the basic lemming cycle. Data on the number of breeding geese and waders in Arctic areas show three-year cycles, supporting this hypothesis. There are two alternative explanations for such a prey switch. The switch to the alternative prey could be due to a functional prey response, which assumes that the proportion of birds in fox diet should be related to lemming population phase due to a type III functional response between foxes and lemmings. The numerical switch explanation on the other hand, assumes that bird numbers should be related to lemming population phase because of a time lag in the numerical response between foxes and lemmings. With data on the diet and population numbers of Arctic foxes, Arctic lemmings and Arctic birds from eight different sites in northern Siberia, we tested these hypotheses. The use of birds in fox diet was not related to lemming population phase. Instead, we found a time lag in numerical response to lemmings, thus supporting the numerical switch explanation for the alternative prey hypothesis.

KEYWORDS

predation, lemming cycle, geese, waders, *Vulpes lagopus*

Introduction

Predation is a powerful process in terrestrial ecological communities (Sinclair et al., 2003). Most attention has so far been paid to the larger predators (e.g. Owen Smiths and Mills, 2008; Ripple et al., 2000) but there is an increasing interest in how meso-carnivores function in mammal communities (Roemer et al., 2009; Ims et al., 2017; van Schaik et al., 2025). Studies have shown a strong top-down effect of predation control on a preferred prey (e.g. Elmhagen et al., 2010), but also a cascading effect on secondary prey populations (Terborgh and Estes, 2013).

Most of these studies have been performed in complex mammal communities including many species. However, in ecological systems with fewer links, the community effects can be more pronounced and easier to study. Arctic mammal communities have very few but dominating species where Arctic lemmings (*Lemmus* spp, *Dicrostonyx* spp.) for example show dramatic fluctuations in their population dynamics (Krebs, 2013; Gauthier et al., 2024). During some years densities can be very high, followed by a sharp decline and crash in numbers. These density changes are known to follow a more or less cyclic pattern of three to four years between peak years and have attracted scientists for more than a century (Collett, 1912; Elton, 1949; Stenseth and Ims, 1993; Chitty, 1996; Krebs, 2013). These cyclic dynamics of lemming numbers are of substantial interest in analyses of Arctic ecosystems (Krebs et al., 2003; Ims and Fuglei, 2005; Krebs, 2013; Ims et al., 2017). Similar cyclic pattern can be seen for many birds of prey and mammalian carnivores (Pitelka et al.1955; Finerty, 1980; Bety et al., 2002; Legagneux et al., 2012). Further, breeding success of Arctic birds such as waders and ducks have also been shown to follow the lemming cyclicity, often with one-year time lag (Summers et al., 1998; Bety et al., 2001; Blomqvist et al., 2002; Gauthier et al., 2003). Many studies have therefore suggested that Arctic predators preying on lemmings reach high densities during peak years, but switch to alternative prey during years of low lemming density, and thereby might force other prey species into the basic lemming cycle, the so called "Roselaar - Summers hypothesis" or "the alternative prey hypothesis" (Roselaar, 1979; Angelstam et al., 1984; Summers, 1986; Summers et al., 1998; Blomquist et al., 2002). Recent warming in Arctic areas have severe consequences (Post et al., 2009) and have raised concerns for disruption to the population dynamics both of lemmings (Kausrud et al., 2008; Coulson and Malo, 2008); Schmidt et al., 2012; Ehrich et al., 2020; Soininen et al., 2025; but see Gauthier et al., 2024) and of Arctic birds (Aharon-Rotman et al., 2015). This can have profound effects on several ecological processes (Ims et al., 2008).

Data on the number of breeding geese and waders in Arctic areas typically indicate three-year cycles, supporting "the alternative prey hypothesis" (Summers et al., 1998). Further, Summers et al. (1998) found a strong cross-correlation between Arctic fox (*Vulpes lagopus*) numbers and first-year brent geese (*Branta bernicla*), indicating that the breeding success of geese was better in years when lemming numbers increased than during lemming peak years. It was suggested that predators, especially the Arctic fox, after a decline in lemming numbers would switch diet from lemmings to birds (Roselaar, 1979; Summers and Underhill, 1987, 1998, Blomquist et al., 2002; Gauthier et al., 2003). Most studies have noted how the phase of the lemming cycle affects different species of Arctic birds. But interestingly, the apex of the widely accepted "alternative prey hypothesis" in Arctic areas, i.e. the mechanism behind a proposed switch in predator diet, is not clear.

The relationship between predators and their prey is governed by two major characteristics of the predator: their behavioral (functional) response to changes in prey numbers, and their numerical response to such changes. There are some scenarios in which Arctic foxes could affect the prey fluctuations observed by Summers et al. (1998). One possibility is that Arctic foxes towards *lemmings* show a type III sigmoid response function typical of generalist predators (Taylor, 1984), where they readily switch to birds when lemming numbers decline. If so, the proportion of birds in fox diet should be related to the *phase* of the lemming cycle but independent of bird *numbers*. The switch to the alternative prey would in this case be due to a functional prey response. We call this the functional response hypothesis. If Arctic foxes instead show a type II functional response to lemmings (Angerbjörn et al., 1999) the switching to birds would be both weak and late.

An alternative explanation is that the cross-correlation pattern between foxes and birds is an effect of a delayed numerical response of fox numbers to lemming numbers, whereby fox numbers would be highest when the lemming population declines (which indeed was found by Angerbjörn et al., 1999). The switch to the alternative prey in this case would then be due to a numerical explanation. We call this the numerical response hypothesis. The observed variation in breeding success of for example geese would thus be an effect of a variation in predator numbers only, but not the result of a behavioral switch in diet preferences. In this case the number of birds should be related to the *phase* of the lemming cycle. The functional response to *birds* in this case could be of several types. A specialist (type II) functional response would emphasize fluctuations more than would a proportional (type I) response, as the bird population at intervals would be driven to very low levels by the predator. A type III response function to *birds* would instead tend to stabilize the predator-prey system (Taylor, 1984).

In a study of Arctic foxes and geese, Wilson and Bromley (2001) pointed out that both numerical and functional response should be taken into account in analyses of prey switch and cyclic lemming populations. They demonstrated a similar numerical pattern as in other studies (e.g. Gauthier et al., 2003), but they had no quantitative data on functional response. In this study we attempt to test the two alternative mechanisms using a set of data from 17 study sites across Northern Siberia (Angerbjörn et al., 1999). Thus, instead of temporal data that would be more natural to use in these analyses, we have used a geographical data set where natural variation within one season has given us contrasts in both predator and prey numbers and thereby generating comparable data as the temporal data set would. This assumes that there are similar ecological functions through Northern Siberia.

Materials and methods

Our study was performed during a ship-based expedition along the north coast of Siberia in the summer of 1994, where we visited 17 study sites from the Kola Peninsula in the west to Wrangel Island in the east (Figure 1; Hedberg, 1995). At each site, colleagues censused lemming populations, focusing on the Siberian lemming *Lemmus sibiricus* (Erlinge et al., 1999) and the collared lemming *(Dicrostonyx torquatus)* (Fedorov et al., 1999; Fredga et al., 1999), while we surveyed Arctic fox dens and collected scats for diet analysis (Angerbjörn et al., 1999; Wiklund et al., 1999). All these inventories were about 10 kilometer apart (Hedberg 1985) and in similar habitats. From eight sites, 1 to 10, we also performed a quantitative survey of the abundance of birds during the first leg of the expedition (Svensson, 1995). There are thus two data sets, one for the first eight sites

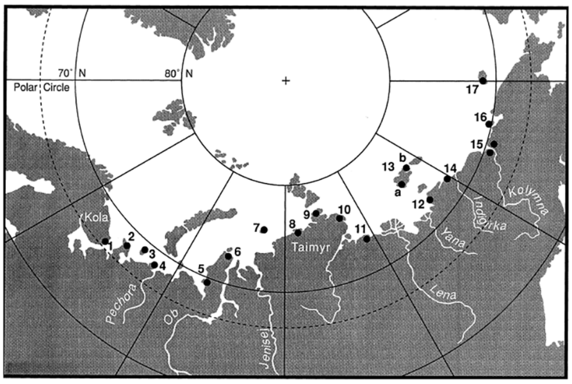

FIGURE 1
Map of the study area. Site names and numbers are seen in Table 2.

including bird inventories (Table 1) and the total set of 17 sites including estimates of abundance of lemmings and Arctic foxes (Table 2).

Arctic fox dens are usually situated in characteristic landforms and have lush vegetation due to digging and fertilization, making them relatively easy to locate at a distance (e.g. Smits et al., 1989; Prestrud, 1992; Dalerum et al., 2002). When scanning through the landscape we could identify dens from several kilometer distance and sometimes even at 10–20 kilometers. By walking at ridges we could thus scan through the landscape and cover large areas. A single visit at a den was sufficient to detect if it was occupied or not, and further inspections clarified whatever if it was a breeding den with a litter of Arctic foxes. When single foxes visit dens during the summer, there are no or very few food remains and no clear run ways (Dalerum et al., 2002). Given the open and relatively homogenous tundra landscape, and well-established den monitoring routines, we assumed that we found a similar proportion of dens in all inventoried areas (Angerbjörn et al., 1999). The number of occupied dens multiplied by two was used as an index of density of breeding Arctic foxes (Angerbjörn et al., 1999). The area inventoried at each site varied from 35 to 160 km^2, mostly depending on the time spent at each site (Table 1). During the expedition, we covered 1464 km^2 and inspected 142 Arctic fox dens (Wiklund et al., 1999).

We collected Arctic fox scats (feces) at all occupied dens. Fresh scats, from the summer of 1994, were separated from older scats by appearance. We ignored scats that were two years or older, as determined by extensive weathering, generally being white and brittle, or overgrowth of vegetation from previous seasons. Fresh and old scats contained similar proportions of migrating birds (Angerbjörn et al., 1999), indicating that scats on dens were from summers only, making age separation easier. Scats were dried at 90°C and prey remains were identified using reference material. In the analysis of scats we identified bird groups, rodent species, reindeer *Rangifer tarandus*, mountain hare *Lepus timidus*, insects and plant material, as far as possible. We could distinguish bird remains from Anseriformes and Galliformes (Day, 1966; Brom, 1986), but excluded waders since they are difficult to identify in fox scats (Day, 1966; Brom, 1986; Elmhagen et al., 2000), and passerines because of their minor importance for Arctic foxes (Dalerum et al., 2002; Ehrich et al., 2017). Egg shells are underestimated in scats and we only found less than 1% at the different sites. Molecular methods with DNA coding (Schmidt et al., 2022) or stable isotopes (Samelius et al., 2007) would be needed to reveal the amount of eggs consumed. Thus. given with the problems of egg identification and bird inventories, our estimates regarding birds should be

TABLE 1 Number of birds observed along line transects at the eight different sites in Siberia including the dominating species in each bird group on each site.

Site	Observ. Length km	Observ. Time (h)	No. Birds/ 10 h	No. Birds observed				Dominating species, no. obs.		
				Ducks	Divers, merganser	Geese, swans	Grouse	Ducks	Divers, merganser	Geese, swans
1	15.5	5.7	103	25	7	51	27	Clangula hyemalis 16	Gavia stellate 7	Anser fabilis 39
2	12.2	9.4	136	34	13	82	20	Anas crecca 11	Mergus meganser 5	Anser fabilis 44
3	14.3	8.6	400	2	4	216	182	Anas acuta 2	Gavia arctica 4	Anser albifrons 189
4	15.8	7.8	265	99	10	130	36	Clangula hyemalis 58	Gavia arctica 5	Anser fabilis 63
5	42.7	17.2	69	10	1	40	19	Clangula hyemalis 8	Gavia arctica 1	Anser albifrons 23
8	30.8	13.8	74	23	1	45	6	Polystica stelleri 15	Gavia arctica 1	Anser albifrons 30
9	27.1	9.8	116	9	0	107	0	Somateria spectabilis 9	0	Branta bernicla 107
10	32.8	12.9	22	10	0	10	2	Somateria spectabilis 8	0	Branta bernicla 10

TABLE 2 Summary of lemming and arctic fox inventories.

Site		Date	No. trapped/24h		Area km2	Fox/ 100km2	% in fox diet					Population
			Lemmus	Dicro			Lem Dicro		Lemmings	Birds	Fresh Fox scats	Phase
Kola Peninsula	1	9.6	0.89	0.00	109	3.67	26.12	0.00	26.1	21.8	48	Low
Kanin Peninsula	2	11.6	0.00	0.00	79	2.53	0.00	35.00			2*	Low
Kolguyev Island	3	14.6	0.00	0.00	70	5.71			0.0	98.2	19*	n/a
Pechora Bay	4	16.6	0.00	4.80	84	7.14	24.97	13.89	38.9	41.2	62	Low
W Yamal Penins	5	18.6	12.71	16.47	93	10.75	44.81	42.65	87.5	4.16	166	Extended peak
N Yamal Penins	6	21.6	0.00	8.73	39	5.13	80.94	6.76	87.7	2.00	50	Peak/decline
NW Taymyr Peninsula	8	24.6	36.26	4.60	79	10.13	51.02	12.84	63.9	29.3	35	Extended peak
Chelyuskin Peninssula	9	27.6	29.54	48.92	65	6.15	39.25	60.55	99.8	0.00	25	Peak/decline
NE Taymyr Peninsula	10	30.6	23.52	2.40	104	9.62	64.49	30.46	95.0	0.57	35	Extended peak
Olenëkskiy Bay	11	6.7	2.04	0.51	90	2.22	88.62	8.72	97.3	0.67	30	Low
Yana Delta	12	12.7	14.88	9.12	67	26.87	79.83	16.37	96.2	3.20	50	Increase
N.S.I. Faadeyevskiy	13a	10.7	51.76	0.00	100	28.00	98.80	0.00	98.8	0.53	75	Peak
N.S.I. Kotel'nyy	13b	12.7	40.26	0.00	35	28.57	60.45	28.78	89.2	0.00	40	Peak/decline
Indigirka/ Lopatka	14	15.7	14.29	0.57	130	24.62	89.66	9.84	99.5	0.20	50	Decline
Kolyma Delta	15	18.7	36.00	11.00	110	5.45	52.91	40.09	93.0	7.00	10	Increase
Ayon Island	16	20.7	1.20	0.00	50	8.00	50.47	35.03	85.5	0.00	30	Low
Wrangel Island	17	25.7	33.00	24.00	160	12.50	35.33	64.23	99.6	0.44	45	Peak

Site numbers, dates (day.month) and names follow Hedberg (1995). Asterisk (*) denotes data that were excluded from calculations; at site 3 due to absence of rodents, at site 2 due to small sample size. N.S.I., New Siberian Islands. Data on arctic foxes are from Angerbjörn et al., 1999 and population phase of *Lemmus* from Erlinge et al., 1999. For bird data see Table 1.

considered underestimations. However, these shortcomings would be similar in all areas and therefore not cause a systematic bias.

We used a modified frequency of occurrence measure to estimate the amount of each prey category (Angerbjörn et al., 1999; Elmhagen et al., 2000). When there were remains from more than one species in a single scat, we took into account the proportion of each prey species by dry volume. For example, one scat with 40% *Lemmus* and 60% *Dicrostonyx* plus another scat with 60% *Lemmus* and 40% *Dicrostonyx*, were considered to be equivalent to one scat with 100% *Lemmus* and one with 100% *Dicrostonyx*. We call this semi-quantitative measure "percent whole scat equivalents" (% WSE) (Angerbjörn et al., 1999; Elmhagen et al., 2000). Sample sizes remain the same as for frequency of occurrence. The advantage of this measure is that the relative amount of each prey category in the feces is taken into account. This is especially important for rare prey items that occur in small quantities in each scat. With a strict frequency of occurrence measure, these would be over-estimated.

We noted all birds observed along systematic line transects at the eight sites in June (Table 1; Svensson, 1995). We chose routes to cover representative samples of the most important habitats. All transects were on low elevation tundra up to 15 km from the coast. During slow walks (the same speed on all transects), all birds seen or heard were recorded. The length of the transects differed between sites (Table 1), and we have thus used number of birds per 10 hours transect walk as an index of bird densities. We had to work during different hours a day, but light conditions do not change much between day and night in the Arctic summer. The main inventories were made between 09:00 and 21:00 (86%) and a few in the early mornings (06:00 – 09:00: 7%) or late evening (21:00 – 24:00: 7%). The weather conditions were stable with little rain (Svensson, 1995). In this paper we have used an estimate of the number of birds of interest for Arctic foxes, i.e. the sum of ducks, geese, swans and ptarmigan (Anseriformes and Galliformes). For a more detailed description of the bird surveys, see Svensson (1995). Since we stayed at each site only 1–3 days, the breeding season for the birds was different during the expedition. However, we moved successively to higher latitudes through June, and therefore visited the different sites at approximately the same phenological time. The data emanate from the nest building, laying or early incubation period at sites 1-10. The statistical analyses are linear and non-linear regressions performed in excel.

Population densities of lemmings were estimated by snap trapping. However, different methods were used when trapping the two lemming species present. Relative density estimates of the Siberian lemming, *Lemmus sibiricus*, were obtained according to a standardized grid snap-trapping program with 300 snap-traps (Erlinge et al., 1999). With data on lemming demography and dendrochronological methods, Erlinge et al. (1999) determined the phase of the population cycle for the *Lemmus* (Table 2). Traps for the collared lemming, *Dicrostonyx torquatus*, on the other hand, were set on selected sites with 200 Sherman live traps and 50 snap-traps (Fedorov et al., 1999; Fredga et al., 1999), and the results are not directly comparable to those from the grid trapping for *Lemmus.* We therefore calculated a "total lemming index" for each site (Angerbjörn et al., 1999; Wiklund et al., 1999), based on total number of trapped lemmings (both *Lemmus* and *Dicrostonyx*) per 24 hours with a constant number of 550 traps. This is the lemming density index used throughout this study.

Results

The basic patterns in abundance of birds, lemmings and arctic foxes showed large variation over this vast area with clear population peaks of lemmings on especially the Arctic islands in eastern Siberia (Table 2) but also on Taymyr and Yamal Peninsulas (Table 2). The Arctic fox density followed this with similar high densities. For the birds the highest abundance was also on an island but in western Siberia, Kolguyev Island, followed by the close Pechora Bay (Table 1) with the dominating species White-fronted and Bean goose. However, on the Yamal Peninsula, Brant goose showed highest abundance (Table 1). Among the ducks, Long-tailed duck and King eiders were common (Table 1).

Arctic fox diet was dominated by lemmings of both *Lemmus* and *Dicrostonyx* genera. In populations with high lemming densities, there were between 60 and 99% lemmings in Arctic fox scats (Table 2). However, foxes also utilized birds to some extent and on Kolguyev Island (Table 2), where rodents are absent, birds constituted 98% of their diet. The highest bird density was also found on Kolguyev Island. Although we found rodent remains in one of the Arctic fox scats ($n = 41$) from Kolguyev Island, it is likely that this was from a migrating fox. We have therefore excluded data from that site in analyses concerning lemmings.

The numerical response of breeding Arctic foxes (per 100 km^2) to density of birds (observed per 10 h) showed a negative trend and thus no numerical relationship ($y = 8.2 - 0.009*x$; $r^2 = 0.13$; $P > 0.05$) (Figure 2). However, the numerical response of breeding Arctic foxes to lemmings (no. trapped per 24 h) showed signs of a numerical time lag (Figure 3, see further Angerbjörn et al., 1999).

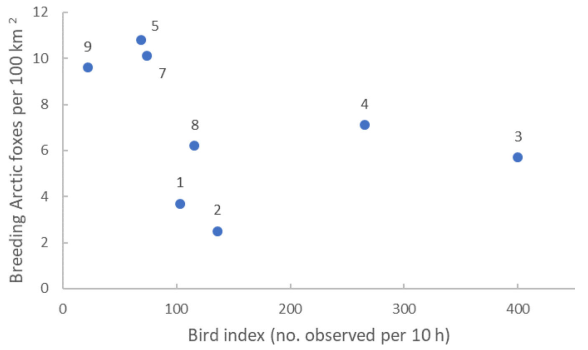

FIGURE 2
The relationship between bird density (no. of observed birds per 10h) and density of breeding Arctic foxes (per km^2), and in relationship to lemming population phase (Erlinge et al., 1999), from eight sites in northern Siberia.

The bold arrows in Figure 3 show the population trend for the lemmings (Table 2) and the thin arrows indicate the direction of a limit population cycle (e.g. Hesaaraki and Moghadas, 2001). There would thus be a high density of foxes the year after a crash as predicted by the numerical switch explanation. Further, there was a tendency that bird density was higher at sites where the lemming population dynamics was in a low phase compared to where it was in peak phase (Figure 2; ANOVA: F (1,4) = 4.70, P = 0.09).

When we compared the amount of birds and lemmings in fox scats, the percentage of birds in fox diet was not related to the lemming population phase (ANOVA, F (3,19) = 0.76, P = 0.54), contradicting the functional switch explanation. On the other hand, there was a clear functional response for foxes preying upon birds, i.e. the percentage of birds in fox scats was related to bird density (Table 2, Figure 3). The response function for birds (Figure 4) was a linear type I function ($y = 0.0032*x - 0.0493$, $r^2 = 0.60$, $P<0.01$). This

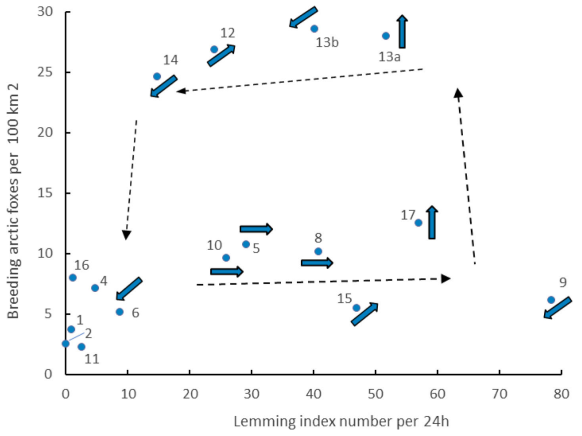

FIGURE 3
Numerical response of Arctic foxes to different population densities of lemmings (*Lemmus* and *Dicrostonyx* spp. combined). Fox density was measured as number of breeding adults per 100 km^2 and lemming trap indices as no. trapped per 24 h for each study site (Table 2). Arrows indicate the direction of the lemming population phase (Table 2). See further Angerbjörn et al. (1999) and Erlinge et al., 1999.

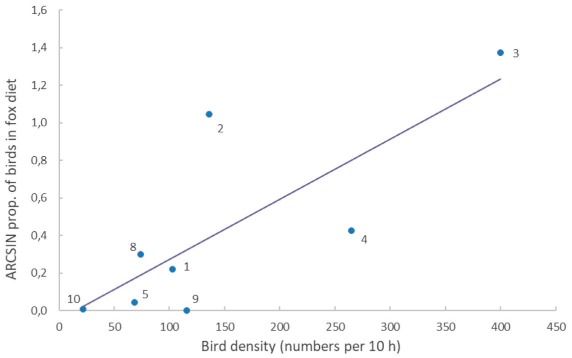

FIGURE 4
The functional response of arctic foxes to different population densities of birds (Table 1). The diet of Arctic foxes was measured as the arcsin of the percentage of whole scat equivalents (WSE) for each site (Table 2). Fitted are the functions of a straight line of a type I functional response curve.

indicates that Arctic foxes prey on birds with little behavioral specificity but rather in direct relation to their availability. On the other hand, Arctic foxes show a strong functional response to lemming species of both genera with a type II functional response ($y = 94.9 * x/(x + 0.57)$; Angerbjörn et al., 1999).

Discussion

Our results indicates that the picture is somewhat more complicated than originally proposed by Roselaar (1979) and Summers et al. (1987, 1998). The variation in reproductive success observed in Arctic geese (e.g. Bety et al., 2002; Blomqvist et al., 2002) cannot be explained only by a diet switch in the Arctic fox, i.e. a switch due to the functional response hypothesis. We found no relationship between percentage of birds in fox diet and population phase for lemmings, and no evidence for a specific behavioral response other than a linear increase of birds in diet with increased bird density. Instead, there was a tendency that bird density was related to the phase of the lemming cycle, as many other studies have found (Summers et al., 1998; Blomqvist et al., 2002; Bety et al., 2002). However, for the numerical hypothesis we plot the number of breeding Arctic foxes against the lemming index and we get a pattern suggesting a time lag based on the population phase for the rodents (Erlinge et al., 1999). This also indicates a pattern of a classic limit cycle for a predator-prey system that can be generated with a functional response (Hesaaraki and Moghadas, 2001). It would be very interesting to analyze the empirical predator-prey data with the theoretical framework in e.g. Hesaarake and Moghadas (2001). Although not formally tested, this indicates a time lag in numerical response for foxes preying on lemmings (Angerbjörn et al., 1999, see also Macpherson, 1969), thus supports the numerical response hypothesis. This would result in a high density of Arctic foxes the year after a lemming population peak. The functional response of Arctic foxes preying on their major prey, the lemmings, was a steep type II, which would postpone the switch to birds and therefore strengthen the effect on bird numbers. Angerbjörn et al. (1999) showed that the functional response to *Lemmus* was of type II but for *Dicrostonyx* they found a type III response, although *Lemmus* is considered as the dominating species in Siberian tundra areas (Danell et al., 1999; Ims and Fuglei, 2005). This could actually indicate a limit cycle (Hessaraki and Moghadas, 2001). Altogether, our results indicates that the population dynamics of lemmings influence breeding Arctic birds through a time lag in the numerical response that Arctic foxes show towards especially *Lemmus*. There might be another relationship between *Dicrostonyx*, Arctic foxes and birds, which could explain some anomalies in the breeding pattern of birds (Spaans et al., 1998). There might be similar difference in how Arctic foxes hunt different geese species or waders, but we were unable to detect any patterns of this in our data. More detailed studies, including longer visits during different phases of the lemming cycle, would be needed to validate this conclusion.

Arctic foxes seem to be specialized on *Lemmus* with a steep functional II response but show a type III response function to *Dicrostonyx* suggesting a stabilizing effect on the latter (Angerbjörn et al., 1999). The predation pattern further indicates that Arctic foxes exploit birds in an opportunistic way in relation to availability (Bantle and Alisauskas, 1998; Elmhagen et al., 2000, Dalerum and Angerbjörn 2000). There are thus similarities in how Arctic foxes utilize birds and *Dicrostonyx*. However, in areas where *Lemmus* are absent or rare, *Dicrostonyx* might assume the role of the dominating, and thus preferred, prey species as for example on Greenland (Dalerum and Angerbjörn 2000). However, Schmidt et al. (2008) found a type III functional response for Arctic foxes and *Dicrostonyx* lemmings in Greenland. An interesting question is why a predator like the Arctic fox is not perfectly opportunistic, but shows preference for certain prey types. As shown on islands without rodents, or in contacts with man, Arctic foxes can quickly adapt to new food types and hunting techniques. Yet, in Siberia and Fennoscandia they are specialized on *Lemmus* (Angerbjörn et al., 1999; Elmhagen et al., 2000; Norén et al., 2023). It might be an effect of specific search images and hunting techniques, but this question remains unresolved.

Similar prey switching cases have been studied in a few other mammalian communities. Angelstam et al. (1984, 1985). found evidence that the mountain hare (*Lepus timidus*) population was forced into a red fox-vole cycle of four years through an alternative prey switching in the boreal ecosystem in Fennoscandia. Red foxes showed a time lag in numerical response to their main prey, *Microtus agrestis* and *Myodes glareolus*, and a type II functional response to both vole species (Lindström, 1982). There is no information on to what extent the secondary prey is consumed in relation to population phase of the primary prey species. However, all other information indicates that the cyclic population fluctuations for the alternative prey populations can be explained by a delayed numerical response. In boreal areas in North America, the dominating mammalian herbivore is the snowshoe hare (*Lepus americanus*) with its 10-year cycle. Predators like the Canadian lynx (*Lynx candensis*), great horned owl (*Bubo virigianus*) and coyote (*Canis latrans*) follow these cycles, but through prey switching different grouse populations and squirrels are also forced into the same cycle (Bergerud, 1983; Keith, 1974; Keith et al., 1977, O'Donoghue et al., 1997, 1998). The predators showed a delayed numerical response to their main prey, the snowshoe hare, both in the Alberta and Yukon studies (Keith et al., 1977; Rohner, 1996; O'Donoghue et al., 1997). The functional response for lynx and great horned owl to snowshoe hares was of type II in both studies, and for coyotes a type II in the Yukon but type III in Alberta (Keith et al., 1977; O'Donoghue et al., 1998).

In another red fox-vole system in southern Sweden, Erlinge et al. (1984) instead found that generalist predators stabilized vole fluctuations by switching between rabbits and voles due to a numerical response. Reid et al. (1997) came to the same conclusion when red foxes could switch between Arctic ground squirrels, *Spermophillus paryii*, and lemmings, and thereby stabilizing lemming fluctuations. Red foxes in Arctic areas do not prey on lemmings to the same extent as Arctic foxes do (Smits et al., 1989; Frafjord, 1995; Elmhagen et al., 2002). Thus, in these cases red foxes functioned as generalist predators and could stabilize prey populations through a high population density. It is possible that cases where cyclic predator population cause secondary prey populations to cycle are confined to animal communities with few species and low productivity (Boutin, 1995), where even "generalist" predators behave as specialists (O'Donoghue et al., 1997).

This study gives support to the hypothesis that lemmings are key species in Arctic ecosystems and that changes in lemming abundance can cause cascade effects in several other organism groups. Lemming population fluctuations affect Arctic foxes, which in turn affect breeding success and population numbers of Brent geese. These observed cascade effects were caused by changes in predator numbers with a time lag, not by changes in predator behavior, thus supporting the numerical switch explanation for the alternative prey hypothesis.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/supplementary material.

Ethics statement

The animal study was approved by Försöksdjursorganisation vid Stockholms universitet. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

AA: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing. MT: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing – review & editing. SS: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Writing – review & editing.

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Conflict of interest

The authors declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

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