SUPPORTING ONLINE MATERIAL

Cyclic dynamics in a simple vertebrate predator-prey community

Olivier Gilg, Ilkka Hanski & Benoît Sittler

In our model (main article), the numbers of lemmings predated by the arctic fox, the long-tailed skua and the snowy owl were calculated based on the functional and numerical responses of the predators presented in Fig. 1 (main article). All these species feed mostly on lemmings, which account for >90% of their diet when lemming densities are >1 ind./ha. At lower lemming densities, the main alternate prey are birds (ptarmigan, waders and passerines) for the snowy owl, small birds, fishes, invertebrates and berries for the long-tailed skua, and arctic hare, muskox carrion, birds, eggs, invertebrates and berries for the arctic fox (O. Gilg et al. in prep.).

Below, we present a more detailed description of the methods used to calculate (i) the functional and (ii) numerical responses of these predators to the lemming density, (iii) the field-estimated parameter values (Table S1), and (iv) how we implemented the numerical responses in the model (the functional responses were simply added to the prey equation as presented in the main article).

Additionally, we describe (v) how we estimated the lemming density at snowmelt *(N')* based on the density of winter nests for 1988-2002 and on direct live-trapping for 1998-2002. We present (vi) the empirical support for lack of space or food limitation in lemming dynamics. We describe (vii) the assumptions involved in the calculation of the functional and numerical responses of the stoat. Finally, we present (viii) the parameter values used for calculating the results in Fig. 3 and the justification for these values (Table S2).

Functional responses

Functional responses can be calculated by plotting the daily rates at which prey are consumed by an individual predator (daily consumption rate, DCR) against the estimated lemming density *N* for the same time period *(S1-S4)*.

Avian predators. To calculate DCR for avian predators, we monitored the birds in the field. The monitoring involved five pairs (10 adult birds) of snowy owls in 1998-1999, three pairs of long-tailed skua in both 1998 and 1999 and one pair of long-tailed skua in 2002 (total: 14 adult birds). One to two trained ornithologists observed birds from hides with a telescope during 3 (skua) and 6 hour (owl) monitoring bouts. The aim was to cover all hours of the 24 hours and hence to sample possible circadian variation in predators' activity. Monitoring always involved the two adults of a breeding pair, but during incubation only one individual had to be looked for since only the male snowy owl hunts (and feeds the female) while the skuas take turns at the nest. Additional monitoring bouts were done in 2000 and 2002 for non-breeding long-tailed skuas at randomly chosen points within the study area. In this case, all individuals (single or in groups) that could be seen were monitored simultaneously. DCR was calculated by pooling the results for several monitoring bouts as follows:

$$DCR = 24 \cdot \frac{\sum n_i}{\sum (P_i \cdot h_i)}, \qquad \text{eqn (S1)}$$

where n_i is the number of lemmings predated during monitoring bout i lasting h_i hours and during which P_i individual predators were monitored. Eqn (S1) was used to calculate DCR for breeding pairs of both species before hatching (P=2) and for non-breeding long-tailed skua in 2000 and 2002.

Following hatching, the number of lemmings captured by breeding adults constantly increases to meet the age-dependent needs of the offspring and hence eqn (S1) cannot be used as such. For snowy owl, the weight W_t of a t-day old young follows a growth curve during the ≈ 45-day long fledging period *(S5-S9)* that can be described by Ricklefs's equation *(S10)*:

$$W_t = \frac{A}{1 + e^{-k(t-t_i)}}, \qquad \text{eqn (S2a)}$$

where A is the asymptotic (adult) body weight, k is a constant and t_i is the age in days at which the inflection point of the curve ($W_t = A/2$) is reached.

The daily food requirements of young owls (X_t) follow a similar but steeper curve than W_t, the daily needs being already maximal after 20-25 days *(S9, S11)*. According to a detailed feeding experiment *(S9)*, the daily food requirements of a young bird can be approximated by a variant of the previous equation, where A' is the asymptotic feeding rate in g per day (i.e. the daily food requirements of an adult bird):

$$X_t = \frac{A'}{1 + e^{-2k\left(t - \frac{t_i}{2}\right)}}. \qquad \text{eqn (S2b)}$$

The growth curve of young long-tailed skuas has a similar shape than that of the owl though their fledging period is only ≈ 25 days long *(S12-S15)*. Values for k and t_i have already been published for NE Greenland *(S13)*. Eqn (S2b) was thus used for both the owl and the skua, and from the point of view of food consumption, every juvenile of age t was considered to

represent a fraction X_t /A' of a "functional adult". Hence, DCR calculated based on the monitoring of breeding pairs with hatched young was estimated as

$$DCR = 24 \cdot \frac{\sum n_i}{\sum \left(\left(2 + \sum \frac{X_t}{A'} \right) \cdot h_i \right)}, \qquad \text{eqn (S3a)}$$

We note that X_t/A' is calculated separately for each young since hatching is asynchronous and hence the young in the same nest have different ages.

Contrary to long-tailed skua, owls use large hunting territories and the hide was not always close enough to the birds to allow specific identification of the prey captured during the monitoring bout. Hence, the number of lemmings caught during a monitoring bout (n in eqns S1 and S3a) was calculated by multiplying the total number of vertebrate prey individuals captured during the monitoring bout by the proportion of lemmings found in the pellets at the same period.

The outlier for long-tailed skua in Fig. 1 refers to August 1998 when large lemmings (≥ 45 g) accounted for an unusually high fraction of the population. Such lemmings are difficult to catch, kill and swallow by this predator that shows a marked preference for small lemmings (O. Gilg et al. in prep.). Indeed, if we only consider small lemmings (< 45 g) while plotting N on the x-axis, eqn (S4b) fits the data much better.

Arctic fox. Fox scats were collected in 1998 to 2002 from seven different dens and from the vicinity of our base camp to include as large a number of different individuals as possible (e.g. at least eight different individuals in 1998 when four of the dens were occupied by breeding adults). The results were analyzed following Dalerum and Angerbjörn *(S16)*. Dry weights of prey remains found in scats can be used to estimate the number of prey individuals of each food category eaten by mammalian predators *(S17)*. We used the factor of 28 previously applied for

the collared lemming *(S18, S19)* to convert the total mass of undigested lemming remains (L) found in a fox scat sample to the lemming biomass consumed. Following these previous studies, we estimated DCR for the time period during which scats were collected by first calculating the average proportion of lemmings found in a single scat as $28L$ divided by the mass of the scat sample, s. This result was then multiplied by the daily defecation rate *d (S18, S19)* and divided by the average live weight of lemmings, *w (S20)*,

$$DCR = \frac{28 \cdot L \cdot d}{s \cdot w}. \qquad \text{eqn (S3b)}$$

Numerical responses

The numerical responses were investigated based on data collected in 1988 to 2002. Long-tailed skua response was investigated in the 15-km² intensive study area, snowy owl and arctic fox responses in the entire study area of 75 km². Numerical response of adult predators and their reproductive output (number of fledged birds and weaned mammals) are presented separately.

Snowy owl. With the exception of 1999 (only 50 km² mapped), snowy owl nests were mapped annually over the entire study area. In the first census in the beginning of June to the beginning of July, we recorded the breeding pairs and the mean clutch size, while subsequent visits to some nests allowed an assessment of the breeding success. Non-breeding adults were extremely rare (one immature in 1990 and one adult in 1992) and they never stayed for long. They were ignored in the calculation of the numerical response.

Long-tailed skua. Breeding pairs and clutch sizes were documented for all years but the number of territorial pairs was mapped precisely from 1998 to 2000 (the years when we arrived at the study area in the beginning of June). Territorial pairs can be accurately counted only in

early summer, because in low lemming years skuas tend to leave their territories shortly after their arrival, in early June, though they remain in the general area in pairs or in larger groups *(S21)* and therefore continue to be active lemming predators. Breeding success was calculated for some pairs from 1988 to 1996 and for all pairs from 1997 to 2002.

Arctic fox. Breeding foxes were counted over the entire study area by visiting the seven known dens *(S16)*. Individual variation in coat coloration was also used to identify non-breeding adults. Non-breeding adults are common during low lemming years, but in these years foxes regularly visited our base camp and hides and were therefore easy to record. A separate study devoted to fox home-ranges *(S22, S23)* and involving ear tagging (young and adults) and radio-tracking (adults) was also helpful for distinguishing the different individuals met in the field. Dens suspected to be occupied (fresh scats or prey remains, dug entrances) were also monitored over the summer to record the minimum number of weaned young.

In Fig. 1, the outliers for the snowy owl refers to the year 1994 when the snow cover in the study area was 80% on July 1st, meaning exceptionally unfavorable breeding conditions for a bird laying eggs in May. The outlier for the stoat refers to the winter 2001-2002, when stoat survival rate was higher than expected from the lemming densities (Fig. 2), probably as a result of exceptional food availability (several large mammal carcasses in the study area). These favorable local conditions for the stoat might well explain the long-lasting low lemming phase recorded since 2000 (see main article).

Fitting the predator responses

To distinguish between the type II and type III functional responses, we first plotted the predation rate (DCR / N) against lemming density (N). A positive slope observed over any range of prey abundances is indicative of positive density dependence and hence type III response, whereas a

negative slope indicates a type II response *(S24)*. We then fitted the classical functions of functional responses used for predator-prey modeling *(S25-S27)* including studies on small rodent dynamics *(S28-S30)*,

Type II: $DCR = c\,N / (D + N)$ (eqn S4a)

Type III: $DCR = c\,N^2 / (D^2 + N^2)$ (eqn S4b)

where c is the maximum per capita consumption rate, N is lemming density per ha, and D is the half-saturation constant. The lemming density needed for each DCR estimate was calculated by assuming a linear change in density between the two closest trapping sessions. Parameter c was determined based on data in the literature and our own data. Finally, D was estimated by iteration. In one instance (long-tailed skua), we had to use a different function ($W N^e / [D^e + N^e]$ with $e > 2$) to fit the data. In this case, the values of both D and e were estimated by iteration.

Numerical responses of rodent predators are usually fitted with linear, logarithmic or curvilinear functions *(S2, S3, S31)*. Since the density of breeding owls, skuas and foxes is limited at high prey density by the predators' territorial behavior or by the number of available breeding sites (dens) as well as by their life history traits (maximal clutch or litter size), we used sigmoid functions similar to eqn (S4b) or functions with a threshold value (for species that do not breed at low lemming densities). The numerical functions were fitted as follows:

Numerical response for adults:

sigmoid function $b\,N'^2 / (Y^2 + N'^2)$ (eqn S5a)

step function $b\,(N' - N'_{crit}) / (Y + N' - 2\,N'_{crit})$ (eqn S5b)

Reproductive success:

sigmoid function $b'\,N'^2 / (Y'^2 + N'^2)$ (eqn S6a)

step function $b'\,(N' - N'_{crit}) / (Y' + N' - 2\,N'_{crit})$ (eqn S6b)

where b is asymptotic density of adults, b' is asymptotic breeding success (obtained by multiplying 2b by the maximal clutch or litter size), Y and Y' are lemming densities at which the slopes of the curves inflect and N'_{crit} is threshold lemming density below which the predator does not even attempt to breed. In the numerical responses, N' refers to the lemming density at snowmelt. We determined distinct numerical responses for both adults and young to be able to calculate the total response mechanistically for different times of the summer (i.e. before and after the birth of the young).

The estimated parameter values are summarized in Table S1.

Table S1. Parameter values for the responses of the arctic fox, the snowy owl and the long-tailed skua.

Functional responses		
W_o	Maximum predation rate for the owl (lemmings per day)	4.7
D_o	Slope of the type III functional response (e = 2) for the owl	1.08
W_l	Maximum predation rate for the skua (lemmings per day)	4.4
D_l	Slope of the type III functional response (e = 4) for the skua	2.2
W_f	Maximum predation rate for the fox (lemmings per day)	3.8
D_f	Slope of the type III functional response (e = 2) for the fox	0.13
Numerical responses (adults)		
b_o	Maximum owl density (individuals per ha)	0.00366
Y_o	Slope of the numerical response for adult owls	2.86
P_l	Skua density (individuals per ha)	0.02
b_f	Maximum fox density (individuals per ha)	0.0008
Y_f	Slope of the numerical response for adult foxes	11
Numerical responses (young)		
b'_o	Maximum density for young owls (fledglings per ha)	0.011
Y'_o	Slope of the numerical response for young owls	4
b'_l	Maximum density for young skuas (fledglings per ha)	0.016
Y'_l	Slope of the numerical response for young skuas	6
b'_f	Maximum density for young foxes (weaned young per ha)	0.0028
Y'_f	Slope of the numerical response for young foxes	5.3

Implementation of the numerical responses

Adult owls $P_o = \frac{(2 \cdot b_o) \cdot (N'-2)}{(Y_o + N'-4)}$ from May 1st (arrival) to September 30 (departure) when *N' > 2*;

with *N'* replaced by *N* before snowmelt (June 15).

Young owls $P_{yo} = \frac{b'_o \cdot (N'-2)}{Y'_o + N'-4} \cdot \left(\frac{1}{1 + e^{-0.36 \cdot ("age\ in\ days"-9)}} \right)$ from June 25 (hatching) to September 30

when $P_o > 0$. Note that the second part of the function (similar in skua and fox), adapted from Ricklefs's logistic growth curve *(S10)*, allows us to implement the young progressively from hatching to mid-fledging as "adult equivalents" in order to weight their total response according to their age (constant values from published growth curves; *S5-S9, S12-S15*).

Adult skua $P_l = 0.02$ from June 5 to August 15.

Young skua $P_{yl} = \frac{b'_l \cdot N'^2}{Y'^2_l + N'^2} \cdot \left(\frac{1}{1 + e^{-0.464 \cdot ("age\ in\ days"-4.55)}} \right)$ from July 14 to August 15.

Adult fox $P_f = \frac{\left[0.04 + (b_f - 0.04)\right] \cdot N'^2}{Y_f^2 + N'^2}$ from May 1st to October 22 with *N'* replaced by *N*

before snowmelt (June 15).

Young fox $P_{yf} = \frac{b'_f \cdot N'^2}{Y'^2_f + N'^2} \cdot \left(\frac{1}{1 + e^{-0.36 \cdot ("age\ in\ days"-9)}} \right)$ from June 15.

Lemming density

Lemming winter nests made of grasses and sedges become very apparent after snowmelt when they lie on the ground. The numbers of winter nests have been counted in the intensive study area in 1988-2002 *(S32-S34)*. To estimate the lemming density at snowmelt for the period 1988-2002, we calculated the regression between lemming winter nest counts and spring density estimates

(first live-trapping sessions following snowmelt) for the five years (1998-2002) for which the latter data were available. The power function that was transformed to a straight line fitted the data well ($R^2 = 0.99$; $p < 0.01$),

$$\ln N' = 1.15 + 1.35 \ln W \qquad \text{(eqn S7)}$$

where N' is the estimated spring density in ind./ha and W is the density of winter nests per ha as counted in the complete search of the 15 km^2 study area. Fig. S1 below illustrates the close correlation between the density estimates.

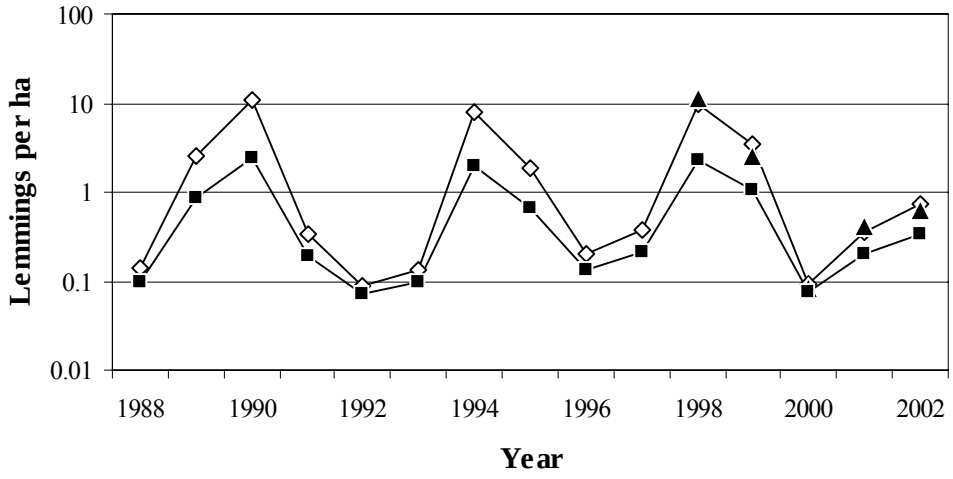

Fig. S1. Time series of the numbers of lemming winter nests per ha after snowmelt (squares) and spring densities (ind./ha) estimated from the density of winter nests (eqn S7; diamonds) for the period 1988-2002. Triangles show direct estimates of the spring densities (live trapping).

Lack of space or food limitation in lemming dynamics

The lemming population could be limited by the availability of burrows, which they absolutely need in the high-Arctic environment. However, the numbers of old burrows are so great in our study area (153 per ha on average and > 300 per ha in typical lemming habitats; *S20*) that it is not plausible to assume them to be limiting.

Considering the daily requirements of lemmings in relation to the above ground net production of vascular plants at similar tundra sites *(S35-S37)*, it is apparent that lemming density could be much higher and hence food is unlikely to limit lemming population growth. Evidence of lemming browsing can be seen locally (e.g. within one meter around the occupied burrows) but during the 15-yr study we have not observed a situation where a substantial fraction of the suitable host plants would have been consumed even in small areas. Furthermore, the steep lemming declines always occur in summer in our study area *(S20)*, i.e. during maximal primary production.

Stoat dynamics

Stoat density index. To assess the dynamics of stoats for 1988-2002, we recorded the numbers of lemming winter nests that had been predated and occupied by stoat during the winter *(S32)*. If the duration a stoat occupies a particular nest is density-dependent (e.g. longer during peak years when lots of prey can be found within a short distance), this index would be biased (more winter nests occupied per stoat at low prey density). However, since the mean number of scats found around the stoat-occupied nests in different years was fairly constant (mean: 12.3 ± 1.04 S.E.) and not correlated with N' or N'_{year-1} ($p > 0.1$), we rejected this assumption. Lack of density dependence is also supported by Fitzgerald *(S38),* who showed that the mean number of

winter nests used by small mustelids over the winter season remained constant over a vole cycle regardless of the vole density.

Numerical response. We assume a population of even sex ratio and that each female is mated annually *(S39)*. Each mated female is assumed to produce a constant number of weaned young per litter (v) in early July. Thus we increase the number of stoats in the model by a factor of v on the first of July. We assumed that stoat density decreases continuously due to mortality, which has an S-shaped dependence on lemming density

$$\frac{\mathrm{d}P}{\mathrm{d}t} = -P \cdot \left(d_{high} - \left(d_{high} - d_{low} \right) \cdot \left(\frac{1}{2} + \frac{\arctan \cdot \left(b \cdot \left(N - N_{crit} \right) \right)}{\pi} \right) \right) \qquad \text{(eqn S8)}$$

where d_{high} is the maximal stoat mortality rate, d_{low} the minimal rate, N_{crit} the lemming density at which stoat mortality is $(d_{low} + d_{high})/2$, and b is the slope of the S-shaped mortality function *(S30)*.

Functional response. Predation by stoat was modeled with a type III functional response, $cPN^2/(N^2+D^2)$, where c is the maximum per capita predation rate of the stoat, P is stoat density and D is the predation half-saturation constant for the stoat. We allowed for food caching while selecting the value for c (references in Table S2). Type III functional response was used to incorporate a probabilitistic "refuge" for the lemming at very low densities, when lemmings are so dispersed (less than 10 per km²) that they must become very hard to locate for the stoat. In this situation, with stoat densities being minimally ≤ 1 per 15 km², it would be unrealistic to use the type II functional response, which assumes a steeply increasing predation rate for the lowest observed prey densities. It seems inevitable that stoats use to some extent alternative food sources when the lemming density is minimal, and in fact stoats in NE Greenland have been observed to use birds, eggs, insects, berries, carrion and even the feces of other mammalian predators (*S40-S43*, O. Gilg et al. in prep.).

Parameter values for the lemming and the stoat

Parameter values used in the calculations for Fig. 3 are summarized in Table S2.

Table S2. Parameter values of the lemming and the stoat and their sources and justification.

Parameter	Value(s)	Source
r_w	4	30% of females reproduce monthly, 4 young per litter, 10% mortality before maturity at the age of 2 months *(S19, S44)*
r_s	0, 0.4, 0.8	Maximum in summer 0.8 because no young mature, but not all adults probably reproduce *(S20, S45-S47)*
v	4	unpublished data from the region (n = 6)
c	1000	Calculated based on daily food requirement of 1.9 lemmings *(S48-S51)* plus 45% surplus killing *(S30, S52-S54)*
D	0.08, 0.1, 0.12	Based on Fig. 1.
N_{crit}	D	Based on the dependence of the stoat on lemmings
d_{low}	0.0, 0.1, 0.2	As assumed for weasels *(S30, S54)*
d_{high}	3.5, 4, 4.5	As assumed for weasels *(S30, S54)*
b	25	To obtain a steep function in eqn (S8)

r_w = lemming growth rate in winter

r_s = lemming growth rate in summer

v = number of weaned young (both sexes) produced per female per year by the stoat

c = maximum per capita predation rate of the stoat (lemmings per year)

D = half-saturation constant of the stoat's functional response

N_{crit}, d_{low}, d_{high} and b, parameters of the function describing stoat mortality rate as a function of lemming density (eqn S8).

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