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Cyclic Dynamics in a Simple Vertebrate Predator-Prey Community

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Cyclic Dynamics in a Simple Vertebrate Predator-Prey Community

Olivier Gilg,[1,2]* Ilkka Hanski,[1] Benoît Sittler[3]

The collared lemming in the high-Arctic tundra in Greenland is preyed upon by four species of predators that show marked differences in the numbers of lemmings each consumes and in the dependence of their dynamics on lemming density. A predator-prey model based on the field-estimated predator responses robustly predicts 4-year periodicity in lemming dynamics, in agreement with long-term empirical data. There is no indication in the field that food or space limits lemming population growth, nor is there need in the model to consider those factors. The cyclic dynamics are driven by a 1-year delay in the numerical response of the stoat and stabilized by strongly density-dependent predation by the arctic fox, the snowy owl, and the long-tailed skua.

The cyclic dynamics of boreal and arctic populations of small rodents is one of the most intensively studied phenomena in population ecology. Many (*1*–*4*), although not all (*5*, *6*), researchers now agree that the most likely mechanism that maintains cyclic dynamics in boreal vole populations is predation by specialist mustelid predators. In contrast, interaction with food resources is thought to drive the dynamics of at least some lemming populations (*7*). Even in the case of vole dynamics, competition among prey for space or food is thought to play a key role in halting prey population growth at high density, thereby allowing the predator population to catch up with their faster-reproducing prey (*1*, *3*, *8*–*10*).

One of the simplest vertebrate predator-prey communities is that of lemmings and their dependent predators in the high-Arctic tundra in Greenland. It constitutes only one mammalian prey, the collared lemming (*Dicrostonyx groenlandicus*), and four predators, the stoat (*Mustela erminea*), the arctic fox (*Alopex lagopus*), the snowy owl (*Nyctea scandiaca*), and the long-tailed skua (*Stercorarius longicaudus*) (*11*, *12*). The open tundra landscape and the continuous daylight in summer in the high Arctic provide particularly favorable conditions for fieldwork on vertebrate predators. We studied the densities, breeding success, and diet of the four predators in a 75-km^2 area in the Karup Valley in northeast Greenland (72°30′ N, 24°00′ W), from 1988 to 2002.

Lemming densities were estimated with live trapping for 1998 to 2002 (*11*, *13*) and with regression between live-trapping results and lemming winter nest counts (*12*, *14*) for the other years (*15*). The winter nests of lemmings are made of grass within snow beds and are easily located on the ground after snowmelt. We made a complete count of the nest numbers in an area of 15 km^2 every spring for 1988 to 2002. Although a varying number of lemmings may use the same nest (*16*, *17*), the winter nest count in our large study area should closely reflect the actual number of lemmings. The correlation between the spring densities, as estimated by live trapping, and the winter nest count for the years 1998 to 2002 is high ($R^2 = 0.99$, $P < 0.01$) (fig. S1).

The stoat density was estimated from the number of lemming winter nests predated and occupied by stoats in the 15-km^2 area (*12*, *13*). Stoats always use lemming nests in winter, and stoat-occupied nests are easily distinguished by the abundance of lemming fur within the nest (*12*, *18*).

Daily predation rates were plotted against the current (daily) lemming density (N) to estimate functional responses of predators. Daily predation rates were estimated from scat samples for arctic foxes ($n = 927$) and stoats ($n = 663$), from direct observations for skuas (n=475 hours), and from pellet samples and direct observations for snowy owls ($n = 3419$ pellets and 245 hours of observation). In the open landscape and in the continuous daylight of summer, the behavior of individual predators can be closely monitored over areas as large as 5 km^2.

Predator densities were plotted against lemming density at snowmelt to estimate numerical responses. With the exception of the stoat, separate responses were estimated for adults and weaned or fledged young (*15*).

The daily consumption rate of the avian predators is somewhat higher than that of the mammalian predators, but the latter are more efficient at catching prey at low lemming densities (predation half-saturation constant < 0.2 lemmings/ha) than are the former (≥ 1) (Fig. 1, upper row). The numerical responses of the predators are species specific. The nomadic snowy owl only settles and breeds in areas where lemming density at snowmelt (N') exceeds a threshold of $\approx$2 lemmings/ha. The constant adult density in summer of the migratory long-tailed skua is five times as high as that of the snowy owl when the latter is present, but the skua breeds successfully only when $N' > 1$. The arctic fox shows elevated breeding success when $N' > 1$ but maintains a relatively constant adult density, except in peak lemming years ($N' \approx 10$) (Fig. 1, middle row), when fox density may increase greatly.

The stoat is the only predator that shows a delayed response to changes in prey density, with highest numbers seen the year after the lemming peak (Fig. 2, top). The results for the

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stoat in Fig. 2 are based on the counts of lemming winter nests occupied by the stoat, rather than on population size estimates, but our field observations support the assumption that the winter nest count gives a reliable picture of the long-term dynamics (*15*).

The results in Fig. 2 demonstrate a 4-year cycle in lemming and stoat numbers from 1988 to 1998. The years 1999 to 2002 show a somewhat deviating pattern, possibly indicating that this cycle will be 5 years long. The occurrence of 4-year population cycles in lemmings is supported by another source of information. The trapping records for the arctic fox in northeast Greenland from 1935 until 1960 showed distinct peaks in the winters of 1937–38, 1941–42, 1946–47, 1950–51, 1954–55, and 1958–59 (*19*), at intervals of 4, 5, 4, 4, and 4 years. These trapping records most likely reflect changes in lemming density.

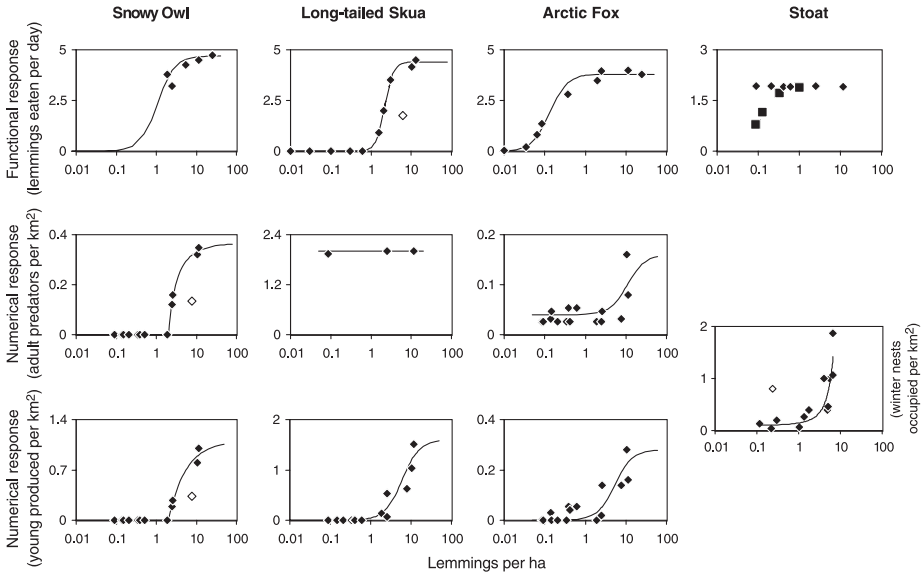


Fig. 1. Predators' responses to lemming density. Functional responses (**top**) are related to the current (daily) lemming density (*N*), whereas the numerical responses (**middle** and **bottom**) are related to the lemming density at snowmelt (*N*′). The numerical response of the stoat includes adults and weaned young and is delayed (*x* axis is the average lemming density at snowmelt for the past 2 years). The functional response of the stoat (**top right**) shows estimates based on winter (diamonds) and summer (square) scats. Open symbols are outliers resulting from unusual climatic or demographic situations (*15*). The numerical response of adult skuas could only be assessed for 1998 to 2000, when we arrived at the study area in the beginning of June and before the skuas started to flock. The species is known to have stable densities (*28*).

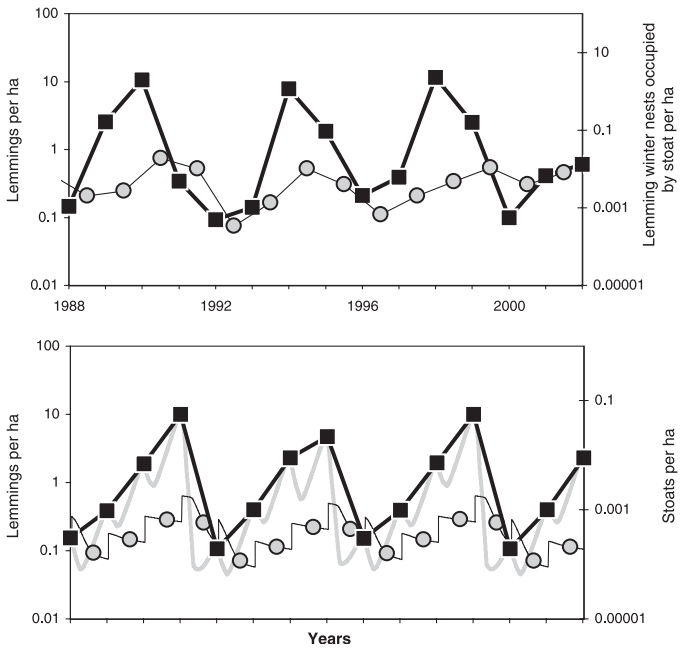


Fig. 2. Empirical (**top**) and model-predicted (**bottom**) time series for the lemming (squares) and the stoat (circles). Data points for the lemming are at snowmelt and for the stoat at midwinter. The lemming density estimate was calculated on the basis of absolute lemming winter nest counts for 1988 to 2002 and live-trapping density estimates for 1998 to 2002 (*15*). The gray line (bottom) shows the lemming dynamics predicted by the model; the bold black line represents the overall lemming dynamics to be compared with the empirical time series. There is a correspondence in cycle length, amplitude, and maximum lemming densities. Parameter values for the predicted series: $r_s = 0.8$, $r_w = 4$, $v = 4$, $c = 1000$, $D = 0.1$, $N_{crit} = 0.1$, $d_{low} = 0.1$, $d_{high} = 4$, and $b = 25$. v, number of weaned stoats produced per female per year; c, maximum per capita predation rate of the stoat, in lemmings per year; b, slope of the mortality function for the stoat (table S2).

The dynamic part of the model involves the lemming and the stoat. Reproduction in the collared lemming is continuous, with overlapping generations and with a higher rate of reproduction in winter than in summer (*11*, *20*–*22*). The maximum observed lemming densities were ~10 individuals per ha (Fig. 2, top). This density could potentially be much higher (*11*, *23*–*25*). There is an excess of burrows available for lemmings in our study area, and there is no evidence that food is a limiting factor (*15*). Because there is no evidence for space or food limitation, lemming dynamics were modeled by continuous-time exponential growth, with different growth rates for winter (r_w) and for summer (r_s, from June 15 to September 25).

The dynamics of the stoat were modeled by assuming that all females produce one litter per year and that stoat mortality is an S-shaped function of lemming density (*15*).

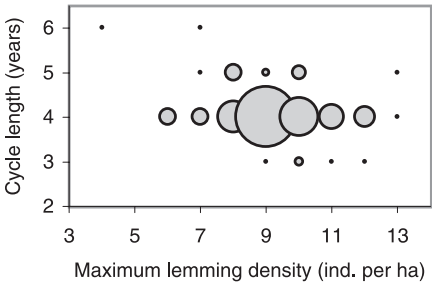


Fig. 3. Cycle lengths and maximum densities predicted by 81 parameter combinations given in table S2. Two combinations are not included that led to noncyclic dynamics or to the lemming population increasing exponentially. Circle width is proportional to the number of parameter combinations yielding the cycle length and maximum lemming density indicated in the figure (smallest circle, 1 parameter combination; largest circle, 17 combinations).

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Predation by stoat was modeled with a type III functional response (*3*) to incorporate the possibility of stoats finding alternative prey at lowest lemming densities, when lemmings are so dispersed (less than 10 per km^2) that they must become very hard for stoats to locate (*15*). In this situation, with stoat density $\leq$1 per 15 km^2, it would be unrealistic to use a type II functional response, which assumes a steeply increasing predation rate for the lowest prey densities.

We analyzed the model numerically by keeping the parameters for the arctic fox, the snowy owl, and the long-tailed skua fixed at the values estimated in Fig. 1 and reported in table S1. Of the remaining parameters (table S2), the summer growth rate of the lemming (r_s), the predation half-saturation constant of the stoat (D), and the mortality rate parameters of the stoat (d_{low}, d_{high}, and N_{crit}) (*15*) have more uncertainty than the others. We ran model simulations for many combinations of these parameters (table S2). The model mostly predicts complex dynamics, but with a strong regular component, which most frequently has a period of 4 years (Figs. 2 and 3). The most notable difference between the predicted and observed dynamics is in the shape of the cycle: The increase phase of the cycle appears to be shorter in empirical results than in model predictions (Fig. 2).

Turchin *et al.* (*7*) have argued that Norwegian lemming oscillations, characterized by sharp and angular peaks, are driven by interactions with food plants, but our study suggests that similarly sharp peaks can also be observed for predator-regulated lemming populations.

The notable feature of the present modeling results is that there is no food or space limitation in the lemming dynamics; in other words, there is no intrinsic prey density dependence. This is supported empirically, because there is no evidence for food or space limitation in the field, or for any other mechanism, apart from predation, contributing to population regulation. The predicted dynamics are generated by a combination of destabilizing predation by the stoat and strongly stabilizing predation by the three other species of predators. This is an example of cyclic predator-prey dynamics in which the prey dynamics are entirely determined by predation.

If one of the avian predators is completely removed from the model, the dynamics change: The lemming escapes from the control of the predators. If removed, the arctic fox is less influential to lemming dynamics, which remain qualitatively unchanged, unless the summer growth rate of the lemming (r_s) is higher than 0.25 (which value is within the feasible range for r_s) (table S2). Removing the stoat, which has a much lower predation rate than the avian predators for most of the cycle (Fig. 1), does not allow the lemming to escape predator control as long as $r_s < 0.33$. However, removing the stoat leads to noncyclic dynamics, because the delayed numerical response of the stoat is the driving force of the multiannual fluctuations. In this simple community, all the predators have distinct life histories and responses to changing prey population size, which should help them coexist on the single prey (*26*, *27*).

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A Four–Base Paired Genetic Helix with Expanded Size

Haibo Liu, Jianmin Gao, Stephen R. Lynch, Y. David Saito, Lystranne Maynard, Eric T. Kool*

We describe a new molecular class of genetic-pairing system that has a native DNA backbone but has all four base pairs replaced by new, larger pairs. The base pairs include size-expanded analogs of thymine and of adenine, both extended by the width of a benzene ring (2.4 Å). The expanded-diameter double helices are more thermodynamically stable than the Watson-Crick helix, likely because of enhanced base stacking. Structural data confirm a right-handed, double-stranded, and base-paired helical form. Because of the larger base size, all the pairs of this helical system are fluorescent, which suggests practical applications in detection of natural DNA and RNA. Our findings establish that there is no apparent structural or thermodynamic prohibition against genetic systems having sizes different from the natural one.

Previous studies aimed at making altered forms of DNA have focused mainly on changes to the phosphodiester backbone (*1*–*5*). Because the bases, rather than the backbone, encode information, it was not clear whether all of the four base pairs could be replaced and still function in specific sequence recognition and spontaneous self-assembly. This is particularly the case where non–Watson-Crick geometries are contemplated. Earlier studies aimed at replacing one or more of the natural base pairs (*6*–*11*) have used structures compatible with Watson-Crick purine-pyrimidine pairing.

The designs of size-expanded DNA bases are shown in Fig. 1. Each base is larger than the natural analog by 2.4 Å, the width of an inserted benzene ring, converting a bicyclic purine into a three-ring analog and a mono-

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