ABSTRACT: The cyclicity of Arctic populations of small rodents is a subject with a long history and a large literature (Batzli, 1992) in which the question ‘What drives the cycle?’ has received many answers, among them that the source of the cycle is either rodent interaction with food or the interaction with predators or both. Another question concerns the confinement of the cycle to Arctic conditions. The paper by Gårding (2000) presented a simple mathematical model of the combined predator-prey-food interaction based on a general eater-food interaction in which cycle length is an explicit decreasing function of the average birth rate of eaters. In the combined interaction, the cycle length is the same function of the sum of the average birth rates of predators and prey. Numerical fits of these models make it possible to answer the questions above. The results are that the short 3–5 year cycles of the Arctic rodents: lemming (*Lemmus lemmus*) and vole (*Microtus agrestis*) are mainly driven by interaction with food while the ten year cycle of the Canadian snowshoe hare (*Lepus americanus*), is driven by interaction with its predator – lynx. Rodents in the Arctic live and breed in burrows and experience predation pressure when surfacing. This explains their interaction with food. The greater variety and easier availability of food in a temperate climate accounts for a missing rodent interaction with food. The paper starts with a presentation of the eater-food interaction model itself, its simple but unfamiliar mathematics and its points of credibility. At the end of the paper some current hypotheses about the nature of the rodent cycle are seen in the light of the model used here.

KEY WORDS: Arctic cycle, eater-food interaction, vole, lemming, snowshoe hare.

The model. In stable situations a population of eaters may interact with their food in the sense that there is a balance between population size and available food supply. Here we shall consider a model of this interaction between a population of eaters and its food in a very simplified situation. The population is supposed to be of one species which has an annual breeding period and feeds from an annual supply of food, whose amount is influenced by consumption one year earlier. The size of the adult population and the amount of its food are supposed to be registered annually at some fixed time of the breeding season. The basic mechanism determining annual changes of population size and food amount is put into abstract form below as a mathematical model of interaction with food. Described in words it says in particular that an increase (decrease) of food one year means more (less) surviving offsprings at the next count. The model
applies both to eaters of plant food and to predators and their prey.

The model has units chosen so that one unit of the species consumes on the average one unit of food annually. To start the mathematics let $P$ and $F$ be the size of the adult population and the amount of its food, counted in units and observed at some date of the breeding season the same year. When these numbers are equal, the model is at an equilibrium where the size of the population and its food amount remain the same at the next count.

The model presents annual predictions of population and food counts when the two numbers are different. The predictions are

$$P \rightarrow P + a(F - P), \quad F \rightarrow F - P + B$$

(1)

where the arrow means ‘predicted to be the next year’; $B$ is the annual renewal of food, supposed to be constant, and $a$ is an average annual birth rate of the population, defined as the inverse of the average life span of the population. Note that this average birth rate $a$ can be observed in the field by observing the average life span $A$ of the species. In fact in the average population the inverse of $A$ is the average death rate which equals the birth rate. We note in passing that (1) shows that decreased birth rate flattens the population curve.

A pair $P, F$ with $P=B, F=B$ reproduces itself under iteration and represents an equilibrium where the eater population has precisely enough to eat to live and breed and compensate for deaths to maintain its size next year. When this does not happen, when $F>P$, say, $F-P$ extra units of food are available. By assumption they represent annual food for the same number of units of an eater population which, normally, would breed $a(F-P)$ new ones. We now assume that the excess of food has the same effect on the original $P$ units of the eater population resulting in a population size of $P + a(F - P)$ units at the next count. At least when $F-P$ is small relative to $P$ this computation appears to be realistic. When $F<P$ the same reasoning now applies to units of missing food with $a(F-P)$ negative. This explains the first equation (1). When $F>P$, the second formula (1) adds $F-P$ uneaten units of food to the $B$ units of food renewal. This motivates the entire formula (1) at least when the pair $P, F$ is not too far from he equilibrium. Note that the population increases when $F>P$ and that food increases when $B>P$. Note also that the formula (1) is just a food balance and ignores the way that death and breeding occur during the year.

The true nature of the formula (1) appears when it is iterated from year to year as shown in the Fig1. The upper part shows how 14 iterated values of $P$ and $F$ vary with time. Initial values are $P=120$, $F=80$ units with $B=100$ and the average birth rate is put to 0.7. Note that the food curve rises ahead of the population curve. The lower part shows the same iterations in the $P, F$-plane. The iterated points form a cyclic orbit going clockwise around and almost closing up after seven steps, the cycle length being 7.3 years. By (1) $P$ increases above the diagonal where $F=P$ while $F$ increases left of the line $P=B$ and decreases to the right. These two lines divide the orbit into four parts with different modes of change.

Some linear algebra (Gårding 2000) shows that Fig.1 represents a general situation which can be described as follows. When $a<4$ iterations of (1) with the same $a$ and $B$ but arbitrary starting points produce a family of cyclic orbits in the $P, F$-plane with coordinates $P, F$. They are all similar and of elliptic form with the same center $P=F=B$ and the same cycle length. When $a=4$ the orbits are chaotic. Only orbits contained in the first quadrant where $P$ and $F$ are positive make physical and ecological sense. A step outside can be seen as extinction.

All cycles produced by iteration of (1) with a fixed $a$ have the same length counted in years. More precisely, the cycle length equals $360/w$ years where $w$ (less than half a turn and counted in degrees) is an angle whose cosine is $1-a/2$. The following table taken from Gårding (2000) shows some values of $a$ and the corresponding cycle lengths in years (Table 1).

**Stability.** In practice only population changes are registered and cyclic ones when observed are always a bit irregular. In the theory similar irregularities can be achieved during the iteration by chance deviations of
Fig. 1. The eater-food cycle with an average birth rate 0.7. Eaters start at 120, food at 80 units. The top shows variation with time in years, the bottom shows the cycle in an eater-food plane with eaters on the horizontal axis. The cycle length is 7.3 years.
Lars Gårding

the two parameters – food renewal and average birth rate. Moderate modifications of this kind will result in cycles that do not quite close up but cycle length defined as the number of years between two consecutive maxima of the population will vary very little. The theoretical cycle length is in fact very stable under chance deviations from fixed values of the parameters. But drastic changes may even destroy an approximate periodicity or lead to theoretical extinction.

Numerical fits of the model. A first credential of the eater-food model is perhaps that it has an equilibrium and produces credible orbits starting near the equilibrium. The model makes the cycle length depend on the average birth rate of the eaters; that is also compatible with common sense. In fact, during a cycle the size of the population changes by births and deaths back to its original size and the speed of this process clearly increases with an increasing birth rate. But the decisive credential of the model is its numerical fit. In fact, it predicts correct cycle lengths in two classical cases, for the Arctic rodents lemming (*Lemmus lemmus*) and vole (*Microtus agrestis*) and the Canadian snowshoe hare (*Lepus americanus*).

The Arctic lemming eats grass and moss, lives and breeds in burrows and is the prey for predators like weasel, Arctic fox and some birds. This makes for two interactions, one with food and one with predators. Predation pressure in the barren landscape makes it dangerous for lemmings to leave the underground and this makes interaction with food probable. By informed estimates (Sam Erlinge, oral communication) the average life span of a lemming is between 4 and 8 months giving an average birth rate between 3 and 1.5 and hence, by the table, a cycle length between 3 and 4 years which fits observation. On the other hand, the average life span of the lemming predators above can be estimated to between 1 and 3 years giving a birth rate between 1 and 1/3 years which, by the table (see above), gives a cycle length of more than six years. Actually, this is not a contradiction since the two interactions may be simultaneous and in this case there is a theory (Gårding 2000) which says that the cycle length of lemmings is determined by adding the two birth rates. This makes the cycle length a little bit shorter, but the interaction of lemmings with food is still the main source of lemming cycles. The situation is analogous for the vole.

The Canadian snowshoe hare eats bark and grass and its main predator is lynx. The ambulant hare shares its abundant food with many other species and it is therefore unlikely that its consumption influences the amount of available food. This rules out an interaction with food. Lynx is the main predator of the Canadian snowshoe hare and the hare has a population cycle of ten years. According to the statistics of Brand and Keith (1979) the average life span of lynx is 2.6 years giving an average birth rate of 0.38 and, by the table, a cycle length of 10 years predicted by the model and observed in the field.

Absence of a rodent cycle in a temperate climate. As said above, the rodent-food interaction in the Arctic is created by special circumstances i.e. underground living under predation pressure in a barren landscape. In a temperate climate with a varied and abundant food supply and protecting vegetation, these conditions simply cease to exist. It is therefore natural to assume that only interaction with predators remains. With reasonable predator average life spans between 1.5 and 3 years it gives theoretical cycle lengths around 7–9 years. Such a long cycle is sensitive to chance influences created by a varied fauna. According to Erlinge (1987) and references quoted there, no trace of cyclicity has been observed in Southern Sweden.

Hypotheses about the Arctic rodent cycle. The model for eater interaction with food sheds light on some current hypotheses

<table>
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<tr>
<th>parameter $a$</th>
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about the nature and cause of the Arctic rodent cycle.

1. In his recent review of the problems with the lemming cycle (Stenseth 1999) and in other papers by the same author (Stenseth 1995) rodent population statistics is analysed in terms of a time series where the data for two consecutive years determine the data for the following ones. Using the statistical model the author argues as follows: "an order two process cannot correspond to a system where both food and predators interact with voles in a dynamic way exhibiting closed loops." Later the same idea is formulated in other words: "Tentatively we may conclude that an order two process seems to suggest that voles and lemmings are controlled either from below or above – but not from both below and above" (Stenseth 1999, p. 161).

As explained above, the interaction model says that interaction with food is the main ingredient of the Arctic rodent cycle and that simultaneous interaction with predators is possible and only shortens the cycle a little. Stenseth's statement 'not by both' seems to be an overinterpretation of the power of the time series to distinguish causes of action.

2. In Seldal et al (1994) the authors prove that eaten food defends itself by getting poisonous and argue that this effect could explain the periodic sharp decline in lemming populations. The length of the cycle is not explained but the basic observation shows in itself that there is a strong interaction between lemmings and their food so that the eater-food model applies giving an estimate of the cycle length. On the other hand, the model exhibits a prerequisite for Seldal's observation, namely that the eater curve rises after the maximum of the food curve (see Fig 1). This creates a time interval when the eaters are close to their maximum but food supply goes down to a minimum.

3. The nature of classical snowshoe hare cycle is the object of several papers, (Krebs 1994, Krebs and Stenseth 1995, Krebs et al. 2001). Their main conclusion is that interaction with predators is the main force of the cycle, but all of them advance arguments to show that the snowshoe hare cycle must also be at least partly driven by interaction with food. Seen from the predator-rodent-food model (Gårding 2000) this statement is not credible since it gives the wrong cycle length. In fact, the average annual birth rate of hares is at most 1 giving a value of $a+b$ of a bit over 1 which, by the table, corresponds to cycle lengths around 6–7 years. Note that the ambulant ways of hares can only mean a weak interaction with food. The third paper above ends with the conclusion that "The hare cycle is produced by an interaction between predation and food supplies ... “. This interaction, which occurs via the hare population, is made explicit in the model for a predator-prey-food interaction (Gårding 2000): when predators eat hares they also influence food supply indirectly. But, as pointed out above, the cycle length of this composite interaction is too short to fit the hare cycle. Hence the hare-food interaction is negligible compared to the lynx-hare interaction.

4. Turchin et al. (2000) have observed that the cycle amplitudes for lemmings and voles are very different, those of voles being more regular. This leads them to the conclusion that the lemming cycle is driven by food and the vole cycle by predation. Since the vole cycle is five years long our model shows that the vole predators in that case should have average life spans of $1/1.4=0.7$ years which is not possible. Instead, the difference between vole and lemming population curves is explained by the flattening effect of decreased average birth rate. The lemming and the vole cycles fit well with the predator-prey-food model of Gårding (2000), interaction with food playing the first fiddle.

5. Using the Lotka-Volterra equations for the predator-prey interaction, Turchin and Hanski (1997) simulated the current hypothesis that many-sided predation performed by so called generalists decreases the amplitudes of the rodent cycle and, in a temperate climate, makes it loose its cyclic character.

This reasoning disregards the rodent-food interaction which according to the model given here is the main source of Arc-
tic cyclicity. As argued above it seems very probable that this interaction and the accompanying short cycle simply disappear in the relatively dense and differentiated vegetation of a temperate climate.

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REFERENCES


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