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Research note

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## APPLICATIONS OF THE EATER-FOOD MODEL TO PREDATOR-PREY-FOOD CYCLES

**ABSTRACT:** This note gives five applications of the eater-food interaction model (Gårding 2005) where cycle length is a function of the eater average birth rate defined as the inverse of average life span. The model extends to an analysis of predator-prey-food cycles (Gårding 2000). Here the cycle length is the same as that of an eater-food interaction whose average 'birth rate' is the sum of the average birth rates of the predator-prey and prey-food interactions.

The model. In the eater-food interaction model the sizes  $E$  and  $F$  of eaters and food observed annually are predicted to be  $E + a(E - F)$  and  $F - E + B$  in the following year,  $B$  being a constant annual supply of food. Here  $E$  and  $F$  are counted in units so that one unit of eater eats on the average one unit of food annually and  $a > 0$  is an average annual birth rate of eater supposed to be less than 4. Annual iterations of this step produce eater cycles (in the  $E$  and  $F$  planes) centred at the point  $E = F = B$ , having the same cycle length, depending only on  $a$ . Initial pairs which are close to the centre give physically and ecologically meaningful cycles with positive  $E$  and  $F$ . This somewhat abstract construction fits the cycle lengths and average life spans observed in some classical Arctic cycles (Gårding 2000). Relations between the pa-

rameter  $a$  and cycle lengths up to 10 years is given in Table 1.

The predator-prey-food interaction is composed of the predator-prey interaction and the prey-food interaction, both of the eater-food type. Let  $a$  and  $b$  be the birth rate of predator and prey respectively assumed to be observed in an eater-food interaction. A known theorem (Gårding 2000) says that the triple has a cycle whose length is the same as that of an eater-food interaction cycle with the birth rate  $a + b$ . In the applications below only the cycle length of the triple interaction is known as well as the sum  $a + b$ . The average birth rates  $a$  and  $b$  have to be established by estimating the average life spans of predator and prey living under simple interactions. Such estimates may not be conclusive but they are at least helpful in a situation where substantial clues are missing.

### APPLICATIONS

1. *The Arctic triple weasel-vole-food.* The paper by Turchin *et al.* (2000) deals with the Arctic cycle of voles *Microtus agrestis*. Based on a comparison between population curves of lemmings and voles it is claimed that in contrast to lemmings the interaction of voles

with food is negligible and that the five year cycle of voles is driven only by interaction with its main predator, the weasel. This drastic assumption is contradicted by the observations made by Sun *et al.* (2005) that the consumption of voles *Microtus oeconomus* Pallas in Alpine meadows has a great impact on vegetation.

Here we shall estimate the parameter  $a$  for the weasel-vole interaction and  $b$  for the vole-food interaction knowing that their sum should give a five year cycle. The average life spans of weasel and vole are here both close to 1 year and if we assume that  $a = b = 1$  we get a cycle length of 4 years. Now the simple interactions involved have slightly longer life spans, say around 1.4 years for weasels and 1.2 years for voles. This gives  $a = 0.7$ ,  $b = 0.8$  with the sum 1.5 corresponding to a cycle length close to the observed five years. Hence the weasel-vole-food interaction should be driven both by the predator-prey interaction and the prey-food interaction. The precise choices of life spans made above do not influence this conclusion.

2. *The Arctic lemming cycle.* Replacing voles by lemmings the above observed cycle length shrinks to 4 years and we must have  $a + b$  close to 2. The average life span of lemmings is about 0.5 years which makes for  $b$  larger than 1, for instance  $b = 1.5$ . This makes room for predators with life spans around 2 years,  $a = 0.5$ ; for instance foxes and Snowy Owls. This set-up fits the view that inter-

action with food is the main driver of the lemming cycle. But if we have a shorter cycle length from the beginning, say 3 or 3.5 years the situation opens for a predator with a shorter life span, for instance weasels.

3. *Effect of several predators.* A combined predator population like weasels and Snowy Owls with eater-food average birth rates 1 and 0.5 have average birth rates of, say 0.75. Adding an estimated birth rate for the lemming-food interaction, say 0.9, gives the parameter 1.65 for the combined interaction corresponding to cycle length below 4 years.

4. *Cycle dependence on latitude.* The vole cycle in Scandinavia is longer in the north (Turchin and Hanski 1997). We try to explain this as an effect of a longer snow cover. Snow cover protects and preserves food and makes prey more difficult to get. Hence longer lasting snow cover increases the average life span  $1/b$  of voles but seems to leave  $1/a$  unchanged. Then  $a + b$  decreases and cycle length increases fitting observation (*ibidem*).

5 *Wrangel Island, (Alaska).* This region has no weasels (S. Erlinge, personal communication). The predators hunting for the lemmings are foxes and Snowy Owls with average life spans estimated to be close to two years. The long snow cover gives the lemming a long life span close to a year, say 0.9 year. This makes the parameter  $a + b$  equal to 2.25 corresponding to an observed cycle length of 5 years (Litvin and Ovsjannikov 1990).

Table 1. Relations between average birth rate ( $a$ ) and cycle lengths up to 10 years.

Average birth rate $a$	Average life span (years)	Cycle length (years)
3.62	0.28	2.5
3	0.38	3
2	0.5	4
1.38	0.72	5
1	1	6
0.753	1.3	7
0.586	1.7	8
0.408	2	9
0.38	2.6	10

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