Mammalogy Lecture 15 – Arvicoline Population Cycles

Population Cycles: For the most part, populations tend to be fairly stable, or at least when they fluctuate, there's usually an identifiable correlate that we can associate with population size. However populations of some species undergo dramatic population cycles.

A. There are well-studied predator-prey cycles of lynx and snowshoe hares.

These are in-phase 10-year cycles that have been studied for decades.

Krebs et al. (2018) summarize this research and support the earlier conclusion that this is primarily driven by predation.

Hare mortality is due to predation. Predation-induced stress causes these snowshoe hare to decrease reproductive output; this causes hare populations to crash. Because the lynx are specialists, the predator populations follow in crashing. It takes a couple generations for hare populations to rebound due to maternal effects.

So this appears to be driven by a single factor, the specialist predator-prey dynamics.

B. Cricetid rodents in the subfamily Arvicolinae, the voles and lemmings, are well known for dramatic population cycles, but the drivers of these cycles are more complex.

1. Examples – *Myodes* (*Clethrionomys) rufocanus* in the Kola peninsula.
   - *Dicrostonyx* in Alaska.
   - Several well-studied species of *Microtus*.

2. Characteristics of arvicoline cycles
   - Peak population densities may actually be 1-2 orders of magnitude higher than trough densities. The highest reported densities are *M. montanus* of 20,000 per hectare, but there are good scientific records of over 1000 *M. pennsylvanicus*/hectare, also recorded in *M. oregoni*.
   - Growth phase is very rapid
   - Crash is very abrupt
   - There is a lag; typically, in arvicolines there are 1-5 years between peaks.
   - This periodicity seems to be fairly regular, that is non-random, at least with respect to the temporal aspect, although the amplitude of the peak can vary.
   - In addition, there is a latitudinal component. There is a correlation between the tendency to cycle and latitude; northern populations exhibit more cyclicity. **Especially true in Scandinavia** (where lots of research has focused).

There has been some controversy over whether or not these cycles are statistically regular. Some studies have reported that the cycles are too variable to be statistically regular, whereas other studies have reported that they are statistically periodic.

Regardless of the issue of statistically regular periodicity, the presence of these populations is well established and well-studied.

C. Biologists have been struck by this phenomenon for some time, and a great deal of work has been undertaken to uncover the cause of these cycles.

Rapid growth is easy to explain; these have classically "r-selected" reproductive traits.

Large litter sizes; up to 12.

Polyestrous; up to 17 litters per year in captivity.

Short generation times; gestation can be as short as short as 21 days.

Rapid post-natal maturation; with 1st reproduction occurring as soon as 15-21 days after birth.

Thus, there can be as little as 36 days from conception to 1st reproduction.

1. Extrinsic Hypotheses have been proposed.

a. Food - Herbivore/Plant interactions --- Batzli and Pitelka (1971. J. Mammal. 52:141.)

There's a density-dependent effect of herbivory on food supply

At low vole densities, plants are unaffected by herbivory.

At high densities, there is a selective reduction of plant biomass.

A high rate of herbivory induces the production of chemical defenses by plants. This compromises the quality of forage available to voles, which in turn, causes the crash.

The time lag is explained as the time that plant populations take to recover. Truchin & Batzli (2001. Ecology, 82:1521) demonstrated that plants regrow exponentially and used this to model vole cycles.

Slide: Dotted line represents a mathematical model based only on food and a time lag corresponding to plant recovery.

Actual populations seem to fit predictions of the mathematical models extremely well, so this hypothesis has been tested experimentally.

When voles are raised in enclosures and given supplemental food, we still eventually see a population crash. Exhaustion of food resources alone can't explain crash.

These studies have been repeated again and again. Supplemental food just can't prevent a crash. Therefore, the food depletion can't be the only explanation.

b. Predators - (Hanski et al. 1991, 2001)

In northern Scandinavia, there are specialist predators ---> *Mustela nivalis*
M. erminea

The idea is that specialist predators oscillate with prey (as is the case with snowshoes and lynx), and predators drive the cycle.

In southern Scandinavia, the predators are more generalist and keep populations relatively low because the predator populations never crash.

This would explain the latitudinal variation.

However, the correspondence between specialist predators and latitude doesn't hold in North America.

Furthermore, populations in predator-free enclosures still crash (e.g., Graham and Lambin 2002. J. Animal Ecol. 71:946).

Thus, predation by specialist predators alone can't explain arvicoline population cycles as it does for snowshoe hare population cycles.

2. Intrinsic Hypotheses - Chitty behavioral/genetic hypothesis. (Krebs. 1978. Can. J. Zool. 56:2463.).

Based on the observation that there is a higher proportion of large aggressive voles in peak populations. This is known as the **Chitty Effect.**

The idea is that there is a genetic basis to both size and aggressive behavior, and that selection is operating within a cycle.

It's complex, but the crux is as follows:
At low densities, selection will favor amicable voles that put much energy into reproduction rather than aggression.

As densities increase, selection will favor fighters; they'll get resources, but won't be very reproductively active, therefore the population will crash

At first, the Chitty hypothesis was criticized on the grounds that a single cycle is too short a time period for selection to operate.

However, allozyme studies have demonstrated that allele frequencies in a sample from a trough can be significantly different than those in a sample from a peak. So significant genetic change can actually occur in this short a time period (w/in a cycle).

This led to a general acceptance of the Chitty hypothesis.

However, the traits involved (large size and aggressive behavior) have very low heritabilities (Boonstra & Boag. 1987. Evolution. 41:929). Therefore, even though genetic change within a cycle can be driven by selection, the response to selection is only possible if traits are heritable; this is not true for the crucial traits.

3. Multifactorial Hypothesis – Lidicker's model (Lidicker 1988. J. Mammal. 69:225.).

Focuses on *M. californicus* and posits that intrinsic and extrinsic factors interact.

Specifically, there are eight factors that affect vole numbers directly, and these include intrinsic factors like dispersal rates, reproduction and mortality, as well as extrinsic factors like parasites, predators, and vegetation.

Further, these are posited to have their effects at different stages during the cycles.

This has been criticized as being untestable in the literature.

5. Multifactorial Hypothesis - Social Fence (Hestebeck 1982. Oikos, 39:157.)

There is a density threshold called the "social fence."

At low densities – Intrinsic factors will dominate the dynamics.
Scattered social groups
Group size is regulated by dispersal - there is free dispersal.
Little aggression because there are plenty of resources.

At high densities - Resources become scarce.
Food may become limiting.
Dispersers experience increased aggression because of lower relatedness.
Further dispersal will be curtailed, and population may increase to the point of exhausting resources.
Extrinsic factors will dominate.
Population will crash.

Food becomes limiting, this contributes to other effects such as increased aggression.

Predators are incorporated by Pantry Effect; predation increases greatly at high vole densities because of a positive feedback, even among generalist predators. This contributes to crash.

Accounts for large aggressive animals present at high population densities.

Population cycles in arvicolines is a complex phenomenon; the explanation isn't going to be simple, and multifactorial hypotheses will be required (Oli. 2019. Mammal Review, 49:226).

However, one difficulty that such a complex hypothesis presents is that it is incredibly difficult to test. We can reject single factor hypotheses as being sufficient; however discerning among the various multifactorial hypotheses is very difficult (in my opinion).