 

Cyclic population dynamics of lemmings (*Lemmus lemmus*) and Arctic Fox (*Alopex lagopus*) – and implications for conservation

A REVIEW

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Summary

Several species - for instance geese, waders, stoat (Mustela erminea), roughlegged buzzard (Buteo lagopus), skua (Stercorarius parasiticus, S. longicaudus and S. pomarinus), herring gull (Larus argentatus), glaucous gull (L. hyperboreus), arctic fox (Alopex lagopus), snowy owl (Nyctea scandiaca) and plants - in the arctic and alpine ecosystems are much affected by the lemming population´s four-year cyclicity with peaks of high magnitude. It has cascade effects in the entire tundra ecosystems and induce cyclicity in several other animals.

The arctic fox, red-listed as acute threatened, is one of the species strongly affected by lemmings´ population dynamics since lemmings are an important part of the diet.

There are several theories about the causes of the cycles though there is no consensus among scientists: Climate change, bottom-up and top-down cascades, social interactions and toxic defend mechanisms in plants are plausible causes. Lately the cyclicity has decreased and it seems to be strongly connected with global warming.

Keywords: Lemming (Lemmus lemmus), arctic fox (Alopex lagopus), cyclicity, tundra, population dynamics, conservation.

Introduction

In the most northern of Europe the landscape is alpine or arctic. Here we find the lemmings and arctic foxes.

Already in the 16th century the archbishop Olaus Magnus in Uppsala noted that the lemmings where abundant every third year. His theory was that predation from polecat and weasel had a contributory cause for the cyclicity, something that is still considered.

The underlying reasons why the lemming populations fluctuate in a cyclic way is not clear but probably the main reasons are grazed plants (herbivory) or predation (Norrdahl 1995, Turchin et al. 2000, Ekerholm et al. 2001, Krebs 2011). Other factors like social interactions and climate are also discussed (Krebs 2011, Hansson Frank 2016) but there is no consensus among scientists.

Cyclicity is shown by many mammals around the world, but it is most obvious in northern ecosystems and in the lemmings which, with its role as key species, also influences cyclicity in other species abundance (Ims & Fuglei 2005). The fact that the phenomena occur in other related species could imply that the underlying processes are alike (Stenseth & Ims 1993). Although there is cyclicity in all arctic rodents this article will mainly focus on the rodent lemming (Lemmus lemmus).

The arctic fox is red listed as acute endangered and is since 1928 protected (fridlyst) in Sweden. It has had – like the lemmings - an important place in the tundra ecosystem since the last ice age. As a result of high hunting pressure, the Fennoscandian population of arctic foxes experienced a drastic bottleneck in the early 20th century. After 70 years of protection the population showed no signs of recovery (Hersteinsson et al. 1989). Conservation actions with culling of red foxes, release of foxes from captive breeding program and supplementary feeding started 1998 (Keeling Hemphill 2020). In 2022 unusually many (164 litters) arctic foxes were born, and genetic variation had increased considerably (Keeling Hemphill 2020). Since the arctic foxes´ population is very small now we can not expect that the impact on the system will be great. Therefore, it might be hard to see any clear results in research on the interaction. But since arctic foxes and lemmings are so closely interconnected one can wonder “what is the hen and what is the egg”. Turchin et al. (2000) claims that significantly bigger populations of foxes will make the cyclicity disappear. But probably the answer to the question is more complex.

Methods

The focus of this literature review is lemming density changes in relation to arctic foxes on the Scandinavia tundra. Scientific papers regarding relations and interactions between arctic foxes and lemmings as predator and prey were noted on internet in Oktober 2023. Keywords used in the search were “arctic fox”, “lemmel” and “cyclic” both separate and together (and the Swedish words for them). Then the papers that explained the theories regarding the cyclic population peaks in lemmings were used.

The ecology of lemmings

The lemmings are small (12-15 cm) rodents that in the winter live in grass-covered tunnels and dens under the snow. Different tunnels are used for different purposes; food storage, give birth or for latrine (Knaust 2014). They prefer a lot of snow in the winter, and in the summer, they move to semiaquatic areas. In autumn they can move long distances, up to 200 kilometers, especially when the population density is high. In Swedish this extraordinary dispersal is called "lämmeltåg" and it occurs only in this species (Lemmus lemmus). Every 30th year some individuals even spread to the forest but these small populations seldome survive (Hentonen & Kaikusalo 1993).

When populations are big the lemmings reside in bogs with lots of herbs and willow thickets or on moors with lichen (Saetnan et al. 2009). The diet consists mainly of mosses, lichens, herbs, sedge, and wavy hairgrass (Saetnan et al. 2009, Soininen et al. 2013) but the diet varies both regional and between different habitat (Soininen et al. 2013). The digestive capacity is only 30 percent of the intake while they have a high metabolism. They eat up to eight times their own body weight in a day (Ims & Fuglei 2005). The high grazing pressure affects both flora and fauna (Saetnan et al. 2009, Soininen et al. 2013).

The reproduction of lemmings is fast. They reproduce from the beginning of March to the middle of September with a pause around snow melting (Kuksov 1975). When the population is dense the females become fertile later and the litters are smaller (Kukosv 1975, Erlinge et al. 2000). On the other hand, when the population is small and it is early in the season, the females become sexually mature already after weaning, 14-20 days old. The size of litters was between 5,1 and 7,8 in the years 1964-1974 (Kuksov 1975).

The pregnancy is 20 days and after the birth of a litter (5-7 young) they can mate again (Semb-Johansson et al. 1993). The mating season is all year round except from the autumn to the middle of the winter (Ims & Fuglei 2005). It means that they can have 4-5 and up to 6 litters in a good year. The lemmings can become three years old. So… six pups five times a year is 30 pups/year or 90 pups in one female lifespan.

In years of abundance, every fourth year, the populations can become between 25 and 200 times (and sometimes up to 1000 times) larger than in the low phase (Krebs 1993). The time and magnitude of the crash varies but it comes during the summer or winter (Stenseth & Ims 1993).

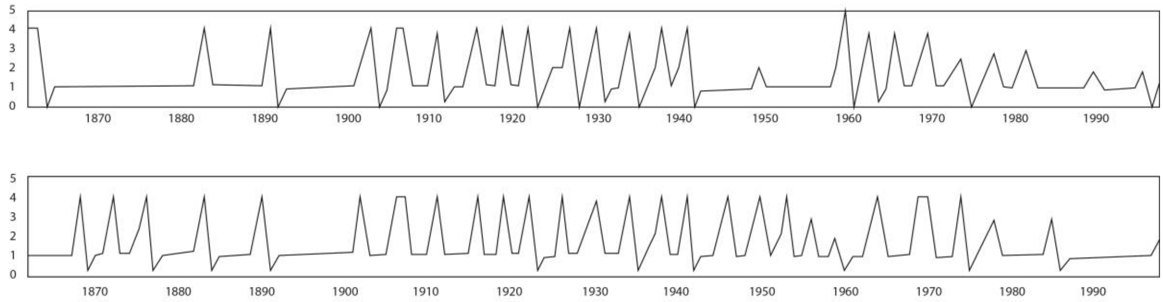

Fig. 1: Lemming densities between 1860 och 2000, in two different regions of Sweden. 0=crash, 1=low density, 2= increase, 3= small/local peak, 4=normal peak, 5= high peak. Drawn from illustration in Angerbjorn et al. (2001).

The ecology of arctic foxes

The arctic fox is red listed as endangered (artfakta.se). There are now (2023) about 550 adult individuals in Scandinavia (Eide et al. 2022). The species is a generalist, and they can eat anything from berries to carcasses but live mainly on lemmings. Therefore, the population dynamics shows a pattern that vary cyclic with the lemmings´ peaks (Elton 1924, Angerbjörn et al. 1999, Elmhagen et al. 2011). The arctic foxes have litters mainly the years when the lemmings are abundant, and then the litters are large (Ims & Fuglei 2005), about 7 pups on average and up to 18 pups (Meijer et al. 2013). The arctic fox litter sizes show a linear relation to the densities of lemming (Lemmus lemmus) (Angerbjorn et al. 2002). The arctic foxes reproduce in March-April and the pups are born in July-August (Svenska Fjällrävsprojektet 2022). One month after the pups are born, they go outside the den (Meijer et al. 2013). The arctic fox can become 5-8 years (artfakta.se).

Some arctic foxes that live by the coast or on islands and eat birds and carcasses from marine mammals´ don´t show this cyclic pattern in reproduction. They have litters more frequent but instead smaller litters, 4-5 pups every year (Ims & Fuglei 2005).

Even though the genetic variation in the arctic fox has increased it probably still suffers from the bottleneck with only 40 to 60 individuals that it has gone through (Angerbjörn et al. 2013). Inbreeding can often affect fertility.

Besides the missing lemming peaks, climate change, competition with red foxes and hybridization with foxes from fur-farms are growing causes for the arctic foxes´ trouble to recover (Svenska Fjällrävsprojektet 2022).

In a project in the years 2003-2008 the arctic foxes where fed during years when lemmings where few, and in addition red foxes where hunted. It was a success for the arctic fox, the population doubled (Svenska Fjällrävsprojektet 2022). One especially interesting result from the observation was that the arctic foxes litter size was bigger in the fed individuals, but *the cyclic variation still existed*. Another interesting result was that the foxes that were *not* fed had more pups in the lemmings rise phase than in the decline phase. So there seems to be an adaptation to expected lemming peaks, but we don´t know the mechanism behind this (Meijer et al. 2013).

The arctic fox lives in lifelong pairs that defend a home area around a good den. Together the parents raise the pups and sometimes the pups stay after getting sexually mature at nine months of age. Consequently, there can be several litters in the same den (Norén et al. 2012, Elmhagen et al. 2014). The females most often get their first litter at two years of age and about 10 percent of the pups survive the first winter (artfakta.se). So… seven pups per year and with ten percent surviving… will be 0,7 pups per year or 4,2 pups per female´s lifespan.

Why cyclicity?

This apparent cyclicity is a complex phenomenon. There is no consensus regarding the factors that controls the population dynamic with lemmings and other arctic rodents (Krebs 2011).

The trophic cascades top-down (predation) and bottom-up (grazing pressure) could be underlying mechanisms (Ims & Fuglei 2005). Other possible explanations could be social interactions or abiotic factors; climate, weather, snow depth… (Angerbjörn et al. 2001, Kausrud et al. 2008, Gilg et al. 2009).

It should be mentioned that the lemmings are bigger and slower than voles, and they try to scare the predators instead of running away. That makes them an easy catch for the predators (Hellström et al. 2014) which lessens the predation pressure on other prey and thus also generate cyclicity in other species (Ims et al. 2013).

CLIMATE CHANGE

The cyclicity has been decreasing lately. One theory is that it depends on a warmer climate (Kausrud et al. 2008).

When the high-amplitude population cycles collapse they will probably affect important ecosystem functions (Ims et al. 2008). The weather regulates the vegetation, and the snow is important for the lemmings´ reproduction. A lot of snow gives a higher survival rate during the winter months since the snow also isolates against the cold (Bilodeau et al. 2012). A warmer climate with ice close to the ground can prevent the lemmings from grazing during winter months. Less snow also means less shelter from predators

(Korslund & Steen 2006). Snow depth and climate change can explain lower peaks in lemming population growth.

Ims et al. (2008) points out that the dynamics of how climate change interacts with demography likely is differing among ecosystems.

Between 1860 and 1998 there are data on the cycles of lemmings, but in the beginning of the 1980th, around the same time as the climate change is globally alerted, the pattern gets more unusual and unpredictable. Warmer weather shrinks the lemmings´ natural habitat. A decrease in lemmings will affect many other species in the delicate ecosystem (Nyström 2011).

BOTTOM-UP AND TOP-DOWN CASCADES

The food chains on the tundra are perhaps an important key to explain the four-year cyclicity. The diet in the lemmings is different in different habitats (Soininen et al. 2013) but they have a high intake of food and a fast growth. That means that there is a high grazing pressure that affects both flora and fauna (Hanson Frank 2016).

The amount of food limits the number of herbivores. Low availability of vegetation decreases herbivores populations and low availability of herbivores limits the predators. But when there is abundant of food for the herbivores, populations can grow and the predators´ populations also (Ims & Fuglei 2005).

When the population of predators grow, they decrease the herbivores and then the vegetation can recover. But predators often have slower populations growth than prey, so the peaks of prey and predators are displaced.

On the other hand, when there are few predators there can be many herbivores. The lemmings can increase rapidly, and so they decrease the vegetation (Ims & Fuglei 2005) and reach the carrying capacity of the system.

Angerbjorn et al. (2002) found that the arctic foxes´ numerical response to lemmings´ abundant years had a time lag of one year. Both the carrying capacity of the vegetation and the displaced growth peaks of prey and predator populations are considered to be driving forces behind the cyclic phenomenon (Reid et al. 1995, Wilson et al. 1999).

The lemmings decline phase after a peak is *prolonged* until the predators´ populations also has decreased due to less food and high competition (Reid et al. 1995, Wilson et al 1999).

Turchin et al. (2000) mentions that if the arctic foxes´ population grows and regulate themselves, then the cyclicity will disappear and the system will get stable. He also says that the sharp population peaks imply that lemmings are functional predators, and that is confirmed by their long migrations that occurs in search for new moss.

TOXIC DEFENDMECHANISM IN PLANTS

Some plants produce toxins when grazed and that is enough to create cyclicity in the lemmings (Jensen & Doncaster 1999, Kent et al. 2005). The theory is that the lemmings eat the preferred plants first and then they switch to other plants that are less nutritious and produce toxins when grazed (Jensen & Doncaster 1999). Some toxins like silicon dioxide (SiO_2) stays in the plant up to a year (Soininen et al. 2013b).

SOCIAL INTERACTIONS

The cyclicity could also be a matter of self-regulation together with external factors (Stenseth et al. 1996, Andreassen et al. 2013).

During the increase in the population some individuals disperse to new areas around the original area. The original area then can´t expand and the competition of food increases there (Andreassen et al. 2013).

In the peak phase the lemming males move over open space to mate or to defend females. That makes them easy targets for predators. The crash phase could then probably be initiated and enhanced by predation of males. When a dominant male disappears a new male kills the litters of the first male (Andreassen & Gundersen 2006, Korpela et al. 2011, Andreassen et al. 2013). When the litters are killed the females move more and thus become targets for predation. Groups that are dissolved are more susceptible for predation. During the years when the population size is small the risk for predation is also higher because the lemmings are scattered and must move more to find each other. That keeps the population low in numbers (Andreassen et al. 2013).

Another theory is that the cyclicity is because lemmings reproduce under heavy snow which is beneficial for them (Turchin et al. 2000, Ims et al. 2010).

They are also benefited from big populations of other prey like voles because then the predation pressure gets lower on the lemmings (Turchin et al. 2000, Ims et al. 2010).

Discussion

The unsolved mystery with the cycles of the lemmings is something of the arctic scientist´s holy grail. The reasons behind the cyclicity in lemmings is not fully defined although several theories are discussed and researched. The understanding of the underlying mechanisms of the cyclic phenomenon is important to know for a successful conservation work with all the species that live in the delicate ecosystems of the tundra. There are a few different theories about the phenomenon, and they don´t contradict each other. The cycles could be a result of several concurrent factors.

Climate change has a big effect on the unique ecology of alpine and arctic tundra. A deeper knowledge of how arctic ecosystems are affected by the climate change would facilitate the conservation work for several species. A warmer climate will have consequences for both the ecology of lemmings, their predators, and the landscape. There is at suspicion that the climate change has caused the decrease in the cyclicity of lemmings in the resent years (Kausrud et al. 2008). An interesting study would be to compare the peaks with snow depth.

There is a probability that the one-year displaced peaks of population growth in lemmings and foxes makes the decline steeper and keeps cyclicity going.

Different studies of the ecosystems on the tundra shows that both top-down and bottom-up-systems can exist there. In the arctic Canada for instance the primary production is high, and it is not limiting the populations. That indicates that the decrease in the lemming populations there might be predator driven. But in Scandinavia the arctic foxes′ population is acute endangered, with a small population, so here the bottom-up theory becomes more probable (if one factor is enough). Few predators (or no predators) decrease the top-down effect and thus have a stronger effect on the primary production.

Several studies (Jensen & Doncaster 1999, Turchin et al. 2000, Turchin & Batzli 2001, Krebs et al. 2010, Soininen et al. 2013b, Hoset et al. 2014) are leaning towards the theory of resource-controlled ecosystems. We know that some plants get toxic when grazed. Could the vegetation in some other way also be cyclic, either in abundance or nutrition or is the toxicity enough to explain the crash? More studies of the lemmings′ diet in different seasons and the plants′ resilience and recovery time to hard grazing would be a welcome and important insight. Slow growing plants like mosses could maybe show cyclicity due to periodic heavy grazing.

Other rodent species also have cycles in population size which makes it extra interesting. Could there be a similar cause or are they not at all connected?

Regarding social factors it is hard to know what magnitude inner social factors (like male aggression and lack of food due to large density) really have. This would be an interesting area to study closer.

It would be interesting to search for other common patterns in the interactions between the mammal species in the tundra ecosystems. There might be found a missing factor. And, since the arctic foxes now are few, it would be fascinating to see the functions in a system with many more foxes.

To be able to anticipate the future for the lemmings and arctic fox one needs to include all the factors that are involved, not least competitive species, for instance the red fox, that benefits from warmer climate. Animals and plants that now live south of the artic and alpine area will, together with warmer temperatures, move north and compete with now existing species.

It is possible that all these theories are right and that they all affect the cyclic population dynamics of the lemmings and foxes. Radchuk et al. (2016) confirms that a model which include both predation and intrinsic factors (dispersal and sociality) yields cycle periods that resembles those in the nature.

Since the results of the different studies vary the conclusion could be that the cyclicity has different factors in different habitats. It is not impossible that all the theories are working together in a complicated collaborating system.

The complexity of the problem makes it harder to plan conservation strategies for the two species, the arctic fox, and the lemming. Though it seems that the conservation actions made for the arctic fox - feeding, breeding, and hunting the red fox - are working. Maybe the population can grow on its own from here, but it will need monitoring. The lemming´s biggest threat right now is warmer weather with less snow and more ice. Climate change will affect the whole tundra ecosystem and, of course, the whole planet. For that we need the world leaders to act in a broad, brave, and acute way.

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