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Arctic lemmings are not simply food limited – a comment on Oksanen *et al.*

We appreciate the attempt by Oksanen *et al.* (2008: *Evol. Ecol. Res.*, **10**: 415–434; http://evolutionary-ecology.com/issues/v10n03/hhar2304.pdf) to link possible evolutionary changes to the history of colonization of the Arctic by lemmings. However, we do not agree that lemming evolution and colonization history help us to understand current lemming population dynamics.

Oksanen *et al.* (2008) note that field exclosures in Fennoscandia show evidence of moss overgrazing by lemmings. Habitat degradation is clearly visible in peak lemming years, especially in critical wintering habitat such as snowbeds. Based on this evidence and their analysis of lemming populations through time, Oksanen *et al.* reach generalizations about lemming–vegetation interactions across the Arctic. Their food-limitation model generates a time-lag owing to the overuse of mosses by *Lemmus* (during years of peak lemming abundance) followed by the delayed recovery of mosses.

It is true that previous models assumed a recovery time for mosses of 2 years (Turchin and Baltzi, 2001: *Ecology*, **82**: 1521–1534). But recovery time of these plants following severe overgrazing appears much longer in northern Fennoscandia, on the order of 10 years (Oksanen *et al.*, 2008). After overgrazing, recovery of mosses (and even vascular plants) is indeed slow in the Arctic. But the period typical of most lemming cycles is 3–5 years. A 10-year recovery time-lag cannot generate a 3- to 5-year population cycle.

Moreover, the time-series analyses in Oksanen *et al.* have a troubling technical flaw. Of the 15 time-series that they use, 13 are based on index values rather than estimates of population density. Indices may overestimate or underestimate density and the bias may itself depend on density (Anderson, 2003: *Wildlife Soc. Bull.*, **31**: 288–291). So one cannot reliably calculate per capita population growth rates based on indices.

We are convinced that the generalizations of Oksanen *et al.* do not apply in the Arctic regions where we have worked. No study conducted in the Canadian Arctic in the past 40 years has ever noted evidence of widespread habitat degradation, including mosses, after a lemming peak. Recent evidence from lemming exclosures in both wet and mesic tundra sites at Bylot Island (G. Gauthier, unpublished data) also fails to support the overgrazing hypothesis. The food limitation hypothesis for *Lemmus* population cycles may apply in Fennoscandia but not in Canada.

Oksanen *et al.* also generalize their food depletion hypothesis to *Dicrostonyx* populations. However, *Dicrostonyx* eat very little moss, and yet are highly cyclic in several places where *Lemmus* are scarce (Walker Bay) or absent (Greenland). In Canada, we have never seen *Dicrostonyx* food resource depletion after peak populations.

In addition, we do not believe that one can describe population dynamics and evaluate a mechanistic model from census data taken only once or twice a year. By using annual and semi-annual censuses, Oksanen *et al.* ignore seasonality. Yet moss is a dominant part of *Lemmus* diet only in winter. In summer, *Lemmus* eat mostly other plants, especially graminoids. If the food-limitation hypothesis were true, the most difficult period for lemmings in peak years would be the end of winter, when mosses become increasingly depleted. Therefore, the end of winter and early spring would be the time when *Lemmus* should experience decreased reproduction and a population decline. After the snow melts and new food supplies are renewed, *Lemmus* populations should grow rapidly. However, in peak lemming years, the strongest reproductive output often occurs under the snow in late winter and spring. Populations of lemmings peak shortly after snow melt and then decline or even crash during the summer (Millar, 2001: *Ecoscience*, **2**: 145–150).

The summer decline is often associated with increased predation mortality. In previous research, we found evidence for a strong role of predators in lemming cycles at some Canadian sites (Reid *et al.*, 1995: *Oikos*, **73**: 387–398; Wilson *et al.*, 1999: *Oikos*, **87**: 382–398). Nonetheless, Oksanen *et al.* reject the predator hypothesis either by pointing out weaknesses in these studies or by arguing that they were conducted at coastal sites where predators may benefit from allochthonous exchanges with the marine environment. We do not dispute some of these weaknesses, but we believe that the food-limitation hypothesis has at least as many.

To reach convincing conclusions, one needs detailed seasonal data on changes in actual numbers. But there are hardly any winter data on lemming and northern vole populations. We also need data on how predation, parasitism, food shortages, and social processes affect population changes. Empirical field studies that might provide such data are still scarce for lemmings and limited to a few sites in the circumpolar world for too short a period to rely on at this point. Therefore, we conclude that the jury is still out on what factors drive the lemming cycles in many parts of the Arctic and that the conclusions of Oksanen *et al.* are premature.

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