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On the implications of currently available data on population fluctuations of arctic lemmings – reply to Gauthier *et al.*

Gauthier *et al.* (2009: *Evol. Ecol. Res.*, **11**: 483–484) raise two major questions about our recent paper (Oksanen *et al.*, 2008: *Evol. Ecol. Res.*, **10**: 415–434). Can the evolutionary background of a species provide clues for its current population dynamics? And can patterns revealed by imperfect data be used for testing population dynamical hypotheses?

We interpreted the evolution of arctic lemmings as an indication of a shift from predator control to resource limitation. This shift provides clues for population dynamical hypotheses if adaptations carry a cost. Predator-controlled herbivore guilds are structured by apparent competition, where success depends on the r/a ratio (Holt, 1977: *Theor. Popul. Biol.*, **12**: 276–290), i.e. the ratio of reproductive capacity to vulnerability. Conversely, food-limited herbivore guilds are structured by resource competition, where the outcome depends on R^*, i.e. the lowest resource density at which the organism can still survive (Tilman, 1982: *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press). If there is a trade-off between properties minimizing a (speed and agility) and R^* [the ability to exploit depleted resources (Oksanen, 1992: *Evol. Ecol.*, **6**: 15–33)] and the more agile voles are present, regulation by predators should lead to exclusion of arctic lemmings (Oksanen, 1993: *Linn. Soc. Symp. Ser.*, **15**: 425–437; K. Kyrö, L. Oksanen, and T. Oksanen, unpublished data).

In their second major point, Gauthier *et al.* (2009) argue that snap trapping indices are too inaccurate to be used for testing population dynamical conjectures. Inaccuracies in the database can reduce the likelihood of detecting differences between the objects of study but cannot account for the statistically significant contrasts between arctic lemmings and reference voles. Moreover, we have focused on robust predictions. According to the predation-based models (Hanski *et al.*, 2001: *Ecology*, **82**: 1505–1520; Gilg *et al.*, 2003: *Science*, **302**: 866–868), rodent densities must not increase more than four-fold during the year preceding the peak, while a more than 20-fold increase is predicted by the food-based models (Turchin *et al.*, 2000: *Nature*, **405**: 562–565; Turchin and Batzli, 2001: *Ecology*, **82**: 1521–1534). During the year preceding the peak, the density indices for *Lemmus* spp. increased, on average, by 67-fold and those for *Dicrostonyx* spp. by 37-fold, whereas the indices for the reference voles increased less than two-fold. Due to trap saturation at high densities, all these estimates are downward biased. But this bias only strengthens the point that just before the peak, arctic lemmings are increasing at a rate that resident specialized predators cannot match.

As for the other points, the Barrow model is taxonomically neutral and requires only that lemmings exploit both depletable and annually renewed forage plants. The model can be applied to *Dicrostonyx* spp. if we assume that woody plants form the depletable part of the diet. With original parameter values, the Barrow model generates the 3- to 5-year cycles discussed by Gauthier *et al.* (2009). To reconcile this model with the longer periods of Fennoscandian cycles, we must assume lower growth rates for depletable forage plants. Studies on plant growth rates can thus be used to test the model.

Gauthier *et al.* (2009) claim that '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'. The visibility of herbivore impacts depends on the frequency of the disturbance. During a decade with low lemming densities, the species composition of Fennoscandian snowbed vegetation changes profoundly, making the impacts of lemming outbreaks obvious. In cycles with a shorter period, there is less time for the vegetation to change qualitatively, and biomass changes may not be easily observed. The detailed plant population studies of Berg *et al.* (2008: *Adv. Ecol. Res.*, **40**: 275–298) reveal strong lemming impacts on dwarf shrubs in northeast Greenland, and lemmings also seem to regulate the moss cover at Barrow, Alaska (Oksanen, 1983: *Am. Nat.*, **122**: 45–52; Pitelka and Batzli, 2007: *Acta Theriol.*, **52**: 323–336). Moreover, depletion of woody plants can be difficult to detect. We did not detect the impacts of grey-sided voles on dwarf shrubs visually, but by marking shoots and by experimentally introducing and excluding voles (Oksanen and Oksanen, 1981: *Rep. Kevo Subarctic Res. Stat.*, **17**: 7–31; Hambäck and Ekerholm, 1997: *Oikos*, **80**: 276–288; Hambäck *et al.*, 2004: *Oikos*, **106**: 85–92; Olofsson *et al.*, 2004: *Oikos*, **106**: 324–334).

As pointed out by Gauthier *et al.* (2009), the food-based models predict that lemming populations crash in the post-peak winter, whereas according to them lemming densities peak right after the snow melt and decline or crash during the summer. They cite Millar (2001: *Ecoscience*, **8**: 145–150), but that study focuses on reproductive biology and does not discuss the timing of crashes. The data compiled by us include one summer crash (at Barrow 1965); all other documented crashes have occurred in winter. Moderate summer declines, attributable to avian predation, occur often in coastal areas. According to the indices, all studied inland populations, including the one studied by Krebs (1964: *Arct. Inst. N. Am., Tech. Paper*, **15**: 1–104) at Baker Lake, Canada, peaked in late summer and crashed in winter.

We see the coast versus inland contrast as part of a broader question concerning the impact of marine-based subsidies on food web dynamics in unproductive terrestrial systems (Polis and Hurd, 1996: *Food Webs: Integration of Patterns and Dynamics*, pp. 275–285. New York: Chapman & Hall). The experiments demonstrating the impact of predation on lemmings (Reid *et al.*, 1994: *Oikos*, **73**: 387–398; Wilson *et al.*, 1999: *Oikos*, **87**: 382–398) were conducted at the coast, and refer to populations which we do not regard as cyclic. [The densities of the lemmings of Wilson *et al.* (1999) varied only within the range 1 to 10 individuals per hectare.] Moreover, coastal predators do use marine-based prey (Sitter *et al.*, 2000: *Arctic*, **53**: 53–60). Studies conducted on the coastal tundra make an important contribution to our understanding of the arctic. The arctic coastline is long and a substantial part of the tundra is coastal, especially in the high arctic where much of the inland area is made up of ice caps and polar deserts. Nevertheless, results obtained from coastal areas need not be representative of the inland tundra.

While the available time trajectory data do corroborate the Barrow model, other ideas, which have not yet been rigorously modelled, could also account for their patterns. We are currently analysing an idea in the context of the low arctic tundra where productive willow scrublands still occur, which we call the 'pacemaker hypothesis'. It presupposes that the period of the cycle is set by predator–vole–lemming interactions in small patches of productive pacemaker habitat. The dramatic increase in the pre-peak year happens primarily in the widespread unproductive habitats; there lemmings crash due to starvation in the post-peak winter.

We agree with Gauthier *et al.* (2009) that the enigma of arctic lemming cycles is far from solved. Experimental results and long-term records are few. Thus, large geographical and/or interspecific differences in population dynamics of arctic lemmings might remain to be detected. To date, however, the only clear difference detected between the dynamics of different populations of arctic lemmings is the greater frequency of summer declines in coastal areas, which fits the food-based hypotheses.

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