

# Vole cycles and predation

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In a recent article in *TREE* [1], Madan K. Oli claimed that an experimental reduction of weasel density in Kielder Forest [2] shows that specialist mammalian predators are neither sufficient nor necessary to drive multiannual population cycles of field voles *Microtus agrestis*. Here, we argue that this claim is misleading because he overlooked three important issues: the uniqueness of the Kielder Forest vole cycles compared with elsewhere; the limitations in the Kielder Forest experiment to test current predation hypotheses; and the contribution of other recent experiments on predation and vole cycles.

The multiannual vole cycles in Kielder Forest and in northern Europe (northern vole cycles) differ in at least three fundamental ways to suggest that the Kielder Forest experiment provides limited insight into the role of predators in vole cycles elsewhere. First, in the low phase of northern vole cycles, densities of voles are much lower than in Kielder Forest (<1 ha<sup>-1</sup> versus 25–50 ha<sup>-1</sup>). Northern vole cycles are also characterized by 50- to 500-fold differences between peak and lowest densities, whereas vole cycles in Kielder Forest are low amplitude cycles with only tenfold differences between peaks and lows that would provide greater interannual stability in food supply for vole-eating predators. Second, spatial synchrony of Kielder Forest vole cycles is much smaller than that of northern vole cycles (8–20 km versus 70–500 km [3–5]) to provide a more reliable prey base across small areas. Third, in northern Europe, but not in Kielder Forest, field voles fluctuate in close temporal synchrony with other arvicoline rodents and even with shrews, all showing their lowest densities simultaneously [4,6], which again would alter food supply of predators. Current dynamic population models of the northern vole cycles predict that delayed density-dependent impact by predators drives vole cycles [7], but comparable models for the Kielder Forest predator–prey system do not exist. Hence, we feel that Oli erred when he concluded, ‘a leading hypothesis of population cycles, the specialist predator hypothesis, has now been conclusively contradicted’ [1], assuming that ‘population cycles’ also includes the large-scale northern vole cycles.

We suggest two important limitations that might have caused the lack of response by voles in the weasel reduction experiment in Kielder Forest [2]. First, the

experiment was conducted on a small spatial scale: three paired reduction and control areas, each only 5–12 ha and 2–4 km apart. As the home range size of weasels is 10–40 ha at high vole densities and 120–220 ha at low vole densities [8], each reduction area was smaller than the home range of a single weasel. Second, only the densities of the smallest member of the vole-eating predator assemblage, the common weasel, were reduced [2]. Because the densities of other mammalian and avian predators preying on voles were high in Kielder Forest [9], it seems probable that these other predators, together with weasels immigrating from surrounding areas to reduction areas, could easily have compensated for the weasels that were removed.

Oli’s paper [1] also gives a misleading picture of the predator reduction experiments conducted in northern Europe. The study in Kielder Forest is not the only one that has ‘large-scale, replicated field experiments, conducted in natural settings’. We have experimentally reduced densities of all main mammalian and avian predators in three or four large unfenced areas (2.5–3 km<sup>2</sup> each) in each phase of the three-year vole cycle. These large-scale replicated manipulations increased the autumn density of voles by two- to fourfold in the three phases of the vole cycle, retarded the initiation of decline of the vole cycle and prevented the summer decline of vole populations [10,11]. Unfortunately, Oli implied that the latter three-year experiment [11] was fenced and only short term [1].

The case of the Kielder Forest and recent data from other areas of temperate Europe [8,12] now suggest that the influence of predators on population fluctuations of voles is more multifaceted than was previously thought. But confounding this cycle with the entirely different northern vole cycles appears unhelpful for understanding vole dynamics in either zone.

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### Letters Response

## Response to Korpimäki *et al.*: vole cycles and predation

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Korpimäki *et al.* [1] argue that I overlooked some important issues in a recent article in *TREE* [2]. They correctly point out that Kielder Forest vole cycles are somewhat different than Fennoscandian vole cycles. Species- or habitat- specific differences in population dynamics are to be expected, and a general hypothesis of vole cycles should explain cyclic fluctuations in abundance of voles in more than one geographic locations. The Kielder Forest experiment (I.M. Graham, PhD thesis, University of Aberdeen 2001; [3]) was specifically conducted to test the specialist predator hypothesis on Kielder Forest voles, and it is unclear how differences between Kielder Forest and Fennoscandian vole cycles or the lack of mathematical models for Kielder Forest vole cycles could have influenced the results of the experiment.

Few field experiments that span large spatial and temporal scales are perfect, and perhaps there is room for improvement in the Kielder Forest experiment, as noted by Korpimäki *et al.* Nevertheless, this experiment remains one of the most rigorous experimental tests of specialist predator hypothesis. It was well designed and provided rigorous estimates of important demographic variables. Spatial scale of the experiment, although smaller than that used by some recent studies (e.g. [4]), was apparently adequate to test specialist predator hypothesis [5].

If density-dependent predation by specialist predators was necessary and sufficient to cause population cycles, experimental removal of weasels (specialist predators of Kielder Forest voles) should stop cyclic fluctuations in vole abundance [6]. The Kielder Forest experiment (I.M. Graham, PhD thesis, University of Aberdeen 2001; [3]) has convincingly shown that removal of weasels did not substantially impact vole survival or alter the cyclic dynamics of the experimental populations. These results

can lead to only one conclusion: specialist predators are neither necessary nor sufficient to cause population cycles in Kielder Forest field voles. Although findings of the Kielder Forest experiment do not eliminate the specialist predator hypothesis as a potential explanation of population cycles elsewhere, the results clearly contradict predictions of the hypothesis for Kielder Forest vole cycles. Given the rigorous experimental design, I see no reason to question the results of this experiment until future experiments show otherwise. Consequently, my conclusions stand as before.

It is well known that vole population cycles are characterized by phase-related changes in reproductive rate, age at maturity, age structure and body mass [6–11]. Hypotheses of vole cycles must also explain the biological changes associated with cyclic fluctuations in abundance [6], but it is unclear how predation can cause these changes. The challenge for Lambin's research group (and for other ecologists) is to devise and/or test hypotheses that can explain cyclic fluctuations in abundance, as well as phase-related changes in biological attributes of the Kielder Forest vole cycles.

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