

# Population cycles of small rodents are caused by specialist predators: or are they?

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**Predation by specialist mammalian predators has been hypothesized to be the primary cause of multi-annual density fluctuations ('population cycles') in voles. Using a series of replicated field experiments, Isla Graham and Xavier Lambin have now shown that specialist mammalian predators are neither necessary nor sufficient to drive field vole *Microtus agrestis* population cycles. These findings conclusively contradict the specialist predator hypothesis. The search for the mechanisms underlying the spectacular dynamics of cyclic vole populations must, therefore, continue.**

Many populations of voles and lemmings in northern latitudes exhibit cyclic fluctuations in abundance with a periodicity of 3–5 yrs. These fluctuations ('population cycles') have been the subject of much research, starting with a classic paper by Charles Elton early in the last century [1]. In spite of seven decades of research and a plethora of hypotheses, population cycles remain one of the most important and unresolved issues in ecology [2–5]. One of the leading hypotheses of population cycles invokes predation as the underlying mechanism of population cycles [3,6–8]. The idea that predator–prey interactions can generate cyclic numerical dynamics has its roots in early predator–prey models [9]. However, recent studies indicate that, whilst both specialist and generalist predators can potentially influence prey population dynamics, only specialist mammalian predators can potentially cause cyclic fluctuations in prey abundance [6,7]. This idea, called the specialist predator hypothesis, has received much attention in recent years. The essence of the hypothesis is that delayed density-dependant mortality owing to predation by specialist mammalian predators drives the dynamics of cyclic vole populations [10]. Recent theoretical and experimental studies in the Fennoscandia appear to corroborate the specialist predator hypothesis [6,10–13], but comparable experimental tests of the hypothesis elsewhere were lacking until now. A recent study by Isla Graham and Xavier Lambin ([14]; I.M. Graham, PhD thesis, University of Aberdeen, 2001) of a cyclic field vole *Microtus agrestis* population in northern England provides the first rigorous test of the specialist predator hypothesis outside the Fennoscandia.

## The experiment

Graham and Lambin's study is unique in several respects. First, they used large-scale, replicated field experiments, conducted in natural settings, and monitored vole populations with the use of live-trapping methods. Second, the study spanned all phases of a population cycle (April 1996–April 2001). Third, they tested all predictions and an important assumption of the specialist predator hypothesis within the framework of 'strong inference' [15]. Finally, Graham and Lambin not only monitored the abundance of voles and predators in paired control-manipulated sites, but also provided explicit estimates of several demographic parameters. This enabled direct demographic comparisons of control and manipulated population pairs to be made. By contrast, most previous tests of the specialist predator hypothesis (1) were based on short-term studies, focusing on the decline or low phase of a cycle; (2) employed enclosures or snap-trapping methods; or (3) have failed to provide estimates of demographic parameters [11,12].

## The hypothesis and predictions

If specialist mammalian predators are in fact necessary and sufficient to cause population cycles, and if an experiment involved removal of specialist mammalian predators from manipulated sites, one would predict that: (1) vole populations at control sites should exhibit multi-annual cycles whereas those at manipulated sites should not; (2) the crash of the population during the decline phase should not be observed in manipulated sites; (3) survival rate in control sites should be lower than that in manipulated sites; and (4) the survival differences between control and manipulated sites should be necessary and sufficient for changing a cyclic population to being noncyclic or vice versa. Moreover, theory suggests that there must be a delayed numerical response of specialist predators to prey abundance for predation to cause cyclic fluctuations in vole abundance [6,7,10], and the specialist predator hypothesis assumes such a response. This assumption must also be tested.

Graham and Lambin rigorously tested both these predictions and the assumption ([14]; I.M. Graham, PhD thesis, University of Aberdeen, 2001). The study population, located at the Kielder Forest in northern England, exhibited cyclic fluctuations in abundance with a periodicity of 3–4 years. Vole densities ranged from 25 ha<sup>-1</sup> during the low phase to 413 ha<sup>-1</sup> during the peak phase.

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The weasel *Mustela nivalis* was the main specialist mammalian predator, and fed almost exclusively on voles. The authors monitored vole populations in three sites under natural conditions, and in three manipulated sites where weasels were live trapped and removed. Each control site was paired with a manipulated site with similar habitat characteristics, which enabled direct demographic comparisons between the two to be made. Weasel populations were also monitored at all six sites, and the effect of predation by weasels on vole survival was modeled using mark–recapture techniques [16].

The results are intriguing. First, vole populations fluctuated similarly in control and manipulated sites, and there was no significant divergence in population trajectories between the two (I.M. Graham, PhD thesis, University of Aberdeen, 2001; Graham and Lambin, pers. commun.). Moreover, weasel removal did not prevent the crash of the population during the decline phase of the cycle at any predator removal site. Second, although survival rates were generally higher in manipulated sites, these survival differences had little influence on vole population dynamics. These observations are consistent with recent findings that adult survival rates have little potential influence on the growth rates of populations characterized by early maturity and high reproductive rates (e.g. [17]). Finally, Graham and Lambin found no evidence to suggest that the numerical response of weasels to temporal changes in vole abundance was delayed density dependent. These results clearly contradict predictions and the main assumption of the specialist predator hypothesis, and led the authors to conclude that predation by specialist mammalian predators is neither necessary nor sufficient to cause multi-annual fluctuations in the field vole abundance. This study, therefore, conclusively rejected the specialist predator hypothesis as the mechanism underlying population cycles, at least for the Kielder Forest field vole population.

By contrast, predator removal experiments have been reported to have prevented the crash phase, induced rapid population growth, or increased peak densities in western Finland [11,12,18]. These findings are consistent with the predation/specialist predator hypothesis and, if true, would establish predation as the mechanism underlying vole population cycles. Why are the results of these studies and those of Graham and Lambin so different?

Korpimäki and Norrdahl's [11] study lasted only a few months during two decline phases, and provided no information about the effect of predators on vole populations during other phases of cycles. Moreover, this study employed snap-trapping techniques to monitor vole populations, which can substantially disrupt the natural dynamics of the study populations. Klemola *et al.*'s study [12] was also conducted during the decline or low phase of the cycle, and employed predator-proof enclosures to protect manipulated populations from predators. Enclosed vole populations are known to grow to extremely high densities [2,19]. Thus, rapid increases in enclosed vole populations in the studies by Klemola *et al.* might be attributable, at least in part, to the 'fence effect' [2,19]. Neither of these studies documented effects of predation on vole populations during phases of the cycle other than the

low or decline phases. The continuation of the latter study [18] encompassed the increase phase of a cycle, but did not address other concerns (e.g. fence effect). Thus, the differences between the findings of Graham and Lambin's study and those conducted in western Finland [11,12,18] might be, at least in part, because of methodological differences. However, population-dynamic differences between the Fennoscandian and English vole populations [20] might also have contributed to differences in results obtained by the two research groups.

## Conclusion

So, do specialist mammalian predators initiate and drive vole population cycles? The answer seems to be a resounding 'no', at least for the Kielder Forest field voles. Given their rigorous experimental design, there seems to be little ground to question Graham and Lambin's main conclusion that specialist mammalian predators are neither necessary nor sufficient to drive field vole population cycles in northern England. Similar experiments elsewhere (particularly in Japan and North America) would be required to test the generality of Graham and Lambin's conclusions.

Population cycles have fascinated many ecologists, and the causes of the high-amplitude, multi-annual fluctuations in abundance have been fervently debated for seven decades [2,3,5,21]. Given that a leading hypothesis of population cycles, the specialist predator hypothesis, has now been conclusively contradicted, the search for causes of spectacular cyclic fluctuations in small mammal abundance must continue.

## Acknowledgements

I thank E. Bruna, I.M. Graham and X. Lambin for helpful comments on the article.

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doi:10.1016/S0169-5347(03)00005-3

## Letters

## Do queens select sperm?

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In their recent Research Update in *TREE* discussing the genetic caste determination in certain hybrid populations of the harvester ant *Pogonomyrmex barbatus* [1], Ashe and Oldroyd highlight an interesting problem for queen ants. Because queens are homozygous and workers are heterozygous at a particular locus, successful queens are not only obligatorily polyandrous, but must also mate with males of two different haplotypes to form a successful colony containing both workers and alate queens [2,3]. Authors of one of the original papers reviewed [2] report an average effective mate number of 3.34 and calculate that, with random mating, ~26% of triple-mated queens would be unable to produce both workers and reproductive offspring. Ashe and Oldroyd [1] postulate that mating frequency is low because females have evolved sophisticated precopulatory mate choice that involves the ability to distinguish between males of different genotypes.

We would like to point out an additional problem facing these queens that might make these ants a superb model for examining the relationship between sexual selection and social evolution. As indicated by Volny and Gordon [2], 'a genetic system of caste determination will constrain the ability of a colony to adjust its ratio of workers to reproductives according to its changing needs in different seasons and stages of life'. The problem therefore is that without some sophisticated means of organizing or otherwise discriminating between the two sperm haplotypes and selectively utilizing the competing sperm within her reproductive tract, queens will be unlikely to produce selectively advantageous proportions of female reproductives and workers. In particular, there is likely to be a massive overproduction of reproductive females, because reproductive output of ants is often <10% than that of worker production over a queen's lifetime [4]. Even if females could somehow manage to mate strategically so as

to obtain the right proportion of the two sperm haplotypes, some form of 'sperm choice' [5] would still be required to modulate temporal variation in the production of female reproductives. Colonies of *P. barbatus* typically do not produce reproductives during the first five years of their existence – the time required to build a sufficient worker force [6]. Even after colonies begin production of reproductives, worker production remains continuous, whereas reproductives are only produced seasonally in preparation for the mating flight [2].

Sperm choice by females is challenging to demonstrate and so has been a contentious issue among evolutionary ecologists [5,7–9]. Natural selection for the physiological capacity to selectively use different sperm should have been extremely strong in these harvester ants. They could provide a unique and relatively easy opportunity for unequivocal demonstration of female sperm choice.

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PII: S0169-5347(02)00057-5