Population cycles in microtines: the senescence hypothesis

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Summary
The cause of population cycles in microtines (voles and lemmings) remains an enigma. I propose a new solution to this problem based on a crucial feature of microtine biology, shifts in age structure, that has been ignored until now. Empirical evidence indicates that age structure must shift markedly towards older animals during declines because of three characteristics of the previous peak year: a shortened breeding season, total replacement of the breeding population from peak to decline and density-dependent social inhibition of maturation of young. Declines become inevitable as populations composed of older animals survive and reproduce poorly because of the effects of senescence, possibly interacting with the experiences of peak density and I present both theoretical and empirical evidence for this hypothesis. Although a variety of physiological systems deteriorate with aging, I focus on a crucial one – the inability of older animals to effectively maintain homeostasis in the face of environmental challenges because of a progressive deterioration in the endocrine feedback mechanisms involved in the hippocampal–hypothalamic–pituitary–adrenal axis. Microtine populations will not exhibit cycles where age structure shifts are prevented owing to extrinsic factors such as intense predation. Six testable predictions are made that can falsify this hypothesis.

Keywords: age structure; population demography; microtines; population cycles; senescence

Introduction
Many microtine populations (lemmings and voles) go through regular multi-annual fluctuations in numbers (commonly known as cycles) (Krebs and Myers, 1974; Taitt and Krebs, 1985). Although many hypotheses have been advanced to explain this phenomenon, all extant hypotheses are still controversial and in question (Taitt and Krebs, 1985; Boonstra and Boag, 1987; Nelson, 1987; Lidicker, 1988; Gaines et al., 1991; Lambin and Krebs, 1991a). It is remarkable that even though the study of cycles is the bailiwick of population ecologists, the importance of age structure, a concept central to demography, has been virtually ignored (Krebs and Myers, 1974; Taitt and Krebs, 1985). Here, I elaborate a new hypothesis for cycles that (1) directly considers the role of age structure shifts whereas others have not, (2) considers the consequences of these age structure shifts, specifically that reproduction and survival vary as a function of age for evolutionary reasons (i.e. the theory of senescence; Rose, 1991) and, in doing so, (3) offers a more broadly based explanation that can account for population cycles in microtines.

The problem and a new hypothesis
The central enigma in understanding microtine cycles is knowing the cause(s) of population declines and the period of low numbers that often accompanies these declines. Experiments have
manipulated the environments of voles, but have been unable to arrest population declines. Therefore, whatever changes occur must be intrinsic. Declines cannot be stopped by transferring animals from declining populations to areas from which animals from an increasing population have just been removed (Krebs, 1966), by adding food (Krebs and DeLong, 1965; Cole and Batzli, 1978; Desy and Thompson, 1983) or by removing predators (Pearson, 1966, 1971). Interactions among these potential causes may prove relevant (e.g. predation and food; Desy and Batzli, 1989), though these have not yet been shown to be necessary and sufficient to explain declines. Nor can these interactions account for the fact that most decline animals, when removed to the optimal conditions of the laboratory, continue to exhibit poor performance with respect to reproduction and growth when compared with animals removed from other phases of the cycle (Newson and Chitty, 1962; Krebs, 1966; Mihok and Boonstra, 1992). One obvious and previously ignored change through the population cycle is the shift in age structure towards older animals during declines.

The essence of the hypothesis is that density-dependent social inhibition during the spring and early summer of the peak year of the cycle forces young animals to delay maturation until the next breeding season when they are old (Fig. 1). Old age, acting either separately or in conjunction with the experience of peak density during the previous summer and winter, impairs the viability of these animals and their young and precipitates the decline. Thus, declines will necessarily follow peaks because of the lags in age of first reproduction. This hypothesis is therefore based on two critical assumptions: (1) that age structure shifts significantly throughout a cycle and (2) that, in older populations, the effects of senescence become more pronounced, leading to reduced survival and reproductive success. Below, I review the theory and evidence for these assumptions and I describe a plausible physiological mechanism by which aging (senescence) may affect fitness in microtines.