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Model of microtine cycles caused by lethal toxins in non-preferred food plants

Adam Kent[a], Susanne Plesner Jensen[b], C.Patrick Doncaster[a,*]

[a]*School of Biological Sciences, Biodiversity and Ecology Division, University of Southampton, Bassett Crescent East, Southampton SO16 7PX, UK*
[b]*Evolutionary Biology Group, School of Clinical Medical Sciences, University of Newcastle upon Tyne, 4th Floor William Leech Building, Newcastle upon Tyne NE2 4HH, UK*

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Abstract

A recent model of microtine cycles has hypothesized that plant chemical defences can drive the precipitous decline phase, through periodic lethal toxin production (PLTP) by non-preferred plant foods. Here we enumerate possible mechanisms using a previously published model of optimal foraging by one consumer (microtine rodent) of two types of food plant (1 preferred and 1 non-preferred). Rate constants for each of the model parameters were sought from the extensive literature on vole cycles. For a range of likely values of input parameters, we evaluated model fit by applying five empirically derived criteria for cyclic behaviour. These were: cycles with a period length of 2–5 yr, peak densities of 100–350 voles per ha and trough densities of 0–25 ha^{-1}, ratio of peak to trough densities of 10–100, and the occurrence of a catastrophic collapse in the vole population followed by a prolonged low phase. In contrast to previous models of food-induced microtine cycles, the optimal foraging model successfully reproduced the first four criteria and the prolonged low phase. The criterion of population collapse was met if the non-preferred food began producing lethal toxins at a threshold grazing intensity, as predicted by PLTP. Fewer criteria could be met in variations on the model, in which the non-preferred food was equally as nutritious as the preferred food or was continuously toxic.

Keywords: Lemmings; Population cycles; Population regulation; Voles; Wound-induced responses

1. Introduction

Populations of many small microtine rodents undergo regular cycles in high latitudes and altitudes of the northern hemisphere, though not the southern hemisphere. Voles (*Microtus* spp. and *Clethrionomys* spp.) and lemmings (*Lemmus* spp. and *Myopus* spp.) in particular show remarkably regular oscillations of population size, with cycle frequencies much longer than a generation (Hairston, 1994) and typically having a periodicity of between 2 and 5 years (Myllymäki, 1977; Remmert, 1980). These populations usually decline in the summer, autumn and winter following a population peak, with the lowest densities reached by the second summer (Bunnell et al., 1975). Not only are the declines recurrent but they are also characterized by changes in the distribution of microtine body weights and survival rates (Chitty, 1967).

Much is known about the biology and ecology of both voles and lemmings (e.g. Stenseth and Ims, 1993a), yet it remains one of the longstanding unresolved problems of population ecology to understand the processes driving their population cycles.

Explanations have been sought amongst two principal intrinsic factors: social organization and senescence, and two extrinsic factors: predation and nutrition (e.g. reviews by Stenseth and Ims, 1993b; Klemola et al., 2003; Turchin, 2003). Amongst the explanations relating to nutrition, plant chemical defences have rarely been considered despite their capacity for lethal toxin production (Freeland, 1974). Most studies have

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*Corresponding author. Tel.: +23 80594352; fax: +23 80594459.
E-mail address: cpd@soton.ac.uk (C.P. Doncaster).

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dismissed food toxicity as an explanation for microtine cycles, on the basis that microtines should evolve resistance to toxins or preferences for non-toxic food (reviewed in Jensen and Doncaster, 1999; see also Turchin and Hanski, 2001).

The aim of this paper is to quantify a model for toxin-induced cycles in tundra habitat that was developed verbally by Jensen and Doncaster (1999). They hypothesized that a precipitous decline in microtines can be caused by wound-induced production of lethal toxins by non-preferred plant species that are eaten only when overgrazing has depleted availability of preferred food plants. This hypothesis for periodic lethal toxin production (PLTP) contrasts with previous hypotheses involving plant toxins, which have either focused on preferred food plants eaten throughout all phases of the microtine cycle (e.g. Andersson and Jonasson, 1986; Berger et al., 1977; Bergeron, 1980; Bergeron et al., 1987; Jean and Bergeron, 1986; Jung and Batzli, 1981, Seldal et al., 1994), or have assumed that the non-preferred food plants were already producing lethal toxins at the time of the switch (Freeland, 1974).

It may be wondered why we need another hypothesis for microtine cycles when a number of recent predation-based models have successfully reproduced cyclicity in vole population densities (e.g. Hanski et al., 1993; Hanski and Korpimäki, 1995; Turchin and Hanski, 1997). The model parameters such as the generalist predation function and the experimental support for these models have been taken from studies in non-tundra areas, such as southern Sweden (Erlinge et al., 1983) and agricultural habitats in Finland (e.g. Klemola et al., 2000a, b; Korpimäki and Norrdahl, 1991a, b, 1998), which see high levels of immigration of predators. Predator-induced microtine cycles in these areas are consistent with a model of PLTP-induced microtine crashes causing predators to migrate away from tundra habitat. We therefore suggest that PLTP in tundra may be driving predator-induced cycles at lower altitude or latitude.

Our objective for this paper is to reproduce several key characteristics of microtine cycles in tundra regions, including periodicity and population crash, with an optimal foraging model that allows a consumer to switch between preferred and non-preferred food sources. We use parameter values obtained from the literature on microtines in a model developed by Křivan (1996) and Křivan and Sikder (1999), which we adapt to allow toxin production by a non-preferred food in response to grazing pressure.

1.1. PLTP hypothesis

The verbal model of Jensen and Doncaster (1999) describes a geometrically increasing population of a microtine species in high latitude and or altitude tundra with a relatively small range of food plants. The microtine population depletes a preferred food source to levels that can no longer sustain the population. As a result, previously non-preferred food plants are included in the diet. At least one of these plants responds to a threshold level of grazing pressure by producing toxins that interfere with the grazers' nutrient uptake, suppress breeding and ultimately cause death (e.g. Berg, 2003; Tahvanainen et al., 1991). These effects coupled with some level of microtine emigration lead directly to the collapse of the population. Predators that have increased in numbers during the years of microtine increase and peak subsequently disperse into neighbouring regions in response to the disappearance of their prey. This in turn causes secondary crashes of first the resident microtine populations and then their predators in these areas. During the long low phase, the preferred food plants of the microtines regenerate in the tundra areas followed by a gradual recovery of the microtine population, augmented by immigration from surrounding areas. This dilutes any evolved resistance to the toxins, which is further reduced in subsequent generations that feed only on preferred foods with no toxin production.

Jensen and Doncaster (1999) offered a number of indirect sources of evidence supporting a role for PLTP, and argued that direct evidence was lacking only because it had not been sought amongst non-preferred foods at the cusp of a population crash. They proposed three plants as likely candidates: the crowberry *Empetrum nigrum nigrum*, the northern crowberry *E. n. hermaphroditum* and the Arctic blueberry *Vaccinium uliginosum*, all of which feature in the diet of microtines only when preferred food plants have been depleted (e.g. Hambäck and Ekerholm, 1997; Berg, 2003; Hambäck et al., 2004) and are known to have chemical defences that include PLTP.

1.2. Population dynamics of optimal foraging and PLTP

Křivan (1996) and Křivan and Sikder (1999) introduced a simple deterministic model of population dynamics in continuous time for a predator with an optimal choice of prey types between more or less nutritious alternatives. The model applies optimal foraging theory (Stephens and Krebs, 1986) to population dynamics of a predator with a functional response to independently renewing prey (Rosenzweig and MacArthur, 1963; see also review by Oksanen et al., 2001). It assumes that the more profitable of two prey types will always be included in the diet when encountered, whereas the less profitable type will be included only if the density of the profitable alternative falls below a critical threshold. We apply this model to the PLTP hypothesis, with the predator representing a microtine rodent, the more profitable prey type