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REVISIT BROWN LEMMING POPULATION CYCLES IN ALASKA: EXAMINATION OF STOICHIOMETRY

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Abstract. Resource-consumer models have been applied to explain population cycles of small mammals such as brown lemmings in Alaska. All these models only consider food quantity for small mammals. However, food quality can potentially be a key factor driving the population cycle. To capture both food quantity and quality in the resource-consumer model, we apply the newly emerged method "ecological stoichiometry", which deals with the balance of fundamental elements in living organisms. A group of stoichiometric models are discussed in this paper for brown lemmings in Alaska, where food quality is measured by phosphorus and food quantity is measured by carbon. Within the framework of our models, we define an index to compare the relative importance of food quality and food quantity. Simulations of this index show that brown lemming cycles in Alaska are mainly controlled by food quantity. Bifurcation diagrams illustrate that the cycle period is an increasing function of the nutrient availability but a decreasing function of the nutrient requirement of lemmings. A striking result arises: high nutrient availability and small nutrient requirement of lemmings drive the low points of the population cycle to be extremely small, leading to high probability of lemmings' extinction. However, high nutrient availability and small nutrient requirement of lemmings should both benefit lemmings. This paradox needs further examination in theoretical and empirical studies. In addition, we perform sensitivity analysis of periodicity with respect to all parameters.

Key words. stoichiometry, brown lemmings, population cycle, period, amplitude, bifurcation, sensitivity, phosphorus, carbon, and nutrient.

1. Introduction

Large-scale high-amplitude oscillations in populations of small rodents, such as brown lemmings in Alaska, have been a long-term inspiration to considerable influential and thought provoking papers [8, 12]. Many researchers believe that such population fluctuations are generated by consumer-resource interactions. Pioneering works on resource-consumer dynamics include the classical Lotka-Volterra predator-prey model [18, 23], the Rosenzweig-MacArthur model [20], and Bazykin model [4, 5].

All existing consumer-resource models for interpreting small mammal population cycles only consider energy flow between trophic levels, which implicitly depends on quantity of available food (measured in carbon). However, carbon is not the only element in living organisms. Other elements such as phosphorus and nitrogen are also vital constituents in organism and population growth: phosphorus is an essential component of nucleic acids, and nitrogen is essential to build proteins. The scarcity of any of these elements can severely restrict population growth. Hence, the consideration of nutrient cycling, or stoichiometry, can be essential for predictive population models. Most of existing stoichiometric models are developed for trophic interactions in aquatic ecosystems [1]. Little work has been done in modeling stoichiometry of trophic interactions in terrestrial ecosystems. To our knowledge,

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this is the first modeling paper to discuss stoichiometric effects on small mammal population cycles.

Similar to aquatic trophic interactions, there is often a mismatch in the elemental composition of food and consumers, and this mismatch strongly affects the performance of individual consumers and the transfer efficiency of carbon. Terrestrial grazers such as rodents [9] and insects [10] have high demands for dietary nitrogen and phosphorus. Consumers have high nutrient contents whereas autotroph have low and highly variable nutrient contents. The growth rate hypothesis suggests that herbivore growth efficiency is positively related to growth rate and nutrient contents in the autotroph [7, 21].

Lemming populations can be severely limited by low nutrient contents of mosses (the median P:C ratio about $0.0015gP/gC$), which is only $1/40$ of the biomass P:C ratio of lemmings (about $0.06gP/gC$). As an empirical example, Lindroth et al. (1984) [15] developed artificial diets in their lab to assess the calcium and phosphorus requirements of the brown lemming and found that female lemmings on different diets grew similarly but reproduced differently. This suggests that reproduction rate could be affected by forage quality. However, such a laboratory experiment can not clearly explain whether the forage quality is a controlling factor or only a minor factor in the whole population cycle. This modeling paper plays the role in bridging the food quality factor and the population dynamical model with the aim of uncovering effects of food quality on lemming population fluctuations.

Three models are discussed in this paper. The first model is a phenomenological model, which is the main part of this paper. We define an index to quantify the relative importance of food quality and food quantity on controlling the lemming population cycle. We find three regions, separated by this index, on the parameter space: I) cyclic population completely controlled by food quantity, II) extinction, III) cyclic population partially controlled by food quality. The realistic parameter region of brown lemmings locates in Region I, that is, for brown lemmings in Alaska food quality is less limiting than food quantity. We numerically perform bifurcation analysis to examine how the amplitude and the period of lemming cycles depend on key parameters. We find that the cycle period is strongly positively related to the nutrient availability but strongly negatively related to the nutrient requirement of lemmings. The cycle amplitude is extremely large when the nutrient availability is large or the nutrient requirement of lemmings is small. An extremely large amplitude leads to extremely small low points which probably drive lemmings to go extinct, thus high nutrient availability and small nutrient requirement of lemmings are negative for brown lemmings to survive in Alaska. This observation contradicts to what we believed to be. This paradox would be tested in a field experiment. In addition, we compute the normalized forward sensitivity indices of the cycle period with respect to all parameters. The sensitivity analysis shows the relative importance of all parameters on the period as well as the robustness of our modeling results. The second model is a mechanistically derived stoichiometric model. This model is much more complicated than the phenomenological model but both models have almost same results. The third model is a modification of the phenomenological model by introducing a quantity ceiling such that the quantity and quality indicators have the same structure and similar properties. This more realistic model gives heavier food quality limitation on the lemming population cycle than the first model.

Our models suggest that food quality has large effects on lemming population dynamics but food quantity is always a more limiting factor than food quality