

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 autotrophs 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

TABLE 1. Parameters in stoichiometric moss-lemming systems

Par	Meaning	Value	Reference
u	Maximum moss growth rate	$2/yr$	Wang 2007 [24]
q	Minimum $P : C$ ratio of mosses	$0.00057gP/gC$	Fagan 2006 [11]
P	Total mass of phosphorus in the entire system	$0.1 - 0.5kg/ha$	Hobbie 2002 [13]
θ	Constant $P : C$ ratio of lemmings	$0.06gP/gC$	Batzli 1980 [3]
a	Maximum moss consumption rate by a lemming	$1071/yr$	Powell 2002 [19], Turchin 2001 [22]
c	Half-saturation constant for moss consumption	$63kgC/ha$	Wang 2007 [24]
b	Conversion rate of mosses into lemmings	$0.1 - 0.713$	Powell 2002 [19]
d	Lemming death rate	$6.4/yr$	Turchin 2001 [22]
\hat{c}	Maximum phosphorus uptake rate of mosses	$70gP/gC/yr$	Wang 2008 [25]
\hat{a}	Phosphorus half-saturation constant of mosses	$0.05kg/ha$	Wang 2008 [25]
\hat{d}	Phosphorus loss rate of mosses	$18/yr$	Wang 2008 [25]

throughout the lemming cycle in Alaska. Similarly, Kendall et al. (2005) [14] proposed that food quality was an important but not the most pivotal factor in the pine-moth interaction.

2. A Phenomenological Model

In this section, we introduce a phenomenological model incorporating both food quality and food quantity limitations for lemmings. We estimate parameter values carefully from literature, most of which are empirical studies. We define an index and run numerical simulations for the model. Finally, we perform bifurcation and sensitivity analyses.

2.1. Model Formulation. Following Table 10-4 of Batzli et al. (1980) [3], relatively large amounts of phosphorus and calcium are retained for lemming production, thus these nutrient elements may be more limiting for lemmings. In this paper, we consider phosphorus as the key nutrient element for lemmings.

As a first attempt, the phosphorus limitation is studied under the same three assumptions of LKE model [16], which are 1) fixed total phosphorus, 2) flexible moss stoichiometry versus fixed lemming stoichiometry, and 3) all phosphorus is either in mosses or in lemmings. Because sunlight is sufficient in Alaska, it is unnecessary to involve energy limitation through the carrying capacity, which is the only difference between the ‘‘phenomenological’’ model here and the LKE model [16]. Let x be the moss density (kgC/ha) and y be the lemming density (kgC/ha). Both mosses and lemmings are measured in carbon biomass. Therefore, the phenomenological stoichiometric moss-lemming system takes the following form:

$$(1) \quad \begin{cases} \frac{dx}{dt} = ux \left(1 - \frac{q}{(P - \theta y)/x} \right) - \frac{axy}{x + c}, \\ \frac{dy}{dt} = b \min \left\{ 1, \frac{(P - \theta y)/x}{\theta} \right\} \frac{axy}{x + c} - dy. \end{cases}$$

Meanings of all parameters are listed in Table 1.

2.2. Parameter Estimation. We estimate all parameters in the phenomenological model (1) carefully and conclude their values in Table 1, except three parameters $\hat{c}, \hat{a}, \hat{d}$ that are introduced in the mechanistic model (2).

Approximately 45% of moss or lemming dry weight is carbon. We apply this fact to convert units in the parameter estimation. To estimate the minimum P:C ratio of mosses, we find a few empirical studies on phosphorus content of mosses. Table 10-4 of [3] shows that phosphorus concentration in forage is $2mg/gdw$, thus $q \ll 0.002gP/0.45gC = 0.0044(gP/gC)$. Figure 2 of [2] shows that the mean phosphorus content of mosses is $20\mu molP/g$, thus $q \ll 20\mu molP/g \times 31\mu g/\mu mol = 600\mu gP/gdw = 0.0006gP/gdw = 0.0006gP/0.45gC = 0.0013gP/gC$. Fagan (2006) [11]'s database shows that the mean P:C ratio of arctic mosses is $0.0013gP/gC$, the median P:C ratio of arctic mosses is $0.0015gP/gC$, the minimum P:C ratio of arctic mosses is $0.00057gP/gC$, and the maximum P:C ratio of arctic mosses is $0.0052gP/gC$. Hence, we choose the minimum P:C ratio of mosses $q = 0.00057gP/gC$. Since the soil extractable phosphorus is $0.01 - 0.05gP/m^2$ (see Figure 2 of [13]), the total phosphorus in the system $P = 0.01 - 0.05gP/m^2 = 100 - 500gP/ha = 0.1 - 0.5kgP/ha$. The phosphorus concentration of lemmings is about $27mg/gdw$ (see Table 10-4 of [3]), thus the P:C ratio of lemmings $\theta = 0.027gP/0.45gC = 0.06gP/gC$. The dry weight of a lemming is about $14g/ind. = 6.3gC/ind. = 0.0063kgC/ind.$, then the maximum food consumption rate by a lemming is $15kg/(yr \cdot ind.) = 6.75kgC/(yr \cdot ind.) = 6.75/0.0063/yr = 1071/yr$ (see Table 2 of [19], Table 2 or 3 of [22]), which is used as the approximation of the parameter a . The half-saturation constant $c = 140kg/ha = 63kgC/ha$ [24]. The conversion efficiency $b = 0.1 - 0.713$ (see Table 1 of [19], and [22]). According to Turchin et al. (2001) [22], the averaged lemming death rate $d = 10.7 \times (5 \times 0.63 + 0.44)/6 = 6.4/yr$. The maximum moss growth rate $u = 2/yr$ was estimated in Wang 2007 [24].

2.3. Index Definition and Simulation. To show the importance of food quality and food quantity on lemming population dynamics, we introduce the indicator for moss quality

$$ID_{quality} = \min \left\{ 1, \frac{(P - \theta y)/x}{\theta} \right\}$$

and the indicator for moss quantity

$$ID_{quantity} = \frac{\text{actual per unit consumption}}{\text{maximum consumption}} = \frac{x}{x + c}.$$

To quantify the relative importance of food quality and food quantity, we define the index for determining the more limiting factor

$$INDEX = \frac{ID_{quality}}{ID_{quantity}}.$$

When $ID_{quality} < 1$ (yellow part in Figure 1), the moss quality is bad. When $ID_{quality} = 1$, the moss quality is good (green part in Figure 1). When $INDEX > 1$ (black part in Figure 1), the lemming population cycle is more limited by food quantity. When $INDEX < 1$, the lemming population cycle is more limited by food quality, which does not exist in Figure 1. See the panel (b) of Figure 2 for the case $INDEX < 1$ (red color).

We obtain some insights from the simulated time-series (Figure 1). Food quality is bad at peaks of the moss biomass time series. Whenever mosses are abundant, then its quality is low. This is consistent to observations from stoichiometric studies for aquatic ecosystems. However, even at peaks the lemming population is more limited by food quantity instead of quality as we can observe from the lemming population time series. This simple observation suggests that food quality may not be a major factor controlling the lemming population cycle in Alaska.

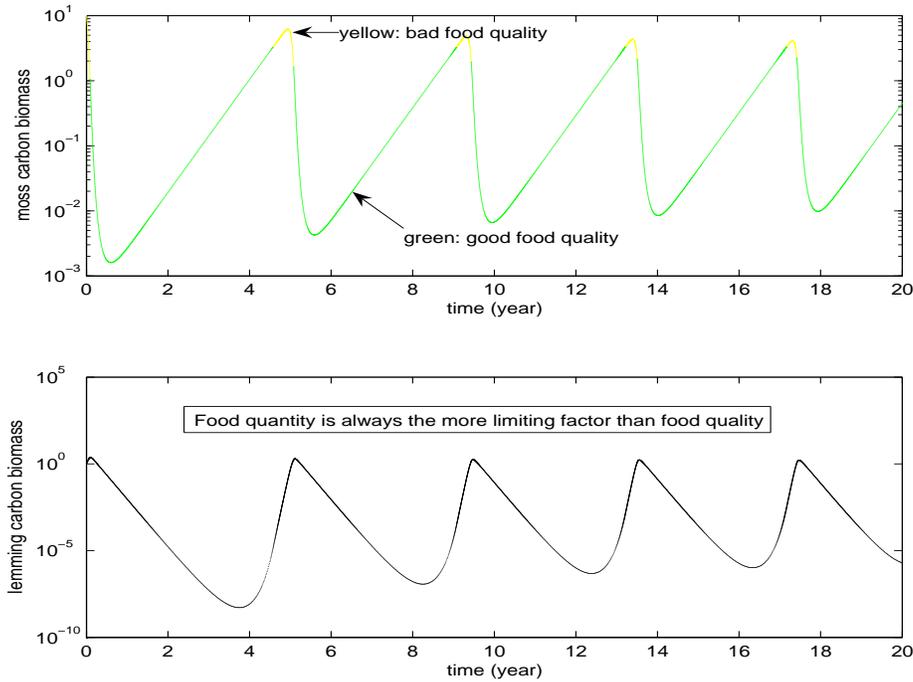
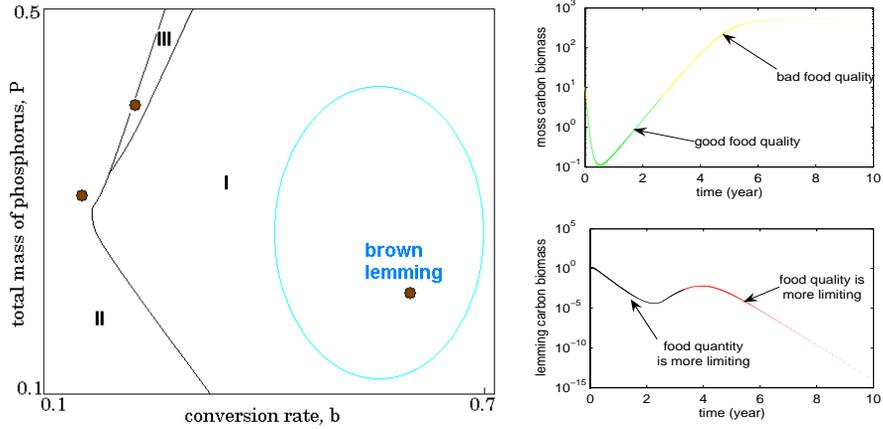
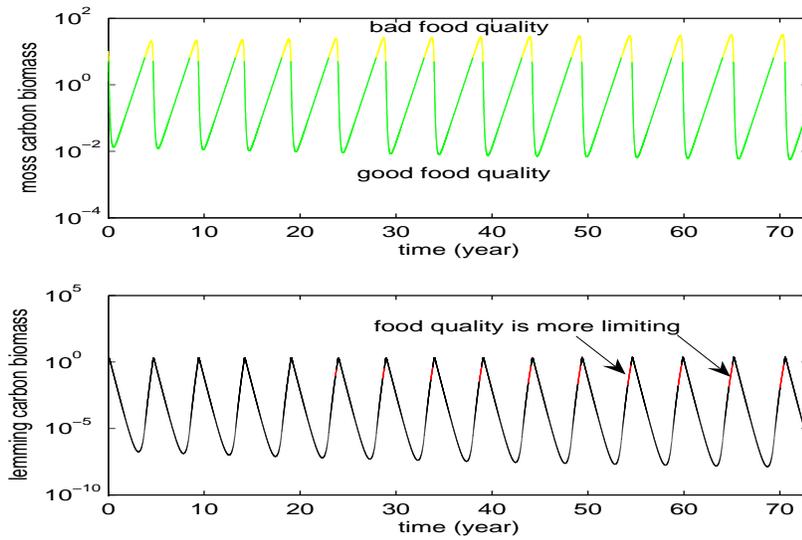


FIGURE 1. The phenomenological stoichiometric moss-lemming model (1) with $P = 0.2\text{kg/ha}$, $b = 0.6$. Also, this solution is for the sample point in Region I of Figure 2. The lemming population is always more limited by food quantity than food quality, because the index is greater than one all the time.

To further examine this conclusion, we thoroughly test the possible parameter region of b (conversion rate of mosses into lemmings) and P (the total mass of phosphorus in the entire system) in Figure 2 (a) for the brown lemmings. There are three possible regions with different outcomes. Sample points (small bullets) are chosen to generate numerical solutions for all these three regions (see Figure 1 and Figure 2 (b)(c)). Figure 2 shows that the solution in Figure 1 represents the whole region I. In Region III, food quality affects the lemming population more than food quantity in part of the cycle (Figure 2 (c)). It greatly affects the increasing stages of the population cycle. The species go extinct in the region II, and it is always induced by the limitation of food quality. To explain these phenomena, we return to the algorithm for plotting these regions. Two cases are considered: (1) existence: for this case, there are two subcases (i) food quantity is always more limiting (Region I), or (ii) food quality is more limiting in part of the population cycle (Region III); (2) extinction: for this case, there are also two subcases (i) the extinction is induced by food quality (Region II), or (ii) the extinction is induced by food quantity, but this subcase never exists. With this algorithm, implications of our three parameter regions are transparent. The phenomenon that extinction is always triggered by food quality makes biological sense, because when the lemming population becomes extremely low (close to extinction), considerable amount of



(a) Possible parameter region for the brown lemming (b) The solution for the sample point ($P = 0.3kg/ha, b = 0.15$) in Region II



(c) The solution for the sample point ($P = 0.4kg/ha, b = 0.22$) in Region III

FIGURE 2. Possible outcomes in the biologically reasonable parameter region: In Region I, brown lemmings persist and their population is more limited by food quantity all the time; In Region II, brown lemmings go extinct and it is induced by the imitation of food quality; In Region III, brown lemmings persist and food quality is more limiting during part of increasing stages. The region inside the big ellipse is the most likely parameter region for brown lemmings in Alaska, which suggests that food quantity is always more limiting throughout the population cycle.

mosses grow up and meanwhile nutrient contents of mosses go down dramatically such that the lemming population cannot bounce back from the low point.

2.4. Bifurcation Diagrams. To examine how the amplitude and the period of the population cycle depend on key parameters such as P, θ, b , we perform bifurcation analysis for the model (1). In our simulation results, bifurcation points locate outside the biological ranges of studied parameters, thus we cannot see any bifurcation point in these bifurcation diagrams.

The numerical technique is to apply the command “ode23s” in Matlab to solve the model (1) along biologically reasonable values of the studied parameter. To obtain the cycle amplitude for each value of the parameter, we choose maxima and minima after fluctuations are stabilized to the limit cycle. The unstable steady state is computed by applying the command “fsolve”. We set the right-hand sides of the model to be zero and then apply “fsolve” to obtain the internal steady state for each value of the parameter. The difficult part is to compute the cycle period for each value of the studied parameter. We first run the simulation for a long enough time such that fluctuations are stabilized to the limit cycle, then we compute shifts between two consecutive maxima and between two consecutive minima, both of which can give the cycle period.

Our bifurcation diagrams in Figure 3 show that key parameters can dramatically change the amplitude and the period of the population cycle. In the biological ranges of parameters P, θ, b , there are always a globally attracting limit cycle and an unstable internal equilibrium surrounded by the limit cycle (see panels (a)(c)(e)). When the nutrient availability P or the conversion efficiency b increases, the cycle amplitude increases dramatically (see panels (a)(e)). Especially, when P is large, the low points will be extremely small, which may drive brown lemmings in Alaska to go extinct. This contradicts to what we believed to be: higher nutrient availability should be good for lemmings. This paradox can be examined in a field experiment. The cycle period increases as P or b increases (see panels (b)(f)). Note that the cycle period is almost a monotonically increasing function of b except when the parameter b is extremely small. In comparison, the parameter P has very strong effects on the periodicity. When P reaches 0.5, the period is over 9 years. Our sensitivity analysis in Section 2.5 confirms the strong dependence of periodicity on P . When the cell quota of lemmings θ (representing nutrient requirement of lemmings) increases, the cycle amplitude shrinks dramatically, that is, the higher requirement on nutrient is good for lemmings to survive. This observation is also opposite to what we believed to be and should be further tested. The cycle period is a decreasing function of θ (see panel (d)). The panel (g) gives an example for visible limit cycles along a parameter; the panel (e) is the simplified version of the three-dimensional plot in panel (g). The same idea is applied to the panels (a)(c). These numerical results illustrate that cyclic populations need more complicated strategies to survive, since the common methods for protecting lemmings may even drive them to go extinct.

We plot the two-dimensional bifurcation diagram in Figure 4. For each pair of (b, P) , we compute the maximum and the minimum of the lemming population/carbon component of the limit cycle obtained after solutions are stabilized. With two loops for b and P , we obtain all maxima and minima of the lemming carbon biomass for the whole $b - P$ plane. Eventually, we plot both matrices of maxima and minima to obtain the two-dimensional bifurcation diagram in Figure 4, which illustrates that the lemming population always fluctuates in the existence regions I and III of Figure 2(a).

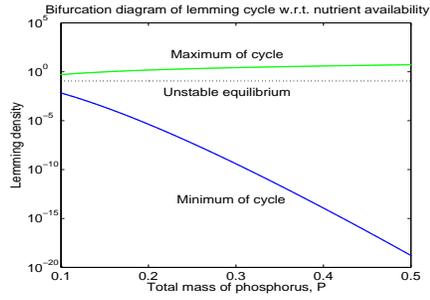
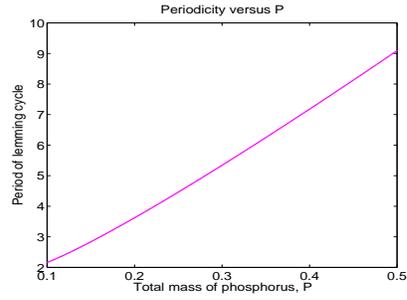
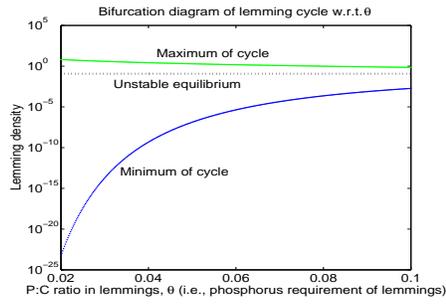
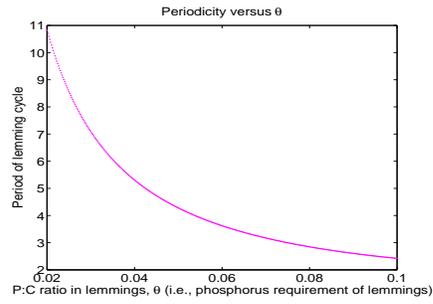
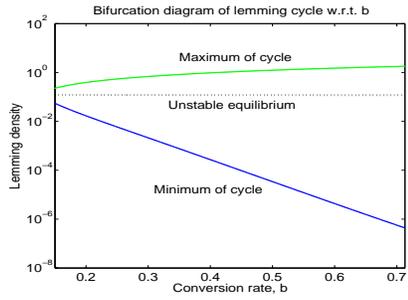
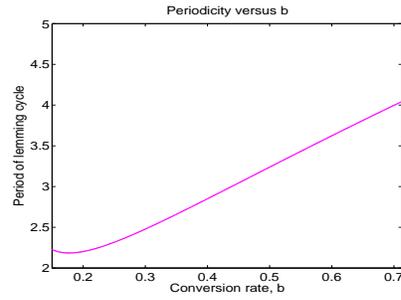
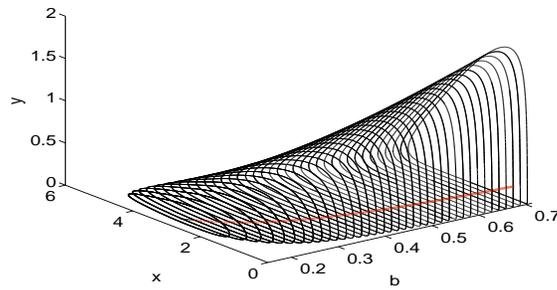
(a) Cycle amplitudes along P values(b) Cycle periods along P values(c) Cycle amplitudes along θ values(d) Cycle periods along θ values(e) Cycle amplitudes along b values(f) Cycle periods along b values(g) Limit cycles and unstable internal equilibria along b values

FIGURE 3. Dependence of cycle amplitudes and periods on key parameters: nutrient availability (P), nutrient requirement of lemmings (θ), and conversion rate (b).

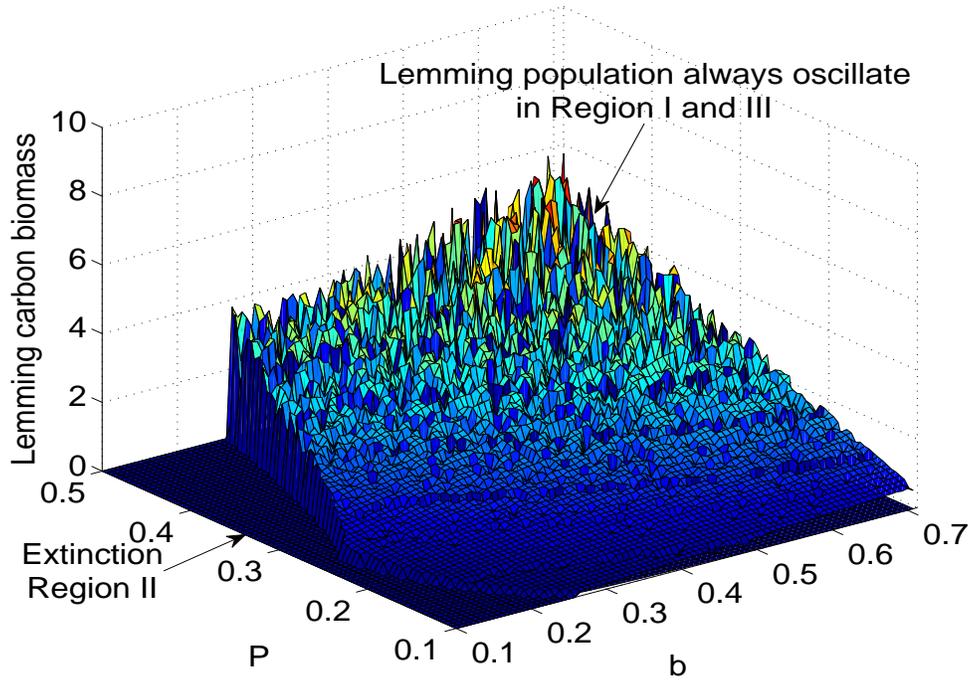


FIGURE 4. The two-dimensional bifurcation diagram for the parameters b and P . This graph exhibits the extinction K-shaped region II and indicates that the lemming population always oscillates in the regions I and III.

2.5. Sensitivity Analysis. We discuss the sensitivity of the cycle period with respect to all parameters. Sensitivity analysis provides useful information on whether each parameter strongly or weakly affects the periodicity and how each parameter changes the cycle period (positively or negatively).

The normalized forward sensitivity index [6] is defined as

$$\gamma_{par}^{period} = \frac{\partial period}{\partial par} \cdot \frac{par}{period}.$$

To estimate the derivative in the definition, we apply the central difference derivative approximation:

$$\frac{\partial period}{\partial par} = \frac{period(par + h) - period(par - h)}{2h} + O(h^2).$$

We take the first part of the right-hand side as the approximation for the derivative. This is a second-order approximation, which is much better than the approximation from the definition of derivative (first-order). In our computations of sensitivity indices, we choose $h = 1\% \cdot par$. Substitute the derivative approximation into the

TABLE 2. Sensitivity analysis of periodicity with respect to all parameters with (b, P) in Region I

Par	Baseline value	Baseline period	Period(par+h)	Period(par-h)	Sensitivity index
u	2	3.6235	3.5917	3.6557	-0.8831
q	0.00057	3.6235	3.6231	3.6239	-0.0110
P	0.2	3.6235	3.6561	3.5912	0.8955
θ	0.06	3.6235	3.5917	3.6559	-0.8859
a	1071	3.6235	3.6534	3.5934	0.8279
c	63	3.6235	3.5910	3.6563	-0.9011
b	0.6	3.6235	3.6464	3.6005	0.6334
d	6.4	3.6235	3.5894	3.6580	-0.9466

formula of sensitivity index, we obtain

$$\begin{aligned}
 \gamma_{par}^{period} &= \frac{period(par+h) - period(par-h)}{2h} \cdot \frac{par}{period} \\
 &= \frac{period(1.01 \cdot par) - period(0.99 \cdot par)}{2 \cdot 0.01 \cdot par} \cdot \frac{par}{period} \\
 &= \frac{period(1.01 \cdot par) - period(0.99 \cdot par)}{0.02 \cdot period}.
 \end{aligned}$$

In Region I, the baseline values of parameters P and b are $P = 0.2, b = 0.6$ as in Figure 1. Sensitivity indices of the cycle period are computed in Table 2. In this case, model predictions are robust because absolute values of all indices are less than one. The most irrelevant parameter to period is the minimum moss cell quota, q . All other parameters have comparable absolute values of sensitivity indices.

In Region III, the baseline values of parameters P and b are $P = 0.4, b = 0.22$ as in Figure 2(c). Sensitivity indices of cycle period are computed in Table 3. Some sensitivity indices in this case have large absolute values, that is, model predictions for Region III are less robust than those for Region I. Absolute values of sensitivity indices of parameters P, θ, c, b are much larger than one, which means that the cycle period strongly depends on these parameters. The parameter θ represents the nutrient requirement of lemmings, the parameter c represents the food consumption efficiency of lemmings, and the parameter b represents the conversion efficiency of mosses to lemmings. The most sensitive parameter is P , representing the nutrient availability in the ecosystem. From both Tables 2 and 3, we can further observe that the period of the lemming cycle strongly positively depends on the nutrient availability, P .

Comparing Tables 2 and 3, we find that sensitivity indices of each parameter have same sign, except the parameter b . The cycle period is positively related to parameters P, a and negatively related to parameters u, q, θ, c, d . In Region I the parameter b has positive effects on the cycle period, while in Region III b has strong negative effects on the cycle period.

Sensitivity results for Region I are robust since population fluctuations are quickly stabilized to the limit cycle. However, for Region III it is almost impossible to numerically obtain stabilized fluctuations. Hence, sensitivity results for Region III are not as robust as those for Region I. When (b, P) is within Region II, lemmings go extinct due to bad food quality, thus the periodicity cannot be discussed.

TABLE 3. Sensitivity analysis of periodicity with respect to all parameters with (b, P) in Region III

Par	Baseline value	Baseline period	Period(par+h)	Period(par-h)	Sensitivity index
u	2	6.2090	6.1318	6.2868	-1.2482
q	0.00057	6.2090	6.1337	6.2975	-1.3191
P	0.4	6.2090	7.4259	5.7819	13.2388
θ	0.06	6.2090	5.8250	6.9220	-8.8340
a	1071	6.2090	6.2473	6.1683	0.6362
c	63	6.2090	5.7767	7.0361	-10.1417
b	0.22	6.2090	5.8217	7.0009	-9.4959
d	6.4	6.2090	6.1869	6.2340	-0.3793

3. A Mechanistic Model

In this section, we extend this phenomenological model to a “mechanistic” model that relaxes the third assumption in the LKE model: phosphorus in the system is divided into two pools (the herbivore and the plant). Free phosphorus outside organisms was incorporated and the dynamical equation of phosphorus in the plant was explicitly derived in Wang et al. (2008) [25]. Compared to the WKL model in [25], the only difference is that the mechanistic model here has no light limitation.

The main purpose of introducing this mechanistic model is to test the robustness of our results in the phenomenological model.

The mechanistic model is provided by

$$\begin{aligned} \frac{dx}{dt} &= ux \left(1 - \frac{q}{p/x} \right) - \frac{axy}{x+c}, \\ \frac{dy}{dt} &= b \min \left\{ 1, \frac{p/x}{\theta} \right\} \frac{axy}{x+c} - dy, \\ \frac{dp}{dt} &= g(p_f)x - \frac{p}{x} \frac{axy}{x+c} - \hat{d}p, \\ \frac{dp_f}{dt} &= -g(p_f)x + \hat{d}p + \theta dy + \left(\frac{p}{x} - b \min \left\{ \theta, \frac{p}{x} \right\} \right) \frac{axy}{x+c}, \end{aligned}$$

where $g(p_f)$ is the phosphorus uptake rate of the producer and $g(p_f) = \frac{\hat{c}p_f}{\hat{a} + p_f}$. p is the density of phosphorus content in the producer, p_f is the density of free phosphorus in media. Compared with the phenomenological model, the mechanistic model has three additional parameters \hat{c} (maximum phosphorus uptake rate of mosses), \hat{a} (phosphorus half-saturation constant of mosses), \hat{d} (phosphorus loss rate of mosses). We estimate their values by scaling the corresponding values of algae in [25] and considering the difference between mosses and algae.

Let $P = \theta y + p + p_f$, then $\frac{dP}{dt} = 0$, which means P is a constant, which is the total phosphorus in the entire system. We can use this to reduce the system to be

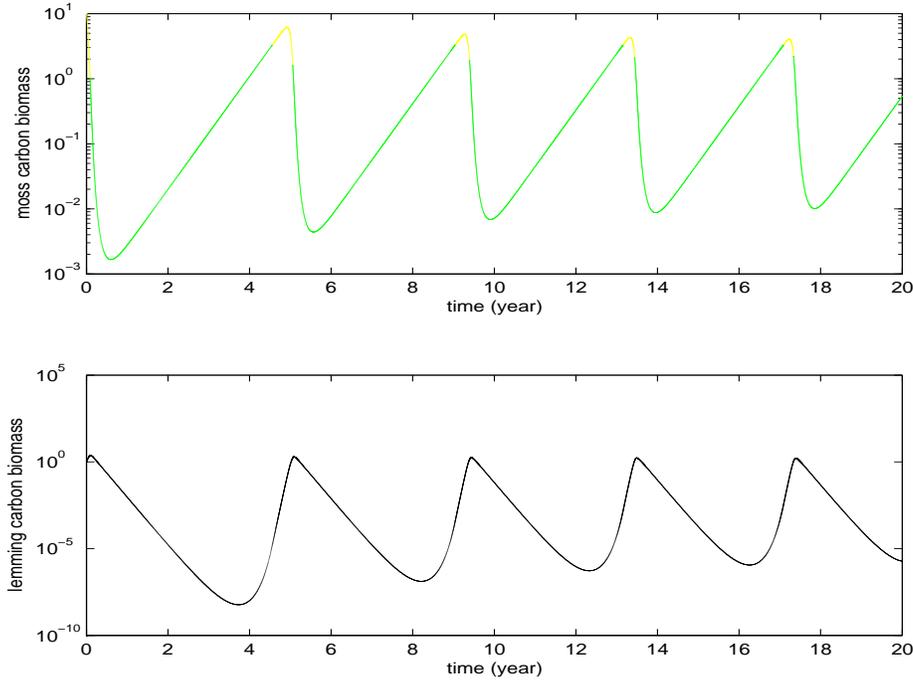


FIGURE 5. The mechanistically derived stoichiometric model with $P = 0.2\text{kg/ha}$, $b = 0.6$

a three-dimensional system:

$$\begin{aligned}
 \frac{dx}{dt} &= ux \left(1 - \frac{q}{p/x} \right) - \frac{axy}{x+c}, \\
 \frac{dy}{dt} &= b \min \left\{ 1, \frac{p/x}{\theta} \right\} \frac{axy}{x+c} - dy, \\
 \frac{dp}{dt} &= g(P - \theta y - p)x - \frac{p}{x} \frac{axy}{x+c} - \hat{d}p.
 \end{aligned}
 \tag{2}$$

The simulation in the mechanistic model (2) in Figure 5 is almost same as the corresponding simulation in the phenomenological model. This observation validates the robustness of our results in the phenomenological model, especially for Region I. The reason for this similarity is that the nutrient (phosphorus) equation is much faster process than moss and lemming equations. Therefore, we can use the quasi-steady state approximation to obtain the phenomenological model. To test this explanation, we can slower the nutrient process by reducing the nutrient uptake rate unrealistically, then the mechanistic model has quite different behaviors from the phenomenological one (see [25] for this game).

Besides the robustness test for the phenomenological model, we introduce this mechanistic model for terrestrial trophic interactions, because the mechanistic model can be easily extended to a general model with multiple nutrients, multiple producers and multiple herbivores, whereas the phenomenological model cannot. After we expand this mechanistic model to a general multi-species model, we can discuss

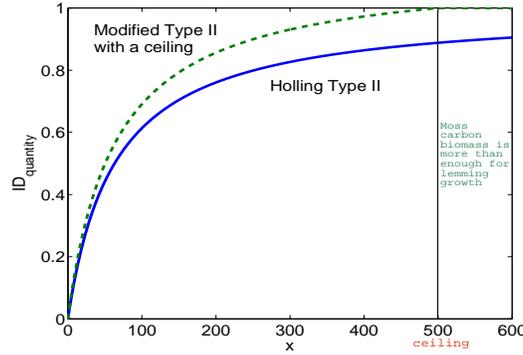


FIGURE 6. The comparison of the modified quantity indicator with the Holling Type II quantity indicator.

the biodiversity problem. How many producers can coexist under multiple nutrient elements? How many consumer species can coexist under multiple producers and multiple nutrients? In Loladze et al (2004) [17]’s paper, there is a relatively “large window” of parameters for coexistence compared to the possibility of coexistence in evolution. One can imagine that providing more nutrient elements more species can coexist, but the parameter window should be smaller which is closer to reality.

4. Introducing A Quantity Ceiling

The models in the previous sections lead to the food quality with a ceiling but food quantity without a ceiling. The more realistic version is to introduce a ceiling for food quantity as well, then $ID_{quantity}$ is not always less than one. The case $ID_{quantity} = 1$ means the sufficient food quantity for lemming growth. This modification also makes the quantity indicator more comparable to the quality indicator. Hence, we incorporate a maximum requirement of moss quantity for lemming growth in the phenomenological model:

$$(3) \quad \begin{cases} \frac{dx}{dt} = ux \left(1 - \frac{q}{(P - \theta y)/x} \right) - a \min \left\{ \frac{x_m + c}{x_m} \frac{x}{x + c}, 1 \right\} y, \\ \frac{dy}{dt} = b \min \left\{ 1, \frac{(P - \theta y)/x}{\theta} \right\} a \min \left\{ \frac{x_m + c}{x_m} \frac{x}{x + c}, 1 \right\} y - dy. \end{cases}$$

Here, x_m is the threshold for mosses, above which the moss quantity is enough for lemmings. In this system, the indicator for moss quantity becomes

$$ID_{quantity} = \min \left\{ \frac{x_m + c}{x_m} \frac{x}{x + c}, 1 \right\}.$$

This function is close to the original Holling Type II functional response when the threshold x_m is large enough, for example, $x_m = 500$ in Figure 6.

Figure 7 illustrates that the modified phenomenological model (3) gives stronger food quality limitation on the lemming population cycle than the original phenomenological model (1), because Region II is larger in the modified model. When the threshold x_m approaches infinity, the result of b - P plane in the ceiling model (3) approaches that in the original phenomenological model (1).

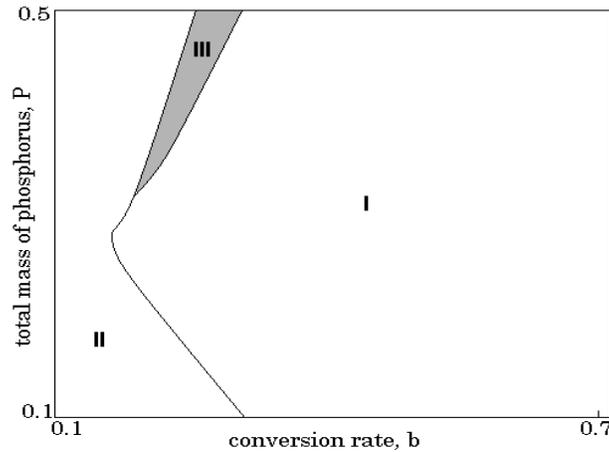


FIGURE 7. The region test of the parameter space (b, P) with $x_m = 500$: Region II for food quality limitation is larger than that in the original phenomenological model.

This modified model slightly improves the original model with more biological details and opens up the possibility of larger effects of food quality on small mammal population cycles.

5. Concluding Remarks

To summarize, we have provided numerical simulations for the following conclusions: 1) Brown lemming cycles in Alaska are mainly controlled by food quantity; 2) The cycle period is positively related to the nutrient availability but negatively related to the nutrient requirement of lemmings; 3) High nutrient availability or small nutrient requirement of lemmings leads to high probability of lemmings' extinction by driving the low points of the population cycle to be extremely small; 4) For Region III, the cycle period is most sensitive to the nutrient availability; 5) Results for Region I are robust whereas results for Region III are not as robust; 6) Results of the mechanistic model with realistic parameter values are consistent to results of the phenomenological model; 7) The ceiling model, a modification of the phenomenological model, shows the possibility of larger effects of food quality on small mammal population cycles.

Our models can be improved in various ways. Droop's equation was applied to obtain the nutrient-limited moss growth in LKE model, WKL model, and models in this paper. The original derivation and data verification of Droop's equation was specially for the nutrient-limited phytoplankton growth in aquatic ecosystems. Hence, Droop's equation was correctly used in LKE and WKL models that deal with producer-grazer interactions in aquatic ecosystems; however, it might be problematic to apply the same equation for the nutrient-limited moss growth in a terrestrial ecosystem. A new version of Droop's equation needs to be derived for the nutrient-based growth of terrestrial plants through empirical studies. Besides mosses, vascular plants are another important food resource for brown lemmings in Alaska. The vascular plants regrow from their roots [22], not grow logistically, thus Droop's equation is definitely not the correct form for the nutrient-dependent growth of vascular plants. Again, we need a modified version of Droop's equation.

To our knowledge, this is the first modeling paper to discuss stoichiometric restrictions on terrestrial small mammals. Results of this paper may guide some future field studies of nutrition in terrestrial ecosystems. For some terrestrial herbivores, it is possible that food quality has larger effects than food quantity on dynamics of herbivore populations. Even when food quantity has larger effects, nutritional status of living organisms and nutrient enrichment of environment can greatly affect population dynamics according to the bifurcation and sensitivity analyses in this paper. Therefore, there are great needs for further empirical and theoretical studies on stoichiometric aspects of terrestrial ecosystems.

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