The roles of predator maturation delay and functional response in determining the periodicity of predator–prey cycles

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ABSTRACT

Population cycles in small mammals have attracted the attention of several generations of theoretical and experimental biologists and continue to generate controversy. Top-down and bottom-up trophic regulations are two recent competing hypotheses. The principal purpose of this paper is to explore the relative contributions of a variety of ecological factors to predator–prey population cycles. Here we suggest that for some species – collared lemmings, snowshoe hares and moose in particular – maturation delay of predators and the functional response of predation appear to be the primary determinants. Our study suggests that maturation delay alone almost completely determines the cycle period, whereas the functional response greatly affects its amplitude and even its existence. These results are obtained from sensitivity analysis of all parameters in a mathematical model of the lemming–stoat delayed system, which is an extension of Gilg's model. Our result may also explain why lemmings have a 4-year cycle whereas snowshoe hares have a 10-year cycle. Our parameterized model supports and extends May's assertion that time delay impacts cycle period and amplitude. Furthermore, if maturation periods of predators are too short or too long, or the functional response resembles Holling Type I, then population cycles do not appear; however, suitable intermediate predator maturation periods and suitable functional responses can generate population cycles for both prey and predators. These results seem to explain why some populations are cyclic whereas others are not. Finally, we find parameterizations of our model that generate a 38-year population cycle consistent with the putative cycles of the moose–wolf interactions on Isle Royale, Michigan.

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1. Introduction

The search for the cause of mammalian population cycles, most notably of voles, lemmings, snowshoe hares (*Lepus americanus*), mice and their predators [14], has become one of the greatest adventures in all of science. Recent advances have uncovered at least an outline of the underlying causes [12,14], although many details remain obscure. In particular, the precise roles played by the amount and quality of food for primary consumers, along with predation – so-called 'bottom-up' and 'top-down' mechanisms, respectively – are still open for debate. This uncertainty is reflected in three questions posed by Hudson and Björnstad [7]. First, what precise ecological mechanisms generate population cycles? Second, do these mechanisms apply to all cyclic populations? Finally, do these mechanisms explain why some populations are cyclic whereas others are not?

Over the years, a variety of ecological mechanisms have been proposed as causes of population cycles [10]. Some researchers have argued that the 'cycles' are nothing more than stochastic fluctuations, but this view is undermined by obvious synchrony across broad, even continental, geographic regions [11]. Ecological dispersal, cyclic weather patterns, parasitic and other diseases and even the sun spot cycle have all joined food supply, predation and stochasticity as potential causes. Recently, however, the evidence appears to point increasingly towards trophic interactions, either bottom-up or top-down, as the primary culprits [14].

For example, cycles in brown lemming (*Lemmus trimucronatus*) populations at Point Barrow, Alaska, appear to be driven by bottom-up regulation [34,33]. Turchin and coworkers found evidence for this conclusion in the shape of the population density curve at its peaks. If cycles were driven primarily by predators, then prey peaks should be 'blunt', because by the time predator density increases sufficiently to cause a decline in prey population size, the prey would have spent a prolonged period of time at its peak. However, lemming populations exhibit very sharp peaks, with

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rarely more than one observation period at the peak [33]. Therefore, predators are probably not causing cycles in the Point Barrow brown lemming population.

In contrast, evidence suggests that cycles in collared lemming (*Discrostonyx groenlandicus*) populations in Northeast Greenland are driven by predation. This system is well studied and astoundingly simple, with this single prey species hunted essentially by only four predator species [4]. A mathematical model studied by Gilg et al. [3] predicted cycles with a periodicity that matched field data very well over a 15 year time span, a remarkable result primarily because the model was parameterized with independent field data instead of being fit to the field data with a statistical procedure. In the model, cycles were driven by stoat or short-tailed weasel (*Mustela ermina*) predation, although predation from other species was necessary to keep the lemming population under control in models with no other regulation mechanism.

To make matters more complicated, recent evidence has forced ecologists to examine hypotheses that include both bottom-up and top-down forces acting together. These ideas were introduced mainly by Oksanen et al. [24], and summarized nicely by Korpimaki et al. [14]. They conclude that, at least for voles, lemmings and snowshoe hares, the increase phase of the cycle occurs largely because individuals are more likely to survive, not because females increase reproductive output. Population density plateaus when food becomes scarce and is driven into the decrease phase as predator populations become so dense that the prey population can no longer sustain predation losses.

In this paper, we introduce a series of mathematical models that extend earlier models of this complex phenomenon. The models are founded on the collared lemming system studied earlier by [3]. First, in Section 3, we extend a simple ordinary differential equation model to include a time delay in the predator equations representing the time it takes for predators – stoats in this instance – to mature. The results predict field data reasonably well when the lemming's intrinsic growth is described by a generalized logistic model and the predation term takes a Holling Type III form. The carrying capacity in the logistic growth includes food limitation and also three other more generalist predators. Through sensitivity analysis, we obtain four key parameters whose effects on the period are strongest. In addition, we show that the type of functional response also strongly affects the existence of the population cycle. We modify the model for the snowshoe hare–lynx (*Lynx canadensis*) interaction of boreal North America in Section 4 and parameterize the modified model with field data to fit the observed 10-year snowshoe hare cycle. Comparing those four key parameters in Section 5 for the 4-year lemming cycle and the 10-year snowshoe hare cycle, we conclude that cycle periodicity may be primarily controlled by the delay in predator maturation. This conclusion may explain why lemmings have a 4-year cycle whereas hares have a 10-year cycle. Further, we explore whether this delay in maturation of predators can explain why some species cycle and others do not. Finally, to test our hypothesis, we determine if our model can generate 38-year population cycles observed in the moose–wolf interactions on Isle Royale National Park in Lake Superior.

2. Formulation of the lemming–stoat model

We begin by first modeling the collared lemming system studied by Gilg et al. [3]. Collared lemmings live on the tundra of arctic North American, Siberia and Greenland. In the area of the study [3], approximately 30% of the females breed monthly, producing, on average, four young per litter, giving this population a relatively large reproductive potential. Juveniles mature in about 2 months [2,40]. The major sources of mortality include predation by stoats, arctic foxes (*Alopex lagopus*), snowy owls (*Nyctea scandiaca*) and long-tailed skuas (*Stercorarius longicaudus*).

All four major predators play key roles in the lemming cycle. However, stoats appear to have the most profound impact. Stoats are the most specialized predator, and the only one with a clearly delayed numerical response. Indeed, stoat populations cycle with the lemmings', tending to hit minimal density in the winter just before the lemming population's peak, and in turn peaking the winter before the lemming's hit bottom [4]. Further evidence suggests that the lemming density is held down for at least two successive years by stoat predation, which may help explain why, at the low point, the lemming population density tends to become exceedingly small, far smaller than in most other cyclic species.

In a previous paper [39], we considered several mathematical model formulations of the moss–lemming interaction. If the lemming density is relatively low, then its death is still induced by predation, because food supply is abundant, which is the case for collared lemmings in Greenland. However, we also follow [3] by describing the functional response of stoat predation on lemmings as Holling Type III. This form reflects the difficulty predators have finding lemmings when their density reaches its low point and prey becomes extremely scarce – less than 10 animals per km^2; indeed, evidence suggests that in such conditions stoats will switch to alternate prey or disappear from the study area [4]. This assumption tends to underestimate rather than overestimate the predators' responses, so the estimated impact of predation on lemming population dynamics should be conservative. In the model, we denote the maximum predation rate as η and the 'half-saturation' constant as D. (Notations are summarized in Table 1.)

In the simplest model, with no time delay, we assume that in the absence of predation, lemming populations will grow logistically with intrinsic growth rate b and 'carrying capacity' K. In addition, stoats suffer a per capita mortality rate that also depends on prey availability, generally reflecting the physiological effects of starvation. These assumptions lead us to the following simple model:

$$\begin{cases} \dfrac{dx}{dt} = bx\left(1 - \dfrac{x}{K}\right) - \dfrac{\eta x^2}{D^2 + x^2}y, \\ \dfrac{dy}{dt} = \dfrac{\xi \eta x^2}{D^2 + x^2}y - d(x)y, \end{cases} \tag{1}$$

Table 1
Parameters in lemming–stoat system.

Parameters	Meaning	Median value	Range
b	Maximal growth rate of lemmings	3.92/year	N.A.
K	Lemming carrying capacity	17 ind./ha	$\geqslant 12$
η	Maximum per capita predation rate of the stoat	730 ind./year	600–1000
D	Half-saturation constant of the stoat's functional response	0.1	0.08–0.12
ξ	Conversion rate of lemming to stoat	0.004	0.002–0.01
d_h	The maximal stoat death rate	4/year	3.5–4.5
d_l	The lowest stoat death rate	0.1/year	0–0.2
N_c	The lemming density at which stoat mortality is $(d_l + d_h)/2$	0.1	N.A.
b_1	The slope of the S-shaped mortality function	25	N.A.
τ	Stoat maturation delay	1/4 year	0–0.5
d_j	Stoat juvenile mortality rate	4/year	0–6

where x represents the lemming density and y that of stoats. The first equation is identical to the model of spruce budworm outbreaks studied by Ludwig et al. [15]. Parameter ξ is the conversion rate of lemming mass to stoat mass. Stoat mortality is described by the function $d(x)$. In particular, we set

$$d(x) = d_h - (d_h - d_l)\left(\frac{1}{2} + \frac{\arctan(b_1(x - N_c))}{\pi}\right) \qquad (2)$$

to match Gilg et al. [3]. Because stoats are top predators in this food chain, we ignore stoat self-limitation. Lemming self-limitation is represented by the logistic form of the basic growth term.

2.1. Parametrization of the lemming–stoat model

Values for parameters D, d_h, d_l, N_c and b_1 in Eqs. (1) and (2) were obtained from Gilg et al. [3] and its supporting online material, and are summarized in Table 1. The carrying capacity, K, is necessarily above 12 per ha, which is a value one of us (Gilg) has observed in the field. The maximal growth rate of collared lemmings is about 3.92/year. A stoat is often considered, according to its physiological needs, to kill and consume two rodents per day (i.e., $\eta = 730$/year). However, stoats are also known to 'surplus kill' on a regular basis – kill and hide more prey than needed; some prey are eventually eaten later, but some probably also rot and are therefore 'lost'. Hence, considering that surplus killing might account for as much as 1/3 of the total number of prey killed, the maximum per capita predation rate may be as high as 1000/year. On the other hand, stoats do not feed exclusively on lemmings. Therefore, we choose the maximal per capital predation rate of stoats in the range 600–1000.

2.2. Behavior of the simple lemming–stoat system

The numerical solution of model (1), with parameter values from Table 1, is shown in Fig. 1. Realistic parameter values generate population cycles in both predator and prey with suitable periodicity, but with amplitudes far larger than the field data suggest. Therefore, we hypothesize that sustained 4-year oscillations result from different mechanisms than those modeled in (1). In particular, we propose that the time delay caused by maturation of the predator is necessary to explain the cycle amplitude and periodicity. The predator maturation delay is the time lag required for a newly born predator to reach sexual maturity and start reproducing. We explore this hypothesis in more detail in the next section.

3. The lemming–stoat model with delay

To evaluate the hypothesis that lemming population cycles are controlled by the delay associated with predator maturation, we have extended model (1) as follows:

$$\begin{cases} \frac{dx}{dt} = \frac{bx(1-(x/K)^\theta)}{(1-K^{-\theta})} - \frac{\eta x^2}{D^2+x^2}y, \\ \frac{dy}{dt} = \xi\eta \exp(-d_j\tau)\left[\frac{x^2(t-\tau)y(t-\tau)}{D^2+x^2(t-\tau)}\right] - d(x)y, \end{cases} \qquad (3)$$

where τ is the time delay associated with predator maturation. The exponential term in the stoat equation represents juvenile mortality, so d_j is the per capita juvenile mortality rate. We also generalize lemming self-limitation. Here, we use a generalized logistic form primarily because the standard logistic tends to produce population minima (10^{-3}) that may be too low. The relationship between a population size and its growth rate is recently estimated by Sibly et al. [29]. For mammals, θ should be negative in the growth term of x-equation. We find $\theta = -0.3$ produces an excellent fit to the empirical data. Parameter values used in numerical solutions are listed in Table 1.

3.1. Dynamics of the lemming–stoat model with delay

All simulations of model (3) were run for 20 years. However, for data fitting we used only 6.2–20 year segments in regions where the dynamics had settled into its asymptotic behavior. The model produces cycles with reasonable period and amplitude compared to the field data (Fig. 2). However, the lemming peaks are lower than the actual data suggests, probably because the model is still a simplification of the system and is not designed to provide detailed numerical predictions. The population minima are also lower than the data, but the field data points are annual maxima (density at snowmelt) while the model provides continuous estimates. If we plot all summer trappings as Gilg et al. did (Fig. 2 in Gilg et al. [4]), we can actually see a strong summer decrease, consistent with the model results. The model predicts a periodicity of just over 4 years, which may be the actual average, since most lemming cycles in NE Greenland have a 4 year period but some have 5.

Sharp peaks in the data arise because the breeding population strongly declines after the snowmelt as predation by nomadic and migratory predators increases. However, the model's peaks are rounded because this seasonality and additional predation are not included. Hence, we cannot use peak shape to infer regulation mode – top-down or bottom-up – as in Turchin et al. [34],
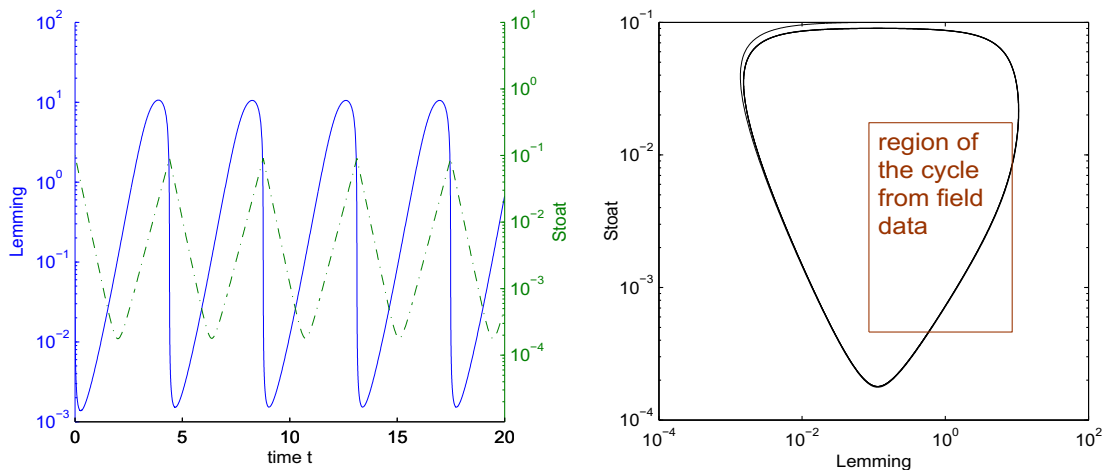

Fig. 1. A typical solution of the simple lemming–stoat ODE system with parameter values in Table 1. In the left panel, the solid line is for lemmings while the dash-dot line is for stoats. In the right panel, the typical solution is compared to the region of field data.
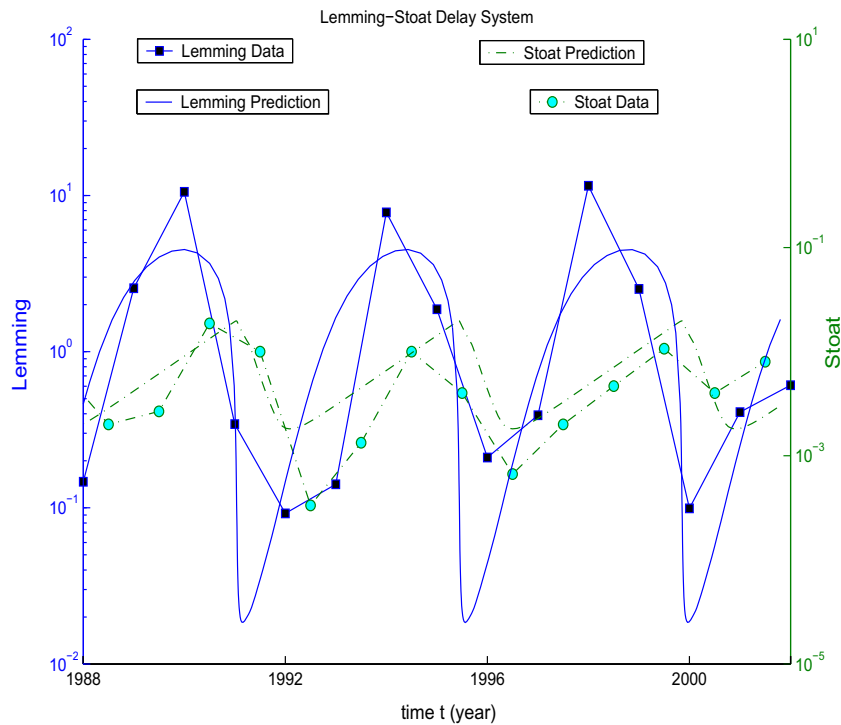
Fig. 2. Lemming–stoat dynamics predicted by model (3) compared to empirical data (points).

because in our case sharp peaks in annual census data may still be consistent with 'blunt' peaks predicted by the model.

Stoat predation remains very low during the lemming increase phase but then eventually causes the lemming population to collapse as young stoats mature and become independent predators (Fig. 2). Biologically, juvenile dispersal and acquisition of territories marks the end of the maturation delay period [9,30]. After the lemming population reaches its minimum and begins to rebound, the stoat population continues to decline over the subsequent year until the following breeding season. Since breeding occurs in a discrete season, the decline might continue for a few months to 1 year at most.

3.2. Sensitivity analysis

To determine the model's sensitivity to parameter estimates, we perturbed each parameter by 50% both up and down, and assessed the perturbation's effect on cycle period and amplitude. We also performed a similar analysis to determine the model's sensitivity to assumptions on predation functional response. In particular, we compared all three Holling Type functions. Figs. 3 and 4 show the results. The (red) horizontal lines represent period and amplitude in the default model.[1]

Fig. 3 suggests that the cycle period is the most sensitive to d_j, τ, η and ξ. Increasing maturation death rate (d_j) and delay (τ), or decreasing predation rate (η) and conversion rate/yield constant (ξ), enlarge the period of the lemming cycle (Fig. 3). Assuming a Holling Type II instead of the Holling Type III functional response also increases the period.

Amplitude of the lemming cycle is largely insensitive to changes in parameters (Fig. 4), but the type of functional response has a large effect. Using the Holling Type II instead of the Holling Type III increases the amplitude of the cycle from 2 to 6 orders of mag-

nitude. In addition, decreasing d_j, τ or θ changes cycle amplitude from 2 orders of magnitude to 1.

This analysis suggests that η, ξ, d_j and τ are key parameters, as they have large impacts on periodicity. This conclusion is supported by bifurcation analysis (Fig. 5), which shows that, indeed, maturation death rate (d_j) and delay (τ) are strongly positively related to cycle period, whereas predation rate (η) and conversion rate/yield constant (ξ) are strongly negatively related to cycle period. In addition, panel (a) of Fig. 5 supports an intriguing hypothesis. As maturation delay for the predator increases by only a couple of months, the period increases dramatically. The snowshoe hare–lynx predator–prey system of Boreal Canada famously has a 10-year period, and lynx mature more slowly than stoats. Could this difference in maturation delay explain why one system cycles with a 4-year period and the other with a 10-year period? To realistically answer this question, we should carefully examine other parameters and the type of functional response for the hare–lynx interactions (see the next section).

4. 10-year snowshoe hare cycle

To evaluate the viability of this hypothesis, we modify model (3) to represent the lynx–hare system. The 10-year cycle of this system is thought to result from the interaction between predation and food supplies [13,12], although here we focus on predation. We are particularly interested in the effect of predator maturation time on the cycle period. Stenseth et al. [32], using a combined approach of empirical, statistical and mathematical modeling, demonstrated that lynx–hare interactions cause delayed density-dependent regulation of population growth. Lynx is a hare specialist, so we only explicitly model predation by lynx. Additional predation on hares, by coyotes (*Canis latrans*) for example, will be lumped with other causes of mortality. Also, the functional response of lynx is well described by Holling Type II [22]. These considerations yield the following model:

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[1] For interpretation of the references to color in the text, the reader is referred to the web version of this paper.
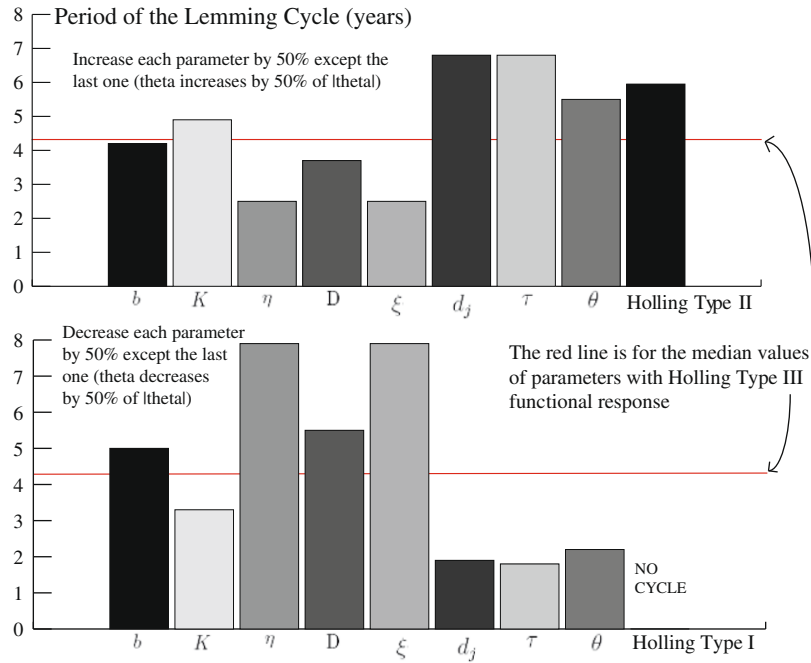
Fig. 3. Period sensitivity analysis of model (3) for all the parameters and different functional responses.
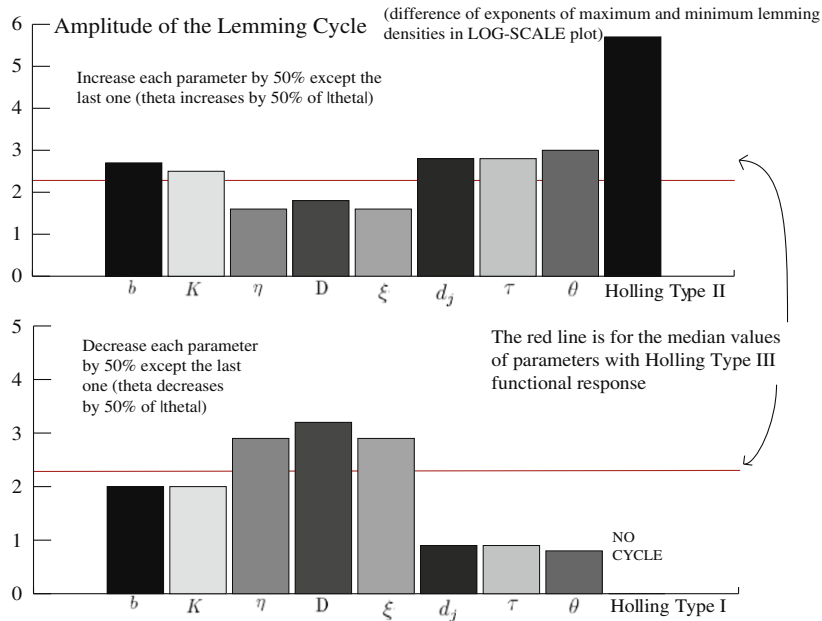

Fig. 4. Amplitude sensitivity analysis of model (3) for all the parameters and different functional responses.

$$\begin{cases} \frac{dx}{dt} = \frac{bx(1-(x/K)^\theta)}{1-K^{-\theta}} - \frac{\eta x}{D+x}y, \\ \frac{dy}{dt} = \xi\eta\exp(-d_j\tau)\left[\frac{x(t-\tau)y(t-\tau)}{D+x(t-\tau)}\right] - dy. \end{cases} \qquad (4)$$

Reproductive output in snowshoe hares varies throughout the cycle from a low of 6.9 young per female during the decline phase to a maximum of 18.9 during the second year of the low and early increase phases [31]. Hence, the maximal growth rate of snowshoe hares is less than 9.5/year assuming a sex ratio of 1:1.

Hares are killed by coyotes at a rate that varies from 0.3 to 2.3 hares/day, with the greatest predation pressure occurring 1 year before the cycle peaks. Lynx predation varies from 0.3 to 1.2 hares/day, with the highest pressure 1 year after the peak. Coyote predation rates are highest early in the winter [22]. Assuming coyotes kill hares at rate 0.3/day for 9 months (spring-fall) and with rate 2.3/day for 3 months (winter), then the additional annual mean predation rate by coyotes is 0.8(/day). The maximum predation rate η equals the maximum lynx kill rate plus the additional predation rate by coyotes. Since the maximum lynx predation rate is 1.2/day, η=730/year.

From Fig. 5 of O'Donoghue et al. [22], we can calculate the half-saturation constant, D. When $x = D$, the per capita predation
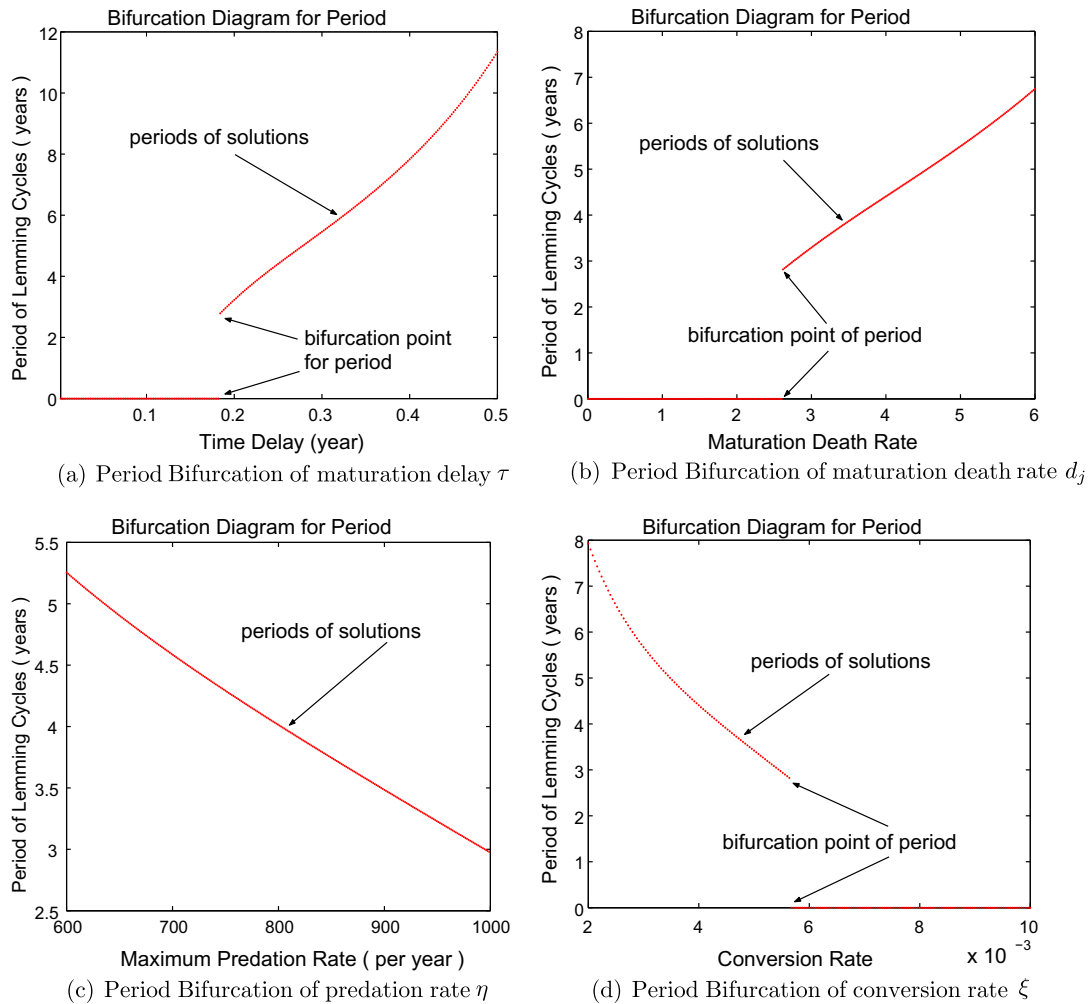
Fig. 5. Period bifurcations for key parameters in model (3).

rate is $\eta/2 = 365/\text{year} = 1/\text{day}$. When the killing rate is 1/day, $x = 70/(100 \text{ ha}) = 0.7/\text{ha}$, which is just the value of D. Therefore, $D = 0.7$.

Female lynx give birth to up to five offspring per litter, with only one litter each year. Therefore, assuming a 1:1 sex ratio, $\xi\eta = 5/2 = 2.5(/\text{year})$.

We estimate the lynx maturation delay $\tau = 1.5$ years from Murdoch et al. [19]. Note that this maturation delay may be affected by the near absence of the coyote and lynx (especially juveniles) that occurs just after the hare population crashes [21,23].

Numerical solutions of model (4) with these parameter values (summarized in Table 2) produce cycles with a 10-year period (Fig. 6).

5. Comparison and interpretation

From Fig. 3, one can see that increasing maturation death rate (d_j) and delay (τ), or decreasing predation rate (η) and conversion rate/yield constant (ξ), can enlarge the period of population cycles, so at first glance any of these parameters may explain the different cycle periods of lemmings and snowshoe hares. The values of η and ξ are very close for both systems, so they are unlikely explanations. The juvenile mortality rate, d_j, of lynx (0.5/year) is much smaller than that of stoats (4/year). This difference would tend to make the period of the hare cycle shorter than the lemming's, in contradiction to reality. However, the maturation delay, τ, of lynx (1.5 years) is much larger than that of stoats (3 months). This dif-

Table 2
Parameter values for the snowshoe hare–lynx system.

Parameters	Median value	Range	Reference
b	5/year	$\leqslant 9.5$	Stefan anjd Krebs [31]
K	8 ind./ha	2–10	Krebs et al. [12]
η	730 ind./year	400–1000	O'Donoghue et al. [22]
D	0.7	0.1–1	O'Donoghue et al. [22]
$\xi\eta$	2.5/year	0.25–4	Literature
d	0.3/year	0–0.5	Literature
d_j	0.5/year	0.3–0.5	Literature
τ	1.5 year	N.A.	Murdoch et al. [19]
θ	−0.1	(−0.3)–0	Numerical test

ference tends to oppose the effect of juvenile mortality, making the period of the hare cycle much longer than that of the lemming cycle as observed in reality.

Furthermore, assuming a Holling Type II functional response, as in the snowshoe hare–lynx model, instead of the Holling Type III, as in the lemming model, also increases the period, as is clear from the sensitivity analysis (Fig. 3). Therefore, functional response can potentially explain, at least in part, why lemming cycles have a 4-year period whereas hares cycle every 10 years.

Our models suggest that both maturation delay of predators and type of functional response are key determinants of the period length of population cycles. Which of these factors is more important can be inferred from Fig. 3. Because lynx mature much more
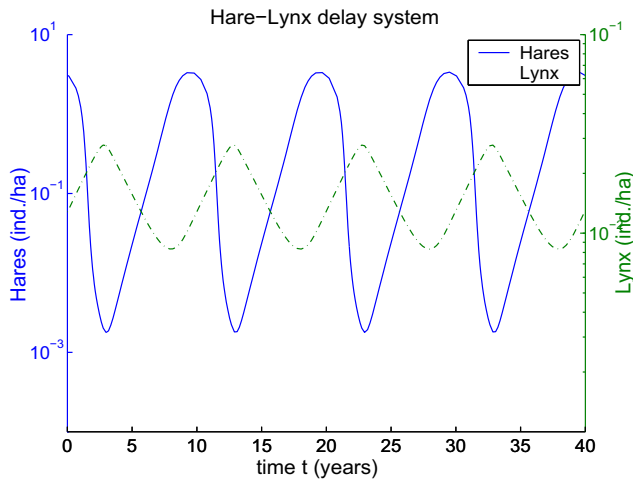
Fig. 6. Hare–lynx delayed system with parameter values in Table 2 produces the 10-year snowshoe hare cycle. The solid line is for hares while the dash-dot line is for lynx.

slowly than stoats, the value of τ used in the hare–lynx model is much larger than its maximum value in Fig. 3, which only represents a 50% increase from τ for stoats. The longer period of the snowshoe hare cycle compared to the lemmings, therefore, is explained more by maturation delay than type of functional response (Fig. 5(a)). This observation suggests that the maturation delay of predators almost completely determines the period of population cycles.

In addition to its effects on period, functional response also plays a dominant role in determining the amplitude of population cycles (Fig. 4). In particular, a Holling Type II functional response, as opposed to the Holling Type III, greatly increases the cycle amplitude. This observation may explain why the amplitude of the snowshoe hare cycle is larger than that of the lemming cycle, probably because the functional response of lynx to snowshoe hare is Holling Type II while that of stoat to lemming is Holling Type III.

Simple mathematical stability analysis shows that predator maturation periods that are either too short or too long actually inhibit generation of population cycles. Intuitively, if the time to maturation is too short, then the cycle period is zero; if too long, then the period appears to approach infinity for finite τ, above which, solutions approach the interior (positive) steady state. If even longer than this threshold τ, then solutions approach the predator extinction steady state, and prey approach their carrying capacity K (see below). Also, even if the predator maturation period is intermediate and able to produce cycles, but the functional response is the Holling Type I, then no cycles will arise (Figs. 3 and 4). These observations may explain why only a few species have well-defined population fluctuations.

These results match those of Gourley and Kuang [5], who analyzed a similar delayed prey–predator system. Their model differed from ours in that they assumed $\theta = 1$, a constant predator death rate and a general functional response. Since our simulations suggest that both θ and the prey-dependent predator death rate, d, only affect the system slightly, our results should coincide with those of Gourley and Kuang [5]. From their stability curve of the interior steady state, one can see that there exists three threshold values of the maturation delay, $0 < \tau_1 < \tau_2 < \tau_3$, such that no cycles exist when $\tau < \tau_1$; cycles arise when $\tau_1 < \tau < \tau_2$; and cycles disappear again when $\tau_2 < \tau < \tau_3$. If the delay is so large that $\tau > \tau_3$, then the interior steady state disappears and the predator extinction steady state $(K, 0)$ becomes globally asymptotically stable; hence, there are no cycles in this case either – more precisely, there exist no globally asymptotically stable limit cycles. Fig. 7

shows that all four of these cases also exist in our lemming–stoat delay system (model (3)). If the functional response resembles either the Holling Type II or III, then there is a range in which the maturation delay, $\tau_1 < \tau < \tau_2$, allows the existence of population cycles. This range depends on all the other parameters and the type of functional response.

6. Multi-decade moose cycle on Isle Royale

The well-studied moose–wolf predator–prey system on Isle Royale in Lake Superior provides another opportunity to test predictions generated by this modeling approach. Wolves (*Canis lupus*) are the top predator on the island, and moose (*Alces americanus*) are their primary prey. Importantly, no other predators capable of taking down a moose – notably black bears (*Ursus americanus*) – exist on the island to compete with the wolves for moose [27]. Also, the Isle Royale ecosystem has been under essentially continuous study since the late 1950s [25,1,8,35]. Therefore, not only do the conditions fit the basic assumptions of the model, but essentially all parameters can be estimated from the outstanding data these ongoing studies have produced.

Moose calves on Isle Royale are born typically in May and June [20,1], although in the model we make no provision for a pulsed reproductive season. Therefore, we interpret b as the maximum per moose birth rate under ideal conditions. Moose typically have one calf, occasionally two. Therefore, the largest realistic upper limit for b would be 0.7/year, assuming all cows have twins, all adults survive and the sex ratio is 1:1. However, this number is almost certainly high, given that on Isle Royale, over 80% of cows bearing young will lose their calves. On the other hand, in 1982, the fraction of the Isle Royale moose population made up of 8-month-old calves reached a peak of about 24% of the total population [27,35].

The remaining parameters for the moose equation are easier to decipher. The Isle Royale moose population reached an observed peak of about 3000 before wolves were introduced to the island [20]. Therefore, we set $k = 3000$. (*Note:* in this model our density is scaled in units of number of individuals on the island.)

Although Vucetich et al. [38] and Jost et al. [8] suggested a ratio-dependent functional response for the moose–wolf system on Isle Royale, here we opt for a Holling Type II functional response, with the form

$$\frac{\eta x}{x + D},$$

as suggested by Hayes and Harestad [6] for moose in the Yukon. We choose the Holling function to make contact with our previous models; clearly, the data support density-dependent predation on Isle Royale.

The wolf population growth rate as a function of kills was analyzed by Vucetich and Peterson [36]. The simplest model they consider – a linear relationship between per capita kill rate and per capita wolf population growth rate – performed reasonably well based on their criteria, so we use it to generate our (first approximation) estimate of ξ. In particular, the slope parameter (estimated from their Fig. 2) is approximately 0.48; that is, if one assumes that.

$$\frac{1}{y}\frac{dy}{dt} = b_0 + b_1 f(x, y),$$

with b_0 and b_1 constants and $f(x, y)$ the kill rate (estimate of the functional response), then $b_1 \approx 0.48$. Inasmuch as the data from Vicetich and Peterson [36] includes both wolf reproduction and mortality, and our ξ represents wolf reproduction only, equating $\xi = b_1$ yields a lower bound. Therefore, we somewhat arbitrarily set our default value to 0.35. Wolf mortality on Isle Royale peaked at 54% in both 1981 and 1998 [37,35], which equates to a rate of
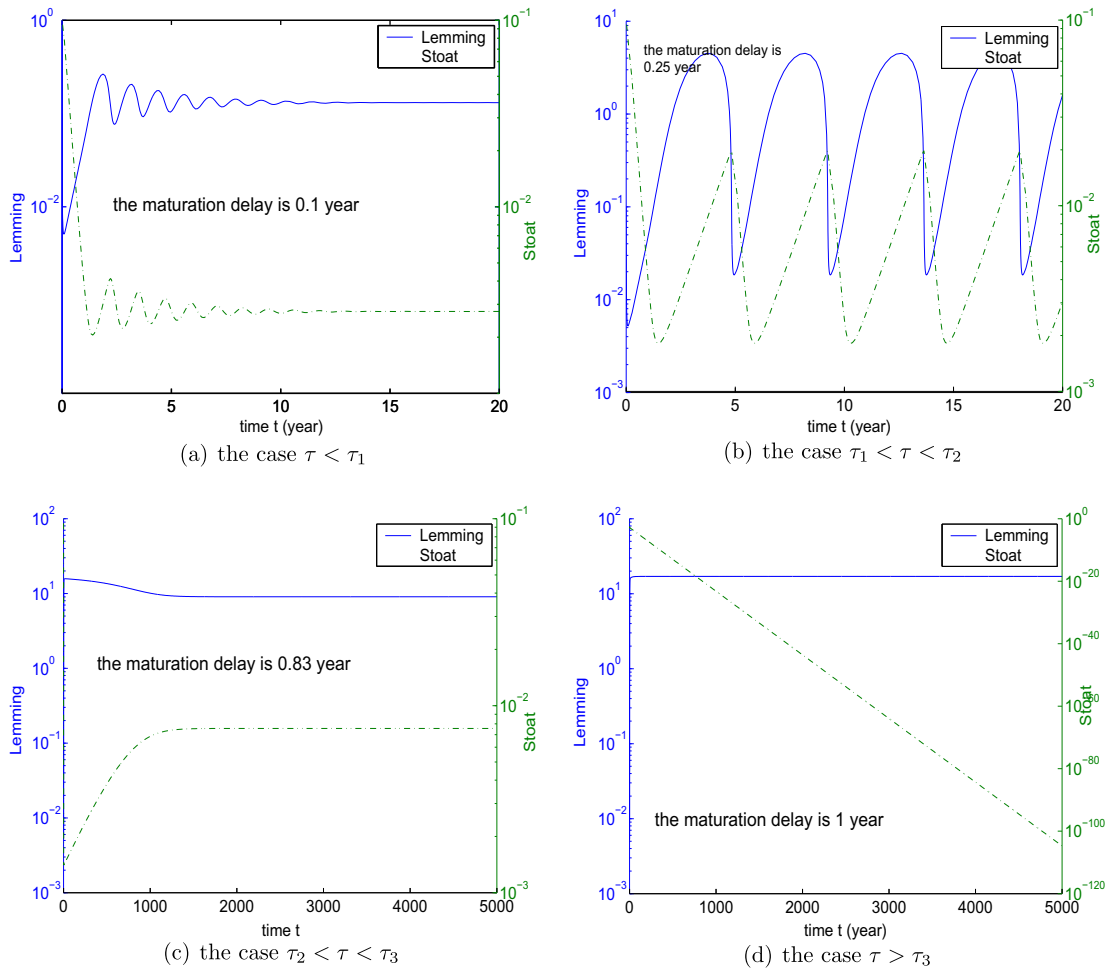
Fig. 7. The qualitative effect of the maturation delay in our lemming–stoat delay system (model (3)). The solid lines are for lemmings while the dash-dot lines are for stoats.

0.78/year for d_h. In other years, no wolves died, suggesting $d_l = 0$. To estimate N_c we used data published on the Isle Royale moose–wolf study website maintained by John Vucetich to regress percent wolf mortality on moose population size, which yields the following regression equation:

$$\%\text{Mortality} = -9.095 \times 10^{-3}x + 34.778$$

with x the moose population size. Since N_c represents the moose population at which wolf mortality reaches half maximum (given that $d_l = 0$), this regression equation yields the estimate $N_c \approx 855$. However, this value must be used with caution given the great amount of noise evident in the data, and the obvious effect of demographic stochasticity and other random processes affecting the system [36]. Therefore, we recommend a broad range for this parameter.

Mech [18] reports that wolves begin exhibiting breeding behavior at 22 months of age, suggesting $\tau = 1.8$ years given that wolves breed in a discrete season. Thus, we assume 1–4 years as the range for τ. Our model best fits the 38-year period when τ is the lower boundary value. Note that the maturation period of wolves is usually longer than 1 year. This observation leads to a question whether 38 year is the realistic period of moose–wolf cycles. The 38-year cycle was originally suggested by Peterson et al. [26]. However, the evidence was rather weak and has a large uncertainty (±13 years). The later paper by Post et al. [28] paints a more complex picture. They found that the period was much shorter – 20–21 years – than that suggested by Peterson et al. [26].

Mortality of young wolves varies greatly with age. Puppies in their first 5–10 months suffer mortality ranging from 57% to 94%, whereas older juveniles – from this range to between 17 and 22 months – experience mortality of about 45% [18]. So, in the worst case, juvenile mortality (through 22 months) can reach $1 - (0.06)(0.55) = 0.967$ (96.7%), and in the best case can approach 76.4%. These values generate an estimate of d_j ranging from 2.88 to 6.82.

Numerical solutions of our delayed predator–prey model with realistic parameter values from Isle Royale (summarized in Table

Table 3
Parameter values for the moose–wolf system on Isle Royale National Park.

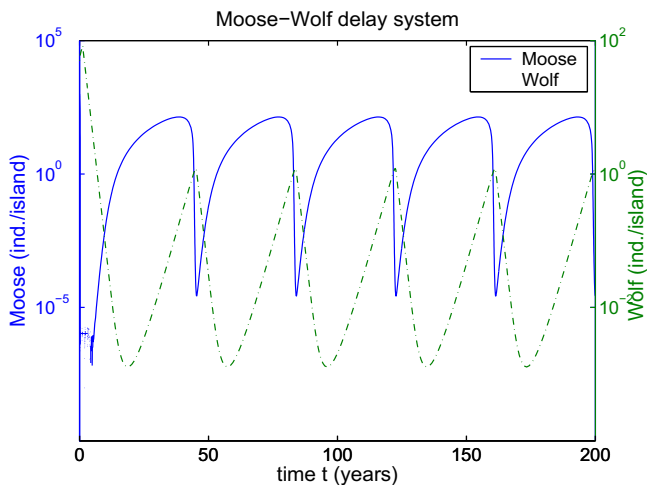| Parameters	Value we choose	Range	Reference
b	0.68	<0.7	Vucetich and Peterson [35]
K	3000	2500–3000	Murie [20]
η	80	NA	Literature
D	5	NA	Literature
ξ	0.35	<0.48	Vucetich and Peterson [36]
d_h	0.78	NA	Vucetich and Peterson [35]
d_l	0	NA	Vucetich and Peterson [35]
N_c	855	500–1500	Published data
b_1	0.48	NA	Vucetich and Peterson [36]
τ	1	1–4	Mech [18]
d_j	2.9	2.88–6.82	Mech [18]
θ	−0.3	NA	Numerical test

Fig. 8. Moose–wolf delayed system with parameter values in Table 3 produces the 38-year moose cycle. The solid line is for moose while the dash-dot line is for wolves.

3) can produce cycles with a 38-year period (Fig. 8), as originally suggested by Peterson et al. [26].

7. Summary and discussion

In this paper, we construct and parameterize a series of mathematical models to explore why some predator–prey interactions exhibit population cycles while others do not, and what determines the period and amplitude of such cycles should they exist. Many similar studies using mathematical models exist. Ours is unique because it combines an extension of the traditional logistic growth of prey with a discrete delay representing predator maturation, a prey-dependent death rate among predators and both Holling Type II and III functional responses. We also estimate parameters and the functional response from field data for three independent predator–prey systems: lemming–stoat (arctic North America, Greenland and Europe), snowshoe hare–lynx (boreal Canada) and wolf–moose (Isle Royale National Park).

Reasonable parameterizations of our models for all three systems can generate cyclic behavior with the proper period in each case, namely 4, 10 and 20–40 years for lemmings, hares and moose, respectively. Sensitivity and bifurcation analyses identified four key parameters that could possibly determine cycle period and amplitude in these models. We found that one of these four parameters, predator maturation delay, along with the type of functional response, are the key determining factors of the period and amplitude of cycles in all three systems. These observations lead to the primary hypothesis generated by this study – the details of predator–prey cycles, especially the period and amplitude, are determined primarily by the length of time it takes for predators to mature and how predation responds to changes in prey density (functional response). Furthermore, the predator maturation delay primarily determines cycle periodicity, and functional response controls amplitude.

The idea that a predator maturation delay can cause population cycles is nothing new. Indeed, May [16,17] also studied general mathematical models of predator–prey systems, concluding that time delay, cycle period and cycle amplitude were all correlated. Our work, with more tactical models parameterized to represent specific systems, support May's conclusion.

Gourley and Kuang [5] showed, in similar models to the ones studied here, that predator maturation delay generated cyclic

behavior. These researchers also observed that time delays that were either too short or too long obliterated the cycles. Our results confirm these observations – cycles are generated only by intermediate time delays. In addition, as generally known from previous predator–prey models, sufficient nonlinearity in function response is required to generate cycles – cyclic behavior is impossible for Holling Type I functional response.

As more and more data on predator–prey systems accumulates, the hope of a simple 'smoking gun' explanation of population cycles fades. For example, it has become fairly clear that both top-down and bottom-up mechanisms are required to explain the 10-year snowshoe hare cycles, and which mechanisms predominate depends on the phase of both predator and prey populations [13,12]. Similarly, on Isle Royale, density-dependent mechanisms appear to limit the moose population when the wolf population is in decline, but when wolf numbers are increasing, moose enter a cyclic dynamic driven by predator–prey interaction [28]. Thus, we take care here not to suggest that we have an explanation of population cycles. Nevertheless, our results highlight the potential roles of predator maturation delay and functional response as universal causal mechanisms of population cycles in most mammalian predator–prey systems.

Acknowledgments

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