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Modelling the Canada lynx and snowshoe hare population cycle: the role of specialist predators

Rebecca Tyson · Sheena Haines · Karen E. Hodges

Abstract Mathematical models of the snowshoe hare (*Lepus americanus*) and Canada lynx (*Lynx canadensis*) population cycles in the boreal forest have largely focused on the interaction between a single specialist predator and its prey. Here, we consider the role that other hare predators play in shaping the cycles, using a predator–prey model for up to three separate specialist predators. We consider the Canada lynx, coyote (*Canis latrans*) and great horned owl (*Bubo virginianus*). Our model improves on past modelling efforts in two ways: (1) our model solutions more closely represent the boreal hare and predator cycles with respect to the cycle period, maximum and minimum hare densities and maximum and minimum predator densities for each predator, and (2) our model sheds light on the role each specialist plays in regulation of the hare cycle, in particular, the dynamics of the raptor appear to be crucial for characterising the low hare densities correctly.

Keywords Population dynamics · Boreal population cycles · Mathematical model · Differential equations · Snowshoe hare minimum density · Canada lynx · Multiple predators · Predator-prey model · Coyote · Great horned owl

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Introduction

The population cycle of the snowshoe hare (*Lepus americanus*) has been a focus of scientific interest for the past century (Boonstra et al. 1998; King and Schaffer 2001; Korpimäki et al. 2004; Krebs et al. 2001a). Hudson Bay furrier records (MacLulich 1957), along with extensive ecological research (Keith et al. 1984; Krebs et al. 2001a), have given us a wealth of information on the demography of snowshoe hare populations throughout boreal North America. These populations are characterised by striking high-amplitude multi-year cycles with a period of 8–11 years (MacLulich 1957; Stenseth et al. 1998).

Many hypotheses and mathematical models have been proposed to explain the northern snowshoe hare cycle (King and Schaffer 2001; Korpimaki and Krebs 1996; Royama 1992; Schaffer et al. 2001; Zhang et al. 2007). Some consensus has emerged that predation plays a key role in the cycle (Korpimäki et al. 2004; Krebs et al. 2001a; Ruesink and Hodges 2001; Turchin 2003, but see Inchausti and Ginzburg 2002). The Canada lynx(*Lynx canadensis*) is a specialist predator of the hare (O'Donoghue et al. 1998), and Hudson Bay trapping records show that lynx populations fluctuate in an 8–11-year cycle closely linked with that of the snowshoe hare (Elton and Nicholson 1942; Vik et al. 2008). Existing predator–prey models (see Turchin 2003 for a review of the models listed above) capture many traits of the cycle, particularly the period and amplitude. Few, however, discuss the maximum and minimum densities of hares and lynx during the population cycle, and none address the role of other specialist predators on the hare. It is important to develop models that fit observed densities, as well

as cycle periods. The low minimum densities have very real impacts on many species in the boreal forest food web (Ruesink and Hodges 2001), so models that do not capture low densities are failing to describe an important aspect of the population cycle.

In this paper, we seek to investigate these two omissions by previous researchers. Since the minimum hare densities observed in the boreal forest are much lower than existing models predict, we have yet to understand what drives the hare density to such low values during the cycle troughs (Boonstra et al. 1998; Hodges et al. 1999). Predation by lynx is apparently not sufficient. Snowshoe hares, however, are subject to predation by a myriad of mammalian and avian predators (Stenseth et al. 1997). Furthermore, the Kluane study in the Yukon Territory provides data indicating that, in addition to the lynx, both the coyote (*Canis latrans*) and the great horned owl (*Bubo virginianus*) populations respond to fluctuating hare densities as specialist predators (O'Donoghue et al. 2001; Rohner et al. 2001). It is thus possible that these predators each play an important role in shaping the dynamics of the hare population cycle.

We assess model fit to empirical data through three cycle probes for the prey, and three cycle probes for each specialist predator: period, hare maximum density, hare minimum density and, for each specialist predator, maximum density, minimum density and lag. The predator lag is defined as the time between the maximum of the prey cycle and the subsequent maximum of the predator cycle. Using these cycle probes, we address two central questions. First, can a bi-trophic predator–prey model of the lynx–hare system generate simulated cycles that match boreal forest cycles if multiple predators are included? Second, what is the role played by each specialist hare predator in the lynx–hare cycle dynamics? Our work is a significant extension of current models, which have concentrated on capturing the qualitative rather than quantitative behaviour of the lynx–hare system, and which have included only one specialist predator.

The model

We base our investigation on the model used by Hanski and Korpimaki (Hanski and Korpimäki 1995) to analyse vole population dynamics in Fennoscandia. Voles and their predators exhibit distinct 4-year cycles

in the northern parts of the voles' range. The model equations are

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - \frac{\gamma N^2}{N^2 + \eta^2} - \frac{\alpha NP}{N + \mu}, \tag{1a}$$

$$\frac{dP}{dt} = sP\left(1 - \frac{qP}{N}\right), \tag{1b}$$

where N and P are the prey (vole) and specialist predator population density, respectively. We use the same model, but with parameters appropriate for the snowshoe hare and its predators. We refer to this model as the "*basic* model".

Equation 1a has logistic growth of the hare population, with r the hares' intrinsic rate of population growth and k the carrying capacity. The second term in the prey equation represents predation by generalist predators, which are assumed to have a sigmoid (type III) functional response (O'Donoghue et al. 1998). The parameter γ describes the maximum yearly rate of generalist predation in terms of kills per area, and η is the hare density at which the yearly generalist predation rate is half of γ. The third term in Eq. 1a reflects specialist predation on hares. Specialist predators are assumed to have a type-II functional response (O'Donoghue et al. 1998; Turchin 2003). The three most important hare predators in the boreal forest are the lynx, coyote and great horned owl, and the functional response of each of these is well described by the type-II response (Krebs et al. 2001b). The parameter α is the maximum killing rate of hares by specialist predators, and μ, the half-saturation constant, is the hare density at which specialist predation is at half α.

The predator equation (Eq. 1b) consists of a single logistic growth term with a prey-dependent carrying capacity, N/q. This formulation of predator dynamics is analogous to a logistic growth model with variable predator territories that change in size according to prey abundance (Turchin 2003). Thus, as the hare population decreases, the predator carrying capacity, N/q, also decreases. The parameter q is the equilibrium density ratio of hares to predators (Turchin and Hanski 1997), and s is the intrinsic rate of increase of the predator population.

We allowed the specialist predator P in Eq. 1 to represent just lynx, or a predator complex of lynx and other specialist predators. We considered three predator complexes: lynx and coyote (lynx:coyote–hare system), lynx and owl (lynx:owl–hare system) and all three specialists (lynx:coyote:owl–hare system). Since a proportion p_i of hare deaths is due to each predator,

we sought to represent the combination of specialist predators as a single combined predator by taking combined parameter values. The resulting predator parameter values were weighted sums of the individual parameter values, using the predation pressure proportions p_i as the weights. For example, if hare predation pressure was due to lynx, coyote and great horned owl in the ratio $p_l : p_c : p_g = 0.6 : 0.3 : 0.1$, then $\alpha = (p_l\alpha_l + p_c\alpha_c + p_g\alpha_g) = 0.6\alpha_l + 0.3\alpha_c + 0.1\alpha_g$. The s, q and μ combination parameters were calculated in the same way. We used data on hare mortality in the boreal forest as a guideline for plausible p_i values.

Additional specialist predators are explicitly included in the model by adding, for each predator, an equation analogous to Eq. 1b, and a separate specialist predation term in Eq. 1a. The result is the following system of equations:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - \frac{\gamma N^2}{N^2 + \eta^2} - \sum_i \frac{\alpha_i N P_i}{N + \mu_i}, \quad (2a)$$

$$\frac{dP_i}{dt} = s_i P_i \left(1 - \frac{q_i P_i}{N}\right), \quad \forall i. \quad (2b)$$

The index i denotes predator type and can be l (lynx), c (coyote) or g (great horned owl).

In any study of model fit to data, it is important to know how many degrees of freedom are available in the model. To do this here, we must rescale the model variables and, thereby, uncover the relevant dimensionless parameter groupings. In nondimensional form, the model becomes

$$\frac{dn}{dt^*} = n(1 - n) - \frac{\gamma^* n^2}{n^2 + (\eta^*)2} - \sum_i \frac{\alpha_i n p_i}{n + \mu_i^*}, \quad (3a)$$

$$\frac{dp_i}{dt^*} = s_i^* p_i \left(1 - \frac{p_i}{n}\right), \quad \forall i, \quad (3b)$$

where the rescaled variables and dimensionless parameter groupings are

$$n = \frac{N}{k}, \qquad p_i = \frac{q_i P_i}{k}, \qquad t^* = rt, \qquad \gamma^* = \frac{\gamma}{kr},$$

$$\eta^* = \frac{\eta}{k}, \qquad \alpha_i = \frac{\alpha_i}{q_i}, \qquad \mu_i^* = \frac{\mu_i}{k}, \qquad s_i^* = \frac{s_i}{r}.$$

The prey equation (Eq. 3a) has two generalist predation parameters, plus two parameters for each specialist predator. The predator equations (Eq. 3b) each have just one parameter.

Below, we investigate models with one, two and three specialist predators, using parameter values from field research. The multiple predator models we consider are:

- The *LC* model: lynx, coyote, snowshoe hare
- The *LG* model: lynx, great horned owl, snowshoe hare
- The *LCG* model: lynx, coyote, great horned owl, snowshoe hare

Parameter estimation

The parameter values we used (Table 1) were chosen based on field studies, primarily from the comprehensive ecosystem study at Kluane Lake, Yukon (Krebs et al. 2001b), which included several different study sites. Snowshoe hare densities at each site were estimated by mark-recapture live-trapping, thus providing high-quality estimates of hare densities in this system. We supplemented these values with data from other sources if parameters were not well estimated by the Kluane study or if other studies showed widely divergent values, indicating that model behaviour should be tested over a broad range. Below, we outline how the various parameter values were determined in the literature.

Intrinsic rate of population increase values were determined from direct measurements of population increase (r) or from annual litter size data (ρ) coupled with survival rates of the young (δ). Given ρ and δ, the corresponding annual rate of population increase is determined from

$$r = \ln(\rho\delta).$$

The snowshoe hare carrying capacity (k) is estimated from observations of maximum hare densities observed in the field. The generalist predation rate (γ) has been measured on control grids in Kluane. The generalist half-saturation constant (η) cannot be directly measured in the field, and so we use a range of values. We selected a plausible range by using measured values for specialist predator half-saturation constants (μ) for a variety of predators as a guideline.

Predator half-saturation constants (μ_i) are determined from functional response curves fitted to predation data plotted as a function of prey density. Maximal daily kill rates (α_i) are estimated from field data and from functional response curves. These values are then multiplied by 365 days/year to give the yearly saturation killing rate.

Table 1 Parameters for the model equations Eqs. 1 and 2

	Description (units)	Source	Range	Default value	
				Basic model	*LCG* model
r	Hare intrinsic rate of increase (/yr)	(a)(f)	1.5–2.0	8.0	5.0
k	Hare carrying capacity (hares/ha)	(a)(e)	4.0–8.0 (12)	1.75	1.75
γ	Generalist killing rate (hares/(ha·yr))	(a)	0.1–2.0	0.1	0.1
η	Generalist half-saturation constant (hares/ha)		0.5–2.0	1.25	1.25
α_l	Lynx saturation killing rate (hares/(lynx·yr))	(b)(d)	438–577	505	505
α_c	Coyote saturation killing rate (hares/(coyote·yr))	(b)(d)	840–876	–	858
α_g	Great horned owl saturation killing rate (hares/(owl·yr))	(c)	50–150 (250)	–	100
μ_l	Lynx half-saturation constant (hares/ha)	(d)	0.2–0.4	0.3	0.3
μ_c	Coyote half-saturation constant (hares/ha)	(d)	0.5–1.1	–	0.8
μ_g	Great horned owl half-saturation constant (hares/ha)	(c)	0.05–0.25	–	0.15
s_l	Lynx rate of population increase (/yr)	(e)(f)	0.7–1.0	0.85	0.8
s_c	Coyote rate of population increase (/yr)	(f)(g)	0.5–1.2	–	0.55
s_g	Great horned owl rate of population increase (/yr)	(c)	0.2–0.5	–	0.35
q_l	Hare:lynx equilibrium ratio (hares/lynx)	(b)	150–1200	212	500
q_c	Hare:coyote equilibrium ratio (hares/coyote)	(b)	330–2500	–	1075
q_g	Hare:great horned owl equilibrium ratio (hares/owl)	(c)	50–250	–	100

Parameters values derived from the data (column 4) are measured or calculated as described in "Parameter estimation". Default parameter values for the *basic* and *LCG* (columns 5 and 6) models are chosen midway through the observed range except in cases where the model solutions did not cycle. For the *basic* model, therefore, it was necessary to set k and q_l at the extreme low and high end of the observed ranges, respectively. Sources are Hodges et al. (2001) (a), O'Donoghue et al. (2001) (b), Rohner et al. (2001) (c), O'Donoghue et al. (1998) (d), Ruggerio et al. (2000) (e), King and Schaffer (2001) (f) and Windberg (1995) (g)

The hare:predator equilibrium ratio q_i determines the carrying capacity of the environment for the predator, and is very difficult to estimate with certainty. The ratio can be calculated using predator energetic needs (prey/predator/year), or from demographic data. Generally, estimates derived from energetic needs are two to three times lower than estimates derived from demographic data, and so the plausible range of values is relatively large compared to the other parameters of the model.

Model analysis

It is not possible to determine the characteristics of the limit cycle solutions to our models analytically, and so we carried out a numerical study. Each parameter was varied through the range of biologically realistic values from boreal North America (Table 1), and for some of the parameters, we also investigated values outside the realistic range in order to better understand the solution behaviour.

For each set of parameter values, we obtained numerical solutions to the model equations using a fourth-order Runge Kutta scheme. Numerical solutions were run for 600 years, and then the first 500 were discarded so that transient behaviour was not included in our analysis. In every case, the steady state behaviour for N and P_i was either a limit cycle or a constant equilibrium.

The period, maximum population density and minimum population density of the cyclic solutions for N and P_i were measured from the numerical time series. These probes were then compared to field data.

We explored a wide range and combination of parameter values in our investigations. For the discussion below, we found it useful to choose default parameter values in the middle of each plausible parameter range (Table 1). The two exceptions to this rule are k and q_l in the *basic* model, which had to be chosen at the extreme high and low end of the plausible range, respectively, in order for the default parameter set to yield population cycles in the solutions. We used the model solutions obtained with these default values as a starting point to examine how the cycle characteristics of the model solutions depended on variations in the model parameters.

Parameter sensitivity

We investigated the sensitivity of the model solutions to variation in individual model parameters, and also did some work in which we varied multiple parameters simultaneously. Changes in the numerically generated time series were observed with respect to the cycle probes identified in "Introduction". Results for the *basic* and *LCG* models are shown in Fig. 1. In the interest of brevity, the figure shows the sensitivity of just two cycle probes, hare maxima and minima, to
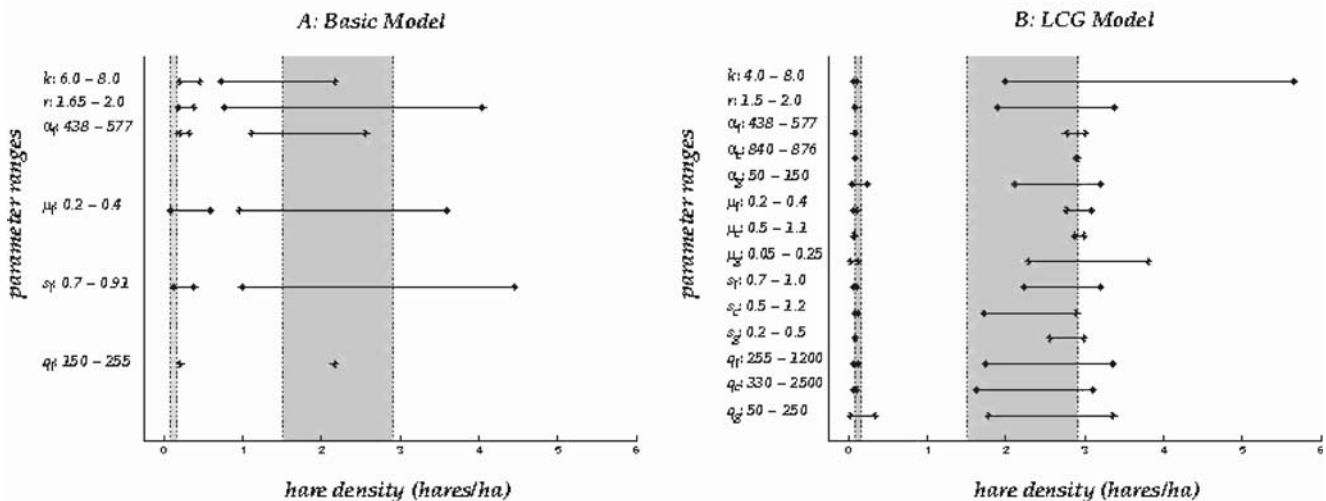
Fig. 1 Sensitivity of the hare minimum and maximum densities to model parameters. Results are shown for the **a** *basic* and **b** *LCG* models. Model behaviour was tested for all parameters held at their default values (Table 1, except for the one parameter being varied. The *grey rectangles* show the range of observed low and high densities across several sites in the Yukon. Ranges over which each parameter was varied are listed on the vertical axis, across from the corresponding cycle response ranges. The parameter ranges correspond to the range of plausible values for each parameter (see Table 1), except in cases where the model did not yield cycles for parameter values at either end of the range. Solutions with cycle amplitude (maximum density divided by minimum density) of less than 1.5 were deemed non-cyclic, since cycles of such low amplitude would be difficult to detect in the field, given the individual confidence limits around each density estimate

individual parameter variations when all other parameters are held constant at the default values (Table 1). The corresponding cycle periods showed relatively little sensitivity to variations in parameter values, remaining generally within the plausible range of values. Cycle periods generally fell within the range of 8–9 years for the *basic* model, and 9–12 years for the *LCG* model. Similar sensitivity results were obtained for model parameters fixed at other plausible values. Below, we describe the full response of the model solutions, in terms of all of the cycle probes, to variations in the model parameters.

All of the models gave rise to periodic limit cycle oscillations for a wide range of parameter values. Figures 2 and 3 show sample population density time series from the *basic* and *LCG* models obtained with default parameter values (the default values are listed in Fig. 1). Consistent with time series from the boreal forest, the predator cycles lag 1–2 years behind the hare cycle.

Hanski and Korpimäki (1995) analysed the *basic* model of Eq. 1a in parameter ranges appropriate for the vole food web, and found that parameters *r*, *s*, *k* and *μ* had the strongest influence on model dynamics. Using values appropriate for the Canada lynx and snowshoe hare, we also found that these parameters are important (Fig. 1-A). The parameters *r* and *s* (intrinsic rate of hare and predator population increase) have the strongest influence on cycle length, with low values increasing the cycle period to 10–11 years, and higher values decreasing the cycle period to 7–9 years. These parameters also affect predator lag, with lag decreasing with increasing *s* or decreasing *r*. Parameter *k* (hare-carrying capacity) has a strong effect on cycle amplitude, with increasing values increasing peak densities significantly while increasing low densities only slightly.

The parameter *μ* (predator half-saturation constant) has strong effects on the model dynamics, as small decreases in *μ* significantly affect cycle amplitude, both increasing peak densities and lowering low densities. For the default values of these four parameters, the model always predicts stable limit cycles. In contrast, at low values for *r* and *k* and at high values for *s* and *μ*, the limit cycle collapses to a stable equilibrium point.

The hare:predator equilibrium ratio, *q*, also has important effects on the model dynamics. Additionally, *q* is the most difficult parameter to estimate, and so sensitivity of the model to changes in *q* is highly relevant. For the *basic* model, *q* has little effect on cycle period and only a minor effect on cycle amplitude, but it is the most important parameter in shifting the model from a stable equilibrium point to a stable limit cycle. The range of values for which the model exhibits stable limit cycles is small relative to the range of plausible values for *q*
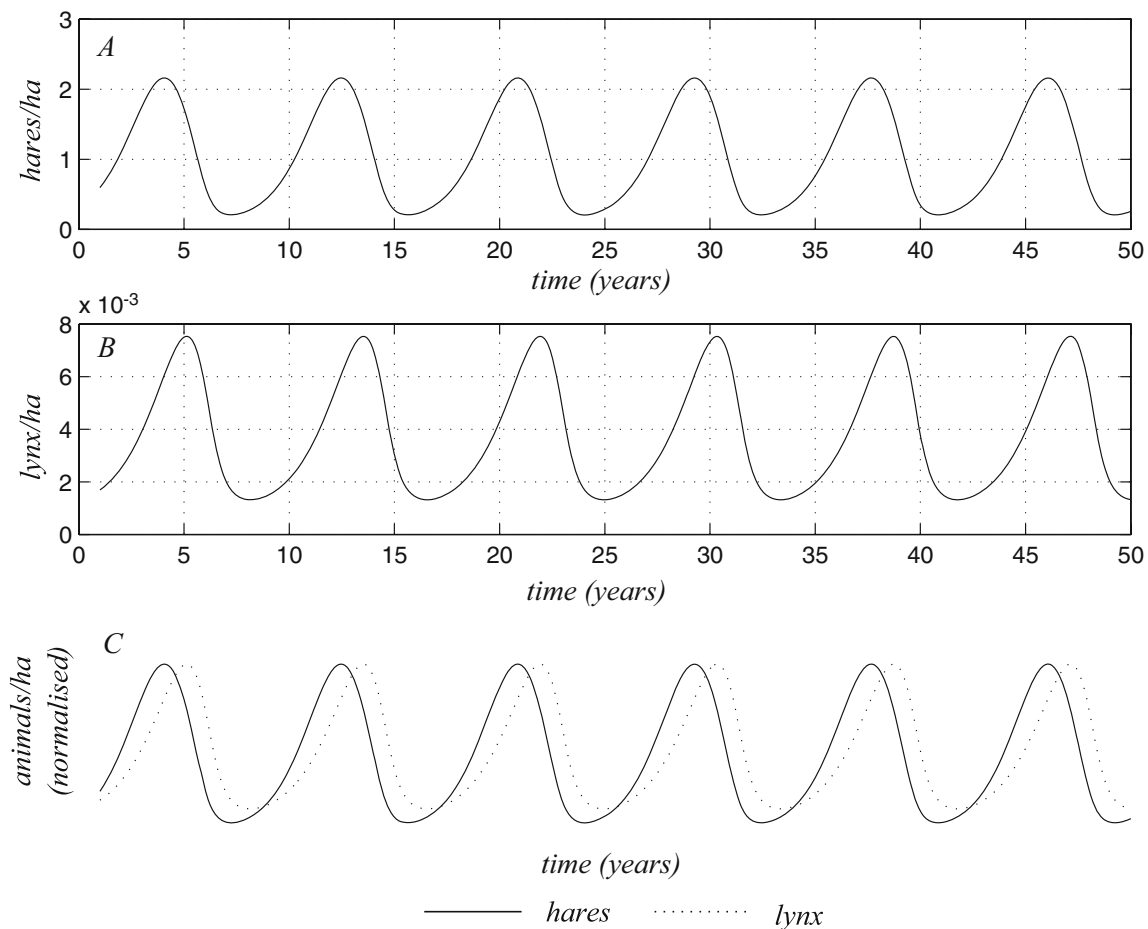
Fig. 2 Sample time series for the *basic* model. The hare and lynx time series are shown separately in **a** and **b**, respectively, and together in **c**. The hare and lynx population densities are normalised in **c** to lie between 0 and 1 so that the two time series can be easily viewed together, showing the predator lag. Parameter values are: $r = 1.75, k = 8, \gamma = 0.1, \eta = 1.25, \alpha = 505, \mu = 0.3, s = 0.85$ and $q = 212$

(Fig. 4); for all predator combinations investigated, the largest range of q values that evinces cycles is 125–300 hares/predator, and most combinations only cycled for q within 150–275 hares/predator.

In the multiple-predator *LC*, *LG* and *LCG* models, the parameters r, k, s_i and μ_i all have similar effects on model dynamics as they do in the single predator model (sensitivity results for the *LCG* model are shown in Fig. 1b; results for the *LC* and *LG* models are not shown). The model solutions respond differently, however, to changes in the parameters q_i. Increasing any of the three hare:predator equilibrium ratios, q_i, to their maximum values increased the cycle period, as in the *basic* model, but beyond this simple relationship, the three parameters affected the model in quite different ways. The hare:lynx ratio q_l is the only ratio that affected the stability of the model. The lowest estimated values for q_l led to stable equilibrium solutions in all of the multiple-predator models. In contrast, q_c and q_g

had little to no effect on the existence of limit cycle solutions, but did affect cycle amplitude. Increasing either q_c or q_g reduced cycle amplitude, with q_g having a much stronger effect than q_c. Between the default and maximum values for q_g, the cycle amplitude increased tenfold.

Comparison of model solutions to field data

The performance of each model with respect to the boreal cycles at Kluane Lake, Yukon Territory, described by Krebs et al. (2001b), is summarised in Table 2. For each model and realistic parameter values, we show the best match to the data that we were able to obtain. A match was recorded if the probe values from the simulated time series fell within the range for the natural boreal time series. The *LCG* model came closest to a
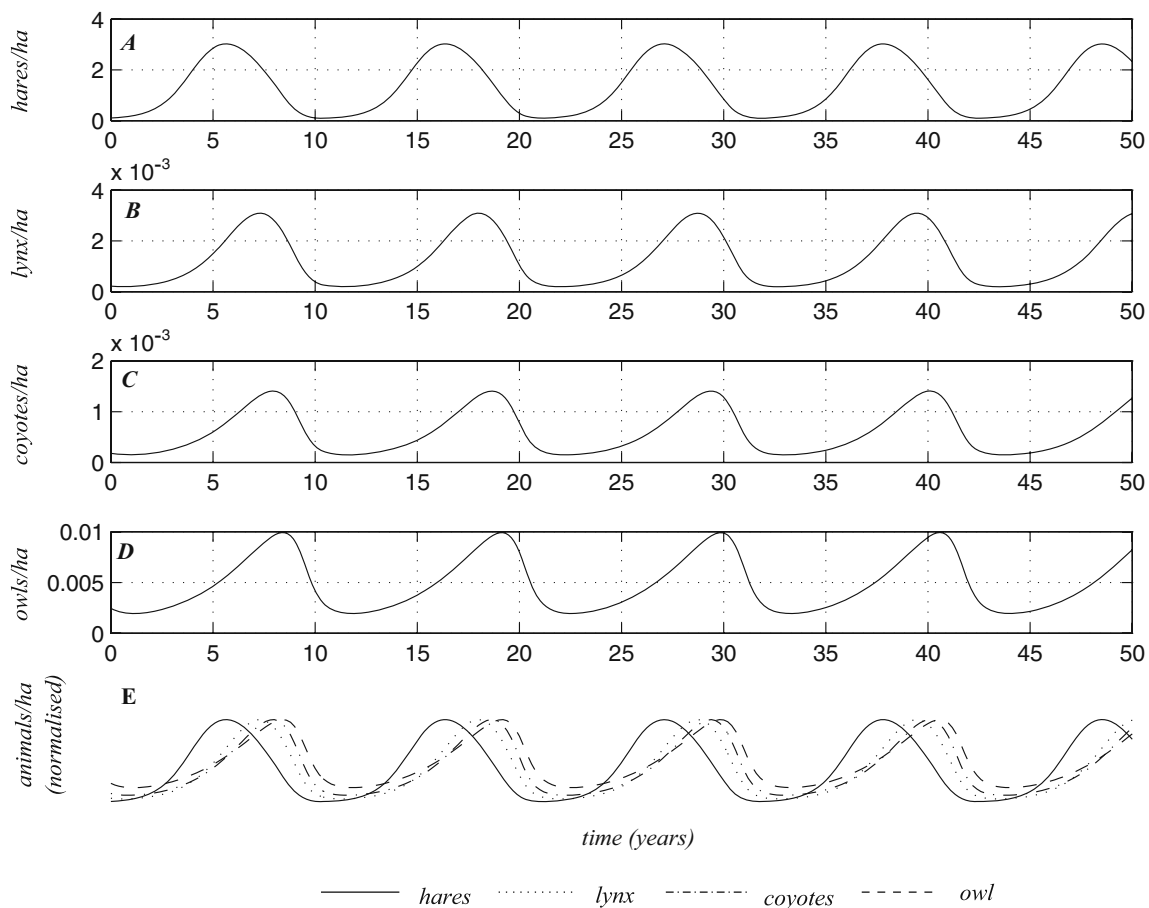
Fig. 3 Sample time series for the *LCG* model. The hare, lynx, coyote and great horned owl times series are shown separately in **a**–**d**, in that order, and together in **e**. The hare and predator populations are each normalised in **e** to lie between 0 and 1 so that the four time series can be easily viewed together, showing the separate predator lags. Parameter values are: $r = 1.75$, $k = 5$, $\eta = 1.25$, $\alpha_l = 505$, $\mu_l = 0.3$, $s_l = 0.85$, $q_l = 700$, $\alpha_c = 858$, $\mu_c = 0.8$, $s_c = 0.55$, $q_c = 1075$, $\alpha_g = 100$, $\mu_g = 0.15$, $s_g = 0.35$ and $q_g = 100$

satisfactory match to the data. We discuss the fit of each individual model below.

The *basic* model

For the *basic* model, we found that, with a single predator, the model can capture cycle period, predator lag and maximum hare densities, but fails to accurately describe minimum hare densities or predator densities at either the maximum or minimum of the cycle. As described in "The model", the single predator was either lynx or a predator complex of lynx with one or two other specialist predators. The best match to boreal cycles was obtained with the lynx:owl–hare system but, though predicted hare minimum densities were lower than in either of the other two systems, the simulated cycles could still only match cycle period and predator lag.

To obtain cyclic behaviour in the model solutions, it was necessary to keep q values within the low end of the tested range. Doing so, however, resulted in higher predator densities. For the lynx–hare model, it appears that, for lynx alone to exert sufficient predation pressure on the hare to cause population cycles at all, the population densities of lynx would have to be well above any that have been recorded throughout North America.

The *LC* and *LG* models

Consistent with our results for the *basic* model, we found that predator–prey cycles can occur with only the mammalian predators included—lynx and coyote (*LC* model)—but that hare population densities during the low phase still remain well above their observed densities. As with the *basic* model, cycles are predicted only
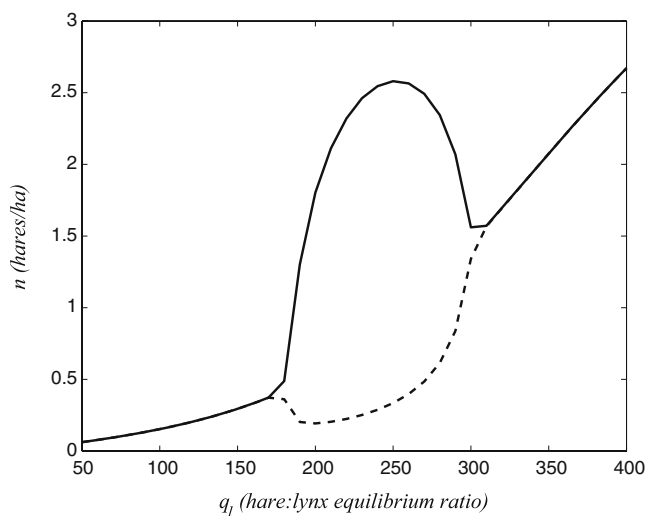
Fig. 4 Bifurcation plot showing the maximum (*solid curve*) and minimum (*dotted curve*) hare populations from the *basic* model of Eq. 1a as functions of the hare:predator equilibrium ratio q. When the two curves coalesce, the maximum and minimum are equal and the hare population is not cycling. The values of the other parameters are $r = 1.75$, $k = 8$, $\gamma = 0.1$, $\eta = 1.25$, $\alpha = 505$, $\mu = 0.3$ and $s = 0.85$

for the lowest range of hare:predator ratios, q_i. This result means that, as with the *basic* model, predator densities remain well above those observed at Kluane.

In the two predator models, we found that the range of parameter values for which the model showed cycles was larger than for any predator complex in the single-predator models. In particular, we found that we use a much wider range of plausible values for the hare:predator equilibrium ratios (q_i), and still obtain cyclic solution behaviour. Predator numbers, however, were still not fully in line with Kluane population densities.

When we analysed the model with lynx and great horned owl as the two specialist predators (*LG* model), predicted dynamics were quite different from those discussed thus far. Hare densities at all phases of the cycle were in much closer agreement with observed densities, which seems to be a result of the much lower half-saturation constant for great horned owl predation, μ_g. Great horned owl densities were in fairly close agreement with the Kluane data, but lynx densities could not be brought down to a plausible range of values.

Table 2 Summary of model fit to the cycle probes

Probe		Data[a]	Basic model				LC & LG models		LCG model
			l	l:c	l:g	l:c:g	l&c	l&g	l,c&g
Hare density (/ha)	max	1.5–2.9	√	√	×	√	√	√	√
	min	0.08–0.16	×	×	×	×	×	×	√
Pred. complex density (/100 km²)	max	varies	–	×	×	√	–	–	–
	min	varies	–	×	×	√	–	–	–
Lynx density (/100 km²)	max	30–45	×	–	–	–	×	×	√
	min	0–3	×	–	–	–	×	×	√
Coyote density (/100 km²)	max	9–30[b]	–	–	–	–	×	–	√
	min	1–5[b]	–	–	–	–	×	–	√
Owl density (/100 km²)	max	90[c]	–	–	–	–	–	√	√
	min	20[c]	–	–	–	–	–	√	√
Predator lag (years)	l	1–2	√	√	√	√	√	√	√
	c	1–2	–	–	–	–	√	–	√
	g	1–2	–	–	–	–	–	√	√
Period (years)		9–11	√	√	√	√	√	√	√
Performance									
# Dimensionless model parameters			5	5	5	5	8	8	11
# Probes to match			6	6	6	6	9	9	12
# Matched			3	3	2	5	5	7	12

Predators are denoted l (lynx), c (coyote) and g (great horned owl). Where predators are combined in a complex, the appropriate minimum and maximum predator densities are the sum of the individual maximum and minimum densities for each included species. A √ (×) appears in the table where simulation values fell inside (outside) the acceptable range defined by the data. A dash indicates that the probe was not available for that model

[a] All data values were obtained from Kluane (Krebs et al. 2001a; Boutin et al. 1995), except as noted below. The ranges of values either reflect different study areas (e.g., hare density) or the uncertainty around estimates (e.g., maximum lynx densities)

[b] Coyote density values from Kluane were supplemented with data from central Alberta (Nellis and Keith 1976) and eastern Canada (Dumont et al. 2000; Mosnier et al. 2008; Patterson and Messier 2001)

[c] It was not possible to determine data ranges for the great horned owl density, and so, only the single values measured at Kluane are reported. We accepted simulation time series as fitting the great horned owl data if the maximum values fell within 30% of the observed value, and if the minimum values fell within 10% of the observed value. These ranges are consistent, or more restrictive, than the observed ranges for the hares and other predators

The *LCG* model

The most striking difference between the *LCG* model and all of the other models is the effect of the hare:predator ratios, q_v. In the bifurcation plots (Fig. 5), we set all parameters at the default values given in Table 1 and explored how each ratio (q_l, q_c and q_g) affected the model dynamics. Limit cycle solutions are obtained for a much larger range of values than can be used for q or q_i in any of the other models. In contrast, if we use the estimated hare:predator ratios that give cycles in the *basic* model (150–250 hares/predator, with the predator being either one species or a predator complex), the *LCG* model converges to a stable equilibrium point.

The estimated ranges for the q_v parameters are quite large (see Table 1), especially for the lynx and coyote. As mentioned in "Parameter estimation", the lower bounds are determined from calculations based on energetic needs, while the upper bounds are based on observed population densities. In the *LCG* model, the larger values of q_v yield cycles of approximately 9–10 years, with predator densities and cycle lags of 1–2 years, consistent with field observations (Krebs et al. 2001a).

An exhaustive search through parameter space was not possible, due to the large number of parameters, but we found a number of different parameter sets for which the model solutions provided a satisfactory fit to the data (Table 3). In particular, with the *LCG* model,
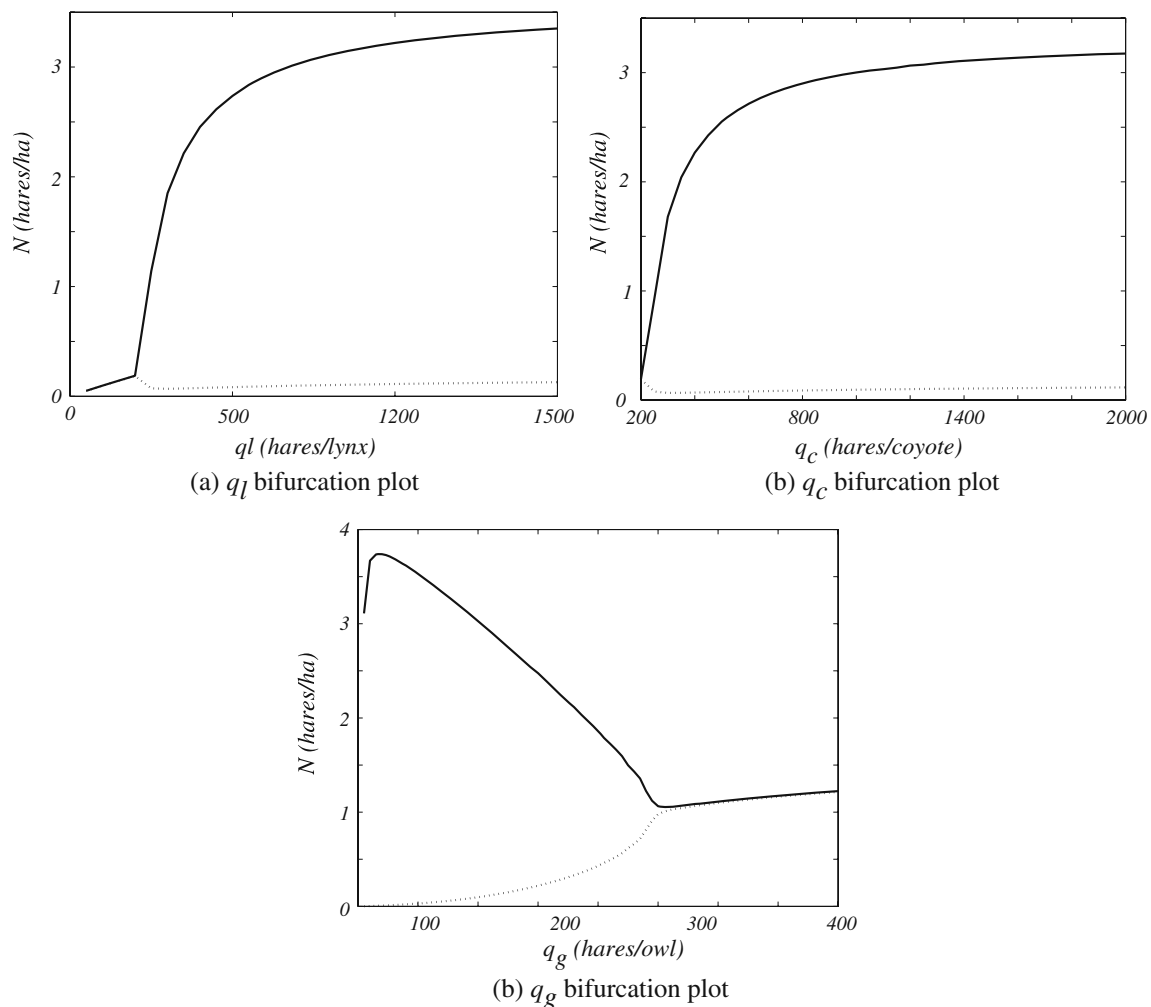

Fig. 5 Bifurcation plots for the *LCG* model showing the maximum (*solid curve*) and minimum (*dotted curve*) hare densities as functions of q_l, q_c or q_g. When the two curves coalesce, the maximum and minimum are equal and the hare population is not cycling. When not being varied, q_l, q_c and q_g were held at 700, 1,075 and 100, respectively. All other parameter values were $r = 1.75$, $k = 5$, $\gamma = 0.1$, $\eta = 1.25$, $\alpha_l = 505$, $\mu_l = 0.3$, $\alpha_c = 858$, $\mu_c = 0.8$, $\alpha_g = 100$, $\mu_g = 0.15$, $s_l = 0.85$, $s_c = 0.55$ and $s_g = 0.35$. **a** q_l bifurcation plot, **b** q_c bifurcation plot and **c** q_g bifurcation plot

Table 3 We found a number of parameter sets for which the *LCG* model yielded solutions with cycle probes that produced a satisfactory match to the data

Source		Data[a]	LCG model	
			Parameter set 1	Parameter set 2
Hare density (/ha)	max	1.5–2.9	2.4	2.2
	min	0.08–0.16	0.11	0.17
Lynx density (/100 km^2)	max	30–45	37	25
	min	0–3	3	3
Coyote density (/100 km^2)	max	9–30[b]	14	28
	min	1–5[b]	2.0	5
Owl density (/100 km^2)	max	90[c]	110	65
	min	20[c]	19	21
Predator lag (years)	lynx	1–2	1.2	1.2
	coyote	1-2	1.7	1.6
	owl	1–2	1.9	2.1
Period (years)		9–11	9.5	9.7

The probe values from two such parameter sets are shown. The model parameter values are as reported in Fig. 6 (parameter set 1) and Fig. 7 (parameter set 2)

[a] All data values were obtained from Kluane (Krebs et al. 2001a; Boutin et al. 1995), except as noted below

[b] Coyote density values from Kluane were supplemented with data from central Alberta (Nellis and Keith 1976) and eastern Canada (Dumont et al. 2000; Mosnier et al. 2008; Patterson and Messier 2001)

[c] It was not possible to determine data ranges for the great horned owl density, and so, only the single values measured at Kluane are reported. For these cases, we accepted simulation time series as fitting the great horned owl data if the maximum values fell within 30% of the observed value, and if the minimum values fell within 10% of the observed value. These ranges are consistent with, or more restrictive than, the observed ranges for the hares and other predators

it was finally possible to match the hare minimum densities, while still keeping predator numbers inside a reasonable range. The fits to cycle probes corresponding to two such parameter sets are shown in Table 3. These two parameter sets are quite different, and illustrate the type of cyclic behaviour that can be obtained with the *LCG* model.

The role of each specialist predator

The *LCG* model allows us to explore the different effects of predation by lynx, coyote and great horned owl. Using the parameter values identified in "Parameter estimation", our model predicts that great horned owl predation is particularly important. While the lynx and coyote predation parameters have relatively minor effects on cycle amplitude and period, the parameters relating to great horned owl predation are much more significant. This result can be explained in terms of the magnitude of great horned owl predation at low prey densities. The predation characteristics of the great horned owl, as captured in the parameters α_g and μ_g, are very different from those of the other two specialist predators. The saturation killing rate (α_g) is significantly lower than that of either the lynx or the coyote. This means that, at high hare densities, great

horned owls cause less hare mortality, per capita, than either lynx or coyotes. The much higher population of great horned owls, however, counteracts this effect. More importantly, the half-saturation constant (μ_g) is lower than the associated parameter for the lynx and coyote. Consequently, the great horned owl can cause significant mortality at low hare population densities. In our model, this owl predation is what makes the snowshoe hare population lows drop to the numbers observed at Kluane.

This result suggests that the great horned owl is a very different sort of predator from the lynx or coyote. The total response of each predator is given by

$$TR_i = \frac{\alpha_i N P_i}{N + \mu_i} \qquad (4)$$

and is a measure of the number of hares killed per hectare per year by each predator class (lynx, coyote, great horned owl). The difference between the great horned owl and other predators is evident when we consider the predation fraction, the proportion of hare deaths by predation that are due to a particular predator:

$$\Phi_i = \frac{TR_i}{\sum_j TR_j}, \qquad (5)$$

where j is summed over all predators in the model. Predation impact for each predator is obtained by taking the total response for that predator and dividing by hare density:

$$\Psi_i = \frac{TR_i}{N}. \tag{6}$$

Plots of predation fraction and predation impact as functions of hare density are shown for two different sets of parameters in Figs. 6b and 7b. The figures show predation fraction and predation impact over one period and, since the cycles are not perfectly symmetric, each curve appears as a closed loop rather than a single curve. Both of these parameter sets yield cycles that provide a reasonable match to the cycle probes (Table 3). Indeed, a large number of parameter sets were found that provided a satisfactory fit to the data; these two were chosen for illustrative purposes. From the figures, we see that what distinguishes great horned owl predation from lynx and coyote predation is the behaviour at low hare densities. Whereas the curves for lynx and coyote predation impact have positive slopes for low hare densities, the great horned owl predation impact has a negative slope.

This result is due directly to the form of the functional response of the specialist predators. The effect of the Holling Type II response is easily seen if we consider the dimensionless equations (Eq. 3) and compute the change in predation impact with changes in hare density.

When there are two predators, the slope of the predation impact curve for predator i is given by

$$\frac{d\Phi_i}{dn} = \left(1 + \frac{\alpha_j^* p_j (n + \mu_i^*)}{\alpha_i^* p_i (n + \mu_j^*)}\right)^{-2} \left(\frac{\mu_i^* - \mu_j^*}{(n + \mu_j^*)^2}\right), \tag{7}$$

where j indicates the other predator in the model. Since all of the parameters and variables are nonnegative, we immediately conclude that the sign of $d\Phi_i/dn$ is given by

$$\text{sgn}\left(\frac{d\Phi_i}{dn}\right) = \text{sgn}(\mu_i^* - \mu_j^*) = \text{sgn}\left(\frac{\mu_i}{k} - \frac{\mu_j}{k}\right)$$
$$= \text{sgn}(\mu_i - \mu_j),$$

and that it does not change with prey density, n. For the lynx, coyote and great horned owl parameters (Table 1), we generally have

$$\mu_g < \mu_l < \mu_c, \tag{8}$$

though, at the lowest and highest possible values of μ_l and μ_g, respectively, there is possible overlap in the
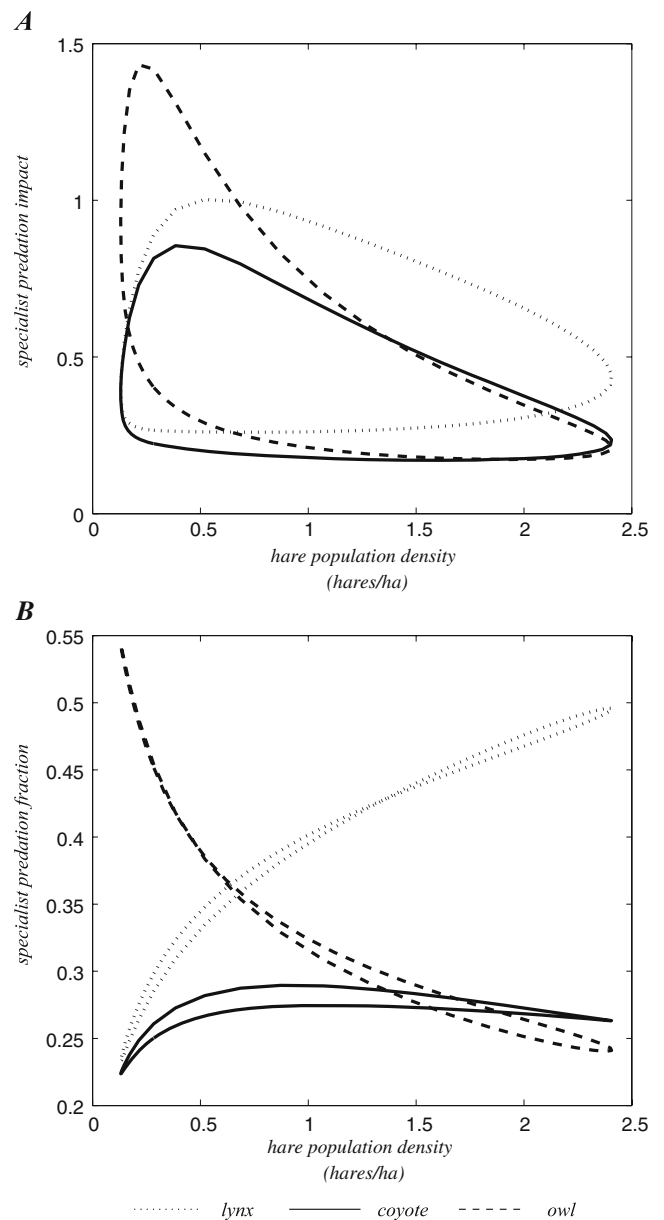

Fig. 6 Phase plane plots of the **a** specialist predation impact (defined in Eq. 6) and **b** specialist predation fraction (defined in Eq. 5) vs hare density for the *LCG* model. The predation impact curves (**a**) all have similar shape, though the great horned owl predation impact is smaller than the predation impact of lynx or coyote for large hare densities, while the opposite is true at low hare densities. The predation fraction curves (**b**) behave quite differently. These curves highlight the relative importance of each specialist. The lynx and coyote predation fraction curves have a slope that decreases as hare density decreases, while the great horned owl predation fraction *increases*. Parameter values are $k = 5$, $r = 1.75$, $\gamma = 0.1$, $\eta = 1.25$, $\alpha_l = 400$, $\alpha_c = 800$, $\alpha_g = 70$, $\mu_l = 0.3$, $\mu_c = 0.4$, $\mu_g = 0.1$, $s_l = 1$, $s_c = 0.6$, $s_g = 0.5$, $q_l = 500$, $q_c = 1100$ and $q_g = 100$. *Dotted lines*, lynx; *solid lines*, coyote; *broken lines*, owl
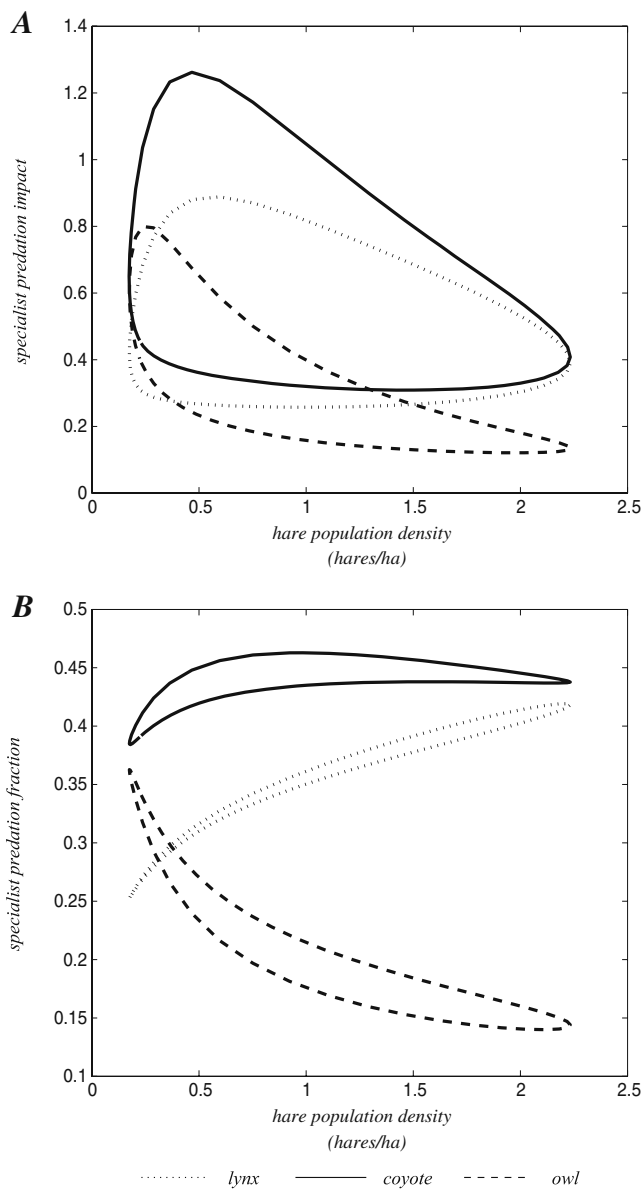
the field data, and so we assume that Eq. 8 holds. In this case, we see that, in the *LC* model, we have

$$\frac{d\Phi_c}{dn} > 0, \qquad \frac{d\Phi_l}{dn} < 0, \tag{9}$$

while in the *LG* model, we have

$$\frac{d\Phi_l}{dn} > 0, \qquad \frac{d\Phi_g}{dn} < 0. \tag{10}$$

Consequently, in the *LC* model, the predation impact of coyotes decreases as n decreases, while in the *LG* model, the predation impact of great horned owls *increases* as n decreases. Thus, the great horned owl is a more important predator at low hare densities. The predation impact of lynx varies depending on the model (*LC* or *LG*).

When there are three predators, the slope of the predation impact curve is given by

$$\frac{d\Phi_i}{dn} = \frac{1}{\alpha_i^* p_i} A B, \tag{11}$$

where

$$A = \left(1 + \frac{\alpha_j^* p_j}{\alpha_i^* p_i} \frac{(n + \mu_i^*)}{(n + \mu_j^*)} + \frac{\alpha_k^* p_k}{\alpha_i^* p_i} \frac{(n + \mu_i^*)}{(n + \mu_k^*)}\right)^{-2}, \tag{12}$$

$$B = \left(\frac{\alpha_j^* p_j (\mu_i^* - \mu_j^*)}{(n + \mu_j^*)^2} + \frac{\alpha_k^* p_k (\mu_i^* - \mu_k^*)}{(n + \mu_k^*)^2}\right). \tag{13}$$

The sign of A is always positive, and so the sign of $d\Phi_i/dn$ depends only on the sign of B. When Eq. 8 holds, we immediately have

$$\frac{d\Phi_c}{dn} > 0, \qquad \text{and} \qquad \frac{d\Phi_g}{dn} < 0. \tag{14}$$

Thus, the two-predator and three-predator models predict the same predation impact slopes (compare Eqs. 9 and 10 with Eq. 14) for coyotes and great horned owls. The sign of $d\Phi_l/dn$ is less clear, as it is composed of the sum of a positive term $(\alpha_g^* p_g(\mu_l^* - \mu_g^*)/(n + \mu_g)^2)$ and a negative term $(\alpha_c^* p_c(\mu_l^* - \mu_c^*)/(n + \mu_c)^2)$. Furthermore, it is possible that, for some parameter values, the sign will change throughout the n cycle. In our model, lynx respond to changing hare densities in different ways depending on current hare density. For the other two predators, however, it is clear that the predation impact of the coyote decreases as n decreases, but that the predation impact of the great horned owl *increases* as n decreases.

This result is drawn entirely from the predation term in the prey equation. Therefore, any predator–prey model in which specialist predation appears as a Holling type II functional response will predict an increase in great horned owl predation impact at low

Fig. 7 Phase plane plots of the specialist predation impact (**a**) (defined in Eq. 6) and specialist predation fraction (**b**) (defined in Eq. 5) vs hare density for the *LCG* model. For this parameter set, the predation impact curves again have similar shape, and the great horned owl predation impact increases in importance as hare density decreases, though remaining below the lynx and coyote curves. This pattern is illustrated in the predation fraction curves (**b**). Again, the lynx and coyote predation fraction curves have a slope that decreases as hare density decreases, while the great horned owl predation fraction *increases*. Parameter values are $k = 5$, $r = 1.75$, $\gamma = 0.1$, $\eta = 1.25$, $\alpha_l = 505$, $\alpha_c = 550$, $\alpha_g = 70$, $\mu_l = 0.3$, $\mu_c = 0.4$, $\mu_g = 0.15$, $s_l = 0.9$, $s_c = 0.6$, $s_g = 0.35$, $q_l = 700$, $q_c = 500$ and $q_g = 150$. *Dotted lines*, lynx; *solid lines*, coyote; *broken lines*, owl

lynx and great horned owl parameters such that $\mu_l \leq \mu_g$. In this range of parameter values, however, we did not find any model solutions that satisfactorily matched

prey densities (assuming $\mu_g^* < \mu_i^*$, where i is in the set of other predators in the model). A series of plausible predator–prey (single predator) models are presented in Turchin (2003), and all of them model specialist predation as a Holling type II functional response.

Discussion

We examined the solution behaviour of a series of predator–prey models for the snowshoe hare population cycles in the boreal forest. Our models incorporated one, two or three separate specialist predators, including the lynx, coyote and great horned owl. We found that, by including three separate specialist predators (the *LCG* model), we were able to obtain hare–predator cycles that matched several cycle probes, namely, the period, predator lag and maximum and minimum population densities for hares and each specialist predator. The single specialist predator model (the *basic* model) and models of two specialist predators (the *LC* and *LG* models) did not provide acceptable quantitative descriptions of the hare cycle. Our model is the first to provide a quantitative match to cycle probes that include peak and low densities. Although low densities can be difficult to estimate accurately from field data (Mills et al. 2005), all of the snowshoe hare density estimates were based on reliable mark-recapture live-trapping (Boulanger and Krebs 1996), thus providing high-quality information about this important phase of the cycle. Our model is the first to capture the very low minimum hare densities observed in the boreal forest near Kluane Lake (Hodges et al. 1999).

With each additional specialist predator, we have four more parameters at our disposal, but only three more cycle probes to match (the lag and maximum and minimum densities for each new specialist). Thus, one could argue that the improved fit is simply due to having more parameters available (Ginzburg and Jensen 2004). When counting parameters, however, the relevant equations are the dimensionless ones. In Eq. 3, each new predator introduces just three new parameters (s_i^*, β_i^* and μ_i^*). Thus, for each new predator, the number of new probes matches the number of new parameters. In addition, each new parameter is constrained to the appropriate biologically plausible range. Also, for the bulk of our investigations, we treated the generalist predation parameters as fixed, leaving us with just three, six and nine parameters (in the *basic*, two-predator and three-predator models, respectively). Altogether, these constraints suggest that the better

match between the *LCG* model and field data is not due simply to additional degrees of freedom.

In the multiple-predator models, we made the important discovery that, without a predator with a very low half-saturation constant, such as the great horned owl, hare numbers in the model never reach lows that are close to those observed in real systems. While the lynx alone, or the lynx and coyote in combination, can provide sufficient predation mortality to cause population cycles in the lynx–hare or lynx:coyote–hare systems, the hare:predator ratios must be well below the lowest hare:predator ratios calculated from population densities observed at Kluane. With the addition of the great horned owl to the model, we have a predator with a hare:predator ratio that is realistically within a low range, and therefore, the hare:predator ratios for the lynx and coyote can be increased to the more realistic values for these mammals, with the model still predicting stable limit cycles. This result suggests that the great horned owl is a necessary component in any complete description of the snowshoe hare cycle. Field work on great horned owls in Kluane (Rohner et al. 2001) also suggests that the great horned owl may be an important specialist predator, especially at low hare population densities.

Contrary to previous work with predator–prey systems (Sokol-Hessner and Schmitz 2002), we found that, for our series of models, a single-predator complex is not equivalent to modeling each individual predator separately. The cycles obtained from the *basic* model with the lynx:coyote:owl predator complex provided the best single-predator model match to the Kluane data, producing reasonable cycle period, predator maximum density, predator minimum density and prey maximum density, but could not match the prey minimum density observed in the field. The same was true of the *LC* and *LG* models. It was only with the *LCG* model that we were able to match all of the cycle probes we considered. This result is due to the differences in the predators' nonlinear response to prey levels. Our result is an argument in favour of more complex predator–prey models in situations where the predators respond differently to prey densities.

Looking more closely at the role of each specialist predator in shaping the hare cycle, we found that the coyote predation impact decreases as hare density decreases, while the great horned owl predation impact *increases* as hare density decreases. For the parameter values that worked best, we found that lynx predation impact also tended to decrease with hare density. Thus, our model suggests that the great horned owl is a very different predator. Indeed, in our model, it is the increased great horned owl predation impact at low hare

densities that drives the hare minima to appropriately low levels. This pattern is due directly to the fact that, in Eqs. 1a and 2a, we modeled predation by each specialist predator as a Holling type II functional response (Holling 1965), a form widely accepted in the ecological literature (Turchin 2003). Other functional forms for specialist predation have been suggested (Turchin 2003), but the Holling type II is generally preferred, as it has a strong mechanistic connection to the predation process.

The field data regarding predation impact are contradictory. The importance of raptor predation has been noted by researchers (Hanski and Korpimäki 1995; Korpimäki and Norrdahl 1991a, b) studying rodent population cycles, and dietary data gathered from owl pellets at Kluane (Rohner et al. 2001) suggest that the great horned owls have increasing predation impact at low hare densities. This research supports the model results we present here. In contrast, mortality data from radio-collared hares gathered at Kluane (Hodges et al. 2001) do not show this pattern in predation impact. Part of the problem in interpreting these field data is that, at low numbers of hares, sample sizes for either method become quite small and our confidence in the estimates is lower than when hare densities are high. Given the contradictory field data, we are uncertain how well the model matches the genuine predation pattern at low hare density.

We have achieved our goal of developing a model of the Canada lynx and snowshoe hare cycle that provides a good match to the period, predator lags, minimum and maximum prey densities and minimum and maximum densities for each predator. An important next step in our research is to repeat the investigation performed here with other plausible predator–prey models (Strohm and Tyson 2009). We will then be able to draw more general conclusions about the importance of additional specialist predators to the hare population cycle.

In this paper, we were particularly interested in capturing the population density cycles and in understanding the separate roles of the lynx, coyote and great horned owl. We note here that the cycles produced by our model also show the asymmetry typical of the boreal forest cycles (troughs are longer than peaks), but not the irregularity in peak densities. Recent work (Stone and He 2007) with tritrophic models based on Rosensweig–MacArthur interaction terms (without generalist predation) shows that these can have a property called "uniform phase-growth and chaotic amplitude" (UPCA) that captures both cycle asymmetry and irregular peak densities. It is possible that UPCA cycles are a fundamental property of the lynx–hare cycles.

Our contribution in this paper is to show that, under one plausible modelling framework (Eq. 2), the lynx, coyote and great horned owl each play a crucial role in the population dynamics of the Canada lynx and snowshoe hare.

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