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Evaluation of predator numerical responses

Jim Hone[A,E], *Charles Krebs*[A,B], *Mark O'Donoghue*[B,C] *and Stan Boutin*[D]

[A]Institute for Applied Ecology, University of Canberra, Canberra, ACT 2601, Australia.
[B]Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
[C]Department of Environment, PO Box 310, Mayo, Yukon Y0B 1M0 Canada.
[D]Department of Biological Sciences, University of Alberta, Edmonton, AL T6G 2E9, Canada.
[E]Corresponding author. Email: Jim.Hone@canberra.edu.au

Abstract. We evaluated hypotheses of the dynamics of predators (lynx) relative to prey (snowshoe hares) and predator abundance in the Yukon, Canada. The hypotheses were that predator (lynx) dynamics are influenced by prey density, or by both prey and predator densities. Annual lynx population growth rate (r), estimated from lynx counts, was positively related to previous hare density and negatively related to previous lynx density, as described by the best-fitting additive model ($R^2 = 0.85$). Annual lynx growth rate (r) estimated from lynx tracks was positively related to the ratio of hares per lynx in the best-fitting model ($R^2 = 0.55$). There was most support for the prey- and predator-dependent hypothesis of predator dynamics. Projected lynx tracks showed similar trends to observed abundance but lagged one year, emphasising the need for evaluation of projected predator trends.

Introduction

Many studies of herbivore and predator dynamics have estimated a numerical response, defined here as the relationship between annual instantaneous population growth rate (r) and food availability (Caughley 1977; Bayliss 1987; Sibly and Hone 2002). Examples of such forms of the numerical response for predators include red fox (*Vulpes vulpes*) eating rabbits (*Oryctolagus cuniculus*) in Australia (Pech and Hood 1998) and barn owls (*Tyto alba*) eating field voles (*Microtus agrestis*) in Scotland (Hone and Sibly 2002). A different form of numerical response of lynx (*Lynx canadensis*) to snowshoe hares (*Lepus americanus*) in Canada has been described (Boutin *et al*. 1995; O'Donoghue *et al*. 1997) although that response described a relationship between lynx density and hare density, not between lynx r and hare density. It is the latter approach that is investigated here.

Predators such as lynx and prey such as snowshoe hares in North America show 9–10-year cycles in abundance. Fur data obtained from trappers comprise much of the long-term data on lynx cycles and dynamics (Elton and Nicholson 1942; Akcakaya 1992; Royama 1992; Stenseth *et al*. 1997). It is often assumed that trends in such data reflect real trends in predator populations (Royama 1992). While trends in the fur data probably broadly reflect real trends, the analysis and interpretation of predator datasets would be simpler if data reflecting real trends could be used, and that is the approach used here.

Predator dynamics may be influenced by prey density or by both prey and predator densities. These hypotheses are represented here by a range of prey-dependent and ratio-dependent (Abrams and Ginzburg 2000) models and evaluated using field data. The combined prey-and-predator hypothesis could be formulated as ratio-dependent or additive models. Both approaches are investigated in this study.

We aimed to evaluate the predator–prey hypotheses using six models of predator numerical responses relating predator annual r and prey density, and predator annual r and prey and predator densities. An aspect of model selection, calibration versus projection, is also examined. The predator is the lynx and the prey is the snowshoe hare; however, the results are used to examine general issues in predator–prey dynamics.

Materials and methods

Modelling

We selected a set of candidate numerical response models (Table 1) based both on published models and a new model derived here. The candidate models are alternative hypotheses in the sense of Chamberlin (1965) and as described for alternative hypotheses of rodent cycles (Turchin and Hanski 2001) and alternative numerical responses of mice (Ruscoe *et al*. 2005). The models are simple deterministic, non-demographic and non-spatial models. The models are whole-of-population models, in contrast to those of Akcakaya (1992), King and Schaffer (2001) and Choquenot *et al*. (2001), which are based on effects of food (hares) on demographic rates. The models used here have few parameters, as suggested generally by Ginzburg and Jensen (2004). This is needed in this study as the dataset is small. The models are described here in words and equations (Eqns 1–6), and are shown diagrammatically in Fig. 1. Hence, Fig. 1 shows the models as hypotheses and does not show any data.

Model 1 is the linear numerical response model, which is a simple positive relationship between lynx annual r ($= \ln(L_t/L_{t-1})$) and prey density (H_{t-1}) (Fig. 1*a*) and is the original described by Lotka and Volterra (Pielou 1969; May 1981). The equation for the first model was

$$r = -a + bH_{t-1}. \qquad (1)$$

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The linear numerical response was a good description of the dynamics of barn owls to field vole (Hone and Sibly 2002). Ideally, such a model should have a maximum population growth rate (Berryman *et al.* 1995); however, this model has no such maximum. The model is a representation of the Stenseth *et al.* (1997) hypothesis of the dependence of predator dynamics on prey abundance. Note that all subsequent models are representations of the hypotheses (Akcakaya 1992) of prey and predator effects on predator dynamics.

Model 2 is an additive model that assumes a linear, positive effect (Fig. 1*b*) of prey (H_{t-1}) and a linear, negative effect of density (L_{t-1}) on lynx annual *r* (Pielou 1969; Sinclair and Krebs 2001, table 3.1). The equation for the second model was

$$r = aH_{t-1} - bL_{t-1}. \tag{2}$$

The model assumes no intercept. Model 3 is the second model (Fig. 1*b*) but with an intercept and assumes a threshold density of hares for a lynx population to occur (i.e. $r = 0$, $L^* = 0$, then $H^* = -a/b$). The equilibrium threshold is a mathematical property of the model. It is not implied that a lynx population would stay at such an equilibrium for any great length of time. The equation, after Pielou (1969, p. 71), was

$$r = a + bH_{t-1} - cL_{t-1}. \tag{3}$$

The parameters a and c have been described as relating to predator dynamics in the absence of the favoured prey (H = 0) (Pielou 1969, p. 71). Both the second and third models have no maximum growth rate. Model 3 is a version of the density-dependence–rainfall model of Dennis and Otten (2000), although here has a term for food (H) rather than rainfall.

Model 4 is a ratio model (positive ratio) and it assumes a linear, positive effect (Fig. 1*c*) of prey per predator (H_{t-1}/L_{t-1}). The equation of the fourth model was

$$r = -a + b(H_{t-1}/L_{t-1}). \tag{4}$$

The equation is recognised as a linear approximation of a relationship expected to be a curve (concave down) with a maximum. The positive ratio model is a whole-of-population model. In contrast, the ratio model of Akcakaya (1992) assumed that predator fecundity was positively related to the ratio of prey per predator.

Model 5 (negative ratio) was a form of the ratio model (Leslie 1948; Pielou 1969, pp. 72–74) described for wolves (*Canis lupus*) and moose (*Alces alces*) in North America (Eberhardt and Peterson 1999), for ferrets (*Mustela furo*) and rabbits in New Zealand (Barlow and Norbury 2001) and for least weasel (*Mustela nivalis*) and field vole in Scandinavia (Hanski *et al.* 2001). The equation used here was

$$r = r_m - r_m J(L_{t-1}/H_{t-1}) \tag{5}$$

which describes a negative, linear relationship between lynx annual *r* and the ratio of predators per prey (L_{t-1}/H_{t-1}) (Fig. 1d) and a positive, curved (concave down) relationship between *r* and prey per predator (H_{t-1}/L_{t-1}). Model five has a maximum growth rate (r_m) and satisfies that condition described by Berryman *et al.* (1995). At equilibrium ($r = 0$), parameter $J = H_{t-1}/L_{t-1}$.

Model 6 is based on a Gompertz equation and was derived as follows. The Gompertz equation is a density-dependent model describing a curved (concave up) relationship between *r* and predator density (L_{t-1}) (May *et al.* 1974). That is, $r = -\beta\ln(L_{t-1}/K)$. It is assumed that lynx carrying capacity (K) is proportional to prey density; that is, $K = cH_{t-1}$. A similar assumption was made in a study of wolf dynamics (Eberhardt and Peterson 1999). Substituting that into the Gompertz equation and rearranging gives

$$r = \beta\ln c + \beta\ln(H_{t-1}/L_{t-1}). \tag{6}$$

The equation describes a positive curved (concave down) relationship between lynx annual *r* and the prey/predator ratio (H_{t-1}/L_{t-1}) (Fig. 1e) with a coefficient of β reflecting the efficiency of converting food (hares) into predator population growth. At high levels of prey per predator, the growth rate *r* is high although it increases at a decreasing rate and does not have a maximum. Hence the model does not satisfy that condition of models described by Berryman *et al.* (1995). In between very

Table 1. The goodness of fit of models of annual growth rate (*r*) of a lynx population

All models had three parameters, except for the additive with intercept model, which had four. RSS = residual sums of squares, R^2 = coefficient of determination, and w_i are Akaike weights. The best models for each dataset are shown in bold

Model	RSS	R^2	AIC_c	ΔAIC_c	w_i
Lynx counts					
Linear (Model 1)	3.193	0.13	1.475	15.791	0.000
Additive (Model 2)	**0.552**	**0.85**	**–14.316**	**0**	**0.805**
Additive with intercept (Model 3)	0.549	0.85	–7.177	7.139	0.023
Positive ratio (Model 4)	0.823	0.78	–10.724	3.592	0.134
Negative ratio (Model 5)	2.088	0.43	–2.348	11.968	0.002
Modified Gompertz (Model 6)	1.096	0.70	–8.146	6.170	0.037
Lynx tracks					
Linear (Model 1)	3.613	0.10	2.586	6.112	0.017
Additive (Model 2)	1.978	0.44	–2.836	0.690	0.250
Additive with intercept (Model 3)	1.829	0.39	3.659	7.185	0.010
Positive ratio (Model 4)	2.722	0.32	0.037	3.563	0.059
Negative ratio (Model 5)	1.882	0.53	–3.284	0.242	0.312
Modified Gompertz (Model 6)	**1.832**	**0.55**	**–3.526**	**0**	**0.353**

low and very high values of the ratio H_{t-1}/L_{t-1} is an equilibrium ($r = 0$).

The Ivlev (Ruscoe *et al.* 2005) and Mitscherlich (McCarthy 1996) non-linear numerical response models have a maximum population growth rate and were investigated here. However, no valid parameter estimates were obtained because the computer software could not achieve convergence. Hence the models were not considered further. Given those outcomes, more complex numerical response models with more parameters were not investigated.

In summary, the models capture the distinction between prey-dependent and prey-and-predator-dependent hypotheses of predator (lynx) dynamics and are represented in Fig. 1. The linear numerical response and the ratio models (positive, negative and modified Gompertz) capture the distinction between prey-dependent and ratio-dependent models of the type reviewed by Abrams and Ginzburg (2000).

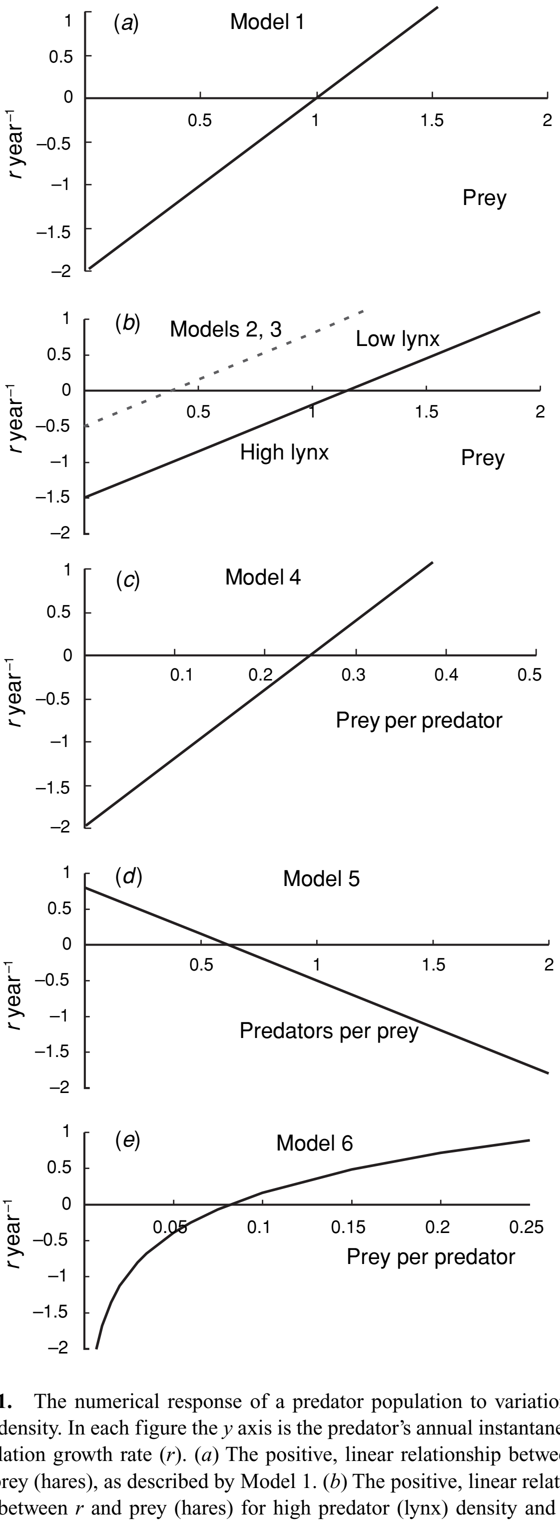

Fig. 1. The numerical response of a predator population to variation in prey density. In each figure the *y* axis is the predator's annual instantaneous population growth rate (r). (*a*) The positive, linear relationship between r and prey (hares), as described by Model 1. (*b*) The positive, linear relationship between r and prey (hares) for high predator (lynx) density and low predator (lynx) density, as described by the additive model (Model 2), and the additive model with intercept (Model 3). (*c*) The positive, linear relationship between r and prey (hares) per predator (lynx), as described by the positive ratio model (Model 4). (*d*) The negative, linear relationship between r and predator (lynx) density per unit of prey (hares), as described by the negative ratio model (Model 5). (*e*) The positive, curved relationship between r and the natural logarithm of prey (hares) per predator (lynx), as described by the modified Gompertz model (Model 6).

Study methods

We obtained data on lynx and snowshoe hare density in the Kluane area in the Yukon, Canada (Krebs *et al.* 2001). Population density of lynx per 100 km^2 was estimated by assessment of snow tracks and intensive radio-tracking of lynx as described by O'Donoghue (1997) and O'Donoghue *et al.* (2001). The lynx data were for winter (November to March inclusive) for an area of 350 km^2. Lynx count data comprised one complete lynx cycle (1987–95). We estimated snowshoe hare density per hectare by mark–recapture using the jackknife estimator as described by O'Donoghue *et al.* (1997). The hare data were for autumn (October to November inclusive) and are the mean for 3–4 sites in 1987–95 and 2 sites in 1996–2004. The hare study sites included the habitats that occurred across the region and included the habitats of the larger lynx study area. The area of each site was 1 km^2.

We also obtained data on lynx from tracks in snow. These are indices of lynx abundance and O'Donoghue *et al.* (2001) reported a significant positive correlation (correlation coefficient = 0.95) between the counts of lynx and lynx tracks. The track data used here were calculated slightly differently from those used by O'Donoghue *et al.* (2001), but the track data and count data used in the present study were still highly correlated (correlation coefficient = 0.82, d.f. = 7, $P = 0.007$) during the years 1987–95 inclusive. The tracks were counted along a 25-km transect that crossed the study area during each winter (October to March inclusive), on days after fresh snowfall (O'Donoghue *et al.* 2001). The data are expressed as the mean lynx tracks per track night per 100 km. The track data were divided into two sets, namely 1987–95 inclusive for calibration and 1996–2004 inclusive for projection and evaluation of the best models from the calibration phase. The first lynx cycle was slightly shorter (8 years) when estimated from tracking data compared with count data (9 years). To avoid confounding data type and sample size, the same period (9 years) was used for each dataset.

Analysis

We estimated lynx (L) annual instantaneous population growth rate (r) as $\ln(L_t/L_{t-1})$ (Caughley 1977). Lynx count data and, separately, lynx track data were used to calibrate the models and assess model fit for the period 1987–95 inclusive. Lynx track data for the second period (1996–2004 inclusive) were used to evaluate the accuracy of projected lynx density. That is, we estimated lynx density one year ahead (Year *t*), based on the observed lynx and hare density both in Year *t*–1.

The analysis described here uses data collected at different spatial scales. The lynx density was estimated over 350 km^2 and hares over >2–4 km^2; however, the habitats in the various areas were similar. If hares and lynx densities are synchronous over large areas, as has been reported (Krebs *et al.* 2001), then the different scales should not bias the results.

The parameters in each model were estimated by least-squares regression analysis using SAS version 8.2 (Freund and Little 1986). Model fit was assessed by Akaike's Information Criterion corrected for small sample size (AIC$_c$), which was calculated by using the estimated residual sums of squares and estimated number of parameters (Burnham and Anderson 2002). Models with $\Delta\text{AIC}_c > 4$ are considered to have considerably less support than models with $\Delta\text{AIC}_c < 2$ (Burnham and Anderson 2001, 2002; Richards 2005). Akaike weights (w_i) were estimated and interpreted as strength of evidence (Burnham and Anderson 2002). We compared observed and projected (one year ahead) lynx track counts during the second lynx cycle (1996–2004 inclusive) by a paired *t*-test assuming a mean difference of zero between observed and projected lynx track counts, and also by regression analysis.

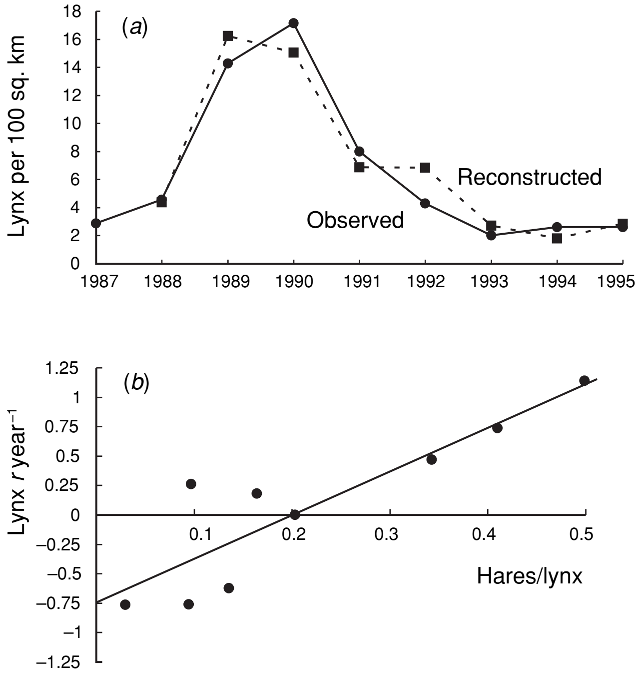

Fig. 2. (*a*) Trends in lynx density per 100 km^2. The solid line and dots show the observed density, and dotted line and squares show reconstructed (1988–95 inclusive) density. The reconstructed density was estimated using the additive model with no intercept (Eqn 7). Year 1987 refers to the winter of 1987–88. (*b*) The observed data (solid circles) and fitted relationship (positive ratio model) between lynx annual instantaneous growth rate (r) and the ratio of hares (per hectare) per lynx (per 100 km^2). The data are from 1987–95 inclusive.

Results

Lynx density, as assessed by count data, peaked in the winter of 1990–91 (Fig. 2*a*). The model with the lowest AIC$_c$ was the additive model with no intercept (Table 1).

The fitted additive model with no intercept was

$$r = 0.817\text{H}_{t-1} - 0.131\text{L}_{t-1} \qquad (7)$$

and shows a positive effect of food (hares) and a negative effect of predators (lynx). The standard errors (SE) of the coefficients were 0.132 (t = 6.18, P < 0.0005) and 0.021 (t = –6.00, P < 0.0005) respectively, showing that both coefficients were highly and equally significant. The regression was highly significant (F = 20.02, d.f. = 2, 7, P = 0.0013, R^2 = 0.85). The additive model reconstructed aspects of the observed lynx dynamics during 1988–95 inclusive (Fig. 2*a*); however, the reconstructed peak in the lynx cycle was one year earlier than that actually observed (Fig. 2*a*), and the reconstructed trough in lynx counts was one year after the observed trough (Fig. 2*a*).

The second-lowest AIC$_c$ was the positive ratio model (Fig. 2*b*) with ΔAIC_c of 3.592 (Table 1). There is no obvious trend in the data towards a maximum value of lynx annual r. The other models differed substantially from the best model ($\Delta\text{AIC}_c > 6$) (Table 1).

The lynx track counts showed cycles in abundance of lynx similar to those shown by the lynx count data. In both datasets lynx abundance in the first cycle peaked in 1990 and was at a low in 1993. Analysis of the lynx track data showed that the

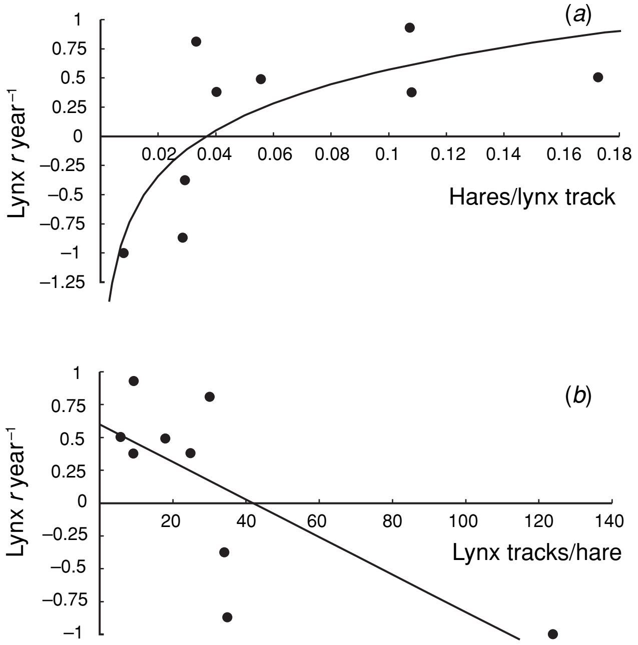

Fig. 3. (*a*) The observed data (solid circles) and fitted relationship (modified Gompertz model in Eqn 8) between lynx annual instantaneous growth rate (r) and the ratio of hares per lynx track (hares per hectare/lynx tracks per night per 100 km). The data are from 1987–95 inclusive. (*b*) The observed data (solid circles) and fitted relationship (negative ratio model in Eqn 9) between lynx annual instantaneous growth rate (r) and the ratio of lynx tracks per hare. The data are from 1987–95 inclusive.

model with the lowest $\mathrm{AIC_c}$ was the modified Gompertz model (Table 1). The fitted relationship (Fig. 3*a*) was

$$r = 1.879 + 0.568\ln(\mathrm{H}_{t-1}/\mathrm{L}_{t-1}) \tag{8}$$

which was significant (F = 8.387, d.f. = 1, 7, P = 0.023, R^2 = 0.55). The coefficient (β = 0.568) had a 95% confidence interval of 0.104–1.031 so included 1.0. The standard error of the intercept was 0.625.

The model with the second-lowest $\mathrm{AIC_c}$ was the negative ratio model with $\Delta\mathrm{AIC_c}$ of 0.242 (Table 1). The fitted negative ratio model (Fig. 3*b*) was

$$r = 0.600 - 0.014(\mathrm{L}_{t-1}/\mathrm{H}_{t-1}) \tag{9}$$

which was significant (F = 7.980, d.f. = 1,7, P = 0.026, R^2 = 0.53). The 95% confidence interval of the intercept (0.600 = annual r_m) was 0.037–1.162. The intercept (0.600) corresponds to an estimate of the maximum annual finite population growth rate (λ) of $\lambda = e^{0.600} = 1.82$.

The third-best model was the additive model with $\Delta\mathrm{AIC_c}$ of 0.690 (Table 1). The fitted additive model was

$$r = 0.576\mathrm{H}_{t-1} - 0.027\mathrm{L}_{t-1} \tag{10}$$

which was not quite significant (F = 3.93, d.f. = 2,7, P = 0.072, R^2 = 0.44). The other models differed substantially ($\Delta\mathrm{AIC_c} > 3$) from the best model (Table 1) so were not considered further.

The numerical response models were a poorer fit, as assessed by R^2, to the lynx track data than to the lynx count data. The best-fit model with the track data had R^2 = 0.55 (Table 1), and for the lynx count data R^2 = 0.85 (Table 1). Similarly, the Akaike weight of the best model for the track data was 0.353 (Table 1), which was lower than the Akaike weight (0.805) for the best model for the count data (Table 1).

The best model of the lynx track data, the modified Gompertz model, reconstructed the main features of lynx dynamics though peaked one year late (Fig. 4). In the projections (one year ahead) the main difference to the observed data was also a one-year lag (Fig. 4). A paired t-test of observed versus projected lynx tracks was not significant (t = 0.508, d.f. = 8, P > 0.40). Using the modified Gompertz (the best fit) model, a linear regression of observed (x) and projected (y) lynx tracks (Fig. 5) was significant (R^2 = 0.64, d.f. = 7, P = 0.01). The slope was 0.696 (0.228–1.165 95%CI) so the 95%CI included 1.0 (the slope of the line of equality). Using the negative ratio (the second-best fit) model, a linear regression of observed (x) and projected (y) lynx tracks (Fig. 5) was also significant (R^2 = 0.64, d.f. = 7, P = 0.01). The slope was 0.872 (0.284–1.460 95%CI) so the 95%CI included 1.0. Using the additive (the third-best fit) model, a linear regression of observed (x) and projected (y) lynx tracks (Fig. 5) was highly significant (R^2 = 0.85, d.f. = 7, P = 0.0004). However, the slope was 0.453 (0.282–0.623 95%CI) so the 95%CI did not include 1.0. Hence the latter projected track estimates were negatively biased (Fig. 5) though were highly correlated with observed tracks.

Discussion

The results show clear evidence of a numerical response relationship between annual predator (lynx) r and prey (hare) and predator density. The results complement the earlier results of a positive relationship between lynx and hare densities (O'Donoghue *et al.* 1997, O'Donoghue *et al.* 2001). The results in the present study provides more support for the hypothesis that predator (lynx) dynamics are related to both prey (snowshoe hare) density and predator density (Akcakaya 1992), than the hypothesis that predator dynamics are related solely to prey density (Stenseth *et al.* 1997).

Ratio-dependence has been suggested (Arditi and Ginzburg 1989; Akcakaya 1992; Berryman *et al.* 1995) as an appropriate form of modelling of predator–prey dynamics, although authors disagree on the approach (Abrams and Ginzburg 2000). Clearly, further research is required to evaluate support for models that assume additive (Model 2) or ratio-dependent (modified Gompertz, Model 6) effects of prey and predators on predator dynamics.

In many models (positive ratio, negative ratio, and modified Gompertz) the effect of lynx density operates as an effect of food per head (H/L). In two models (additive, and additive with an intercept) there is an effect of food (H) on predator dynamics (r) and an extra effect of predator density (L). So what is the extra effect of density (L) not explained by the effect of food (H)? The extra effect may be an effect of alternative food (Pielou 1969), self-regulation (Caughley and Krebs 1983), intraspecific

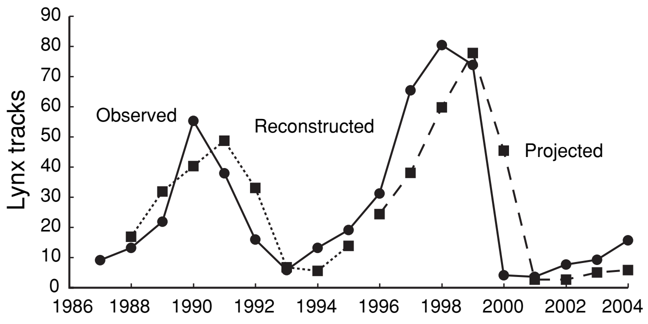

Fig. 4. The observed lynx track data (solid circles and solid line), reconstructed lynx track data (1988–95 inclusive; dotted line and squares) and projected (1996–2004 inclusive; dashed line and squares) lynx track data. The reconstruction and projection used the best-fit model, the modified Gompertz model (Eqn 8).

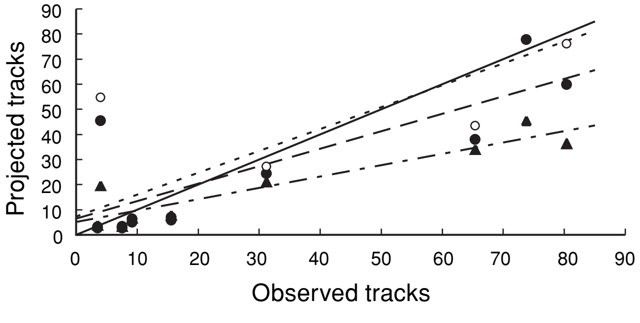

Fig. 5. Observed and projected lynx track data during 1996–2004 inclusive. Projected tracks were estimated using the modified Gompertz model (solid circles and dashed line) from Eqn 8, using the negative ratio model (open circles and dotted line) from Eqn 9, and using the additive model (solid triangles and dashed and dotted line) from Eqn 10. The solid line is the line of equality.

interference competition, as suggested for modelling other species (Hone and Sibly 2002; Sibly and Hone 2002), possible effects of pathogens (Ruscoe *et al.* 2005; Hone and Clutton-Brock 2007) or some lynx are killed by other predators as a type of intraguild predation. O'Donoghue (1997) reported kills of lynx by wolf, wolverine (*Gulo gulo*) and other lynx. Another possibility is that effects of other predators are positively correlated with lynx density, and the other predators kill hares and modify hare foraging behaviour.

The two measures of lynx density are highly correlated but not perfectly so, and hence some differences between the two model-selection analyses (Table 1) were expected. Such differences may reflect the slightly longer period over which the track counts occurred each year. Reconstructed lynx dynamics showed some differences, such as peaking one year ahead using count data (Fig. 2) and one year late using track data (Fig. 4). Further, use of the best-fitting model for projecting predator track density one year ahead showed broad support with observed data but lagged one year. The lag may be associated with some ecological factor not included in the model. The projection results wherein projection was only one year ahead for any year caution against long-term projections.

The additive model (Eqn 7) implies that at equilibrium ($r = 0$) a linear, positive relationship occurs between lynx abundance and hare abundance with the regression going through the origin. That is, there is no threshold hare abundance. A threshold of 0.5 hares ha^{-1} has been suggested for lynx persistence (Ruggiero *et al.* 2000).

The estimate of the maximum annual finite population growth rate (λ) of lynx from the negative ratio model was 1.82, which was consistent with estimates in the literature. Estimates in other studies were 2.4 (cited in Akcakaya 1992, and equivalent to $r = 0.88\ \mathrm{year}^{-1}$), 2.28 (Slough and Mowat 1996), 1.86 (Royama 1992) and 1.34 (Brand and Keith 1979). Several numerical response models did not have a maximum value for the annual growth rate or could not estimate such a maximum with the small dataset used here. Use of a larger dataset should reduce the latter problem and increase the biological realism of the numerical response models.

The wider implications of the results are that analysis of predator dynamics should evaluate the effects of prey and predator densities on predator annual r, and not solely prey or predators. The details of how to combine prey and predator densities in models, namely as additive or ratio effects, requires further research. The classification of predation as prey-dependent or ratio-dependent (Abrams and Ginzburg 2000) is probably too restrictive and the additional options of additive predator effects, and additive and multiplicative predator effects, need further study. Predator effects may also be related to other predators through interference and resource competition and intraguild predation, and not solely effects of lynx. Also there is a need to evaluate support for theoretical models using field data in both a calibration phase and a projection (new data) phase, as done in the present study.

Acknowledgements

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References

Abrams, P. A., and Ginzburg, L. R. (2000). The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution* **15**, 337–341. doi:10.1016/S0169-5347(00)01908-X

Akcakaya, H. R. (1992). Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. *Ecological Monographs* **62**, 119–142. doi:10.2307/2937172

Arditi, R., and Ginzburg, L. R. (1989). Coupling in predator–prey dynamics: ratio-dependence. *Journal of Theoretical Biology* **139**, 311–326. doi:10.1016/S0022-5193(89)80211-5

Barlow, N. D., and Norbury, G. L. (2001). A simple model for ferret population dynamics and control in semi-arid New Zealand habitats. *Wildlife Research* **28**, 87–94. doi:10.1071/WR99090

Bayliss, P. (1987). Kangaroo dynamics. In 'Kangaroos. Their Ecology and Management in the Sheep Rangelands of Australia'. (Eds G. Caughley, N. Shepherd and J. Short.) pp. 119–134. (Cambridge University Press: Cambridge.)

Berryman, A. A., Gutierrez, A. P., and Arditi, R. (1995). Credible, parsimonious and useful predator–prey models – a reply to Abrams, Gleeson and Sarnelle. *Ecology* **76**, 1980–1985. doi:10.2307/1940728

Boutin, S., Krebs, C. J., Boonstra, R., Dale, M. R. T., Hannon, S. J., Martin, K., Sinclair, A. R. E., Smith, J. N. M., Turkington, R., Blower, M., Byrom, A., Doyle, F. I., Doyle, C., Hik, D., Hofer, L., Hubbs, A., Karels, T., Murray, D. L., Nams, V., O'Donoghue, M., Rohner, C., and Schweiger, S. (1995). Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* **74**, 69–80. doi:10.2307/3545676

Brand, C. J., and Keith, L. B. (1979). Lynx demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management* **43**, 827–849. doi:10.2307/3808267

Burnham, K. P., and Anderson, D. R. (2001). Kullback–Leibler information as a basis for strong inference in ecological studies. *Wildlife Research* **28**, 111–119. doi:10.1071/WR99107

Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodel Inference. A Practical Information-theoretic Approach.' (Springer Verlag: Berlin.)

Caughley, G. (1977). 'Analysis of Vertebrate Populations.' (Wiley: New York.)

Caughley, G., and Krebs, C. J. (1983). Are big mammals simply little mammals writ large? *Oecologia* **59**, 7–17. doi:10.1007/BF00388066

Chamberlin, T. (1965). The method of multiple working hypotheses. *Science* **148**, 754–759. doi:10.1126/science.148.3671.754

Choquenot, D., Krebs, C. J., Sinclair, A. R. E., Boonstra, R., and Boutin, S. (2001). Vertebrate community structure in the boreal forest. In 'Ecosystem Dynamics of the Boreal Forest. The Kluane Project'. (Eds C. J. Krebs, S. Boutin and R. Boonstra.) pp. 437–462. (Oxford University Press: Oxford.)

Dennis, B., and Otten, M. R. M. (2000). Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. *Journal of Wildlife Management* **64**, 388–400. doi:10.2307/3803237

Eberhardt, L. L., and Peterson, R. O. (1999). Predicting the wolf–prey equilibrium point. *Canadian Journal of Zoology* **77**, 494–498. doi:10.1139/cjz-77-3-494

Elton, C., and Nicholson, M. (1942). The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology* **11**, 215–244. doi:10.2307/1358

Freund, R. J., and Little, R. C. (1986). 'SAS System for Regression.' (SAS Institute Inc.: Cary, NJ.)

Ginzburg, L. R., and Jensen, C. X. J. (2004). Rules of thumb for judging ecological theories. *Trends in Ecology & Evolution* **19**, 121–126. doi:10.1016/j.tree.2003.11.004

Hanski, I., Henttonen, H., Korpimaki, E., Oksanen, L., and Turchin, P. (2001). Small-rodent dynamics and predation. *Ecology* **82**, 1505–1520.

Hone, J., and Clutton-Brock, T. H. (2007). Climate, food, density and wildlife population growth rate. *Journal of Animal Ecology* **76**, 361–367. doi:10.1111/j.1365-2656.2006.01200.x

Hone, J., and Sibly, R. M. (2002). Demographic, mechanistic and density-dependent determinants of population growth: a case study in an avian predator. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **357**, 1171–1178. doi:10.1098/rstb.2002.1118

King, A. A., and Schaffer, W. M. (2001). The geometry of a population cycle: a mechanistic model of snowshoe hare demography. *Ecology* **82**, 814–830.

Krebs, C. J., Boutin, S., and Boonstra, R. (2001). 'Ecosystem Dynamics of the Boreal Forest: the Kluane Project.' (Oxford University Press: Oxford.)

Leslie, P. H. (1948). Some further notes on the use of matrices in population mathematics. *Biometrika* **35**, 213–245.

May, R. M. (1981). Models for interacting populations. In 'Theoretical Ecology. Principles and Applications.' 2nd edn. (Ed. R. M. May.) pp. 5–29. (Blackwell: Oxford.)

May, R. M., Conway, G. R., Hassell, M. P., and Southwood, T. R. E. (1974). Time delays, density-dependence and single-species oscillations. *Journal of Animal Ecology* **43**, 747–770. doi:10.2307/3535

McCarthy, M. A. (1996). Red kangaroo (*Macropus rufus*) dynamics: effects of rainfall, density dependence, harvesting and environmental stochasticity. *Journal of Applied Ecology* **33**, 45–53. doi:10.2307/2405014

O'Donoghue, M. (1997). Responses of coyotes and lynx to the snowshoe hare cycle. Ph.D. Thesis, University of British Columbia, Vancouver.

O'Donoghue, M., Boutin, S., Krebs, C. J., and Hofer, E. J. (1997). Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* **80**, 150–162. doi:10.2307/3546526

O'Donoghue, M., Boutin, S., Murray, D. L., Krebs, C. J., Hofer, E. J., Breitenmoser, U., Breitenmoser-Wuersten, C., Zuleta, G., Doyle, C., and Nams, V. O. (2001). Coyotes and lynx. In 'Ecosystem Dynamics of the Boreal Forest: the Kluane Project.' (Eds C. J. Krebs, S. Boutin, and R. Boonstra.) pp. 275–323. (Oxford University Press: Oxford.)

Pech, R., and Hood, G. (1998). Foxes, rabbits, alternative prey and rabbit calicivirus disease: consequences of a new biological control agent for an outbreaking species. *Journal of Applied Ecology* **35**, 434–453. doi:10.1046/j.1365-2664.1998.00318.x

Pielou, E. C. (1969). 'An Introduction to Mathematical Ecology.' (Wiley: New York.)

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* **86**, 2805–2814. doi:10.1890/05-0074

Royama, T. (1992). 'Analytical Population Dynamics.' (Chapman and Hall: London.)

Ruggiero, L. F., Aubry, K. B., Buskirk, S. W., Koehler, G. M., Krebs, C. J., McKelvey, K. S., and Squires, J. R. (2000). The scientific basis for lynx conservation: qualified insights. In 'Ecology and Conservation of Lynx in the United States.' (Eds L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires.) pp. 443–454. (University Press of Colorado: Boulder.)

Ruscoe, W. A., Elkington, J. S., Choquenot, D., and Allen, R. B. (2005). Predation of beech seed by mice: effects of numerical and functional responses. *Journal of Animal Ecology* **74**, 1005–1019. doi:10.1111/j.1365-2656.2005.00998.x

Sibly, R. M., and Hone, J. (2002). Population growth rate: an overview. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **357**, 1153–1170. doi:10.1098/rstb.2002.1117

Sinclair, A. R. E., and Krebs, C. J. (2001). Trophic interactions, community organization, and the Kluane ecosystem. In 'Ecosystem Dynamics of the Boreal Forest: the Kluane Project.' (Eds C. J. Krebs, S. Boutin, and R. Boonstra.) pp. 25–48. (Oxford University Press: Oxford.)

Slough, B. G., and Mowat, G. (1996). Lynx population dynamics in an untrapped refugium. *Journal of Wildlife Management* **60**, 946–961. doi:10.2307/3802397

Stenseth, N. C., Falck, W., Bjornstad, O. N., and Krebs, C. J. (1997). Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 5147–5152. doi:10.1073/pnas.94.10.5147

Turchin, P., and Hanski, I. (2001). Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecology Letters* **4**, 267–276. doi:10.1046/j.1461-0248.2001.00204.x

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