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Biases in the estimation of the demographic parameters of a snowshoe hare population

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Summary

1. Survival rates and natalities for a population of snowshoe hares in the Yukon were estimated independently of and simultaneously with estimates of population change during the increase phase of a hare cycle.

2. Simple demographic models are used to show that even though the estimated survival rates and natalities were high relative to previously published estimates, the observed demographic parameters are unable to explain the extent of population increase, and we conclude that some of these parameters must be underestimates.

3. A sensitivity analysis is used to examine the potential influence of changes in these demographic parameters on the population growth rate. During most years of the hare cycle the population growth rate is potentially most sensitive to changes in juvenile postweaning survival. Only during crash years is adult survivorship likely to be a more important determinant of the rate of population change.

4. Examination of previously published data sets on two full population cycles suggests that while survival rates are positively correlated with population growth rates, their incorporation into demographic models results in frequent underestimation of the rate of population increase.

Key-words: biased parameter estimation, demographic parameters, population elasticities, population growth rates, population sensitivity analyses, snowshoe hare cycles, survival rates.

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Introduction

Population dynamics has a great advantage over community dynamics in having an arithmetic of numerical change. If changes in numbers in a population are tracked over a time period, estimates of birth, death and migration rates should be consistent with these changes. Surprisingly, very few vertebrate ecologists use this powerful arithmetic to check on the accuracy of their estimated parameters of births and deaths. In this paper population arithmetic is applied to a fluctuating population of snowshoe hares (*Lepus americanus* Erxleben) to see whether it is possible to reconstruct the numerical population changes from independent estimates of the components of births and deaths. This analysis leads to the conclusion that empirically measured survival rates are likely to be underestimated. A sensitivity analysis of snowshoe hare demography was then conducted to understand better the consequences of underestimating different age-specific survival rates for our predictions. In order to evaluate the generality of these findings, this analysis is extended using two previously published data sets to examine the demography of snowshoe hares over their full population cycle.

Snowshoe hares are typical of small mammals in having a high birth rate and a correspondingly high death rate. Individual females may have 3–4 litters during the summer, spaced at approximately 5-week intervals, with litter sizes from 3 to 8, so that as many as 20 offspring may result from one breeding season. The maximum rate of increase of snowshoe hares is thus tenfold per year, assuming an even sex ratio. Observed rates of increase over the 10-year population cycle vary from about 0·2–4·0 per year, with correspondingly high variation in both birth and

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death rates over the cycle (Krebs *et al.* 1986; Keith 1990).

Methods

PARAMETER ESTIMATION

Population sizes, and survival and natality rates were collected between April 1995 and April 1996 as part of the Kluane Boreal Forest Ecosystem Project. During this period the snowshoe hare population in the area underwent a cyclic population increase (Krebs *et al.* 1995). Five 36-ha study grids were located in the Shakwak Trench, a glacial valley near Kluane Lake, Yukon Territory (60°57′N, 138°12′W). As part of a concurrent study, two of the grids (Food 1 and Food 2) had commercial rabbit food spread *ad libitum* every 5–10 days along four equally spaced cutlines running the length of the grid (Krebs *et al.* 1992).

Population estimates for each grid were based on 3–6 night trapping sessions conducted in March 1995, October 1995 and March 1996. All estimates were calculated using the jack-knife estimator in the program CAPTURE (July 1991 version, White, Burnham & Otis 1982; Boulanger & Krebs 1996). In order to divide the autumn population estimates into adult and juvenile cohorts, the proportion of juveniles in the trapped population on each grid during the autumn census was determined and was assumed to reflect the true proportion in the population. Because some hares trapped in the autumn could not be definitively classified as juveniles or adults, the minimum and maximum proportion of juveniles on each grid was obtained by assuming all the unclassifiable individuals were either adults or juveniles, respectively.

Survival of adult and juvenile hares was monitored using radio-collared and radio-tagged individuals. Survival curves were calculated using a Kaplan–Meier procedure, which allowed for staggered entry of animals into the study (Pollock *et al.* 1989) and were calculated for each age cohort within each treatment (food addition or control). The Kaplan–Meier procedure was also used to estimate 28-day survival. In this paper, the term '28-day survival' is used to refer to the average probability of surviving a 28-day time period, obtained by back calculating from the observed survival probabilities estimated over considerably longer periods (usually spring 1995–96). Survival estimates were not calculated separately for males and females, as previous studies have indicated survival does not differ between the sexes (Meslow & Keith 1968; Keith & Windberg 1978; Boutin 1984; Keith *et al.* 1984; Boutin & Krebs 1986; Krebs *et al.* 1986; O'Donoghue 1994; Gillis, 1999). Details of the methods used to monitor survival can be found in Krebs *et al.* (1992) and Boutin *et al.* (1986) (adult hare survival), Gillis (1999) (postweaning juvenile survival), O'Donoghue (1994) (preweaning survival) and Stefan (1998) (preweaning survival).

Breeding in snowshoe hares is synchronous among females. Mean parturition date and litter size for each of the litter groups on each treatment were determined by placing pregnant females in cages immediately prior to parturition and counting the number of young born (Stefan 1998; methods as in O'Donoghue & Krebs 1992).

Unless otherwise stated, all parameters used in this paper were empirically measured; where they had to be estimated, estimates were based on previous studies.

POPULATION PROJECTION

The demographic parameters were incorporated into a simple demographic model that permitted expected population sizes to be calculated from values observed at a previous time. The model assumed that the ratio of males and females was equal and took the form:

$$E(\mathrm{Adults}_{\mathrm{Spring96}}) = LA_{365}\mathrm{Adults}_{\mathrm{Spring95}} + \frac{\mathrm{Adults}_{\mathrm{Spring95}}}{2} \times \begin{bmatrix} LA_{P1}m_1L1_{pre-w}L1_{365}+ \\ LA_{P2}m_2L2_{pre-w}L2_{365}+ \\ LA_{P3}m_3L3_{pre-w}L3_{365}+ \\ LA_{P4}m_4L4_{pre-w}L4_{365} \end{bmatrix} \qquad \text{eqn 1}$$

where all parameters are defined in Tables 1 and 2.

Using a similar approach it was possible to subdivide this projection into periods from spring 1995 to autumn 1995:

$$E(\{\mathrm{Adults}+\mathrm{Juveniles}\}_{\mathrm{Fall95}}) = LA_{183}\mathrm{Adults}_{\mathrm{Spring95}} + \frac{\mathrm{Adults}_{\mathrm{Spring95}}}{2} \times \begin{bmatrix} LA_{P1}m_1L1_{pre-w}L1_{183}+ \\ LA_{P2}m_2L2_{pre-w}L2_{183}+ \\ LA_{P3}m_3L3_{pre-w}L3_{183}+ \\ LA_{P4}m_4L4_{pre-w}L4_{183} \end{bmatrix} \qquad \text{eqn 2}$$

and from the autumn of 1995 to the spring of 1996:

$$E(\mathrm{Adults}_{\mathrm{Spring96}}) = LA_{184\text{–}365}\mathrm{Adults}_{\mathrm{Fall95}} + \overline{LJ}_{184\text{–}365}\mathrm{Juveniles}_{\mathrm{Fall95}} \qquad \text{eqn 3}$$

where $\mathrm{Juveniles}_{\mathrm{Fall95}}$ is the number of juveniles in the autumn of 1995 and again all other parameters are defined in Tables 1 and 2.

Establishing the significance of differences between the observed and expected abundances is complicated by lack of any definite knowledge about the shapes of the distributions of these quantities. Two approaches were adopted in addressing this problem.

Standard deviations of the expectations were estimated from the variance of the appropriate sums and products, using appropriate combinations of the following relationships and approximations:

Table 1. Survival parameter definitions and values. All estimates were obtained using a Kaplan–Meier procedure, which allows for staggered entry of radio-collared individuals into the study (Pollock *et al.*, 1989). Standard errors are provided in parentheses. Spring 1995 corresponds to 1 April 1995; Autumn 1995 to 1 October 1995; and Spring 1996 to 1 April 1996

Parameter	Definition	Control*	Food
	Adult survival		
LA_{P1}	from Spring 95–1st litter parturition	0·91 (0·051)	0·84 (0·084)
LA_{P2}	from Spring 95–2nd litter parturition	0·79 (0·066)	0·59 (0·099)
LA_{P3}	from Spring 95–3rd litter parturition	0·65 (0·073)	0·56 (0·098)
LA_{P4}	from Spring 95–4th litter parturition	0·63 (0·073)	0·56 (0·098)
LA_{183}	from Spring 95 to Autumn 95	0·61 (0·074)	0·52 (0·095)
LA_{365}	from Spring 95 to Spring 96	0·35 (0·067)	0·36 (0·083)
$LA_{184\ 365}$	from Autumn 95 to Spring 96	0·58 (0·084)	0·70 (0·095)
LA_{28}	28-day survival from Spring 95 to Spring 95	0·92 (0·89–0·94)†	NA
	Juveniles: pre-weaning survival		
$L1_{pre\text{-}w}$	litter 1, from birth to weaning	0·58 (0·113)	0·27 (0·115)
$L2_{pre\text{-}w}$	litter 2, from birth to weaning	0·61 (0·074)	0·17 (0·083)
$L3_{pre\text{-}w}$	litter 3, from birth to weaning	0·60 (0·089)	0·46 (0·096)
$L4_{pre\text{-}w}$	litter 4, from birth to weaning	0·60 (0·089)‡	0·35 (0·096)‡
$\bar{L}_{pre\text{-}w}$	all litters combined§	0·60 (0·50–0·70)†	NA
	Juveniles: post weaning		
$L1_{183}$	litter 1, from weaning to Autumn 95	0·92 (0·077)	0·88 (0·118)
$L2_{183}$	litter 2, from weaning to Autumn 95	0·80 (0·126)	0·80 (0·179)
$L3_{183}$	litter 3, from weaning to Autumn 95	0·68 (0·158)	0·50 (0·251)
$L4_{183}$	litter 4, from weaning to Autumn 95	1·00 (0·000)	1 (0·000)‡
$L1_{365}$	litter 1, from weaning to Spring 96	0·49 (0·134)	0·21 (0·179)
$L2_{365}$	litter 2, from weaning to Spring 96	0·64 (0·145)	0·57 (0·187)
$L3_{365}$	litter 3, from weaning to Spring 96	0·15 (0·099)	0·42 (0·070)
$L4_{365}$	litter 4, from weaning to Spring 96	0·004 (0·272)‡¶	0·20 (0·137)
$\overline{LJ}_{184\text{-}365}$	Juveniles from Fall 95 to Spring 96 (all litters combined)§	0·49 (0·085)	0·51 (0·098)
$\overline{LJ}_{28}$	28-day survival from Spring 95 to Spring 96 (all litters combined)§	0·91 (0·87–0·94)†	NA

* Estimate based on hares collared on control grids 1 and 3.

† 95% confidence intervals provided in parentheses.

‡ Estimated value and standard error.

§ For all litters combined, survival information from all litter groups was pooled and the estimate recalculated. Therefore, the value is not an average of the survival of the individual litter groups.

¶ All collared hares died or disappeared within 1 month of collaring. Survival estimate was obtained by extrapolating survival rate over the time period it was measured to the entire year.

Table 2. Reproductive information from the 1995 breeding season. Variance is provided in parentheses

	Control*		Food	
	Mean litter size	Mean parturition date	Mean litter size	Mean parturition date
Litter 1 (m_1)	3·4 (0·8)	22 May	4·2 (6)	10 May
Litter 2 (m_2)	6·9 (2·6)	20 June	7·0 (3·2)	10 June
Litter 3 (m_3)	5·6 (3·2)	28 July	6·4 (8·4)	20 July
Litter 4 (m_4)	4†	3 September‡	4†	27 August‡

* Data from control grids 1 and 3.

† Estimated value.

‡ Estimated by adding 37 days (average gestation period) to mean third litter parturition date.

$$\sigma^2_{XY} = \sigma^2_X\mu^2_Y + \sigma^2_Y\mu^2_X + \sigma^2_X\sigma^2_y \qquad \text{eqn 4a} \qquad \mu_{XY} = \mu_X\mu_Y \qquad \text{eqn 4d}$$

$$\sigma^2_{X\pm Y} = \sigma^2_X + \sigma^2_Y \qquad \text{eqn 4b} \qquad \mu_{X\pm Y} = \mu_X \pm \mu_Y \qquad \text{eqn 4e}$$

$$\sigma^2_{cY} = c^2\sigma^2_Y \qquad \text{eqn 4c} \qquad \mu_{cX} = c\mu_X \qquad \text{eqn 4f}$$

where σ_{XY} is the standard deviation of the product of two independent random variables, X and Y, with mean μ_X, μ_Y and standard deviations σ_X and σ_Y, respectively, and c is a constant. The parameters were assumed to be independent of each other, and the standard errors of the estimate of the mean initial population sizes were included in the calculation of the standard deviations of the expectations. The variances used for each parameter were the squared standard errors associated with the mean parameter estimates, with the exception of litter size values (m_{1-4}), for which the directly observed variance in litter size was used. Calculating the standard deviations of the expectations in this way makes no assumptions about the shapes of the underlying distributions of parameters and initial population size. The mean and standard deviation of the difference between expected and observed abundances is calculated using equations 4b and e. An upper limit on the p-value corresponding to the null hypothesis that this difference is zero can be obtained using Chebyshev's inequality (Kalbfleisch 1985): $P\{|X-\mu_X|/\sigma_X \geq t\} \leq t^{-2}$, this inequality is applicable to any distribution.

Our second approach was a bootstrap procedure. We approximated the distribution of initial population estimates, selected an initial population size, and subjected each member of this population to a series of Bernoulli trials, representing transitions in the demographic process for which we had empirically obtained survival probability and natality estimates (Tables 1 and 2). The survival probability estimates were drawn from sampling distributions with the same mean and standard deviations as those reported in Table 1, distributions were assumed to be uniform. Litter sizes were assumed to be Poisson distributed with empirically determined means obtained from Table 2. The mean number of surviving animals from 5000 such simulations corresponded almost exactly with those obtained from equations 1, 2 and 3. The initial population estimate (N) was assumed to be described by a modified exponential gamma distribution:

$$f(N) = c\frac{|h|}{\Gamma(a)}\exp[ah(N-u)]\cdot\exp[-e^{h(N-u)}] \qquad \text{eqn 5}$$

with parameters a, h, and u selected in order to give the same mean and asymmetric 95% confidence intervals as the observed estimates, and c is a normalization constant. The variances of the exponential gamma distributions selected in this way were always greater than the variances from CAPTURE, often by at least a factor of two. The bootstrapping procedure permitted the estimation of upper and lower 95% confidence intervals around the mean predictions derived from equations 1, 2 and 3, and a statistical test of the null hypothesis that there were no differences between observed and predicted hare numbers. Reported p-values from this procedure are the overlap between the normalized distributions of predicted hare numbers from the bootstrapping procedure and a modified exponential gamma distribution fitted to the mean and confidence intervals of the observed hare numbers corresponding to the predictions.

SENSITIVITY ANALYSIS

Pre- and postweaning survival probabilities were calculated by pooling all litters from all control grids. Adult and postweaning survival probabilities were adjusted to 28 day time periods. Eqn 1 was used to extract the annual per capita growth rate (λ) for the population from spring 1995 to spring 1996:

$$\lambda = \frac{1}{2}\begin{bmatrix} LA_{28}^{1.86}m_1\bar{L}_{pre-w}\overline{LJ}_{28}^{10.11} + \\ LA_{28}^{2.89}m_2\bar{L}_{pre-w}\overline{LJ}_{28}^{9.07} + \\ LA_{28}^{4.25}m_3\bar{L}_{pre-w}\overline{LJ}_{28}^{7.64} + \\ f_4 LA_{28}^{5.57}m_4\bar{L}_{pre-w}\overline{LJ}_{28}^{6.39} \end{bmatrix} + LA_{28}^{13} \qquad \text{eqn 6}$$

The exponents are calculated from how many 28-day time periods constitute the appropriate period of time (for example there are 13 28-day periods in 1 year, hence LA_{28} must be raised to the 13th power to predict adult annual survival). The parameter f_4 is the fourth litter pregnancy rate, and from here on is assumed to be 85% (pregnancy rates for the first three litters were maintained at 100%). The population sensitivities and elasticities (defined in Table 5) with respect to each of the constituent parameters can be calculated using the partial derivative of equation 6 taken with respect to each parameter and evaluated using the observed parameter values (as outlined in Caswell 1989). Sensitivities were calculated as:

$$s_{LA_{28}} = \left.\frac{\partial\lambda}{\partial LA_{28}}\right|_*, \quad s_{\bar{L}_{pre-w}} = \left.\frac{\partial\lambda}{\partial \bar{L}_{pre-w}}\right|_*,$$

$$s_{\overline{LJ}_{28}} = \left.\frac{\partial\lambda}{\partial \overline{LJ}_{28}}\right|_*, \quad s_{f_4} = \left.\frac{\partial\lambda}{\partial f_4}\right|_*, \quad s_{m_i} = \left.\frac{\partial\lambda}{\partial m_i}\right|_*, \qquad \text{eqn 7}$$

where asterisks denote evaluation of the derivative at the observed parameter values reported in Tables 1 and 2), and elasticities as:

$$e_{LA_{28}} = \left.\frac{LA_{28}}{\lambda}\frac{\partial\lambda}{\partial LA_{28}}\right|_*, \quad e_{\bar{L}_{pre-w}} = \left.\frac{\bar{L}_{pre-w}}{\lambda}\frac{\partial\lambda}{\partial \bar{L}_{pre-w}}\right|_*,$$

$$e_{\overline{LJ}_{28}} = \left.\frac{\overline{LJ}_{28}}{\lambda}\frac{\partial\lambda}{\partial \overline{LJ}_{28}}\right|_*, \quad e_{f_4}\left.\frac{f_4}{\lambda}\frac{\partial\lambda}{\partial f_4}\right|_*, \quad e_{m_i} = \left.\frac{m_i}{\lambda}\frac{\partial\lambda}{\partial m_i}\right|_*, \qquad \text{eqn 8}$$

If these elasticities are multiplied by the coefficient of variation (CV) that has been associated with year to year variation in these parameters, then the units of parameter perturbation are measured in standard deviations of the parameter in question, in effect combining the proportional sensitivity of the growth rate to the parameter with the observed empirical variation in that parameter (see Tienderen 1995; Steen &

Erikstad 1996). The *CVs* reported here are calculated from data chosen selectively from the literature. Only studies which had estimates for at least five continuous years of a cycle were included and information from noncyclic and experimentally manipulated populations was excluded. In studies in which data from more than one grid or study area were available, the coefficient for each study site was calculated and then the sites within a study were averaged. For adult and postweaning juvenile survival our coefficients of variation were based on yearly (spring–spring) survival, which was standardized to 28-day time intervals. In doing this, it was assumed that postweaning juvenile hares were present from 1 June to 31 March of each year.

PREVIOUSLY PUBLISHED DATA

To reconstruct population changes of snowshoe hare populations for Kluane, Yukon from 1977 to 1984 and Rochester, Alberta from 1962 to 1975, natality estimates, mean parturition dates of each litter and survival rates of adults and juveniles were incorporated from several sources into the expression for population growth rate (equation 6). For simplicity, only survival rates were permitted to change in the model, with natality and parturition dates held constant. As reproductive rates were not measured directly for the Kluane population for the years 1977–84, 1995 values were used for natality and parturition dates (Stefan 1998). This year was the first of the population increase phase and reproductive parameters were at a 10-year high. For the Rochester population, natality estimates and mean parturition dates for 1967 were used (Cary & Keith 1979), the year of increase corresponding to 1995 at Kluane.

The 28-day adult survival rates reported by Krebs *et al.* (1986) for the Kluane population from 1977 to 1984 were used, averaged over the cyclic control grids (Silver Creek, Beaver Pond, 1050, and Gribble's). For the Rochester population, the mean adult survival for 365 days (Keith & Windberg 1978) was converted to 28-day survival rates for 1962–75. Juvenile survival estimates for both areas were based on the number of recruits per female from birth to the following spring. Juvenile recruitment estimates, based on live trapping, were taken from Krebs *et al.* (1986) for the Kluane population and from Keith & Windberg (1978) for Rochester. Predicted values of population growth rate were compared directly with those observed for each population.

Results

The basic demographic parameters are summarized in Tables 1 and 2. Figure 1 shows how adult survival varied through the year, and also shows that this survival rate is well modelled by assuming a constant 28 day survivorship.

The comparison of observed hare numbers in the spring of 1996 and the numbers predicted projecting from the spring of 1995 is made in Table 3. The projections all substantially underestimate the observed increase in hare numbers. The observed population

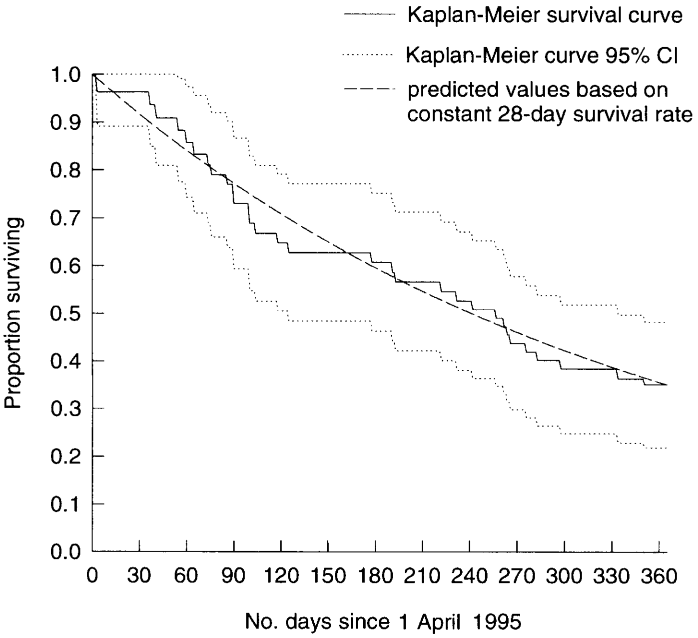

Fig. 1. Comparison of Kaplan–Meier survival curve (with 95% CI) and survival curve derived from constant 28-day survival for adult snowshoe hares, Kluane Lake 1995–96. Twenty-eight day survival refers to the average 28-day survival over the entire study period and assumes an exponential decline, while the Kaplan–Meier curve is based on a daily survival estimate and does not assume shape of decline.

Table 3. Observed and predicted hare numbers on each of the five grids, projected from spring 1995 to spring 1996. Parentheses enclose the standard deviation of the observed or predicted value. 95% CI obtained from the program CAPTURE (White *et al*., 1982) for observed population estimates and 95% CI obtained by the bootstrap procedure for the predicted population estimate are given below. The prediction is derived from equation 1, the conservative P-values test the null hypotheses that the difference between the observed abundance for spring 1996 and the prediction is equal to zero. The test is performed using Chebyshev's inequality, which is valid for any distribution of the difference. The bootstrap *P*-value uses the overlap between the bootstrapped distribution of expected abundances and a modified exponential gamma distribution fitted to observed spring 1996 census information to test the null hypothesis that the observed spring 1996 abundance is not different to the bootstrapped expectation

Grid	Observed Spring 1995	Observed Spring 1996	Predicted Spring 1996	Conservative *P*-value	Bootstrap *P*-value
Control 1	11 (1·98) 9–19	36 (1·51) 34–40	22 (6·29) 11–44	0·217	0·104
Control 2	5 (1·52) 4–11	25 (2·13) 24–38	10 (3·68) 1–28	0·082	0·050
Control 3	17 (1·85) 15–24	53 (3·36) 50–65	34 (8·55) 22–58	0·237	0·059
Food 1	31 (5·18) 25–47	130 (11·32) 113–159	34 (10·27)	0·025	–
Food 2	52 (8·07) 41–74	191 (18·07) 163–235	56 (16·95)	0·034	–

growth rate averaged over the five grids was 3·8, the growth rates that result from the use of the demographic parameters underestimate this figure by between 30 and 75%. Evaluation of the significance of these underestimates is complicated by the absence of any knowledge about the probable distribution of the expectations, however, even a conservative evaluation of the difference is significant on the food addition grids, and a Fisher's combined probability test for an effect on all three control grids using the conservative *P*-values from the application of Chebyshev's inequality yields $\chi^2 = 10{\cdot}94$, (6 d.f., $P = 0{\cdot}090$). A Fisher's combined probability test on the bootstrapped *P*-values indicates a significant discrepancy ($\chi^2 = 16{\cdot}18$, 6 d.f., $P = 0{\cdot}013$) on the three control grids taken together.

Closer inspection of the first half of this projection period, spring 1995 to autumn 1995 (Table 4a-b), is suggestive of the origin of the observed discrepancies. The severity of the underestimates of the total population is moderated (as they have less time to compound) but is still very substantial on the food grids (Table 4a). However, if the analysis is conducted exclusive of recruitment, then the projections fall mostly midway within the possible range of observed adult numbers (Table 4b). Inspection of the second half of the projection (autumn 1995 to spring 1996) once again reveals consistent underestimation (Table 4c), significantly so on three out of five occasions. Taken together, these results suggest that while adult survivorship is underestimated, the principal source of error originates in the estimates of recruitment parameters.

The sensitivities and elasticities are reported in Table 5. The elasticities suggest growth rate is potentially at least five times more sensitive to changes in adult and postweaning juvenile survival probabilities than to changes in preweaning survival, and at least 15 times more sensitive relative to changes in litter size parameters. Furthermore, analysis of three different hare populations reveals that the observed coefficient of variation in 28-day juvenile survival is consistently about twice that observed in adult survivorship. This suggests that throughout the hare cycle, variation in the 28-day juvenile survival rate is three times as influential in snowshoe hare demography as variation in 28-day adult survivorship and preweaning survivorship, and 30 times as important as variation observed in litter sizes and fourth litter pregnancy rates (Table 5). The analysis predicts that the absence of a fourth litter will decrease the growth rate by ≈ 15% (but note that this is likely to be an overestimate because the low fourth litter survival parameters have been pooled with the higher survival rates of earlier litters). In Table 5 the sensitivities and elasticities are evaluated using the observed demographic parameters for the increase year 1995–96. In Fig. 2(a) the elasticities have been calculated for values of adult and juvenile postweaning survivorship observed for the years 1977–84 (data from Krebs *et al.* 1986). The results suggest that juvenile survival remains the most sensitive demographic parameter over most of the cycle, the important exception being in sharp decline years when adult survival assumes prime influence (Fig. 2a). This result is also observed for the parameters of a cyclic hare population in Alberta (Fig. 2b) using the data from Keith & Windberg (1978). In decline years $\overline{LJ}_{28}$ falls to such low values that small changes to any of the recruitment parameters are unlikely to affect the population dynamics.

Use of pooled data on juvenile survivorship results

Table 4a. Observed and predicted hare numbers on each of the five grids, projected from spring 1995 to autumn 1995. Otherwise details as for Table 3

Grid	Observed Spring 1995	Observed Adults + juveniles$_{\text{autumn95}}$	Predicted Adults + juveniles$_{\text{autumn95}}$	Conservative *P*-value	Bootstrap *P*-value
Control 1	11 (1·98)	62 (4·33)	46·80 (10·50)	0·558	0·213
	9–19	56–75	22–87		
Control 2	5 (1·52)	28 (4·21)	21·27 (6·85)	1·000	0·309
	4–11	24–42	3–55		
Control 3	17 (1·85)	102 (9·66)	72·32 (12·94)	0·366	0·100
	15–24	89–128	43–110		
Food 1	31 (5·18)	140 (13·01)	62·82 (18·46)	0·086	0·002
	25–47	119–171	35–110		
Food 2	52 (8·07)	255 (18·61)	105·37 (30·39)	0·057	0·000
	41–74	225–300	72–170		

Table 4b. Observed and predicted adult hare numbers on each of the five grids, projected from spring 1995 to autumn 1995. The range of observed adults in the autumn results from assuming all trapped animals in the unclassified cohort are juveniles (lower value) or adults (upper value)

Observed Grid	Observed Spring 1995	Observed Adults$_{\text{autumn95}}$	Predicted Adults$_{\text{autumn95}}$
Control 1	11	2–8	6·69 (1·44)
	9–19		
Control 2	5	0–7	3·04 (0·995)
	4–11		
Control 3	17	9–18	10·34 (1·65)
	15–24		
Food 1	31	5–38	16·12 (4·18)
	25–47		
Food 2	52	3–60	27·04 (6·64)
	41–74		

Table 4c. Observed and predicted hare numbers on each of the five grids, projected from autumn 1995 to spring 1996. Predictions are based on assuming that autumn-trapped animals in the unclassified cohort are all adult (this assumption gives the largest predicted spring populations). Otherwise details as for Table 3

Grid	Observed Autumn 1995	Observed Spring 1996	Predicted Spring 1996	Conservative *P*-value	Bootstrap *P*-value
Control 1	62 (4·33)	36 (1·51)	31·27 (4·93)	1·000	0·165
	56–75	34–40	23–41		
Control 2	28 (4·21)	25 (2·13)	14·53 (2·09)	0·087	0·018
	24–42	24–38	9–23		
Control 3	102 (9·66)	53 (3·36)	52·31 (7·89)	1·000	0·997
	89–128	50–65	39–72		
Food 1	140 (13·01)	130 (11·32)	83·22 (12·47)	0·130	0·001
	119–171	113–159	67–110		
Food 2	255 (18·61)	191 (18·07)	146·93 (19·78)	0·370	0·035
	225–300	163–235	120–180		

in a predicted growth rate for the control grids of 2·4, compared with the observed value of 3·8. The influences of the three dominant parameters on this growth rate are shown in graph form in Fig. 3a–c. The topography of these surfaces close to the observed values is described by the sensitivities reported in the second column of Table 5. The dominant influence of postweaning juvenile survivorship is apparent. The discrepancy between observed and predicted growth rates is not resolved even when survival parameters are inflated to their upper 95% confidence limits. Figure 4a and b shows contour plots of the effects of different combinations of $\overline{LJ}_{28}$ and LA_{28} on predicted population growth rate. Overlayed on this figure are measured combinations of $\overline{LJ}_{28}$ and LA_{28} together with the observed corresponding population growth rates for the Kluane and Rochester populations shown for the full cycle. Observed and predicted growth rates are positively correlated for both populations (for the Kluane population $r = 0{\cdot}67$; for the

Table 5. The sensitivities, elasticities and observed coefficients of variation for the principal demographic parameters governing the studied snowshoe hare population as described by equation 6

Parameter	Parameter value (control grids)	Sensitivity s_i	Elasticity e_i	Observed coefficients of variation (CV)	CV e_i
28-day adult survival (LA_{28})	0·92	13·08	4·95	4·3†, 9·5‡, 17·0§	0·508
28-day juvenile postweaning survival ($\overline{LJ}_{28}$)	0·91	19·03	7·14	8·4†, 19·3‡, 31·9§	1·419
Preweaning survival (30-day) ($\bar{L}_{pre\text{-}w}$)	0·60	3·45	0·85	60¶	0·513
Litter 1 size (m_1)	3·4	0·11	0·15	10¶	0·015
Litter 2 size (m_2)	6·9	0·11	0·30	17¶	0·052
Litter 3 size (m_3)	5·6	0·11	0·25	18¶	0·045
Litter 4 size (m_4)	4·0	0·09	0·15	?	?
Fourth litter pregnancy rate (f_4)	0·85	0·44	0·15	††	††
Growth rate (λ from eqn 6)	2·44				

Sensitivities measure the change in λ (denoted $\Delta\lambda$) resulting from a change in a focus parameter, a_i, (denoted Δa_i). It is the partial derivative of the growth rate taken with respect to the focus parameter, evaluated at the observed value of the focus parameter, (i.e. the ratio $\Delta\lambda$: Δa_i). Elasticities measure the proportional change in λ (i.e. $\Delta\lambda/\lambda$) resulting from a proportional change in the focus parameter (i.e. the ratio $\Delta\lambda/\lambda$: $\Delta a_i/a_i$). The coefficient of variation in the fifth column reflects annual variability observed in this parameter as deduced from various multiyear studies (†Keith & Windberg 1978; ‡Krebs *et al.* 1986; §Krebs *et al.*, 1995; ¶Stefan 1998). The last column, CVe_i, indicates the proportional change in the growth rate resulting from a perturbation to the focus parameter, when this perturbation is measured in units of the standard deviation of the focus parameter. This last column therefore combines the sensitivity of the growth rate to a parameter change, together with the degree of variability actually observed in this parameter (e.g. if $\overline{LJ}_{28}$ was increased by 5% of its observed standard deviation, λ would increase by 0·05 × 1·419 × 100 = 7·1%, i.e. from 2·44 to 2·61). The observed value of λ averaged over all control grids was 3·8.

††$f_4 = 0$ results in 15·3% reduction in λ, while $f_4 = 1$ results in 2·7% increase.

Rochester population $r = 0·91$). Note that even though the natalities used in these reconstructions are from a year of high hare density increases (with high rates of preweaning survival likely), the observed growth rates are still frequently underestimated.

Discussion

This analysis reveals significant discrepancies between estimates of population changes deduced from trapping methods, and those predicted on the basis of observed demographic parameters derived from radio-telemetry studies. While the discrepancies are consistent (there was not a single expectation that exceeded the observed population estimate) and the magnitude in some cases substantial, evaluating their significance is problematic. Despite improvements made to the program CAPTURE in the 1991 release, variances from the jack-knife estimator associated with estimated population sizes are sometimes suspected of being negatively biased (Rosenberg, Overton & Anthony 1995; J.D. Boulanger & E. Rexstad, personal communication). For these reasons we have attempted to be conservative in our statistical evaluation of the encountered discrepancies. For a specified standard deviation, Chebyshev's inequality applies to the maximally dispersed distribution and the bootstrapping procedure is conservative in a number of respects (variances in initial population sizes are overestimated by the exponential gamma distribution, by a factor of at least two for the spring to spring predictions; and variances around litters sizes are considerably overestimated by use of a Poisson distribution).

While survival parameters were estimated from telemetry studies and therefore do not confound dispersal with mortality, we recognize that we have omitted the effects of dispersal from the census study. We first ask if the observed underestimation in population growth might be explained by immigration into our study areas. Because the snowshoe hare cycle is synchronous over most of Western Canada and Alaska (Keith 1990), there are unlikely to be any large scale movements into the study area. However, there are certainly small scale movements within the study area. In particular, areas provided with supplemental food in the form of rabbit feed attract immigrants (Boutin 1984). The discrepancies in Food 1 and Food 2 are interpreted as a strong indication of the role of immigration in driving population changes in supplemental food areas. This is shown particularly clearly in Table 4c for the winter period during which numbers on the food grids fell only slightly, in spite of all the winter losses of radio-tagged hares (Table 1).

The control areas also show an underestimation of population increase from 1995 to 1996 and this cannot be explained by movements. We can see no reason to expect immigration into the control grids and we reject this hypothesis to explain the discrepancies. This leaves only four possibilities: (i) that reproductive parameters are underestimated; (ii) that adult survival is underestimated; (iii) that juvenile survival after weaning is underestimated; and (iv) that juvenile survival

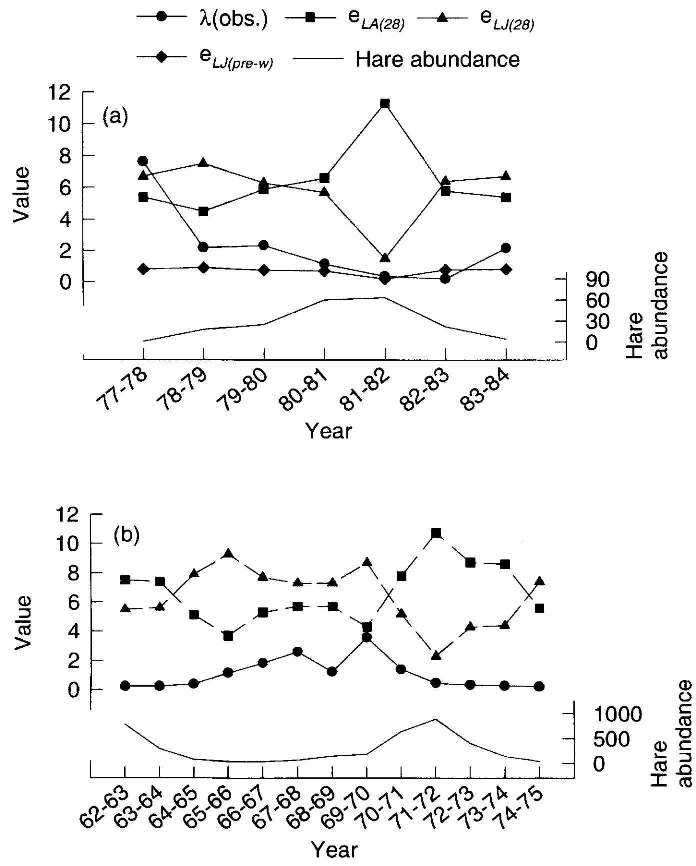

Fig. 2. Elasticities for the demographic parameters evaluated over a snowshoe hare cycle. (a) a Kluane population over the years 1977–84, data from Krebs *et al.* (1986); (b) a population from Rochester, Alberta, over the years 1962–75, data from Keith & Windberg (1978). Observed growth rates and elasticities evaluated at values of adult and juvenile postweaning survival rates observed over each annual period (other parameters held constant and as reported in Table 5). The important conclusion is that elasticities remain fairly unchanged throughout the cycle except during years of population crash, when adult survivorship replaces juvenile postweaning survivorship as the most sensitive parameter.

before weaning is underestimated. We reject the idea that reproductive parameters are biased, because they are at or above similar estimates available in the literature and agree with independent data from road-killed autopsies (C.I. Stefan, unpublished data). Also, because the elasticities of litter sizes are all very low, it is unlikely that any believable change in these reproductive estimates could balance the demographic equation.

Adult survival estimated from mark–recapture models like Jolly–Seber have, in the past, underestimated adult survival estimated from radio-telemetry by as much as 15% (Boutin & Krebs 1986). We therefore predict that using trapping data to estimate survival as opposed to telemetry would result in an even greater underestimate of growth rate. W. Hochachka (unpublished information) compared adult hare survival of individuals that were radio-collared and those not collared in the same population and showed that hare survival was decreased by radio-collaring. W. Hochachka (unpublished information) speculated that the trauma of live-trapping was the major cause of this additional mortality, because hares that were captured more often suffered a greater reduction in survival. Hare mortality rates might also be increased in the live-trapping areas because predators were attracted to these areas in winter as a result of ease of access on packed snowshoe trails (Murray & Boutin 1991). We would thus tentatively suggest that the adult survival rates presented in Table 1 might be underestimated by no more than 5%. If we increase adult hare survival by 5% (from 0·923 per 28 days to 0·969), we still cannot balance the demographic equation (Fig. 3a,b). It is concluded that a negative bias in adult survival is part of the reason for the observed discrepancy on the control grids, but it is unlikely to be the whole explanation.

It is not clear which of the two components of juvenile survival could be biased. We can only observe that, in general, the postweaning survival of juveniles is nearly as high as adult survival, and because on biological grounds it seems likely that being a juvenile is at least slightly more risky than being an experienced adult, we would guess that the observed postweaning survival estimate is accurate to within 1–2%. We suspect that the preweaning survival estimate is also nega-

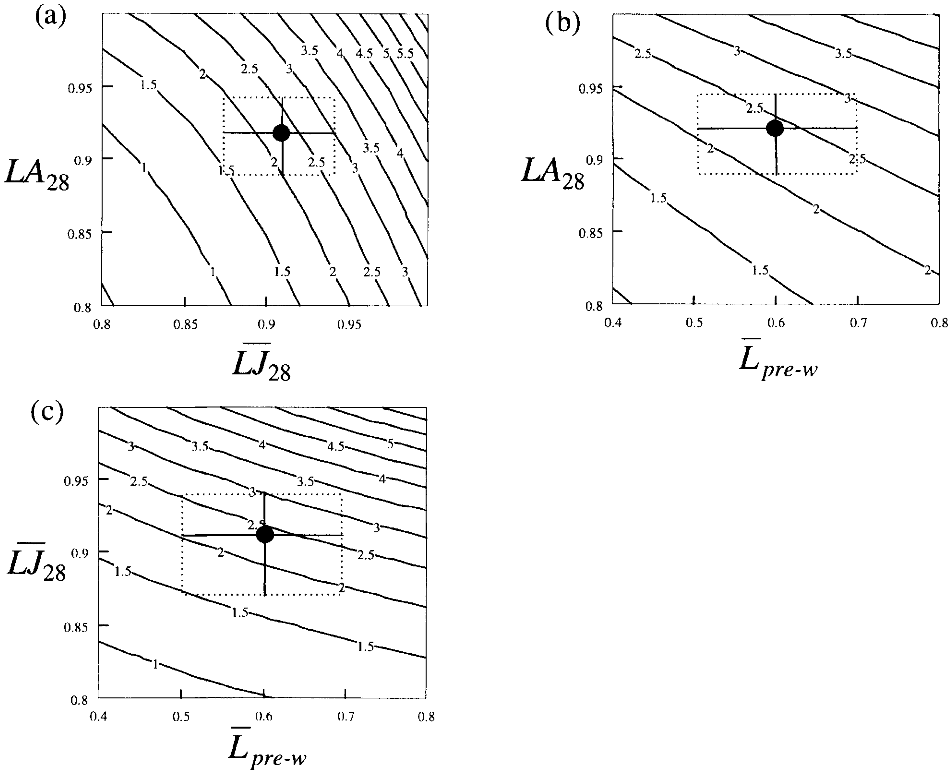

Fig. 3. Contour plots illustrating the dependency of hare population growth rate, λ, on the three critical demographic parameters as revealed by the sensitivity analysis. (a) juvenile postweaning survival pooled across litters ($\overline{LJ}_{28}$), and adult survival (LA_{28}); (b) juvenile preweaning survival ($\overline{L}_{pre\text{-}w}$) pooled across litters, and adult survival (LA_{28}); (c) juvenile preweaning survival ($\overline{L}_{pre\text{-}w}$) pooled across litters, and juvenile postweaning survival ($\overline{LJ}_{28}$) pooled across litters. Demographic parameters calculated from combined data for all three control grids. The predicted value of λ (from equation 6) for these grids was 2·4, the observed average value of λ was 3·8. The dashed boxes indicate the extent of the 95% CI for the parameter estimates in each dimension. Note that even at the upper 95% limit for each parameter, the boxes do not overlap with the $\lambda = 3{\cdot}5$ contour.

tively biased. We do not know this for certain, but we anticipate that the disturbance of caging pregnant females and moving the marked juveniles back into the field may increase losses at least slightly in this life stage. If adult survival rates were increased by 4%, and juvenile postweaning survival by 2%, then preweaning survival would require $\approx$ 13% increase to explain the observed discrepancies. However, the growth rate is extremely sensitive to juvenile postweaning survival, a 3% increase in this parameter would require only a 5% increase in preweaning survival rates.

In conclusion, the demographic equation does not balance for snowshoe hares. This imbalance is most credibly corrected by making small changes ($<$ 5%) to all survival parameters. We think that hare survival estimated from radio-telemetry is likely to be negatively biased, and that the effects of caging pregnant females prior to parturition may have a negative impact on estimation of preweaning survival. We suggest that additional work needs to be undertaken to determine exactly why radio-collared hares suffer added mortality and to reduce any impact of live-trapping on individuals. The use of alternative methods to estimate recruitment would also be useful to increase the accuracy of our estimates of preweaning mortality.

The sensitivity analysis is fully consistent with longstanding conclusions that juvenile survivorship is of prime importance in determining changes in snowshoe hare populations (Green & Evans 1940; Keith & Windberg 1978; Krebs *et al.* 1986). It should be noted that the derivatives in Table 5 are the slopes of curves evaluated at particular parameter values, and are likely to be misleading if used for very large parameter perturbations. The model makes few questionable assumptions. For the year from March 1995 to March 1996 we are satisfied that adult survivorship is well modelled as a constant value independent of seasonal modification (see Fig. 1). However, this may not always be true, and past studies have found autumn and early winter survivorships to correlate more highly with growth rate than survival rates over other seasons (Krebs *et al.* 1986). The model assumes that all demographic parameters apply equally and independently to members of the population, i.e. that no covariances exist among demographic parameters as they apply to individuals at any particular time. The existence of such covariances could conceivably introduce systematic bias into the predictions of the model.

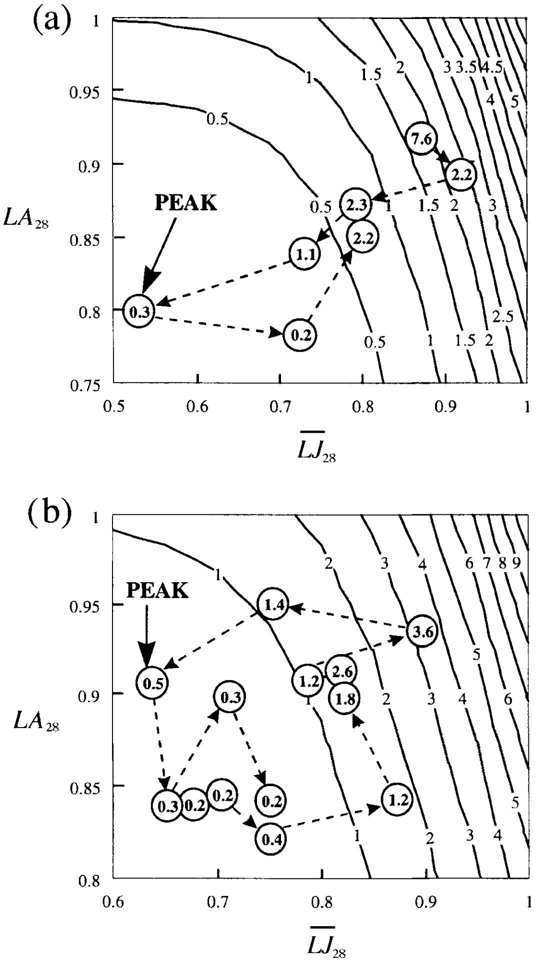

Fig. 4. The same as Fig. 3(a), but showing extended axes. Plotted on (a) are combinations of $\overline{LJ}_{28}$ and LA_{28} obtained from trapping data for a Kluane hare population for the years 1977–84. The numbers inside the discs indicate the observed value of λ for that year. The sequence starts with an observed value of 7·6 for 1977–8, and ends with a value of 2·2 for 1983–4. The hare population peaked with an observed $\lambda = 0{\cdot}3$ in 1981–82. Note that once again, there is a consistent tendency to underestimate observed growth rates. All other demographic parameters used in the calculation of the predicted growth rates are for the year 1995–6 and are shown in column 2 of Table 5. (b) Combinations of $\overline{LJ}_{28}$ and LA_{28} obtained from the study by Keith & Windberg (1978). The sequence starts with an observed growth rate of 0·2 for 1962–3 (the middle disc in the lower left hand corner) and ends with a value of 0·2 in 1974–5.

Cyclic snowshoe hare populations are highly dynamic and it is perhaps not surprising that their growth rates are most sensitive to juvenile survivorship. Only in crash years, when juvenile survivorship is so low that small changes make no difference, does λ become more sensitive to adult survival rates.

Previous studies have found correlations between measures of survival and population growth rate; for example Krebs *et al.* (1986) observed correlations between adult autumn survival and population growth rate ($r = 0{\cdot}49$), and juvenile autumn survival with population growth rate ($r = 0{\cdot}60$). Keith & Windberg (1978) observed analogous correlations of 0·65 and 0·8. In this study correlations were noted between observed and expected growth rates (where expected growth rates are generated using equation 6) of 0·67 and 0·91 for these two data sets, respectively. That it is possible to achieve these correlation values without accounting for annual variation in natality is indicative of the insensitivity of growth rate to these parameters. The possibility that these populations are sensitive to different demographic parameters at different stages of the cycle (see Fig. 2) may help to explain why correlation coefficients between growth rates and different survival rates are not higher. High sensitivities are a prerequisite for tight correlations.

We encourage other population ecologists to utilize simple methods to check on the accuracy of their estimates of demographic components. In particular, the data presented here suggest considerable caution should be used in inferring missing demographic components from the demographic equation. Using changes in numbers and estimated death rates to infer birth rates can lead to misleading interpretations of demographic change if the death rate estimates are strongly biased.

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