

Modeling the reintroduction of lynx to the southern portion of its range

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Abstract

We modeled populations of lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*) to determine prey densities required for persistence of lynx translocated to the southern portion of the species' range. The models suggested that a density of 1.1–1.8 hares/h is required for lynx persistence; these densities are higher than those reported for most hare populations across the USA. We found that lynx dispersal and density-independent mortality substantially increased the hare density required for lynx persistence. Reintroduction success was associated with number of release events, total number of animals released, and timing of release relative to the phase of the hare population cycle. However, no release protocol could override the negative effects of low prey density or high population losses. We conclude that successful lynx reintroduction requires high hare densities and minimal anthropogenic disturbance; few areas in the contiguous USA currently possess such qualities.

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1. Introduction

Reintroduction, the act of releasing animals to regions of their native range where populations are extirpated (IUCN, 1995), has become an important, albeit controversial, form of wildlife management (Griffith et al., 1989; Brocke et al., 1992; Reading and Clark, 1996; Wolf et al., 1996). Given the limited success and substantial cost of reintroduction efforts, and the threatened/endangered status of many reintroduced species, restoration programs should endeavor to ensure the successful establishment of released populations. However, few operational guidelines currently exist to maximize the success of such release programs.

Griffith et al. (1989) and Wolf et al. (1996) found that the most important factor determining reintroduction

success was the availability of high quality habitat. In addition, proximity to core of historic range, number of animals released, and length of the reintroduction program can further influence translocation success (Griffith et al., 1989; Wolf et al., 1996). However, given the variability in quality of release sites and in demographic attributes among released species, factors identified as having been important in past reintroductions may be of limited importance to current or future release programs. Thus, the World Conservation Union recommends that species being considered for reintroduction should be subject to population modeling prior to any release, in order to determine an optimal release strategy (IUCN, 1995).

In general, population viability analysis is useful for identifying variables important to species reintroduction. Several studies have made use of such tools to produce desirable release protocols (e.g., Lubow, 1996; Bustamante, 1998; Saltz, 1998). Such modeling efforts are especially important for certain taxa, such as carnivores, because of their substantial spatial requirements and complex relationships with prey and the environment (Griffith et al., 1989; Yalden, 1993; Wolf et al., 1996).

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The Canada lynx, *Lynx canadensis*, occurs throughout the boreal forests of Canada and Alaska, but populations in the contiguous USA, which historically inhabited the coniferous forests of the Rocky Mountains, the upper Midwest, and the Northeast, exhibit patchy distribution and low numbers (US Fish and Wildlife Service, 2000). In March 2000, lynx populations in the USA were listed as threatened under the Endangered Species Act (USA Fish and Wildlife Service, 2000), an action that is testament to the need to restore viable lynx populations to areas where numbers currently are depressed or extirpated. Accordingly, Colorado Division of Wildlife reintroduced lynx native to Canada and Alaska within their state boundaries during 1999 and 2000 (USA Fish and Wildlife Service, 2000; Shenk, 2001), and Idaho recently considered a similar effort (W. Melquist, Idaho Department of Fish and Game, personal communication). However, an earlier (1988–1992) attempt to reintroduce lynx to Adirondack Park, New York, resulted in equivocal success, with several lynx dying from collisions with vehicles while others dispersed beyond park boundaries. At present, the occurrence of lynx in New York remains suspect (Brocke et al., 1992; USA Fish and Wildlife Service, 2000). Thus, there is a need to determine factors potentially associated with the success of lynx reintroduction and recovery in the southern portion of their range.

We modeled the population dynamics of lynx and their main prey, snowshoe hares, *Lepus americanus*, to evaluate release protocols and habitat characteristics (hare densities) that would promote lynx population persistence following translocation. We predicted that the total number of lynx released and the number of release events both would influence reintroduction success positively (Griffith et al., 1989; Wolf et al., 1996).

2. Model and results

2.1. Model parameters

For many carnivore populations, prey abundance is a critical characteristic of habitat quality (Carbone and Gittleman, 2002). Lynx are specialist predators of snowshoe hares (Saunders, 1963; Nellis et al., 1972; Brand et al., 1976), and throughout North America the distribution, habitat use, and population dynamics of lynx and hares are known to be integrally linked (McCord and Cardoza, 1984; McKelvey et al., 2000; Mowat et al., 2000). Although lynx may consume alternative prey when snowshoe hares are scarce, hares make up the largest portion of the lynx diet in nearly all studies (see Quinn and Parker, 1987; Koehler and Aubry, 1994; Aubry et al., 2000 for reviews). Thus, lynx recruitment, survival, and population dynamics are

closely tied to hare availability both in northern (Quinn and Parker, 1987; Poole, 1994; O'Donoghue et al., 1997; Mowat et al., 2000) and southern (Koehler, 1990; Koehler and Aubry, 1994; Apps, 2000; Aubry et al., 2000) portions of the lynx range. Indeed, Royama (1992) and Stenseth et al. (1997) demonstrated, using time-series analysis of trapping returns from northern Canada, that lynx populations are solely regulated by prey (i.e., hare) availability. Accordingly, we considered that a model characterizing lynx demographic responses to habitat quality in the context of hare densities was the appropriate method for evaluating lynx release protocols.

We used data from studies of northern (i.e., Canada and Alaska) lynx and hare populations to parameterize our model, assuming that (1) lynx reintroduced to the United States would originate from northern locales, and (2) translocated lynx would exhibit similar ecological and demographic relationships with prey as in their native (northern) habitat. Thus, while lynx in southern habitats may differ ecologically from those in northern habitats, we believed that animals emanating from a particular geographic area would retain their original behavioral traits and relationships to prey.

We established relationships between lynx survival and productivity relative to hare densities by obtaining estimates for each of the demographic attributes of interest from the literature (Appendix A). This procedure enabled us to pool data from multiple studies to examine the relationship between lynx demographic attributes and hare density estimates. The published studies were conducted throughout the northern portion of the lynx range, and included lynx/hare population fluctuations characterized by a variety of amplitudes (e.g., O'Donoghue et al., 1997; Slough and Mowat, 1996). Thus, the data used to parameterize our model are representative of lynx/hare populations under a variety of ecological conditions. We used a logistic equation (i.e. sigmoidal curve) to describe the relationships between lynx demographics and hare densities because (1) survival and productivity should increase monotonically with increasing hare densities, but (2) there must be physiological limits to survival and productivity that are largely independent of prey density (i.e., survival cannot be higher than 1 or lower than 0; productivity cannot exceed the physiological capabilities of female lynx). To ascertain the validity of the logistic equation relative to other candidate models, we compared data-fit among a suite of potentially relevant equations using Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Burnham et al., 1998; Anderson et al., 2000). We focused our analyses on type I (linear) and type II (exponential association, power fit, etc.) functions (Table 2; see Messier, 1994; O'Donoghue et al., 1998), but limited our comparisons to equations that produced a biologically realistic relationship (i.e.,

Table 1

Correlation coefficients of best-fit equations for the relationship between each demographic variable and various indices of snowshoe hare abundance^a

Demographic parameter	Hare density (time <i>t</i>)	Hare density (<i>t</i> –1)	Per-capita hare density	% Change in hare density $\frac{[t-(t-1)]}{(t-1)}$
Adult survival	$r = 0.27^b$	–	$r = 0.53^b$	$r = 0.82^a$
Kitten survival	$r = 0.96^a$	$r = 0.59^b$	–	$r = 0.69^b$
Adult productivity	$r = 0.82^a$	$r = 0.51^b$	$r = 0.30^b$	$r = 0.49^b$
Yearling productivity	$r = 0.81^a$	$r = 0.18^b$	$r = 0.12^b$	$r = 0.76^{ab}$
Dispersal	–	–	–	$r = 0.45$

^a For the relationships between adult and yearling productivity and same-year hare densities, the correlation coefficients are given for the logistic equation, rather than the best-fit equation (see text). The absence of a correlation coefficient indicates that no biologically realistic relationship fit the data. Within each demographic parameter, coefficient estimates with different superscripts are different statistically at the $\alpha = 0.05$ level (see text for description of statistical tests).

monotonically increasing survival or productivity over the range of hare densities considered).

We also examined the relationship between lynx dispersal and hare density. Because we expected dispersal to be a monotonically decreasing function of hare abundance with a lower limit of zero, we focused our curve-fitting on hyperbolic and similar relationships, while comparing the models to other curve-fits using the above procedures. In all cases, changes in AIC_c values > 2.0 were considered significant statistically (Burnham et al., 1998).

In some circumstances, the relationship between a particular demographic parameter and same-year hare densities was non-existent, weak, or biologically unrealistic (see below). Therefore, to more fully assess lynx demographic responses, we also considered time-delayed (*t*–1) hare densities, hare densities per capita (lynx), and annual change in hare densities as alternate correlates. For each demographic variable, we chose the measure of hare abundance that was the best predictor of the demographic response, as determined via the correlation coefficient (*r*) of the best-fit equation.

However, for each demographic variable, we used bootstrapping of the best-fit equations to compare statistically the relationships between the different measures of hare abundance. An equal number of samples were drawn (with replacement) from the original data, the best-fit equation was re-fit to the new data set, and the new correlation coefficient was calculated. This procedure was repeated 1000 times for each relationship, and the 95% rank interval of the distribution of the differences in correlation coefficients was examined. If the rank interval did not contain 0, then we concluded that the strength of the two relationships was different statistically (Table 1).

Hare density of the same year was the best predictor of kitten survival, adult productivity, and yearling productivity (Table 1). Yet, for adult survival, our analysis revealed that the best association was with annual change in hare densities (Table 1; Fig. 1). Previous researchers have noted that lynx survival typically is poor during the decline in hare numbers but is high during the low phase of the hare cycle (Breitenmoser et al., 1993; O’Donoghue et al., 1997); this observation

Table 2

AIC_c values of the logistic and other equations fitted to lynx demographic data^a

Equation name	Equation	Adult survival	Kitten survival	Adult productivity	Yearling productivity	Dispersal
Logistic	$y = \frac{a}{1 + be^{-cx}}$	–111.55	–76.20	–0.56	8.47	–61.77
Rational function	$y = \frac{a + bx}{1 + cx + dx^2}$	–107.37	–	0.77	–	–
Quadratic	$y = a + bx + cx^2$	–	–63.67	–	9.85	–
Linear	$y = a + bx$	–92.72	–61.33	5.54	7.24	–60.40
Exp. Assoc. (1)	$y = ae^{bx}$	–91.83	–51.44	18.31	11.63	–
Exp. Assoc. (3)	$y = a(b - e^{-cx})$	–89.97	–61.92	0.22	11.06	–57.53
Constant only	$y = a$	–86.83	–36.26	40.10	17.21	–61.43
Michaelis–Menton	$y = \frac{ax}{b + x}$	–	–62.45	–0.99	7.84	–
Exp. Assoc. (2)	$y = a(1 - e^{-bx})$	–0.93	–62.61	–1.75	7.84	–41.55

^a The lower the AIC_c value, the better the equation fit the data. The absence of an AIC_c value indicates the fitted relationship was biologically unrealistic (e.g., kitten survival must be a monotonically increasing function of hare density), and thus was ignored. Demographics were correlated with hare densities from the same year, except for adult survival and dispersal, which were correlated with % annual change in hare densities.

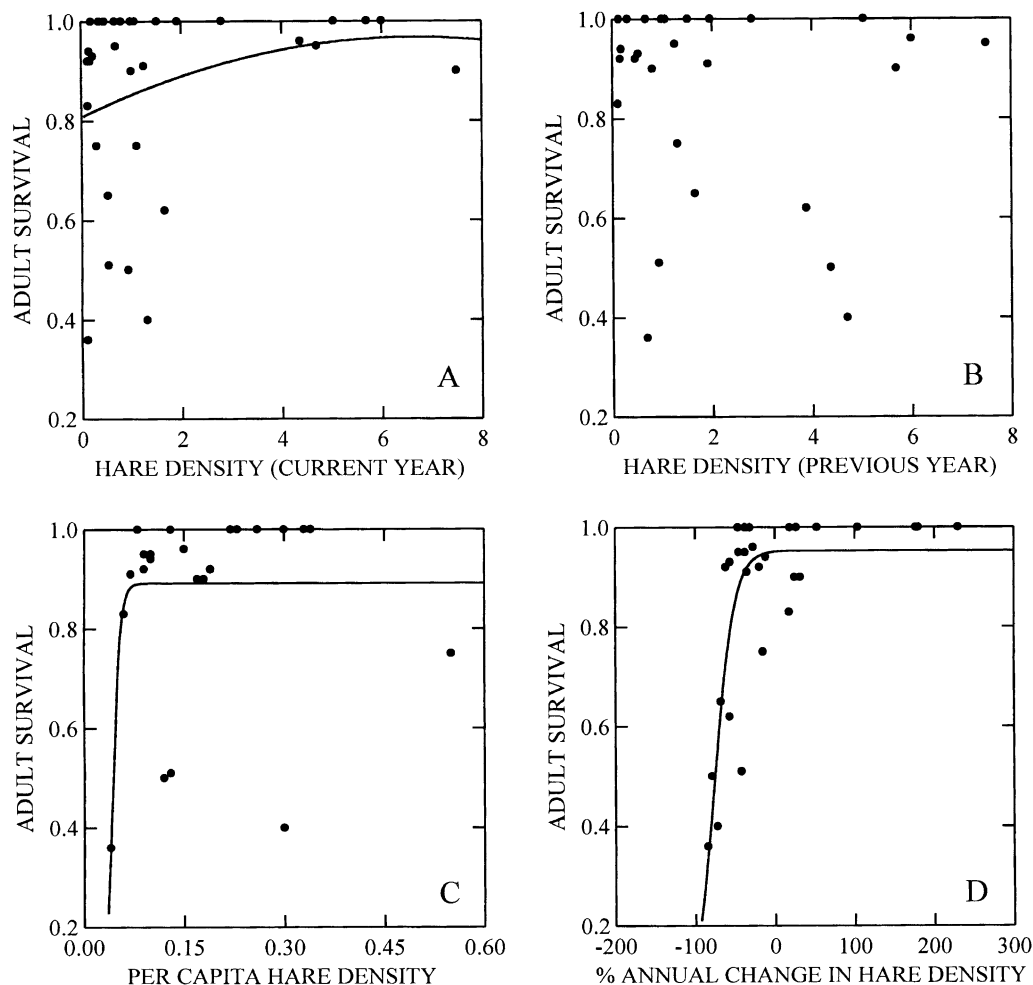


Fig. 1. Relationships between adult lynx survival and various measures of snowshoe hare abundance. Each data point represents a single year from a published lynx study. Lines represent the equations that fit the data best, based on AIC_c values. (a) Adult survival versus same-year hare densities; best-fit equation was a quadratic equation ($r=0.27$, $P < 0.001$). (b) Adult survival versus previous year hare densities. (c) Adult survival versus per-capita hare densities; best-fit equation was a logistic equation ($r=0.53$, $P < 0.001$). (d) Adult survival versus % annual change in hare density; best-fit equation was a logistic equation ($r=0.82$, $P < 0.001$). The relationship between adult survival and % change in hare densities was used in the model:

$$S_3 = \frac{0.9487}{1 + 0.0021e^{-8.0086\left(\frac{h_t - h_{t-1}}{h_{t-1}}\right)}}$$

supports the modeled relationship between survival and change in hare density. Similarly, dispersal was only associated with annual change in hare density (Table 1). Therefore, we used the relationships between annual change in hare density and survival or dispersal in our modeled system. We also used the relationship between adult survival and change in hare density to represent yearling lynx survival, due to the paucity of published yearling data. For all other demographic variables, we used the relationships with same-year hare densities.

For all demographic variables, the logistic equation provided the best fit to the data, except in the cases of adult and yearling productivity (Table 2; Figs. 1 and 2). For adult and kitten survival, the logistic equation was statistically superior to all other equations (all $\Delta AIC_c > 4.18$ in both cases; Table 2), while for dispersal the logistic equation was only qualitatively superior to all

other equations (all $\Delta AIC_c > 0.34$; Table 2). For both yearling and adult productivity, the fit of the logistic equation was not best among tested equations, but was statistically indistinguishable from equations with better fit to the data (Table 2). Thus, because of its intuitive appeal as well as its generally strong ability to describe lynx demographics in relation to hare densities, we used the logistic equation to describe all relationships between lynx demographics and hare density (Figs. 1 and 2).

The relationships depicted in Figs. 1 and 2 support the contention that lynx are primarily snowshoe hare specialists, but are able to utilize alternative prey when hares are scarce (see also O'Donoghue et al., 1998; Aubry et al., 2000). If lynx did not rely heavily on snowshoe hares, then survival and productivity likely would not be related as closely to hare density. However,

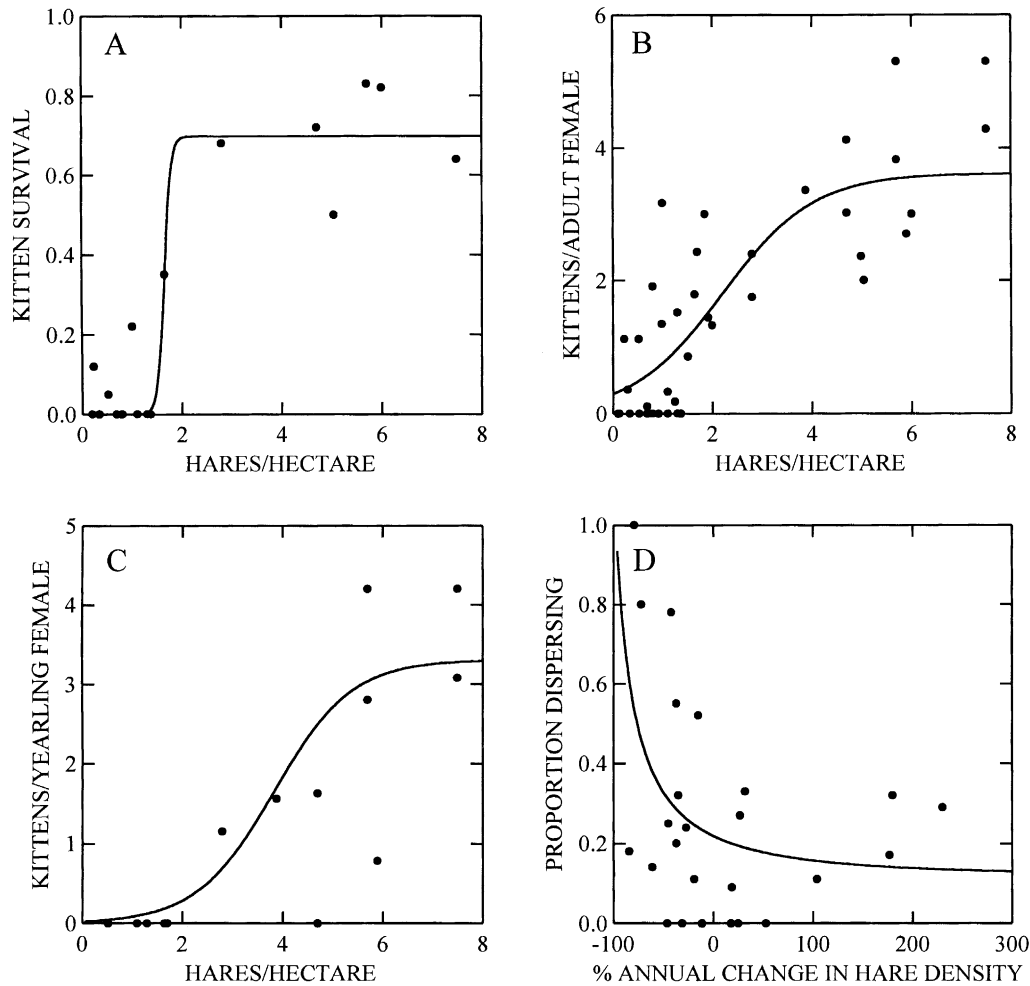


Fig. 2. Relationships between various lynx demographic parameters and hare abundance. Each data point represents a single year from previous lynx studies. (a) Kitten survival versus hare density: $S_1 = \frac{0.6984}{1+2.63 \times 10^{10} e^{-14.5421h}}$; $r=0.96$, $P < 0.001$. (b) Productivity of adult female lynx (# kittens produced/female, including non-productive females) versus hare density: $F_2 = \frac{3.6121}{1+11.1641 e^{-1.0897h}}$; $r=0.82$, $P < 0.001$. (c) Productivity of yearling female lynx versus hare density: $F_3 = \frac{3.3059}{1+142.8857 e^{-1.0367h}}$; $r=0.81$, $P < 0.001$. (d) Lynx dispersal versus % annual change in hare density: $D = \frac{0.1233}{1-0.4363e^{-0.7164\left(\frac{h_t-h_{t-1}}{h_{t-1}}\right)}}$; $r=0.45$, $P < 0.001$.

if lynx were obligate predators of snowshoe hares, unable to utilize alternative prey, then all lynx productivity and survival curves should decrease to zero with declining hare densities, which not all do (Figs. 1 and 2). Thus, our parameter equations incorporate, to a certain extent, the use of alternative prey by lynx at low hare densities. Visual inspection of Figs. 1 and 2 suggests that kitten survival is the demographic factor that is most negatively influenced by low hare densities; this interpretation is supported by authors who have noted that when hares are scarce, poor recruitment likely is the primary determinant of lynx population decline (Koehler and Aubry, 1994; Mowat et al., 2000).

2.2. Deterministic model

We used each of the generated relationships (Figs. 1 and 2) to calculate lynx survival and reproductive rates relative to site-specific hare densities and annual changes

in hare densities. These demographic rates were then used in a standard Leslie population projection matrix:

$$A_h = \begin{pmatrix} 0 & 0.5F_2(h) & 0.5F_3(h) \\ S_1(h) & 0 & 0 \\ 0 & S_2(\Delta h) & S_3(\Delta h) \end{pmatrix}, \quad (1)$$

where A_h is the population projection matrix at hare density h . We assumed that kittens are born with sex ratio at parity and we only modeled females in the population. Furthermore, in our basic, deterministic model, hare densities do not change from year to year, and thus the yearling and adult survival rates were those estimated for a 0% change in hare density (potential importance of changing hare density is addressed in cyclic and stochastic models, see below). Finally, in this initial model, we assumed that the population was closed, or that immigration equaled emigration, and thus we did not include the effects of dispersal in our calculations. Thus, the basic deterministic model was a

simple discrete-time model with increments to the population occurring annually.

We chose not to include density-dependence in any of our model simulations because (1) the lack of strong relationships between lynx demographics and per-capita resource abundance suggests that density-dependent effects probably are minimal in lynx–hare systems, and (2) reintroductions typically involve relatively few animals released into a relatively large area. Thus, the probability that released individuals will compete for food or space likely is small. In preliminary analyses, model results were altered negligibly by inclusion of density-dependence.

For the deterministic model, a successful reintroduction was considered to be one in which the finite rate of increase in lynx numbers (λ) was at least 1.0, implying population persistence. In the deterministic models, λ at any particular hare density was determined from the dominant eigenvalue of the matrix at that hare density (Caswell, 2001).

The deterministic model predicts that 1.52 hares/h are required for the positive growth of a reintroduced lynx population. For comparison, Keith (1990) found that density estimates of adult hares during the spring–summer period in southern, “non-cyclic” populations ranged from 0.01 to 2.06 hares/h, whereas estimates that included juveniles (taken during summer–fall) ranged from 0.02 to 3.95 hares/h. Murray (2000) later showed that hare densities from studies in the contiguous USA and southeastern Canada (latitude $< 49^\circ$ N) averaged 0.81 ± 0.16 (mean \pm SE, $n = 14$) and 1.38 ± 0.36 ($n = 12$) hares/h in spring and fall, respectively.

Because southern hare populations may undergo periodic cycles of low amplitude (Hodges, 2000; but see Murray, 2000), we also modeled cyclic hare populations, with amplitudes ranging from those typical of cyclic boreal populations to smaller fluctuations poten-

tially experienced in the southern range. We used a sinusoidal equation to depict cyclic hare population trends:

$$h_t = \bar{h} + \frac{\text{magnitude}}{2} \cos\left(\frac{2\pi t}{10}\right), \quad (2)$$

where magnitude is equal to the difference in high and low hare densities (twice the amplitude of the sine wave), and t is time in years. Although natural hare population cycles tend to have prolonged low phases (Boonstra et al., 1998), the sinusoidal equation often has been used in models of hare dynamics due to its adequacy in describing hare population trends (e.g., Bulmer, 1974). Indeed, a test of the fit of the sinusoidal curve to published hare cycle data (Meslow and Keith, 1968; Krebs et al., 1986; Slough and Mowat, 1996; O’Donoghue et al., 1997) revealed a strong fit (r ranged from 0.96 to 0.99 for all data sets). Using an alternate method of generating the hare cycle in our modeled system probably would not change our results substantially.

We modeled a range of cycle magnitudes from 0.5 to 8.0 hares/h (differences between high/low hare densities); these values are representative of those typically seen in cyclic populations (e.g., Keith and Windberg, 1978; Keith, 1990; Boutin et al., 1995). In our modeled system, lynx demographic rates were estimated annually from the cyclic hare densities and our parameter relationships. The demographic rates were then used in a population projection, and the geometric mean λ was measured over 100 years.

In the presence of cyclic hare populations, the mean hare density required for lynx population persistence first decreases then increases with increasing cycle magnitude (Table 3). However, at cycle magnitudes ≥ 6.0 hares/h, the minimum mean hare density required for lynx population persistence generates a hare cycle in

Table 3
Minimum mean hare density required for lynx reintroduction success in a variety of cyclic hare populations^a

Cycle magnitude	Low hare density	Mean hare density	High hare density	High/low hare density
0.00	1.52	1.52	1.52	1.00
0.50	1.16	1.41	1.66	1.43
1.00	0.72	1.22	1.72	2.39
1.50	0.31	1.06	1.81	5.84
2.00	0.15	1.15	2.15	14.33
2.50	0.09	1.34	2.59	28.78
3.00	0.08	1.58	3.08	38.50
3.50	0.07	1.82	3.57	51.00
4.00	0.06	2.06	4.06	67.67
4.50	0.05	2.30	4.55	91.00
5.00	0.02	2.52	5.02	251.00
5.50	0.01	2.76	5.51	551.00
6.00	0.00	3.00	6.00	–

^a Units for all columns except high/low hare density are hares/h. Low and high hare densities are the trough and peak of the cycle represented by the particular cyclic magnitude and minimum mean hare density. At or above cycle magnitudes of 6.0 hares/h, the minimum required mean hare density produces hare populations that go extinct during the low in the cycle.

which hares go extinct during the low phase in the cycle. Thus, the minimum mean hare density required for lynx population persistence is lower than the minimum mean density possible in a cycle with magnitude greater than 6.0 hares/h. These results imply that in our modeled system, lynx population persistence is assured at high cycle magnitude.

2.3. Parameter uncertainty

The regression equations used to describe lynx demographics are characterized by substantial error (Figs. 1 and 2). However, our generated relationships have relatively good correlation coefficients despite the fact that the data were collected from different locales, during different phases of the hare cycle, and using different methods; this fact only supports our assertion that lynx demography is determined largely by snowshoe hare abundance. However, we used bootstrapping and sensitivity and elasticity analyses to examine how slight changes in our demographic relationships would influence the results of our deterministic model. For each parameter used in the model, we randomly selected an equal number (see Appendix for sample sizes) of points (with replacement) from the original data, re-fit the logistic equation to the new data set, and examined how the minimum hare density required for lynx population persistence was impacted by the changes in parameter estimates. This procedure was repeated 100 times for each parameter, providing us with a range of estimates for the minimum required mean hare density associated with uncertainty in that parameter.

Bootstrapping indicated that the model largely was insensitive to variations in the data associated with most demographic variables; the 95% rank intervals for the threshold hare density required for lynx population persistence were similar to the estimate obtained from the deterministic model for changes in adult survival (1.47–1.57 hares/h), adult productivity (1.51–1.56 hares/h), and yearling productivity (1.51–1.53 hares/h). Alterations to the demographic relationship for kitten survival, however, resulted in a 95% rank interval for the threshold hare density required for lynx persistence of 1.15–1.88 hares/h, indicating a higher degree of uncertainty in model results due to error associated with this demographic attribute. The 95% rank interval for all bootstrapped parameters combined was 1.06 to 1.86, further supporting the notion that uncertainty in parameter estimates for kitten survival had the largest potential impact on model results. Nonetheless, the lower bound of this latter 95% rank interval exceeds hare densities seen in much of the contiguous USA (Keith, 1990; Murray, 2000).

Sensitivity and elasticity analyses suggested that λ was most impacted by changes in adult survival, especially at low hare densities (Fig. 3). Above a threshold of

approximately 1.5 hares/h, the sensitivity and elasticity of λ to adult survival decreased, and to the other parameters increased, until densities above approximately 4.0 hares/h. Above 4.0 hares/h, population growth was impacted most by absolute or relative changes in kitten survival (Fig. 3). However, such high hare densities are rarely seen for more than 2–3 years in cyclic northern populations (e.g., Slough and Mowat, 1998; Poole, 1994), and have not been reported for southern populations (Keith, 1990; Murray, 2000). Results from sensitivity/elasticity analysis coupled with our bootstrap-analysis of parameter uncertainty suggest that while the growth of our modeled lynx population is most impacted by changes in adult survival at low hare densities, our regression equation describing this demographic attribute is relatively robust to slight changes in the original data used to generate the equation.

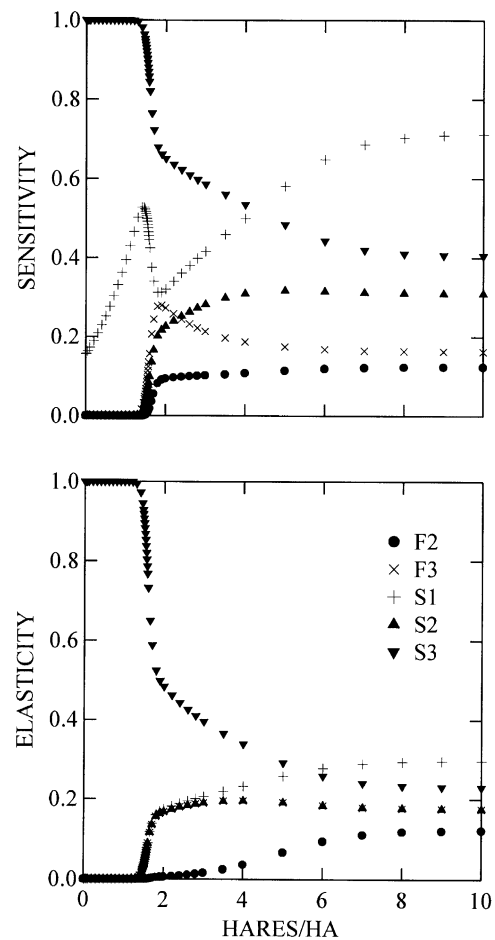


Fig. 3. Relationships between hare density and the sensitivity and elasticity of the finite rate of growth (λ) of the reintroduced lynx population in our (deterministic) modeled system. Parameters (F2, S1, etc.) represent the appropriate demographic variable and age class in the Leslie matrix.

2.4. Stochastic models

Our deterministic models may provide limited realism regarding snowshoe hare–lynx population dynamics. For example, snowshoe hare populations in the western mountains of the United States may exhibit weakly cyclic, stable, or irruptive dynamics relative to populations in Canada and Alaska (Hodges, 2000; Murray, 2000).

Accordingly, we modeled hare numbers stochastically by generating random annual hare densities according to a user-defined mean hare density and standard deviation, and the normal distribution curve. In our stochastic models, we assessed the potential population growth of our modeled lynx population and the probability of a successful reintroduction by examining population projections over 100 years; each reintroduction was iterated 500 times. The probability of success was defined as the percentage of iterations in which population persistence (i.e., geometric mean $\lambda \geq 1.0$) over 100 years was attained.

The addition of stochastic hare numbers had a small influence on the results of the non-cyclic model. In the absence of stochasticity, the relationship between hare density and probability of success was a step function, but when stochasticity was included, the relationship became logistic (Fig. 4a). The probability of lynx persistence increased between 0 and 100% within a small range of hare densities, with the width of that range expanding with increasing standard deviation in hare densities.

We also added stochasticity to hare populations that were modeled cyclically. We modeled inter-year variation in cycle magnitude by adding stochastic variation,

according to a user-defined standard deviation (variability around the sinusoidal curve) and the normal distribution. We tested a range of values for this variation up to 0.3 at cycle magnitude of 0.8 hares/h.

Modeling hares cyclically with stochastic variation about the sin curve produced similar results to modeling hares with random stochasticity. Increasing random variation in cyclic hare densities resulted in an increase in the probability of success, between 0 and 100%, within a small range of hare densities, with the width of that range expanding with increasing variation (Fig. 4b). Thus, the above simulations suggest that lynx translocation is best achieved in areas supporting a relatively high hare density and/or areas with hare cycles of moderate magnitude, but that stochastic patterns of variability in hare numbers have relatively minor impacts on lynx population persistence.

2.5. Factors associated with translocation success

Hare population trends remain poorly understood in the United States, but populations may exhibit cyclic dynamics with attenuated amplitude (Hodges, 2000; Murray, 2000). Thus, in order to test factors associated with successful lynx reintroduction, we used a cyclic model with magnitude of 0.8 hares/h and stochastic variation with standard deviation of 0.2 to depict possible demographic trends in southern hare populations. At these levels of magnitude and variation, the ratio of cyclic highs and lows would average 1.8-fold, and range from approximately 1-fold to 4-fold; these values seem to be similar to attenuated fluctuations seen in the New England States and Eastern Canada (Hodges, 2000; Murray, 2000). However, qualitative results of the

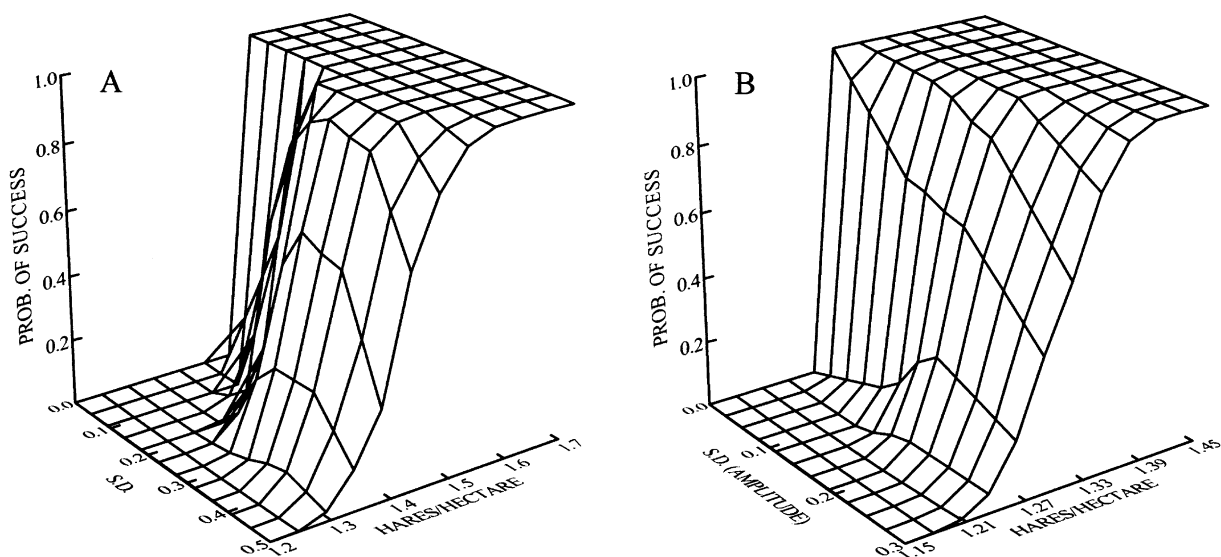


Fig. 4. Relationships between probability of successful reintroduction (success = geometric mean $\lambda \geq 1.0$), mean hare density, and variability in non-cyclic or cyclic hare densities. (a) Relationship between probability of success, mean hare density, and standard deviation in stochastic hare densities. (b) Relationship between probability of success, mean hare density, and variation in the sinusoidal equation, with magnitude of cycle = 0.8.

following model simulations are not affected by the magnitude or nature (cyclic or non-cyclic) of hare population fluctuations (except for effects of dispersal; see below).

2.5.1. Dispersal

Our initial analyses assumed population closure, an assumption that we relaxed in later model iterations, in which dispersal was examined explicitly. In a reintroduced lynx population, immigration rates should equal zero, and thus dispersal from the population may be an important source of loss of individuals (e.g., Brocke et al., 1992). Therefore, we added dispersal to our model by removing annually yearlings and adults from the population (kittens usually stay with the mother for the first year; Poole, 1995; Slough and Mowat, 1996); the proportion removed was determined from the % change in hare density from the previous year, as described by the relationship in Fig. 2.

The addition of dispersal to the model increased the hare density associated with a given probability of success by approximately 0.6 hares/h. However, given that dispersal in our modeled system is a function of the annual change in hare density (Fig. 2), the effects of dispersal are dependent on the variation in annual hare densities. If annual variation in hare densities were lower than that generated by the cycle magnitude and stochasticity used here, the effect of dispersal would be diminished. However, even with stable hare densities, dispersal increases the hare density required for reintroduction success by approximately 0.3 hares/h.

2.5.2. Human-induced losses

Because human-caused mortality (e.g., trapping, collisions with vehicles, etc.) can be a substantial source of loss in a reintroduced population (e.g., Brocke et al., 1992), we examined the effect of including such mortality on the results of the reintroduction. Insufficient evidence exists to suggest whether such mortality is likely to be density-dependent or density-independent; thus, we assumed arbitrarily that human-caused mortality would be density-independent by removing 0–60% of the population annually.

The addition of a density-independent source of loss to the population had marked effects on the results of the model. The mean hare density associated with a particular probability of success increased exponentially, with each 5% increase in density-independent population losses resulting in approximately a 10% increase in the mean hare density associated with the given probability of success. Thus, while the hare density associated with an 80% probability of population persistence was 1.34 hares/h in the absence of density-independent losses (under the above-stated model scenario), at rates of 20, 40, and 60% density-independent mortality, the mean hare density associated with the

same probability of population persistence was approximately 1.9, 2.5, and 4.0 hares/h, respectively.

2.5.3. Timing and length of reintroduction

In previous model iterations, the reintroduction occurred during the high phase of the hare cycle. We initially chose this point because of the increased availability of lynx from source populations and the increased number of prey in the release area; previous lynx transplants in New York (Brocke et al., 1992) and Colorado (Kloor, 1999; Shenk, 2001) occurred during the high phase of the hare cycle in Canada. We tested how releasing animals during different phases of the cycle affected the minimum mean hare density required for lynx population persistence in our cyclic, stochastic model. Phase of the hare cycle at time of release affected the probability of population persistence if the probability of success initially was low (maximum = 25%). The probability of success was highest if the reintroduction occurred during the decline phase of the hare cycle, followed by the low phase, high phase, and incline phase. However, the hare density associated with a given probability of success only changed minimally (maximum $\Delta = 0.05$ hares/h). These results imply that although the probability of population persistence in reintroduced lynx might be increased slightly depending on the phase of reintroduction, such actions likely cannot overcome chronically poor hare densities.

We also tested the importance of length of release program on the success of reintroduction. While keeping the total number of animals released constant ($n = 200$ lynx), we varied the number of years during which lynx were released from 1 to 40 years. If the probability of reintroduction success initially was low, that probability increased with increasing number of release efforts. However, the effect of increasing the number of releases was only marginal, with a maximum 20% increase in probability of success experienced from a 40-year increase in number of releases. The hare density associated with a given probability of population persistence only changed minimally (maximum $\Delta = 0.05$ hares/h).

2.5.4. Number of animals released

When the criterion for success in our modeled system was at least an equal number of animals after a given time period as that released (i.e., $\lambda \geq 1.0$), and demographic stochasticity was not a significant factor, then number of animals released did not influence the probability of success. However, if the success criterion was static (e.g., > 50 lynx or > 0 lynx) then the number of animals released could influence the probability of success. At low hare densities, increasing the number of lynx released may seem to provide some success over a given monitoring interval, but such changes mask the inevitable extinction in systems with poor prey availability. For example, at hare densities of 1.10 hares/h, a

reintroduction of 100 animals in our modeled system provided a high probability (95%) of having ≥ 1 lynx at the end of 100 years. However, the same reintroduction had a 0% chance of providing ≥ 1 lynx at the end of 200 years. The mean λ of the 500 modeled populations was 0.96 (± 0.01 ; 95% C.I.); thus in no case would the population persist over the long term. By comparison, a similar reintroduction at a mean hare density of 1.3 hares/h results in a high probability of success even at the end of 1000 years (99% of simulated populations had > 1 lynx). Thus, while the number of lynx released may decrease the probability of extinction due to stochastic hare numbers, the number released cannot override the negative effects of chronically poor prey densities on lynx population persistence.

The number of lynx released may be important in overcoming potential effects of demographic stochasticity. In order to explore such effects, we determined randomly the number of lynx suffering each fate (survive or die), with the probability of survival equal to that predicted by the parameter equations at the given hare density (Akçakaya, 1991). Similarly, we determined randomly the number of kittens born to adult and yearling lynx according to a Poisson distribution and the mean number of kittens per female adult and yearling, respectively (Akçakaya, 1991). We tested the importance of demographic stochasticity in our deterministic model for reintroduced populations ranging from 3–1000 lynx.

Inclusion of demographic stochasticity affected the probability of successful reintroduction of populations below approximately 250 lynx, with probabilities of success declining exponentially with decreasing release numbers (Fig. 5). However, sizeable effects (i.e. $\geq 25\%$

change) on the probability of success did not occur until release population size decreased below 50 lynx. In addition, the effects of demographic stochasticity were easily compensated for by marginal increases in prey density, with the necessary change in hare density decreasing with increasing size of the released lynx population (Fig. 5). Thus, while demographic stochasticity may have negative effects on the probability of persistence of a reintroduced lynx population, especially those populations that initially have small sizes, the effects likely are small compared to the effects of prey availability.

3. Discussion

The results of this modeling exercise suggest that, in addition to the direct effect of hare densities on lynx population demography, five factors may influence the likelihood of a successful lynx reintroduction: (1) dispersal from the reintroduced population; (2) density-independent losses, such as those potentially resulting from anthropogenic factors (e.g., trapping, hunting, and vehicle collisions); (3) phase of the prey population cycle during which the reintroduction occurs; (4) duration of the release program; and (5) number of animals released. However, the contribution of the above five factors to persistence of transplanted lynx generally is less important than the effects of hare densities.

Dispersal from the reintroduced population increases substantially the hare density associated with a given probability of success. Our analysis of dispersal suggests that its importance in reintroduced lynx populations should depend, in part, on the dynamics of the prey population. However, dispersal apparently has been an important source of population losses in the lynx reintroduction in New York and Colorado (Brocke et al., 1992; Kloor, 1999; Shenk, 2001). Release protocols exist that can potentially reduce the dispersal of translocated individuals (e.g., soft release, food provisionment, specific age, sex, and pregnancy status in the released cohort; seasonal timing of release; see Logan et al., 1996; Linnell et al., 1997). Thus, every effort should be made to reduce dispersal rates in reintroduced populations; additional research on methods of further reducing dispersal rates in transplanted animals is warranted.

In our system, if density-independent losses removed as little as 10% of the reintroduced population per year, the mean prey density required for a particular probability of success increased by approximately 20%. In general, species with relatively long lifespan and low productivity should be affected most severely by density-independent mortality (e.g., condors, *Gymnogyps californianus*, Mestel, 1993; lynx, Brocke et al., 1992; otters, *Lutra canadensis*, Erickson and Hamilton, 1988). Insufficient data exists to suggest whether human-caused

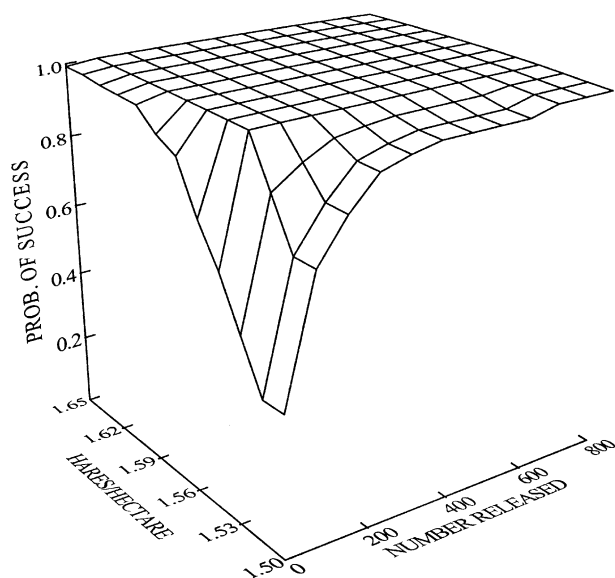


Fig. 5. Effect of demographic stochasticity on probability of success. Without the demographic stochasticity, the probability of success is 1.0 at 1.52 hares/h, regardless of release size.

mortality is density-dependent or density-independent in lynx. However, regardless of the nature of the relationship, human-caused mortality has been substantial in past lynx reintroductions: of 96 lynx reintroduced to Colorado in 1999–2000, at least 12 (12.5%) died within a few years of release due to collisions with vehicles, shooting, or other anthropogenic causes (Shenk, 2001). Similarly, collisions with vehicles allegedly were the primary determinant of lynx reintroduction failure in New York (Brocke et al., 1992; Kloor, 1999). Even in the presence of overwhelming public support and limits on human activities in release areas, anthropogenic factors may still contribute to mortality. Nonetheless, given the relatively large effect that small increases in density-independent losses can have on reintroduced populations, every effort should be made to minimize such losses.

Our model predicts that releasing lynx during the decline phase of a cycle may have a positive impact on reintroduction success. Intuitively, releasing lynx when prey are most abundant should produce the most positive results. In our model, however, lynx released during the decline phase of the cycle quickly experienced increasing prey numbers for an extended period of time, which should be demographically advantageous early in a reintroduction program, particularly for kitten survival. Alternatively, lynx released during the high or incline phases of the cycle should quickly experience an extended period of declining or low hare numbers (i.e., reduced adult survival and productivity, no kitten survival). Similarly, lynx translocated from Canada during the peak in hare numbers likely will be thrust into areas with low prey densities, which effectively would constitute a large negative change in hare densities, and thereby should reduce adult survival. Given the relatively stable hare populations in the USA, lynx translocated from Canada during the low in hare numbers likely would experience a relatively smaller change in hare densities, which should decrease initial starvation and dispersal rates.

A number of reintroduction programs have attributed their success, at least in part, to a large sample of released animals and/or long-lasting release programs (e.g., Erickson and Hamilton, 1988; Smith and Clark, 1994). However, Griffith et al. (1989) found that the effects of increasing release numbers on probability of success quickly becomes asymptotic and, therefore, difficult to justify from a simple cost standpoint. Our results support and expand upon these conclusions. In our modeled system, habitat quality (i.e., prey abundance) was much more important than number of animals released or length of the reintroduction program. Furthermore, releasing large numbers of animals may only increase the probability of attaining some arbitrary criterion of success (e.g., $N > 10$), but not increase the probability of attaining true population persistence

($\lambda > 1.0$). Indeed, in many of the translocations reviewed by Griffith et al. (1989), the reintroduced population was monitored only for a short period of time (i.e., < 20 years), implying that greater numbers of released animals only may have made reintroduction programs ‘appear’ more successful. Thus, assessing the rate of population change following transplant should be more revealing about reintroduction success than a simple enumeration of the population after an arbitrary time period.

Habitat characteristics often are much more important to the success of a reintroduction than release protocols (Griffith et al. 1989; Wolf et al. 1996). Consistent with that theme, past carnivore reintroductions often have been preceded by field investigations of prey population ecology (e.g., Brocke et al., 1992; Seidel et al., 1998). While field studies can provide necessary information on prey abundance in the release area, they reveal little about the importance of prey to reintroduction success. Population viability modeling can assist in determining the abundance of prey required for reintroduction success. For example, pellet counts (Krebs et al., 1987) were used to index snowshoe hare abundance in preparation for lynx reintroduction in Colorado (Kloor, 1999). Yet, in the absence of an associated modeling exercise, predictions regarding required prey densities, likely outcomes of reintroduction, optimal release protocols, and probable causes of failure, cannot easily be derived. In general, reintroduction efforts lacking the necessary preliminary data and analyses ultimately will provide limited inference to conservation biologists.

The models herein may be useful for determining the minimum prey abundance required for successful lynx reintroduction. Ruggerio et al. (2000) suggested that a density of approximately 0.5 hares/h is required for lynx population persistence. Although this value is only a rough estimate of prey requirements, these authors’ attempt to estimate a hare density threshold attests to the need for such values in lynx conservation efforts. Our basic models suggest that if hare populations are stable, the minimum prey abundance required for the persistence of a reintroduced lynx population likely ranges between 1.1 and 1.8 hares/h, although secondary demographic factors such as dispersal further increase this threshold hare density. The demographic relationships generated herein suggest that kitten survival is the demographic variable that most likely drives population decline at hare densities below this threshold. Hare populations that are characterized by stochastic or cyclic dynamics may further influence the minimum mean hare density required for lynx population persistence; however, these changes may be relatively small. Finally, although release protocols might have a positive effect on the probability of lynx population persistence (see above), none of these factors may compensate for poor prey abundance. Thus, in support of the findings of Griffith et al. (1989), our results suggest that, determi-

nistic effects related to the relationship between hares and lynx likely have the largest impact on the success of lynx reintroduction.

Many locales in the USA apparently do not have sufficient hare densities to support a lynx population translocated from the northern range, including Colorado where reintroductions are ongoing (Kloor, 1999). However, many states that currently have snowshoe hares historically also have had lynx populations. This discrepancy could be due to: (1) a recent decline in hare numbers in the contiguous USA following anthropogenically-induced habitat alteration (e.g., fire suppression or timber harvest; Scott et al., 1999); (2) lynx populations at the southern extent of their range possibly having more generalist feeding behavior and thus less reliance on hares than northern lynx populations; or (3) reduced connectivity between northern and southern lynx populations and the possibility that southern lynx populations historically were continually bolstered by the periodic influx of animals from Canada (see Mech, 1973; Mech, 1980; Schwartz et al., 2002). Early reports of lynx in the southern range were not associated with any rigorous population viability assessment, implying

that the historical status and persistence of southern lynx populations remains unclear. However, regardless of the reason why current hare densities in the contiguous USA may be insufficient to support viable lynx populations, the successful recovery of lynx may only be possible when the key factors contributing to the apparent decline of the species in the southern portion of its range are more fully understood and addressed.

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Appendix A

Year	Hare density (hares/h.) ^a	Natural adult survival	Dispersal (%)	Pregnancy rate (adult)	Adult litter size	Adult productivity ^b	Kitten survival rate (adult mother)	Pregnancy rate (yearling)	Yearling litter size	Yearling productivity ^b	Study location	Author
1964–1965	1.37 ^c			0.67		0.00	0.00				Alberta, Canada	Nellis et al. (1972)
1965–1966	0.79			0.00		0.00	0.00					
1966–1967	0.80			1.00	4.0	0.00	0.00					
1967–1968	1.85			1.00	3.5	3.00						
1971–1972	4.99			0.67	3.5	2.36				Alberta, Canada	Brand et al. (1976)	
1972–1973	2.00			1.00	1.3	1.33						
1973–1974	0.69				1.5	0.00	0.00					
1974–1975	0.34					0.00	0.00					
1971–1972	3.88 ^d			0.73	4.6	3.36		0.40	3.9	1.56	Alberta, Canada	Brand and Keith (1979)
1972–1973	1.65	0.62		0.46	3.9	1.79	0.35	0.00	0.0	0.00		
1973–1974	0.52	0.65		0.33	3.4	1.12	0.05	0.00	0.0	0.00		
1974–1975	0.23	0.93		0.33	3.4	1.12	0.12					
1977–1978	10.00 ^e			0.75	3.3	2.48		0.67	3.7	2.48	Nova Scotia, Canada	Parker et al. (1983)
1978–1979	5.90 ^f			0.71	3.8	2.70		0.29	2.7	0.78		
1979–1980	1.70			0.64	3.8	2.43		0.00	0.0	0.00		
1984–1985	1.96 ^g		0.00								Alaska, USA	Staples (1995)
1985–1986	1.06	1.00 ^h	0.00									
1986–1987	0.67	1.00	0.20									
1987–1988	0.46	1.00	0.00									
1988–1989	0.18	0.92	0.14									
1989–1990	0.16	0.94	0.00									
1990–1991	0.13	0.92	0.11									

(continued on next page)

Appendix A (continued)

Year	Hare density (hares/h.) ^a	Natural adult survival	Dispersal (%)	Pregnancy rate (adult)	Adult litter size	Adult productivity ^b	Kitten survival rate (adult mother)	Pregnancy rate (yearling)	Yearling litter size	Yearling productivity ^b	Study location	Author
1986–1987	0.80	1.00	0.17									
1987–1988	1.00	0.90	0.00				0.22					
1988–1989	2.80	1.00	0.32	0.50	3.5	1.75	0.68					
1989–1990	5.70	1.00	0.11	1.00	5.3	5.30	0.83	1.00	4.2	4.20	Yukon, Canada	Slough and Mowat (1996)
1990–1991	7.50	0.90	0.33	1.00	5.3	5.30	0.64	1.00	4.2	4.20		
1991–1992	4.70	0.95	0.55	0.84	4.9	4.12	0.72	0.00	0.0	0.00		
1992–1993	1.30	0.40	0.80	0.00	0.0	0.00	0.00	0.00	0.0	0.00		
1993–1994	1.10	0.75	0.52	0.00	0.0	0.00	0.00	0.00	0.0	0.00		
1986–1987	0.80			0.71	2.7	1.91						
1987–1988	1.00			0.83	3.8	3.17						
1988–1989	2.80			0.75	3.2	2.40		0.50	2.3	1.15	Yukon, Canada	Slough and Mowat (1996)
1989–1990	5.70	From carcasses	0.81	4.7	3.82			0.68	4.1	2.80		
1990–1991	7.50			0.93	4.6	4.28		0.70	4.4	3.08		
1991–1992	4.70			0.76	4.0	3.02		0.48	3.4	1.63		
1992–1993	1.30			0.38	4.0	1.52		0.00				
1993–1994	1.10			0.33	1.0	0.33						
1986–1987	0.30 ⁱ	0.75	0.00	0.18	2.0	0.36						
1987–1988	0.99	1.00	0.29	0.45	3.0	1.35						
1988–1989	1.51	1.00	0.00	0.29	3.0	0.86						
1989–1990	1.92	1.00	0.27	0.48	3.0	1.44						
1990–1991	1.25	0.91	0.32	0.09	2.0	0.18					Yukon, Canada	O'Donoghue et al. (1997)
1991–1992	0.69	0.95	0.25	0.06	2.0	0.11						
1992–1993	0.11	0.36	0.18	0.00	0.0	0.00						
1993–1994	0.13	0.83	0.00	0.00	0.0	0.00						
1994–1995	0.36	1.00	0.17									
1988–1989	5.04 ^j	1.00	0.17 ^k	0.50	4.0	2.00	0.50					
1989–1990	6.00	1.00	0.09	0.75	4.0	3.00	0.82				Northwest Territories, Canada	Poole (1994)
1990–1991	4.37	0.96	0.24									
1991–1992	0.92	0.50	1.00	0.00		0.00						
1992–1993	0.53	0.51	0.78	0.00		0.00						
1996–1998	0.20	1.00		0.55	1.8		0.00				BC, Canada	Apps (2000)

^a Hare densities over winter (except for Parker et al. 1983, which are summer densities).

^b If not provided in literature, productivity calculated as pregnancy rate \times average litter size. Productivity may not equal rate \times size if provided in literature.

^c Hare density for Nellis et al. (1972) cited in Brand et al. (1976).

^d Hare density for Brand and Keith (1979) cited in Todd et al. (1981).

^e Hare density in Parker et al. (1983) is for optimal habitat (about 12% of total habitat).

^f Hare density in 1978–1979 for Parker et al. (1983) was average of other 2 years.

^g Hare density in Staples (1995) calculated from pellet counts using equations from Krebs et al. (1985).

^h Survival in Staples (1995) calculated from radio days and known mortalities.

ⁱ All demographic values in O'Donoghue et al. (1997) estimated from graphs.

^j Hare densities and lynx survival in Poole (1994) calculated from graphs.

^k Dispersal from Poole (1997).

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