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GEOGRAPHICAL GRADIENTS IN DIET AFFECT POPULATION DYNAMICS OF CANADA LYNX

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Abstract. Geographical gradients in the stability of cyclic populations of herbivores and their predators may relate to the degree of specialization of predators. However, such changes are usually associated with transition from specialist to generalist predator species, rather than from geographical variation in dietary breadth of specialist predators. Canada lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) populations undergo cyclic fluctuations in northern parts of their range, but cycles are either greatly attenuated or lost altogether in the southern boreal forest where prey diversity is higher. We tested the influence of prey specialization on population cycles by measuring the stable carbon and nitrogen isotope ratios in lynx and their prey, estimating the contribution of hares to lynx diet across their range, and correlating this degree of specialization to the strength of their population cycles. Hares dominated the lynx diet across their range, but specialization on hares decreased in southern and western populations. The degree of specialization correlated with cyclic signal strength indicated by spectral analysis of lynx harvest data, but overall variability of lynx harvest (the standard deviation of natural-log-transformed harvest numbers) did not change significantly with dietary specialization. Thus, as alternative prey became more important in the lynx diet, the fluctuations became decoupled from a regular cycle but did not become less variable. Our results support the hypothesis that alternative prey decrease population cycle regularity but emphasize that such changes may be driven by dietary shifts among dominant specialist predators rather than exclusively through changes in the predator community.

Key words: alternative prey; Canada lynx; *Lepus americanus*; *Lynx canadensis*; population cycles; snowshoe hare; specialist/generalist predation hypothesis; stable isotope ratios.

INTRODUCTION

The availability of alternative prey can have a strong impact on the population dynamics of predator–prey systems. Complex population dynamics (e.g., population cycles) often occur in areas of low prey diversity, where specialist predators consume primarily a single prey species (Hansson and Henttonen 1988, Hanski et al. 1991). When alternative prey are available, predators may increase their dietary breadth when their primary prey decline, which generally increases stability and dampens population cycles (Hansson and Henttonen 1988, Klemola et al. 2002).

The diversity of mammalian prey available generally follows a latitudinal gradient, increasing from north to south in the Northern Hemisphere (Hanski and Henttonen 1996, Willig et al. 2003). Thus, changes in the cyclic dynamics of predators and their prey may also be expected to follow a similar gradient. In Fennoscandia, fluctuations in numbers of microtine rodents and their predators decrease in amplitude and period with

latitude, becoming irregular in southernmost Fennoscandia, corresponding to a change in the predator complex from microtine specialists (weasels) in the north to generalist predators (raptors and foxes) in the south (Hansson and Henttonen 1988, Hanski et al. 1991). This spatial variation in prey diversity may also affect degree of specialization of a given predator species. Stoats (*Mustela erminea*), for example, are thought to be specialists on microtine rodents in the northern parts of their range but semi-generalists farther south where there are more alternative prey, based on changes in their population dynamics with latitude (Hanski et al. 1991, Hanski and Henttonen 1996, Johnson et al. 2000). Likewise, North American mink (*Mustela vison*) population dynamics appear to be related to the types and diversity of prey available, with stronger trophic interactions between mink and muskrat (*Ondatra zibethicus*) harvest data suggesting increased specialization on muskrats in areas of lower prey diversity (Erb et al. 2001). However, testing the mechanism behind these changes in the population dynamics of predator and prey requires an explicit examination of the dietary breadth and plasticity of a specialist predator across its range and the relationship of dietary variation to differences in cyclic dynamics.

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In the northern boreal forests of North America, Canada lynx (*Lynx canadensis*; see Plate 1) rely extensively on snowshoe hares (*Lepus americanus*) as prey, and the numbers of both lynx and hares fluctuate dramatically, with a period of ~10 years (Keith 1963). This well-known association often is considered as a classic example of predator–prey population cycles, yet in southern boreal forests, lynx and hare populations appear to be less cyclic, with densities more similar to population lows from their cyclic counterparts (Keith 1963, 1990, Koehler and Aubry 1994, Murray 2000). Geographic variation in the structure of lynx population dynamics is influenced by large-scale climatic changes (Stenseth et al. 1999), and may also be related to geographic variation in the prey assemblages available and prey species consumed by lynx. During cyclic lows in hare density, northern lynx consume more alternative prey, especially red squirrels (*Tamiasciurus hudsonicus*; Brand et al. 1976, O'Donoghue et al. 1998), suggesting that lynx may forage opportunistically in response to low hare densities. Lynx in southern boreal forests, where the available prey diversity is much greater, may also rely extensively on red squirrels and other alternative prey (Koehler 1990, Apps 2000).

However, the generality of the prediction that lynx are facultative specialists on snowshoe hares (O'Donoghue et al. 2001), consuming greater amounts of alternative prey in areas of greater prey diversity, is unknown. Thus, our objective was to determine variation in the diet of lynx across their range, and to quantify the relative importance of snowshoe hares across a latitudinal gradient. If the use of alternative prey by predators affects their population dynamics, a relationship between lynx dietary specialization and the cyclicity of their population fluctuations is expected.

METHODS

Stable isotope ratios ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) in animals are related to those of their foods, with predicted enrichment in consumer tissues due to trophic fractionation (DeNiro and Epstein 1978, 1981). For consumers of foods with distinct isotopic signatures, this technique can provide estimates of the relative importance of different prey types. We obtained samples of tissue (mostly hair) for stable isotope analysis from museum collections and free-ranging animals captured in field studies. Our samples included representatives of many species of mammals and birds that have previously been identified as prey of lynx (Quinn and Parker 1987) in order to determine the isotopic distinctiveness of different prey species. For most of these species, samples were chosen opportunistically, irrespective of geographic origin. We also collected samples of lynx, snowshoe hares, and red squirrels (the most common alternative prey of lynx; see Aubry et al. 2000) from across their range to determine geographic changes in the isotopic signatures of each species and the degree of specialization on hares by lynx. Metabolically inactive tissues like



PLATE 1. Canada lynx (*Lynx canadensis*). Photo credit: D. L. Murray.

hair do not resorb or turnover, so their stable isotope ratios record the diet of individuals integrated over a finite period of growth. Lynx molt twice per year, in October/November and again in April/May, and the timing of molt of snowshoe hares and red squirrels is similar (Banfield 1977, Quinn and Parker 1987). This molt pattern, in which the previous coat is shed and replaced by new hairs twice each year, is typical of many, but not all, terrestrial furbearers (see Worthy et al. 1987). Thus, the stable isotope ratios of our hair samples are standardized to reflect diet during the molting period, regardless of the exact date of collection (Roth 2002).

Hair samples were cleaned with soap and water to remove surface oils and debris, dried at 90°C, and homogenized with scissors. Muscle samples were freeze-dried and powdered with mortar and pestle. Since the carbon isotope ratios of lipids differ substantially from other compounds (DeNiro and Epstein 1978), variations in lipid concentration can significantly influence $\delta^{13}\text{C}$ measurements. Therefore, we removed lipids from muscle samples using a Soxhlet apparatus with petroleum ether for more than eight hours. Ether was then evaporated off in a drying oven. Stable isotope ratios of hair and feathers were measured on a continuous flow isotope ratio mass spectrometer in the Idaho Stable Isotopes Laboratory at the Department of Forest Resources, University of Idaho. Stable isotope ratios of muscle samples were measured on a similar instrument at the University of Central Florida, calibrated with working standards from the Idaho laboratory. Stable isotope signatures are expressed in delta notation as parts per thousand (‰) as follows: $\delta X = [(R_{\text{smp}}/R_{\text{std}}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N and R is the corresponding sample/standard ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The standards for ^{13}C and ^{15}N are Pee Dee Belemnite (PDB) and atmospheric N_2 , respectively. Measurement precision was within 0.1‰ for C and 0.2‰ for N.

Elevated concentrations of CO₂ in the atmosphere over the last few hundred years have led to an exponential decrease of atmospheric δ¹³C values, which can be approximated by δ¹³C_{atm} = -6.429 - 0.0060 exp(0.0217[t - 1740]), where *t* is the year (Feng 1998). This change in atmospheric δ¹³C would affect the isotope ratios of plant tissues when they fix carbon during photosynthesis, and then would be transferred to herbivores and higher trophic levels. Therefore, we used this equation to adjust our calculated stable-carbon isotope ratios to year 2000 atmospheric stable-carbon isotope levels. We calculated the δ¹³C_{atm} value in the year the sample was collected, and the difference between that value and the δ¹³C_{atm} value for year 2000 was subtracted from the δ¹³C value measured in the sample.

To establish the uniqueness of snowshoe hares among known prey species with respect to isotopic signatures, we performed a hierarchical cluster analysis using mean δ¹⁵N and δ¹³C of hair or feather samples from potential prey species. The clustering method and resemblance measure applied to the species' means were average linkage and Euclidean distance, respectively (see, for example, Rencher 2002: Chapter 14). From the results of the cluster analysis a dendrogram was constructed to display graphically the relative differences among snowshoe hares and the other prey species.

We examined temporal variability in the isotopic signatures of red squirrels and snowshoe hares using hair collected from a study population in central Idaho (Wirsing et al. 2002). To examine geographic variation in the isotopic signatures of these species, we used hair samples collected across their range and fit separate models relating δ¹⁵N and δ¹³C to longitude, latitude, and their interaction. We then compared lynx and hare stable isotope ratios across their range to determine changes in the degree of specialization on hares by lynx. For both lynx and hares, we fit separate models relating carbon and nitrogen stable isotope ratios to longitude, latitude, and their interaction for each season, and compared the differences between the two species. As specialization on hares by lynx increases, we expect the isotopic differences between the species to decrease.

We used the stable isotope ratios of lynx, hares, and squirrels to calculate the proportion of snowshoe hares in the diet of lynx for several locations using a two source linear mixing model for each isotope (Phillips 2001). This analysis assumed that snowshoe hares and red squirrels were the only prey consumed. Although other prey species clearly will be consumed by lynx in different parts of their range, we considered red squirrels to be an appropriate representation of alternative prey because they occur throughout the distributional range of lynx, and most studies of lynx diet in both northern and southern boreal forests have found red squirrels to be the most significant alternative prey (Obbard 1987, Aubry et al. 2000). Estimates of the proportion of hares in the lynx diet were calculated from the mean δ¹⁵N and δ¹³C of each species at each location based on the

equation $R_{lynx} = p \times (R_{hare} + e) + (1 - p) \times (R_{sqr} + e)$, where *R* is δ¹³C or δ¹⁵N, *p* is the proportion of hares in the diet, and *e* is the trophic shift for that isotope (3‰ for nitrogen and 0.5‰ for carbon; McCutchan et al. 2003). These estimates are sensitive to estimates of isotopic trophic shift (McCutchan et al. 2003), but the patterns of relative hare consumption across North America should be robust to variability in trophic shift. Separate estimates were calculated using the carbon and nitrogen data, and then averaged together.

We compared these diet estimates to characteristics of the population dynamics of lynx from each region determined from published lynx harvest numbers (Elton and Nicholson 1942, Novak et al. 1987, Healy 2001; see also Statistics Canada, 2005, *available online*).⁷ We used the number of lynx pelts in the harvest as an index of population size, recognizing that pelt prices and trapper effort may also affect harvest (Gamara and Sole 2000). To determine the presence and intensity of population cycles in these data, we performed a spectral analysis of the natural-log-transformed numbers of lynx harvested each year in each state or province using the Lomb normalized periodogram (Kendall et al. 1998). We used spectral power to reflect the height of the spectral peak and determined the significance of the spectral peak by $P = 1 - (1 - e^{-z})^n$, where *z* is the peak height and *n* is the number of data points in the time series (Kendall et al. 1998). We compared this estimate of peak height with our diet estimate to determine whether the degree of specialization on snowshoe hares was related to population cyclicity. We also compared lynx diet to the SD of the natural-log-transformed harvest numbers, a measure of variability that is independent of the chronology of events and therefore does not necessarily reflect cyclicity (Heath 2006).

RESULTS

We measured the stable isotope ratios in hair samples from 284 lynx from across their range and found significant spatial variation (Appendix A). To determine the source of that variation and the relative importance of snowshoe hares compared to other prey species in the lynx diet, we evaluated differential isotopic signatures among prey species. We analyzed 580 samples from 25 potential prey species of lynx (Appendix B) and included the 15 species represented by more than one sample in the hierarchical cluster analysis. Snowshoe hares had the lowest values of both δ¹⁵N and δ¹³C and, as the last species to cluster with the other 14 species in the dendrogram, were distinct from all other prey species (Appendix C). Red squirrels and flying squirrels (*Glaucomys sabrinus*) were the next most distant group, linking together midway through the clustering.

Hare and squirrel hair samples collected from the same site in central Idaho in 1998–1999 differed

⁷ (<http://www.statcan.ca/>)

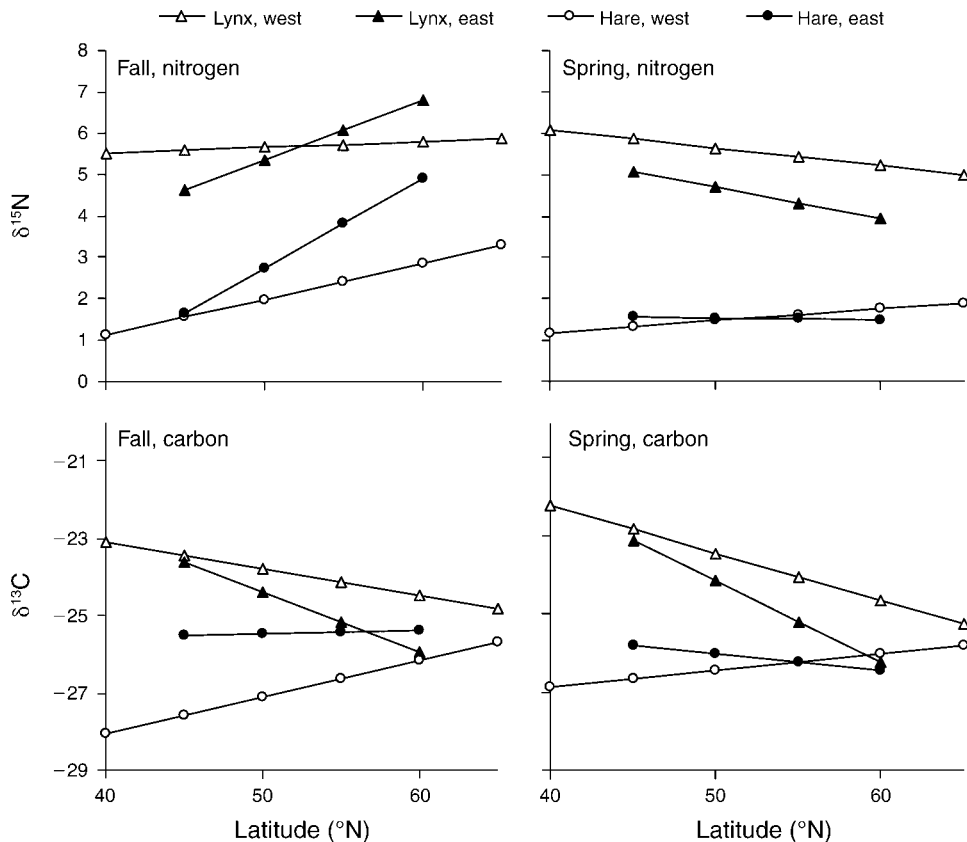


FIG. 1. Stable isotope differences between lynx (triangles) and snowshoe hares (circles) across latitudes and seasons. Open symbols are model output for western North America (120° W), and solid symbols are model output for eastern North America (70° W). For carbon, species (hare/lynx) interacted significantly with latitude ($F_{1,472} = 59.05$, $P < 0.001$), longitude ($F_{1,472} = 41.14$, $P < 0.001$), season ($F_{1,472} = 4.99$, $P = 0.026$), and longitude \times season ($F_{1,472} = 5.29$, $P = 0.022$). For nitrogen, species interacted significantly with latitude ($F_{1,472} = 10.50$, $P = 0.001$), longitude ($F_{1,472} = 13.02$, $P < 0.001$), and season ($F_{1,472} = 4.95$, $P = 0.027$).

significantly in both $\delta^{13}\text{C}$ (ANOVA, $F_{3,46} = 179$, $P < 0.001$) and $\delta^{15}\text{N}$ ($F_{3,46} = 57.8$, $P < 0.001$) after considering season and year, and muscle samples from a subset of these hares and squirrels also differed substantially (carbon, $F_{1,24} = 644$, $P < 0.001$; nitrogen, $F_{1,24} = 107$, $P < 0.001$). Seasonal and annual variation in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ occurred for red squirrels, but not hares (Appendix D). The stable isotope ratios of both prey species also varied geographically, but despite this variability, red squirrel signatures differed substantially from snowshoe hares across their entire range (Appendix E).

The differences in lynx and snowshoe hare stable isotope ratios decreased with latitude for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in both seasons (Fig. 1). Since the isotopic signatures of hares are lower than any other prey species, the approach of lynx signatures to the hare values suggests greater specialization on snowshoe hares in northern areas. Likewise, differences between lynx and hares decreased with longitude for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in spring and fall (Fig. 1), indicating a diet more specialized on snowshoe hares in the eastern part of the

range. Sex did not affect either $\delta^{13}\text{C}$ ($F_{8,215} = 1.05$, $P = 0.40$) or $\delta^{15}\text{N}$ ($F_{8,215} = 1.85$, $P = 0.070$) of lynx, after considering longitude, latitude, season, and their interactions. Our lynx hair samples included 156 with age information, but since all subadults (< 2 years old) were collected west of 100° W longitude and only one of those was collected in summer, we restricted our age analysis to fall samples in western North America. Age class (adult vs. subadult) did not affect either $\delta^{13}\text{C}$ ($F_{4,111} = 1.91$, $P = 0.11$) or $\delta^{15}\text{N}$ ($F_{4,111} = 1.32$, $P = 0.27$). Cycle phase did affect $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of lynx (Appendix F), but the broad spatial patterns (increased specialization on hares in the north and east) persisted regardless of cycle phase.

We estimated the proportion of snowshoe hares in the diet of lynx for each state or province (Table 1). Eight of the 12 lynx time series we examined (Appendix G) had significant spectral peaks (Table 1). The mean percentage of hares in the lynx diet was correlated with spectral power, reflecting peak height ($r = 0.815$, $n = 12$, $P = 0.001$; using only estimates with statistically significant spectral peaks, $r = 0.697$, $n = 8$, $P = 0.055$; Fig. 2).

TABLE 1. Estimated percentage of hares in the diet of lynx, and spectral analysis of lynx time series.

Jurisdiction	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
	Snowshoe hare	Red squirrel	Canada lynx	Diet (%)	Snowshoe hare	Red squirrel	Canada lynx	Diet (%)
Alaska	1.55	4.09	5.44	65	-25.71	-20.77	-24.14	78
Alberta	1.14	4.89	6.09	48	-25.36	-20.25	-23.48	73
British Columbia	1.82	7.18	5.17	93	-25.98	-18.68	-24.50	86
Idaho	1.06	6.92	5.80	70	-27.16	-20.39	-23.49	53
Manitoba	3.07	6.41	6.73	80	-26.10	-21.60	-23.84	61
Minnesota	1.31	4.66	5.54	63	-26.61	-21.79	-23.99	56
Newfoundland	0.66	5.15	5.03	70	-25.91	-21.53	-23.76	62
Northwest Territories	2.93	5.44	5.93	100	-25.84	-20.42	-25.02	94
Ontario	2.01	4.50	5.80	68	-25.88	-21.58	-23.83	64
Quebec	1.66	4.72	4.81	95	-26.08	-20.06	-24.22	77
Washington	0.87	4.28	5.73	45	-27.73	-18.03	-23.29	59
Wyoming†	1.37	5.60	5.30	78	-25.05	-18.92	-22.24	62
Yukon	1.89	3.84	5.04	92	-25.96	-20.45	-23.20	59

† Mean and SD were calculated from the natural-log-transformed harvest numbers.

‡ For Wyoming, we had samples for stable isotope analysis, but no time series data were available.

** $P \leq 0.01$.

However, the overall variability in abundance (SD of transformed abundance) was unrelated to diet (cyclic populations only, $r = -0.418$, $n = 8$, $P = 0.30$; all jurisdictions, $r = -0.537$, $n = 12$, $P = 0.072$). Thus, although external sources of irregular fluctuations in abundance were unrelated to diet, populations of lynx with greater specialization on hares had more distinct cycles.

DISCUSSION

Our results indicate that lynx are in fact facultative specialists on snowshoe hares (O'Donoghue et al. 2001), given that they consume significant amounts of alternative prey when they are available. These alternative prey species, therefore, can be important to lynx populations at lower latitudes. Furthermore, the degree of prey specialization correlates with local population dynamics, with increasing specialization on snowshoe hares leading to truly cyclic dynamics. This correlation demonstrates the mechanism by which predation patterns may generate geographical gradients in population cycles (Hansson and Henttonen 1988, Hanski et al. 1991). Specialist predators unable to make use of alternative prey species when their primary prey decline drive those prey to very low levels. When predator numbers subsequently decline, prey increase rapidly in the absence of predation pressure. When predators are able to switch to alternative prey, however, the fluctuations are decoupled from a true cycle. This result provides direct empirical support for the hypothesis that changes in diet breadth can contribute to latitudinal gradients in population cyclicity.

Overall variability in abundance, however, did not decrease with increased consumption of alternative prey; in fact, accepting a slightly larger α (0.07) would suggest an increase in population variability with increased use of alternative prey. The persistence of variability in southern lynx populations in the absence of population

cycles suggests that lynx may respond to variability in other food sources that are independent of changes in hare abundance, such as fluctuations in red squirrel populations with seed crop size (Obbard 1987). In models of lynx-hare population dynamics, including alternative prey in the lynx diet can lead to complicated dynamics (Gamarra and Sole 2000). Both cyclicity (reflected in the spectral power of the time series) and variability (reflected in the SD of log-transformed abundance) are important components for understanding predator-prey population dynamics.

The use of alternative prey in areas of higher prey diversity could explain the historical occurrence of lynx

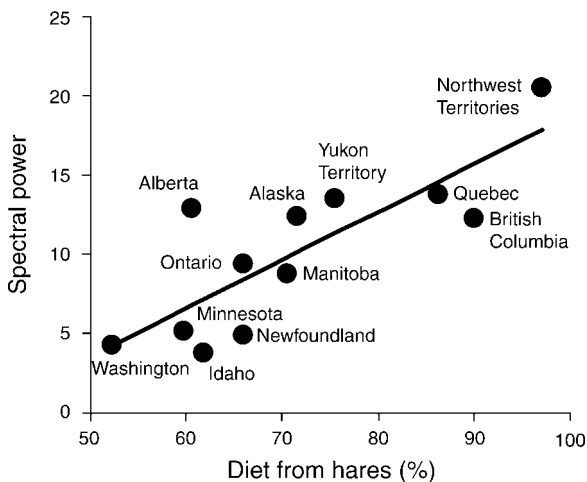


FIG. 2. Relationship between lynx diet and population cyclicity. Each point reflects a different jurisdiction (state, province, or territory). Spectral power reflects peak height estimated from a spectral analysis of natural-log-transformed lynx harvest numbers using the Lomb normalized periodogram (Table 1; Kendall et al. 1998). Diet estimates were calculated from the average lynx, hare, and squirrel stable isotope ratios (Table 1).

TABLE 1. Extended.

Mean diet (%)	Time series length (yr)	Period (yr)	Spectral power	Mean (SD)†
72	64	8.7	12.34**	7.449 (0.684)
60	84	9.5	12.85**	7.686 (1.084)
90	84	9.5	12.27**	7.543 (0.758)
62	25	7.4	3.77	2.527 (1.283)
71	84	9.6	8.74**	6.759 (1.293)
60	41	11.7	5.07	3.905 (1.328)
66	52	9.6	4.85	5.569 (0.870)
97	84	9.1	20.47**	7.329 (0.764)
66	84	9.4	9.32**	7.121 (0.710)
86	84	9.4	13.73**	7.372 (0.787)
52	20	10.4	4.20	2.419 (0.972)
70				
76	84	9.1	13.45**	6.739 (0.900)

within the contiguous United States. Because of a general dearth of hares, a viable lynx population could be supported there only if the degree of prey specialization is much lower than in their northern counterparts during cyclic peaks (Steury and Murray 2004). The results of this study suggest that management of potential lynx habitat need not focus exclusively on snowshoe hares, and consideration of potential habitats suitable for lynx reintroduction in the southern part of their range should include red squirrels and other alternative prey species.

The difference in the stable isotope ratios of snowshoe hares and red squirrels is related to the diets of these two species. Snowshoe hares rely extensively on leafy vegetation or woody browse as food (Keith 1990), whereas red squirrel diet is comprised of conifer seeds, mushrooms, and animal protein (Obbard 1987, Vernes et al. 2004). These food sources differ isotopically and this difference would be transferred up trophic levels to consumers and their respective predators (DeNiro and Epstein 1981, Dawson et al. 2002). Geographical variation in the stable isotope ratios of herbivores (Appendix E) likely reflects isotopic variability in plants and soils, which can vary with altitude, mean annual precipitation, and temperature (Hultine and Marshall 2000, Amundson et al. 2003). The temporal variability in red squirrel stable isotope ratios (Appendix D) is expected because their diets vary seasonally and yearly with changes in food availability, especially seed production (Vernes et al. 2004), which may confound our ability to examine spatial patterns for red squirrels over a wide time span and could explain the discrepancies in the two estimates of lynx diet provided by the carbon and the nitrogen stable isotope ratios (Table 1). Although hare diet varies seasonally as well, from herbaceous and leafy material in summer to woody browse in winter, the isotopic differences in these food sources were not substantial enough to be reflected in the hare tissues.

Specialist predators may not solely generate the high-amplitude population cycles in the north, as herbivory

by hares seems to interact synergistically with predation to generate cycles in this system (Krebs et al. 2001). But the increased consumption of increasingly available alternative prey by lynx, as well as the addition of other generalist predators as latitude decreases, appears to decouple lynx and hare population dynamics from a regular cycle. Although we did not investigate the population dynamics of hares, the ability of lynx to shift to alternative prey could reduce the fluctuations in southern hare populations, even though lynx populations remained variable (but noncyclic). The effects of alternative prey on predator-prey interactions are often counterintuitive when fluctuations occur in all three species (Abrams et al. 1998). Investigating the response of lynx to changes in abundance of other food sources in their southern range would help elucidate the indirect effects of alternative prey in cyclic systems.

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APPENDIX A

Spatial variation in the stable isotope ratios of lynx (*Ecological Archives* E088-169-A1).

APPENDIX B

Stable isotope ratios of lynx and their potential prey (*Ecological Archives* E088-169-A2).

APPENDIX C

Dendrogram for hierarchical cluster analysis on prey species (*Ecological Archives* E088-169-A3).

APPENDIX D

Seasonal and annual variability in stable isotope ratios of snowshoe hare and red squirrel hair samples from Clearwater National Forest, Idaho, USA (*Ecological Archives* E088-169-A4).

APPENDIX E

Geographic variation in stable isotope ratios of snowshoe hare and red squirrel hair samples collected across Canada and the northern United States (*Ecological Archives* E088-169-A5).

APPENDIX F

Effect of cycle phase on lynx stable isotope ratios (*Ecological Archives* E088-169-A6).

APPENDIX G

Lynx time series data from harvest records (*Ecological Archives* E088-169-A7).