

Assessment of Canada Lynx Research and Conservation Needs in the Southern Range: Another Kick at the Cat

DENNIS L. MURRAY,¹ *Department of Biology, Trent University, Peterborough, ON K9J 7B8, Canada*

TODD D. STEURY, *Department of Biology, Washington University, St. Louis, MO 63130, USA*

JAMES D. ROTH, *Department of Biology, University of Central Florida, Orlando, FL 32816, USA*

ABSTRACT The ecology of Canada lynx (*Lynx canadensis*) and their main prey, snowshoe hares (*Lepus americanus*), is poorly understood in southern Canada and the contiguous United States compared to the boreal forest of Canada and Alaska, USA, where both species are well studied. However, given recent listing of lynx under the Endangered Species Act, accurate understanding of lynx and snowshoe hare ecology and conservation requirements in the United States is a high priority. We critically examined unchallenged perceptions and important research needs related to lynx and hare ecology and conservation at the southern extent of their range. Contrary to popular dogma, lynx do not require old-growth forest for denning, but further research on lynx and hare use of fragmented landscapes at lower latitudes is required. The contention that southern lynx are subject to higher interference or exploitative competition compared to their northern counterparts remains without strong empirical support. Lynx rely more on red squirrels (*Tamiasciurus hudsonicus*) and possibly other alternate prey at lower latitudes, but hares are the predominant food type for lynx across their range. Southern lynx and hare populations do not exhibit periodic cyclicity, but harvest statistics suggest that lynx abundance in the southern range is highly variable, implying that numerical fluctuations likely are fueled by immigration from Canada. Southern lynx population viability in the absence of ingress is suspect and thus maintaining connectivity with northern areas of occupancy should be a priority. Successful conservation of lynx populations in the contiguous United States will require 1) improved understanding of lynx population and habitat ecology at lower latitudes, 2) protection and management of large tracts of lynx and snowshoe hare habitat, and 3) ensured connectivity between lynx populations at the core and periphery of the species' range. However, in light of the numerous challenges facing conservation of populations of many species at their southern distributional limit, the long-term prognosis for lynx in the southern range currently is uncertain. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1463–1472; 2008)

DOI: 10.2193/2007-389

KEY WORDS Canada lynx, conservation, habitat, population dynamics, snowshoe hare.

Canada lynx (*Lynx canadensis*) populations and those of their main prey, snowshoe hares (*Lepus americanus*), undergo 9-year to 11-year cycles across the boreal forest of Canada and Alaska, USA (Keith 1963, Royama 1992, Krebs et al. 2001). Lynx and hare populations have been subject to extensive research in the boreal forest, where it is understood that 1) lynx respond functionally and numerically to fluctuations in hare abundance (Keith et al. 1977; O'Donoghue et al. 1997, 1998b); 2) lynx population cycles lag behind those of hares by 1–2 years (Keith et al. 1977, Royama 1992, Boutin et al. 1995, Stenseth et al. 1998); and 3) both species exhibit quasi-synchrony in their population cycles across large geographic areas (Keith 1963, Smith 1983, Ranta et al. 1997, Stenseth et al. 1999). A variety of hypotheses may explain underlying causes of lynx–hare population cycles (see Keith 1963, Royama 1992, Murray 2003), but currently most ecologists agree that tri-trophic interactions between predators, hares, and winter browse are primary determinants (Royama 1992, Krebs et al. 1995, Stenseth et al. 1997, King and Schaffer 2001, Krebs et al. 2001).

Lynx and snowshoe hare distributions overlap extensively across the boreal forest of Canada and Alaska (Anderson and Lovallo 2003, Murray 2003), with lynx being most abundant in areas where hare densities are high (Mowat et al. 2000). Both species currently range southward into southeastern Canada and including parts of Maine, Minnesota, Wyoming, Montana, Idaho, and Washington, USA. Historically, lynx were reported in at least 24 states

(McKelvey et al. 2000a), although many reports probably involved transient animals rather than residents. Lynx were previously extirpated and currently are being restored to Colorado, USA (Shenk 2006), whereas restoration to New York, USA, during 1988–1990 apparently failed (Brocke et al. 1992). Lynx are absent in southern parts of the Rocky and Appalachian mountains where hares are at the most southern extent of their range. Herein we refer to lynx and hare populations as northern if they occur in the boreal forest of Canada and Alaska, and southern if they occupy forests in southern Canada and the contiguous United States.

Southern lynx and hare populations do not reach the high densities observed during cyclic peaks in the boreal forest (Keith 1990, Aubry et al. 2000, Hodges 2000, Murray 2000), and, until recently, southern populations of either species had not received research attention commensurate with that afforded to their northern counterparts. The recent listing of lynx as Threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 2000) prompted a spate of research activity on the ecology of southern lynx (e.g., Schwartz et al. 2002; Hoving et al. 2004, 2005; Steury and Murray 2004; Squires and Ruggiero 2007) and southern hares (e.g., Murray et al. 2002, 2005; Wirsing and Murray 2002; Mills et al. 2005; Homyack et al. 2006), but considerable uncertainty and disagreement remain regarding their ecology and conservation at lower latitudes.

We address key topics related to southern lynx and snowshoe hare ecology that either have not been tested adequately or received conflicting (and in some cases

¹ E-mail: dennismurray@trentu.ca

misleading) support in the literature. These topics are 1) lynx and hare habitat requirements, 2) lynx competition with other carnivores, 3) lynx reliance on hares, 4) lynx and hare population cyclicality, 5) lynx population viability, and 6) lynx population connectivity. However, rather than provide an extensive review of these topics (e.g., Aubry et al. 2000, Hodges 2000, Anderson and Lovallo 2003, Murray 2003, Ellsworth and Reynolds 2006), we seek specifically to quell error and uncertainty, identify issues needing further research, and make recommendations for improving conservation and management of lynx in the contiguous United States.

DO SOUTHERN LYNX HAVE SPECIFIC HABITAT REQUIREMENTS?

Mowat et al. (2000) concluded that lynx in the boreal forest consistently prefer mid-successional forests with intermediate to high stem densities; open areas and mature forest are used but not preferred. At the stand level, lynx habitat selection largely reflects that of hares, both seasonally as well as through the hare population cycle (O'Donoghue et al. 1998a, Mowat and Slough 2003), implying that hare suitability may be used generally as an index of lynx habitat requirements at the stand level. In the southern range, lynx prefer a variety of habitat types including mid-successional coniferous forests and edge habitat with moderate to abundant understory cover (Koehler et al. 2008, Maletzke et al. 2008, Vashon et al. 2008b), whereas areas with low forest cover tend to be avoided (Koehler et al. 2008, Vashon et al. 2008b). Although lynx may sometimes select mature forests in the southeastern distribution (Vashon et al. 2008b), such habitat always constitutes a broader forest mosaic within the home range. Hares may be found in mature forests, provided that understory cover is adequate, but we reject the suggestion (Buskirk et al. 2000a) that viable hare populations can occur in old-growth forest (see Hodges 2000).

Lynx responses to landscape-scale habitat features are poorly known, in part because studies in the boreal forest tend to occur in areas having largely homogenous forest structure with limited human disturbance (e.g., Slough and Mowat 1996, O'Donoghue et al. 1998b). The paucity of similar homogeneity in the United States (Aubry et al. 2000, Buskirk et al. 2000b, Carroll et al. 2001) implies that northern studies provide limited insight regarding broad-scale habitat requirements and space-use patterns in southern lynx (see Buskirk et al. 2000a). Southern lynx need to travel longer distances and through more undesirable (e.g., unforested) habitat (e.g., Koehler et al. 2008); therefore, their home ranges may need to be larger and encompass a diversity of habitat types to include sufficient prey biomass (Aubry et al. 2000, but see Vashon et al. 2008a). For snowshoe hares, large-scale forest fragmentation or maturation can be deleterious because as hares become increasingly restricted to small patches with adequate cover, higher predation rates from a variety of carnivores tend to increase local extinction risk (Wolff 1981, Keith et al. 1993, Wirsing

et al. 2002; see also Barbour and Litvaitis 1993). Notwithstanding important contributions in this Special Section to our understanding of habitat ecology of southern lynx, additional research is critical for quantifying lynx habitat requirements and responses to landscape alteration at lower latitudes. This point is especially relevant in light of anticipated further habitat fragmentation and loss in the southern lynx range, and the likelihood that ongoing climate change will influence both distribution and abundance of prey such as snowshoe hares at lower latitudes.

Lynx den site selection may be distinct from their general habitat-use patterns. Initially, lynx dens in the southern range were recognized as being associated with both mature forest and horizontal structure in the form of overblown trees and woody debris (Koehler 1990, Squires and Laurion 2000). Although mature forest and horizontal structure tend to be correlated on the landscape, and thus it may not be clear specifically which criterion is required for successful denning, forest age per se is unlikely to have a direct influence on lynx den location if sites are chosen for their protective cover for kittens. More recent work also associates lynx den sites with both mature stands and horizontal cover in southern lynx range, with the latter apparently playing a primary role (see Moen et al. 2008, Organ et al. 2008, Squires et al. 2008). In the boreal forest, where linkage between stand age—structural size and horizontal ground cover may be weaker, lynx dens are almost always associated with overblown trees and rarely with mature stands (Slough 1999). Thus, we conclude that cover is the requisite habitat attribute for lynx denning, meaning that popular dogma such as “lynx depend on old growth forest, the habitat for denning” (Defenders of Wildlife 2007) clearly is spurious. We question if such assertions are perhaps driven by attempts to use lynx as a vehicle for enhancing protection of old-growth forests, rather than being objective interpretations of scientific findings.

ARE SOUTHERN LYNX SUBJECT TO INCREASED COMPETITION?

Interspecific competition among carnivores may be weaker in the boreal forest because of lower diversity and abundance of the vertebrate predator–prey community. Cougars (*Puma concolor*), bobcats (*Lynx rufus*), and fisher (*Martes pennanti*) are found exclusively in the southern lynx range, and lynx mortality from these carnivores has been reported at lower latitudes (Koehler et al. 1979, Aubry et al. 2000, Squires and Laurion 2000). Although southern lynx are known to kill coyotes (*Canis latrans*; T. Shenk, Colorado Division of Wildlife, personal communication), northern lynx allegedly are killed by coyotes, wolves (*Canis lupus*), and wolverines (*Gulo gulo*; O'Donoghue et al. 1995, 1997; Slough and Mowat 1996). Yet, mortality from strife with other carnivores may be observed rarely in northern lynx populations because trapping is the primary cause of death and may be compensatory with other mortality sources (Brand and Keith 1979, Mowat et al. 2000). Thus, the rarity of reports identifying lynx mortality from interspecific

interactions in the northern range should not be construed as evidence that interference competition is more important in the southern lynx range.

Interference competition also may be manifest through spatial exclusion, and lynx in Nova Scotia, Canada, apparently were displaced by an expanding bobcat population (Parker et al. 1983). Along the same line, Buskirk et al. (2000*b*) suggested that lynx competition with coyotes in the southern range could be intensified through increased spatial overlap where hard-packed snow trails (i.e., due to snowmobiles) are prevalent. This argument presumes that winter habitat restriction of coyotes and perhaps other carnivores is limited by snow conditions and that trails allow occupancy in areas that otherwise would be inaccessible (Buskirk et al. 2000*b*, Ruediger et al. 2000). However, the sympatric distribution of lynx and coyotes across much of their ranges and their common reliance on prey such as snowshoe hares (O'Donoghue et al. 1998*a, b*) implies that lynx-coyote competition should not be unique to the southern range. Although a recent study (Bunnell et al. 2004) suggests that snowmobile trails can improve coyote winter access to remote areas, a more rigorous comparison (Kolbe et al. 2007) suggests that coyote habitat-use patterns are unlikely to be sufficiently modified by snowmobile trails such that lynx would be affected. Indeed, exactly how coyotes could functionally and significantly displace or outcompete lynx if they are largely restricted to hard-packed trails is unclear. Yet, the issue of snowmobile trails harming southern lynx populations has been adopted without strong empirical support. For example, the United States Fish and Wildlife Service states that "snowtrails packed by humans facilitate the movement of potential lynx competitors into the deep snow habitats of the lynx" (U.S. Fish and Wildlife Service 2000:16080; see also Buskirk et al. 2000*b*). Such statements have been widely touted by nongovernment organizations as justification for increased lynx protection, perhaps ultimately as a general means of achieving greater restrictions on anthropogenic activities in wilderness areas. Although the possibility that the United States Forest Service will restrict snowmobile access in lynx range (see Bunnell et al. 2004) may be warranted from a precautionary standpoint, the question of increased lynx competition and the role of snowmobile trails should be scrutinized more closely.

The primary cause of snowshoe hare death is predation, both in northern (Keith et al. 1977, 1984; Boutin et al. 1986; Murray et al. 1997; Hodges et al. 2001) and southern (Keith et al. 1993, Cox et al. 1997, Wirsing et al. 2002, Etcheverry et al. 2005) areas. The predator community relying on hares is broad across its geographic range, and studies from northern regions reveal a relatively minor role of lynx predation on the total mortality of hares (see Hodges et al. 2001; see also Keith et al. 1977, 1984; Boutin et al. 1986). Comparable data for southern lynx populations are not available, but predation rates on hares at lower latitudes where lynx are absent are not higher or more consistent across time than those in northern areas (Sievert and Keith

1985, Keith et al. 1993, Cox et al. 1997, Wirsing et al. 2002). In theory, the greater diversity and higher biomass of alternate prey at lower latitudes should benefit facultative hare predators to the detriment of lynx if the latter species fails to respond functionally to increased prey breadth (Aubry et al. 2000, Buskirk et al. 2000*b*). Yet, the possibility that southern lynx are subject to higher exploitative competition remains untested.

Finally, recent evidence of hybridization between lynx and bobcats in Minnesota (Schwartz et al. 2004) as well as more recently in Maine and New Brunswick, Canada (Schwartz et al., unknown date), has prompted an additional conservation concern for southern lynx. Although the current prevalence and viability of lynx-bobcat hybrids is poorly understood, this could have important implications to prospects for lynx population recovery and persistence at lower latitudes, especially given recent northward expansion of bobcat range into the northern United States and southern Canada (see Anderson and Lovallo 2003).

ARE SOUTHERN LYNX GENERALIST PREDATORS?

Southern snowshoe hare population densities are comparable to those observed during cyclic lows in the boreal forest (Keith 1990, Murray 2000). Thus, conceivably southern lynx may respond to low hare densities similarly to northern lynx when hares are scarce. Buskirk et al. (2000*b*) discussed high coyote dietary plasticity being a function of variable prey availability, and suggested that lynx fail to exhibit comparable adaptive responses to changes in snowshoe hare density. However, comparison of the foraging patterns of lynx and coyotes during a hare population cycle in the Yukon, Canada, revealed that both the number of kills and prey biomass from various prey species actually were more variable for lynx than coyotes, and that lynx relied mostly on red squirrels (*Tamiasciurus hudsonicus*) during the period of hare paucity (O'Donoghue et al. 1998*a, b*). Thus, although lynx are specialists of snowshoe hares, they possess more generalist foraging patterns than originally thought, which may have important implications to their prey choice at lower latitudes.

Several authors (Koehler 1990, Apps 2000, Squires and Ruggiero 2007, Maletzke et al. 2008) noted that red squirrels are included in the diet of southern lynx, but northern lynx also eat red squirrels (O'Donoghue et al. 1998*a, b*) and until recently it was unclear if food choice was more varied at lower latitudes. Roth et al. (2007) have shown that isotopic signatures of historical samples from southwestern lynx have higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than those from elsewhere across the geographic range. Isotopic signatures for the southern range are less reflective of those for snowshoe hares but rather indicate higher reliance on alternate prey, including red squirrel (Fig. 1). This suggests that southwestern lynx are relatively generalized feeders (Roth et al. 2007) and historically had lower reliance on snowshoe hares than did lynx in the boreal forest. However, hares were estimated to compose >50% of the biomass of

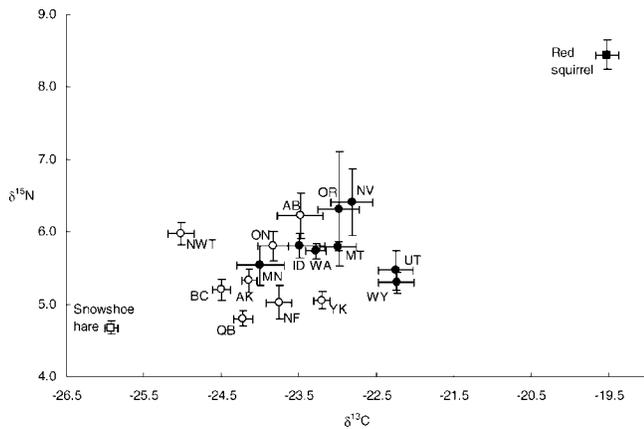


Figure 1. Stable isotope ratios (\bar{x} + SE) of Canada lynx hair from northern, cyclic populations (open circles) and southern, noncyclic populations (closed circles), and of snowshoe hares and red squirrels averaged across their range (squares). Hare and squirrel values have been adjusted for trophic shift (3‰ for nitrogen and 0.5‰ for carbon; McCutchan et al. 2003). Note that isotope ratios for most other potential prey were intermediate ($\delta^{15}\text{N}$: 56.5%, $n = 23$ species; $\delta^{13}\text{C}$: 94.7%, $n = 19$ species) to those for hares and squirrels (see Roth et al. 2007).

lynx diet in all populations studied by Roth et al. (2007; see also Aubry et al. 2000); thus, we surmise that forest practices aimed at promoting lynx habitat should emphasize snowshoe hares as prey because of their predominance in lynx diet, as well as the likelihood that alternate prey species have less restrictive habitat requirements (e.g., see Obbard 1987).

If observed differences in diet breadth between northern and southern lynx are innate and not due to behavioral plasticity reflecting local prey availability, implications of the above findings are that attempts to restore southern lynx populations via transplant of northern animals (e.g., Brocke et al. 1992, Shenk 2001) likely will fail. Alternatively, if observed differences are simply due to behavioral plasticity in feeding patterns, then even transplanted lynx should persist in habitats with a paucity of hares. Ongoing work to document food habits and predator-prey relationships among transplanted lynx (Shenk 2006) should be helpful in differentiating between these possibilities. Furthermore, answers to this question also will help forecast how southern lynx will respond to anticipated northward shift in the southern distribution and abundance of snowshoe hares, following climate change.

DO SOUTHERN LYNX AND HARE POPULATIONS CYCLE?

The possibility that southern lynx populations do not cycle has fueled longstanding debate (see Keith 1963, Aubry et al. 2000, McKelvey et al. 2000a) but surprisingly little rigorous analysis. However, southern lynx populations are unlikely to cycle unless southern hares also do so, or unless lynx numerical variability is driven by ingress of animals from northern populations rather than on-site recruitment (see below). Yet, recent assessment of population cyclicality among southern hares provided conflicting results (Keith 1990, Hodges 2000), whereas other vertebrate species are known to exhibit latitudinal declines in both cyclic amplitude and

propensity for population variability (Turchin 1996, Turchin and Hanski 1997, Hanski et al. 2001, Willig et al. 2003). We contend that previous qualitative analyses of cyclicality for lynx and hares lack the rigor necessary to test the hypothesis of cyclic attenuation with latitude.

We analyzed lynx (Table 1) and snowshoe hare (Table 2) harvest data using spectral analysis (Kendall et al. 1998) and nonlinear time series models (Turchin 2003). Spectral analysis revealed that lynx population cycles were closely tied to latitude, with 8 of 11 time series from the northern boreal forest showing significant evidence of an 8-year to 10-year cycle, and Nova Scotia exhibiting marginally significant cyclicality (Table 1). In contrast, time series from Washington, Idaho, Montana, and Minnesota failed to show similar cyclic patterns (Table 1). When the above analysis was restricted to the first 20 years to control for uneven sampling (see Kendall et al. 1998), 8 northern populations were cyclic (spectral peak all $P < 0.016$, cycle period range 8.4–13.4 yr) and 3 were not (all $P > 0.23$). Results from nonlinear time series models generally were comparable to those for spectral analysis, with autocorrelation at the dominant period of most northern time series being indicative of cyclicality, whereas those for time series from the southern range were not (Table 1). However, we noted that northern time series averaged marginally lower variability compared to those from southern jurisdictions (northern: 0.393 ± 0.028 , $n = 10$; southern: 0.503 ± 0.042 , $n = 5$; Mann-Whitney U chi-square approximation = 3.375, $df = 1$, $P = 0.066$), thereby suggesting a decrease in the relative magnitude of lynx population fluctuations with latitude.

Our analysis of snowshoe hare harvest statistics revealed that the 2 hare populations from Canada were cyclic using either spectral analysis or nonlinear time series modeling (Table 2). Results for several jurisdictions in the southern range (i.e., MI, MN, NY) were equivocal, whereas remaining southern populations exhibited no evidence of cyclicality (Table 2). Yet, unlike lynx population time series, variability for hares increased with latitude (northern: 0.452, $n = 2$; southern: 0.214 ± 0.051 , $n = 6$; Mann-Whitney U chi-square approximation = 4.000, $df = 1$, $P = 0.045$).

Although we recognize limitations imposed by available harvest time series data, our analysis essentially supports the hypothesis that cyclic dynamics are attenuated among southern lynx and snowshoe hare populations, with the important distinction that variability in numerical fluctuations decreases with latitude among lynx and instead increases for hares. If we accept these trends at face value, they suggest that southern lynx populations fluctuate irruptively despite largely stationary southern hare populations. Because high numerical variability is generally recognized as predisposing populations to increased extinction risk (Saether et al. 1996, Morris and Doak 2002), fluctuations in southern lynx populations require close assessment in the context of long-term population viability. Furthermore, it remains possible that southern lynx-hare

Table 1. Results of spectral analysis and nonlinear time series modeling of Canada lynx population time series from harvest data, United States and Canada, 1919–2003. Analyses were restricted to time series collected after 1900 and having ≥ 20 data points.^a

Jurisdiction	Yr	Spectral analysis ^b			Nonlinear time series analysis ^c		
		Peak	<i>P</i>	Period	ACF(<i>T</i>)	$2/\sqrt{n}$	Variability
AK ^d	1934–2003	12.343	<0.001	8.7	0.480	0.241	0.288
NT	1919–2003	20.472	<0.001	9.1	0.517	0.218	0.330
YT	1919–2003	13.450	<0.001	9.1	0.462	0.218	0.389
BC	1919–2003	12.270	<0.001	9.5	0.357	0.218	0.327
AB	1919–2003	12.845	<0.001	9.4	0.523	0.218	0.468
SK ^d	1919–2000	5.168	0.37	9.6	0.375	0.222	0.473
MB	1919–2003	8.735	0.013	9.6	0.370	0.218	0.558
ON	1919–2003	9.322	0.008	9.4	0.320	0.218	0.307
PQ	1919–2003	13.733	<0.001	9.4	0.362	0.218	0.340
NS	1919–1980	6.656	0.073	9.4	0	0.277	0.374
NF	1951–2003	4.849	0.34	9.6	0.046	0.256	0.445
WA ^d	1961–1983	4.196	0.26	10.4	0.096	0.426	0.446
ID	1957–1982	3.769	0.44	7.4	0.101	0.400	0.546
MT ^d	1950–1998	2.012	0.95	9.7	0.193	0.289	0.618
MN ^d	1934–1984	5.072	0.99	8.6	0.371	0.283	0.531

^a Lynx harvest data are from Novak et al. (1987) up to 1984 and updated with unpublished data from the International Association of Fish and Wildlife Agencies (<www.iafwa.org>) and Statistics Canada (<www.statscan.ca>).

^b For spectral analysis, time series were transformed to natural log and detrended by subtracting the fit of a linear model and the mean. Lomb–Scargle periodograms generated Fourier spectra that accommodated unevenly sampled data (Lomb 1976). Populations were considered as cyclic if $P < 0.05$, where $P = 1 - (1 - e^{-z})^n$, and z is the corresponding spectral peak and n is the sample size (Horne and Baliunas 1986, Kendall et al. 1998). Cycle period was calculated as $1/\text{spectral frequency}$.

^c For nonlinear time series models, autocorrelation at the dominant period (ACF[*T*]) was calculated and cyclicity was deemed significant where $\text{ACF}(T) > 2/\sqrt{n}$ (Turchin 2003). Variability was calculated as $\text{SD}(\log_{10}[N])$ (Stenseth and Framstad 1980).

^d Missing values were interpolated for nonlinear time series analysis and corrected sample size was used to calculate $2/\sqrt{n}$.

populations that were formerly cyclic have experienced dampened oscillations in recent years (see Ims et al. 2007).

ARE SOUTHERN LYNX POPULATIONS VIABLE?

Assessment of southern lynx population viability has been structured in terms of the hare density required for lynx persistence (e.g., Ruggiero et al. 2000, Steury and Murray 2004). Previously, we examined conditions promoting lynx population viability in the southern range by modeling lynx demography relative to snowshoe hare abundance, using

lynx–hare data collected in the northern range (Steury and Murray 2004). We found that survival and dispersal among adult lynx were strongly influenced by relative (rather than absolute) hare density, with rapid decline in hare abundance resulting in low survival and high dispersal of lynx (Steury and Murray 2004). More gradual hare population decline failed to elicit comparably poor population demography, even when absolute hare density was low. Thus, it seems that southern lynx may experience adequate survival and low dispersal when hare densities are consistently low, but rapid declines in hare density tend to promote mortality and

Table 2. Results of spectral analysis and nonlinear time series modeling of snowshoe hare population time series from harvest data, United States and Canada, 1911–1998. Analyses were restricted to time series collected after 1900 and having ≥ 20 data points.

Jurisdiction	Years	Spectral analysis ^a			Nonlinear time series analysis ^b		
		Peak	<i>P</i>	Period	ACF(<i>T</i>)	$2/\sqrt{n}$	Variability
NT (Hudson Bay Company)	1911–1936	9.946	0.001	10.3	0.613	0.392	0.448
ON	1911–1935	9.101	0.003	10.4	0.633	0.400	0.457
MI	1937–1997	12.459	0.002	12.8	0.084	0.256	0.186
WI	1931–1997	4.945	0.38	13.8	0.054	0.244	0.410
MN	1942–1995	8.358	0.013	9.5	0.051	0.272	0.329
ME	1948–1983	1.837	0.99	8.5	−0.255	0.333	0.131
NY ^c	1932–1951	5.582	0.073	8.8	0.634	0.447	0.119
CT	1923–1955	4.043	0.44	9.6	0.337	0.348	0.113

^a Snowshoe hares harvest data are from Keith (1963) and Murray (2000). For spectral analysis, time series were transformed to natural log and detrended by subtracting the fit of a linear model and the mean. Lomb–Scargle periodograms generated Fourier spectra that accommodated unevenly sampled data (Lomb 1976). Populations were considered as cyclic if $P < 0.05$, where $P = 1 - (1 - e^{-z})^n$, and z is the corresponding spectral peak and n is the sample size (Horne and Baliunas 1986, Kendall et al. 1998). Cycle period was calculated as $1/\text{spectral frequency}$.

^b For nonlinear time series models, autocorrelation at the dominant period (ACF[*T*]) was calculated and cyclicity was deemed significant where $\text{ACF}(T) > 2/\sqrt{n}$ (Turchin 2003). Variability was calculated as $\text{SD}(\log_{10}[N])$ (Stenseth and Framstad 1980).

^c Missing values were interpolated for nonlinear time series analysis and corrected sample size was used to calculate $2/\sqrt{n}$.

emigration. If hare population dynamics are less variable in the southern range as was suggested by the time series analysis we presented in the previous section (see also Keith 1990, Hodges 2000, Murray 2000), then the proposed lynx sensitivity to variable hare densities (Steury and Murray 2004) may have limited relevance in the southern range. However, these demographic responses may offer insight into sources of low survival and high dispersal among transplanted lynx in New York (Brocke et al. 1992) as well as initially in Colorado (Kloor 1999, Shenk 2001). Because source animals were livetrapped from northern areas with relatively high hare abundance, and quickly released to sites where hares were scarce, animals that remained in the release area and survived the transplant likely were those that adapted quickly to drastic changes in prey abundance. Improved transplant success in the second phase of the Colorado effort was at least partly related to modified handling protocols, including soft-release following longer acclimation periods.

Our analysis (Steury and Murray 2004) also indicated that kitten production and survival were related to absolute hare abundance, with threshold hare densities <1.5 hares/ha leading to markedly low (and likely unsustainable) recruitment rates. Snowshoe hare densities across most of the southern range are consistently below this threshold (Keith 1990, Hodges 2000, Murray 2000), implying that despite reported on-site recruitment of lynx kittens born in the southern range (e.g., Shenk 2006), such recruitment may be too low to offset local mortality and dispersal rates. However, we remain mindful of the caution offered by Buskirk et al. (2000b) about making inferences on the ecology of southern lynx based on knowledge gained from northern animals, and the general relationships we modeled (i.e., adult survival as a function of changes in hare densities, kitten survival as a function of absolute hare densities, etc.) are likely to hold if population dynamics of northern and southern lynx are comparable. Indeed, if southern lynx are sufficiently less reliant on hares (see Roth et al. 2007), or if southern hare numbers are suitably stationary so as not to subject resident lynx to dramatic interannual fluctuations in prey abundance, then threshold hare densities and lynx demographic responses described by Steury and Murray (2004) may be overly conservative. Further studies clearly are needed to better determine the relationship between prey abundance and lynx demography in the southern range.

ARE SOUTHERN LYNX POPULATIONS RELIANT ON INGRESS FROM CANADIAN LYNX?

If, however, Steury and Murray (2004) are correct in their assessment of the current potential for southern areas to support lynx, then existing populations may be maintained only as part of a larger metapopulation with the boreal forest. For instance, irruptive behavior in southern lynx numbers (Mech 1973, 1980) may not reflect on-site differences in population dynamics but rather periodic emigration of lynx from Canada to the contiguous United

States. We provided some support for this position in our aforementioned analysis showing decreasing lynx population variability with latitude.

Cyclic lynx and hare population dynamics are largely synchronous across the boreal forest of Canada and Alaska, although synchrony in both species tends to diminish as populations become increasingly distant from the continental core (Smith 1983, Ranta et al. 1997). Stenseth et al. (1999) identified distinct geographical regions where lynx populations are synchronous, leading to the speculation that climatic factors may limit lynx dispersal and gene flow (Stenseth et al. 2004a, b). Because lynx can disperse over long distances, especially following hare population declines (Poole 1997, Mowat et al. 2000), their localized dispersal between snowshoe hare populations at slightly different phases of the cycle likely synchronizes regional dynamics (Stenseth et al. 1999, Krebs et al. 2001). By extension, lynx populations in the boreal forest may provide rescue for southern lynx populations if southward dispersal occurs following cyclic declines in hare abundance. This trend could have important implications for lynx conservation in the southern range, especially given the proximity of most areas recognized as lynx habitat within the contiguous United States to the international border with Canada (see U.S. Fish and Wildlife Service 2006).

Southward migration of lynx across the international border could account for the periodic pulses in lynx harvest observed in the contiguous United States (McKelvey et al. 2000a, b), and lynx population fluctuations in the United States could either be synchronous or time-delayed relative to adjacent Canadian populations depending on whether emigration is fast and pulsatile versus slow and continuous. We used cross-correlation analysis of lynx harvest numbers from Washington, Idaho, Montana, and Minnesota to evaluate correlation with harvest numbers from the most proximate lynx populations in Canada. We compared correlations between populations ranging from $t-0$ to $t-4$ and speculated that increasing correlation with increasing time lag should reflect delays in emigration of lynx from north to south. This analysis expands on that of McKelvey et al. (2000a) by using ln-transformed population time series to correct for bias in lynx harvest data (Keith 1963, Royama 1992), and excludes fur return statistics from New Hampshire, USA (due to small sample size), and instead includes Idaho.

Individual correlation coefficients for lynx harvest time series from each of the 4 southern jurisdictions were nonsignificant (with Bonferroni correction), so we focused our attention on qualitative trends in correlation. For Minnesota and Montana, correlation coefficients generally declined from positive to negative with increasing delays (Fig. 2), implying that those populations may be synchronous with their northern counterparts either through rapid ingress of northern animals following hare population declines or from fluctuations in resident populations acting in synchrony with those in Canada. In contrast, for Idaho and Washington, correlation coefficients tended to increase

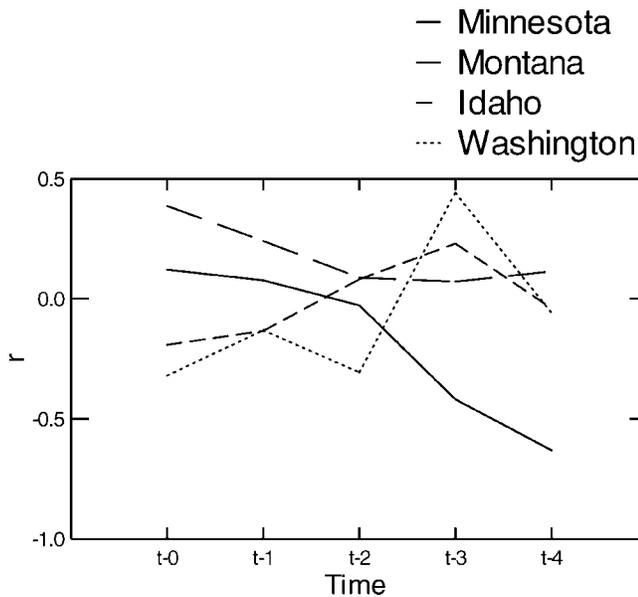


Figure 2. Correlation coefficients between time-lagged Canada lynx harvest time series in the contiguous United States versus time series from adjacent Canadian populations, 1934–1998.

from negative to positive up to $t-3$ (Fig. 2), suggesting that numerical responses may be offset and that immigration could have occurred into the southern range over several years.

Genetic analyses of lynx populations offer more robust evidence of linkage between northern and southern lynx populations. Schwartz et al. (2002) revealed an absence of genetic isolation by distance along the Rocky Mountain corridor, implying that lynx populations from Alaska to Montana are largely panmictic and that immigration from Canada likely is an important source of recruitment into southern populations. It follows that international conservation efforts should prioritize identification and protection of lynx migration corridors between Canada and the United States. Yet, despite the absence of evidence for genetic isolation in the Schwartz et al. (2002) analysis, some degree of gene flow restriction may occur across the North American distribution of lynx (Rueness et al. 2003b; see also Stenseth et al. 2004a), and genetic isolation also is apparent at lower latitudes near periphery of the species' range (Schwartz et al. 2003). Genetic structuring and restricted gene flow also is known for other felids such as Eurasian lynx (*Lynx lynx*; Rueness et al. 2003a), bobcat (Millions and Swanson 2007), and cougar (Anderson et al. 2004), so it seems likely that dispersal barriers are relevant to dynamics of southern lynx populations as well.

The above evidence for genetic structuring in southern lynx implies that population restoration efforts should be mindful of the source of animals used in the transplant. For example, the New York transplant received lynx from Yukon (Brocke et al. 1992), whereas Colorado restoration was achieved with animals from Alaska, and British Columbia, Yukon, Manitoba, and Québec, Canada (T. Shenk, personal communication). We submit that to the fullest extent possible, lynx restoration efforts should not use distant

source populations nor mix genotypes from a variety of areas. In fact, extensive mixing of genotypes from disparate regions is not sound conservation practice (Storfer 1999, Crandall et al. 2000), and in the present case probably would not even be possible if lynx transplants either had a higher scientific profile or stronger federal oversight. It follows that future lynx transplant efforts such as that being considered for Washington (Koehler et al. 2008) should strive to maintain potential local adaptation and historically representative gene pools.

MANAGEMENT IMPLICATIONS

Our review and analysis reveal several conclusions that are important to the long-term persistence of southern lynx populations. Forest management should favor an abundance of stands with intermediate to high stem density as well as largely continuous forest coverage with few openings. Managing specifically for lynx denning habitat should not be necessary, provided that some areas have abundant ground cover with overblown trees or other structure. From the prey perspective, habitat management in the southern range should focus on providing suitable patches that are sufficiently large to minimize local extinction risk of snowshoe hares. Snowmobile and other anthropogenic trails have disputable effect in promoting lynx competition with other carnivores, and their impacts should be more fully understood to test the validity of anticipated restrictions on recreational activities in lynx habitat. Stand-alone viability of lynx populations in the southern range is questionable and in need of further study, especially in the context of lynx demographic responses to fluctuating abundance of hares and alternate prey. Determining on-site juvenile recruitment rates via late-winter track surveys will help reveal the importance of arguably the key demographic feature determining population status of southern lynx. Finally, because several southern lynx populations are likely to be reliant on emigration from Canadian populations following cyclic decline of northern hares, lynx habitat protection needs to include large, continuous tracts of landscape that are contiguous with the international border. Yet, over the next decades southern lynx populations inevitably will be influenced by ongoing habitat loss and fragmentation as well as the effects of climate change and attendant shifts in habitat, prey base, and competitor guild. Ultimately, the extent of such changes and whether lynx are able to adapt to them will determine not how, but if, this species can persist in its current southern range.

ACKNOWLEDGMENTS

We are grateful to J. McDonald and J. Vashon for inviting us to participate in the lynx symposium, and to C. J. Krebs, J. McDonald, M. O'Donoghue, and J. Ray for helpful reviews.

LITERATURE CITED

Anderson, C. R., Jr., F. G. Lindzey, and D. B. McDonald. 2004. Genetic structure of cougar populations across the Wyoming basin: metapopulation or megapopulation. *Journal of Mammalogy* 85:1207–1214.

- Anderson, E. M., and M. J. Lovallo. 2003. Bobcat and lynx. Pages 758–786 in G. A. Feldhamer and B. Thompson, editors. *Wild mammals of North America*. Volume II. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Apps, C. D. 2000. Space-use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains: a study. Pages 351–371 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Aubry, K. B., G. M. Koehler, and J. R. Squires. 2000. Ecology of Canada lynx in southern boreal forests. Pages 373–396 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Barbour, M. S., and J. A. Litvaitis. 1993. Niche dimensions of New England cottontails in relation to habitat patch size. *Oecologia* 95:321–327.
- Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, M. Blower, A. Byrom, F. I. Doyle, C. Doyle, D. Hik, E. L. Hofer, A. Hubbs, T. Karels, D. L. Murray, V. Nams, M. O'Donoghue, C. Rohner, and S. Schweiger. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. *Oikos* 74:69–80.
- Boutin, S., C. J. Krebs, A. R. E. Sinclair, and J. N. M. Smith. 1986. Proximate causes of losses in a snowshoe hare population. *Canadian Journal of Zoology* 64:606–610.
- Brand, C. J., and L. B. Keith. 1979. Lynx demography during a snowshoe hare decline in Alberta. *Journal of Wildlife Management* 43:827–849.
- Brocke, R. H., K. A. Gustafson, and L. B. Fox. 1992. Restoration of large predators: potentials and problems. Pages 303–315 in D. J. Decker, M. E. Krasny, G. R. Goff, C. R. Smith, and D. W. Gross, editors. *Challenges in the conservation of biological resources: a practitioner's guide*. Westview Press, Boulder, Colorado, USA.
- Bunnell, K. D., J. T. Flinders, M. L. Wolfe, and J. A. Bissonette. 2004. Quantifying the potential impacts of coyotes and snowmobiles on lynx conservation in Utah and the Intermountain West. Western Forest Carnivore Committee Meeting, Whitefish, Montana, USA.
- Buskirk, S. W., L. F. Ruggiero, K. B. Aubry, D. E. Pearson, J. R. Squires, and K. S. McKelvey. 2000a. Comparative ecology of lynx in North America. Pages 397–418 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Buskirk, S. W., L. F. Ruggiero, and C. J. Krebs. 2000b. Habitat fragmentation and interspecific competition: implications for lynx conservation. Pages 83–100 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications* 11:961–980.
- Cox, E. W., R. A. Garrott, and J. R. Cary. 1997. Effect of supplemental cover on survival of snowshoe hares and cottontail rabbits in patchy habitat. *Canadian Journal of Zoology* 75:1357–1363.
- Crandall, K. A., R. P. Bininda-Emonds, G. M. Mace, and R. K. Wayne. 2000. Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution* 15:290–295.
- Defenders of Wildlife. 2007. Lynx background and recovery. <http://www.defenders.org/programs_and_policy/wildlife_conservation/imperiled_species/lynx/background_and_recovery.php?ht=>. Accessed 25 Jul 2007.
- Ellsworth, E., and T. D. Reynolds. 2006. Snowshoe hare (*Lepus americanus*): a technical conservation assessment. United States Department of Agriculture Forest Service, Rocky Mountain Region, Moscow, Idaho, USA. <<http://www.fs.fed.us/r2/projects/scp/assessments/snowshoehare.pdf>>. Accessed 22 Oct 2006.
- Etcheverry, P., M. Crête, J.-P. Ouellet, L.-P. Rivest, M.-C. Richer, and C. Beaudoin. 2005. Population dynamics of snowshoe hares in relation to furbearer harvest. *Journal of Wildlife Management* 69:771–781.
- Hanski, I., H. Henttonen, E. Korpimäki, and L. Oksanen. 2001. Small rodent dynamics and predation. *Ecology* 82:1505–1520.
- Hodges, K. E. 2000. Ecology of snowshoe hares in southern boreal and montane forests. Pages 163–206 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Hodges, K. E., C. J. Krebs, D. S. Hik, C. I. Stefan, E. A. Gillis, and C. E. Doyle. 2001. Snowshoe hare demography. Pages 141–178 in C. J. Krebs, S. Boutin, and R. Boonstra, editors. *Ecosystem dynamics of the boreal forest*. Oxford University Press, Oxford, United Kingdom.
- Homyack, J. A., D. J. Harrison, J. A. Litvaitis, and W. B. Krohn. 2006. Quantifying densities of snowshoe hares in Maine using pellet plots. *Wildlife Society Bulletin* 34:74–80.
- Horne, J. H., and S. L. Baliunas. 1986. A prescription for period analysis of unequally sampled time series. *Astrophysics Journal* 302:757–763.
- Hoving, C. L., D. J. Harrison, W. B. Krohn, W. J. Jakubas, and M. A. McCollough. 2004. Canada lynx *Lynx canadensis* habitat and forest succession in northern Maine, USA. *Wildlife Biology* 10:285–294.
- Hoving, C. L., D. J. Harrison, W. B. Krohn, R. A. Joseph, and M. O'Brien. 2005. Broad-scale predictors of Canada lynx occurrence in eastern North America. *Journal of Wildlife Management* 69:739–751.
- Ims, R. A., J.-A. Henden, and S. T. Killengreen. 2007. Collapsing population cycles. *Trends in Ecology and Evolution* 23:79–86.
- Keith, L. B. 1963. Wildlife's ten-year cycle. University of Wisconsin Press, Madison, USA.
- Keith, L. B. 1990. Dynamics of snowshoe hare populations. Pages 119–195 in H. H. Genoways, editor. *Current mammalogy*. Plenum Press, New York, New York, USA.
- Keith, L. B., S. E. M. Bloomer, and T. Willebrand. 1993. Dynamics of a snowshoe hare population in a fragmented habitat. *Canadian Journal of Zoology* 71:1385–1392.
- Keith, L. B., J. R. Cary, O. J. Rongstad, and M. C. Brittingham. 1984. Demography of a declining snowshoe hare population. *Wildlife Monographs* 90.
- Keith, L. B., A. W. Todd, C. J. Brand, R. S. Adamcik, and D. H. Rusch. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. *Proceedings of the International Congress of Game Biologists* 13: 151–175.
- Kendall, B. E., J. Prendergast, and O. N. Bjørnstad. 1998. The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. *Ecology Letters* 1:160–164.
- King, A. A., and W. M. Schaffer. 2001. The geometry of a population cycle: a mechanistic model of snowshoe hare demography. *Ecology* 82: 814–830.
- Kloor, K. 1999. Lynx and biologists try to recover after disastrous start. *Science* 285:320–321.
- Koehler, G. M. 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. *Canadian Journal of Zoology* 68:845–851.
- Koehler, G. M., M. G. Hornocker, and H. S. Hash. 1979. Lynx movements and habitat use in Montana. *Canadian Field-Naturalist* 93: 441–442.
- Koehler, G. M., B. T. Maletzke, J. A. Von Kienast, K. B. Aubry, R. B. Wielgus, and R. H. Naney. 2008. Habitat fragmentation and the persistence of lynx populations in Washington State. *Journal of Wildlife Management* 72:1518–1524.
- Kolbe, J. A., J. R. Squires, D. H. Pletscher, and L. F. Ruggiero. 2007. The effect of snowmobile trails on coyote movements within lynx home ranges. *Journal of Wildlife Management* 71:1409–1418.
- Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair. 2001. What drives the 10-year cycle of snowshoe hares. *BioScience* 51:25–35.
- Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112–1115.
- Lomb, N. R. 1976. Least-squares frequency analysis of unequally spaced data. *Astrophysics and Space Science* 39:447–462.
- Maletzke, B. T., G. M. Koehler, R. B. Wielgus, K. B. Aubry, and M. A. Evans. 2008. Habitat conditions associated with lynx hunting behavior during winter in northern Washington. *Journal of Wildlife Management* 72:1473–1478.
- McCutchan, J. H., W. M. Lewis, C. Kendall, and C. C. McGrath. 2003.

- Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390.
- McKelvey, K. S., K. A. Aubry, and Y. K. Ortega. 2000a. History and distribution of lynx in the contiguous United States. Pages 207–264 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- McKelvey, K. S., S. W. Buskirk, and C. J. Krebs. 2000b. Theoretical insights into the population viability of lynx. Pages 21–37 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Mech, L. D. 1973. Canadian lynx invasion of Minnesota. *Biological Conservation* 5:151–152.
- Mech, L. D. 1980. Age, sex, reproduction, and spatial organization of lynxes colonizing northeastern Minnesota. *Journal of Mammalogy* 61: 261–267.
- Millions, D. G., and B. J. Swanson. 2007. Impact of natural and artificial barriers to dispersal on population structure of bobcats. *Journal of Wildlife Management* 71:96–102.
- Mills, L. S., P. C. Griffin, K. E. Hedges, K. McKelvey, L. Ruggiero, and T. Ulizio. 2005. Pellet count indices compared to mark–recapture estimates for evaluating snowshoe hare density. *Journal of Wildlife Management* 69:1053–1062.
- Moen, R., C. L. Burdett, and G. J. Niemi. 2008. Movement and habitat use of Canada lynx during denning in Minnesota. *Journal of Wildlife Management* 72:1507–1513.
- Morris, W. F., and D. F. Doak. 2002. *Quantitative conservation biology*. Sinauer, Sunderland, Massachusetts, USA.
- Mowat, G., K. G. Poole, and M. O'Donoghue. 2000. Ecology of lynx in northern Canada and Alaska. Pages 265–306 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Mowat, G., and B. Slough. 2003. Habitat preference of Canada lynx through a cycle in snowshoe hare abundance. *Canadian Journal of Zoology* 81:1736–1745.
- Murray, D. L. 2000. A geographic analysis of snowshoe hare population demography. *Canadian Journal of Zoology* 78:1207–1217.
- Murray, D. L. 2003. Snowshoe hare and other hares. Pages 147–175 in G. A. Feldhamer and B. Thompson, editors. *Wild mammals of North America*. Volume II. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Murray, D. L., J. R. Cary, and L. B. Keith. 1997. Interactive effects of sublethal nematodes and nutritional status on snowshoe hare vulnerability to predation. *Journal of Animal Ecology* 66:250–264.
- Murray, D. L., E. Ellsworth, and A. Zack. 2005. Assessment of potential bias with snowshoe hare fecal pellet-plot counts. *Journal of Wildlife Management* 69:385–395.
- Murray, D. L., J. D. Roth, E. Ellsworth, A. J. Wirsing, and T. D. Steury. 2002. Estimating low density snowshoe hare populations using fecal pellet counts. *Canadian Journal of Zoology* 80:771–781.
- Novak, M., M. E. Obbard, J. G. Jones, R. Newman, A. Booth, A. J. Satterthwaite, and G. Linscombe. 1987. *Furbearers harvests in North America 1600–1984*. Ministry of Natural Resources, Toronto, Ontario, Canada.
- Obbard, M. E. 1987. Red squirrel. Pages 265–281 in M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. *Wild furbearer management and conservation in North America*. Ontario Ministry of Natural Resources, Toronto, Canada.
- O'Donoghue, M., S. Boutin, C. J. Krebs, and E. J. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 80:150–162.
- O'Donoghue, M., S. Boutin, C. J. Krebs, D. L. Murray, and E. J. Hofer. 1998a. Behavioral responses of coyotes and lynx to the snowshoe hare cycle. *Oikos* 82:169–183.
- O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zutela, D. L. Murray, and E. J. Hofer. 1998b. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79:1193–1208.
- O'Donoghue, M., E. Hofer, and F. I. Doyle. 1995. Predator versus predator. *Natural History* 104:6–9.
- Organ, J. F., J. H. Vashon, J. E. McDonald, Jr., A. D. Vashon, S. M. Crowley, W. J. Jakubas, G. J. Matula, Jr., and A. L. Meehan. 2008. Within-stand selection of Canada lynx natal dens in northwest Maine, USA. *Journal of Wildlife Management* 72:1514–1517.
- Parker, G. R., J. W. Maxwell, L. D. Morton, and G. E. J. Smith. 1983. The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. *Canadian Journal of Zoology* 61:770–786.
- Poole, K. G. 1997. Dispersal patterns of lynx in the Northwest Territories. *Journal of Wildlife Management* 61:497–505.
- Ranta, E., V. Kaitala, and P. Lundberg. 1997. The spatial dimension in population fluctuations. *Science* 278:1621–1623.
- Roth, J. D., J. D. Marshall, D. L. Murray, D. M. Nickerson, and T. D. Steury. 2007. Geographical gradients in diet affect population dynamics of Canada lynx. *Ecology* 88:2736–2743.
- Royama, T. 1992. *Analytical population dynamics*. Chapman and Hall, New York, New York, USA.
- Ruediger, B., J. Claar, S. Mighton, B. Nancy, T. Rinali, F. Wahl, N. Warren, D. Wenger, A. Williamson, L. Lewis, B. Holt, G. Patton, and J. Trick. 2000. *Canada lynx conservation assessment and strategy*. U.S. Forest Service, Bureau of Land Management, National Parks Service, and U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- Ruess, E. K., P. E. Jorde, L. Hellborg, N. C. Stenseth, H. Ellegren, and K. S. Jakobsen. 2003a. Cryptic population structure in a large, mobile mammalian predator: the Scandinavian lynx. *Molecular Ecology* 32: 2623–2633.
- Ruess, E. K., N. C. Stenseth, M. O'Donoghue, S. Boutin, H. Ellegren, and K. S. Jakobsen. 2003b. Ecological and genetic spatial structuring in the Canadian lynx. *Nature* 425:69–72.
- Ruggiero, L. F., K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. 2000. *The scientific basis for lynx conservation: qualified insights*. Pages 443–454 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Saether, B.-E., T. H. Ringsby, and E. Roskaft. 1996. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos* 77:217–226.
- Schwartz, M. K., L. S. Mills, K. S. McKelvey, L. F. Ruggiero, and F. W. Allendorf. 2002. DNA reveals high dispersal synchronizing the population dynamics of Canada lynx. *Nature* 415:520–522.
- Schwartz, M. K., L. S. Mills, Y. Ortega, L. F. Ruggiero, and F. W. Allendorf. 2003. Landscape location affects genetic variation of Canada lynx (*Lynx canadensis*). *Molecular Ecology* 12:1807–1816.
- Schwartz, M. K., K. L. Pilgrim, K. S. McKelvey, E. L. Lindquist, J. J. Claar, S. Loch, and L. F. Ruggiero. 2004. Hybridization between Canada lynx and bobcats: genetic results and management implications. *Conservation Genetics* 5:349–355.
- Schwartz, M. K., K. Pilgrim, K. McKelvey, and L. F. Ruggiero. Unknown date. Using DNA to determine the presence of lynx and identify hybridization between lynx and bobcats. RWU 4201 Wildlife Ecology in Rocky Mountain Landscapes, U.S. Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA. <www.fs.fed.us/rm/wildlife/genetics/pdfs/Lynx_Bobcat_Hybrid.pdf>. Accessed 25 Jun 2007.
- Shenk, T. 2006. Wildlife Commission meeting: November 8, 2006. Lynx fact sheet. Colorado Division of Wildlife, Denver, USA. <<http://wildlife.state.co.us/WildlifeSpecies/SpeciesOfConcern/Mammals/Lynx/>>. Accessed 25 Jun 2006.
- Shenk, T. M. 2001. Post-release monitoring of lynx reintroduced to Colorado. Annual progress report for the USA Fish and Wildlife Service. Colorado Division of Wildlife, Denver, USA.
- Sievert, P. R., and L. B. Keith. 1985. Survival of snowshoe hares at a geographic range boundary. *Journal of Wildlife Management* 49:854–866.
- Slough, B. G. 1999. Characteristics of Canada lynx, *Lynx canadensis*, maternal dens and denning habitat. *Canadian Field-Naturalist* 113:605–608.
- Slough, B. G., and G. Mowat. 1996. Population dynamics of lynx in a refuge and interactions between harvested and unharvested populations. *Journal of Wildlife Management* 60:946–961.
- Smith, C. H. 1983. Spatial trends in Canadian snowshoe hare, *Lepus americanus*, population cycles. *Canadian Field-Naturalist* 97:151–160.
- Squires, J. R., N. J. DeCesare, J. A. Kolbe, and L. F. Ruggiero. 2008.

- Hierarchical den selection of Canada lynx in western Montana. *Journal of Wildlife Management* 72:1497–1506.
- Squires, J. R., and T. Laurion. 2000. Lynx hole range and movements in Montana and Wyoming: preliminary results. Pages 337–350 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. S. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Niwot, USA.
- Squires, J. R., and L. F. Ruggiero. 2007. Winter prey selection of Canada lynx in northwestern Montana. *Journal of Wildlife Management* 71:310–315.
- Stenseth, N. C., K.-S. Chan, H. Tong, R. Boonstra, S. Boutin, C. J. Krebs, E. Post, M. O'Donoghue, N. G. Yoccoz, M. C. Forchhammer, and J. W. Hurrell. 1999. Common dynamic structure of Canada lynx populations within three climatic regions. *Science* 285:1071–1073.
- Stenseth, N. C., D. Ehrlich, E. K. Rueness, O. C. Lingjaerde, K.-S. Chan, S. Boutin, M. O'Donoghue, D. A. Robinson, H. Viljugrein, and K. S. Jakobsen. 2004a. The effect of climate forcing on population synchrony and genetic structuring of the Canadian lynx. *Proceedings of the National Academy of Sciences* 101:6056–6061.
- Stenseth, N. C., W. Falck, K.-S. Chan, O. N. Bjørnstad, and C. J. Krebs. 1997. Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. *Proceedings of the National Academy of Sciences* 94:5147–5152.
- Stenseth, N. C., W. Falck, K.-S. Chan, O. N. Bjørnstad, M. O'Donoghue, H. Tong, R. Boonstra, S. Boutin, C. J. Krebs, and N. G. Yoccoz. 1998. From patterns to processes: phase and density dependencies in the Canadian lynx cycle. *Proceedings of the National Academy of Sciences* 95:15430–15435.
- Stenseth, N. C., and E. Framstad. 1980. Reproductive effort and optimal reproductive rates in small rodents. *Oikos* 34:23–34.
- Stenseth, N. C., A. Shabbar, K.-S. Chan, S. Boutin, E. K. Rueness, D. Ehrlich, J. W. Hurrell, O. C. Lingjaerde, and K. S. Jakobsen. 2004b. Snow conditions may create an invisible barrier for lynx. *Proceedings of the National Academy of Sciences* 101:10632–10634.
- Steury, T. D., and D. L. Murray. 2004. Modeling the reintroduction of lynx to the southern portion of its range. *Biological Conservation* 117:127–141.
- Storfer, A. 1999. Gene flow and endangered species translocations: a topic revisited. *Biological Conservation* 87:173–180.
- Turchin, P. 1996. Nonlinear time-series model of vole population fluctuations. *Researches in Population Ecology* 38:121–132.
- Turchin, P. 2003. *Complex population dynamics*. Princeton University Press, Princeton, New Jersey, USA.
- Turchin, P., and I. Hanski. 1997. An empirically-based model for the latitudinal gradient in vole population dynamics. *American Naturalist* 149:267–276.
- U.S. Fish and Wildlife Service. 2000. Endangered and Threatened wildlife and plants; determination of threatened status for the contiguous USA distinct population segment of the Canada lynx and related rule. *Federal Register* 65:16051–16086.
- U.S. Fish and Wildlife Service. 2006. Endangered and Threatened wildlife and plants; designation of critical habitat for the contiguous United States distinct population segment of the Canada lynx; final rule. *Federal Register* 71:66006–66061.
- Vashon, J. H., A. L. Meehan, W. J. Jakubas, J. F. Organ, A. D. Vashon, C. R. McLaughlin, G. J. Matula, Jr., and S. M. Crowley. 2008a. Spatial ecology of a Canada lynx population in northern Maine. *Journal of Wildlife Management* 72:1479–1487.
- Vashon, J. H., A. L. Meehan, J. F. Organ, W. J. Jakubas, C. R. McLaughlin, A. D. Vashon, and S. M. Crowley. 2008b. Diurnal habitat relationships of Canada lynx in an intensively managed private forest landscape in northern Maine. *Journal of Wildlife Management* 72:1488–1496.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics* 34:273–309.
- Wirsing, A. J., and D. L. Murray. 2002. Patterns in consumption of woody plants by snowshoe hares in northwestern United States. *Ecoscience* 9:440–449.
- Wirsing, A. J., T. D. Steury, and D. L. Murray. 2002. A demographic analysis of a southern hare population in a fragmented habitat: evaluating the refugium model. *Canadian Journal of Zoology* 80:169–177.
- Wolff, J. O. 1981. Refugia, dispersal, predation, and geographic variation in snowshoe hare cycles. Pages 441–449 in K. Myers and C. D. MacInnes, editors. *Proceedings of the International Lagomorph Conference*, 12–16 August 1979, Guelph, Ontario, Canada.

Associate Editor: McDonald.