

The Canada Lynx (*Lynx canadensis*) of Isle Royale: Over-harvest, Climate Change, and the Extirpation of an Island Population

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In the 1930s, the Canada Lynx (*Lynx canadensis*) was extirpated from Isle Royale, a 535-km² island located in western Lake Superior, 22 km from the Ontario and Minnesota shorelines. The first half of the 20th century was a time of change on Isle Royale as Caribou (*Rangifer tarandus*) disappeared, Coyotes (*Canis latrans*) briefly appeared, Moose (*Alces americanus*), Grey Wolves (*Canis lupus*), and Red Foxes (*Vulpes vulpes*) became established, and the habitat was altered by fire, logging, and over-browsing. Although these changes may have contributed to the demise of the Canada Lynx, our results suggest that over-harvest was a primary cause. Assuming a peak carrying capacity of 75 Canada Lynx and harvest rates comparable to those reported from 1890–1935, a population viability analysis indicated that the island population had a 0% chance of surviving 50 years. The analysis also indicated that, even in the absence of harvest, the population had only a 14% chance of persistence for 250 years. However, when 10 Canada Lynx were added to the modeled population every 10th year, the probability of persistence increased to 100%. Our analyses suggest that the island's Canada Lynx population maintained itself by periodic immigration across an ice bridge; therefore, natural recolonization should be possible. However, the probability of ice-bridge formation has declined from 0.8 in the winter of 1958–59 to 0.1 in 2012–13, likely as a result of climate change. The Isle Royale situation exemplifies another impact of climate change and the possible need to augment populations to mitigate the loss of connectivity.

Key Words: Canada Lynx; *Lynx canadensis*; climate change; connectivity; island biogeography; Isle Royale; metapopulation; over-harvest; population viability analysis

Introduction

The historical range of the Canada Lynx (*Lynx canadensis*) includes Alaska, Canada, and, within the conterminous United States, parts of New England, the upper Midwest, and the Rocky Mountains (McKelvey 2000; Anderson and Lovallo 2003; Poole 2003). In recent times, the distribution of the Canada Lynx has been reduced in the southern portion of its range (Laliberte and Ripple 2004; Koen *et al.* 2014), mainly due to a combination of over-harvest, loss of suitable habitat, and changes in faunal communities (Ruggiero and McKelvey 2000; United States Fish and Wildlife Service 2000; Anderson and Lovallo 2003). The species is now listed as “threatened” in the conterminous United States under the U.S. Endangered Species Act (Ruggiero and McKelvey 2000; United States Fish and Wildlife Service 2000; Interagency Lynx Biology Team 2013). In Canada, the species is listed as regionally endangered in Nova Scotia and New Brunswick (Mackinnon and Kennedy 2008).

Canada Lynx were present and seemingly abundant on Isle Royale when Europeans explored the island in 1857 (Palliser 1863). Large-scale lynx trapping on Isle Royale apparently started in the 1890s (Martin 1988). Historical records suggest that there was a resident pop-

ulation of Canada Lynx on Isle Royale until about the 1930s (Adams 1909; Mech 1966; Johnsson *et al.* 1982; Martin 1988). Although there have been a few reports of lynx on Isle Royale since then (Johnsson *et al.* 1982; Martin 1988; Cochrane 1996), there is no evidence of an established breeding population. The island and surrounding islets and waters now constitute Isle Royale National Park, which is managed by the U.S. National Park Service (NPS 1998), whose policies call for restoring extirpated native species when feasible (NPS 2006). A critical step in assessing the feasibility of reintroduction is to determine the cause(s) of the species' extirpation. We reviewed the history of the Canada Lynx on Isle Royale and evaluated possible reasons for extirpation of the species.

Study Area

Isle Royale is a 535-km² island (about 72 km × 14 km) in western Lake Superior, about 22 km from the Ontario and Minnesota shorelines (Figure 1). It is surrounded by about 400 islets. The island is characterized by short cool summers and long cold winters. Mid-winter snow depths average 44 cm (Vucetich and Peterson 2011).

Before European settlement, Isle Royale supported an old-growth boreal ecosystem (Cooper 1913; Cole



FIGURE 1. Location of Isle Royale.

et al. 1997), with Canada Lynx and Caribou (*Rangifer tarandus*) as the largest resident wildlife (Adams 1909; Martin 1988; Cochrane 1996). Indigenous people periodically occupied the island for the purposes of hunting, fishing, and copper mining (Shelton 1997). Settlement by people of European descent occurred from the early part of the 19th century to the first half of the 20th century, primarily for the purposes of fishing and copper mining. Fur trapping, mainly American Beaver (*Castor canadensis*), by European settlers apparently started in the early 19th century (Cochrane 2013), although there is at least one oral history account of a Canada Lynx being trapped in 1873–74 (Cochrane 1996). Significant changes to the island ecosystem occurred in the early 20th century as a result of logging, a large and severe forest fire, and over-browsing by Moose (*Alces americanus*), which colonized the island in 1900–10 (Murie 1934; Mech 1966). In 1940, Isle Royale National Park was established, and hunting and trapping were prohibited.

The island is currently dominated by a mix of Balsam Fir (*Abies balsamea* (L.) Miller)–White Spruce (*Picea glauca* (Moench) Voss)–Trembling Aspen (*Populus tremuloides* Michaux) and Eastern White Cedar (*Thuja occidentalis* L.)–Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh)–Tamarack (*Larix laricina* (Du Roi) K. Koch)–Black Ash (*Fraxinus nigra* Marshall) vegetation types (The Nature Conservancy 1999). The island is recognized for the Grey Wolf (*Canis lupus*) and Moose populations it supports and the long-term research on their ecology (Wolf–Moose Project 2013*). The park is designated as an International Biosphere Reserve and 99% of the island is managed as wilderness under the U.S. Wilderness Act of 1964, which prohibits motorized equipment. There are no permanent human residents and negligible infrastructure.

Canada Lynx are no longer present on Isle Royale. The limited evidence suggests they had a long history of occupation before their extirpation. Cleland (1968) found lynx bone fragments at archeological sites dating back about 2000 years and referred to sites with lynx remains dating back about 600 years (Cleland 1966). In recounting his 1857 visit to Isle Royale, Palliser

wrote “the lynx is the largest animal on the island, and is said to be very common” (Palliser 1863: 23). William P. Scott, an early resident of the island, noted the presence of lynx around 1890 (Scott 1925). Martin (1988: 29) wrote that “commercial exploitation of lynxes was underway on the island by 1897.” Martin (1988) reported that juvenile lynx were harvested on the island, indicating reproduction and an established population.

A University of Michigan biological study conducted in 1904–05 reported lynx as present, apparently abundant, and distributed over much of the island (Adams 1909). The study also reported that “with the possible exception of the White-footed Mouse (*Peromyscus leucopus*), the Hare (*Lepus americanus*) is the most abundant mammal upon Isle Royale” (Adams 1909: 410) and that Red Squirrels (*Tamiasciurus hudsonicus*) “were exceedingly abundant” (Adams 1909: 399), suggesting high-quality habitat for lynx. Based on these reports, we assume that lynx occupied Isle Royale in pre-Columbian times and were abundant at the time of European settlement. However, sometime in the 1930s they were extirpated from the island (Mech 1966; Johnsson *et al.* 1982; Martin 1988).

Methods

We reviewed the scientific and historic literature to identify possible causes for the lynx extirpation. We identified four causes that we critiqued using an inductive qualitative approach; disease, habitat changes, interactions with other predators, and cycles in prey populations. We searched extensively in the peer-reviewed literature for evidence that would support extirpation of Canada Lynx on Isle Royale by each of these possible causes. We summarized results of the literature search qualitatively, and concluded whether there was or was not support for being the cause of extirpation.

Two other potential causes, over-harvest and changes in connectivity, were analyzed quantitatively. Over-harvest was analyzed with a population viability analysis, while changes in connectivity between Isle Royale and the mainland were analyzed by searching for evidence of an ice bridge being formed in each winter that data was available.

To better understand the role that harvest played in the extirpation of the Isle Royale lynx population, we conducted a population viability analysis using VORTEX 9.99 (Lacy and Pollak 2014). We used published vital rates (see Anderson and Lovallo 2003; Steury and Murray 2004; Moen *et al.* 2008), unpublished data from studies in Minnesota (R. Moen, unpublished data), and professional judgement to establish input parameters (Table 1). We conducted sensitivity testing to evaluate and refine model inputs, to identify influential parameters, and to assess the reasonableness of the model (Lacy and Pollak 2014). VORTEX models inbreeding depression using the concept of lethal equivalents whereby 1) new individuals are killed if they have two copies of the same lethal allele, and 2) survival is re-

TABLE 1. Input parameters used in population viability analysis of Canada Lynx (*Lynx canadensis*) on Isle Royale. Values following the \pm symbol are the amount of variability at the peak and nadir of the cyclical scenarios.

Breeding	
Adult females breeding at low density	90% (SD 5)
Adult females breeding at carrying capacity	50% (SD 5)
Mean no. of mates/successful sire	1.5
Inbreeding depression	
Lethal equivalents	3.14
Proportion due to recessive lethal	50%
Reproduction	
Age at first offspring, females and males	2 years
Maximum age of reproduction	10 years
Maximum no. litters/year	1
Maximum no. young/litter	6
Mean no. young/litter	3.3 \pm 1 (SD 0.9)
Sex ratio of young	50:50
Environmental variation concordance of reproduction and survival	Yes
Annual mortality rate, both sexes	
Kitten (age 0–1 year)	45% \pm 20 (SD 10)
Yearling (age 1–2 years)	45% \pm 20 (SD 10)
Adult	10% \pm 5 (SD 5)
Catastrophes	0
Carrying capacity	75 (SD 10)
Starting population	Stable age distribution

Note: SD = standard deviation.

duced as the inbreeding coefficient increases (Miller and Lacy 2005; Lacy *et al.* 2014; Lacy and Pollak 2014). We used the VORTEX version 9.99 default value of 3.14; however, we also ran scenarios assuming no inbreeding depression to better understand the influence of inbreeding on model outputs. We modeled allele frequencies using a single neutral locus and unique alleles for each founder (Lacy *et al.* 2014). For harvest simulations we ran 1000 iterations for 50 years, i.e., the approximate time frame of the reported lynx harvest at the island. For non-harvest simulations, we initially used 1000 years, but ultimately

used 250 years as that period best illustrated the impacts of the various assumptions.

Canada Lynx and their primary prey, Snowshoe Hare, are known to go through an 8–11-year population cycle (Hodges 2000a; Krebs *et al.* 2001: Figure 2). Historical reports from 1900 to the 1930s suggest that the Isle Royale hare population was cyclical (Martin 1988; Allen 1994) as does more recent fieldwork (Vucetich and Peterson 2011). Therefore, we assumed a cyclical lynx population. We used a 10-year sinusoidal function to mimic the cycle. We varied lynx mortality, litter size, and percentage of females breeding to

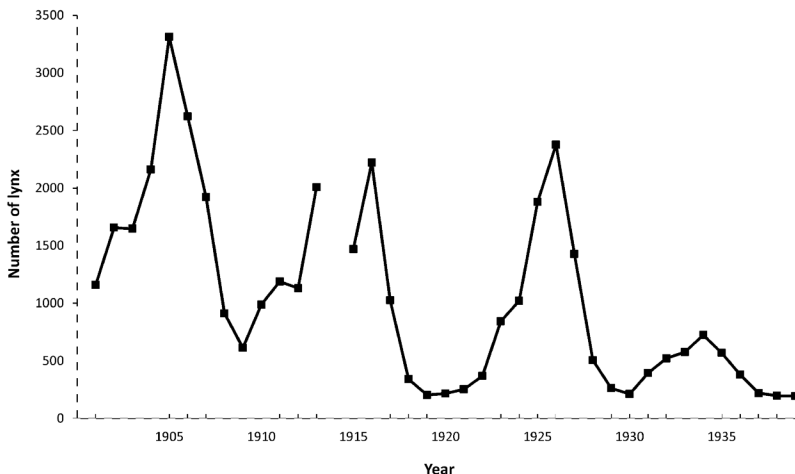


FIGURE 2. Hudson's Bay Company yearly lynx fur returns for the Lakes region (southern Ontario and western Quebec), 1901–39. Source: Elton and Nicholson (1942).

account for changes between the cycle nadir and peak (Table 1). Our closed cyclical model for Isle Royale resulted in a four-fold increase in lynx abundance from nadir to peak. Our cyclic variability was modest compared with that found in northern regions (Poole 1994; Slough and Mowat 1996); however, amplitudes are believed to be smaller in southern ranges (Hodges 2000b). For example, Slough and Mowat (1996) showed a nine-fold change in Snowshoe Hare abundance over a cycle in the Yukon Territory, whereas Vucetich and Peterson (2011) showed only a three- to four-fold change in an index of hare abundance at Isle Royale. There is some evidence that lynx populations in the southern portion of the species range may even be non-cyclical (Hodges 2000b; Murray *et al.* 2008); however, that may be a recent phenomenon (Poole 2003). Nevertheless, we also ran non-cyclical simulations.

An influential input parameter was carrying capacity. Estimates of Canada Lynx densities in Minnesota and Ontario, and Snowshoe Hare pellet surveys on Isle Royale, suggest that the current peak carrying capacity of the island may be 30–40 lynx (Licht *et al.* in prep). However, historical lynx harvests at Isle Royale suggest a population substantially greater than that, at least for brief periods, as evidenced by a minimum of 48 lynx harvested in the winter of 1903–04 and 67 in the winter of 1916–17 (Adams 1909; Foster 1917; Mech 1966; Martin 1988). Poole (2003) reviewed the scientific literature and suggested that lynx populations in mature forests in the more southern ranges had peak densities ranging from 8 to 20 per 100 km²: extrapolating from the mid-point gives a population of 75 lynx for Isle Royale. This peak abundance is plausible based on historical harvests. Therefore, we set carrying capacity at 75 lynx in our baseline model. We also ran simulations with carrying capacities of 38 and 113 lynx; the former approximates the current estimated non-cyclical carrying capacity (D. S. Licht, unpublished data) and the latter approximates the high end reported by Poole (2003).

The historical record from Isle Royale includes harvests of 48 lynx in the winter of 1903–04, 67 lynx in the winter of 1916–17, and over 25 lynx in the early 1930s (Adams 1909; Foster 1917; Mech 1966; Martin 1988). These are likely minimum harvests. For example, the report of 48 lynx captured in 1903–04 was by a father-son combination and primarily from a small portion of the island (Adams 1909). Additional reports of harvests and trapping effort in the 1890–1930s are documented by Martin (1988), Mech (1966), and Cochran (1996), but little additional quantitative information is available. Cumulatively, the reported harvests appear to have the potential to have extirpated the Isle Royale lynx population. The peak historical harvests in 1903–04 and 1916–17 are 13 years apart with the reported harvest in the early 1930s approximately 14–19 years later (Adams 1909; Foster 1917; Mech 1966; Martin 1988). This periodicity does not synchro-

nize with the reported 8–11 year lynx population cycle nor do the reported historical harvests align perfectly with the lynx population peaks for the Lakes region as reported by Elton and Nicholson (1942: Figure 2), creating a conundrum if one assumes the reported large harvests were at population peaks. One possible explanation is that the timing of the population peaks at Isle Royale may have differed from the regional peaks reported by Elton and Nicholson (1942), as lynx population peaks are not synchronous across the species' range (Ranta *et al.* 1997; Stenseth *et al.* 1999). Another plausible explanation is that reported harvests did not occur in years when the lynx population peaked. Anderson and Lovallo (2003) stated that lynx harvest rates may be somewhat independent of lynx density and driven more by pelt prices. Furthermore, in a small area, such as Isle Royale, the addition of just a few trappers or trap lines could cause a substantial change in trapping effort, thereby influencing harvest rates more than lynx density. As a result of these unknowns, we ran simulations where harvest peaks and lynx population peaks were asynchronous and other scenarios where harvest and population peaks coincided by assuming a 13-year lynx cycle. We ran simulations that modeled the reported harvests of 48, 67, and more than 25 lynx; simulations that also included 5 or 10 additional lynx harvested each year to account for unreported harvests; and simulations where we removed 50 lynx every 13th year as well as an additional 5 or 10 lynx in the interim years. We did not find useful information regarding the demographic composition of the lynx harvested at Isle Royale; however, others have reported that adult males typically comprise the majority of lynx harvests (Bailey *et al.* 1986; Quinn and Thompson 1987; Poole 1991). For all harvests, we assumed a composition of 60% adult male, 30% adult female, and 10% kittens split equally between the sexes.

Our initial simulations assumed a closed population. We subsequently posited that lynx might have historically immigrated to Isle Royale every 10 years or so coincident with lynx population peaks farther north. Therefore, we ran simulations that assumed supplementation every 10th year. We altered the default sequence of events in VORTEX so that supplementation (i.e., immigration) occurred before harvest. Carrying-capacity truncation occurred after those events. Henderson (1978) reported about a 12-fold nadir-to-peak increase in lynx harvests in Minnesota from 1940 to the 1970s and Gunderson (1978) reported an eight-fold and two-fold increase in harvested lynx from two sites in Ontario from 1955–58 to 1960–63. We assumed immigration of 10 or 20 adult lynx every 10th year, coinciding with peaks in the resident population: the combination of supplementations and growth of the resident population generally resulted in a five-fold increase from nadir to peak. Although lynx irruptions in Canada sometimes plateau over multiple years (Gunderson 1978), we assumed a single-year influx of im-

migrants as that approximates what was observed in Minnesota (Mech 1973; Henderson 1978). We assumed a 50:50 sex ratio of the immigrants as reported by Mech (1980) for a recently colonized site in Minnesota. When comparing supplementation and non-supplementation simulations, we allowed lynx immigration to occur only if there was an extant population at the time of augmentation.

Although lynx can swim and are known to cross cold rivers (Feierabend and Kielland 2014), the farthest distance we know of a lynx swimming is 3.2 km (Kobalenko 1997); hence, we viewed it as unlikely that immigration occurred via swimming. We thought it more plausible that historical lynx immigration to Isle Royale occurred via an ice bridge between the mainland and the island. In that case, lynx could have recolonized Isle Royale following extirpation, as lynx populations in Minnesota and Ontario have recovered from early-20th-century lows (Poole 2003; Moen *et al.* 2008). Furthermore, lynx invasions from Ontario into Minnesota have been documented since the 1960s (Mech 1973; Gunderson 1978; Henderson 1978). However, we speculated that a decline in ice-bridge formation in recent decades may have prevented lynx recolonization of Isle Royale. We used three datasets to evaluate a possible decline in ice-bridge formation between the mainland and Isle Royale.

We used National Oceanic and Atmospheric Administration (NOAA), Great Lakes Environmental Research Laboratory ice atlases (Assel *et al.* 2002; NOAA Great Lakes Environmental Research Laboratory 2014) to calculate the number of days each winter during 1973–2011 that an ice bridge formed between Isle Royale and the mainland. The ice concentration class with the greatest ice surface area and, therefore, the most potential for crossing by lynx, was the $\geq 90\%$ class. We looked at each daily image and summed the number of days each winter with ice of class $\geq 90\%$ connecting the mainland to the island. We ran a linear regression of the sum of the days against year. The strength of the dataset is that the data were somewhat systematically collected and the dataset allowed the summation of the total number of days an ice bridge formed each winter. Its weakness is that the iciest class could have as little as 90% ice cover which may not be enough for a lynx to traverse from the mainland to the island.

Our second analysis of ice-bridge formation used statements from 1965–66 to 2012–13 Isle Royale Wolf–Moose Project annual reports (Wolf–Moose Project 2013*). Additional data for 1958–59 to 1964–65 and clarification of some ambiguous statements in the annual reports were provided by R. Peterson (personal communication, 2014). For each winter 1958–59 to 2012–13, we assigned either “yes” or “no” for ice-bridge formation. We then ran a logistic regression on the binomial data. The strength of this dataset is that it better captured true ice-bridge formation that could be

traversed by an animal as the primary reason the investigators recorded the observations was for documenting the potential for wolf movement between the mainland and the island. Its weakness is that the total number of days each winter with an ice bridge was not captured, and investigators were only on the island during a portion of the winter (Wolf–Moose Project 2013*).

Our final ice-bridge analysis used 1900–1970 ice-thickness data collected by the National Weather Service (Assel 2004). We evaluated datasets from the Duluth Harbor, Two Harbors, and Keweenaw Waterway stations (Figure 1); these stations had data for 66, 44, and 54 of the years, respectively. We used the annual mean or midpoint of the reported range for each station and regressed that against year. The value of the datasets is that they covered 1900–1970, a period not covered by the other datasets and a time when lynx still occupied Isle Royale. Their weakness is that the data were not collected systematically, the parameter was near-shore ice thickness which might not be strongly correlated to ice surface coverage on the lake, and the stations were a substantial distance from Isle Royale (245 km in the case of Duluth Harbor station).

Results

Qualitative evaluation of possible reasons for the extirpation of Canada Lynx

Disease: Disease can have a catastrophic impact on wildlife, especially small isolated populations (de Castro and Bolker 2005; Cully *et al.* 2010; Descamps *et al.* 2012). The anthropogenic introduction of canine parvovirus to Isle Royale in 1981 was probably a factor in a crash of the island’s wolf population (Peterson *et al.* 1998). Therefore, we evaluated disease as a possible cause of the lynx extirpation.

Lynx are susceptible to a variety of diseases, some of which can be lethal (Anderson and Lovallo 2003). Wild *et al.* (2006) documented Canada Lynx mortality from plague (*Yersinia pestis*) in Colorado; however, that disease is not known to occur in the Isle Royale region. Ryser-Degiorgis *et al.* (2005) reported that sarcoptic mange (*Sarcoptes scabiei*) is the most common infectious cause of death in free-ranging Eurasian Lynx (*Lynx lynx*), but mange is not known to have occurred at Isle Royale. Vashon *et al.* (2012) reported lungworm in Canada Lynx in Maine, but only one of 65 animals in that study was reported to have died from disease. In a sample of 215 Canada Lynx, Biek *et al.* (2002) found a low prevalence of a suite of pathogens. Moen *et al.* (2008) did not find disease to be a significant mortality factor for Canada Lynx in nearby Minnesota. Likewise, *Canada Lynx Conservation and Assessment* (Interagency Lynx Biology Team 2013) does not list disease as a high concern in lynx conservation. We know of no evidence of disease-caused mortality of Canada Lynx on Isle Royale.

Systemic transitional changes in the vegetation community: The vegetation community on Isle Royale has

changed dramatically in the past century due primarily to logging, fire, and Moose overabundance (Murie 1934; Mech 1966; Snyder and Janke 1976). Logging and fire can significantly alter habitat; however, depending on the spatial pattern, severity, and return intervals, these disturbances could increase the abundance of lynx by improving conditions for Snowshoe Hare (Parker *et al.* 1983; Moen *et al.* 2008; Interagency Lynx Biology Team 2013). At an Ontario study site with 27% disturbance due to fire, logging, and insect damage, Quinn and Thompson (1987) found that several lynx population parameters were as good as or higher than they were at a site with only 17% disturbance.

On Isle Royale, over-browsing by Moose might have degraded habitat for Snowshoe Hare. Moose apparently arrived on the island between 1900 and 1910 (Cochrane 2013). The population reached several thousand in the early 1930s, but then starvation caused a population crash in 1933–35 (Krefting 1974). Murie (1934) reported that Snowshoe Hares were scarce in 1930, and Mech (1966) cited island residents who reported seeing fewer hares in the late 1920s and early 1930s than they had in earlier years; whether these changes were due to systemic habitat alteration or natural oscillations in hare populations is not known. Allen (1994) suggested that Moose overabundance on the island resulted in a decline in Snowshoe Hare numbers that may have contributed to the extirpation of lynx. Conversely, some researchers have reported that forage competition between Moose and Snowshoe Hares is limited because of differences in spatial use and browse heights (Dodds 1960; Oldemeyer 1983); however, the severity of the competition likely depends on the degree of browsing. Although the concurrent timing of the Moose irruption and the lynx extirpation raises the possibility of a cause-and-effect relation, confounding processes may have lessened the impact of Moose over-browsing on the lynx population. A die-off of thousands of Moose (Krefting 1974) would have provided a substantial supply of carrion for lynx that could have mitigated the short-term decline in hare abundance as lynx consume carrion when available and during periods of hare scarcity (Saunders 1963; Brand *et al.* 1976). Furthermore, the Isle Royale ecosystem includes alternative prey, specifically Red Squirrels (Adams 1909; Johnson 1969), which should have provided an important and relatively stable secondary prey (O'Donoghue *et al.* 1998) until hare numbers recovered. We suggest that systemic changes in habitat at Isle Royale — primarily related to Moose overabundance — might have contributed to the extirpation of Canada Lynx on the island.

Interactions with other predators: Coyotes appear to have colonized Isle Royale by 1912 (Krefting 1969). In the winter of 1916–17, trappers harvested 60 Coyotes from Isle Royale, but did not extirpate the population (Foster 1917). Cochrane (1996) reported an anonymous 1928 statement that “coyotes are becom-

ing so numerous they threaten other wildlife.” Lynx apparently disappeared from the island in the 1930s (Mech 1966; Johnsson *et al.* 1982; Martin 1988), a time when Coyotes were well established. Therefore, it is conceivable that Coyotes were a factor in the extirpation of lynx. Coyotes are suspected of being exploitative or interference competitors of Canada Lynx where their ranges overlap and may be contributing to range contraction and population declines of mainland lynx populations (Buskirk 2000). However, Murray *et al.* (2008) suggested that the evidence of inter-specific competition between Canada Lynx and Coyotes is weak. According to Cochrane (1996) and Cochrane (2013), Red Foxes (*Vulpes vulpes*) colonized the island in the 20th century; foxes could have competed with Canada Lynx for Snowshoe Hare and other small prey. However, Johnsson *et al.* (1982) reported that Red Foxes were scarce until Coyotes were extirpated, which apparently occurred in the 1950s (Mech 1966). The changing mammalian community, especially the presence of Coyotes, may have been a stress on the Canada Lynx population at Isle Royale.

Cyclical collapse in prey populations: The interacting temporal population dynamics of Canada Lynx and Snowshoe Hare are well known (Elton and Nicholson 1942; O'Donoghue *et al.* 2010), and hare population crashes are typically followed by lynx population crashes (Elton and Nicholson 1942; O'Donoghue *et al.* 2010). Historical and current evidence suggests that Isle Royale's hare population does oscillate (Martin 1988; Allen 1994; Vucetich and Peterson 2011). When Snowshoe Hare populations in Ontario crash, lynx are thought to emigrate in large numbers to Minnesota (Mech 1973; Gunderson 1978; Henderson 1978). Therefore, lynx could have emigrated from Isle Royale in response to a hare population decline.

However, Isle Royale is immediately east of the Ontario–Minnesota border so it is unclear whether Isle Royale would be a source or recipient of lynx during lows in the Ontario cycle. Furthermore, even if some lynx emigrated from Isle Royale during nadirs in the hare cycle, it is unlikely that all lynx would have left. In northern regions, lynx populations persist even through severe declines in hare populations (Poole 1994; O'Donoghue *et al.* 1997). Also, Red Squirrels should have provided an important alternative prey for lynx (O'Donoghue *et al.* 1998). Lynx remains were found on Isle Royale from pre-Columbian times, the species was abundant when the first people of European descent visited the island around 1850, and lynx were common up to the 1930s, suggesting that the population persisted on Isle Royale through numerous hare cycles (Figure 2).

Quantitative analysis of harvest impacts

Assuming a carrying capacity of 75 Canada Lynx, the reported historical harvests of 48, 67, and 25 animals resulted in a modeled 50-year population persistence of 15% (Table 2). When the harvest was increased

TABLE 2. Population viability (50-year) of Canada Lynx (*Lynx canadensis*) on Isle Royale under reported and assumed historical harvest rates, assuming a peak carrying capacity of 75 lynx.

Harvest option	Probability of persistence	Mean no. years of extinct runs	Mean final population size (extant runs only)
Assuming a 10-year population cycle			
48 lynx in year 13, 67 in year 26, and 5/year in years 40–44	0.154	19.9	35.0
53 lynx in year 13, 72 in year 26, and 10/year in years 40–44, plus 5 in each interim year	0.000	17.2	na
Assuming a 13-year population cycle			
48 lynx in year 13, 67 in year 26, and 5/year in years 40–44	0.278	37.8	31.5
53 lynx in year 13, 72 in year 26, and 10/year in years 40–44, plus 4 in each interim year	0.000	19.5	na

Note: na = not applicable.

by five lynx each year, to account for unreported harvest, the probability of persistence was 0% and the median time to extinction was 15 years. Correlating the reported harvest years with a modeled 13-year lynx cycle increased the probability of persistence to 28%, but, when we assumed an additional five lynx were harvested each year, the probability of persistence was 0%. The only harvest scenarios that produced a greater than 50% chance of lynx persistence for 50 years were those that assumed a carrying capacity of 113 lynx and/or no lynx harvest in interim years (Figure 3).

In non-harvest, 1000-year simulations, all of the cyclical and non-cyclical runs resulted in extinction within 400 years. Therefore, we ran simulations for 250 years and they resulted in a 14% chance of persistence for a cyclical population and a 42% chance of persistence for a non-cyclical population (Table 3). When inbreeding was disabled the probability of 250-year persistence increased to 100% for the cyclical scenario (Table 3). Supplementing the island population with 10 immigrants every 10th year increased the probability of persistence to 100% for both the 250-

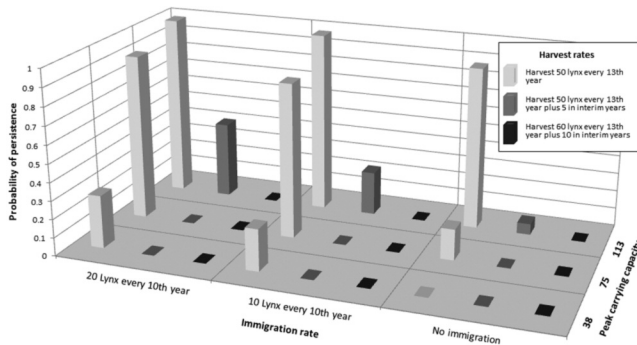


FIGURE 3. Probability of 50-year persistence of a population of Canada Lynx (*Lynx canadensis*) under a range of immigration rates, peak carrying capacities, and harvest rates.

TABLE 3. Population viability (250-year) of Canada Lynx (*Lynx canadensis*) on Isle Royale based on various non-harvest scenarios.

Scenario	Probability of persistence	Mean no. years of extinct runs (SD)	Mean final population size, extant runs (SD)	Final no. alleles*	Final expected heterozygosity
10-year cyclical population with peak carrying capacity of 75 lynx and inbreeding (baseline)	0.136	197.0 (36.1)	12.8 (13.4)	1.70	0.239
Assuming a non-cyclical population	0.417	207.6 (32.7)	19.7 (15.1)	2.01	0.321
Peak carrying capacity of 38 lynx	0.000	72.6 (26.8)	na	na	na
Peak carrying capacity of 113 lynx	0.941	226.0 (24.9)	64.4 (27.8)	3.26	0.510
Assuming no inbreeding depression	1.000	na	68.6 (8.8)	2.39	0.377
Assuming 10 immigrants every 10th year	1.000	na	70.1 (8.7)	37.41	0.926

*Using the VORTEX default infinite allele model.

Note: na = not applicable; SD = standard deviation.

year (Table 3) and 1000-year simulations even when inbreeding was enabled.

Quantitative analysis of changes in connectivity

The number of days each winter with $\geq 90\%$ ice concentration between the mainland and Isle Royale declined significantly ($P < 0.01$) at a rate of 4.5% annually from a modeled 56 days in 1973 to 10 days in 2011 (Figure 4). Based on the Isle Royale Wolf–Moose

Project binomial observations, the probability of an ice bridge forming in 1958–59 was 0.78 whereas in 2012–13 it was 0.10, a significant decline ($P < 0.01$: Figure 5). The Duluth Harbor station showed a significant ($P < 0.01$) annual decline of 0.6% in ice thickness over 1900–70 (Figure 6) whereas the Two Harbors and Keweenaw datasets each showed a 0.2% annual decline over the same period ($P > 0.05$).

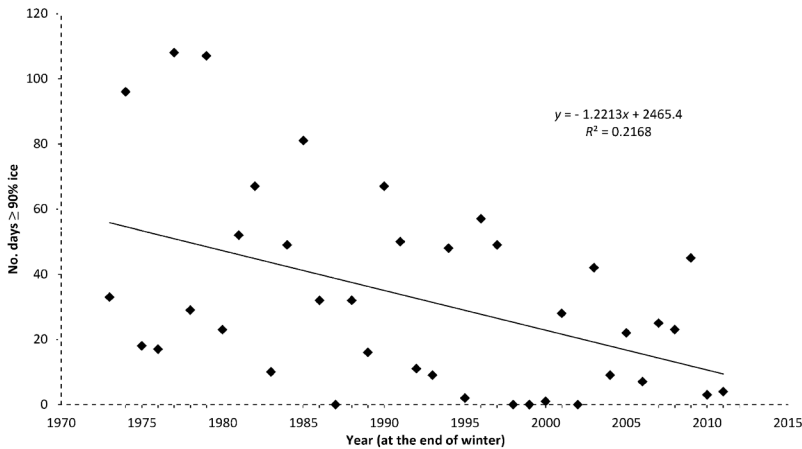


FIGURE 4. Number of days with ice concentration $\geq 90\%$ between Isle Royale and the Minnesota–Ontario shoreline and linear regression trend. Source: Assel (2014*).

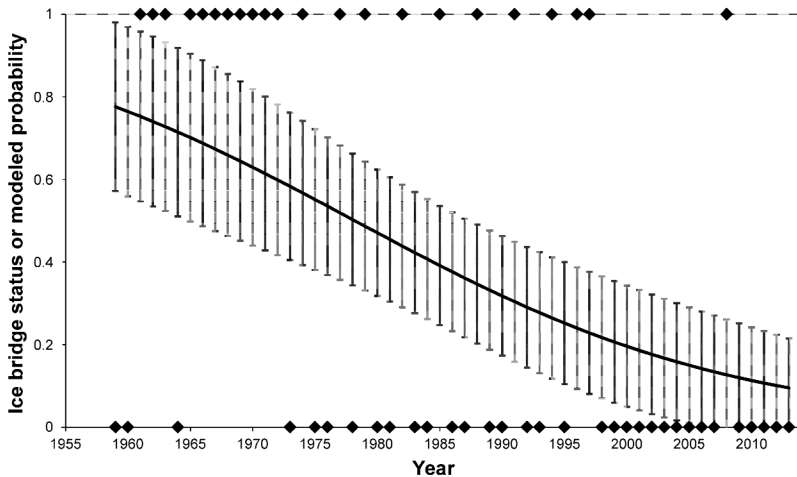


FIGURE 5. Observed (1 = yes, 0 = no) and logistic regression probability of ice-bridge formation based on visual observations. Error bars are approximate 95% point-wise prediction intervals. Source: Wolf–Moose Project (2013*) and R. Peterson (personal communication, 2014).

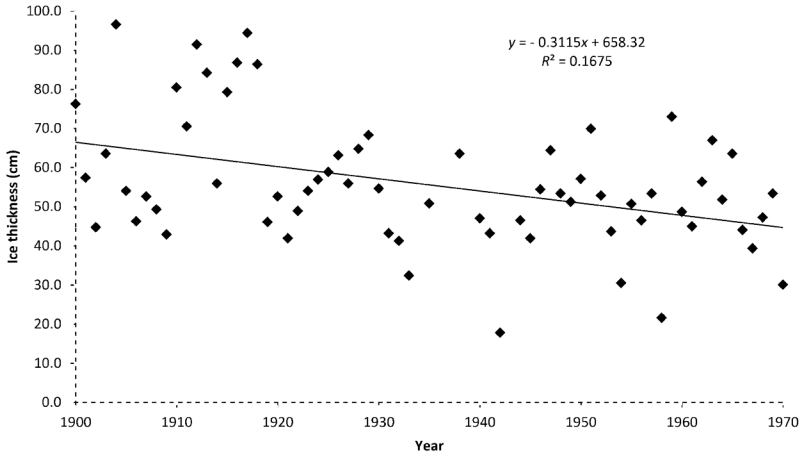


FIGURE 6. February–April ice thickness at Duluth Harbor, Minnesota, 1900–1970. Source: Assel (2004).

Discussion

The reasons for the extirpation of Canada Lynx from Isle Royale may never be fully understood, but, if the historical harvest records are accurate, then over-harvest alone could have caused the extirpation. Lynx populations are susceptible to over-harvest (Bailey *et al.* 1986; Slough and Mowat 1996), and such mortality is added to natural mortality (Brand and Keith 1979; Anderson and Lovallo 2003). Bailey *et al.* (1986) found that 80% of the marked lynx at their study site in Alaska were trapped within a year and Parker *et al.* (1983) estimated that 65% of their study population in Nova Scotia was removed by trapping. The idea that over-harvest caused the extirpation of lynx from Isle Royale has been suggested by others although no quantitative analysis appears to have been conducted. Mech (1966: 16) stated that people are “probably responsible for exterminating the Lynx.” Martin (1988: 2) stated that “lynxes, like marten, were heavily trapped throughout the region during the early 1900s. Once the dominant predator on Isle Royale, they were extirpated in the 1930s after no less than four decades of systematic trapping.”

Our analyses of the long-term viability of Canada Lynx on Isle Royale — even in the absence of harvest — indicate that the population needed immigrants to lessen the impact of inbreeding depression. Regular historical lynx immigration to Isle Royale is plausible. Both Schwartz *et al.* (2002) and Row *et al.* (2012) found high gene flow between lynx populations, even those separated by great distances. Dispersal of lynx appears to be substantial during the post-peak decline in the 8–11 year population cycle, with many animals traveling more than 100 km (Slough and Mowat 1996; Poole 1997). During lows in the Snowshoe Hare population cycle, large numbers of lynx may move southward into northern Minnesota in what has been termed

an “invasion” (Mech 1973; Gunderson 1978; Henderson 1978). Dispersing lynx have been documented venturing hundreds of kilometres into treeless habitats and crossing frozen lakes (Mech 1973; Gunderson 1978; Ward and Krebs 1985; Devineau *et al.* 2010). Cochrane (2013) reported that ice-bridge formation was so substantial between Isle Royale and the mainland in the 1870s that draft horses and dog teams regularly crossed the ice. Thus, it is conceivable, even likely, that lynx historically crossed a 22-km ice bridge between the mainland and Isle Royale and, as a result, the population persisted for a long time. So why did immigration cease and why have lynx not recolonized the island?

The extirpation of lynx at Isle Royale occurred at a time when lynx populations were declining throughout the Great Lakes region due, in part, to unregulated harvest (Johnson 1922; de Vos and Matel 1952). The population decline and range contraction of mainland lynx may have reduced or eliminated immigration to Isle Royale during the period from 1930 to the 1960s. At the same time, changes in ice-bridge formation were occurring.

Our three ice-bridge analyses showed that the frequency of formation of an ice bridge between Isle Royale and the mainland is declining. Our results are corroborated by other studies of Great Lakes ice cover (Magnuson *et al.* 2000; Assel 2003; Wang *et al.* 2012). Assel (1990) showed that the decline in ice formation may have started in the late 19th century. More recently, the NOAA (2009) reported that densely packed ice near Great Lakes shores had declined about 20% from 1973–2002 and that Lake Superior has shown the greatest decrease in total ice cover of all the Great Lakes over the past several decades. Vucetich and Peterson (2011) reported that ice bridges between Isle Royale and the mainland have formed in only 2 of the past 15 years and one of those years was the only

known instance of a wolf immigrating to the island since the 1940s. Vucetich *et al.* (2012) suggested that the decreasing frequency of an ice bridge, along with anthropogenic development along the Lake Superior shoreline (e.g., the Trans-Canada Highway and expansion of the city of Thunder Bay, Ontario) has significantly reduced the likelihood of wolf immigration to the island. Conversely, Mech (2013) suggested that climate change may not lead to a reduction in ice-bridge formation and, hence, there was no need to transplant wolves to the island for genetic augmentation; however, our analyses and corroborating evidence by others (Magnuson *et al.* 2000; Assel 2003; Wang *et al.* 2012) strongly indicate that the frequency of ice-bridge formation between Isle Royale and the mainland is declining due to climate change.

Climate change is widely identified as one of the major threats facing wildlife populations (Thomas *et al.* 2004). In Canada, climate change may disproportionately affect large-bodied mammals more than smaller ones (Imre and Derbowka 2011). The impacts on wildlife are generally thought to be via changes in plant communities, altered phenology, physiological stresses, changes in disease patterns, and escalating catastrophic weather events, among other factors (Gitay *et al.* 2002; Geyer *et al.* 2011; Nichols *et al.* 2011). The Interagency Lynx Biology Team (2013) categorized climate change impacts on lynx as shifts in distribution, changes in periodicity of the Snowshoe Hare cycle, reduction in lynx habitat and population size, changes in demographic rates, and changes in predator–prey relationships. Carroll (2007) and Gonzalez *et al.* (2007) speculated that climate change will decrease snow cover and reduce and degrade boreal habitat, resulting in local extirpations and range decline. We show that climate change can also reduce or eliminate metapopulation processes and contribute to local extirpations.

Conclusion

Our analyses suggest that Canada Lynx were extirpated from Isle Royale due to human activities and that over-harvest alone could have caused the extirpation. However, our analyses also suggest that climate change and the declining frequency of ice-bridge formation may prevent natural recolonization and reduce the viability of a future population, whether naturally recolonized or reintroduced by management. The Isle Royale situation exemplifies the notion that, as climate change reduces or eliminates connectivity, long-term conservation success may require periodic population augmentation to mitigate the loss of connectivity between populations.

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