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Original Research

Use of Non-invasive Genetics to Generate Core-Area Population Estimates of a Threatened Predator in the Superior National Forest, USA

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Abstract

Canada lynx (*Lynx canadensis*) are found in boreal forests of Canada and Alaska and range southward into the contiguous United States. Much less is understood about lynx in their southern range compared to northern populations. Because lynx are currently listed as threatened under the US Endangered Species Act but have recently been recommended for delisting, information on their southern populations is important for lynx recovery, conservation, and management. We used non-invasive, genetic data collected during lynx snowtracking surveys from 2012-2017 to generate core-area estimates of abundance, trend and density in selected core areas of the Superior National Forest of Minnesota, USA. Lynx abundance estimates averaged 41.8 (SD=14.7, range=24-67) during 2012-2017 in the smaller core areas and averaged 52.3 (SD=8.3, range=43-59) during 2015-2017 in the larger core areas. We found no evidence

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for a decrease or increase in abundance during either period. Lynx density estimates were approximately 7-10 times lower than densities of lynx in northern populations at the low of the snowshoe hare (*Lepus americanus*) population cycle. To our knowledge, our results are the first attempt to estimate abundance, trend and density of lynx in Minnesota using non-invasive genetic capture-mark-recapture. Estimates such as ours provide useful benchmarks for future comparisons by providing a context with which to assess 1) potential changes in forest management that may affect lynx recovery and conservation, and 2) possible effects of climate change on the depth, density, and duration of annual snow cover and correspondingly, potential effects on snowshoe hares as well.

Key Words: Abundance, Capwire, Density, Genetic, Hair, Lynx, Non-invasive, Population Estimate, Scat, Track, Trend.

INTRODUCTION

Canada lynx (*Lynx canadensis*, hereafter lynx) are found in boreal forests of Canada and Alaska and range southward into the contiguous United States (McKelvey *et al.* 2000). Much less is understood about lynx in their southern range compared to northern populations (Murray *et al.* 2008). Federally, lynx was listed as threatened under the US Endangered Species Act in 2000 (U.S. Fish and Wildlife Service 2000). The federal listing prompted important research on lynx recovery, conservation, and management in their southern range (Murray *et al.* 2008). Northeastern Minnesota was subsequently designated a lynx recovery core area (U.S. Fish and Wildlife Service 2005) and in 2009 much of the Superior National Forest (SNF) in Minnesota was deemed “critical habitat” (U.S. Fish and Wildlife Service 2009). Lynx were also listed as a Minnesota Species of Special Concern in 2013 (MNDNR 2013) because they were uncommon, they were at the southern edge of their range (McKelvey *et al.* 2000), and they had specific habitat requirements owing, in part, to their main prey being snowshoe hare (*Lepus americanus*) (Burdett 2008; Hanson and Moen 2008). Accordingly, research was conducted to understand factors affecting lynx populations in Minnesota (e.g., Moen *et al.* 2008b).

Analysis of harvest records indicated lynx occurrence in Minnesota since the 1920s (Henderson 1978; Moen *et al.* 2008b). Additional lynx research in Minnesota focused on movements and home range analysis (Mech 1973, 1977; Burdett *et al.* 2007; Moen *et al.* 2008 a, b), physical condition (Mech 1980; Moen *et al.* 2010), reproduction (Mech 1973, 1980; Moen *et al.* 2008a), diet (Hanson and Moen 2008), and measures of prey abundance (McCann *et al.* 2008).

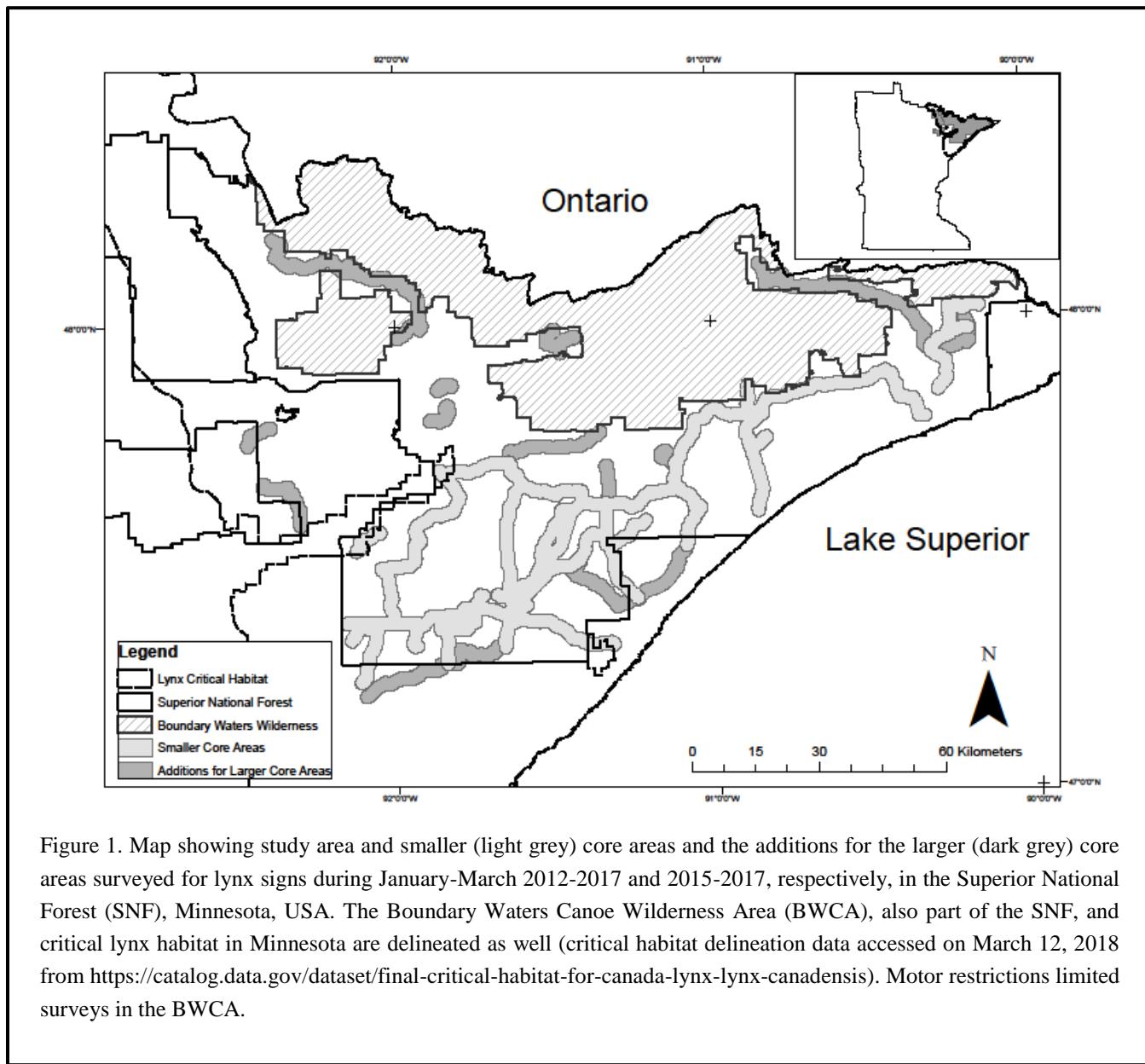
However, because of the low densities of lynx in their southern range it has generally not been considered feasible to determine lynx abundance in all of northeastern Minnesota (Moen 2009) and abundance estimates of smaller core areas in northeastern Minnesota have not been

attempted. Recent advances in capture-mark-recapture analysis methods (Pennell *et al.* 2013) and their application to non-invasive research (Brøseth *et al.* 2010), allowed us to use non-invasive, genetic data from lynx to estimate population abundance, trend, and density in selected core areas with previous lynx presence on the SNF of Minnesota.

MATERIAL AND METHODS

Snowtracking and other methods used to obtain genetic samples have confirmed presence of Canada lynx across the SNF, northeastern Minnesota, USA (48° N, 92° W) since December 2000 (Figure 1) (Catton *et al.* 2017). The study area is in a transition zone between the southern boreal forest of neighbouring Ontario, Canada and the hardwood forests typical of areas farther south in Minnesota (Pastor and Mladenoff 1992). Vegetation is mixed forest with conifers including jack pine (*Pinus banksiana*), white pine (*P. strobus*), red pine (*P. resinosa*), black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*), interspersed with paper birch (*Betula papyrifera*) and quaking aspen (*Populus tremuloides*) (Heinselman 1996). The forested landscape generally includes numerous lakes, swamps, rocky ridges with elevations only occasionally exceeding 600 m above sea level (Heinselman 1996). Summers are characterized as short and warm and winters long and cold with snow typically present from December through April (Heinselman 1996). For additional study area details see Burdett *et al.* (2007). In general, snowshoe hare densities are lower in southern lynx range and are comparable to the lows in the cycle of snowshoe hare populations to the north (Hodges 2000; Murray 2000). Snowshoe hare densities in Minnesota are about 10% of snowshoe hare-density highs in northern Canada (Moen *et al.* 2008b).

Since 2000, ad hoc snow track surveys for lynx have been conducted from November-April in the SNF. To minimize detection bias based on snow conditions, surveys were



generally conducted 1–3 d after fresh snow and lack of high wind. Trained observers primarily searched for lynx tracks by traveling 15–20 km/h on roads and trails by truck and snowmobile. The survey area was divided by forest district and areas of lynx habitat with reliable winter access within each district were surveyed throughout winter. Care was taken to survey different areas within the districts to avoid repeatedly sampling the same roads and trails using the same starting points. When lynx tracks were found, they were generally followed (fresh tracks were usually back-tracked, otherwise fore- or back-tracked) to collect DNA from scat or hair and to determine the number of lynx traveling together. Tracks were followed until sufficient samples and data were collected, generally up to 1.6 km straight line distance from the main survey road. When family groups were detected,

repeat surveys (generally at least 1 week from the initial survey) were conducted to ensure sufficient DNA samples and/or group-number data were obtained. Starting in 2012, several small core areas were surveyed across years allowing for comparisons (Figure 1). These core areas were selected for surveys because of previous lynx presence and dependable winter access. During 2015–2017, an occupancy analysis was conducted that included increased survey effort (each year >3,100 km was surveyed over 954 km of roads and trails) in the SNF and better documentation of survey effort location (Hostetter and Gardner 2016) (Table 1). This allowed us to delineate larger core areas that included repeated surveys (Figure 1).

During snow track surveys, lynx tracks were followed to collect genetic material (usually scat but also hair). Genetic

Table 1. Survey effort (km surveyed for occupancy including by truck and snowmobile; number of days surveyed) during winter lynx snowtracking surveys in the Superior National Forest, Minnesota, USA, January-March 2015-2017 in the larger core area. Prior to 2015, these data were not rigorously recorded but survey effort pertaining to the smaller core areas during 2012-2017 was consistent across years.

	2015	2016	2017
Km surveyed	3170	3289	3668
Days surveyed	35	37	30

Table 2. Frequency distribution of the number of lynx individuals, gender, and the times they were detected (“captured”) during winter surveys in the smaller core areas of the Superior National Forest, Minnesota, USA, January-March 2012-2017.

Captures	2012	2013	2014	2015	2016	2017
1	16	9	20	13	5	11
2	4	8	9	7	7	6
3	0	1	3	6	4	2
4	0	2	1	1	2	1
5	1	1	1	1	1	2
6	2	1	0	0	0	0
7	0	1	0	0	0	1
8	0	0	0	0	0	0
9	0	0	0	0	0	0
10	1	0	0	0	0	0
11	0	1	0	0	0	0
Total individuals detected						
	24	24	34	28	19	23

Female:male of total individuals detected

10:14 13:11 15:19 13:15 10:9 14:9

Total genetic samples

51 65 56 54 44 50

Table 3. Frequency distribution of the number of lynx individuals, gender, and the times they were detected (“captured”) during winter surveys in the larger core areas of the Superior National Forest, Minnesota, USA, January-March 2015-2017.

Captures	2015	2016	2017
1	17	11	15
2	9	10	7
3	6	7	2
4	1	3	1
5	1	1	2
6	0	0	0
7	0	0	1
Total individuals detected			
	34	32	28
Female:male of total individuals detected			
	16:18	18:14	16:12
Total genetic samples			
	62	69	56

samples were sent to the National Genomics Center for Wildlife and Fish Conservation (U.S. Forest Service, Missoula, Montana, USA) for gender and individual ID analysis following protocols described in Pilgrim *et al.* (2005).

Using the results from the lynx genetic analysis, we conducted a capture-mark-recapture using package *capwire* v.1.1.4© (Miller *et al.* 2005; Pennell *et al.* 2013) in program R v3.4.1© (R Core Team 2015). *Capwire* analyzes single session data or multi-session data collapsed into a single session, accounting for individuals that are captured more than once during a sampling session (Brøseth *et al.* 2010; Pennell *et al.* 2013). We used *capwire* to generate annual abundance estimates and 95% confidence intervals for both the smaller core areas from 2012-2017 and the larger core areas from 2015-2017. For both periods, we included samples collected within a circular buffer (linear path) with 1.6 km radius (generally the maximum straight line distance that lynx tracks were followed off of main survey routes) of roads and trails surveyed. *Capwire* tests 3 models of varying capture heterogeneity: 1) Equal Capture Model (ECM) with no heterogeneity, 2) Two Innate Rates Model (TIRM) representing a high capture-probability group and a low capture-probability group, and 3) TIRM-Partitioned Model (TIRM-Part) used for overdispersed data due to either a high number of animals (as determined by *capwire*) being caught only once or a few individuals captured at very high rates compared to others (data are partitioned into 3 groups based on recapture rates, 1 group is added back ad hoc to the TIRM abundance estimate that was generated from the other 2 groups). *Capwire* includes a likelihood ratio test to assess models and also generates additional metrics including alpha (the ratio of capture rates between the high capture-probability group and the low capture-probability group, if no capture heterogeneity alpha=1). When alpha>2, the TIRM model reduces mean relative error and improves coverage compared to ECM and when alpha>3 the TIRM model reduces bias in the population estimate compared to ECM (Miller *et al.* 2005).

Preliminary analyses indicated that including data from the entire snow sampling period (November-April) likely resulted in violations of the population closure assumption so only data from the shorter period (less subject to closure assumption issues) of January-March were analyzed for each winter. It was suggested by a reviewer that we consider shortening the analysis to January-February because of males making wider breeding season movements during March, but our data indicated that “new” males were not disproportionately detected in March. Further, previous research indicated most large-scale movements occurred during summer and fall with less movement during

winter/spring (Moen *et al.* 2008b), providing biological support for our use of the January-March period in our capture-mark-recapture analysis. We assessed linear, 2nd, and 3rd degree polynomial trends in abundance estimates (when sample size permitted) using Statistix v.10.0© at the alpha=0.05 level of significance.

Like other solitary felids, adult female lynx tend to have smaller home ranges than males (Burdett *et al.* 2007). Therefore, to estimate density, we first generated a likely catchment area (for most of the residential lynx captured in our surveys) by placing a circular buffer (with linear path) on the roads and trails surveyed in the core areas with a radius equal to the length of the diameter of the mean female home range (assuming a circle) during winter in northern Minnesota (95% fixed-kernel female, winter home range estimate = 44 km²; diameter = 7.48 km, Burdett *et al.* 2007, Table 2). We used ArcMap v.10.3.1© to place the buffer and calculate the area surrounding roads and trails surveyed for the smaller and larger core areas. If the catchment area overlapped Lake Superior, we clipped the overlap. We then calculated density estimates by dividing the mean abundance estimates from the smaller core areas and larger core areas by the catchment area for each of those surveys.

RESULTS

During January-March 2012-2017, an average total of 25.3 individuals (SD=5.1) were detected each year in the smaller core areas (Table 2). During January-March 2015-2017, an average total of 31.3 individuals (SD=3.1) were detected in the larger core areas (Table 3).

We used the TIRM (and in 1 case, 2017 for the larger core areas, TIRM-Part) abundance estimates from the *capwire* capture-mark-recapture analysis because 1) the *P*-value resulting from the likelihood ratio test supported the model that included capture heterogeneity and/or 2) the alpha metric (ratio of capture rates as detailed above) was >2.

Lynx abundance point estimates ranged from 24 to 67 and averaged 41.8 (SD=14.7) during 2012-2017 in the smaller core areas (Figure 2) and ranged from 43 to 59 and averaged 52.3 (SD=8.3) during 2015-2017 in the larger core areas (Figure 3). We did not reject the null hypothesis of a stable population across years in both the smaller and larger core areas because we found no statistical support for linear, 2nd, or 3rd order polynomial trends (all *P*>0.5) and because comparisons between years revealed a lack of convincing evidence for difference except for a possible increase from 2013 to 2014 (Ramsey and Schafer 2002). This possible “increase” is suspect though because earlier and later years in the 2012-2017 smaller core areas similarly showed a lack

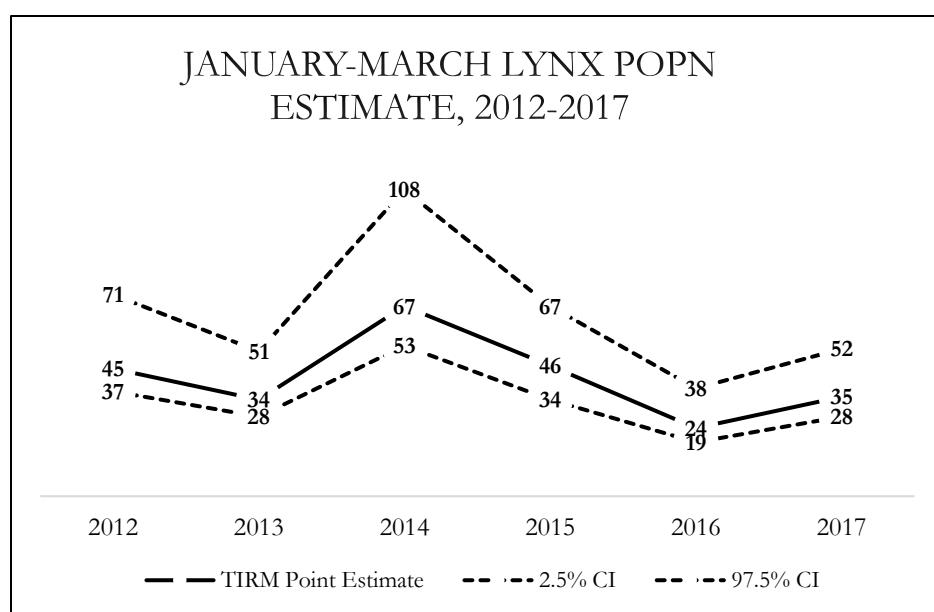


Figure 2. Lynx population TIRM point estimates and 95% confidence intervals generated using capture-mark-recapture analysis of genetic samples for areas consistently surveyed from January-March of 2012-2017 in the Superior National Forest, Minnesota, USA. These areas represent a subset of the areas consistently surveyed during 2015-2017.

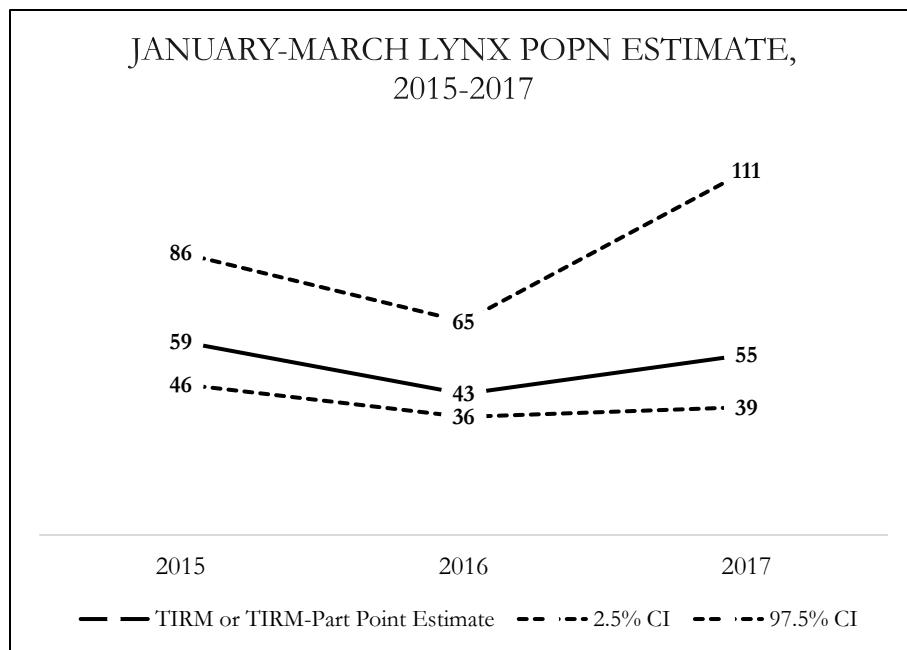


Figure 3. Lynx population TIRM (2015-2016) and TIRM-Part (2017) point estimates and 95% confidence intervals generated using capture-mark-recapture analysis of genetic samples for areas consistently surveyed from January-March of 2015-2017 in the Superior National Forest, Minnesota, USA.

of convincing evidence for difference when compared to either 2013 or 2014 (Ramsey and Schafer 2002). Thus, overall, we find no evidence to suggest the population was not stable during 2012-2017 in the smaller core areas or during 2015-2017 in the larger core areas.

We estimated the catchment area for the smaller core areas (2012-2017) as 6,297 km², and as 10,032 km² for the larger core areas (2015-2017). We estimated the lynx densities in the smaller core areas as 1 lynx/248.9 km² (or 0.4 lynx/100 km²), and in the larger core areas as 1 lynx/320.5 km² (or 0.3 lynx / 100 km²).

DISCUSSION

Our findings represent the first attempt using genetic capture-mark-recapture at estimating abundance and trends of lynx in core areas of the SNF, Minnesota, USA. Estimates such as these can provide important benchmarks for conservation and management of lynx. Our study area was at a southern end of the lynx range in North America, thus making population monitoring more difficult due to potentially higher fluctuations in seasonal distribution compared to more northern core populations, generally lower densities that can exacerbate detection issues, and often less ideal and less homogenous habitat (O'Donoghue *et al.* 1997; Krebs *et al.* 2001; Murray *et al.* 2008). Additionally, significant fluctuations in southern populations may occur during periods of higher immigration from northern populations related to snowshoe hare abundance (Mech 1973; Schwartz *et al.* 2002; Murray *et al.* 2008). During 2014, we detected snowshoe hare in areas where they are typically absent. Our lynx data suggest 2014 may have been a high immigration year given the largest number of individuals were detected, and “new” males were found outside of the typical core areas. Many of the “new” male lynx that were detected during January-March 2014 have not been detected since (supporting our high immigration hypothesis).

Although 2014 was the peak for individuals detected, overall during 2012-2017 the lynx population showed no trend in abundance in the smaller core areas. Results from the 2015-2017 larger core areas generally reflected a similar trajectory as data from the smaller core areas during those years. Moen *et al.* (2008b) concluded that it was unlikely that there were more than about 200 Canada lynx across Minnesota if 25% of northeastern Minnesota was deemed suitable habitat, and if lynx densities were similar to those reported during periods of snowshoe hare lows in northern lynx populations (Poole 1994; Slough and Mowat 1996). The total area for critical habitat for lynx in Minnesota has been estimated at 20,899 km² (Figure 1) (critical habitat delineation data accessed on March 12, 2018 from

<https://catalog.data.gov/dataset/final-critical-habitat-for-canada-lynx-lynx-canadensis>). As expected, our abundance results are lower than the hypothesized 200, because although our study was conducted in the highest quality lynx habitat (of the areas with dependable winter access), it excluded the Boundary Waters Canoe Area Wilderness (BWCA, approximately 4,400 km²) due to motor restrictions, and other areas without reliable winter access. Thus, it covered less than half of Minnesota's critical habitat (Figure 1).

Our density estimates pertaining to the smaller and the larger core areas were similar, and represent approximations because of the methods we used and assumptions therein (e.g., use of genetic capture-mark-recapture to obtain abundance, determination of catchment area, use of average female home range size). Nevertheless, they serve as approximate benchmarks useful for future comparisons within our study area and for broad comparisons with other lynx populations. Because lynx at the southern end of their range often have larger home ranges (due in part to forest heterogeneity and reduced prey abundance; Mech 1980; Burdett *et al.* 2007; Hornseth *et al.* 2014), we expected our density estimates (based, in part, on average female home range sizes) to similarly be lower than northern estimates. Our core area density estimates were approximately 1 order of magnitude lower than the ≤3 lynx/100 km² in the Northwest Territories and in the Yukon Territory during periods of low snowshoe hare abundance (Poole 1994; Slough and Mowat 1996). While these comparisons must be made with caution due to differing methods and assumptions (as stated above), our results demonstrate that lynx density in our study area was lower than those of northern populations.

Recreational activities, forest management practices, and mining activities are all factors that could alter lynx abundance in the Superior National Forest (Murray *et al.* 2008). Our results provide useful benchmark estimates for comparisons with which to assess potential changes in SNF forest management that may affect lynx recovery and conservation. Similarly, our results provide a benchmark for comparisons as climate change potentially alters the depth, density, and duration of annual snow cover and correspondingly, possibly alters snowshoe hare populations (Murray *et al.* 2008; Mills *et al.* 2013; Sultaire *et al.* 2016; Zimova *et al.* 2016).

Ideally, changes in lynx population trend of core areas elucidated by capture-mark-recapture may be better detected by analyzing only resident adult females (females recaptured in subsequent years), provided the sample size and recapture rates are high enough for reasonably precise confidence intervals, because the influx of dispersing males and

breeding males with large territories is a complicating factor. Unfortunately, it is unlikely that the sample size of resident females would be large enough to generate estimates of such precision capable of detecting less than catastrophic change (the sample size would be even smaller for breeding females). Nevertheless, continued capture-mark-recapture of genetic data from core areas could serve as a coarse index for population monitoring. Furthermore, the genetic information gained from these core-area surveys for individual identification (reproduction, relatedness, survival, dispersal) is by itself important for lynx conservation, especially given the recent recommendation to delist lynx (remove threatened status under the Endangered Species Act) (U. S. Fish and Wildlife Service 2018).

To better assess lynx landscape-level population changes, in addition to surveying core areas, distribution surveys (ideally, occupancy surveys) should routinely assess fringe areas that include the edges of known prior distribution extending into areas without prior detections. Core areas (where territorial lynx reside) should host reasonably stable lynx populations. However, in fringe areas, increases in the residential, adult population and/or possible range shrinkage will most likely be detected and may serve as early signals to larger population changes. It may be possible (depending in part on logistical capacity and actual abundance) to formally combine the capture-mark recapture and occupancy data as per Blanc *et al.* (2014). Lastly, we suggest SNF researchers consider conducting further studies in concert with biologists studying lynx immediately to the north because lynx move between the SNF and Canada (Mech 1977, 1980; Burdett *et al.* 2007).

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