



Hybridization between Canada lynx and bobcats: Genetic results and management implications

Michael K. Schwartz^{1*}, Kristine L. Pilgrim¹, Kevin S. McKelvey¹, Edward L. Lindquist², James J. Claar³, Steve Loch² & Leonard F. Ruggiero¹

¹USDA/USFS Rocky Mountain Research Station, 800 E. Beckwith, Missoula, MT 59801, USA; ²USDA/USFS Superior National Forest, 8901 Grand Avenue Place, Duluth, MN 55808, USA; ³USDA/USFS Northern Regional Office, 200 E. Broadway, Missoula, MT 59801, USA (*Author for correspondence: fax: +1-406-543-2663; e-mail: mkschwartz@fs.fed.us)

Received 4 June 2003; accepted 15 August 2003

Key words: Bobcat, DNA, hybridization, Lynx, management, micro satellite, non-invasive genetic sampling

Abstract

Hybridization between taxonomically similar species is an often-overlooked mechanism limiting the recovery of threatened and endangered species. We present molecular genetic data for the first time demonstrating that Canada lynx and bobcats hybridize in the wild. We verify that two microsatellite loci *Lc106* and *Lc110* have non-overlapping allele ranges between Canada lynx and bobcats, and that three putative lynx from Minnesota contain DNA from both bobcats and lynx. Additionally, we use a published test for the 16S rRNA region of mitochondrial DNA (mtDNA) to determine the maternal species; all hybrids had lynx mothers. Fifteen per cent (3/20) of our 'putative lynx' samples were hybrids, although these data are not from a representative sampling effort. Hybridization may be an under-appreciated factor limiting the distribution and recovery of lynx. The presence of hybrids is thus a new factor in the population management of both species with potential implications for hunting and trapping of bobcats.

Introduction

Hybridization between taxonomically similar species has been proposed as a mechanism for limiting species' geographic ranges (Barton 2001). Rare species that come into contact with more common species may be particularly sensitive to this process. While hybridization is common in plant species, there are fewer examples in the Animal Kingdom, and the process has been often overlooked as a significant factor influencing the evolution, range, and distribution of many animals (Dowling and Secor 1996; Rhymer and Simberloff 1996). To understand the conservation and management implications of hybridization it is important to distinguish whether the causes of hybridization are natural or anthropogenic in origin (Allendorf et al. 2001).

Natural hybridization can influence the evolutionary trajectory of a species, providing new genetic material for evolutionary forces to act upon. Determining how to manage cases of natural hybridization may depend, in part, on the kind of the hybridization (Allendorf et al. 2001). For instance, managers may treat hybrids that have arisen from novel contact (e.g., via range expansion) between distinct parental species different from hybrids formed thousands of years ago now proceeding on their own evolutionary tracks as separate entities. In general, it has been recommended that hybrids arising from natural causes be given protected status when needed (Allendorf et al. 2001).

On the other hand, hybridization is often facilitated by anthropogenic disturbances on the landscape. Specifically, the globalization of species

through habitat changes as well as deliberate and accidental translocations have increased contact between previously isolated species. In these cases it has been recommended that hybrids be given less protection under current US law (Allendorf et al. 2001).

Management of hybrids also depends on the genetic consequences of hybridization. The two extreme consequences of hybridization are: (1) the widespread genetic introgression or complete admixture of taxa, and (2) hybridization without genetic introgression (see Allendorf et al. 2001 for an extensive review on categorization of hybridization). Widespread introgression and complete admixture can occur when the hybrids are reproductively fertile and hybrid matings are not avoided, and thus mate with either the parental types or other hybrids (e.g., Goodman et al. 1999). Hybridization without introgression often occurs when the hybrids have post-zygotic reproductive isolating mechanisms (Mayr 1972) rendering them effectively sterile. For example, hybridization without introgression has been documented in bull trout (*Salvelinus confluentus*) in Montana where this species extensively hybridizes with brook trout (*S. fontinalis*), but seldom produces offspring beyond the F₁ generation (Leary et al. 1993; Spruell et al. 2001).

The production of hybrid offspring is problematic for the preservation of rare species. Production of sterile offspring is particularly destructive if females of the rare species are involved in hybrid coupling because small populations are often limited by the number of reproductively fertile females. Production of fertile hybrid offspring is also problematic because the rare species must compete and potentially further hybridize both with the more common species and hybrids.

The Canada lynx (*Lynx canadensis*) is a wide ranging felid (Ward and Krebs 1985; Slough and Mowat 1996; Mowat et al. 2000; Schwartz et al. 2002). The primary core habitat of the lynx is the boreal forest of Canada and Alaska. The southern distribution of native lynx extends into the northern US Rockies, the north Cascades of Washington State, northeastern Minnesota, and western Maine (McKelvey et al. 2000). Lynx are also located in Colorado where a population was introduced in 1999. The lynx was recently listed as 'Threatened' by the United States Fish and Wildlife Service under the US Endangered Species Act

in the contiguous United States (Federal Register 2000).

Bobcats (*Lynx rufus*), a distinct species from lynx (Werdelin 1981; Johnson and O'Brien 1997), are widespread throughout the conterminous United States and reach their northern extent in southern Canada. Lynx and bobcats do not typically occur in the same habitats. However, while bobcats are generally precluded from areas of heavy snow cover, the two will occasionally co-exist and are likely competitors (Aubry et al. 2000; Buskirk et al. 2000).

In Minnesota, the peripheries of lynx and bobcat ranges overlap. Lynx were historically trapped in Minnesota, yet were either present in low numbers or absent from the state between 1993 and 2000 (McKelvey et al. 2000). Photo evidence in 2001 and non-invasive genetic sampling in 2002 confirmed their existence in four counties in northeastern and north-central Minnesota (Figure 1). However, lynx remain concentrated in the northeastern corner of Minnesota despite similar forest habitat continuing to the southwest. Bobcats are infrequently trapped in the northeastern corner of the state, but are common in areas further south (e.g., 0.63% of the bobcats trapped in Minnesota between 1991 and 2002 came from the two northeast counties).

Surveys commencing in 2002 in Minnesota documented lynx presence in the state. During these surveys, many non-invasive genetic samples (i.e., hair and feces) were collected and tested to identify species (Mills et al. 2001). Additionally, three putative lynx were killed (via train, highway, and trapping mortalities in December 2001, November 2002, and December 2002, respectively). Two of the mortalities had slightly abnormal morphology. Specifically, they had large feet and a mostly black tail band, similar to lynx, while also having short ear tufts and compact bodies associated with bobcats. Here we confirm the hybrid origin of these animals and discuss the implications of these data. This represents the first verified hybridization between Canada lynx and the common bobcat in the wild.

Methods

As part of an effort to document the presence and distribution of lynx in Minnesota we collected

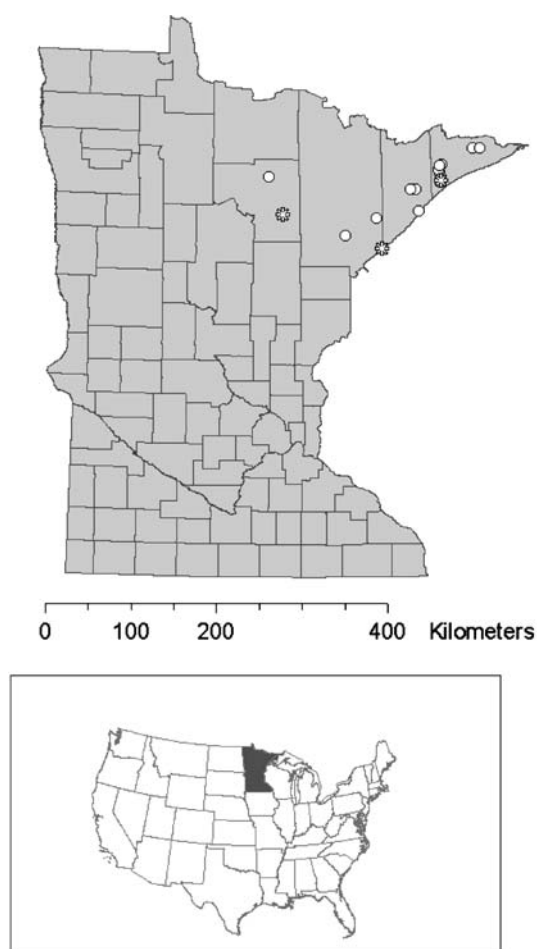


Figure 1. Current distribution of lynx in Minnesota, based on non-invasive genetic sampling surveys (circles), and locations of the Canada lynx-bobcat hybrids (asterisks).

non-invasive genetic samples by following snow tracks associated with putative lynx. When 'lynx' tracks were found, they were followed and hair from daybeds and scats were collected (E. Lindquist, unpublished data). These surveys resulted in 40 non-invasively collected scats and hair samples. Hair and scats were immediately sent to the Rocky Mountain Research Station's Wildlife Ecology unit located in Missoula, Montana. Once in the laboratory, we extracted DNA from each hair sample using the *QIAGEN DNEASY Tissue Kit* (*QIAGEN Inc.*, Germany) and manufacturer protocols, and from each scat using the *QIAMP DNA Stool Minikit* (*QIAGEN Inc.*, Germany).

We established a 'hybrid assay' using differences in the nuclear genome between lynx and

bobcats. This approach was similar to the felid species identification method of Ernest et al. (2000) where species were identified by non-overlapping allele distributions. If two species have non-overlapping allele distributions at a locus, then an F_1 hybrid can be identified by the presence of an allele from both distributions. Our approach had two stages. First, we amplified all samples at microsatellite markers *Lc106* and *Lc110* (Carmichael et al. 2001) and visualized the resultant products on a *LICOR* DNA analyzer (Lincoln, Nebraska, USA). Our PCR reactions for tissues were conducted at volumes of 10 μ l containing 50–100 ng of purified genomic DNA, 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 2.0 mM MgCl₂, 0.2 mM of each dNTP, 0.2 μ M of each primer and 0.5 U *Taq* DNA polymerase. When we used hair and scat samples we modified this protocol by using 2.5 μ l of DNA preparation, along with 2 μ g/ml BSA and 1 U *Taq* DNA polymerase. The thermal profile for the PCR reaction involving DNA from tissue was 94 °C for 5 min, followed by 30 cycles of: 94 °C for 30 s, 56 °C for 30 s, and 72 °C for 30 s. PCR profiles for hair and scat samples were the same, except we increased all steps to 1 min and cycled the reaction 45 times.

Both *Lc106* and *Lc110* have been reported to have non-overlapping allele frequency distributions in lynx and bobcats. Locus *Lc106* has been reported to have alleles between 98 and 110 base pairs (bp) in lynx and either 88 or 90 bp in bobcats; Marker *Lc110* was reported to have allele frequencies between 91 and 103 bp in lynx and to be fixed at 80 bp in bobcats (Carmichael et al. 2000). To ensure that the reported allele frequency distributions were geographically consistent, we evaluated these microsatellites on 108 lynx tissue samples from Alaska, Washington, Wyoming, Montana, Ontario, British Columbia, Yukon Territories, and Northwest Territories (Schwartz et al. 2002, 2003) and 79 bobcat tissue samples from Minnesota, Wisconsin, Wyoming, Colorado, Oregon and Florida. Thirty-eight of the lynx samples were from areas just north of Minnesota in Ontario where bobcats had historically been absent, and 23 of the bobcat samples were from Minnesota counties adjacent to counties where lynx were reported at the time of the survey. The second stage of the hybrid assay was implementation of 16S rRNA mtDNA species identification test (Mills et al. 2001) to determine the direction of

hybridization (i.e., if mtDNA was consistent with lynx, the maternal parent was a lynx; if consistent with bobcat then the maternal parent was a bobcat).

We were also interested in providing an index of the rate of hybridization between lynx and bobcats in our *ad hoc* surveys. While this index is from a non-representative sample, it provides some indication as to the rate of hybridization expected given a more representative sampling strategy. To obtain this index we needed to estimate the number of unique individuals represented by the 40 non-invasive genetic samples and the three putative lynx incidentally killed. Thus, in addition to the two microsatellites used in the hybrid assay we amplified DNA with four additional microsatellite markers described by Carmichael et al. (2000; *Lc109*, *Lc111*, *Lc118*, *Lc120*) using our aforementioned protocols with the exception that markers *Lc109* and *Lc111* were annealed at 54 °C. Probability of identity among siblings ($P_{(ID)Sib}$; Evett and Weir 1998; Waits et al. 2001) using these six microsatellites and the lynx samples collected from Ontario immediately north of our population of interest was 0.005. Using only a four-locus genotype (see below), $P_{(ID)Sib}$ was 0.03, sufficiently low to detect unique individuals based on the criteria of Mills et al. (2000) and Waits et al. (2001).

Because the DNA from hair is subject to allelic dropout and other genotyping errors (Taberlet et al. 1996, 1999; Gagneux et al. 1997; Goossens et al. 1998; Waits and Leberg 2000; Creel et al. 2003) we attempted to analyze each hair or scat sample three times at each locus. Samples that produced scorable products on less than four of six loci were removed from subsequent analyses (18 samples culled from the database), similar to the protocols of Mowat and Paetkau (2002) and Paetkau (2003). We observed four cases of allelic dropout based on three repetitions (twice at *Lc120*, once at *Lc106*, and once at *Lc110*). In these cases, we ran each loci an additional two times and observed consistent heterozygous genotypes. All other loci were consistent across the three runs.

Individual genotypes were considered to be from unique individuals if they differed by more than one allele. However, individuals that differed by only one allele had all replicates of each locus re-scored by an independent observer.

Results

Extensive testing revealed that allele frequencies for loci *Lc106* and *Lc110*, though more variable than reported by Carmichael et al. (2000) at locus *Lc110* in bobcats, do not overlap (Figures 2 and 3,

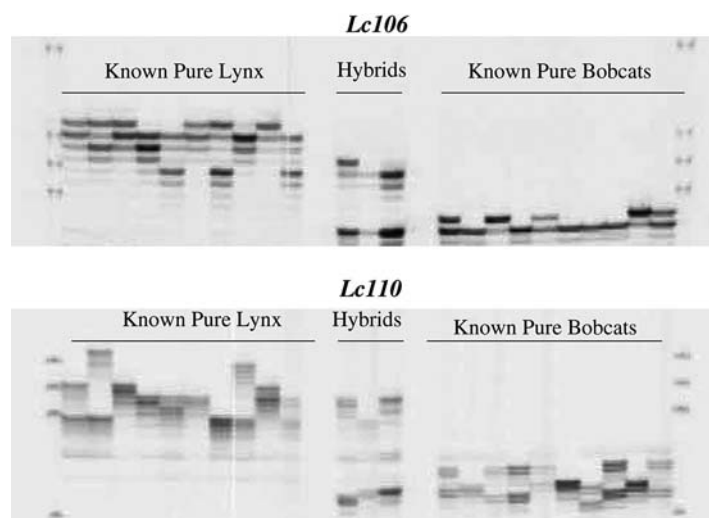


Figure 2. Microsatellite gel image showing lynx, bobcats, and the three hybrids identified in this study. Outer lanes of the gels contain size standards.

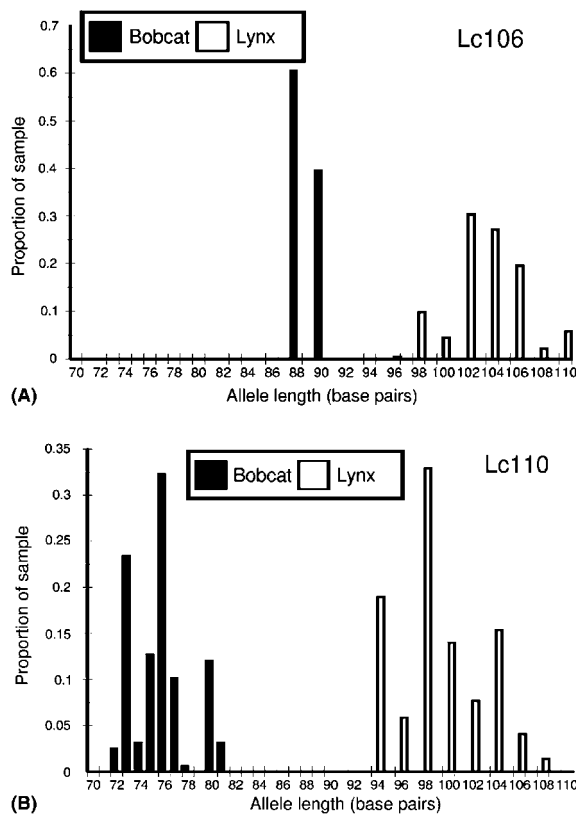


Figure 3. Allele frequencies for lynx and bobcats at loci *Lc106* and *Lc110*. Allele size ranges do not overlap between species at either locus.

Table 1); thus our hybrid test is robust. We detected a minimum of 20 different genotypes that were consistent with lynx based on mtDNA (Mills et al. 2001); 17 were associated with the 40 non-invasively collected scats and hairs from Minnesota (Table 2) and three corresponded to the incidental kills. One hair sample from these 17 individuals (collected in February 2002), and the two tissue samples described as lynx with abnor-

Table 2. Descriptive statistics of the 17 unique lynx (excluding hybrids) identified by non-invasive genetic sampling in Minnesota

Locus	H_e	H_o	A
<i>Lc106</i>	0.78	0.75	6
<i>Lc109</i>	0.76	0.63	5
<i>Lc110</i>	0.77	0.88	6
<i>Lc111</i>	0.73	0.76	5
<i>Lc118</i>	0.79	0.88	5
<i>Lc120</i>	0.67	0.56	4
Averages	0.75	0.74	5.17

H_e is the expected heterozygosity calculated using Nei (1987), H_o is observed heterozygosity, and A is the number of alleles.

mal morphology were hybrids (Figure 2, Table 1). Thus three of 20 individuals were hybrids. Because all three hybrids were identified as lynx based on mtDNA tests, hybridization was between male bobcats and female lynx. At this time we cannot determine whether these hybrids were the result of one or multiple litters from our genetic results, although their geographic (Figure 1) and temporal separation suggest multiple litters.

Discussion

We show here the first confirmed substantiation that wild female lynx mate with wild male bobcats. There have been some anecdotal reports of hybrids in the trapping and fur farm communities. We contacted felid fur farms that claim to have attempted to breed lynx and bobcats in captivity. Only one asserted success in generating Canada lynx–bobcat hybrids, but stated that subsequent attempts to backcross lynx and bobcats failed. Other fur farms were often unsure of the species of

Table 1. Genetic variability for microsatellite loci *Lc106* and *Lc110* for the samples of bobcats ($n = 79$) and lynx ($n = 108$) used to assess the validity of our hybrid test

	Bobcat				Lynx				Hybrid 1	Hybrid 2	Hybrid 3
	Range	H_e	H_o	A	Range	H_e	H_o	A			
<i>Lc106</i>	88–90	0.48	0.52	2	96–110	0.79	0.77	8	88/100	88/98	88/98
<i>Lc110</i>	72–81	0.80	0.77	9	94–108	0.81	0.70	8	75/98	76/94	76/98

Allele ranges are described in base pairs. H_e is the expected heterozygosity calculated using Nei (1987), H_o is observed heterozygosity, and A is the number of alleles. Additionally, the specific genotypes associated with the three hybrid samples are presented.

lynx (*Lynx canadensis*, *Lynx lynx*, or *Lynx pardinus*) they had attempted to breed with bobcats.

Although the test we present may detect any degree of hybridization, it is only fully diagnostic for F₁ hybrids. If hybridization leads to sterile offspring, we diagnosed all hybrids in our samples. However, if hybrids are fertile, our test will provide an underestimate of the number of Canada lynx–bobcat hybrids. As more markers are tested and better reference collections from lynx and bobcats established, we can hope to develop tests (e.g., Spruell et al. 2001; Tranah et al. 2003) to identify future generation hybrids, if they exist. We are currently evaluating additional genetic samples identified as lynx and bobcats based on mtDNA to better determine the extent of hybridization and whether hybrid coupling occurs between male lynx and female bobcats.

While we recognize that our sample is not representative of lynx in northeastern Minnesota, it is interesting that three out of 20 identified individuals (15%) were hybrids. We believe that hybridization is an under-appreciated factor that potentially limits the distribution and recovery of lynx. If the F₁ hybrids are always sterile, the threat to the lynx population is from lost recruitment opportunities (Rhymer and Simberloff 1996; Allendorf et al. 2001). On the other hand, the production of fertile F₁ hybrids may eventually lead to hybrid swarms (Avisé et al. 1984; Forbes and Allendorf 1991), also reducing the range and persistence of pure lynx.

These data have at least two legal implications. First, bobcat trapping is legal in counties that currently contain lynx, while it is illegal to trap lynx anywhere in the conterminous United States. The United States Fish and Wildlife Service, the agency responsible for conserving, protecting, and enhancing the nation's fish and wildlife and their habitats, does not have an official hybrid policy (Allendorf et al. 2001), thus it is unclear if the bobcat–lynx hybrid is protected under the Endangered Species Act. If protection is afforded, bobcat trapping in areas with known lynx could be problematic because both lynx and lynx–bobcat hybrids can be incidentally taken from extant populations. A second legal implication is the identification of a potential threat to lynx recovery. The United States Fish and Wildlife Service is currently reevaluating the conservation needs of lynx (Federal Register 2003). Any factors that may

favor bobcats in lynx habitat may lead to the production of hybrids and thus be potentially harmful to lynx recovery.

Overall, this paper presents evidence that Canada lynx and bobcats hybridize in the wild. Future efforts need to be undertaken to describe the extent, rate, and nature of hybridization between these species, and to understand the ecological context in which hybridization occurs.

Acknowledgements

We thank John Erb, the Minnesota DNR (Division of Wildlife), Dave Kuehn, Mike Kennedy, Tim Lee, and Larry Bickel for their help with sample collection. Yvette Ortega, Rudy King, Roman Biek and Fred Allendorf provided helpful comments on earlier drafts of this manuscript. Cheryl Copeland supplied helpful GIS advice. Cory Engkjer and Carla Burgess provided valuable laboratory assistance. All samples were collected under valid state and national permits.

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