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An Application of Manel's Model: Detecting Bobcat Poaching in Michigan

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Abstract

*The illegal harvest of natural resources (i.e., poaching) has the potential to threaten the persistence of many plant and animal species. In Michigan bobcats (*Lynx rufus*) are distributed throughout the Upper Peninsula (UP) and the northern half of the Lower Peninsula (LP) and are a biologically and economically important species. The popularity of bobcat hunting and trapping in Michigan, along with different harvest regulations between the 2 peninsulas, has created the need for a reliable method of identifying incidences of poaching. Because the bag limit is higher in the UP, we hypothesized that some bobcats harvested in the LP are being registered as originating from the UP. We used 8 polymorphic microsatellite markers and the statistical package STRUCTURE to assign individuals to the population in which they had the highest likelihood of occurrence based on their genotype. We evaluated the influence of using posterior probability threshold values from T > 0.9–0.999 on the number of animals classified as poached. Based on this range, STRUCTURE produced correct assignment rates of 53–82%. All instances of genetic re-assignment involved bobcats claimed as harvested in the UP but genetically assigned to the LP following the suspected method of bobcat poaching in Michigan. This approach provides a reliable method of determining the source population for bobcats harvested in the state and should provide enforcement agencies with a useful way of identifying potential poaching cases.* (WILDLIFE SOCIETY BULLETIN 34(1):150–155; 2006)

Key words

bobcat, Lynx rufus*, Michigan, poaching, population genetics, STRUCTURE.*

One of the greatest threats to the survival of plant and animal species is poaching, which, when defined broadly, is any act that intentionally contravenes the laws and regulations established to protect wild, renewable resources (Muth and Bowe 1998). Recent evidence has shown that poaching is increasing throughout North America (Gregorich 1992, Musgrave and Stein 1993). Unfortunately, poaching often is assigned "folk crime" status (i.e., an act that does not seriously violate public sentiments) and is not always regarded as a serious offence (Muth 1998) nor is its potential negative impact on management efforts recognized. The Convention on International Trade in Endangered Species (CITES) regulates international trade in more than 25,000 species, which is estimated to be worth more than $10 billion (U.S.) annually, with at least $2–3 billion of that illegal (Hemley 1994). Musgrave and Stein (1993) observed that in the United States alone, over $200 million was generated annually from the illegal harvest of wildlife. Although many species may see a direct benefit from the protection gained when recognized by CITES, effective management and enforcement must supplement this protection (Bulte and Van Kooten 2001).

Molecular forensic techniques are available to aid in the enforcement of wildlife harvesting legislation through methods that include, but are not limited to, species identification, DNA fingerprinting, parentage analysis, and determining the population of origin (i.e., birth population) of individuals; the latter application is the focus of this study. Determining the population of origin of an individual is achieved by using hypervariable molecular markers (e.g., microsatellites) and statistical approaches (e.g., allele frequency-based [Paetkau et al. 1995] or fully Bayesian assignment tests [Pritchard et al. 2000]) developed specifically for this purpose (Manel et al. 2002).

A practical application of these methods is to detect whether bobcat (*Lynx rufus*) poaching is occurring in Michigan. The State of Michigan is geographically separated into 2 peninsulas, referred to as the Upper (UP) and Lower Peninsula (LP), which are separated by the Straits of Mackinac consisting of 6 km of open water at the narrowest point. Regulations outlining method of capture, bag limit and hunting and trapping seasons were different in each peninsula at the time of sampling (Michigan Hunting and Trapping Guide 2002). Overall there was a statewide limit of 3 bobcats per season. However, harvest in the LP was limited to 1 bobcat per season, which must be taken by hunting. In the UP up to 3 bobcats could be taken by any combination of hunting or trapping. In all cases bobcat carcasses had to be presented to the Michigan Department of Natural Resources for registration within 5 days of harvest. At this point pelts are given an official seal and the skull or an undamaged canine tooth is collected to determine age, sex, and physical condition of the animal (Cooley et al. 2002). Harvest method, date of capture and harvest location of each individual also are collected at this time.

The potential for poaching to occur arises from the different bag limits in each peninsula. It is possible for a hunter to take more than 1 bobcat, up to the overall limit of 3, from the LP and register as many as 3 of them as having been harvested in the UP. It is not currently possible for state officials to determine the population of origin of any bobcat presented for registration. Following methods outlined by Manel et al. (2002), this study tested the effectiveness of using microsatellite data and STRUCTURE (Pritchard et al. 2000), a Bayesian population-clustering program, to determine if it is possible to identify the population of origin of individual bobcats in an effort to detect instances of poaching.

This method should be particularly useful in Michigan as there is a clear delineation between bobcat populations in the 2 peninsulas and it is unlikely that inter-peninsula dispersal is occurring at a rate sufficient to genetically homogenize popula-

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Figure 1. Harvest locations of the 117 Upper Peninsula and 68 Lower Peninsula bobcats used in this study. Individuals were harvested in the state of Michigan during the 2001–2002 hunting and trapping seasons.

tions. In a study of river crossings by large mammals, Amacher (1983) did not document a single instance of a bobcat crossing the St. Mary's river (0.2–7.0 km wide) 65 km northeast of the Straits, supporting the assumption that inter-peninsula dispersal is rare.

After an individual is genetically assigned to a population, it is then possible to compare the genetic assignment to the harvest location provided to the Department of Natural Resources. Three mutually exclusive outcomes of this comparison can be expected; 1) no significant difference in the number of misassignments between the 2 peninsulas (i.e., individuals reported as being harvested in one population but genetically assigned to another); 2) significantly more individuals genetically assigned to the UP than reported; or 3) significantly more individuals genetically assigned to the LP than reported. Inter-peninsula dispersal best explains outcome 1 because there is no reason for hunters to report bobcats captured in the UP as having been captured in the LP, given that hunters can fill their limit entirely in the UP. Both outcomes 2 and 3 could result from biased dispersal into the LP (outcome 2) or into the UP (outcome 3). However, dispersal biased in such a fashion seems unlikely, as it requires distinct behavioral differences between animals in the 2 peninsulas. Poaching, aided in the form of misreporting harvest locations, also could produce outcomes 2 and 3.

We do not expect to find results consistent with outcome 3 from poaching, as there is no reason for a hunter to falsely report a bobcat as having been harvested from the UP. If inter-peninsula poaching is a problem, we predict our results will be consistent with outcome 2 since a hunter can falsely report an UP harvest location when $\geq$1 bobcats were actually taken from the LP. The ability to detect poaching exemplified by outcome 2 would provide wildlife management officials in Michigan with a reliable method of identifying cases of poaching, aiding in the enforcement of harvest legislation and improving information regarding population sizes in the 2 peninsulas.

Methods

Sample Collection

We obtained tissue samples from the Michigan Department of Natural Resources from bobcats harvested during the 2001–2002 hunting and trapping season. We took a sub-sample of 117 individuals reported harvested from the UP and 68 individuals reported harvested from the LP (Fig. 1). We extracted DNA from tissue samples using QIAGEN DNeasy kits (Qiagen, Valencia, California) following published protocols (Qiagen 2001). Following extraction, we quantified DNA purity with an Eppendorf Biophotometer (Brinkman Instruments, Westbury, New York). We then diluted samples to a working stock of 15ng/µl and stored the remainder of the tissue and extracted DNA at −20°C.

Microsatellite amplification

We typed all bobcats at 8 microsatellite loci using 4 Canada lynx (*Lynx canadensis*) primers (Lc106, Lc109, Lc110 and Lc118; Carmichael et al. 2000) and 4 domestic cat (*Felis catus*) primers (Fca8, Fca35, Fca43 and Fca90; Menotti-Raymond and O'Brien 1995). We performed PCR in a 20-µL cocktail containing 75 ng genomic DNA, 250 µM dNTPs, 0.16 µM of each primer, 1X HotMaster Taq buffer (Brinkman Instruments, Westbury, New York) and 1.5 units of HotMaster Taq polymerase (Brinkman Instruments, Westbury, New York) We conducted amplification on an Eppendorf MasterGradient Thermocycler (Brinkman Instruments, Westbury, New York). Amplification consisted of an initial denaturation step of 2 min at 94°C followed by 3 cycles of 20 s at 94°C, 20 s at 52°C, and 5 s at 72°C. This was followed by 33 cycles of 15 s at 94°C and 20 s at 52°C followed by a terminal extension step of 1 min at 72°C. Following amplification, we analyzed all samples on an ABI 310 Genetic Analyzer using GeneScan Analysis 3.1.2 (Applied Biosystems Foster City, California) software. We determined genotypes using Genotyper 2.0 software (Applied Biosystems, Foster City, California).

Statistical Analyses

We used GENEPOP 3.4 (Raymond and Rousset 1995) to test for deviations from Hardy–Weinberg equilibrium, for genotypic linkage (Bonferroni corrections applied for multiple tests) and genic differentiation between the UP and LP. We calculated Rho_{ST} (Rousset 1996) and F_{ST} (Wright 1969) in GENEPOP 3.4 using the method of Michalakis and Excoffier (1996) and Weir and Cockerham (1984) respectively. We used CERVUS 2.0 (Marshall et al. 1998) to estimate the frequency of null alleles.

We created population clusters using STRUCTURE (Pritchard et al. 2000). We did not use prior population information, as there is a possibility that individual harvest locations had been falsely reported making it inappropriate to place any reliance on use of prior population information in the creation of population clusters. We assumed the UP and LP to be 2 separate populations

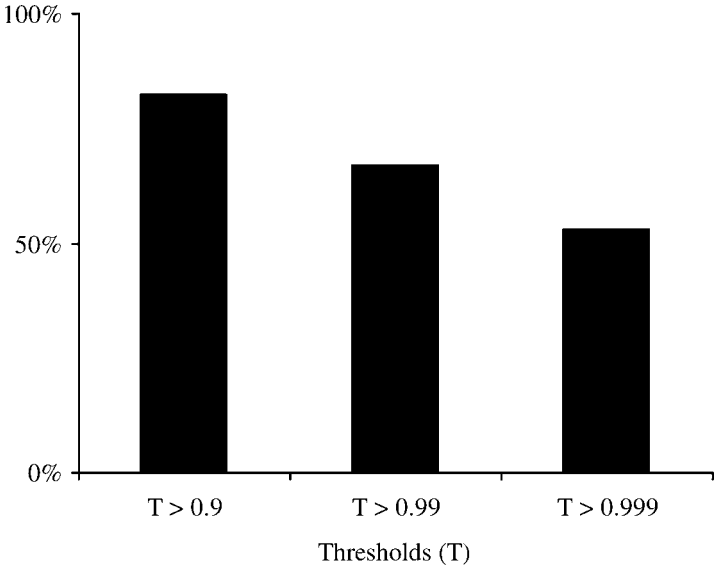

Figure 2. Comparison of the number of bobcats harvested in Michigan during the 2001–2002 hunting and trapping season that were correctly assigned by STRUCTURE (Pritchard et al. 2000) to their population of origin in Michigan based on different probability thresholds (T) defined as the likelihood of them occurring in a given population.

(K = 2) with no admixture (i.e., no gene flow) between populations. An initial burn-in of 100,000 iterations of the Markov chain was followed by a run of 100,000 iterations. We used these parameters because they produced consistent results in replicate runs, as suggested by Pritchard et al. (2000). We assigned individuals to a population if an individual's posterior probability of occurring in that population (T) was above thresholds of T > 0.9, 0.99 and 0.999 (Manel et al. 2002). We considered individuals that fell below the various thresholds to be unassignable and left them in their population of harvest.

Results

Seven of 8 loci were in Hardy–Weinberg equilibrium (following Bonferroni correction). Locus Fca35 was out of Hardy–Weinberg equilibrium due to an excess of homozygotes likely caused by a null allele; Cervus 2.0 (Marshall et al. 1998) estimated null allele frequencies of 12.9% for the UP and 15.9% for the LP. Cornuet et al. (1999) found that slight deviations from Hardy–Weinberg equilibrium had little effect on performance of assignment tests; therefore, we did not remove the locus from this analysis. No loci showed evidence of linkage (following Bonferroni correction).

We detected significant genic differentiation between the UP and LP populations ($P < 0.001$). Presence of separate populations was further supported by F_{ST} and Rho_{ST} values (0.067 and 0.085 respectively) that are relatively high compared to other carnivore species (Paetkau et al. 1999, Schwartz et al. 2002, Cegelski et al. 2003, Rueness et al. 2003).

The percentage of individuals correctly assigned by STRUCTURE ranged from 53.0–82.2% (Fig. 2) depending upon the threshold level used. When we analyzed the UP and LP separately, there was a significant difference (modified Fisher exact test (Ghent 1972); $P < 0.001$) in the distribution of assignments of individuals (Fig. 3). Genetic re-assignments from

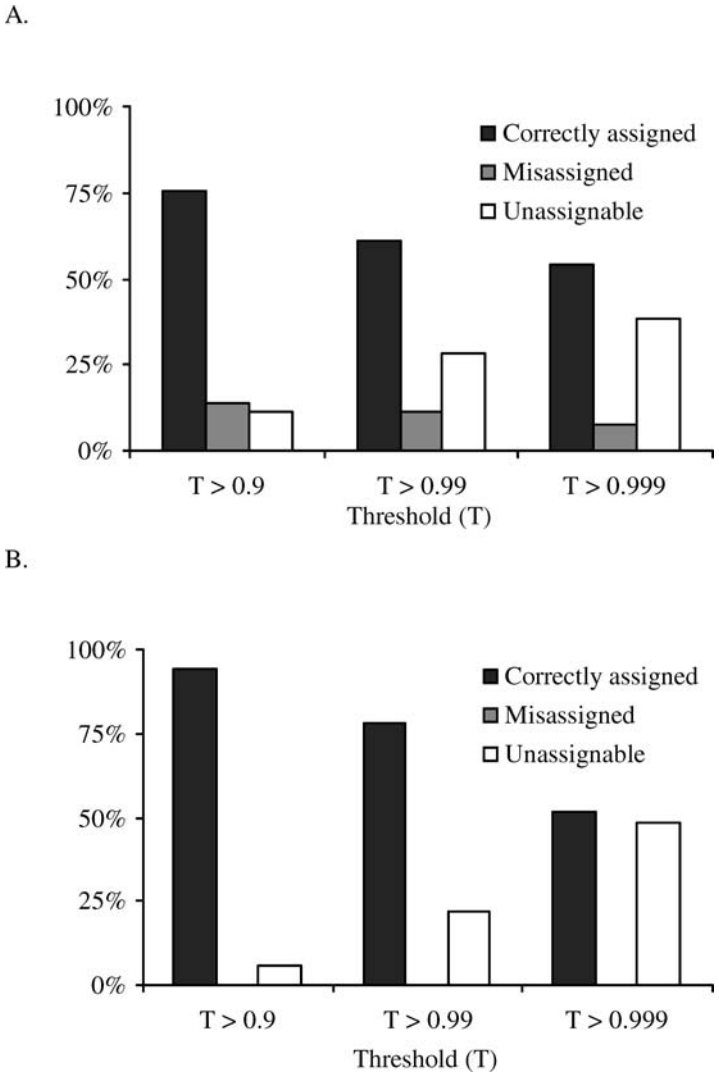

Figure 3. Upper Peninsula (A) and Lower Peninsula (B) assignment results at 3 probability thresholds (T) for bobcats harvested in Michigan during the 2001–2002 hunting and trapping season. Correctly assigned individuals were genetically assigned to the population they were reported harvested in, misassigned individuals were more likely to have come from the other peninsula, and unassignable individuals did not have enough statistical certainty to be unambiguously assigned to a specific peninsula.

the UP to the LP ranged from 7.7–13.7%, depending on the threshold level, but there were no genetic re-assignments from the LP to the UP (animals reported as harvested from the LP but genetically assigned to the UP) regardless of the threshold level used.

After analyzing the results of STRUCTURE, we removed bobcats that were genetically re-assigned at each threshold level from the population in which they were reported as being harvested and added them to their genetically assigned population. We then reanalyzed the revised populations and we found no changes in Hardy–Weinberg equilibrium, linkage, or genic differentiation; however, values of F_{ST} and Rho_{ST} changed (Table 1). Locus Lc109, Lc111, and Fca35 each had significantly more alleles in the UP than the LP ($P < 0.001$) after adjusting for sample size (resampling 1,000 times from the UP; Table 2).

Table 1. F_{ST} and Rho_{ST} values between Upper Peninsula and Lower Peninsula bobcats harvested in Michigan (2001–2002 hunting and trapping season) pre-assignment and after placing misassigned individuals into their assigned population of origin at 3 probability thresholds (T).

		Assignment threshold		
	Pre-assignment	**T > 0.9**	**T > 0.99**	**T > 0.999**
F_{ST}	0.067	0.096	0.094	0.088
Rho_{ST}	0.085	0.104	0.094	0.095

Discussion

Our results provide empirical evidence that the methods of Manel et al. (2002) can be used to detect bobcat poaching in Michigan. Of the 3 mutually exclusive outcomes we predicted, our results are consistent with outcome 2; significantly more individuals were genetically re-assigned to the LP than reported as harvested from there. Since it is unlikely that there is biased dispersal between the peninsulas, the most plausible explanation is that poaching is occurring in the direction expected based on the different harvest limits between the UP and LP.

In addition to being a useful method of detecting poaching, this study is one of the first landscape-scale, practical application of these methods to detect poaching in an instance where it is expected to be occurring. Although Manel et al. (2002) tested this method on a set of natural populations, it was not clear if poaching was occurring in any of the populations. Our data are for a species that the Michigan Department of Natural Resources expects could be experiencing significant poaching. The methods of Manel et al. (2002) could be used in this instance because of the mandatory collection of tissue samples from all bobcats harvested in the state and the rarity of inter-population dispersal. The tissue collection provides access to a sample size sufficient to characterize the unique genetic signature of each population, which results from the limited dispersal between populations.

The difference in the number of misassignments between the peninsulas supports the idea that there is little dispersal occurring. All misassignments, at each of the 3 thresholds, are in the direction that would be expected due to poaching (i.e., bobcats reported as being harvested in the UP but assigned to the LP). If dispersal were occurring, it would be expected that movement between peninsulas would be approximately equal. Differential rates of inter-peninsula dispersal require that ≥ 1 of the following requirements are met: different proximate factors preceding dispersal, a difference in dispersal behavior patterns, or differential mortality for the two dispersal directions. Since no individuals were genetically reassigned from the LP to the UP, even at the least stringent threshold ($T > 0.9$), it is unlikely that any dispersal is occurring. This is further supported by the consistency of genic differentiation between the peninsulas (all $P < 0.001$), the difference in the number of alleles in each peninsula as well as the consistently high F_{ST} and Rho_{ST} values (Table 1).

Although UP and LP bobcat populations are differentiated, problems with assignment may arise which require closer scrutiny if individuals are to be placed in the correct population of origin. An example of such a problem was the difference in the number of alleles we found between peninsulas. Three loci in the UP had a significantly greater number of alleles present than in the LP (Table 2), aiding in the differentiation of populations. However, the number of alleles at locus Lc111 changed at the least stringent threshold ($T > 0.9$) from 3 in each peninsula to 2 alleles in the LP and 3 in the UP at all other thresholds ($T > 0.99$ and $T > 0.999$). This is the result of a single individual harvested in the UP being assigned to the LP at the lowest threshold level. The individual in question had a single allele that was never observed in the LP but was still assigned to the LP at the least stringent threshold due to the characteristics of the rest of its genotype. It is unlikely this individual was actually from the LP, given that the individual remained in the UP when the level of stringency was increased. This provides an example of the potential for this method to incorrectly assign an individual to its supposed population of origin and bias estimates of genetic diversity. However, it also shows how the use of a more stringent threshold can avoid or eliminate this problem. Careful examination of each individual's genotype is necessary to avoid problems that may arise from

Table 2. Genetic diversity indices for 8 microsatellite loci in the Upper (UP) and Lower Peninsula (LP) bobcat populations of Michigan pre-assignment and at T > 0.9–0.999 based on bobcats harvested during the 2001–2002 hunting and trapping season.

		Individual loci																	
		Lc109		**Lc110**		**Lc111**		**Lc118**		**Fca8**		**Fca35**		**Fca43**		**Fca90**		**Mean**	
Population	***n***	**A**	**H_O**	**A**	**H_O**	**A**	**H_O**	**A**	**H_O**	**A**	**H_O**	**A**	**H_O**	**A**	**H_O**	**A**	**H_O**	**A**	**H_O**
Pre-assignment																			
UP	117	10	0.85	5	0.60	3	0.55	5	0.30	6	0.76	8	0.58	6	0.68	6	0.72	6.1	0.63
LP	68	7	0.74	5	0.54	2	0.43	5	0.57	6	0.68	5	0.51	3	0.43	6	0.68	4.9	0.57
T > 0.9																			
UP	101	10	0.86	5	0.60	3	0.54	5	0.29	6	0.76	8	0.61	6	0.70	6	0.71	6.1	0.64
LP	84	7	0.75	5	0.55	3	0.45	6	0.53	6	0.69	5	0.48	3	0.44	6	0.69	5.0	0.57
T > 0.99																			
UP	104	10	0.86	5	0.60	3	0.55	5	0.29	6	0.77	8	0.60	6	0.69	6	0.72	6.1	0.64
LP	81	7	0.74	5	0.55	2	0.44	6	0.54	6	0.68	5	0.49	3	0.44	6	0.68	4.9	0.57
T > 0.999																			
UP	108	10	0.86	5	0.62	3	0.55	5	0.30	6	0.77	8	0.61	6	0.69	6	0.72	6.1	0.64
LP	77	7	0.74	5	0.53	2	0.44	6	0.54	6	0.68	5	0.48	3	0.43	6	0.68	4.9	0.56

T is the probability threshold required to assign an individual to a specific peninsula, *n* the number of individuals analysed, A the number of observed alleles, and H_O the observed proportion of heterozygotes.

incorrect assignments when an animal changes assigned populations based on different thresholds.

The problems associated with incorrect assignments are further highlighted by the changes in F_{ST} and Rho_{ST} values following the replacement of misassigned individuals at each threshold to their correct population of origin. A small number of misassigned individuals can alter estimates of population subdivision. For example, at the lowest threshold ($T > 0.9$), placing the 16 misassigned individuals (misassignment frequency of 8.6%) into their population of origin increases F_{ST} and Rho_{ST} values by 43% and 22% respectively compared to pre-assignment levels (Table 1). Even at the most stringent level ($T > 0.999$), placing the 9 misassigned individuals (misassignment frequency of 4.9%) into their population of origin increases F_{ST} and Rho_{ST} values by 31% and 12%, respectively, compared to pre-assignment levels (Table 1). Failure to place the misassigned animals into their correct population will bias calculations based on these values (e.g., dispersal rates, effective population size and by extension, census population size) making it difficult to accurately model population dynamics, implement effective management decisions and detect poaching.

Management Implications

The use of different thresholds applies a degree of statistical certainty to the assignment of individuals, which allows the results to be used for both forensic and management applications. As suggested by Manel et al. (2002), the most stringent threshold ($T > 0.999$) could be used for forensic cases and would be useful to prosecutors if a poaching case were to proceed to court but may not be appropriate for use in management decisions. The lower thresholds could be used when conducting studies of population structure and testing the sensitivity of population dynamics models by evaluating different levels of poaching. The observed change in poaching rates between the lowest threshold (8.6%) and the highest threshold (4.9%) are great enough that they could alter management decisions. Conservative management would use the lowest threshold levels when modelling population dynamics and setting bag limits. Using different thresholds provides managers with the option of implementing values they believe most accurately reflect the suspected level of poaching.

Conclusions

Molecular biology has proven to be a valuable tool in many aspects of ecology, conservation biology, and wildlife biology. Our results highlight the ability to use molecular markers in management by estimating poaching rates on a large scale. Accurate estimates of poaching will allow managers to more accurately model population dynamics and evaluate harvest rates from management units. We are confident these methods are a successful means of reducing the incidence of poaching.

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