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Distinguishing reintroduction from recolonization with genetic testing

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ABSTRACT

Reintroductions are a common tool for restoring lost biodiversity around the globe and across taxa. The decision to pursue a reintroduction is often based upon the success of past efforts, yet in most cases the assumption that resulting populations are the products of recolonization, is not tested. By collecting data from source populations, reintroduced populations, and natural populations adjacent to reintroductions, it is possible to evaluate the success of past reintroduction events and these data may be used to guide future conservation initiatives. We used the fisher (*Pekania pennanti*), one of North America's most commonly reintroduced species, as a model to conduct an evaluation of reintroduction success. We genotyped 147 individuals at 15 microsatellite loci to determine the genetic contribution of reintroduced individuals to an ostensibly successfully reintroduced population in central Alberta, Canada. Principle component analysis and Bayesian statistical methods converged with confidence on one result: assayed individuals were descended from adjacent native Albertan populations, not putative founders from eastern Canada. A review of fisher reintroduction literature reveals similar patterns: a large proportion of contemporary individuals appear to be the result of recolonization events. Our study has broad implications for conservation as it may imply a 1) over-confidence in past reintroductions, which might lead to significant expenditure of financial and human capital on future initiatives of modest, if any, benefit, and 2) underestimation of some species' ability to disperse and (re-)colonize, highlighting limits to our understanding of functional connectivity. Obtaining appropriate genetic samples in relation to reintroductions will help determine when future reintroduction is likely to be the best conservation initiative.

1. Introduction

Reintroduction – the attempt to re-establish a species in part of its indigenous range (Pavlik, 1996; IUCN, 1998; IUCN/SSC, 2013) – remains a popular management method in conservation biology after a century of use (Hayward and Somers, 2009; Seddon et al., 2014). Considerable contemplation is given to reintroductions as a conservation tool across taxa: in 2016, the Species Survival Commission Reintroduction Specialist Group of the World Conservation Union (IUCN) highlighted 52 on-going case studies encompassing invertebrates, fish, amphibians, reptiles, birds, mammals, and plants (Soorae, 2016). The number of reintroductions being conducted each year is increasing (Seddon et al., 2007), reflecting the conservation community's growing confidence in the strategy compared to other management options. Successful reintroductions are loosely defined as 'establishment of a self-sustaining population' (Seddon, 1999; but see Beck et al., 1994; Sarrazin and Barbault, 1996) and are most commonly undertaken in North America, Australia, and New Zealand (Fischer and Lindenmayer, 2000). Often less empirical examination is given to the real probability for natural recolonization. Many reintroductions are performed in systems perceived to be highly isolated; however, natural recolonization is possible in many areas that demonstrate some form of contemporary, or importantly future, functional connectivity to adjacent populations (Kareiva et al., 1990). With both landscape and climate change altering the occurrence and distribution of biodiversity (Maxwell et al., 2016) the possibility of natural recolonization should be prioritized for many mobile species (Rout et al., 2013).

Context about the dynamics of reintroduced populations may be gleaned from the invasion biology literature. Species invasions and reintroductions are characterized by initiation and expansion stages

Abbreviations: CLM, Cooking Lake Moraine; WW, Willmore Wilderness; NA, Northern Alberta; MB, Manitoba; ON, Ontario

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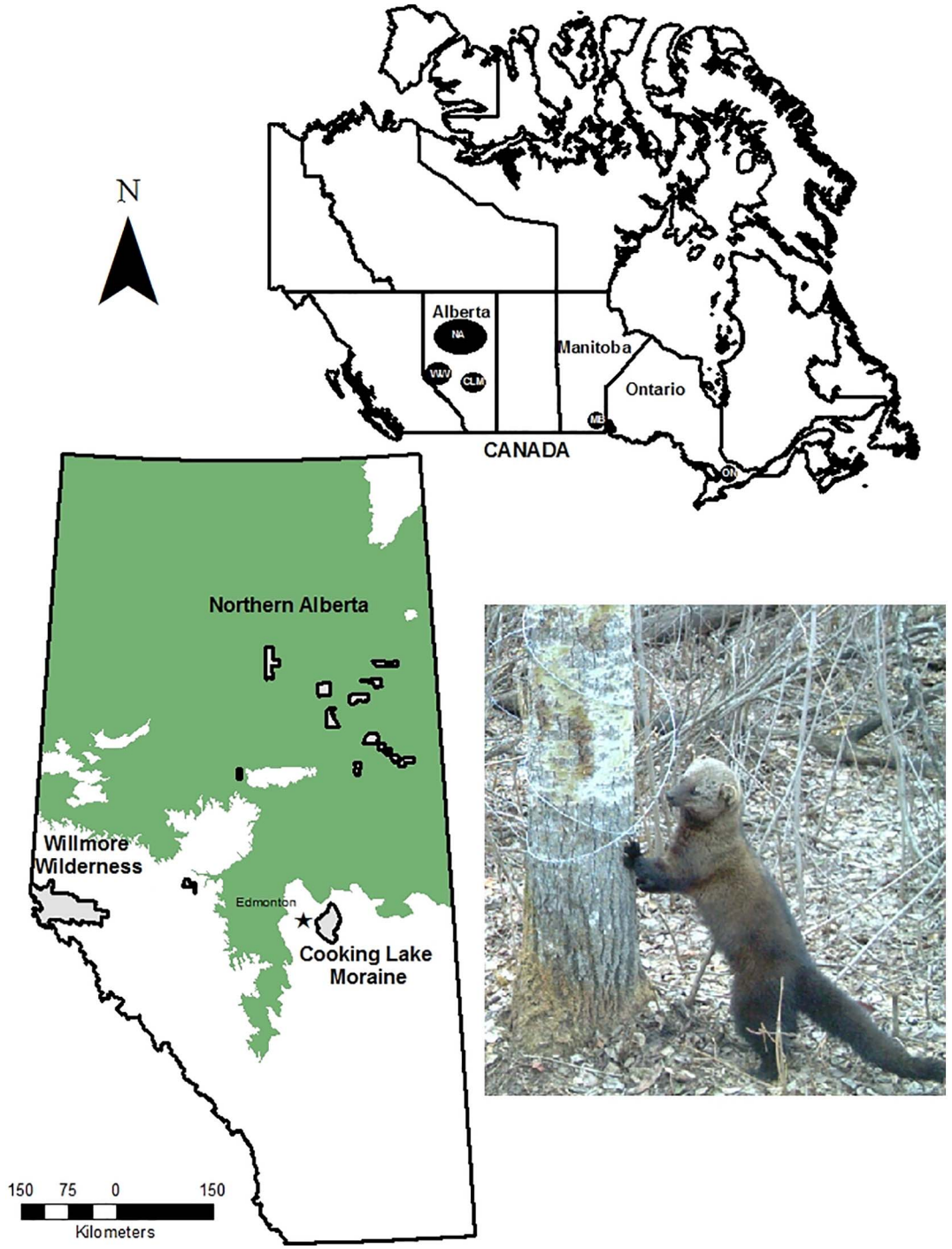

Fig. 1. Fisher DNA samples were collected from 64 sample sites across Alberta's Cooking Lake Moraine (CLM) and compared to four candidate source populations; two adjacent populations in Alberta (Willmore Wilderness in the Rocky Mountains and scattered trap lines throughout northern Alberta) and reintroduction source populations (Manitoba and Ontario) to assess the success of a 1990/1992 fisher reintroduction. Alberta's boreal forest is highlighted in green and a fisher is depicted at a CLM sample site. CLM = Cooking Lake Moraine, NA = northern Alberta, WW = Willmore Wilderness, MB = Manitoba, ON = Ontario. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

prior to establishment (Shigesada and Kawasaki, 1997; Armstrong and Seddon, 2007). Invasive (or exotic) species rarely establish following a single introduction (Shigesada and Kawasaki, 1997). In reintroductions, the probability of establishment can be greatly increased with planning and depends on a suite of limiting factors such as habitat availability and quality, predation, parasitism, and duration in captivity (Seddon et al., 2014). Invasion biology recognizes the 'Tens Rule' where 10% of introduced species establish and a further 10% of these spread (Jeschke and Strayer, 2005). Reintroduction biology recognizes that roughly 20% of reintroductions have been self-described as "successful" (Griffith et al., 1989; Seddon et al., 2014); when compared to the Tens Rule, one might expect this rate may be overestimated and question why more conservation efforts are not being spent on determining the best alternative action.

"Success" is a contested term in reintroduction biology. Definitions vary with project objectives, life history of the species, and the temporal scale of observation (Griffith et al., 1989; Beck et al., 1994; Sarrazin and Barbault, 1996; Seddon, 1999; Haskins, 2015; Robert et al., 2015). The

IUCN provides guidance (IUCN, 1998; IUCN/SSC, 2013), however no definition enjoys a consensus. There are no standards for comparison, and specifically no threshold for discriminating the successful establishment of reintroduced individuals from recolonization events (Robert et al., 2015); just because a species is present in a reintroduction location does not equate to a successful reintroduction. We define 'reintroduction success' as an instance where the reintroduced genetic lineage is maintained in the contemporary population. Using this definition, we question whether reintroduction success is as high as the 20% currently documented (Seddon et al., 2014). Do conservation biologists overestimate reintroduction success, and perhaps underestimate the frequency with which species naturally recolonize former ranges? To distinguish between reintroduction and recolonization success, reintroduction events need to be tested using genetic assessments within a critical time limit; too long and the results will be ambiguous due to accumulation of mutations and/or genetic drift (Nei et al., 1975), and too short risks false declaration of success.

As an example of this larger issue for conservation biologists globally (Olding-Smee, 2005), we re-assessed a previously deemed "successful" fisher (*Pekania pennanti*) reintroduction to Alberta's Cooking Lake Moraine (CLM; 900 km^2; Badry et al., 1997; Proulx and Genereux, 2009; Proulx and Dickson, 2014). The loss of fisher from 40% of its historic range has stimulated frequent reintroduction attempts, making it an attractive model to investigate the probability of reintroduction versus recolonization success (Lewis et al., 2012; Powell et al., 2012). Between 1990 and 1992, twenty fishers were opportunistically reintroduced to the CLM from Steinbach, Manitoba and Bancroft, Ontario, after being held in captivity at Vegreville, Alberta (Badry, 1994; Badry et al., 1997; L. Roy, R. Toews, and J. Bowman pers. com.). The CLM is an area where all evidence indicated the fisher was locally extirpated, due to overexploitation and land-use change, for a minimum of 50 years (Badry et al., 1997). Fishers have frequently been reported by landowners within the CLM since 2007 (Pybus et al., 2009). The CLM is a forested 'terrestrial island' surrounded by a matrix of unsuitable agricultural habitat; extant fisher are hypothesized to be functionally isolated from adjacent Albertan populations. The distinct genotypic signatures of Manitoba, Ontario, and native Alberta (Kyle et al., 2001) provide an opportunity to assess the degree of reintroduction vs. recolonization success by comparing alleles between reintroduction source populations, adjacent Albertan populations, and contemporary CLM samples. With an extant population, we test three non-mutually exclusive hypotheses about the outcome of the CLM reintroduction; 1) a successful reintroduction, wherein the genetic signature of one or both source populations (Ontario and Manitoba) is present within contemporary CLM samples, 2) inadvertent reinforcement, wherein an undetected population was occupying the CLM prior to reintroduction as indicated by unique alleles within CLM samples that do not appear in any other sampled population, or 3) natural recolonization, wherein contemporary fisher individuals are most closely related to animals from adjacent Albertan populations, without genetic evidence of Ontario or Manitoba fishers.

2. Methods

We investigated the ancestry of the contemporary CLM fisher population by comparing microsatellite genotypes to four possible source populations: two adjacent Albertan populations and the two reintroduction source populations (Fig. 1). We consolidated the most recently collected samples from each population (2000–2014). Samples from reintroduction source populations were donated from the original trap-lines sampled in Steinbach, Manitoba (2014 skin; R. Toews pers. com.) and Bancroft, Ontario areas (2000–2003 muscle; sensu Carr et al., 2007, J. Bowman pers. com). CLM fisher DNA samples were collected from 64 stratified-random, non-invasive baited hair traps (sensu Fisher et al., 2011, 2013) in the winters of 2014 and 2016. Fisher populations adjacent to the CLM were sampled via muscle samples donated from fur-harvested individuals in Alberta's boreal forest north of Edmonton (2014), and isolated fisher DNA samples recovered from baited hair traps in Alberta's Willmore Wilderness (Fig. 1) in the Rocky Mountains (2006–2008; Fisher et al., 2011, 2013). All research was performed under the Canadian Council for Animal Care Guidelines (University of Alberta permit #AUP00000518).

We extracted DNA from samples using the QIAGEN DNeasy Blood & Tissue Kit® and protocol (Hilden, Germany). We excluded hair samples that did not contain at least 1 guard hair root or 5 underfur hairs. Muscle and skin samples comprised a ~3 mm^3 clipping. Samples that produced weak or no amplification were analyzed a second time for confirmation, after which we culled 22.8% (87/381) of samples that failed on both attempts. A set of 15-microsatellite loci was used to identify individuals and quantify genetic differentiation among individuals. Primers were developed by Duffy et al., 1998 (*Ggu101* and *Ggu216* in wolverine), Dallas and Piertney, 1998 (*Lut604* in Eurasian otters), Davis and Strobeck, 1998 (*Ma-1*, *Ma-2* and *Ma-19* in American marten, and *Ggu7* in wolverine), Jordan et al., 2007 (*MP144*, *MP182*, *MP055*, *MP114*, *MP175*, *MP227* and *MP247* in fisher), and Fleming et al., 1999 (*Mvis72* in mink and ermine). PCR reactions were performed in a volume of 15 μL containing 50 mM KCl, 160 μM dNTPs, and 0.1% Triton X-100, with primers and *Taq* polymerase optimized to permit co-amplification (Paetkau et al., 1998). PCR thermal cycling ran in a Perkin Elmer 9600 with an initial denaturing step of 94 °C for 1:20 min, 40 cycles of annealing and extension following 94 °C for 20 s, 54 °C for 25 s, and 72 °C for 10 s, followed by 1:05 min at 72 °C. Microsatellite error-checking followed Paetkau (2003) published protocol of reanalyzing mismatching markers in pairs of genotypes that are very similar.

We used three statistical methods to determine the most probable ancestry of contemporary CLM genotypes. First, we compared genetic differentiation between groups using F_{ST} (Wright, 1943), the probability of identity by descent based on allele frequency variation. F_{ST} values range from 0 to 1, with probability of identity by descent increasing as the value approaches zero. We determined F_{ST}, and whether these values were significantly different than zero, in the *diveRsity* package (Keenan et al., 2013) in R (R Foundation for Statistical Computing, 2016). We determined the most probable grouping of samples by genotype-based relationships by qualitatively observing whether sample locations clustered on a biplot with a PCA (Genetix; Belkhir et al., 2004), and quantitatively using MCMC maximum likelihood clustering algorithm (Structure; Hubisz et al., 2009) as well as an assignment test (Geneclass2; Piry et al., 2004). Finally, allele occurrences across sampled populations were screened for any CLM alleles diagnostic of reintroduction or recolonization (Table 1).

3. Results

Both PCA and MCMC identified three distinct provincial clusters (Alberta, Ontario and Manitoba; Fig. S1, Fig. 2). Neither method suggested CLM samples were genetically isolated from northern Alberta or Willmore Wilderness samples. Study areas contained 40 individuals from the CLM, 19 from Willmore Wilderness, 34 from northern Alberta, 29 from Ontario, and 25 from Manitoba (Table S1). Genetic mark-recapture modeling demonstrates that CLM samples represent 47% of the contemporary estimated population (F. Stewart, unpublished data). Within Alberta, F_{ST} was 0.04 between the Willmore Wilderness and the other two study areas, and just 0.02 (marginally greater than zero) between northern Alberta and the CLM. The highest F_{ST} when comparing Alberta samples to other provinces was between Ontario and the Willmore Wilderness (F_{ST} = 0.14; Table S2).

Only 2 of 109 alleles (173 at *Ma*-2, and 136 at *Lut604*) were indicative of reintroduction success; they were found only in the CLM, Ontario, and Manitoba populations. These alleles occurred in few animals in the CLM but are common in Ontario samples, and are only one mutational step away from Albertan alleles (Table 1). We tested

Table 1
Allele presence indicates support for population similarity and mechanism of contemporary fisher occurrence on Alberta's Cooking Lake Moraine. Allele similarities between populations are indicators of reintroduction versus recolonization success. However, alleles that adhere to the microsatellite allele sequence could be the result of a mutation rather than diagnostic of recolonization or reintroduction. Alleles indicating potential mutations are underlined, while alleles diagnostic of either reintroduction or recolonization are bolded.

	Microsatellite	Diagnostic allele	CLM[a] (n = 40)	WW[a] (n = 19)	NA[a] (n = 34)	ON[a] (n = 29)	MB[a] (n = 25)	Microsatellite allele sequence
Reintroduction	*Ma-2*	173	1	–	–	14(3)	3	155, 167, 169, 171, *173*, 175, 177, 179
	Lut604	136	3	–	–	9(1)	5	120, 122, 126, 128, 130, 132, 134, *136*
Recolonization	*Ggu216*	152	2	4	4	–	–	*152*, 154, 158, 160, 162, 164, 166, 168, 170, 172
	MP144	199	20(3)	2	12(2)	–	–	167, 175, 179, 183, 187, 191, 195, *199*, 203, 207
	MP175	179	4	–	3	–	–	151, 155, 159, 163, 167, 171, 175, *179*
	MP182	175	17(1)	2	16(4)	–	–	
		203	1	–	1	–	–	166, ***175***, 183, 187, 191, 195, 199, *203*, *207*
		207	1	–	2	–	–	
	MP247	126	7	3(1)	16(3)	–	–	122, *126*, 130, 134, 138, 142, 146
	Mvis72	258	10	–	2	–	–	***258***, 274, 276, 278, 280, 282, 284

[a] CLM = Cooking Lake Moraine, WW = Willmore Wilderness in Alberta's Rocky Mountains, NA = northern Alberta, ON = Ontario, MB = Manitoba. Units of measurement are the number of individuals sampled within each population. Numbers in brackets represent the number of homozygote individuals.

individual origins using the software Geneclass2 (Piry et al., 2004); no CLM individual showed a statistically meaningful departure from expectation for pure Alberta ancestry (lowest p-value = 0.05 which is not significant after correcting for small sample sizes). There were no alleles unique to the CLM, indicating that inadvertent reinforcement is unlikely. Together, these results provide strong support for recolonization of the CLM from northern Alberta and Willmore Wilderness areas rather than successful reintroduction of founder individuals from Ontario or Manitoba.

4. Discussion

All individuals used in the 1990s CLM fisher reintroduction experiments had experienced months or years of captivity prior to re-introduction, and few individuals remained close to release locations months after reintroduction (Badry, 1994). Here we show evidence that fishers sampled from the Cooking Lake Moraine (CLM) were not derived from the individuals reintroduced from Ontario and Manitoba in the 1990s. Instead it appears that recolonization by Albertan fishers is responsible for the current CLM population. This observation is not uncommon; our review of all fisher reintroductions demonstrated that 47% have been given a different reintroduction status once genetic testing for reintroduction success was performed (Table 2).

Cryptic recolonization has been observed in other commonly reintroduced mammals. In a similar example, Kruckenhauser and Pinsker (2004) reviewed multiple Alpine Marmot (*Marmota marmota*) reintroductions and demonstrated that three contemporary Austrian populations are more closely related to neighboring Austrian populations than putative founders from France. Hicks et al. (2007) concluded that dispersal is much higher in Elk (*Cervus elaphus*) than previously believed because of the astoundingly high genetic diversity within, and low genetic divergence between, western North America's reintroduced

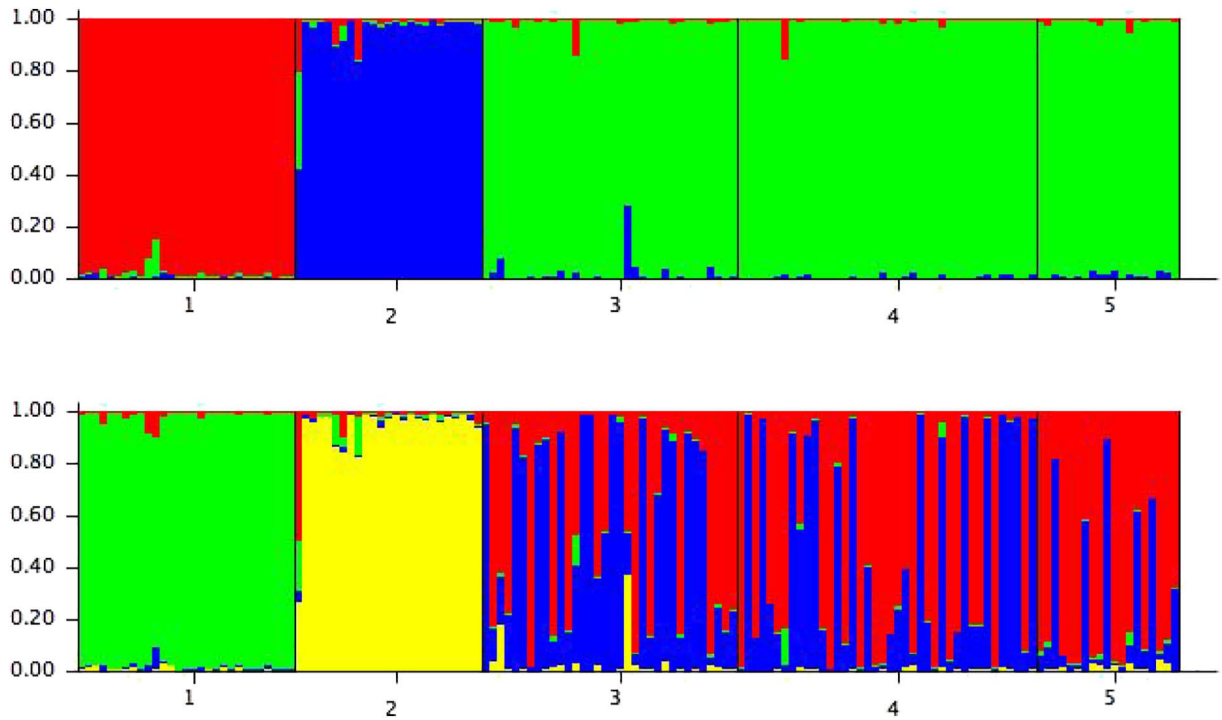

Fig. 2. The probability of population structuring when 3 (upper; $k = 3$), or 4 (lower; $k = 4$), populations are assumed across 15-locus fisher genotype data. Each vertical line represents the probability of population assignment for an individual. Multiple runs under the same conditions converged, and further increases in k did not produce plausible clusters nor did they increase the likelihood meaningfully (Fig. S2). In either situation, Cooking Lake Moraine samples are most closely related to samples from northern Alberta and the Willmore Wilderness. The populations are: 1 - Ontario; 2 - Manitoba; 3 - northern Alberta; 4 - Cooking Lake Moraine; and 5 - Willmore Wilderness in the Rocky Mountains.

Table 2
Implication of genetic work on the status of fisher reintroduction success. Opportunistic genetic sampling provides the ability to re-assess reintroduction success of fisher populations. A status being maintained (Y) demonstrates the genetic results support the original status of the reintroduction. Many genetic tests demonstrate either doubtful (N), or ambiguous (U), contribution of reintroduced individuals to the contemporary genetic population.

Release location	Source location	Years	Status[a]	Genetic reference	Genetic method	Years after release	Status maintained[b]	Original references
Nova Scotia	Ranch	1947–1948	S	(Kyle et al., 2001)	Microsats	53	Y	(Benson, 1959; Dodds and Martell, 1971)
Wisconsin	New York Minnesota	1956–1963	S	(Williams et al., 2000)	Allozymes	37	U	(Irvine et al., 1964; Bradle, 1957; Petersen et al., 1977; Kohn et al., 1993; Dodge, 1977)
Ontario	Ontario	1956	U	N	na	na	na	(Berg, 1982)
Ontario	Ontario (Parry Sound)	1956–1963	S	(Carr et al., 2007)	Microsats	44	U	(Berg, 1982)
Vermont	Maine	1959–1967	S	(Williams et al., 2000; Hapeman et al., 2011)	Allozymes; microsats	33; 44	Y	(Berg, 1982)
Oregon	British Columbia	1961	F	(Aubry and Lewis, 2003)	Microsats; mtDNA	22	Y	(Kebbe, 1961a & b)
Michigan	Minnesota	1966–1968	S	N	na	na	na	(Brander and Books, 1973; Irvine et al., 1964)
Nova Scotia	Maine	1963–1966	S	(Kyle et al., 2001)	Microsats	35	Y	(Dodds and Martell, 1971)
Wisconsin	Minnesota	1966–1967	S	(Williams et al., 2000)	Allozymes	33	U	(Petersen et al., 1977; Kohn et al., 1993; Dodge, 1977)
New Brunswick	New Brunswick	1966–1968	S	(Drew et al., 2003)	mtDNA	35	U	(Dilworth, 1974; Lewis et al., 2012)
West Virginia	New Hampshire	1969	S	(Williams et al., 2000; Drew et al., 2003)	Allozymes; mtDNA	31; 35	U; Y	(Berg, 1982; Lewis et al., 2012)
Minnesota	Minnesota	1968	F	N	na	na	na	(Berg, 1982; Lewis et al., 2012)
Maine	Maine	1972	U	(Drew et al., 2003; Hapeman et al., 2011)	mtDNA; microsats	39; 31	Y	(Lewis et al., 2012)
Manitoba	Manitoba	1972	F	N	na	na	na	(Berg, 1982; Lewis et al., 2012)
New York	New York	1976–1979	S	(Hapeman et al., 2011)	Microsats	32	Y	(Wallace and Henry, 1985; Lewis et al., 2012)
Oregon	British Columbia Minnesota	1977–1981	S	(Drew et al., 2003; Aubry and Lewis, 2003)	mtDNA; microsats	28; 28	Y	(Lewis et al., 2012)
Ontario	Ontario (Manitoulin Is)	1979–1981	S	(Carr et al., 2007)	Microsats	26	Y	(Kyle et al., 2001; Lewis et al., 2012)
Ontario	Ontario (Bruce Peninsula)	1979–1981	S	(Carr et al., 2007)	Microsats	27	U	(Kyle et al., 2001; Lewis et al., 2012)
Alberta	Alberta	1981–1983	F	N	na	na	Y	(Davie, 1984)
Montana	Minnesota Wisconsin	1988–1991	S	(Drew et al., 2003; Vinkey et al., 2006)	mtDNA	12	N	(Roy, 1991; Heinemeyer, 1993)
Michigan	Michigan	1988–1992	S	N	na	na	na	(Lewis et al., 2012)
Connecticut	New Hampshire Vermont	1989–1990	S	(Williams et al., 2000; Hapeman et al., 2011)	Allozyme; microsats	10; 21	Y	(Rego, 1989, 1990, 1991; Lewis et al., 2012)
Alberta	*Ontario Manitoba*	*1990–1992*	*S*	*Stewart* et al.	*Microsats*	*24*	*N*	(Badry et al., 1997; Kyle et al., 2001; Proulx and Dickson, 2014)
Manitoba	Manitoba	1994–1995	S	N	na	na	na	(Baird and Frey, 2000)
Pennsylvania	New York New Hampshire	1994–1998	S	N	na	na	na	(Serfass et al., 2001)
British Columbia	British Columbia	1996–1998	F	N	na	na	na	(Fontana and Teske, 2000; Weir, 2003)
Tennessee	Wisconsin	2001–2003	S	N	na	na	na	(Anderson, 2002)
Washington	British Columbia	2008–2011	S	N	na	na	na	(Lewis, 2014)
California	California	2009–2012	S	N	na	na	na	(Lewis et al., 2012)
Washington	British Columbia	2015–present	O	N	na	na	na	(J. Lewis pers. comm.)

Italics signify research conducted within this journal article.
[a] S = successful re-introduction, F = failed re-introduction, O = ongoing re-introduction.
[b] N = status not maintained after genetic re-assessment, Y = status maintained after genetic assessment, U = unknown status after genetic assessment.

populations. Statham et al. (2012) document the unanticipated continental recolonization of native Red Fox (*Vulpes vulpes*) compared to the perceived reintroduction success from European sources. Such examples highlight two important considerations: 1) that many re-introductions are sub-optimal conservation strategies when compared to the ability of species to naturally recolonize historic ranges, and 2) that re-introductions may provide a catalyst for socially facilitated re-colonization (Parker et al., 2007). In either case, promoting functional connectivity may be a more effective conservation goal.

4.1. Caveats

Within CLM samples, there were two alleles also found among eastern fishers but not among any other fishers from Alberta (Table 1). We suspect these CLM alleles are the products of independent mutations and are not identical by descent to the Ontario alleles, as they are only one mutational step away from other Albertan alleles; each allele may have been the result of a single microsatellite mutation (Waits and Paetkau, 2005). Longer microsatellites mutate more frequently and rates can vary from 10^{-3} to 10^{-4} per locus per generation (Ellegren, 2000). Ideally, genetic samples should be collected at multiple time

points from reintroduction, source, and adjacent populations to document drift.

Post translocation genetic data does not distinguish the exact date, route, or mechanism by which individuals disperse and recolonize former ranges. Our genetic analysis has reduced the possibility of reintroduction success from eastern populations, yet a contemporary CLM population still exists. As in any cryptic recolonization event close to human habitation, there are two possible mechanisms to explain contemporary species occurrence: 1) “paw-power” reflecting multiple routes of natural dispersal, and 2) “horse-power” reflecting unknown (and unsanctioned) translocation. Our genetic analyses found eight of 109 alleles diagnostic of recolonization from northern Alberta and Willmore Wilderness, across 15 loci. We find it unlikely two of these alleles (*MP182* 175 and *Mvis72* 258) are explained by independent mutations because they do not conform to the loci's microsatellite allele sequence (Table 1). Fishers use areas of high forest cover compared to what is available (Badry, 1994; Koen et al., 2007; LaPoint et al., 2013; Koen et al., 2014). Dispersal may happen through unsuitable habitat if distances are small and within a home territory (LaPoint et al., 2013); average dispersal distances are typically less than 30 km for either sex (6–29 km; Aubry and Raley, 2006; Lofroth et al., 2010). However, mustelids can demonstrate amazing feats of dispersal (Carr et al., 2007; Moriarty et al., 2009). We cannot reliably distinguish between “paw-power” and “horse-power” mechanisms of provincial recolonization, but instead demonstrate that recolonization may be an important aspect of range stability. This conclusion suggests that maintaining and enhancing connectivity (and thus opportunities for natural recolonization) may in many cases be a better use of conservation resources than reintroductions.

4.2. Broad conservation implications

If cryptic recolonization is misinterpreted as reintroduction success, it implies that our concept of functional connectivity may be flawed. Functional connectivity is a species-specific concept, and describes how genes, individuals, or populations move through a landscape (Goodwin, 2003; Garroway et al., 2008; Luque et al., 2012; Rudnick et al., 2012). However, if individuals are recolonizing areas that were previously perceived to be functionally disjunct from the rest of the species range, then individuals may be attracted to an anchoring site and move through landscape features more readily than predicted. We therefore recommend conservation biologists attempt to estimate the ability of species to recolonize former ranges by genetically testing past re-introductions, modeling habitat connectivity liberally, and not underestimating the dispersal ability of the study species. There may be situations where connectivity is detrimental to establishing populations (i.e. promoting connectivity with competitor or predator populations). However, if reintroductions are performed, and there is even a small chance of natural recolonization, we recommend investing the time and money into non-invasively sampling the genetic signatures of both reintroduced individuals and proximal populations across a series of time intervals. These genetic measurements inform landscape resistance modeling (Cushman et al., 2006; McRae et al., 2008; Rudnick et al., 2012; Zeller et al., 2012; Koen et al., 2014, 2016; Elliot et al., 2014), and translocation evaluation (Bowman et al., 2016) including the need for assisted colonization in response to climate change (Rout et al., 2013). Such emerging applications in landscape genetics and wildlife management have applicable ramifications on future biodiversity through corridor and conservation area planning (Spear et al., 2005; Balkenhol et al., 2009; Schwartz et al., 2010). The accurate quantification and perception of functional connectivity, which can be empirically documented through recolonization events, is paramount for decision making and implementing the best conservation management techniques.

Our results from the CLM fisher reintroduction (Table 1), fisher reintroduction genetics in general (Table 2), and a sample of mammalian reintroduction events from the literature demonstrate the importance of employing genetic data for comparing reintroductions and recolonizations as optimal conservation strategies. We recommend that given the large amount of money, political capital, public buy-in, and hard work invested in reintroductions – in addition to the great conservation importance of their outcomes – that if recolonization is even minutely probable, reintroduction be treated as a conservation experiment with genetic samples obtained and analyzed from all animals, non-invasive samples obtained from proximal and source populations, and results published that generate and disseminate an objective conclusion about reintroduction vs. recolonization success. Documenting the relative success of reintroductions and recolonizations across varying degrees of functional connectivity helps conservation biologists understand the efficacy of these conservation tools, and quantify the potential of reintroductions providing a catalyst for socially facilitated recolonization, thereby saving valuable future conservation funds. Alternative conservation approaches – such as landscape management to facilitate functional connectivity – must be better assessed for long-term conservation, and may fix some of the very problems that led to extirpation in the first place.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.08.004.

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