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Original Research

Origins and Diversity of the Introduced Southern Red-backed Vole (*Myodes gapperi*) Population in Newfoundland, Canada Based on Mitochondrial Haplotypes: Ecological and Management Implications of a Potentially Invasive Species

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Abstract

Inferences about sources and routes of colonization are important to understanding and managing introduced species. The Southern Red-backed Vole (SRBV; *Myodes gapperi*), not native to Newfoundland, was recently discovered in the western interior of the island, and its range is rapidly expanding. Theories regarding the origin of these animals include migration from an earlier release on a small coastal island, accompaniment of pulpwood imports, or an unsanctioned release as part of Newfoundland Marten (*Martes americana atrata*) recovery efforts. To determine the source, route, and potential timing of introduction to the island, we analyzed mitochondrial control-region sequences of 155 animals from Newfoundland and the two most likely sources, Cape Breton and Labrador. Although Cape Breton and Labrador contain phylogenetically distinct suites of haplotypes, both regions are part of the "eastern" clade of SRBV, indicating that the northeastern-most part of the range was recolonized from an eastern forest refugial lineage isolated during the Pleistocene. The Newfoundland population of SRBV contained only two haplotypes, one found in 89 individuals from multiple sampling locations that clusters with the Cape Breton subclade, and the other found in three individuals from Mine Pond and five from Labrador. We conclude that there have been at least two introductions to the island, with the Cape Breton-sourced introduction occurring earlier than the Labrador event; low diversity is consistent with recent timing of these events. Success of introduced voles in Newfoundland, despite little genetic diversity, probably reflects an exploitable niche for a broadly adapted boreal small mammal.

Key Words: *Myodes gapperi*, mitochondrial DNA, phylogeography, invasive species, Newfoundland Marten recovery plan.

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INTRODUCTION

Introductions involving single or small numbers of individuals will often fail, but in certain circumstances, particularly in island environments (Pauley 1994), populations arising from such events can flourish (Tsutsui *et al.* 2000; Jones and Gomulkiewicz 2012). Factors influencing the success of an introduction include the types of interactions experienced with native flora and fauna, the capacity of the species for rapid reproduction and evolution, and niche availability. Knowledge of the number of introduction events, source populations, and routes of colonization are important to understanding the population dynamics, ecological impacts and possible management of an introduced species (Hulme 2006).

The Southern Red-backed Vole (SRBV; *Myodes gapperi*) is a widely distributed native species in forests of the Hudsonian and Canadian life zones of North America (Merritt 1981), but is an introduced species to the island of Newfoundland, the insular component of Canada's easternmost province, Newfoundland and Labrador. The species was first intentionally introduced from the neighboring mainland component of the province, Labrador, to Camel Island, 2.4 km off the main island of Newfoundland (Figure 1), in 1967 as part of a research program to assess potential competition between SRBV and the native Meadow Vole (*Microtus pennsylvanicus*) (Payne 1974); by 1986, this population was believed to be extirpated (Northcott 1989). In 1999, a population of SRBV was discovered on the main island of Newfoundland during small mammal surveys conducted in the Little Grand Lake area in southwestern Newfoundland (Hearn *et al.* 2006; Figure 1).

Since the discovery of SRBV on the main island of Newfoundland, the species' range has been expanding rapidly (Rodrigues 2012), and the ecological impact of these animals in Newfoundland has yet to be fully realized. As a potentially invasive species, the SRBV raises

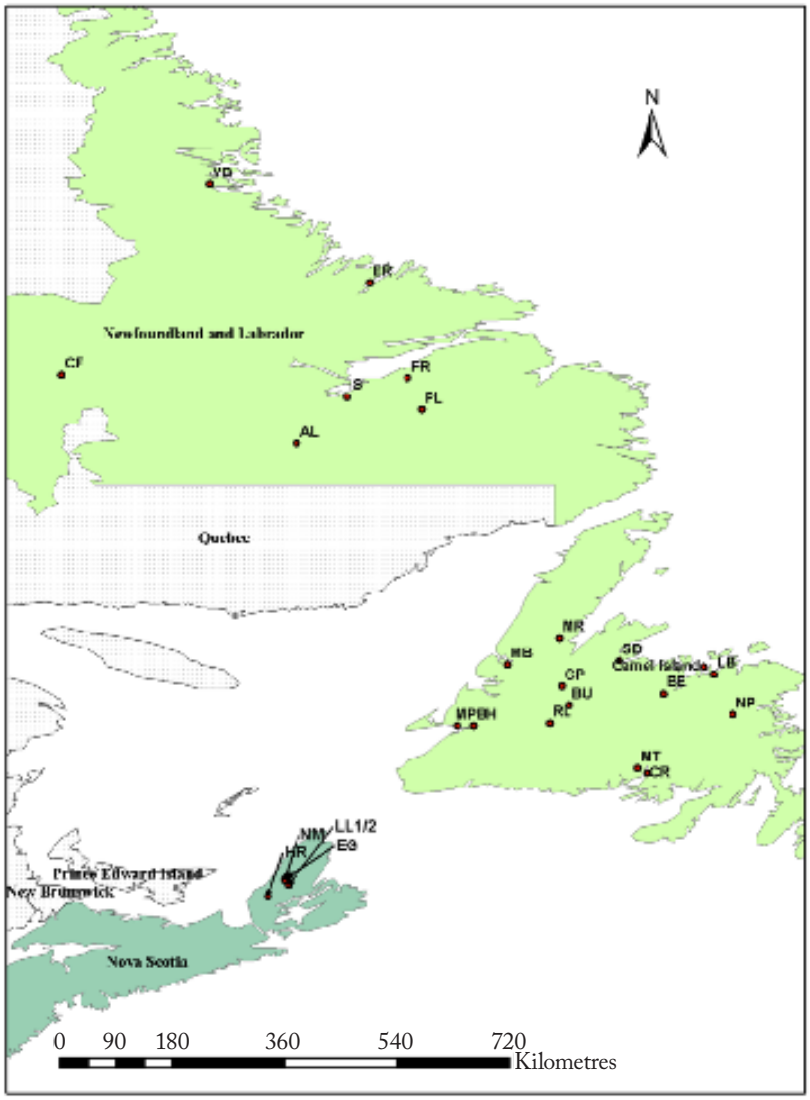

Figure 1. Sampling locations for this study. Locality abbreviations are given in Table 1.

ecological concerns, which include the potential introduction of new diseases and parasites (Moss 2002; for example Q fever caused by the bacterium *Coxiella burnetii*, and diseases associated with the cestodes *Andrya* spp., and the nematodes *Heliginosomum carolinensis* and *Echinococcus multilocularis*), competition with the native Meadow Vole and alteration of predator–prey dynamics (Hearn *et al.* 2006), and seed and seedling predation resulting in lowered tree recruitment, particularly of deciduous tree species, which occur in low numbers in Newfoundland (Kasimos 2007).

Possible explanations for the origin(s) of the current SRBV population include an unintentional introduction with wood chips and pulpwood imported from Labrador into the paper mill in Stephenville, Newfoundland, from 1973 until 2005 (Martin 2006), immigration (e.g., by swimming) or transport from the Camel Island population, or an intentional but unapproved introduction from a mainland population to provide an alternative food source for Newfoundland Marten (*Martes americana atrata*) (Hearn *et al.* 2006), which were endangered at that time (Newfoundland Marten Recovery Team 2010). Newfoundland's closest mainland connections, by distance and as sea transportation routes, are Nova Scotia's Cape Breton Island and Labrador (Smallwood 1981-1994; South 1983) and were thus considered likely source populations for SRBV to Newfoundland.

Runck and Cook (2005) identified three divergent mitochondrial DNA (mtDNA) clades of SRBV throughout their North America range, one west of the Rocky Mountains (western clade), one east of the Appalachian mountains (eastern clade), and a "central clade." Only "central clade" SRBV were found at higher latitudes (Alaska, Northwest Territories, and British Columbia), indicating that postglacial re-colonization of the most northerly parts of the range following the Wisconsin Glacial Maximum (~13,000 years ago) occurred via a mid-continental route. We hypothesize that, due to the geographic barrier to gene flow created by the Appalachian Mountains, we are able to differentiate source populations arising from Cape Breton, representing members of the "eastern clade", from Labrador populations, which may have "central clade" origins.

Documenting the source and genetic diversity of Newfoundland's introduced population of SRBV is important for assessing potential long-term effects of this species. Studies that compare the biology of invasive species in both their native and introduced ranges are increasing in number (e.g., Suarez *et al.* 1999; Tsutsui *et al.* 2000), and both mitochondrial and nuclear DNA are used to identify source populations and routes of invasion, and document genetic variation, in introduced populations (Estoup and Guillemaud 2010; Shi *et al.* 2012). Here, we characterize genetic diversity in the SRBV population of the island of Newfoundland, to identify its origins and potentially infer the frequency and timing of introduction events by comparing mitochondrial control region DNA sequences from animals from Labrador, Cape Breton, and Newfoundland. The data provide the first genetic characterization of SRBV at the northeastern-most limits of their range.

STUDY AREA AND METHODS

Sample Collection

Red-backed Voles were acquired from three different sampling efforts. The majority of specimens came from the Newfoundland and Labrador Small Mammal Monitoring Network (NL SMMN) 2007–2009 (Rodrigues 2010) and represent populations across Newfoundland and Labrador. Specimens from Little Grand Lake and Red Indian Lake, 35 km east of Little Grand Lake, were collected from the first detection events for each area in 1999 and 2001, respectively, during an American Marten prey base study (Hearn *et al.* 2006). Unfortunately, samples from Little Grand Lake were too degraded to yield useable mtDNA. The third group of specimens was specifically collected for this study from Cape Breton (Figure 1) in the spring of 2010. In all cases, small mammals were caught using Victor metal pedal mouse traps (Woodstream Corporation, Lititz, USA), baited with an even mixture of peanut butter and oats. Specimens were kept frozen until processing, although at some more remote sites such as Little Grand Lake it may have been days before specimens were frozen and, therefore, they were subject to decomposition. Except for one specimen in which ear tissue was collected, from all other specimens a 1-cm portion of tail tip was removed and preserved in 95% ethanol. One hundred and eighty-six samples (107 from Newfoundland, 69 from Labrador, and 10 from Cape Breton) were included in this study.

DNA Analysis

DNA was extracted from approximately 10 mg of tissue (1 cm of tail or a 3 mm^2 piece of ear) using the Wizard SV 96 Genomic DNA Purification System (Promega Corporation, Madison, USA), following the manufacturer's protocol, except that DNA was eluted in a final volume of 250 µL.

A 712 bp segment of the mitochondrial control region was amplified using primers RBV-MF (*TGTAAAACGACGGCCAGT*-TCGTACATTAAATTATATTCCCCTA) and RBV-MR (*CAGGAAACAGCTATGAC*-CTTATTTTTGGGGTTTGGTAAG) designed for this study by alignment of 7 SRBV sequences (GenBank Accession Nos. AF367181-AF367187). M13 forward and M13 reverse primer sequences (in italics) were attached to the forward and reverse primers, respectively, to facilitate sequencing PCR products. The 25 µL PCR reaction mix contained: PCR Master Mix (Promega Corporation), 1.5 mM $MgCl^2$, 0.8 µM of each primer, and a minimum of 30 ng of DNA template. A touchdown PCR was performed in a GeneAmp 9700 (Applied Biosystems Inc., Foster City, USA) as follows: 94°C for 2 min; five cycles of 94°C for 30 sec, 56°C to 52°C (decreasing 1°C per cycle) for 30 sec, and 72°C for 1.5 min; 35 cycles of 94°C for 30 sec, 51°C for 30 sec, and 72°C for 1.5 min; and completed with a step of 72°C for 5 min. PCR products were purified by vacuum aspiration on Pall Omega 100k AcroPrep™ molecular weight cut-off plates (Pall Corporation, Port Washington, USA).

Sequencing reactions were performed on C1000 Cycler 96W Systems (Bio Rad Laboratories, Hercules, USA) using the Applied Biosystems Inc. BDT v3.1 chemistry. The cycle sequencing regime consisted of a "hot start" of 98˚C for 5 min prior to the addition of the BDT v3.1, followed by 25 cycles of 96˚C for 10 sec, 50˚C for 30 sec, and 60˚C for 4 min. Sequencing reactions were purified by ethanol precipitation. Sequences were generated by electrophoresis on a 3730 DNA Analyzer (Applied Biosystems Inc.).

Data Analyses

Multiple sequence alignments and consensus sequences for each individual were generated using Sequencher v4.9 (Gene Codes Corporation, Ann Arbor, USA). Number of haplotypes, haplotypic diversity, and nucleotide diversity were calculated for each sampling location and each region using MEGA v5.0 (Tamura *et al.* 2011). Phylogenetic relationships among haplotypes were inferred using MEGA, with maximum composite likelihood distances, the neighbor-joining algorithm, and 500 bootstrap replicates to assess confidence.

Table 1. Sample size, number of haplotypes, and haplotypic and nucleotide diversities in each sampling location or region.

Location (Abbreviation)	*n*	Number of Haplotypes	Haplotypic Diversity (*h*)	Nucleotide Diversity (π)
Newfoundland	**92**	**2**	**0.06**	**0.0012**
Goose Pond (GP)	10	1	0	0
Springdale (SD)	10	1	0	0
North Pond (PD)	8	1	0	0
Loon Bay (LB)	10	1	0	0
Burgeo Highway (BH)	8	1	0	0
Mckenzie's Brook (MB)	9	1	0	0
Milltown (MT)	2	1	0	0
Bay d'Espoir (BE)	4	1	0	0
Conne River (CR)	1	1	0	0
Buchans (BU)	7	1	0	0
Mine Pond (MP)	11	2	0.40	0.0085
Main River (MR)	6	1	0	0
Red Indian Lake (RL)	6	1	0	0
Labrador	**53**	**28**	**0.94**	**0.0041**
Forkin Bridge Road (FR)	7	6	0.82	0.0050
Anne Marie Lake (AL)	8	5	0.69	0.0043
Voisey's Bay (VB)	8	5	0.69	0.0035
Park Lake (PL)	5	4	0.72	0.0021
Innu South Side (IS)	9	5	0.74	0.0037
English River (ER)	8	7	0.81	0.0059
Churchill Falls (CF)	8	2	0.20	0.0006
Cape Breton	**10**	**5**	**0.76**	**0.0032**
North East Margaree (NM)	2	2	0.50	0.0042
Egypt Road (EG)	2	2	0.50	0.0028
Lake O'Law #1 (LLI)	2	1	0	0
Lake O'Law #2 (LL2)	1	1	-	-
Hays River (HR)	3	2	0.44	0.0019

Table 2. Distribution of haplotypes and their frequencies in 25 sampling locations among insular Newfoundland, Labrador, and Cape Breton, Novia Scotia. See Table 1 for location abbreviations and Figure 1 for map.

Haplotype (frequency)	Location (frequency)		
	Newfoundland	Labrador	Cape Breton
1 (89)	GP (10), SD (10), NP (8), LB (10), BH (8), MB (9), MT (2), BE (4), CR, BU (7), MP (8), MR (6), RL (6)		
2 (8)	MP (3*)	FR (2), VB, PL, ER	
3 (7)		CF (7)	
4 (4)		AL (4)	
5 (4)		VB (4)	
6 (4)		IS (3), ER	
7 (3)		IS (3)	
8 (3)			NM, EG, HR
9 (3)			EG, HR (2)
10 (2)		FR, ER	
11 (2)		VB, PL	
12 (2)		VB (2)	
13 (2)		PL (2)	
14 (2)		ER (2)	
15 (2)		ER (2)	
16 (2)			LO1 (2)
17		AL	
18		AL	
19		AL	
20		AL	
21		FR	
22		FR	
23		FR	
24		FR	
25		VB	
26		PL	
27		PL	
28		IS	
29		IS	
30		IS	
31		ER	
32		CF	
33			NM
34			LO2

* Two of these individuals were missing data for three of the 41 variable sites.

RESULTS

Mitochondrial control region sequences (712 bp) were obtained for 155 individuals (92 from Newfoundland, 53 from Labrador, and 10 from Cape Breton; see Table 1).

Among the SRBV sequences, 41 variable sites were observed, which defined 34 haplotypes (Table 2). Of these, 18 were found in single individuals and the remainder was shared. The most common haplotype, haplotype 1, was found in 89 individuals, all from Newfoundland, whereas the others were shared by two to 8 animals. Haplotypes differed from one another at between one and 16 sites; on average ~ 0.8% of sites differed between any pair of haplotypes.

The distribution and frequency of haplotypes among sampling locations and regions are documented in Table 2. Underscoring a lack of genetic diversity in Newfoundland, this population contained only two haplotypes among 92 individuals: the common haplotype 1 found in all sampling areas, and haplotype 2, found in Mine Pond and in several Labrador localities. Both haplotypic diversity and nucleotide diversity were correspondingly very low in Newfoundland. Labrador was observed to be much more diverse, with 28 haplotypes among 54 individuals, and hence much higher measures of haplotypic and nucleotide diversity. Only the Churchill Falls population in Labrador was characterized by low diversity measures. Cape Breton was intermediate between Newfoundland and Labrador with respect to both measures of diversity.

Neighbor-joining analysis identified two clusters among the 34 SRBV haplotypes with 98% bootstrap support (Figure 2). One cluster contained all the individuals from Cape Breton and 89 of the Newfoundland animals (haplotype 1, representing all sampling localities). The other cluster contained all individuals from Labrador as well as the three haplotype 2 voles from Mine Pond, Newfoundland.

To further examine the affiliations of Labrador and Cape Breton animals with the "central" and "eastern" clades, we constructed a phylogeny that included the Labrador and Cape Breton haplotypes identified herein, and seven Genbank Accessions attributed to Matson and Baker (2001), which includes individuals from Washington state, Alberta, New Mexico, Maine, and Maryland. This phylogeny revealed three strongly supported clades of SRBV, one consisting of the Washington sequence (presumed "western"), one containing the New Mexico and Alberta sequences (presumed "central"), and one containing the Labrador, Maryland, Maine, and Cape Breton sequences (presumed "eastern"). The net sequences divergences among these clades (6.5% between control region "western" and "eastern" compared with 5.2% for cytochrome b; 4.1% between control region "central" and 'western' compared with 3.3% for cytochrome b) are broadly consistent with those expected for the 'western' clade, "central" and "eastern" clades of Runck and Cook (2005) respectively, suggesting that although Labrador and Cape Breton haplotypes are phylogenetically distinct and mutually exclusive, they are all part of the "eastern" clade.

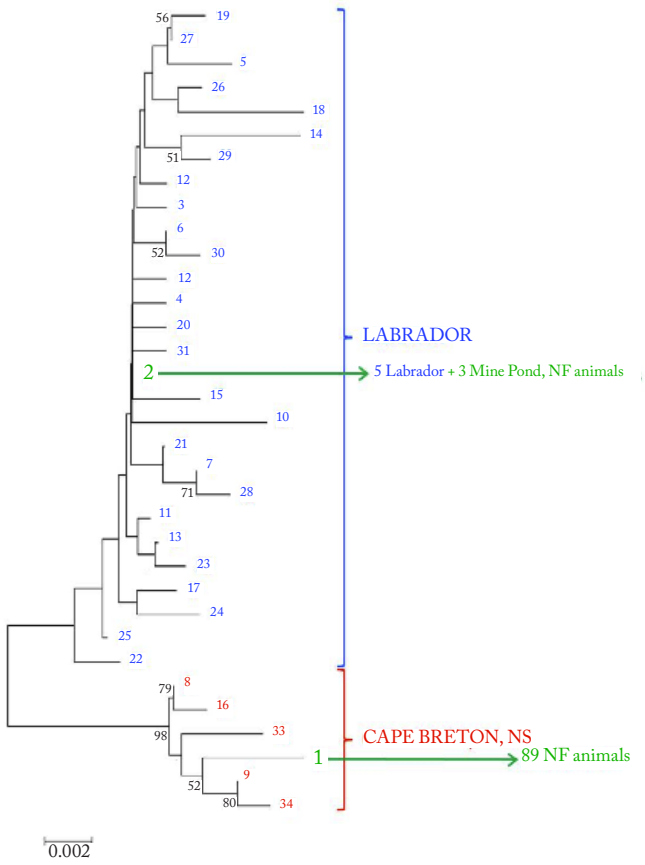

Figure 2. Neighbor-joining phylogeny of 34 mitochondrial control region haplotypes based on composite maximum likelihood distances, with 500 bootstrap replicates. Tips indicate haplotype numbers from Table 2. Blue, red, and green represent Labrador, Cape Breton, and Newfoundland, respectively, except for the case of haplotype 2, which is found in both Labrador and Newfoundland. Numbers above nodes are bootstrap values.

DISCUSSION

SRBV were first discovered on the main island of Newfoundland near Little Grand Lake in 1999 (Hearn *et al.* 2006). Although the possibility that they were present prior to this cannot be definitively eliminated, it is not likely, as trapping had been conducted at that site since 1990, and small mammal surveys were ongoing in other areas of the province before and after the SRBV introduction. The circumstances that led to their introduction are unknown, but this potentially invasive species has spread extensively in Newfoundland (Rodrigues 2012), raising ecological concerns. For example, Meadow Voles have been effectively pushed out of the woodland habitat they used to occupy. The secondary effects of increased predators and effects on alternate prey species may cause changes to species populations that could be significant. Characterizing diversity and identifying sources of this introduced population(s) are important for predicting the potential long-term effects on Newfoundland ecology. In the present study, we analyze mitochondrial control region sequences from Cape

Breton, Labrador, and Newfoundland Southern Red-backed Voles to address these concerns.

Postglacial re-colonization of the northeastern range of Southern Red-backed Voles and subclade differentiation

Of the 34 control region haplotypes, none are shared between Labrador and Cape Breton, and the two suites of haplotypes associated with these two regions are strongly differentiated phylogenetically (98% bootstrap support). Although we expected these two regions to be genetically differentiated, the level of divergence (~1.7% average pairwise sequence divergence between clades or 1.2% net divergence) is low compared with that observed between clades identified with the cytochrome b gene by Runck and Cook (2005). They observed a net divergence of ~3.3% between the "central" and "western" clades, and ~1.2% divergence between subclades within the "central" clade. As the control region is typically more variable than the cytochrome b gene, it follows that, although the Labrador and Cape Breton animals represent genetically differentiated regions, they belong to the same cytochrome b clade, either the "eastern" or the "central," and that the differentiation between them is due to either differences in the timing of postglacial re-colonization or is maintained by ongoing geographic barriers to gene flow, such as the Appalachian mountains.

To further investigate the clade affiliation of these northeastern SRBV populations, we retrieved the GenBank accessions of 7 control region sequences of SRBV from the study of Matson and Baker (2004) and constructed a neighbor-joining phylogeny. This phylogeny recovered the strong signal of the "western" clade (Washington), the "central" clade (New Mexico and Alberta) closely related to the "western" clade, and the "eastern" clade (Maryland and Maine) of Runck and Cook (2005) with comparable net sequence divergences. Our Labrador and Cape Breton sequences clustered strongly with the "eastern" clade, with Maryland, Maine, and Cape Breton haplotypes appearing as a subclade within the "eastern" clade. Although we speculated that SRBV from the "central" clade repopulated Labrador prior to European settlement with the retreat of the Laurentide ice sheet, and "eastern" clade animals dispersed to Cape Breton, both regions appear to have been re-colonized by "eastern" clade animals. Again, the subclade comprising Cape Breton, Maryland, and Maine sequences may represent differentiation due to the barrier to gene flow created by the Appalachians.

We suggest that the northeastern-most part of the SRBV range was not colonized via a continental route following the Wisconsin Glacial Maximum, as were other high latitude areas discussed by Runck and Cook (2005), but rather is associated with an eastern lineage as suggested by Wooding and Ward (1997). Strong differentiation between western and eastern clades described for mammals such as Black Bears (*Ursus americanus*; Wooding and Ward 1997) and American Marten (*Martes americana*; Stone *et al.* 2002) may have arisen from eastern and western forest refugia that formed more than 120,000 years ago and led to long-term partitioning of forest-associated species (Wooding and Ward 1997). These lineages both remained in southern refugia during the Last Glacial Maximum, but eastern lineages appear to have dominated recent postglacial re-colonization of mid-continental areas as rapid continental extension of eastern forests created habitat (Williams *et al.* 1993; Runck and Cook 2005).

Genetic diversity and origins of Newfoundland Southern Red-backed Voles

We found little genetic diversity among SRBV in Newfoundland. Only two haplotypes were found among 92 Newfoundland individuals, compared with 28 haplotypes among 54 Labrador animals, and five among 10 Cape Breton animals. The low haplotypic diversity in Newfoundland is typical for contemporary founder events such as introductions. Furthermore, the two haplotypes found in Newfoundland are from two well-separated phylogenetic clusters, one associated with Labrador and one with Cape Breton. This indicates a minimum of two introduction events, one from each of two main points of ground or sea entry to the island of Newfoundland. The most common haplotype in Newfoundland (shared by 89 out of 92 animals) is not found in the other locations we studied, although it clusters with Cape Breton haplotypes. The second haplotype in Newfoundland (representing three of 92 animals) is also found in Labrador, where it is relatively common and well dispersed. Unfortunately, the complete lack of variability among Newfoundland SRBV associated with either the Cape Breton or the Labrador introduction indicates that we are unable to date these events on the basis of mutational divergence. Nonetheless, the high frequency of the Cape Breton-like haplotype (96.7%) and its widening distribution across the island suggests that these animals were introduced before the animals from Labrador.

The fact that the Cape Breton-like haplotype has spread a straight-line distance of 300 km easterly across the island from its presumed point of entry near Little Grand Lake around 1999, a movement of 23km/yr, calls into question the actual time of introduction. Comparatively, a study of the spread of the introduced Bank Vole (*Myodes glareolus*), the European equivalent of the North American Red-backed Vole, in Ireland determined a rate of spread of only 2 to 4.5km per year (Smal and Fairley 1984). Numerous small mammal surveys were conducted across Newfoundland and in particular in western Newfoundland in the years before discovering the SRBV, and none of these surveys documented the presence of the animals (Knox and Brazil 1992; Thompson and Curran 1995; Forsey 1998; GMNP 2002; Adair 2003; Hearn *et al.* 2006). Furthermore, small mammal survey data collected from 1999–2012 provide evidence for a west-to-east dispersal direction and range expansion rates that would make it entirely possible for the SRBV to have expanded their range by 300 km in 13 years (B.J. Hearn, 2012, Natural Resources Canada, unpublished data; Rodrigues 2012).

The second haplotype found in Newfoundland is also relatively common and well dispersed in Labrador. In 1967, the species was intentionally introduced from Labrador to Camel Island, a small island 2.4 km from the coast of Newfoundland (Figure 1), as part of a

research program to assess potential competition between SRBV and the native Meadow Vole. Consequently, it is possible the Labrador-type haplotype could have arisen from Camel Island Red-backed Voles through their migration and colonization of Newfoundland. However, surveys done in 1986 and 1989 (Northcott 1989) on Camel Island in Notre Dame Bay found no remaining SRBV. Furthermore, the ≥10-year gap between the demise of SRBV on Camel Island and their detection near Little Grand Lake makes it unlikely that Labrador-haplotype animals came from Camel Island.

Interestingly, a mitochondrial DNA study of the Bank Vole in Ireland also revealed only two haplotypes, signifying a minimum of two founding females in that introduction (Ryan *et al.* 1996). Both haplotypes were found at moderate frequencies, unlike here, consistent with the longer time period since that event (~1940), and were distributed heterogeneously among localities. Ryan *et al.* (1996) concluded that local founder events caused by the patchiness of suitable habitat and the territoriality of females led to the heterogeneous distribution of the two haplotypes. If similar local founder events occur in Newfoundland, the dominance of the Cape Breton SRBV haplotype may limit the establishment of the Labrador SRBV haplotype. But currently both haplotypes have been found at the same site (Mine Pond site, Figure 2). The contiguity of forest habitat in Newfoundland (Lee *et al.* 2010) may prevent the haplotype exclusion found in Ireland's much patchier landscape.

Consequences of the Southern Red-backed Vole introduction to Newfoundland

Large or repeated biotic introductions, particularly from multiple source populations, can provide the genotypic variability needed for the successful colonization of introduced species while avoiding the harmful effects of inbreeding (Keller and Waller 2002; Biebach and Keller 2012). Biotic introductions with limited genetic variability may also thrive in their introduced range due to the absence of competitors, predators, parasites, or diseases that would normally limit population growth in native ranges (Sanders and Suarez 2011). The absence of some or all of these factors may explain the results from our study, in which the introduction and subsequent colonization of SRBV in Newfoundland have been successful despite their extremely limited genetic variation.

Though SRBV generally do not experience population cycles in North America (Boonstra and Krebs 2011), small mammal monitoring data from Labrador during 2007-2011 (Rodrigues 2012), a system dominated by SRBV, have shown a dramatic and uniform population decline from the initial monitoring in 2007 to its lowest point in 2009 followed by a gradual population increase. If Newfoundland SRBV populations begin experiencing similar island-wide declines, low genetic variability may exacerbate the depth of the population crash and the time to subsequent recovery. It is recommended that any future evaluations of the genetic composition of the SRBV in Newfoundland should be done in conjunction with population monitoring. Future research should also consider the impact of SRBV on the functional and numerical responses of predator populations, and the direct and indirect effects on alternative prey species and species of concern, e.g., Arctic Hare (*Lepus arcticus*) and Newfoundland Marten.

Concluding Comments and Future Directions

Success of introduced voles in Newfoundland despite lack of genetic diversity, while most likely reflecting niche availability and availability of suitable forest type, raises some ecological concerns. SRBV could introduce new diseases and parasites (Moss 2002), add to seed and seedling predation (Kasimos 2007), compete with and restrict habitat use by native species, and alter predator–prey dynamics on the island (Hearn *et al.* 2006).

Continued monitoring of SRBV populations and their genetic variability in Newfoundland will improve our understanding of the effects of genetic admixture of the Mine Pond-Labrador shared haplotype and the Cape Breton-like haplotype, as well as future infusions of voles to the island. Supplementing mtDNA control region analysis with a panel of nuclear microsatellite loci will better enable these types of investigation.

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