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SHORT NOTE

Red foxes (*Vulpes vulpes*) at their expanding front in the Canadian Arctic have indigenous maternal ancestry

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Abstract The red fox (*Vulpes vulpes*) expanded its distribution over large parts of the Canadian Arctic during the twentieth century and is now considered a threat to the arctic fox (*Vulpes lagopus*). Some authors have proposed that the European red fox, introduced in Eastern North America during the eighteenth century, may have spread and caused the species' expansion in the Arctic. Assessing the biological origin of red foxes in the Nearctic is critical to determine whether their presence constitutes a case of an invading exotic species. We analyzed genetic material obtained from four red foxes at Herschel Island (Yukon) and Bylot Island (Nunavut), at the northern expanding front of the species. Samples from Bylot provide the northernmost genetic information on red fox obtained worldwide. We identified mitochondrial DNA haplotypes in red foxes from both Arctic locations that were phylogenetically divergent from those in Eurasia, but shared with neighboring indigenous North American populations. Thus, our results indicate that the twentieth century expansion of red foxes in the Canadian Arctic involved nearby populations potentially benefiting from habitat changes, rather than an exotic species invading new habitats.

Keywords Genetics · Mitochondrial DNA · Phylogeography · Species expansion · *Vulpes lagopus* · *Vulpes vulpes*

Introduction

From the 1920s to the 1960s, the red fox (*Vulpes vulpes*) expanded its distribution over vast expanses of tundra in the eastern Canadian Arctic (Marsh 1938; Macpherson 1964). It was hypothesized that the species invaded unproductive tundra habitats following an increase in ecosystem productivity caused by climate warming (Hersteinsson and Macdonald 1992) or by food subsidies generated by the sedentarization and expansion of human communities in the Arctic (Gallant 2014). In either case, the range expansion of red foxes in the Canadian Arctic generates concern about the fate of its smaller tundra-dwelling counterpart, the arctic fox (*Vulpes lagopus*). Studies in other regions have found competition between the two species to have a strong negative effect on arctic foxes (Tannerfeldt et al. 2002; Dalén et al. 2004; Angerbjörn et al. 2013).

Kamler and Ballard (2002) hypothesized that most modern North American red foxes derive from European ancestry resulting from colonial introductions to the eastern USA, followed by continent-wide expansions. Although DNA samples from North American red foxes have yet to support this hypothesis (Aubry et al. 2009; Sacks et al. 2010; Statham et al. 2012a, 2014), few samples have been examined from the US Eastern Seaboard, where European red foxes were apparently introduced, or the high Arctic, where red foxes have recently expanded, thus leaving open the origin of red fox in the Nearctic.

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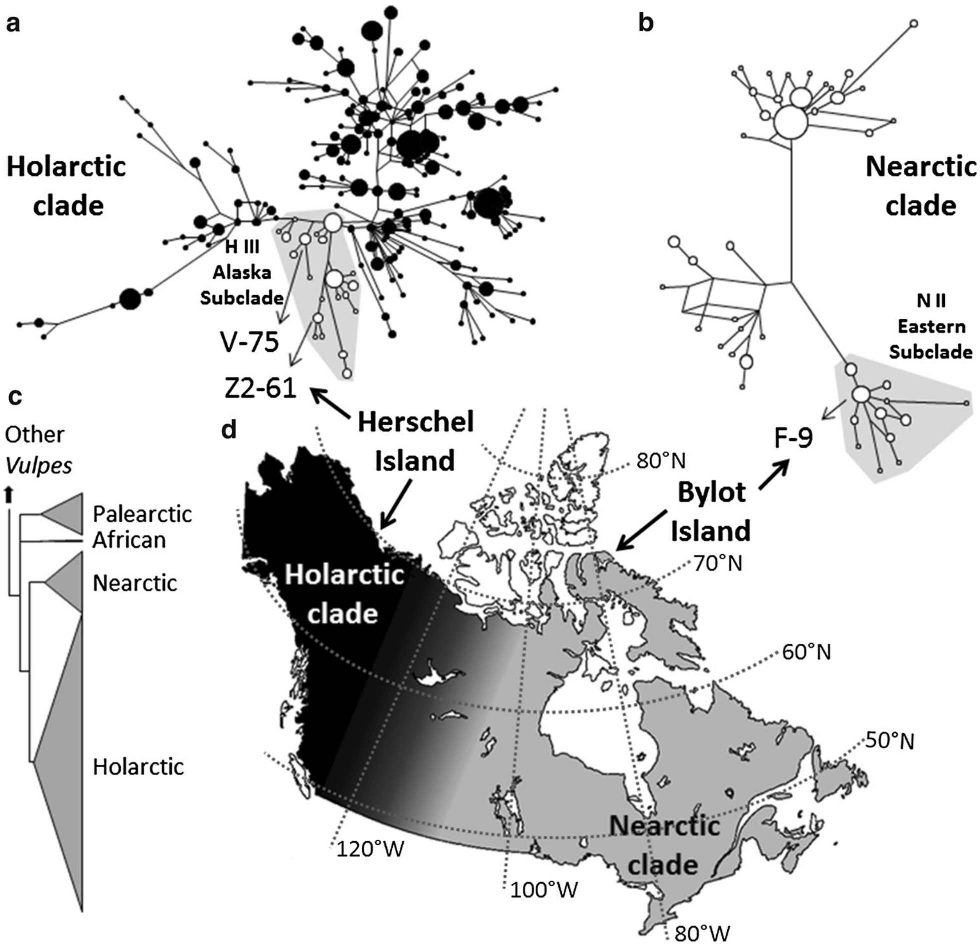

Fig. 1 Mitochondrial clade and subclade assignment of haplotypes identified in red foxes (*Vulpes vulpes*) at their northern range limit in the Canadian Arctic. The haplotype networks were based on concatenated cytochrome *b* and D-loop sequences, and were split into the Holarctic (**a**) and Nearctic (**b**) clades for easier visualization (the relevant subclades are indicated with a gray background). The phylogenetic tree (**c**) displaying the relationship between the major mitochondrial clades/lineages within red fox is adapted from Statham et al. (2014). The red fox distribution map (**d**, *shaded areas*) is modified from Macdonald and Reynolds (2008) to reflect the presence of red foxes on Bylot Island, while the approximate geographic distribution of North American red fox mitochondrial DNA lineages (**d**, *dark* and *gray shadings*) is modified from Statham et al. (2012a)

Resolving the origin of Nearctic red foxes is important. First, differences in tolerance and aggressiveness between red fox forms might exist, with implications on the future outcome of competition between red and arctic foxes in the Nearctic. Second, management decisions regarding expanding populations of red foxes in the Nearctic could drastically differ according to whether they are of North American or European origin. We investigated mitochondrial DNA (mtDNA) from two red fox populations located at the northern edge of the western and eastern Canadian Arctic, in the context of a worldwide phylogeographic analysis to determine whether matrilines were of North American or European origin.

Materials and methods

Sample collection

We collected genetic samples from red fox that were live trapped on Herschel Island (69°34′N, 138°54′W), off the northern coast of the Yukon, and Bylot Island (72°53′N, 79°42′W), at the northern tip of Baffin Island in Nunavut (Fig. 1d). Gallant et al. (2012) and Szor et al. (2008) provide more details on the study areas. We sampled one adult mated pair on Herschel in July 2009 and one adult mated pair on Bylot in July 2011. We captured foxes using padded leghold traps (Softcatch # 1, Oneida Victor Ltd., Euclid, OH, USA), ear tagged each individual, and collected and stored the resulting ear plugs in 70 % ethanol (Cameron et al. 2011; Tarroux et al. 2012). We anaesthetized foxes through injection of medetomidine (0.05 mL/kg) and ketamine (0.03 mL/kg), and used atipemazole (0.05 mL/kg) as reversal. Capture and handling techniques for fox were approved by the Animal Care Committee of Université du Québec à Rimouski (permit # CPA32–08–62 R1-R3), the Joint Park Management Committee of Sirmilik National Park of Canada (permit # SNP-2011-8212), and Qikiqtaruk-Herschel Island Territorial Park (permit # 09-04-Inu).

Molecular analyses

We extracted DNA from the four red fox ear samples using a Qiagen DNeasy Blood and Tissue kit. For comparison to previously published red fox phylogeographic data, we amplified two mtDNA regions; a portion of the cytochrome *b* gene using the primer pair RF14724 and RF15149 (Perrine et al. 2007) and a 343 bp portion (including insertions and deletions) of the D-loop using the primers VVDL1 and VVDL6 (Aubry et al. 2009). We used the polymerase chain reaction (PCR) protocol of Aubry et al. (2009). PCR products were cleaned up, sequenced, and analyzed as described in Statham et al. (2012a).

We compared the resulting arctic red fox sequences to a database of 916 individual red fox sequences from North America and Eurasia (Inoue et al. 2007; Aubry et al. 2009; Sacks et al. 2010; Edwards et al. 2012; Statham et al. 2012a,b; Statham et al. 2014). We conducted statistical analyses on 697 bp long concatenated cytochrome *b*/D-loop sequences. We assigned haplotypes to clades and subclades by creating median-joining networks (Bandelt et al. 1999) in Network 4.6.1.0 (www.fluxus-engineering.com). We generated pairwise Φ_{ST} statistics among sampling sites using the program Arlequin 3.5 to resolve the relationship between red foxes from the two arctic islands and those from around the world (Nei and Li 1979; Excoffier and Lischer 2010).

Results

We identified two haplotypes from Herschel Island, V-75 and Z2-61 (Table 1). Both of these haplotypes belong to the Alaskan subclade (H III), which belongs to the Holarctic clade (Fig. 1a). We identified one haplotype, F-9, in both adults from Bylot Island (Table 1). This haplotype belongs to the Eastern subclade (N II), which belongs to the Nearctic clade (Fig. 1b). The Φ_{ST} analysis indicated no significant differentiation between samples from Herschel Island and Alaska or between Bylot Island and Eastern North America (Table 2).

Table 1 Mitochondrial haplotypes found in red fox (*Vulpes vulpes*) populations in the Canadian Arctic and their presence in other North American and Eurasian regions

Location	*n*	V-75	Cytochrome *b*/D-loop haplotype				
			%	Z2-61	%	F-9	%
Herschel island	2	1	50	1	50	–	–
Bylot island	2	–		–		2	100
Alaska	51	6	11.8	4	7.8	–	–
Western Canada[a]	29	–	–	–	–	1	3.4
Eastern Canada[b]	24	–	–	–	–	7	29.2
Eastern USA[c]	21	–	–	–	–	5	23.8
Western USA[d]	130	–	–	–	–	–	–
Europe	289	–	–	–	–	–	–
Asia	372	–	–	–	–	–	–

The sequence data from the reference populations are from Inoue et al. (2007), Aubry et al. (2009), Sacks et al. (2010), Edwards et al. (2012), Statham et al. (2012a,b), and Statham et al. (2014)

[a] Western Canada consists of Alberta, British Columbia, Northwest Territories, and Yukon

[b] Eastern Canada consists of Manitoba, Newfoundland, Nova Scotia, Ontario, and Quebec

[c] Eastern USA consists of Georgia, Maine, Michigan, New York, North Carolina, and West Virginia

[d] Western USA consists of the indigenous red fox populations in the Cascade Range, Great Basin, Rocky Mountains, Sacramento Valley, and Sierra Nevada

Discussion

All red fox mitochondrial haplotypes we found in the Canadian Arctic were North American in origin (Fig. 1). The two haplotypes we identified on Herschel Island were previously found only in Alaska (Table 1). Both of them belong to the Alaskan subclade, which predominates in Alaska and Western Canada. Individuals we analyzed from Bylot had haplotype F-9, belonging to the Eastern subclade (Aubry et al. 2009). This subclade predominates in populations throughout eastern North America, and haplotype F-9 is relatively common in Newfoundland and Ontario (Aubry et al. 2009; Statham et al. 2012b). The Φ_{ST} analyses generally confirmed these North American affinities, and together the results excluded Europe as a potential source.

Archeological evidence supports the interpretation that these animals are native in origin, as the red fox was present several centuries ago in the Yukon North Slope (Nagy 1988) and 2,000 years ago in northern Quebec (Monchot and Gendron 2011). These times predate European-Inuit contact in both regions and reinforce our conclusion that red foxes expanded into the Arctic from neighboring native populations.

These results contradict the hypothesis that red foxes of exotic origin were involved in the twentieth century expansion of red fox into the Arctic (Kamler and Ballard 2002). Kamler and Ballard's hypothesis was based on a review of the literature and relied heavily on interpretations about changes in frequencies of color phenotypes. We doubt that fur color can be used reliably to indicate population of origin because there was considerable spatial and temporal variability in fur color within North American red foxes. For example, Butler (1951) reported that historically, fur graders in Quebec recognized several variants of red fox pelts according to the region where they were caught, whereas Merriam (1900) described many regional red fox variants in North America.

Our sample sizes in this study were small in absolute terms, but we sampled the only known breeding red foxes on both Bylot Island and Herschel Island. On Bylot Island, up to 110, mostly Arctic fox dens have been monitored yearly since 1993 (Cameron et al. 2011; Gauthier et al. 2013), and never more than one reproductive red fox den

Table 2 Genetic relationship (Φ_{ST}) between red foxes (*Vulpes vulpes*) from the Canadian Arctic and those from other regions of Eurasia and North America

	Europe	Asia	Alaska	Western Canada	Western USA	Eastern Canada	Eastern USA
Herschel	0.23*	<0.01	<0.01	0.04	0.71**	0.66**	0.70**
Bylot	0.66**	0.40**	0.68**	0.51**	0.59**	<0.01	<0.01

* $P = 0.054$

** $P \leq 0.05$

has been found in a given year. The same applies to Herschel Island, where 34 and 62 dens were visited in 1984–1990 (Smits and Slough 1993) and 2008–2010 (Gallant et al. 2012, 2014), respectively.

It is noteworthy that mtDNA is a single clonally inherited marker passed down through the female line. Therefore, an analysis of high-resolution nuclear DNA markers will be necessary to determine whether the pattern observed in the mtDNA was representative of the entire genome. Nevertheless, our study contributes important information on the origin of red foxes in the North American Arctic.

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