NOTE

Evolution of the Dawson caribou (*Rangifer tarandus dawsoni*)

S.A. Byun, B.F. Koop, and T.E. Reimchen

Abstract: The Dawson caribou (*Rangifer tarandus dawsoni*) was a rare subspecies of caribou that inhabited Haida Gwaii, an archipelago located 80 km off the west coast of Canada. It became extinct during the early part of the 20th century and to this day all that remains of Dawson caribou are several pelts, skulls, and antlers. With the exception of a physical description based on these remains, not much is known about the taxonomy of this subspecies of caribou. Using molecular and ancient-DNA techniques, we sequenced 215 base pairs of the mitochondrial gene cytochrome *b* and compared these sequences with those from conspecifics *Rangifer tarandus caribou* (woodland caribou) and *Rangifer tarandus granti* (barren-ground caribou). These analyses suggest that the Dawson caribou was not genetically distinct. The unique morphology characterizing this extinct form of caribou may have been of recent origin, either from local selection pressures or from environmentally induced phenotypic plasticity.

Résumé : Le caribou de Dawson (*Rangifer tarandus dawsoni*) est une sous-espèce rare du caribou qui vivait dans l'archipel de Haida Gwayii, situé à 80 km au large de la côte ouest du Canada, et qui est disparu au début du 20^e siècle et, à ce jour, tout ce qui reste du caribou de Dawson se résume à plusieurs peaux, crânes et merrains. À l'exception d'une description physique basée sur ces restes, la taxonomie de la sous-espèce est mal connue. Au moyen de techniques moléculaires et de méthodes d'analyse de l'ADN ancien, nous avons procédé au séquençage de 215 paires de bases du gène du cytochorome *b* et comparé les séquences obtenues à celles des autres sous-espèces, *Rangifer tarandus caribou* (le caribou de bois) et *Rangifer tarandus granti* (le caribou de Grant). Les analyses indiquent que le caribou de Dawson n'était pas génétiquement distinct. La morphologie particulière qui caractérise cette forme disparue du caribou peut être d'origine récente, à la suite de pressions de sélection locales ou à cause de la plasticité phénotypique suscitée par l'environnement.

[Traduit par la Rédaction]

Introduction

As the most isolated group of islands in the Pacific Northwest, Haida Gwaii (Queen Charlotte Islands) (Fig. 1) has been the subject of intense study from the perspective of both its complex glacial history and its endemic flora and fauna. One of the most interesting endemics known to Haida Gwaii is the now extinct Dawson caribou (*Rangifer tarandus dawsonii*). The last Dawson caribou seen on the islands (two bulls and a cow) were killed in 1908 (Fig. 2) and the skins and skulls of these 3 individuals were sent to the Royal British Columbia Museum in Victoria. The Dawson caribou is believed to have gone extinct shortly thereafter, sometime during the 1920s or 1930s (Cowan and Guiget 1956; Banfield 1961).

The Dawson caribou was the rarest of all caribou and had the most restricted distribution, and not much is known about this subspecies. Morphological characteristics are largely based on the type skull (Seton-Thompson 1900) and the 3 individuals killed in 1908. Dawson caribou were originally described as small in stature, and are believed to have had a pale-coloured pelage with no distinguishing marks. Their antlers were poorly developed and remarkably irregular, while females appear to have been antlerless (Seton-Thompson 1900; Cowan and Guiget 1956; Foster 1965). They were probably never abundant and the indigenous people of Haida Gwaii, who generally restricted their activities to the coast, knew little about this caribou, which inhabited the dense forest and probably the raised bogs of northern Graham Island (Banfield 1961).

The origin of Dawson caribou is unknown. Haida Gwaii was glaciated (Sutherland Brown and Nasmith 1962), and both Banfield (1961) and Foster (1965) surmised that woodland caribou (*Rangifer tarandus caribou*) arrived on Haida Gwaii during early postglacial times, when lowered sea levels allowed access from the adjacent mainland. However, recent evidence that a coastal refugium capable of sustaining

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S.A. Byun. Department of Biology, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada.
B.F. Koop and T.E. Reimchen.[1] Department of Biology, University of Victoria, Box 3020, Victoria, BC V8W 3N5, Canada.

[1] Corresponding author (e-mail: reimchen@uvic.ca).

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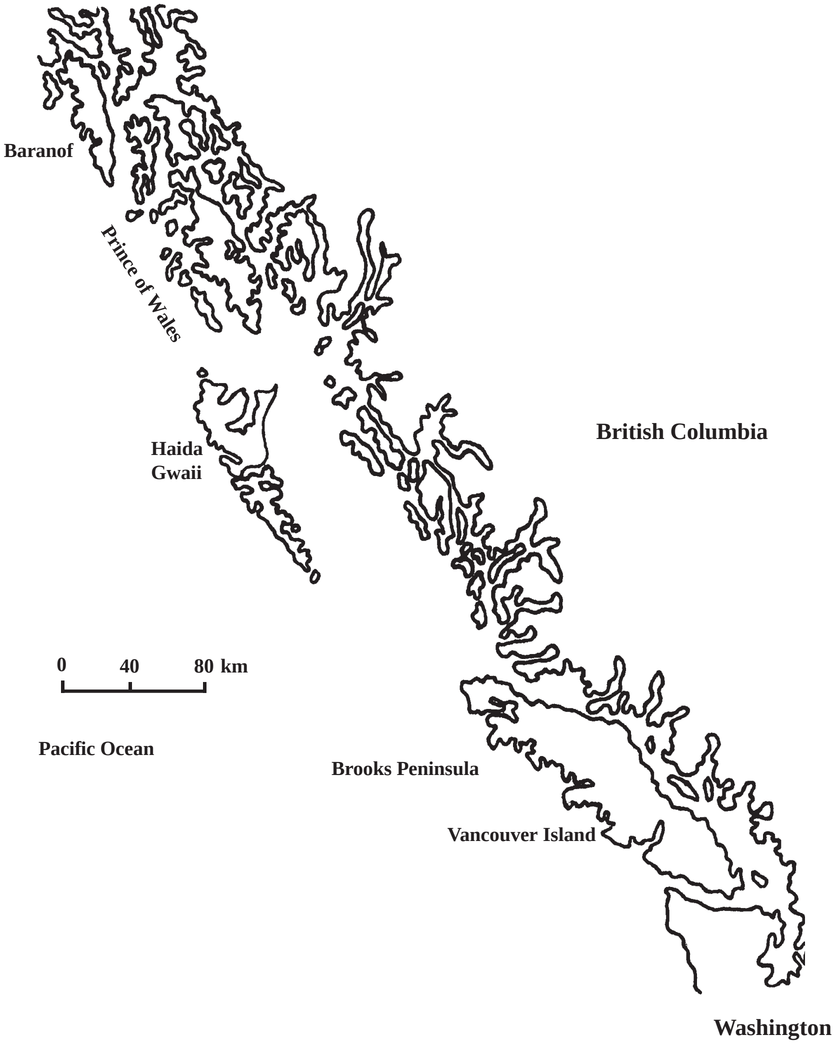
Fig. 1. Haida Gwaii is an archipelago of over 150 islands located about 80 km off the west coast of mainland British Columbia.



large mammals might have existed in the vicinity of this archipelago (Warner et al. 1982; Josenhans et al. 1993; Byun et al. 1997, 1999) raises the possibility that Dawson caribou may have originated from coastal refugial populations and were isolated from the mainland for over 30 000 years. Radiocarbon dating of a recently discovered heavily mineralized caribou antler washed from river gravels on the northeastern corner of Haida Gwaii yielded a date of 40 000 years before present, evidence for preglacial occupation of the islands by caribou (R. Mathewes, personal communication). In this paper we use molecular data to evaluate the relictual status of Dawson caribou.

Methods

Samples

DNA from four *R. t. caribou* (northern British Columbia) and two *Rangifer tarandus granti* (barren-ground caribou, Ray Mountain herd) was obtained from muscle, blood, and antler velvet. DNA from *R. t. dawsoni* was obtained from preserved skin samples from the Royal British Columbia Museum (RCBM 1487, RCBM 1486) as well scrapings of desiccated flesh taken from the type skull (RCBM 1483). Attempts to extract and amplify DNA from the remaining preserved skin sample was repeatedly attempted without success. All tissues were taken using new and sterile scalpel blades and individually stored in sterile microcentrifuge tubes at room temperature. Fresh gloves were used between samples. See Table 1 for sample details.

DNA isolation and amplification

DNA was extracted from blood using a DTAB/CTAB method from Gustincich et al. (1992) modified by Byun (1999). DNA from preserved skin / desiccated flesh was extracted using a modification (Byun 1999) of Doyle and Doyle's (1987) CTAB protocol. A fragment of the mitochondrial (mt) gene cytochrome *b* was amplified using primers H15183 (YCC TCA RAA TGA TAT TTG TCC TCA), L14850 (CCA TCA AAY ATC TCR TCA TGA AA), L15058 (GCT TAT TTA TAC ATG TAG GAC GAG GCC, H15058 CCG GAG CAG GAT GTA CAT ATT TAT TCG), H15144 (GAC ATA TCC TAC AAA TGC TGT AGC TAT TA), and L14968 (TCT CCT CTG TTA CTC ACA TCT GCT GAG ACG TC) designed from aligned cervid sequences from GenBank. For

Fig. 2. The last Dawson caribou (*Rangifer tarandus dawsoni*) seen on Haida Gwaii. They were killed by local hunters around November 1908.

Table 1. Subspecies, geographical locations, and sample sizes for caribou (*Rangifer tarandus*) used in mtDNA extraction.

Subspecies	Location	Sample No.	Sample size	Sample type
caribou	Northern B.C.[a]	na	4	Muscle/antler
granti	Alaska[b]	104342	1	Blood
granti	Alaska	104334	1	Blood
dawsoni	Graham Island (GI)[c]	1486	1	Preserved skin
dawsoni	GI	1487	1	Preserved skin
dawsoni	Virago Sound (GI)	1483	1	Dried muscle
dawsoni?	Blue Jackets Creek (GI)[d]	Flua-004	1	Long bone
dawsoni?	Blue Jackets Creek (GI)	Flua-004	1	Long bone
dawsoni?	Honna River (GI)[e]	F1ua15	1	Long bone

[a] Three samples were from Tucho Lake, Prophet River, and Johiah Lake; the exact locale for the fourth individual was not given.

[b] Both samples were from the Ray Mountain herd in central Alaska.

[c] The sample was obtained from the Royal British Columbia Museum.

[d] The Blue Jackets Creek midden is on the eastern shore of Masset Sound, approximately 2.4 km south of Masset. Unfortunately, these putative Dawson caribou samples did not yield usable DNA. Samples were provided by P. Severs.

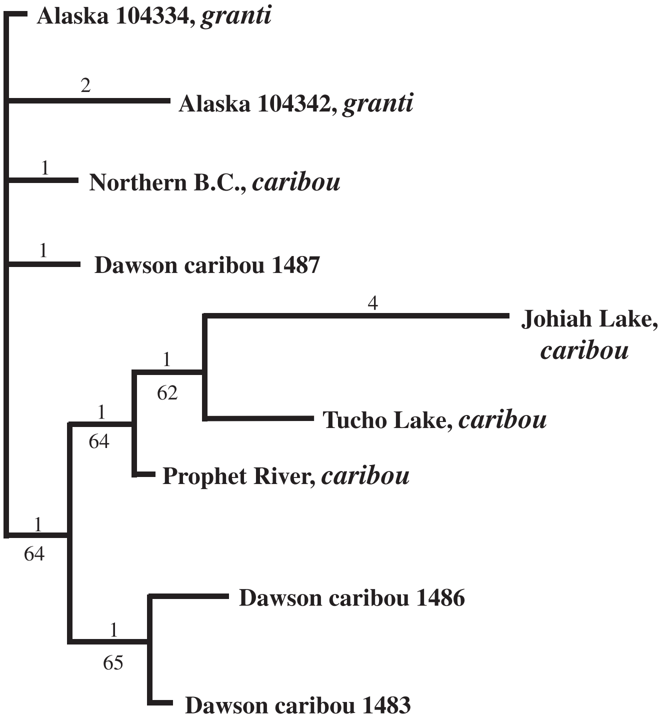
[e] The Honna River Bridge site is about 6.4 km south of Queen Charlotte City on the eastern bank of the Honna River. This sample did not yield usable DNA. The sample was provided by P. Severs.

ancient DNA a range of polymerase chain reaction (PCR) products 86–215 base pairs (bp) were amplified and pieced together to give the longest possible cytochrome *b* sequence. PCR conditions were as follows: initial denaturation at 94°C for 3 min, denaturation at 94°C for 1 min, annealing at 50–55°C for 2 min, extension at 72°C for 2 min, and final extension at 72°C for 7 min. In total, 30–40 cycles were used. PCR fragments of 313–183 bp were obtained from 3 Dawson caribou and 6 caribou from the mainland.

Cloning and sequencing

These PCR fragments were cloned using the TA Cloning Kit (Invitrogen, Carlsbad, Calif.) and subsequently sequenced using the 21mer M13 primer kit (PRISM) on an ABI 373A

Fig. 3. Maximum-parsimony tree. Trees were generated using a branch and bound search of equally weighted characters. The initial tree was obtained by random stepwise addition and branch swapping implemented by tree bisection–reconnection and steepest descent. Data were resampled using 2000 branch and bound bootstraps. Trees generated by both neighbour joining and maximum likelihood had identical topologies to the maximum-parsimony tree.



according to conditions suggested by Applied Biosystems Inc., Foster City, Calif.

Phylogenetic analyses

Sequence consensus from ABI and sequence alignments was generated using Lasergene Navigator (DNASTAR, Madison, Wis.). A minimum of three sequences was used to generate the consensus. These consensus sequences were subsequently analyzed by maximum parsimony (Eck and Dayoff 1966; Fitch 1977), maximum likelihood (Cavalli-Sforza and Edwards 1967), and neighbour joining (Saitou and Nei 1987) using PAUP 4.1 (Swofford 2000).

Results

From the 9 individuals examined, nine haplotypes were identified (GenBank Accession Nos. AF494195–AF494200). Despite the high number of haplotypes, the distance (Kimura's two-parameter model) between haplotypes was relatively low (data not shown). Average intraspecific divergences within *caribou* (0.018) and within *dawsoni* (0.014) were comparable to average intersubspecfic divergences between *granti* and *caribou* (0.016), between *granti* and *dawsoni* (0.019), and between *caribou* and *dawsoni* (0.020). Trees resulting from maximum parsimony, maximum likelihood, and neighbour joining had identical topologies (Fig. 3). In all cases, Dawson caribou was not identified as a distinct lineage.

Discussion

Foster (1965) referred to the Dawson caribou as the most intriguing of all native mammals on Haida Gwaii because of its distinctive morphology and recent extinction. That author surmised that the Dawson caribou was a postglacial migrant derived from the same refugial source populations as *R. t. caribou*. Based on our results involving partial sequences from the mt gene cytochrome *b*, the Dawson caribou is not distinct from either *R. t. caribou* or *R. t. granti,* supporting Foster's (1965) hypothesis that the Dawson caribou is not a glacial relict.

Although we were able to sequence only a short section of the ancient DNA in the museum skins, which limits the robustness of the results, our confidence is increased by the lack of genetic differentiation between caribou subspecies found in other studies. Cronin (1992) also failed to resolve *caribou* and *granti* as distinct mtDNA groups using restriction fragment length polymorphism (RFLP) analysis. While Strobeck (1994) did detect some genetic differentiation between woodland and barren-ground caribou using RFLP analysis and D-loop comparisons, the apparent lack of phylogenetic structure in caribou and the high number of haplotypes found in this study is consistent with what has been found by other workers (J. Purdue, Illinois State Museum, personal communication). This lack of genetic differentiation may be due to high gene flow, retention of ancestral polymorphisms, or a combination thereof. Resolving phylogenetic relationships within caribou will likely require broad analysis of longer sequences with many loci. Given the technical limitations of ancient DNA (for a review see Pääbo et al. 1989) and the specific aim of this study, which was to provide insight for resolving the question of whether the Dawson caribou is genetically unique, further analyses using longer sequences were not considered. Although other markers like the D-loop may provide greater resolution, cytochrome *b* has been an excellent target for assessing relictual status for some of Haida Gwaii's other endemic mammals (Byun et al. 1997).

Comments on morphology

The many divergent characteristics of the Dawson caribou, such as small stature, reduced antler size, and unusual pale pelage colour, are in fact typical of insular ungulates (Foster 1965; Case 1978). This is illustrated by the recent decrease in body size and allometric reduction in antler size of black-tailed deer (*Odocoileus hemionis*) that were introduced to Haida Gwaii in the late 1800s. These rapid changes in body and antler size in black-tailed deer, which are probably nonheritable, have been attributed to a variety of factors including a lack of predators and poor nutrition (Foster 1965).

Caribou bones dated from 4000 to 6000 years of age have been found on Haida Gwaii (Severs 1974; Ham 1990) and these are much larger than their equivalent in recent Dawson caribou. These fossil bones are similar to those of the large barren-ground caribou (Severs 1974; R. Wigen, personal communication) and may be representative of caribou on Haida Gwaii prior to the dwarfing process. Another characteristic of Dawson caribou is the pale-coloured pelage observed in museum skins and this is unusual, as coastal mammals and forest birds from Haida Gwaii tend to be darkly pigmented (Foster 1965). However, the only photographs of Dawson caribou taken at the time of their capture in 1908 (Fig. 2) do not show a pale pelage, which suggests that this characteristic is an artifact of museum preservation (Banfield 1961).

In summary, the Dawson caribou is one of the multiple endemic taxa on Haida Gwaii, which include threespine stickleback, black bear (*Ursus americanus*), marten (*Martes americana*), weasel (*Mustela erminea*), deer mouse (*Peromyscus* spp.), and ground beetles that show morphological distinction from their mainland counterparts (Foster 1965; Moodie and Reimchen 1976; Kavanaugh 1992; Reimchen et al. 1985). The molecular evidence available for these groups (Gach and Reimchen 1987; O'Reilly et al. 1993; Deagle et al. 1996; Byun 1999; Byun et al. 1999; Clarke et al. 2001), including that for the Dawson caribou (this study), suggests that the divergent morphologies are postglacial in origin.

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