

THE PEEL RIVER WATERSHED: ECOLOGICAL CROSSROADS AND BERINGIAN HOTSPOT OF ARCTIC AND BOREAL BIODIVERSITY

Jedediah F. Brodie¹, Joel Berger²

¹David H. Smith Conservation Research Fellow
Faculty Affiliate, Wildlife Biology Program
University of Montana
Missoula, MT 59801, USA
jedediah.brodie@gmail.com

²John J. Craighead Chair and Professor of Wildlife Biology
Division of Biological Sciences
University of Montana
Missoula, MT 59801, USA
joel.berger@mso.umt.edu



This report was produced
by the Yukon Chapter of
the Canadian Parks &
Wilderness Society with
the support and
participation of the
Yellowstone to Yukon
Conservation Initiative.



YELLOWSTONE TO YUKON
CONSERVATION INITIATIVE



Preface



Grizzly bears feeding. Photo: Peter Mather

TABLE OF CONTENTS

Summary	1
Part I: Nexus of floral and faunal interchange	4
Beringia	4
The ice-free corridor	8
Current biota of the Peel River watershed	11
Part II: Biogeographically unique organisms of the Peel	13
Habitat features	14
Fish	14
Terrestrial vertebrates	16
Invertebrates	17
Plants	18
Fungi	19
Part III: Conclusions	21
Acknowledgements	22
Table	23
Literature Cited	27

SUMMARY

The Peel River watershed of the Yukon Territory is a hotspot of arctic and boreal biodiversity in Canada. Essentially the only large tracts of the ancient realm of Beringia to be found in Canada are in the upper Peel River drainage and surrounding areas such as the Porcupine Basin. During the

... the only large tracts of the ancient realm of Beringia to be found in Canada are in the upper Peel River drainage and surrounding areas such as the Porcupine Basin.

Pleistocene glaciations, the steppes of Beringia stretched contiguously from eastern Russia to interior Alaska and the Peel River. This productive landscape offered a refuge for many organisms that subsequently colonized the circumarctic after the ice receded. The exposed Bering land bridge that connected Asia to North America for millions of years provided a route for important exchanges of organisms among the continents. Many of the species entering North America spread through eastern Beringia and then south along a discontinuous “ice-free corridor” running along the eastern edge of the Rocky Mountains. The Peel River ecosystem stands at the junction of Beringia and the

The Peel River ecosystem stands at the junction of Beringia and the ice-free corridor, and was thus a fundamentally critical crossroads in the distribution and exchange of organisms ...

ice-free corridor, and was thus a fundamentally critical crossroads in the distribution and exchange of organisms during the Pleistocene and Holocene.



Ice dams formed during the Pleistocene blocked the flow of the Peel River on several occasions, causing it to switch its flow to drain west into the Yukon River. This facilitated the exchange of aquatic organisms between the Yukon and Mackenzie drainages, and the Peel River thus contains representatives of both of these major river systems. Photo: Theresa Gulliver

The Peel River watershed’s role as biogeographical nexus has left lasting influence on the biota found there today. Many of the organisms in the ecosystem are Beringian relicts, with higher genetic or morphological diversity there than anywhere else in their ranges. For example, mustelid carnivores, voles and lemmings, shrews, collared lemmings, and hares all have high genetic diversity in the eastern Beringian realm. Arctic ground squirrels, purple saxifrage, and fly agaric mushrooms may have originated here and then spread to occupy much of the rest of the arctic. Pockets of spruce, birch, cottonwood, and larch trees survived the glaciations in eastern Beringia and subsequently expanded to form the boreal forests of today. The Ogilvie Mountains to the west of the Peel contain dozens of moss species found nowhere else in the Yukon Territory. Ice dams formed during the Pleistocene blocked the flow of the Peel River on two occasions, causing it to switch its flow to drain west into the Yukon River. This “headwater-switching” facilitated the exchange of aquatic organisms between the Yukon and Mackenzie drainages, and the Peel River thus contains representatives of both of these major river systems.



[Slimy sculpin.]

For example, the Peel River contains remnant Beringian populations of lake whitefish, northern pike, arctic grayling, slimy sculpin, and lake trout that are genetically distinct from others of their species in the rest of Canada.

As a large, substantially intact ecosystem in western Canada, the Peel River drainage is an important storehouse of Arctic and boreal diversity; because of this, its ecological integrity should be safeguarded into the future. There are many other reports summarizing various aspects of the biology and management of the Peel River watershed. Information on fish and fisheries can be found in VanGerwen-Toyne (2003) and Anderton (2006). Kenyon and Whitley (2008) provide an assessment of water resources. Grizzly bear habitat evaluations in the Peel watershed are available in several reports by the Canadian Parks and Wilderness Society (Machutcheon 1997a, b). Green et al. (2008) discuss the international significance of the Peel ecosystem from the viewpoint of wilderness values and recreation aesthetics. The Resource Assessment Report by the Peel Watershed Planning Commission (PWPC 2008) provides an overall summary of various biological and policy aspects of the Peel River management. Our goal for this report is to fill an information gap by providing a review of what makes the Peel River ecosystem ecologically and biogeographically unique.



[*Poa porsildii* is another beringian remnant. Photo: Bruce Bennett]

PART I: NEXUS OF FLORAL + FAUNAL INTERCHANGE

Beringia

At the end of the Pleistocene, about 27-14 thousand years ago (Dyke et al. 2002), global sea levels were lower, connecting Asia and North America via an exposed land bridge. The contiguous region known as “Beringia” included what is now eastern Russia, Alaska (USA), and northwestern Canada. Beringia was mostly ice-free (Brigham-Grette 2001) and served as a refugium for many arctic and boreal organisms. There were other glacial refugia around the northern hemisphere during the Pleistocene, but Beringia was the largest and likely the most important (Hultén 1937, Sanmartin et al. 2001). Many arctic and boreal organisms persisted and even diversified here and then spread throughout the rest of the circumpolar region following glacial retreat (Hultén 1937).

The landscape of Beringia was composed of graminoid and forb steppe (Elias 2001, Swanson 2006) with the grasses dominated by species of *Elymus*, *Festuca*, and *Poa* (Swanson 2006). There were also pockets of conifer forest (Brubaker et al. 2005, Anderson et al. 2006), possibly in moist valley bottom habitats (Zazula et al. 2006b), as well as deciduous trees and shrubs such as *Populus*, *Betula*, and *Alnus* (Brubaker et al. 2005). The transition zones between tundra and forest habitats were in approximately the same locations



[Short-faced bear.]

they are found in today (Bigelow et al. 2003). While all of Beringia was likely a mosaic of arid steppe-tundra, mesic meadows, and forest patches, eastern Beringia was generally more mesic than the western part of the region (Elias et al. 2000). Climate in Beringia during the previous interglacial period (~60-26 thousand years ago) is thought to have been warmer than today, with mean July temperatures in the western Yukon Territory about 5°C higher than at present (Elias 2001). But during the last glacial maximum in the late Pleistocene, the region was probably cold and dry with harsh winters (Elias 2001).

Beringia supported a diverse assemblage of large ungulates; grazers of graminoids and forbs included horses, yaks, mammoth, saiga antelope, and bison, while caribou and woodland muskox consumed more lichen, bryophytes, and fungi (Fox-Dobbs et al. 2008). These animals were hunted by wolves throughout most of the Pleistocene as well as large cats and bears for more intermittent timeframes (Fox-Dobbs et al. 2008). The giant short-faced bear of eastern Beringia appears to have been a specialist on caribou (Fox-Dobbs et al. 2008). The Beringian steppe-tundra may have been similar to the ecosystems of Alaska's north slope today with higher plant diversity, higher availability of nutrients (particularly calcium), and fewer anti-herbivore plant defensive compounds than the Alaskan and Yukon interiors today (Walker et al. 2001).



[*Saxifraga oppositifolia* – a beringian remnant. Photo: Bruce Bennett]

The arid steppe-tundra of western and eastern Beringia was split by the more mesic, shrub-tundra dominated region of the Bering land bridge (now mostly submerged). This wetter zone acted as a dispersal barrier for some species of ungulates, carnivores, and beetles. For example, woolly rhinoceros were only found west of this divide and North American camels, kiangs (a type of horse), bonnet-horned musk ox, and short-faced bears were only found to the east (Guthrie 2001, Elias and Crocker 2008).

Yet the exposed land bridge of Beringia also facilitated the spread of many organisms between Asia and North America. This dry land connection may have lasted for up to 2.25 million of the last 2.5 million years (Elias et al. 2000). Moose (*Alces*), elk (*Cervus*), arvicoline rodents (*Lemmus*, *Dicrostonyx*, *Microtus*), pikas (*Ochotona*), hares (*Lepus*), grayling (*Thymallus*), and bears (*Ursus*) spread eastward (Waltari et al. 2007). Lineages of marmots (*Marmota*), shrews (*Sorex*), and grouse/ptarmigans (*Tetraoninae*) spread westward; different clades of ground squirrels (*Spermophilus*) spread in both directions (Waltari et al. 2007). Other groups may have had their initial development in Beringia and then spread outward in both directions, such as species complexes of *Saxifraga*, *Vaccinium*, and *Amanita muscaria* (Waltari et al. 2007).



Pika. Photo: Jannik Schou

Eastern Beringia, on the North American side of the Bering land bridge, comprises interior Alaska and parts of the Yukon Territory. Most of the Yukon Territory was glaciated during the Wisconsinan advance. Essentially the only large portion of the unique ice-free refugium of Beringia to be found in Canada today is the upper Peel River drainage and adjacent areas such as the Porcupine Basin. Much of the Peel River was glaciated during the Wisconsinan and previous advances but the upper region, west of the Bonnet Plume basin, remained ice-free (Hughes et al. 1981, Zazula et al. 2004). The Peel River, currently a tributary to the Mackenzie, was blocked by ice several times during the Pleistocene, forming large lakes (Bodaly and Lindsey 1977). On at least two occasions these lakes overflowed around the north of the Ogilvie Mountains, forming a contiguous watershed with the westward-flowing Yukon River (Bodaly and Lindsey 1977). These events allowed for exchange of freshwater organisms between the otherwise historically-separated drainages of the Yukon and the Mackenzie. The aquatic biota of the Peel River is therefore quite unique, being an amalgamation of species from both of the two surrounding larger rivers, as well as species that spread north from the Missouri drainage following deglaciation (Bodaly and Lindsey 1977).



Aspen forest. Photo: Peter Sandiford

Massive biotic changes occurred in Beringia following glacial retreat and climate change at the beginning of the Holocene. Most of the region's megafauna were extinct by 11-10 thousand years before present (BP), either through the actions of changing climate (Shapiro et al. 2004), overhunting by humans (Alroy 2001, Burney and Flannery 2005), or both (Nogues-Bravo et al. 2008). The removal of the large ungulates may have triggered or facilitated a strong shift in the vegetation from graminoid and forb dominated steppe tundra (the "mammoth steppe") to mossy tundra (Zimov et al. 1995). Mosses retain more soil moisture than graminoids, so the Beringian tundra today is wetter than at the end of the Pleistocene (Zimov et al. 1995). With a shift toward warmer and wetter conditions, shrub and tree species spread. By 10,000 years BP shrub-birch tundra dominated most of eastern Beringia (Szeicz and MacDonald 2001). Conifer trees spread as well; by 8,000 years BP spruce had expanded upslope in the Mackenzie Mountains east of the Peel River watershed (Elias 2001, Szeicz and MacDonald 2001). The early Holocene may have been warmer than today, with thicker spruce forests and higher treeline (Szeicz and MacDonald 2001).



Mountains of Yukon's Peel Watershed ecosystem stood at the junction of Beringia and the ice-free corridor, and were thus fundamentally critical crossroads in the distribution and exchange of organisms during the Pleistocene and Holocene. Photo: Peter Mather

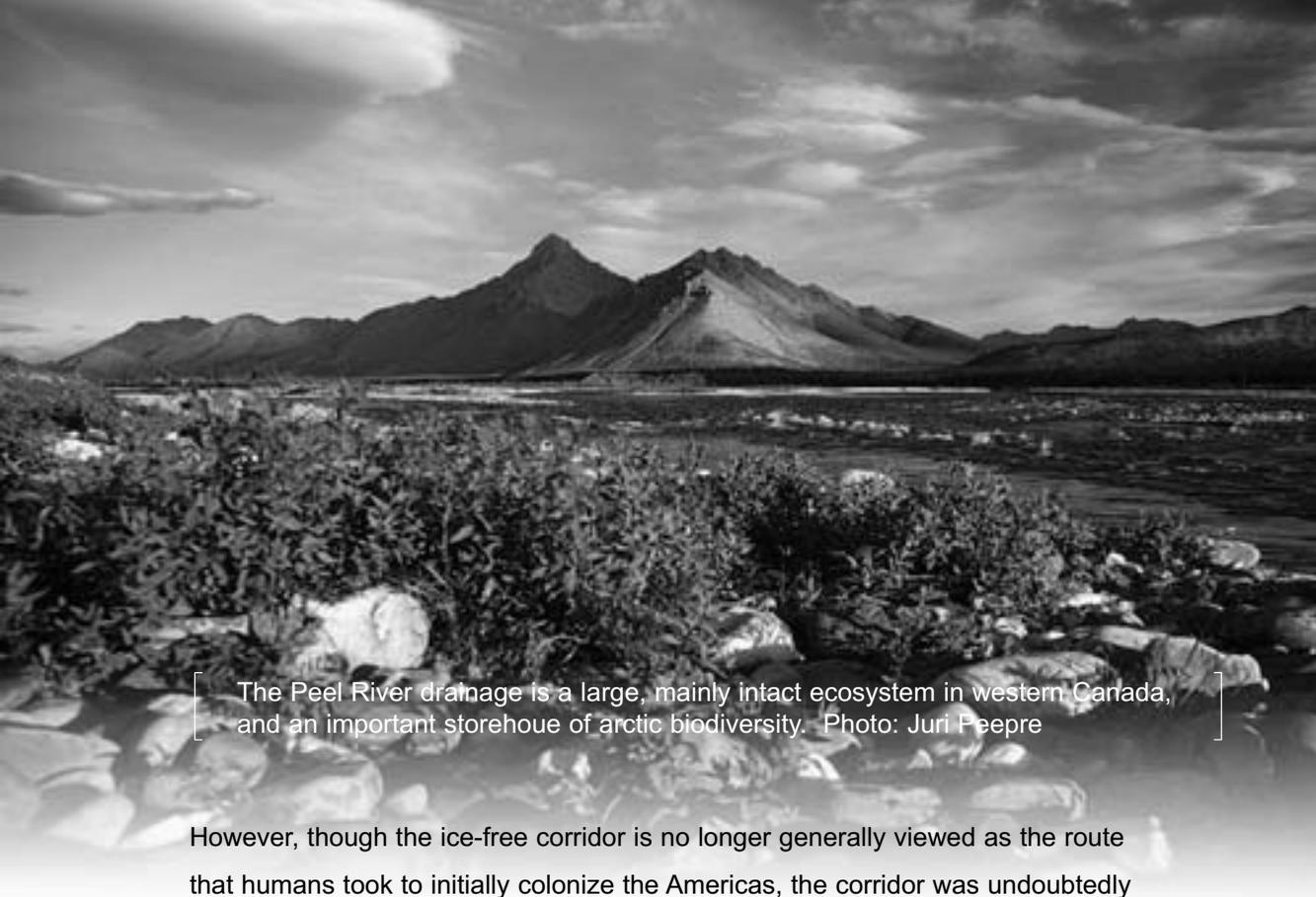
The ice-free corridor

Beringia was an important biogeographic crossroads where organisms spread from the old world to the new, and vice versa. Much of this floral and faunal interchange took place via a long corridor of mostly ice-free habitat that connected the Beringian steppes to the ice-free regions of the continental United States (MacDonald and McLeod 1996). During the last major glaciation, the Wisconsinan advance, much of interior Canada was covered by the vast Laurentide ice sheet while the Canadian west coast was covered by the Cordilleran ice sheet. In between, the ice-free corridor stretched along the eastern edge of the Rocky Mountains.

While today the grazing animals of the northern tundra and the great plains of the continental United States are separated by boreal forest, in the Pleistocene and early Holocene they would have been linked by a corridor of grassy habitat (MacDonald and McLeod 1996). The ice-free corridor may not have actually been a single contiguous path at any one point; much of Alberta was covered by ice during late Wisconsinan glaciation, 28-15 thousand years ago (Burns 1996, Levson and Rutter 1996). Megafauna and conifer fossils show that Alberta was used extensively both before and after the maximum Wisconsinan advance (Burns 1996).

Organisms spreading north along the corridor towards Beringia and Asia, or south towards interior North America would have had faced the Richardson Mountains in the Bodaly and Lindsey 1977, Catto 1996). Thus the Peel River was a critical part of the ice-free corridor, maintaining a route that allowed species to disperse, spread, and intermix. The evidence of this role remains on the landscape today – the Peel River contains a biogeographically unique mixture of organisms by virtue of being located at the junction of Beringia to the west and the ice-free corridor to the south. While most of the Peel River drainage remained ice-free throughout the Pleistocene, a glacial advance did occur in the Bonnet Plume basin, reaching as far as Hungry Creek (Catto 1996). On two occasions, ice blocked the Peel River, forming large lakes in the watershed; these could have been temporary barriers to the dispersal of terrestrial organisms (Catto 1996) but facilitated dispersal and interchange among freshwater species (Bodaly and Lindsey 1977).

The ice-free corridor has been extensively researched for its possible role in allowing humans to disperse from Asia to the Americas. For several decades, the predominant theory of human arrival in the new world was that bands of large-mammal hunters, the Clovis people, migrated down the ice-free corridor from Beringia and rapidly expanded to occupy most of the unglaciated regions of North America as well as spreading throughout South America. But more recent evidence casts doubt on this theory. The earliest estimated dates of human arrival in the unglaciated areas of what is now the United States have been pushed back to >11,000 years ago, prior to the opening of the ice-free corridor (Arnold 2002). These revised dates also significantly pre-date remains in the corridor itself (Beaudoin et al. 1996). Moreover, precise dating of archaeological remains in Alberta suggests that Clovis people colonized southern portions of the ice-free corridor from the south rather than in a wave from the north. A predominant current theory hold that the earliest Americans arrived from Asia by skirting the Cordilleran ice sheet along the Pacific coast (Fagundes et al. 2008). An alternative hypothesis postulates that humans came from Europe via the ice-free edge of the Laurentide ice sheet along the Atlantic coast (Bradley and Stanford 2004).



The Peel River drainage is a large, mainly intact ecosystem in western Canada, and an important storehouse of arctic biodiversity. Photo: Juri Peepre

However, though the ice-free corridor is no longer generally viewed as the route that humans took to initially colonize the Americas, the corridor was undoubtedly important for the dispersal and colonization of many other organisms. For example, the opening of the corridor may have allowed an influx of Beringian bison to reach areas in western Canada farther south (Wilson 1996).

Current biota of the Peel River watershed

The Peel River flows into the Mackenzie, and drains 68,872 km². It has three tributaries arising in the Richardson Mountains to the north, the Caribou, Trail, and Road Rivers, and six tributaries draining from the Ogilvie and Wernecke Mountains to the south and west, the Ogilvie, Blackstone, Hart, Wind, Snake, and Bonnet Plume Rivers (Green et al. 2008). The Peel River ecosystem comprises mountainous terrain mainly covered by boreal forest and tundra. The forests are primarily spruce (*Picea spp.*) with larch (*Larix*), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and balsam poplar (*P. balsamifera*). The shrubs are dominated by birch (*Betula spp.*), willow (*Salix spp.*) and alder (*Alnus spp.*). Large mammalian herbivores in the system include caribou (*Rangifer tarandus*), moose (*Alces alces*), and Dall's sheep (*Ovis dalli*). These animals are hunted by wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*).



The porcupine caribou herd, one of the largest in the western North American arctic, calves on the coastal plain of Alaska but has part of its winter range in the Peel River watershed (CPAWS-YUKON 2002). The headwaters of the Bonnet Plume, Snake, and Wind Rivers in the Mackenzie Mountains support the largest herds of woodland caribou in the Yukon Territory, the Hart River and Bonnet Plume herds, as well as the smaller Clear Creek herd (CPAWS-YUKON 2002). The lower Peel River is important nesting ground for raptors such as peregrine falcons (*Falco peregrinus*), gyrfalcons (*F. rusticolus*), bald eagles (*Haliaeetus leucocephalus*), and osprey (*Pandion haliaetus*), while the north Ogilvie Mountains at the west edge of the Peel watershed have high densities of nesting golden eagles (*Aquila chrysaetos*). The Peel River serves as a migration route for waterfowl, many species of which also nest in the wetlands of the watershed (CPAWS-YUKON 2002). The only two breeding populations of surf-bird (*Aphriza virgata*) in Canada are found in the headwaters of the Peel and Porcupine Rivers (CPAWS-YUKON 2002).

The Peel River contains several fish species that spawn in its waters and then migrate to the Beaufort Sea; many of these are important subsistence food for the local Gwich'in people (VanGerwen-Toyne 2003). These anadromous species include broad whitefish (*Coregonus nasus*), least cisco (*C. sardinella*), arctic cisco (*C. autumnalis*), and inconnu (*Stenodus leucichthyes*) (VanGerwen-Toyne 2003). The Peel River also has reports of apparently stray anadromous chum salmon (*Oncorhynchus keta*) (Stephenson 2006) and some reports of pink salmon (*O. gorbuscha*) (Stephenson 2006). More detailed information on fish of the Peel River can be found in VanGerwen-Toyne (2003) and Anderton (2006).



[Photo: Karsten Heuer]

PART II: BIOGEOGRAPHICALLY UNIQUE ORGANISMS OF THE PEEL

Hultén (1937) initially suggested the ice-free realm of Beringia served as a refuge for boreal and arctic biota during Pleistocene glaciations, and as a source population from which the organisms recolonized the circumarctic during interglacial periods. This hypothesis has been supported for a number of different taxa, which we review below. Indeed, the formerly-contiguous region of Beringia can be considered a critical glacial refuge and a hotspot of genetic diversity for arctic and boreal organisms (Elias 2001, Cook et al. 2005, Geml et al. 2006). Nearly all of western Canada was glaciated during the Wisconsinan advance (Marr et al. 2008). The only large portions of unglaciated Beringia to be found in Canada are in parts of the Yukon Territory, particularly the Peel River drainage and surrounding areas such as the Porcupine Basin and Richardson Mountains (CPAWS-YUKON 2002). There are no known endemic species in the Peel River watershed; this is to be expected, since arctic organisms generally have very large distributions (Hultén 1937). However, the Peel River drainage is nonetheless an incredible storehouse of Canadian biodiversity by virtue of being a large, intact ecosystem and the main representative of Beringia – the hotspot of arctic and boreal biodiversity – in Canada.



[Northern Pike]

Habitat features

The World Wildlife Fund for Nature (WWF) has demarcated biogeographically-distinct “ecoregions” around the world. The Peel River drainage spreads across four ecoregions, the Northern Canadian Shield Taiga, the Northwest Territories Taiga, the Low Arctic Tundra, and the Ogilvie-Mackenzie Alpine Tundra. Of the four, the Peel River is most significant for its coverage of ~20% of the total global area of the Ogilvie-Mackenzie Alpine Tundra ecoregion (Green et al. 2008). More detailed information on ecoregion coverage and other habitat features of the Peel River can be found in Green et al. (2008).

Fish

As reported above (see the Beringia section in Part I), the Peel River effectively switched directions at least twice during the Pleistocene, affording opportunities for dispersal and intermixing among the freshwater organisms of the Yukon and Mackenzie Rivers. Bodaly and Lindsey (1977: 388) report that, “The unusual Pleistocene history of the Peel River system of central Yukon Territory in Canada has been of particular importance to the dispersal of freshwater organisms...The evidence suggests that the Peel region is unique in Canada in that it probably contains relict populations not only of fish but of other animals and plants. These populations are of great intrinsic interest but are potentially susceptible to destruction by man.”



[Lake whitefish.]

Lake whitefish (*Coregonus clupeaformis* complex) survived the late Pleistocene glaciations in Beringia and Mississippi refugia (Franzin 1974); following deglaciation, individuals from the latter refuge spread north to occupy much of the Mackenzie drainage (Bodaly and Lindsey 1977, Franzin and Clayton 1977). Yet the only lake whitefish to occupy the Peel River drainage are in Margaret Lake and the Quartet Lakes; they lack any surface connection to rivers of the Peel drainage and show allelic signatures of a remnant Beringian population rather than dispersal from the Mississippi refuge via the Mackenzie (Bodaly and Lindsey 1977). Likewise, slimy sculpin (*Cottus cognatus*), northern pike (*Esox lucius*), arctic grayling (*Thymallus arcticus*), lake trout (*Salvelinus namaycush*) in the Peel drainage are all of Yukon River origins (Bodaly and Lindsey 1977).

These represent remnant Beringian populations and are thus genetically unique from other Canadian members of the same species. The Peel drainage supports a mixture of long-nosed sucker (*Catostomus catostomus*) races from Beringia as well as Mississippi ancestors (Dillinger et al. 1991). Beringia served as a refuge for long-nosed suckers (McPhail and Taylor 1999) and lake trout (Wilson and Hebert 1998) during the Wisconsin advance. Beringia also protected two separate populations of arctic grayling, a “north Beringia” group in what is now northern Alaska and the Yukon Territory and a “south Beringia” group in western Alaska and British Columbia (Stamford and Taylor 2004).



[Arctic hare.]

Terrestrial vertebrates

There is substantial phylogeographic structure in mustelid carnivores (Fleming and Cook 2002), voles and lemmings (Galbreath and Cook 2004), shrews (Demboski and Cook 2003), arctic ground squirrels (Eddingsaas et al. 2004), collared lemmings (Fedorov and Stenseth 2002), and hares (Waltari et al. 2004) in the eastern Beringia, implying that these species persisted here during the Pleistocene glaciations (Cook et al. 2005). Indeed the arctic ground squirrel (*Spermophilus parryii*) may have evolved in and be well adapted to the steppe-tundra habitats of Beringia (Zazula et al. 2006a, Zazula et al. 2007). The long isolation of Beringian biota during the Pleistocene glaciations has resulted in unique coevolutionary diversification of arvicoline rodents and their endoparasites in the region (Haukisalmi et al. 2004). In some cases these refugia served as source populations from which organisms recolonized the arctic when the glaciers retreated, though in other cases the Beringian populations did not spread but retained unique genetics that continue to set them apart from other arctic populations. For example, lemmings (*Lemmus* spp.) show intraspecific endemism in Beringia that is detectable genetically but not morphologically (Fedorov et al. 2003). The arctic hare *Lepus othus* has a monophyletic Beringian lineage demonstrating the genetic effects of this glacial refuge for this species (Waltari and Cook 2005). The distributions of *L. othus* and *L. arcticus* meet at the Mackenzie River, suggesting that the two species radiated from respective refugia in Beringia and the Canadian high arctic following glacial retreat



Gyrfalcon. Photo: Jannick Schou

(Waltari et al. 2004). Though the Mackenzie River serves as the eastward distributional limit for several Beringian taxa (Waltari et al. 2004), this likely arose only subsequent to glacial retreat since most of the Mackenzie, other than the Peel River drainage, was glaciated during the Wisconsinan advance (Bodaly and Lindsey 1977).

The genetic evidence of Beringian refugia can generally still be found in organisms that do not disperse over large distances, such as the rodents, hares, and shrews discussed above. In contrast, gyrfalcons (*Falco rusticolus*) may have also survived the last glacial maximum in a single refugium such as Beringia, but their dispersal abilities are so great that they are now genetically indistinct across Canada, Alaska, and Norway (Johnson et al. 2007). Still other species colonized Beringia from the south following glacial retreat, such as the southern red-backed vole (*Clethrionomys gapperi*) (Runck and Cook 2005, Jung et al. 2006).

Invertebrates

Morphological and genetic data show that species in the *Ilybius angustior* complex (*Coleoptera: Dytiscidae*) diversified and radiated within the Beringia refugium (Nilsson and Ribera 2007). Small crustaceans in the genus *Daphnia pulex* species complex form the basis for many aquatic food webs across Canada; this lineage persisted and diversified in the eastern Beringia refugium and subsequently colonized other parts of Canada (Weider and Hobæk 2003).

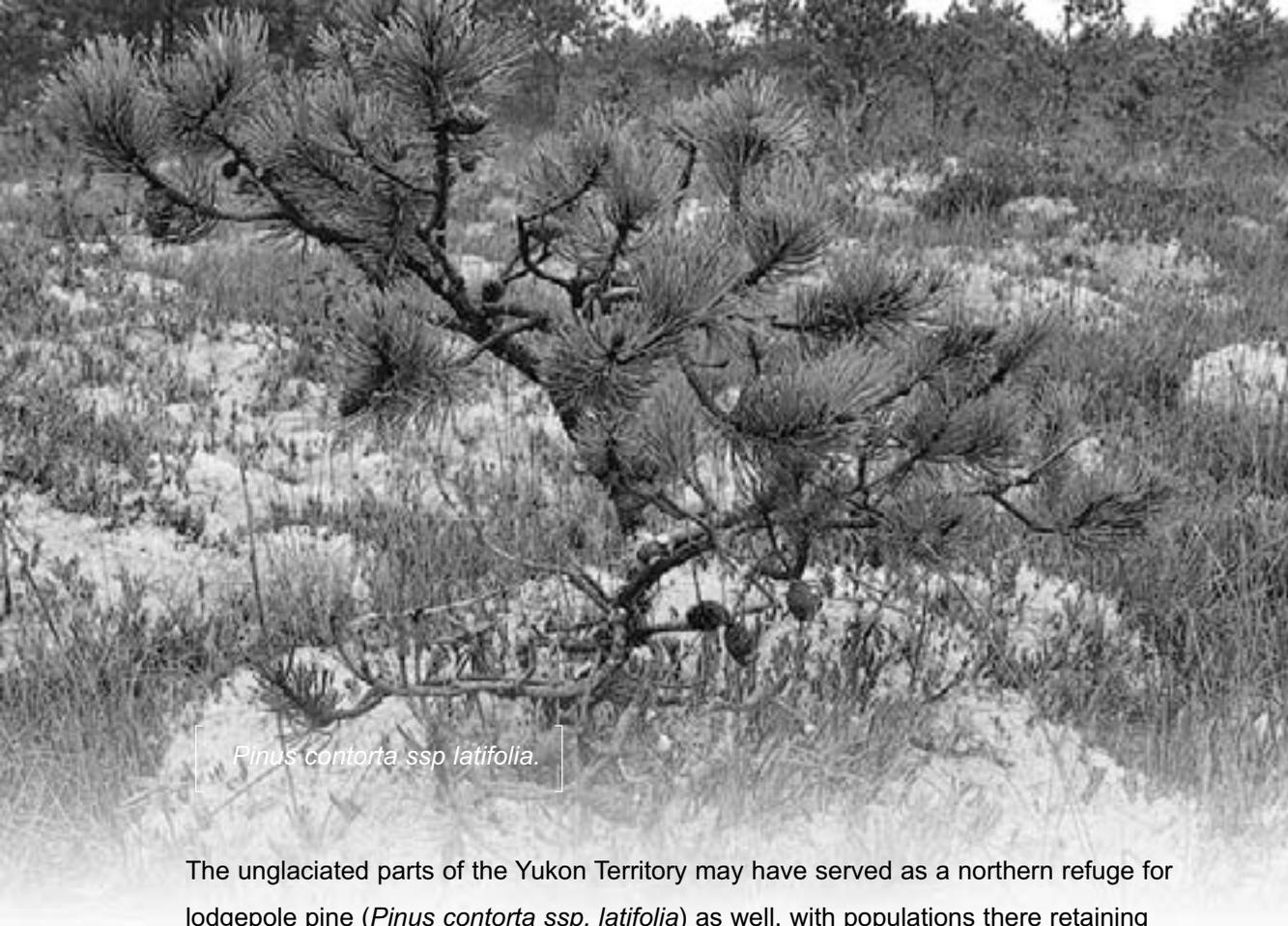


Cassiope tetragona

Plants

Several widespread arctic herbs have high genetic diversity in Beringia compared to the rest of their range, including a *Cassiope tetragona* (Eidesen et al. 2007), *Saxifraga oppositifolia* (Abbott et al. 2000), *Vaccinium uliginosum* (Alsos et al. 2005), and *Oxyria digyna* (Marr et al. 2008). Indeed, *S. oppositifolia* likely originated in Beringia and spread from there to achieve its current circumpolar distribution (Abbott et al. 2000). The circumpolar *Juncus biglumis* survived and diversified in several glacial refugia around the northern hemisphere, including a radiation in Beringia (Schönswetter et al. 2006). Another Beringian relict, *Poa porsildii*, considered vulnerable in Alaska and rare in the Yukon Territory, is found in the upper reaches of the Peel watershed near the headwaters of the Blackstone and Hart (CPAWS-YUKON 2002).

Eastern Beringia, comprised of Alaska and the ice-free portions of the Yukon Territory (primarily the Peel River drainage) also served as important refugium for boreal trees. While Beringia was generally a grassy steppe (Elias 2001, Guthrie 2001), pockets of trees remained in the region and, when the ice sheets melted, these trees spread to help form the boreal forests of today. For example, white spruce (*Picea glauca*) mitochondrial haplotype diversity is currently higher in Alaska than elsewhere in North America, implying that eastern Beringia served as a refugium for spruce (Anderson et al. 2006).



Pinus contorta ssp. latifolia.

The unglaciated parts of the Yukon Territory may have served as a northern refuge for lodgepole pine (*Pinus contorta ssp. latifolia*) as well, with populations there retaining unique haplotypes (Godbout et al. 2008). Fossil pollen also indicates that eastern Beringia contained remnant populations of *Betula* (birch) trees and shrubs and possibly *Populus* (cottonwood) and *Larix* (larch) trees (Brubaker et al. 2005). After the glaciers receded, these refugia served as source populations from which boreal trees and shrubs re-colonized the region. Recently-discovered outbreeding *Cypripedium passerinum* orchids from the Yukon Territory are likely a relict population from the Beringian refugium (Catling and Bennett 2007). Throughout most of the rest of its Canadian range, *C. passerinum* are self-pollinating, an adaptation that probably facilitated rapid colonization of newly exposed lands as the Pleistocene glaciers retreated (Catling and Bennett 2007).

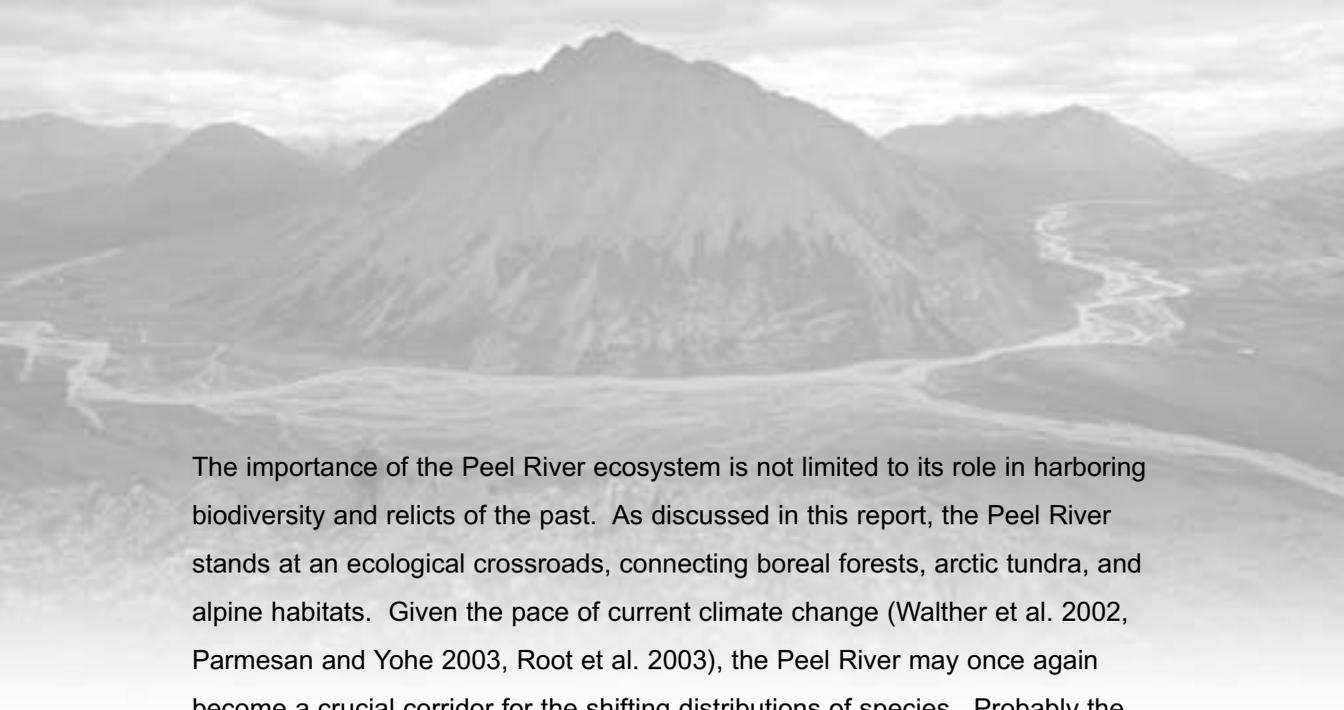
As elsewhere, non-vascular plants are less well-studied in Beringia and the Peel River than their vascular counterparts. Yet the Peel may contain several unique bryophyte taxa. The Ogilvie Mountains, forming the boundary between the watersheds of the Peel and Porcupine Rivers, contain 96 species of moss that may occur nowhere else in the Yukon Territory (Vitt 1976).



Amanita muscaria

Fungi

Fungi receive less scientific attention than many other taxa, but are critical components of many terrestrial ecosystems, helping recycle nutrients and forming mutualistic associations with plants. A widespread and relatively “charismatic” fungus, the fly agaric (*Amanita muscaria*) was recently found to actually consist of three genetically distinct clades throughout its circumpolar range (Oda et al. 2004). Yet all three of these cryptic lineages coexist in eastern Beringia; the region likely served as a glacial refugium for the taxon, from which it diversified and subsequently colonized the northern hemisphere (Geml et al. 2006). Indeed, Geml et al. (2006: 237) state that, “...Beringia is not only the original and longest inhabited region for many plant and animal taxa, but may represent a biodiversity ‘hotspot’ for high-latitude ECM [ectomycorrhizal] fungi as well”. Ectomycorrhizal fungi are soil-based fungi that form mutualistic associations with plant roots, allowing vascular plants greater access to nutrients and water.



Snake River "S-Bend. Photo: Peter Bowers

PART III: CONCLUSIONS

A fundamental finding of the field of conservation biology has been that effective conservation requires the protection of large landscapes (Soule and Terborgh 1999). This is particularly true in boreal and arctic ecosystems (Weaver 2006), where many organisms naturally occur at low densities and range widely. The Peel ecosystem is a large, mainly intact wilderness with great variation in topography and habitat and harboring many unique organisms. By virtue of being the main Canadian representation of the Beringian biogeographic region, it serves as a storehouse of biodiversity for the nation. Green et al. (2008) argue that the presence of the Dempster highway has degraded the western portion of the Peel. This may be true from the standpoint of wilderness aesthetics, yet we feel that the entire Peel ecosystem is critical from ecological and biogeographic perspectives. Although roads have indubitable ecological impacts (Forman and Alexander 1998), in the case of the Dempster highway, these effects are likely to be relatively limited. First of all, the highway is seasonal. Second, and perhaps most importantly, the road has not currently been accompanied by major infrastructure development and associated increases in human impact in the Peel watershed. The road has facilitated caribou hunting, but for many other species the ecological impacts of the Dempster highway are unlikely to propagate very far past the actual roadbed. This is not to say that building roads through wilderness areas is acceptable, only that their creation should not serve as an excuse for further development.

The importance of the Peel River ecosystem is not limited to its role in harboring biodiversity and relicts of the past. As discussed in this report, the Peel River stands at an ecological crossroads, connecting boreal forests, arctic tundra, and alpine habitats. Given the pace of current climate change (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003), the Peel River may once again become a crucial corridor for the shifting distributions of species. Probably the best way that we can manage natural systems so as to ensure resilience to climate change is through protecting large habitat areas and links between different ecosystems (Honnay et al. 2002, Opdam and Wascher 2004, Heller and Zavaleta 2009). The Peel River is exactly such a place – large, untrammled, and providing linkage between different elevations, habitat types, latitudes, and biomes. Moreover, the Peel River ecosystem stands at the northern terminus of the continental-scale habitat connectivity plan envisioned by the Yellowstone to Yukon Project (Schultz 2008).

It would be difficult to predict the extent to which any given development project in the region would degrade the ecological resiliency of the Peel. Yet the best way to avoid the death-by-a-thousand-cuts is to prevent that first cut.

ACKNOWLEDGMENTS

We thank the Canadian Parks and Wilderness Society, specifically Ken Margolis, for instigating and supporting this project, and also the Yellowstone to Yukon Project for financial support. JFB was also supported by a David H. Smith Conservation Research Fellowship through the Society for Conservation Biology and the Cedar Tree Foundation.

Taxon	Common name	Lineage (family)	Beringian diversity	Reference
<i>Amanita muscaria</i> complex	Fly agaric	Fungus (Amanitaceae)	Genetic data show a Beringian origin for the species complex; the highest genetic diversity is still found in Beringia.	Geml et al. (2006)
<i>Cassiope tetragona</i>	Arctic white heather	Vascular plant (Ericaceae)	Species originated in Beringia, has the highest genetic diversity there, and subsequently radiated to a circumpolar distribution.	Eidesen et al. (2007)
<i>Vaccinium uliginosum</i>	Arctic blueberry	Vascular plant (Ericaceae)	Beringian lineage has 7 unique haplotypes.	Alsos et al. (2005)
<i>Juncus biglumis</i>	Two-flowered rush	Vascular plant (Juncaceae)	Genetic data show in situ radiation in western Canadian glacial refugia.	Schönswetter et al. (2006)
<i>Saxifraga oppositifolia</i>	Purple saxifrage	Vascular plant (Saxifragaceae)	cpDNA shows a Beringian origin and subsequent circumpolar radiation.	Abbott et al. (2000)
<i>Oxyria digyna</i>	Mountain sorrel	Vascular plant (Polygonaceae)	Genetic data show high diversity in Beringia.	Marr et al. (2008)
<i>Cypripedium passerinum</i>	Sparrow's-egg lady's-slipper orchid	Vascular plant (Orchidaceae)	A recently-discovered outbreeding morphotype in the Yukon Territory suggests a relictual Beringian population	Catling and Bennett (2007)

<i>Rangifer tarandus</i>	Caribou/reindeer	Mammal (Cervidae)	Most extant caribou share mitochondrial genes from a haplogroup that persisted in Beringia and Eurasia during the Pleistocene.	Flagstad and Røed (2003)
<i>Lepus othus</i>	Arctic hare	Mammal (Leporidae)	Monophyletic Beringian lineage separate from other lineages.	Waltari et al. (2004), Waltari and Cook (2005)
<i>Dicrostonyx groenlandicus</i>	collared lemming	Mammal (Cricetidae)	Haplotypes suggest eastern Beringia refugium during the Pleistocene.	Fedorov and Stenseth (2002)
<i>Lagopus mutus</i>	rock ptarmigan	Bird (Tetraonidae)	mtDNA shows Beringia origin and subsequent spread to Aleutians.	Holder et al. (2000)
<i>Coregonus clupeaformis</i> complex	Lake whitefish	Fish (Coregonidae)	Allelic frequency and gill morphology suggest a remnant Beringian population in Lake Margaret.	Bodaly and Lindsey (1977), Franzin and Clayton (1977)
<i>Cottus cognatus</i>	Slimy sculpin	Fish (Cottidae)	Morphology suggests a remnant Beringian population in the Peel drainage	Bodaly and Lindsey (1977)
<i>Esox lucius</i>	northern pike	Fish (Esocidae)	Morphology suggests a remnant Beringian population in the Peel drainage.	Bodaly and Lindsey (1977)
<i>Thymallus arcticus</i>	arctic grayling	Fish (Salmonidae)	Morphology suggests a remnant Beringian population in the Peel drainage.	Bodaly and Lindsey (1977)

<i>Salvelinus namaycush</i>	lake trout	Fish (Salmonidae)	Morphology suggests a remnant Beringian population in the Peel drainage.	Bodaly and Lindsey (1977)
<i>Catostomus catostomus</i>	long-nosed sucker	Fish (Catostomidae)	cyt b variation suggests Beringian refugium.	McPhail and Taylor (1999)
<i>Ilybius angustior</i> complex	Predatory diving beetles	Insect (Dytiscidae)	Morphological and genetic data show diversification and speciation within the Beringia refugium.	Nilsson and Ribera (2007)
<i>Daphnia pulex</i> complex	Water fleas	Crustacean (Daphniidae)	Genetic data show high diversity and speciation in eastern Beringia.	Weider and Hobæk (2003)

LITERATURE CITED

- Abbott, R. J., L. C. Smith, R. I. Milne, R. M. M. Crawford, K. Wolff, and J. Balfour. 2000. Molecular analysis of plant migration and refugia in the arctic. *Science* 289:1343-1346.
- Alroy, J. 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science* 292:1893-1896.
- Alsos, I. G., T. Engelskjøn, L. Geilly, P. Taberlet, and C. Brochmann. 2005. Impact of ice ages on circumpolar molecular diversity: insights from an ecological key species. *Molecular Ecology* 14:2739-2753.
- Anderson, L. L., F. S. Hu, D. M. Nelson, R. J. Petit, and K. N. Paige. 2006. Ice-age endurance: DNA evidence of a white spruce refugium in Alaska. *Proceedings of the National Academy of Sciences of the United States of America* 103:12447-12450.
- Anderton, I. 2006. Peel River watershed fisheries information summary report - preliminary assessment. Report prepared for the Peel River Planning Commission. Environmental Dynamics Inc., Whitehorse, Yukon Territory.
- Arnold, T. G. 2002. Radiocarbon dates from the Ice-free Corridor. *Radiocarbon* 44:437-454.
- Beaudoin, A. B., M. Wright, and B. Ronaghan. 1996. Late quaternary landscape history and archaeology in the 'ice-free corridor': Some recent results from Alberta. *Quaternary International* 32:113-126.
- Bigelow, N. H., L. B. Brubaker, M. E. Edwards, S. P. Harrison, I. C. Prentice, P. M. Anderson, A. A. Andreev, P. J. Bartlein, T. R. Christensen, W. Cramer, J. O. Kaplan, A. V. Lozhkin, N. V. Matveyeva, D. F. Murray, A. D. McGuire, V. Y. Razzhivin, J. C. Ritchie, B. Smith, D. A. Walker, K. Gajewski, V. Wolf, B. H. Holmqvist, Y. Igarashi, K. Kremenetskii, A. Paus, M. F. J. Pisaric, and V. S. Volkova. 2003. Climate change and Arctic ecosystems: 1. Vegetation changes north of 55 degrees N between the last glacial maximum, mid-Holocene, and present. *Journal of Geophysical Research-Atmospheres* 108.

Bodaly, R. A., and C. C. Lindsey. 1977. Pleistocene Watershed Exchanges and Fish Fauna of Peel River Basin, Yukon Territory. *Journal of the Fisheries Research Board of Canada* 34:388-395.

Bradley, B., and D. Stanford. 2004. The North Atlantic ice-edge corridor: a possible Palaeolithic route to the New World. *World Archaeology* 36:459-478.

Brigham-Grette, J. 2001. New perspectives on Beringian Quaternary paleogeography, stratigraphy, and glacial history. *Quaternary Science Reviews* 20:15-24.

Brubaker, L. B., P. M. Anderson, M. E. Edwards, and A. V. Lozhkin. 2005. Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of Biogeography* 32:833-848.

Burney, D. A., and T. F. Flannery. 2005. Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology & Evolution* 20:395-401.

Burns, J. A. 1996. Vertebrate paleontology and the alleged ice-free corridor: The meat of the matter. *Quaternary International* 32:107-112.

Catling, P. M., and B. A. Bennett. 2007. Discovery of a Possibly Relict Outbreeding Morphotype of Sparrow's-egg Lady's-slipper Orchid, *Cypripedium passerinum*, in Southwestern Yukon. *Canadian Field-Naturalist* 121:295-298.

Catto, N. R. 1996. Richardson Mountains, Yukon-Northwest Territories: the northern portal of the postulated 'ice-free corridor'. *Quaternary International* 32:3-19.

Cook, J. A., E. P. Hoberg, A. Koehler, H. Henttonen, L. M. Wickstrom, V. Haukisalmi, K. E. Galbreath, F. Chernyavski, N. Dokuchaev, A. Lahzuhtkin, S. O. MacDonald, A. Hope, E. Waltari, A. M. Runck, A. Veitch, E. Jenkins, S. Kutz, and R. Eckerlin. 2005. Beringia: intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study* 30:S33-S44.

CPAWS-YUKON. 2002. Yukon wild: natural regions of the Yukon. Canadian Parks and Wilderness Society -Yukon Chapter.

Demboski, J. R., and J. A. Cook. 2003. Phylogenetic diversification within the *Sorex cinereus* complex (Insectivora: Soricidae). *Journal of Mammalogy* 84:144-158.

Dillinger, R. E., T. P. Birt, J. M. Green, and W. S. Davidson. 1991. Postglacial Dispersal of Longnose Suckers, *Catostomus-Catostomus*, in the Mackenzie and Yukon Drainages. *Biochemical Systematics and Ecology* 19:651-657.

Dyke, A. S., J. T. Andrews, P. U. Clark, J. H. England, G. H. Miller, J. Shaw, and J. J. Veillette. 2002. The Laurentide and Innuitian ice sheets during the Last Glacial Maximum. *Quaternary Science Reviews* 21:9-31.

Eddingsaas, A. A., B. K. Jacobsen, E. P. Lessa, and J. A. Cook. 2004. Evolutionary history of the arctic ground squirrel (*Spermophilus parryii*) in Nearctic Beringia. *Journal of Mammalogy* 85:601-610.

Eidesen, P. B., T. Carlsen, U. Molau, and C. Brochmann. 2007. Repeatedly out of Beringia: *Cassiope tetragona* embraces the arctic. *Journal of Biogeography* 34:1559-1574.

Elias, S. A. 2001. Beringian paleoecology: results from the 1997 workshop. *Quaternary Science Reviews* 20:7-13.

Elias, S. A., D. Berman, and A. Alfimov. 2000. Late Pleistocene beetle faunas of Beringia: where east met west. *Journal of Biogeography* 27:1349-1363.

Elias, S. A., and B. Crocker. 2008. The Bering Land Bridge: a moisture barrier to the dispersal of steppe-tundra biota? *Quaternary Science Reviews* 27:2473-2483.

Fagundes, N. J. R., R. Kanitz, R. Eckert, A. C. S. Valls, M. R. Bogo, F. M. Salzano, D. G. Smith, W. A. Silva, M. A. Zago, A. K. Ribeiro-Dos-Santos, S. E. B. Santos, M. L. Petzl-Erler, and S. L. Bonatto. 2008. Mitochondrial population genomics supports a single pre-Clovis origin with a coastal route for the peopling of the Americas. *American Journal of Human Genetics* 82:583-592.

- Fedorov, V. B., A. V. Goropashnaya, M. Jaarola, and J. A. Cook. 2003. Phylogeography of lemmings (*Lemmus*): no evidence for postglacial colonization of Arctic from the Beringian refugium. *Molecular Ecology* 12:725-731.
- Fedorov, V. B., and N. C. Stenseth. 2002. Multiple glacial refugia in the North American Arctic: inference from phylogeography of the collared lemming (*Dicrostonyx groenlandicus*). *Proceedings of the Royal Society of London, B Series* 269:2071-2077.
- Flagstad, Ø., and K. H. Røed. 2003. Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. *Evolution* 57:658-670.
- Fleming, M. A., and J. A. Cook. 2002. Phylogeography of endemic ermine (*Mustela erminea*) in southeast Alaska. *Molecular Ecology* 11:795-808.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207-+.
- Fox-Dobbs, K., J. A. Leonard, and P. L. Koch. 2008. Pleistocene megafauna from eastern Beringia: Paleoeological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. *Palaeogeography Palaeoclimatology Palaeoecology* 261:30-46.
- Franzin, W. G. 1974. Genetic studies of protein variants and their use in a zoogeographic study of lake whitefish, *Coregonus clupeaformis* (Mitchill) in western Canada. Ph.D. Dissertation. University of Manitoba, Winnipeg.
- Franzin, W. G., and J. W. Clayton. 1977. Biochemical Genetic Study of Zoogeography of Lake Whitefish (*Coregonus-Clupeaformis*) in Western Canada. *Journal of the Fisheries Research Board of Canada* 34:617-625.
- Galbreath, K. E., and J. A. Cook. 2004. Genetic consequences of Pleistocene glaciations for the tundra vole (*Microtus oeconomus*) in Beringia. *Molecular Ecology* 13:135-148.
- Geml, J., G. A. Laursen, K. O'Neill, H. C. Nusbaum, and D. L. Taylor. 2006. Beringian origins and cryptic speciation events in the fly agaric (*Amanita muscaria*). *Molecular Ecology* 15:225-239.
- Godbout, J., A. Fazekas, C. H. Newton, F. C. Yeh, and J. Bousquet. 2008. Glacial vicariance in the Pacific Northwest: evidence from a lodgepole pine mitochondrial DNA minisatellite for multiple genetically distinct and widely separated refugia. *Molecular Ecology* 17:2463-2475.
- Green, M. J. B., S. McCool, J. Thorsell, I. Lysenko, and C. Besancon. 2008. Peel watershed, Yukon: international significance from the perspective of parks, recreation, and conservation. Report prepared for Yukon Parks, Department of Environment, Government of Yukon, Whitehorse.
- Guthrie, R. D. 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews* 20:549-574.
- Haukisalmi, V., L. M. Wickstrom, H. Henttonen, J. Hantula, and A. Gubanyi. 2004. Molecular and morphological evidence for multiple species within *Paranoplocephala omphalodes* (Cestoda: Anoplocephalidae) in *Microtus voles* (Arvicolinae). *Zoologica Scripta* 33:277-290.
- Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation* 142:14-32.
- Holder, K., R. Montgomerie, and V. L. Freisen. 2000. Glacial vicariance and historical biogeography of rock ptarmigan (*Lagopus mutus*) in the Bering region. *Molecular Ecology* 9:1265-1278.
- Honnay, O., K. Verheyen, J. Butaye, H. Jacquemyn, B. Bossuyt, and M. Hermy. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* 5:525-530.
- Hughes, O. L., C. R. Harington, J. A. Janssens, J. V. Matthews, R. E. Morlan, N. W. Rutter, and C. E. Schweger. 1981. Upper Pleistocene stratigraphy, paleoecology, and archaeology of the northern Yukon interior, eastern Beringia.1. Bonnet Plume Basin. *Arctic* 34:329-365.

Hultén, E. 1937. Outline of the history of arctic and boreal biota during the Quaternary period: their evolution during and after the glacial period as indicated by the equiformal progressive areas of present plant species. Thule, Stockholm.

Johnson, J. A., K. K. Burnham, W. A. Burnham, and D. P. Mindell. 2007. Genetic structure among continental and island populations of gyrfalcons. *Molecular Ecology* 16:3145-3160.

Jung, T. S., A. M. Runck, D. W. Nagorsen, B. G. Slough, and T. Powell. 2006. First records of the Southern Red-backed Vole, *Myodes gapperi*, in the Yukon. *Canadian Field-Naturalist* 120:331-334.

Kenyon, J., and G. Whitley. 2008. Water resources assessment for the Peel Watershed. Report prepared for the Peel Watershed Planning Commission.

Levson, V. M., and N. W. Rutter. 1996. Evidence of Cordilleran Late Wisconsinan glaciers in the 'ice-free corridor'. *Quaternary International* 32:33-51.

MacDonald, G. M., and T. K. McLeod. 1996. The holocene closing of the 'ice-free' corridor: A biogeographical perspective. *Quaternary International* 32:87-95.

Machutchon, A. G. 1997a. Grizzly bear habitat evaluation, Bonnet Plume River Valley, Yukon. Yukon Wildlands Project, Canadian Parks and Wilderness Society, Whitehorse, Yukon Territory.

Machutchon, A. G. 1997b. Grizzly bear habitat evaluation, Snake River Valley, Yukon. Yukon Wildlands Project, Canadian Parks and Wilderness Society, Whitehorse, Yukon Territory.

Marr, K. L., G. A. Allen, and R. J. Hebda. 2008. Refugia in the Cordilleran ice sheet of western North America: chloroplast DNA diversity in the Arctic-alpine plant *Oxyria digyna*. *Journal of Biogeography* 35:1323-1334.

McPhail, J. D., and E. B. Taylor. 1999. Morphological and genetic variation in northwestern longnose suckers, *Catostomus catostomus*: The Salish sucker problem. *Copeia*:884-893.

Nilsson, A. N., and I. Ribera. 2007. Morphological and molecular species delimitation within the Holarctic *Ilybius angustior* complex with a focus on Beringia (Coleoptera : Dytiscidae). *Aquatic Insects* 29:159-171.

Nogues-Bravo, D., J. Rodriguez, J. Hortal, P. Batra, and M. B. Araujo. 2008. Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biology* 6:685-692.

Oda, T., C. Tanaka, and M. Tsuda. 2004. Molecular phylogeny and biogeography of the widely distributed *Amanita* species, *A. muscaria* and *A. pantherina*. *Mycological Research* 108.

Opdam, P., and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* 117:285-297.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.

PWPC. 2008. Resource assessment report. Peel Watershed Planning Commission, Whitehorse, Yukon Territory.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57-60.

Runck, A. M., and J. A. Cook. 2005. Postglacial expansion of the southern red-backed vole (*Clethrionomys gapperi*) in North America. *Molecular Ecology* 14:1445-1456.

Sanmartin, I., H. Enghoff, and F. Ronquist. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society* 73:345-390.

Schönswetter, P., J. Suda, M. Popp, H. Weiss-Schneeweiss, and C. Brochmann. 2006. Circumpolar phylogeography of *Juncus biglumis* (Juncaceae) inferred from AFLP fingerprints, cpDNA sequences, nuclear DNA content and chromosome numbers. *Molecular Phylogenetics and Evolution* 42:92-103.

Schultz, F. 2008. *Yellowstone to Yukon: freedom to roam*. Braided River, Seattle.

Shapiro, B., A. J. Drummond, A. Rambaut, M. C. Wilson, P. E. Matheus, A. V. Sher, O. G. Pybus, M. T. P. Gilbert, I. Barnes, J. Binladen, E. Willerslev, A. J. Hansen, G. F. Baryshnikov, J. A. Burns, S. Davydov, J. C. Driver, D. G. Froese, C. R. Harington, G. Keddie, P. Kosintsev, M. L. Kunz, L. D. Martin, R. O. Stephenson, J. Storer, R. Tedford, S. Zimov, and A. Cooper. 2004. Rise and fall of the Beringian steppe bison. *Science* 306:1561-1565.

Soule, M. E., and J. Terborgh, editors. 1999. *Continental conservation*. Island Press, Washington, D.C.

Stamford, M. D., and E. B. Taylor. 2004. Phylogeographical lineages of Arctic grayling (*Thymallus arcticus*) in North America: divergence, origins and affinities with Eurasian *Thymallus*. *Molecular Ecology* 13:1533-1549.

Stephenson, S. A. 2006. A review of the occurrence of Pacific salmon (*Oncorhynchus* spp.) in the Canadian western arctic. *Arctic* 59:37-46.

Swanson, D. K. 2006. Biogeographical evidence for the grass (Poaceae) species of Pleistocene Beringian lowlands. *Arctic* 59:191-200.

Szeicz, J. M., and G. M. MacDonald. 2001. Montane climate and vegetation dynamics in easternmost Beringia during the Late Quaternary. *Quaternary Science Reviews* 20:247-257.

VanGerwen-Toyne, M. 2003. Peel River fish study, 2002. Report 03-02, Gwich'in Renewable Resource Board, Inuvik, NT.

Vitt, D. H. 1976. Mosses new to the Yukon from the Ogilvie Mountains. *The Bryologist* 79:501-506.

Walker, D. A., J. G. Bockheim, F. S. Chapin, W. Eugster, F. E. Nelson, and C. L. Ping. 2001. Calcium-rich tundra, wildlife, and the "Mammoth Steppe". *Quaternary Science Reviews* 20:149-163.

Waltari, E., and J. A. Cook. 2005. Hares on ice: phylogeography and historical demographics of *Lepus arcticus*, *L. othus*, and *L. timidus* (Mammalia : Lagomorpha). *Molecular Ecology* 14:3005-3016.

Waltari, E., J. R. Demboski, D. R. Klein, and J. A. Cook. 2004. A molecular perspective on the historical biogeography of the northern high latitudes. *Journal of Mammalogy* 85:601-610.

Waltari, E., E. P. Hoberg, E. P. Lessa, and J. A. Cook. 2007. Eastward Ho: phylogeographical perspectives on colonization of hosts and parasites across the Beringian nexus. *Journal of Biogeography* 34:561-574.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389-395.

Weaver, J. L. 2006. *Big animals and small parks: implications of wildlife distribution and movements for expansion of Nahanni National Park Reserve*. Wildlife Conservation Society Canada Report No. 1, Toronto, Ontario.

Weider, L. J., and A. Hobæk. 2003. Glacial refugia, haplotype distributions, and clonal richness of the *Daphnia pulex* complex in arctic Canada. *Molecular Ecology* 12:463-473.

Wilson, C. C., and P. D. N. Hebert. 1998. Phylogeography and postglacial dispersal of lake trout (*Salvelinus namaycush*) in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1010-1024.

Wilson, M. C. 1996. Late quaternary vertebrates and the opening of the ice-free corridor, with special reference to the genus bison. *Quaternary International* 32:97-105.

Zazula, G., A. Duk-Rodkin, C. E. Schweger, and R. E. Morlan. 2004. Late Pleistocene chronology of glacial Lake Old Crow and the north-west margin of the Laurentide Ice Sheet. Pages 347-362 in J. Ehlers and P. L. Gibbard, editors. *Quaternary glaciations -extent and chronology, Part II: North America: developments in quaternary science, vol. 2b*. Elsevier, Amsterdam.

Zazula, G. D., D. G. Froese, S. A. Elias, S. Kuzmina, and R. W. Mathewes. 2007. Arctic ground squirrels of the mammoth-steppe: paleoecology of Late Pleistocene middens (similar to 24000-29450 C-14 yr BP), Yukon Territory, Canada. *Quaternary Science Reviews* 26:979-1003.



Zazula, G. D., R. F. W. Mathewes, and A. S. Harestad. 2006a. Cache selection by Arctic ground squirrels inhabiting boreal-steppe meadows of southwest Yukon territory, Canada. *Arctic Antarctic and Alpine Research* 38:631-638.

Zazula, G. D., A. M. Telka, C. R. Harington, C. E. Schweger, and R. W. Mathewes. 2006b. New spruce (*Picea* spp.) macrofossils from Yukon Territory: Implications for Late Pleistocene refugia in Eastern Beringia. *Arctic* 59:391-400.

Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin, J. F. Reynolds, and M. C. Chapin. 1995. Steppe-Tundra Transition - a Herbivore-Driven Biome Shift at the End of the Pleistocene. *American Naturalist* 146:765-794.