

An interdisciplinary approach to describing biological diversity

by

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ABSTRACT

The concept of biodiversity – the phenotypic and genotypic variation among organisms – is central to conservation biology. There is growing recognition that biodiversity does not exist in isolation, but rather is intrinsically and evolutionarily linked to cultural diversity and indigenous knowledge systems. In Canada, caribou (*Rangifer tarandus*) occupy a central place in the livelihoods and identities of indigenous people and display substantial variation across their distribution. However, quantifying caribou intraspecific variation has proven challenging. Interdisciplinary approaches are necessary to produce effective species characterizations and conservation strategies that acknowledge the interdependent relationships between people and nature in complex social-ecological systems. In this dissertation I use multiple disciplinary traditions to develop comprehensive and united representations of caribou variation through an exploration of population genetics, phylogenetics, traditional knowledge, language, and visual approaches in the Sahtú region of the Northwest Territories, Canada. First, I examine caribou variation through analysis of population genetics and the relationships Dene and Métis people establish with animals within bioculturally diverse systems. Next, I focus on how the Pleistocene glacial-interglacial cycles have shaped the current patterns of caribou phylogeographic lineage diversification. Finally, I explore how art can be used to facilitate cross-cultural collaboration and externalize the unique heterogeneity of biocultural diversity. The results demonstrate a broad scale understanding of the distribution, spatial organization, and the degree of differentiation of caribou populations in the region. I found evidence for caribou population differentiation that corresponds to the caribou types recognized by Dene people: t̥dzı “boreal woodland caribou,” ʔekwé “barren-ground caribou,” and shúhta ʔepé “mountain caribou.” Phylogenetic results reveal that in their northern margin the boreal ecotype of woodland caribou evolved independently from

the northern Beringian lineage in contrast with southern boreal caribou which belong to the sub-Laurentide refugia lineage. In addition, I demonstrate how art can be used improve communication, participation, and knowledge production among interdisciplinary research collaborations and across language and knowledge systems. A collaborative process of research that facilitates *łeghágots'enetę* “learning together” has the potential to produce sustainable conservation solutions, develop efficient and effective wildlife management policies, and ensure caribou remain an important part of the landscape.

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To
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CHAPTER 1: INTRODUCTION

Variation, patterns, and processes

Recognizing, describing, and understanding patterns of variation in nature is fundamental to conservation biology. The substantial variation observed in the world is a result of three components: 1) DNA and replication; 2) the possibility of mutations; and 3) environmental structure so that groups do not completely overlap (Hey 2001a). Over time the evolutionary processes of genetic drift and natural selection act on organisms' DNA to create lineages that can be distinguished from each other. Until recently, conservation efforts have focused on protecting evolutionary groups that share a common ancestry. However, more attention is being given to the importance of sustaining the essential processes that create and maintain variation (Bowen 1999, Crandall et al. 2000, Moritz 2002). As Otto Frankel pointed out in 1974, the conservation of evolutionary units must occur at an evolutionary time-scale. He was one of the first to examine conservation priorities from a genetics perspective and in doing so argued for optimizing conditions to allow for a continuing evolution (Allendorf and Luikart 2007). The conservation of evolutionary processes requires a comprehensive understanding of the distribution of organisms, interactions between organisms, and how the environment modifies interactions through time (Moritz 2002). Thus, conservation efforts must protect viable populations across large heterogeneous landscapes to ensure processes of gene flow, selection, and drift take place (Moritz 2002).

Patterns of biodiversity can be categorized in myriad ways because variation is expressed across multiple scales, from the gene to the species to the ecosystem (Loh and Harmon 2005, Allendorf and Luikart 2007). Evolutionary groups share traits that are a result of a similar history of genetic drift and the adaptive fixation of beneficial mutations. Different categories represent

groups of organisms where these processes are shared to a certain degree. Depending on the resolution, or the degree of shared processes, the boundaries can be drawn at varying levels of inclusiveness and therefore define diversity differently. Smaller boundaries represent groups that have more traits in common, while more inclusive groupings share only a few key traits. Importantly, the continuum of biodiversity is dynamic and responsive, interacting not just within itself and the abiotic and geophysical diversity, but also with the diversities of human cultures (Loh and Harmon 2005, Gugerli et al. 2008, Gavin et al. 2015).

Determining where, within the ambiguous space of variation, units emerge that merit conservation or resource management priority continues to be one of the most contentious undertakings in biology (Yoon 2010). The question of how to define species has generated considerable debate for several hundred years, resulting in over 24 modern species concepts that have failed to comprehensively address issues of ambiguity (Hey 2001a, Hey et al. 2003, Baker and Bradley 2006, Hey 2006, Mallet 2008, Yoon 2010). Quantifying intraspecific variation, or diversity below the level of taxonomic species, is similarly enigmatic (Hughes et al. 1997, Moritz 2002), but defining, delineating, and identifying intraspecific populations (and subpopulations) remains a central tenet to biological thought (Wright 1951, Schaefer 2006).

Populations exist along a continuum from isolation to panmixia (Waples and Gaggiotti 2006). However, defining the break points between populations on this continuum is as challenging as finding the break points in species delineations. In practice, divisions are based on diverse ecological and political criteria including: taxonomy, phylogenetics, population genetics, morphology, life history traits, behavior, as well as ecological, political and jurisdictional boundaries (Palsboll et al. 2007, COSEWIC 2011). Because populations are often the focal unit for conservation and resource management, their identification has critical implications (Waples

and Gaggiotti 2006). Thus, it is increasingly important to incorporate multiple forms of information (genetic, ecological, or cultural) when attempting to distinguish units (Crandall et al. 2000, Boulet et al. 2007, Gavin et al. 2015). Alternative languages and knowledge systems, for example, can provide an important, largely overlooked, perspective to guide a comprehensive description of the patterns that characterize life (Warren 1996).

Human perception is a complex and active process that emerges through the interacting influences of cultural experiences, cognition, and language (Zhu 2015). People in all societies use language to describe *kinds* of things and to organize and articulate the patterns of repetition found in the world (Lakoff 1990, Hey 2001b). Some researchers argue that language plays an important role in perception and can determine how knowledge is expressed. For example, the structure of a language (expressed through different grammatical patterns) may have a profound influence on memory, conceptualization (e.g., of time and space), and categorization (Deutscher 2010, Fausey et al. 2010, Boroditsky 2011). Because categories are necessary for communication and development of knowledge but are fundamentally entangled in our language and cognitive structure, their employment can sometimes restrain our understanding of natural patterns (Hey 2001b). Examining multiple knowledge systems or languages in parallel can help to overcome some of the limitations imposed by a singular context. Thus, it is possible to consider the same geographic space from several different perspectives – in which each places different emphasis on distinct aspects (or identifiable criteria) of an organism (Fig. 1-1).

Indigenous knowledge, language, and cognitive structures are often relationally entangled and potentially co-evolving with specific places (Davidson-Hunt et al. 2005, Loh and Harmon 2005). In many cases, indigenous traditional knowledge (manifest through language and practices) embodies exceptionally detailed information about local flora and fauna (Warren

1996, Fraser et al. 2006, Nazarea 2006, Ragupathy et al. 2009). Understanding the vocabulary from which differences between cultures arise allows for the creation of new knowledge in dialogue (Newmaster et al. 2006, Rathwell and Armitage 2016). Most importantly, determining where and why similarities and differences between knowledge systems occur can provide opportunities for mutual learning and help to elucidate underlying processes that create structure and drive patterns of biodiversity.

Forces that shape intraspecific variation

Intraspecific variation – the phenotypic and genotypic variation among organisms within a species – arises through the evolutionary processes of recombination, genetic drift, selection, and gene flow. All variation is embedded in an evolutionary context where past lineages have evolved and interacted to form present spatial patterns of diversity (Mallet 2005). Within an evolutionary time scale, contemporary genetic diversity is the foundation that allows for potential future adaptation to environmental change (Allendorf and Luikart 2007). Intraspecific diversity is often the target of conservation units because it tends to represent vital adaptive diversity (of populations) that should arguably be preserved across the geographic range of the species to ensure potential evolutionary success (Crandall et al. 2000). As anthropogenic changes to habitat and climate place increasing pressure on populations it is important to understand how the forces of space (geography) and time (history) interact with evolutionary processes to effectively produce, decrease, or maintain intraspecific variation.

Geographical configuration has profound influences on evolutionary processes. Landscape characteristics can either prevent the movement of animals through barriers or provide corridors that facilitate movement (Schwartz et al. 2009, Sawyer et al. 2011). Mutation,

genetic drift, and selection tend to generate genetic differentiation between populations that are spatially isolated from each other. Delineating population and sub-population structure within a sampled region by evaluating divisions between multilocus genotypes can also allow for the detection of gene flow (Finnegan et al. 2011, Robinson et al. 2012). The role of gene flow as either a constraining (through the neutralization of local adaptations) or a creative (through the addition of new genetic material) force in evolution continues to be debated (Barton 2001, Garant et al. 2007, Fitzpatrick et al. 2015).

At the population level (within a species) gene flow between individuals from differentiated populations (with different allele frequencies) has been termed intraspecific hybridization or introgressive hybridization (Stebbins 1959). In some cases local adaptations may be lost as a result of intraspecific hybridization through outbreeding depression or breakdown of coadapted gene complexes (Rhymer and Simberloff 1996). For example, hatchery-reared salmon that escape and breed with wild populations may reduce important adaptive behaviors, such as timing of spawning, that are necessary for survival and reproduction (Allendorf et al. 2001). Conversely, it is possible that intraspecific hybridization could provide novel genetic material essential to allowing populations to expand and adapt to new environments (Arnold et al. 2008, Hird and Sullivan 2009). This positive gene flow likely plays an essential role in speciation and the generation of diversity (Grant and Grant 2002, Mallet 2005).

Temporal variation has a profound impact on the distribution of species and intraspecific evolutionary processes. Understanding how historic climatic or geologic events, such as glaciations, have shaped populations over time aids assessment of current population structure (Dyke 2004). Glacial expansions and retreats of the Pleistocene influenced the patterns of

biodiversity for many North American species (Weksler et al. 2010) including wolves (Meachen et al. 2016, Schweizer et al. 2016), black bears (Puckett et al. 2015), bison (Heintzman et al. 2016), bighorn sheep (Loehr et al. 2006), mule deer (Latch et al. 2009), and lemmings (Fedorov and Stenseth 2002, Palkopoulou et al. 2016). Phylogeographic analysis can provide insight into the formation of independently evolving lineages and ultimately the mechanisms of speciation and processes responsible for the generation of patterns of diversity (Avice et al. 1987, Malaney and Cook 2013). Long term variation in the spatial distribution of habitats (such as cyclical fire regimes or distribution of mountain valleys) also influences the connectivity of populations and likely plays a role in historic movements, isolating events, and the formation of unique population units (Serrouya et al. 2012). The variation generated or depressed by particular evolutionary histories may be crucial to the formation of differential adaptive potential (Moritz and Potter 2013). Evaluating the historic context of species demographic histories provides insight into contemporary population structure and the influence of adaptation, isolation, and dispersal on population differentiation (Weckworth 2012). Finally, an understanding of historic genetic patterns may allow for predictions of how species will respond or adapt to future disturbances, environmental change, and the impacts of human developments in a changing landscape (Ashcroft 2010, Stewart et al. 2010, Manel and Holderegger 2013, Yannic et al. 2014).

Applied context

The Canadian north presents a unique set of challenges related to wildlife management and conservation due to a complex history of environmental, jurisdictional, and political conflicts (Sandlos 2011). In the early 1900s exclusionary federal policies restricted Dene, Métis, and Inuit people's right to fish and hunt across the Northwest Territories (NWT; Sandlos 2011). Since the

1970s, indigenous peoples in Canada have increasingly gained recognition for their role in the management of natural resources. Constitutional acknowledgement of inherent rights has been followed by a series of court cases affirming the role of indigenous peoples in the management of their traditional territories¹. However, while land claims and associated co-management institutions have further strengthened the formal mechanisms for indigenous governance in land stewardship, indigenous knowledge is rarely included in research or management objectives (McGregor et al. 2010). There is a growing need for clear, implementable approaches that incorporate multiple knowledge sources and recognize the significance of indigenous institutions (Adams et al. 2014, Tondu et al. 2014).

The Sahtú region encompasses 280,238 km² of central Northwest Territories, Canada, surrounding Great Bear Lake (Fig. 1-2). The current political boundaries and institutional structure were defined by the Sahtú Dene and Métis Comprehensive Land Claim Agreement that concluded in 1993 and the Mackenzie Valley Resource Management Act of 1998. There are currently five communities in the region: Délı̄ne, Tulı́'a, Norman Wells (Tłegóhı̄), Fort Good Hope (Rádelı̄ Kóé) and Colville Lake (K'áhbanı́ Túé). Dene people have occupied the region for many thousands of years (Gordon 2003, Gordon 2005, Andrews et al. 2012a) and share a cultural and linguistic (Sahtú Dene or Athapaskan/North Slavey) history (Helm et al. 2000).

Dene and Métis people in the Sahtú self-identify with several social linguistic units and family groups that maintain historic relationships with specific places on the landscape. The main social units are flexible and reflect distinct dialects and cultural diversity that vary between communities and are based on the historical relationships between people, political agreements,

¹Makivik Corp. v Canada (Minister of Canadian Heritage), [1999] 1 F.C. 38. (T.D.)
Haida Nation v British Columbia (Minister of Forests), [2004] 3 S.C.R. 511, 2004 SCC 73
Delgamuukw v British Columbia, [1997] 3 S.C.R. 1010, 1997 Carswell, BC 2358

and economic ties (Petitot 1893, Hara 1980, Rushforth 1984, Helm et al. 2000, Abel 2005). In Tulít'a Dene people self-identify as Shúhta Got'ine “Mountain people,” K'áálo Got'ine “Willow Lake people,” Sahtú or Dél'ine Got'ine “Bearlake/Dél'ine people,” and Dəoga Got'ine “Mackenzie River people.” In Dél'ine the majority of Dene self-identify as Sahtú or Dél'ine Got'ine. In Fort Good Hope and Colville Lake most people self-identify as K'áhsho Got'ine “Tall Willow people” (Hare) and Dela Got'ine². Finally, the community of Norman Wells is unique in that it has an active oil and gas industry and the largest non-indigenous population in the region. Dene and Métis people that reside in Norman Wells have diverse backgrounds and ties to most Sahtú family groups. Prior to the 1960s and 1970s when government intervention forced a shift to life in the communities, Sahtú Dene people lived in the boreal forest along rivers and lakes and in the mountains subsisting on fish and wildlife in a seasonal harvesting cycle (Abel 2005). Dene and Métis people continue to retain a strong cultural and social-ecological relationship with the land (Andrews et al. 2012a, Andrews et al. 2012b, McMillan and Parlee 2013, Harnum et al. 2014).

Under the current institutional structures of the Sahtú Land Claim the ʔehdzo Got'ine Gots'é Nákedı (Sahtú Renewable Resources Board; SRRB) and the five local ʔehdzo Got'ine (Renewable Resources Councils; RRCs) of the Sahtú region are responsible for managing renewable resources including wildlife and habitat. However, successful implementation of the co-management framework has been difficult to achieve due to the lack of conceptual and practical tools available to bring together indigenous and science-based knowledge systems in decision-making (White 2008, Morgan 2012, Miller and Davidson-Hunt 2013). Furthermore, power disparities and a lack of capacity have hindered indigenous environmental governance and stewardship. In light of these challenges, the RRCs passed a joint resolution in September 2012

² Additional fine-scale subgroups of dialects and family-groups also occur in the region.

that called for a renewed commitment to adopt traditional knowledge and Dene law as the guiding principles in caribou research.

Caribou (*Rangifer tarandus*) occupy a central place in the livelihoods and identities of Dene and Métis people and display substantial variation across their distribution. In North America, caribou occur across an extremely diverse expanse of ecological conditions with variable levels of connectivity, natural and human disturbance, and environmental limitations. The ability of caribou to adjust to this variation is apparent in unique phenotypic adaptations that taxonomists have struggled to systematically organize. In 1961 Banfield classified *R. tarandus* in North America into 4 divisions: Barren-ground caribou (*R. t. groenlandicus* and *R. t. granti*); woodland (*R. t. caribou*); Peary caribou (*R. t. pearyi*) and Dawson's caribou (*R. t. dawsoni*) that once occurred on the Haida Gwaii islands of British Columbia. While subdivisions within these designations have also been applied, the main subspecies groupings have remained largely unchanged.

In Canada, endangered species policy can occur below the species level. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) developed and approved guidelines to identify Designatable Units (DUs – discrete and significant biological units that capture irreplaceable components of intraspecific biodiversity) to inform conservation management action (COSEWIC 2009) and in 2011 proposed twelve DUs for caribou (COSEWIC 2011). Three caribou DUs occur in the Sahtú region (Fig. 1-2). In the far north, barren-ground caribou (DU3: Barren-ground Caribou) calve in the open tundra in the spring and migrate to the boreal forest in the winter (Nagy et al. 2011). Barren-ground caribou populations can number in the tens of thousands and have experienced significant population expansions, declines, and fluctuating spatial dynamics that all contribute to high genetic diversity and genetic mixing (Hinkes et al.

2005, Mager et al. 2013). In the Mackenzie Mountains, mountain caribou (DU7: Northern Mountain Caribou) migrate elevationally throughout the year; foraging on terrestrial lichen in valley bottoms during winter and selecting for high elevation alpine tundra plateaus during the summer and fall (Farnell and McDonald 1990, Gullickson and Manseau 2000, Creighton 2006, Polfus et al. 2011, Letts et al. 2012). In the Sahtú, the boreal ecotype of woodland caribou (DU6: Boreal Caribou) occur in small groups throughout the boreal forest and disperses to calve and avoid predators (Stuart-Smith et al. 1997, O'Brien et al. 2006, Brown et al. 2007, Courtois et al. 2007). Nationally, boreal caribou are distributed throughout the boreal forest from the Yukon Territory to Newfoundland and Labrador (COSEWIC 2011), which also comprises the economic, spiritual, and cultural home to over 600 indigenous communities that have relied on caribou for millennia (Anielski and Wilson 2009). The extent of the boreal caribou distribution is bisected by numerous political and jurisdictional boundaries and various ecological assemblages which affect caribou both politically (through provincial, territorial and federal policies) and ecologically. Due to increasing levels of human infrastructure development and population declines throughout their range (Vors and Boyce 2009), boreal caribou have been federally listed as threatened under the Species at Risk Act (SARA).

Defining and delineating geographic ranges of caribou within and between the proposed DUs has proven to be difficult because caribou have the ability to disperse over large distances and overlap between populations is frequent (Boulet et al. 2007, COSEWIC 2011, Klütsch et al. 2016, Pond et al. 2016). Most boreal caribou ranges have not been adequately delineated due to lack of data, poor understanding of movement, and the jurisdictional complications of trans-boundary ranges (Environment Canada 2011). If local population units are poorly defined it will be impossible to identify critical habitat and implement protection actions under the federal

recovery plan. The detailed local-level planning mandatory to guide implantation of recovery actions for boreal caribou under SARA and NWT species at risk processes demands new approaches to conservation that can accommodate diverse views and interests.

There is an especially urgent need for baseline information about the origin, genetic diversity, and distribution of caribou populations in the Sahtú region because of the increased and impending shale-oil development in the central Mackenzie Valley. Over 13,500 km² are currently licensed to oil exploration companies. Increased industrial activity has the potential to impact caribou habitat selection and population dynamics (Dyer et al. 2001, Johnson et al. 2005, Polfus et al. 2011). Thus, understanding both the historic and contemporary structure of caribou populations in the region is important for developing effective management strategies that reflect the evolutionary lineages and population dynamics that exists within the species. Bringing multiple sources of information, knowledge, and ways of knowing into a collaborative and informative research framework will allow the SRRB and local RRCs to provide input into permit applications, cumulative impact assessments, and affirm their management authority.

General approach

In this dissertation I use an interdisciplinary research approach to unite tools and knowledge from different disciplines and knowledge systems to address questions related to caribou conservation. Interdisciplinary research requires that research teams bridge disciplinary boundaries and conduct research in collaboration to address common research goals (Tress et al. 2005, Pretty 2011). Understanding the terminology related to the broad spectrum of integrative research concepts is essential to the application, communication, and evaluation of research outcomes (Tress et al. 2005). To begin, *multidisciplinary research* is characterized by disciplines

working on the same problem in parallel with multiple disciplinary objectives (Tress et al. 2005, Mauser et al. 2013). In contrast, *interdisciplinary research* includes increased levels of integration between unrelated disciplines and knowledge systems to develop new knowledge in collaboration. Finally, *transdisciplinary research* explores relevant research questions with teams of researchers that also engage non-academic decision-makers, practitioners, and the public (Tress et al. 2005, Mauser et al. 2013). While the research in this dissertation does unite traditional knowledge and non-invasive population genetics in an interdisciplinary approach to organize and understand the biological diversity of caribou and inform management and policy decisions, the research goals did not include the co-implementation of policy outcomes or the innovation of solutions to societal problems which exemplify transdisciplinary research (Mauser et al. 2013, Bennett et al. 2016b).

Recent attention to role of social sciences in conservation points to the importance of increasing engagement and interdisciplinary between the social and natural science traditions to optimize the effectiveness of conservation outcomes (Bennett et al. 2016a, Bennett et al. 2016b). The term social-ecological system has been used to describe the intimate linkages between human societies and nature (Folke et al. 2007, Bodin and Tengö 2012). Interdisciplinary methods can help to address and quantitatively study the social and ecological complexity found within social-ecological systems (Pretty 2011). I employed research methods from both the social and natural sciences that included community-based participatory research methodologies, language-based methods, population genetics, phylogenetics, and visual facilitation. These diverse and overlapping approaches required substantial communication and exchange of information between disciplines and collaborators (Mascia et al. 2003, Adams 2007). Bringing together different knowledge systems can be fundamentally challenging due to underlying differences in

how knowledge is constructed and organized (Usher 2000). I prioritized project design and planning at the beginning of the research process to promote transparent communication among academic researchers, community partners, and the local institutions involved in overseeing the research. I also made extensive use of art and visual methods during the research process to help improve communication, encourage participation, and provide accurate representations of the research progress, language, Dene concepts, and results.

Developing and fostering partnerships is foundational to successful community participation in ecological research (Kassam 2009, Bennett et al. 2016a). The SRRB played a key role in facilitating collaborations by promoting ongoing communication with the public and local research partners, developing connections between various research agendas and other co-occurring projects, and providing context for long-term institutional research strategies and programs. The research in this dissertation builds on previous community-based caribou traditional knowledge research sponsored by the SRRB (Délıne First Nation 2005, SENES Consultants Ltd. 2009, Sahtú Species At Risk Working Group 2013, 2014). Existing community research and community research partners were a critical starting point for positive dialogue and were essential to building support from community members on the direction of future caribou research needs. Because different disciplines and institutions frame questions at different scales and conceptual levels, it was imperative that the research process be iterative and flexible in order for emerging questions and issues to be addressed through dialogue (Turner II et al. 2016). The details and background on the community-collaborative research approaches that I used in this dissertation can be found in Appendix 1.

To characterize the genetic relationship between groups of caribou I worked with the RRCs and local participants to non-invasively collect caribou fecal pellet samples across the

region. The resulting genetic information was added to a long-term dataset of caribou genotypes as part of a comprehensive research program administered by Dr. Micheline Manseau and Dr. Paul Wilson (e.g., Ball 2007, Galpern 2012, Klütsch et al. 2012). Phylogeographic and population genetic analyses can help to delineate population units. I analyzed multiple markers (microsatellites and mtDNA) and used multiple statistical approaches to characterize population structure, examine genetic diversity within and among populations, and identify the evolutionary histories of caribou groups.

Research objectives

The dissertation explores the key theme of caribou diversity through an analysis of the spatial organization of caribou and Dene traditional knowledge related to caribou. Understanding how caribou populations are spatially structured on the landscape is a question of interest to managers, ecologists, and indigenous harvesters. Further, identifying caribou populations is an important priority for management and recovery planning. Within the study region caribou belong to three DUs: barren-ground caribou (DU3), boreal caribou (DU6), and northern mountain caribou (DU7; COSEWIC 2011). Data on the boundaries between these designations is limited and most range boundaries do not include information related to genetic divergence. Thus, understanding the distribution, spatial organization, and the degree of population isolation and connectivity between caribou DUs is integral to understanding how different land-use activities affect caribou population dynamics and how management plans should be implemented. The research also explores Dene people's place-based traditional knowledge, practices, and relationships with caribou and examines how language is used to identify different groups and types of caribou in the region (including descriptions of social dynamics within

groups, spatial dynamics, and historic movements). Traditional knowledge can help facilitate the interpretation of the genetic data. The overall goal of the research was to develop a comprehensive understanding of the identities and relationships among caribou populations and Sahtú Dene and Métis people to inform and prioritize resource management efforts.

Dissertation organization

This dissertation uses an interdisciplinary approach to examine the ecological, geographical, genetic, cultural, and historical components of caribou variation in the Sahtú region of the Northwest Territories. **Chapter 2** focuses on caribou variation through analysis of population genetics and an exploration of the relationships Dene and Métis people establish with animals within bioculturally diverse systems. The analysis examines how traditional knowledge, language, and cultural practices provide key insights into the evolutionary processes that have maintained and created the caribou diversity in the region. We present culturally respectful and relevant descriptions of caribou variation through partnerships that respect the lives and experiences of people that depend on the land. The research makes the case that by prioritizing mutual learning, researchers can broaden their understanding of biodiversity and establish a common language for collaboration. **Chapter 3** explores how the glacial-interglacial cycles of the Pleistocene have shaped the current patterns of variation in caribou in the region. We use Approximate Bayesian Computation to test whether woodland caribou colonized boreal habitats from a single southern refugial source or if independent evolution to a common ecotype resulted from diversification within refugia. Our results reveal that in their northern margin, caribou belonging to the boreal ecotype of woodland caribou evolved independently from the northern Beringian lineage. This contrasts with more southern boreal caribou which belong to a

lineage known to have persisted in sub-Laurentide refugia. The results provide an example of intraspecific parallel origins in caribou and contribute important insights into the importance of intraspecific diversification within large Pleistocene refugial basins. **Chapter 4** examines how art and other visual techniques can be used to develop robust cross-cultural collaborations and externalize the unique heterogeneity of biocultural diversity. We provided constructive ideas for using illustrations, diagrams, and other visual aids to increase research potential during all stages of the research process. Our results point to the potential for art to be used to improve communication, participation, and knowledge production among interdisciplinary research collaborations and across language and knowledge systems. The final dissertation appendixes provide additional information and summary statistics for each chapter.

Contributions of the authors

The three main research chapters of the dissertation were prepared for submission and publication in academic journals and include multiple authors. All authors were involved in the conceptual development of the papers and contributed in various ways during the research and writing phases. Due to the contributions of the coauthors to the information presented in this dissertation, the pronoun ‘we’ will be used throughout. In **Chapter 2**, Jean Polfus planned the research, conducted field work, organized logistics of genetic sample collection, held planning, research and reporting meetings, contributed to lab work, analyzed the data, and wrote the first draft of the manuscript. Micheline Manseau, Paul Wilson, and Deborah Simmons guided research design and implementation. Dene co-authors Michael Neyelle, Walter Bayha, Frederick Andrew and Leon Andrew provided expertise in traditional knowledge, Dene language, and Dene concepts; reviewed the draft manuscript; and guided the research process. Cornelya

Klütsch provided support for genetic data analysis and interpretation. Keren Rice prepared linguistic definitions of Dene words and reviewed the analysis of linguistic data. All authors contributed to and commented on several versions of the manuscript, the review by the journal, and gave approval for the final accepted publication.

In **Chapter 3**, Jean Polfus conducted the research, organized logistics of genetic sample collection, contributed to research design, analysis and data interpretation, and wrote the first draft of the manuscript. Micheline Manseau, Paul Wilson, and Deborah Simmons contributed to analysis approach, study design, and data interpretation. Cornelya Klütsch performed the ABC analysis and aided in data interpretation. All authors provided revisions to the manuscript and gave final approval.

Finally, in **Chapter 4**, Jean Polfus planned the research, designed and developed the visual methods and materials, organized and held meetings, and wrote the first draft of the manuscript. Dene co-authors Michael Neyelle, Walter Bayha, Frederick Andrew, and Leon Andrew attended meetings and shared traditional knowledge, Dene language, and Dene concepts. Micheline Manseau and Deborah Simmons guided the research process and study design. Keren Rice helped with translation of Dene language material. Bethann Merkle assisted with the context of arts-based research methods. All authors contributed to and commented on the final manuscript prepared for publication.

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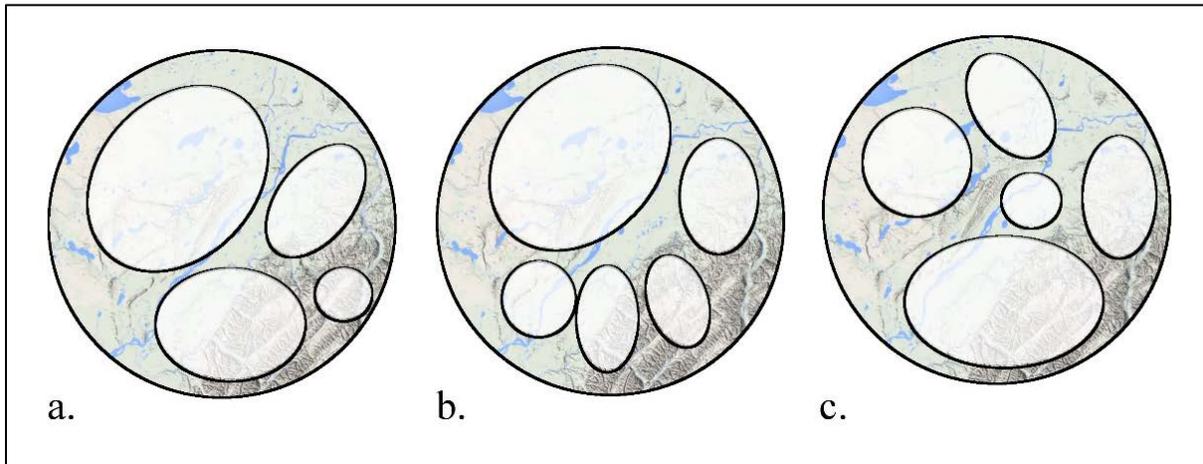


Figure 1-1. Each large circle represents the same hypothetical geographic space which has shaped the observable variation of organisms (not shown) by partitioning processes of gene flow, drift, and natural selection. Patterns in the geographic space can be observed from multiple perspectives: a) might emphasize shared behaviors in relation to other organisms, b) focuses on phenotypic traits that point to an underlying shared evolutionary history, and finally c) examines neutral molecular identities. Importantly, all perspectives provide a unique vantage point from which we can observe the structure of biological variation.

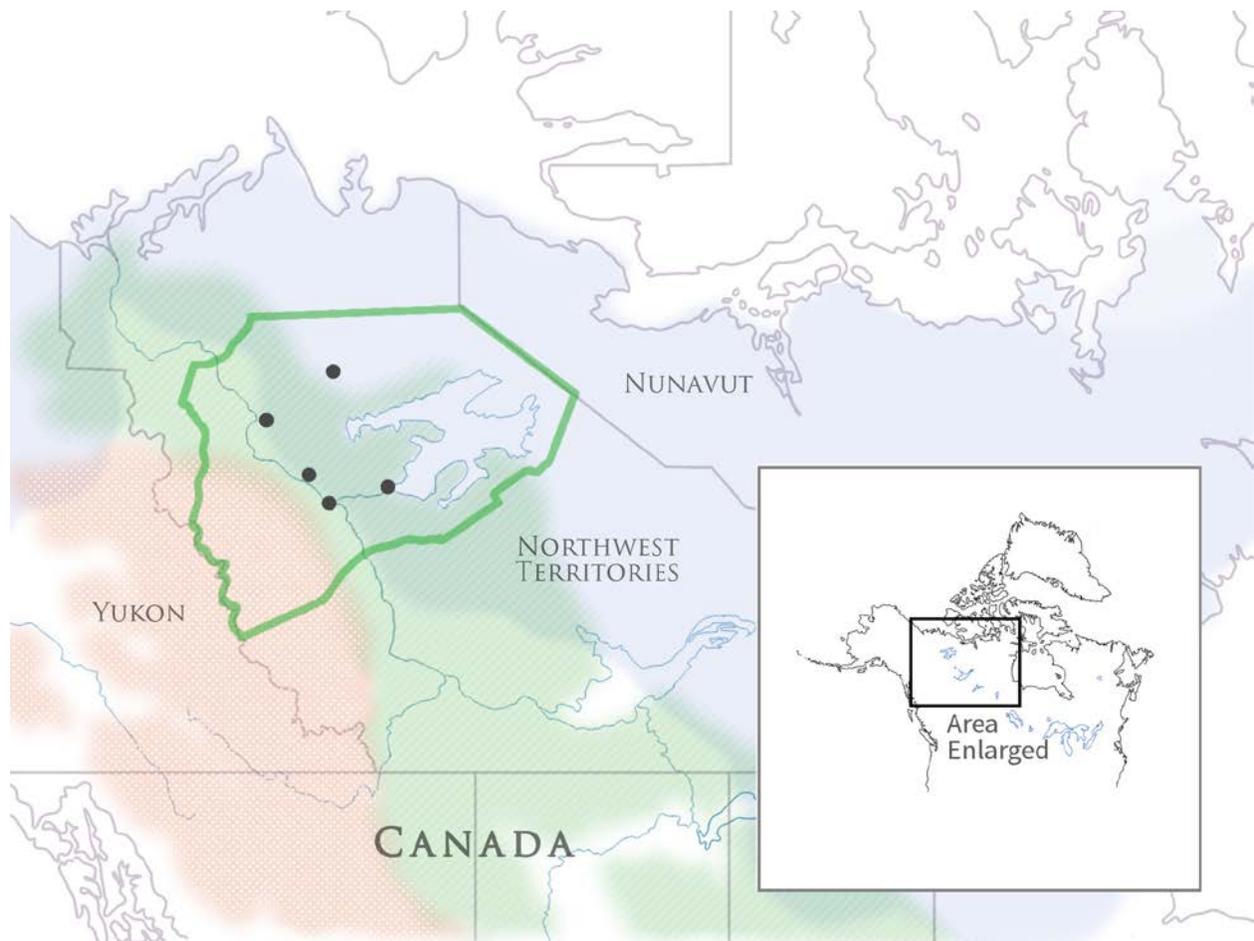


Figure 1-2. Location of the Sahtú region (green border) of the Northwest Territories, Canada. Locations of black dots indicate the five communities of the Sahtú. The shaded regions illustrate the general ranges of barren-ground caribou (blue), the boreal ecotype of woodland caribou (green), and northern mountain caribou (stippled orange) in western Canada.

CHAPTER 2: ŁEGHÁGOTS'ENETE (LEARNING TOGETHER): THE IMPORTANCE OF
INDIGENOUS PERSPECTIVES IN THE IDENTIFICATION OF BIOLOGICAL VARIATION[‡]

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Abstract

Using multiple knowledge sources to interpret patterns of biodiversity can generate the comprehensive species characterizations that are required for effective conservation strategies. Caribou (*Rangifer tarandus*) display substantial intraspecific variation across their distribution and in the Sahtú Region of the Northwest Territories, Canada, three caribou types, each with a different conservation status, co-occur. Caribou are essential to the economies, culture and livelihoods of northern indigenous peoples. Indigenous communities across the north are insisting that caribou research be community-driven and collaborative. In response to questions that arose through dialogue with five Sahtú Dene and Métis communities, we jointly developed a research approach to understand caribou differentiation and population structure. Our goal was to examine caribou variation through analysis of population genetics and an exploration of the relationships Dene and Métis people establish with animals within bioculturally diverse systems. To cultivate a research environment that supported ɫeghágots'enetę “learning together” we collaborated with ʔehdzo Got'ineę (Renewable Resources Councils), elders and an advisory group. Dene knowledge and categorization systems include a comprehensive understanding of the origin, behaviors, dynamic interactions and spatial structure of caribou. Dene people classify tȡdzi “boreal woodland caribou” based on unique behaviors, habitat preferences and morphology that differ from ʔekwę “barren-ground” or shúhta ʔepę “mountain” caribou. Similarly, genetic analysis of material (microsatellites and mitochondrial DNA) from caribou fecal pellets, collected in collaboration with community members during the winter, provided additional evidence for population differentiation that corresponded to the caribou types recognized by Dene people and produced insights into the evolutionary histories that contribute to the various forms. We developed culturally respectful and relevant descriptions of caribou variation through

partnerships that respect the lives and experiences of people that depend on the land. By prioritizing mutual learning, researchers can broaden their understanding of biodiversity and establish a common language for collaboration.

Introduction

Patterns of biological variation are a result of the replication of DNA, the potential for DNA mutations and environmental structure that prevents the complete overlap of groups of organisms (Hey 2001). Significant scientific effort has been allocated toward determining where, within the space of genetic and environmental variation, units emerge that merit identification (Padiál et al. 2010). While the articulation of biological categories is a universal human predisposition (Berlin 1973, Atran 1990), the content of named categories reflects a dynamic exchange between morphological, utilitarian, ecological and perceptual factors, all of which are adapted by different cultures to a particular time and place (Nazarea 2006, Newmaster et al. 2006). The species concept, which has undergone numerous iterations and has been, and continues to be, actively debated by systematists, taxonomists, biologists, and naturalists, illustrates the complexity of assigning objects to categories (Hey 2001). Recently, researchers have begun to acknowledge that many (if not most) species do not have distinct, easy-to-recognize boundaries (Hey 2006, Mallet 2008) and that species may be best described as “poorly differentiated way-stations in a continuous hierarchy of biodiversity” (Mallet 2005:229). However, in order to identify groups that justify protection, such as species or subspecies, scientists and managers require not only a firm understanding of recombination, genetic drift, selection, and gene flow, but also a critical examination of human perception and how people connect with and define their world.

Biodiversity can be categorized in many ways as a result of the inherent complexity and interconnected evolutionary history of life (e.g., introgressive hybridization, horizontal gene transfer, lateral exchange, reticulate evolution, etc.; Mallet 2005, Arnold and Fogarty 2009). Current species taxonomies reflect only one possible grouping structure out of many alternatives

(Atran 1990, Lakoff 1990, Newmaster et al. 2006, Padial et al. 2010). Critics of the hierarchical nature of science-based classification systems cite a lack of flexibility necessary to respond to a world that includes ambiguous boundaries (Hey 2006). The subjectivity inherent in species categories can appear inconsequential when two species or populations are clearly distinct, but in situations involving closely related taxa, intraspecific variation, or geographic overlap, it becomes problematic (Mace 2004). The influence of hybridization and introgression among subspecies, populations and species can be difficult because the conservation of hybrids, which often display a continuum of genotypes, does not fit a discontinuous species-based conservation model (Fitzpatrick et al. 2015). Further, hybridization often necessitates a subjective decision about the “authenticity” of a certain genotype over another and poses a challenge to endangered species policies (e.g., the hybridization of introduced Mallards (*Anas platyrhynchos*) with several species of threatened ducks in New Zealand to the point where all previously considered endemic ducks may be of hybrid origin; Rhymer and Simberloff 1996, Fitzpatrick et al. 2015).

The species *Rangifer tarandus* (known as caribou in North America and reindeer in Scandinavia and Russia) are highly vagile and occur across an extremely diverse spectrum of habitats where they have adapted many different behavioral responses to a range of ecological conditions. Substantial variation in caribou behavior, morphology, life history traits, interactions with other species, movement, diet, and social structures have made attempts to systematically organize and characterize the species challenging. In 1961, Banfield classified *R. tarandus* in North America into 4 divisions based on morphological comparisons: barren-ground caribou (*R. t. groenlandicus* and *R. t. granti*); woodland (*R. t. caribou*); Peary caribou (*R. t. pearyi*) and the extinct Dawson’s caribou that once occurred on the Haida Gwaii islands of British Columbia (*R. t. dawsoni*). A range of subjective subdivisions within Banfield’s designations have since been

applied based on numerous criteria (calving strategies, ecotype designations, seasonal distributions, etc.) resulting in a complicated milieu of inconsistently applied naming conventions that diverge across jurisdictional boundaries. The recent attempt by the Committee on the Status of Endangered Wildlife in Canada to define conservation units for caribou, specifically Designatable Units (DUs – discrete and significant biological units that capture irreplaceable components of intraspecific biodiversity), found that consistent methods and criteria for organizing the variation inherent to the species are not currently available (COSEWIC 2011). Effective categories are needed because units that ignore underlying ecological relationships or misinterpret population structure lead to confusion when implementing recovery plans and conservation policies (Crandall 2009).

For example, in the Sahtú region of the Northwest Territories, Canada, there is considerable overlap among different caribou herds, groups, and types that exhibit unique life histories and have acquired different conservation statuses (Fig. 2-1). In the northern portion of the region, large herds of barren-ground caribou migrate between the open tundra and the boreal forest in response to seasonal pulses of resources and predation pressure (Vors and Boyce 2009, Nagy et al. 2011). In the Mackenzie Mountains, caribou display much smaller scale seasonal migrations between valley bottoms and alpine plateaus (Gullickson and Manseau 2000, Polfus et al. 2011, Letts et al. 2012). Throughout the boreal forest, boreal woodland caribou exhibit sedentary behavior and occur in small groups of ~5-15 individuals (Stuart-Smith et al. 1997, O'Brien et al. 2006, Brown et al. 2007, Courtois et al. 2007). Data on the boundaries and degree of differentiation between these caribou types is currently limited. Understanding how the caribou types are structured in the Sahtú region has legal implications because boreal woodland caribou are listed as threatened by the federal Species at Risk Act (SARA) and the territorial

Species at Risk (NWT) Act and thus warrant specific protection and recovery measures (Environment Canada 2012, Species at Risk Committee 2012). The development of a national recovery strategy and subsequent action plans for boreal woodland caribou conservation has been delayed, in part, due to the complex intraspecific variation that characterizes the species. To date most range boundaries include a poor understanding of long-term caribou movements, gene flow and genetic divergence. Current research examining zones of contact and introgression among caribou subspecies aims to help define evolutionarily significant conservation, management and population units (Weckworth et al. 2012, Colson et al. 2014, Røed et al. 2014, Klütsch et al. 2016); however, alternative sources of knowledge are rarely considered in the context of caribou ecology and conservation (but see O'Flaherty et al. 2008, Mager 2012, Polfus et al. 2014).

Challenges to the classification of *Rangifer* present an ideal opportunity to use multiple knowledge sources to develop a more thorough and complete understanding of caribou population organization and variation (Crandall 2009). Knowledge that arises from indigenous people's ecological relationships is often referred to as traditional knowledge (TK) and encodes ways of knowing and describing environmental diversity (Hunn 2006). While significant scholarly work has defined and critiqued the mechanisms, functions, cultural significance, and cognitive basis of biological classifications (Berlin 1973, Atran 1990, Lakoff 1990, Ingold 2000, Newmaster et al. 2007), there remains space for a more practical consideration of the substantive knowledge indigenous people hold about their environments in the context of conservation (Fraser et al. 2006). Traditional knowledge is a product of a dynamic process of individual engagement with ecosystems that reflects people's capacity to respond to a constantly changing environment (Berkes 2012). Traditional knowledge is neither static nor antiquated. Processes and

institutions guide the production and legitimation of TK as part of a living practice that is constantly updated and renewed (Ingold 2000, Davidson-Hunt 2006). For the purpose of this paper we make the distinction between science and TK. We find it useful not to conflate the two knowledge traditions because the procedures that make up science arose from their own particular social-institutional history and bringing science and TK together requires substantive interpretive and heuristic procedures (Scott 2011). Thus, TK has the potential to provide robust descriptions of species variation that can add value to our understanding of coupled human and natural systems (Fraser et al. 2006, Liu et al. 2007).

Language is one medium by which TK is transmitted and expressed and in the Sahtú it is crucial to the interpretation, organization and articulation of biodiversity (Lakoff 1990, Basso 1996, Hey 2001, Evans 2012). Knowledge holders often need to speak their own language (rather than English) to accurately describe complex components of TK. Examining multiple language systems in parallel allows for descriptions that have the potential to reach beyond one dominant biological classification structure (Davidson-Hunt et al. 2005, Stronen et al. 2014). Languages can express meaning in different ways. This is partially due to the fact that what must be obligatorily expressed in one language need not be obligatorily expressed in another, and thus the structure of the language can implicitly and explicitly affect how speakers engage with the world and influence memory, perception, and categorization (Markman and Hutchinson 1984, Harrison 2007, Deutscher 2010, Boroditsky 2011). Indigenous languages can provide refined and multifaceted descriptions of biodiversity (Hale et al. 1992, Newmaster et al. 2007), alternative ways of examining and relating to non-human animals (Ingold 2011, Miller and Davidson-Hunt 2013) and insight into the underlying processes that create biological structure and drive patterns of biodiversity (Ragupathy et al. 2009, Gavin et al. 2015).

To achieve effective conservation outcomes there is a need to explicitly explore, not only variation itself, but the biocultural forces that shape variation and the relationships people establish within evolutionary systems (Gavin et al. 2015). The concept of biocultural diversity emphasizes the reciprocal relationships and overlapping realms of cultural, biological, and linguistic diversity and the many compelling similarities between languages and species as essential units of culture and nature (Loh and Harmon 2014, Gavin et al. 2015). Recent investigations into the link between biological and cultural diversity have generated important discourse concerning the vital role of TK, language, and diverse knowledge systems in conservation and environmental management (Davidson-Hunt et al. 2012, Gavin et al. 2015).

Land claim settlements across the Northwest Territories have introduced new institutions and governance structures that have the potential to re-frame policies influencing lands and resources. In the Sahtú region, Dene and Métis representatives from local ʔehdzo Got'ıne (Renewable Resources Councils; RRCs) recently passed a resolution that called for a renewed commitment to adopt TK and the laws of the Dene people as the guiding principles for caribou research and management. To support the ambitious goals set forth by the communities we collaboratively developed a research approach to explore questions about caribou variation and differentiation using both traditional and scientific knowledge. We focused on ıghágot'senete “learning together” and acknowledged the complex nature of caribou as part of a dynamic bioculturally diverse system. Our ultimate goal was to support the practices that enhance people’s continued relationships with caribou and promote socially and culturally appropriate solutions to the complex challenges facing caribou conservation. In this article, we discuss the potential for population genetics and TK to deepen our understanding of caribou variation and the robust relationships that people maintain with the species.

Methods

Study area

The Sahtú region surrounds Great Bear Lake and encompasses 280,238 km² of central Northwest Territories (NWT), Canada (Fig. 2-1), an area larger than the United Kingdom with a population of just over 2300 people (Statistics Canada 2012). The current regional boundaries were defined by the Sahtú Dene and Métis Comprehensive Land Claim Agreement that concluded in 1993. Dene people have lived in the region for thousands of years and share a common Sahtú Dene or Athapaskan/North Slavey cultural and linguistic history (Helm et al. 2000). There are currently five communities in the region: Dǎ́lǎᓃ, Tulít'a, Norman Wells (Tǎᓃǎᓃ), Fort Good Hope (Rádelǎ Kǎᓃ) and Colville Lake (K'áᓃᓃ Tǎᓃ). Until the establishment of local government administrations and day schools during the post-WWII period, Dene and Métis peoples led a nomadic existence in a seasonal harvesting cycle (Abel 2005). Despite the shift to a more sedentary way of life in the communities, Sahtú Dene and Métis maintain strong cultural and socio-ecological relationships with the land and wildlife (Andrews et al. 2012a, Andrews et al. 2012b, McMillan and Parlee 2013, Harnum et al. 2014).

There is considerable variation within the Dene language that is spoken across the region, with varieties differing primarily by sounds and vocabulary (Rice 1989). Defining linguistic subgroups of Athapaskan languages is challenging due to historical intergroup communication and overlapping distributions that result in borders which in many ways resemble the ambiguous boundaries of species classifications (Krauss and Golla 1981, Helm et al. 2000). Language in the Sahtú region varies based on specific family roots and community social linguistic units. The main dialect groups are flexible and differ from each other more or less based on family groups

and historical relationships: 1. K'áálq (Willow Lake), Dəoga (Mackenzie River), and Shúhta (Mountain) spoken in Tulít'a; 2. Sahtú (Bearlake) spoken in Délı̨ne; 3. K'áhsho (Hare) and Dala spoken in Fort Good Hope and Colville Lake respectively (Harnum et al. 2014). Fluency in Dene language varies greatly across generations and communities. Elders retain the highest rates of fluency while young people are less likely to speak Dene as their first language. In the Sahtú, an estimated 1000 people are able to converse in the language. In 2014, Délı̨ne reported the highest percent of indigenous people over the age of 15 that could speak Dene (78%; Northwest Territories Bureau of Statistics 2014).

The subarctic landscape of the Sahtú is diverse and encompasses four major ecozones: southern arctic, taiga plains, taiga shield, and taiga cordillera. At treeline, north of Great Bear Lake, tall shrub tundra ecosystems of dwarf birch (*Betula glandulosa*) and willow (*Salix* spp.) transition into boreal forest dominated by conifers: black spruce (*Picea mariana*), tamarack (*Larix laricina*), and white spruce (*P. glauca*). Deciduous stands of trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), mountain alder (*Alnus tenuifolia*) and willow are found in drier and warmer sites. Lichens, mosses, dwarf birch, cotton-grass (*Eriophorum* spp.), Arctic white heather (*Cassiope tetragona*), Labrador tea (*Ledum groenlandicum*), and multiple *Dryas* and *Vaccinium* species make up the ground cover. Dynamic fire cycles establish and control energy flows in the boreal forest. The region contains zones of continuous, extensive discontinuous and intermediate discontinuous permafrost (Heginbottom 2000). The climate is typified by long, cold winters and short, warm summers. Precipitation is low and restricted by a rain-shadow in the Mackenzie Valley which generates milder climates than those to the east and west (Dyke 2000). Mean temperature in Norman Wells is -27.4°C in January and 16.7°C in July (Kokelj 2001).

The Dehcho (Mackenzie River) that flows into the Beaufort Sea dominates the hydrology of the region. Its watershed is the largest in Canada and covers approximately 1.7 million km² (Kokelj 2001). Sahtú Deh (Great Bear River), a major sub-basin, flows from an outlet in Great Bear Lake near Déłıne over low relief landscape and enters Dehcho at Tulít'a. West of Dehcho, the Mackenzie and Selwyn Mountains form the northernmost extension of the Rocky Mountain range and extend along the Yukon/NWT border from British Columbia to the Peel River plateau. Climatic zones vary according to the elevation gradient which ranges from 2,972m (highest peak) to foothills between 200-800m. Major tributaries flowing from the mountains into Dehcho include Begáádó (Keele), Nóggha Chılıne (Carcajou), and Fahfá Nıłıne (Mountain). The Norman Range and Franklin Mountains, which parallel the east side of Dehcho from Fort Good Hope to Wrigley, form a series of steep bedrock ridges and plateaus with elevations of ~1000m (Morgan and Anderson 2013). The region has extensive karst formations including prominent sinkholes, caves, dry valleys, and gorges (Ford 2008).

Ungulates in the region include caribou, moose (*Alces alces*), muskox (*Ovibos moschatus*), mountain goats (*Oreamnos americanu*) and Dall sheep (*Ovis dalli*). The large mammal predator community consists of grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolverines (*Gulo gulo*), wolves (*Canis lupus*), and Canada lynx (*Lynx canadensis*).

Research design

Our community-collaborative research project was developed and implemented within the current institutional and political structures of the Sahtú Land Claim and the Mackenzie Valley Resource Management Act (1998). Under this political structure the ʔehdzo Got'ıne Gots'é Nákedı (Sahtú Renewable Resources Board; SRRB) and the five local RRCs of the Sahtú

Region are responsible for managing renewable resources in the region including wildlife and habitat. The research project initiated a collaborative partnership between the SRRB, RRCs, university researchers, and the NWT Department of Environment and Natural Resources (ENR). We developed partnerships with key knowledge holders, elders and an advisory group with support from the formal institutional structures. In September 2012, the Sahtú RRCs passed a joint resolution supporting the adoption of TK and Dene law as essential components of caribou research. Our research project is a direct outcome of the resolution and was designed to support the initiatives proposed by communities in line with the principals of community-based participatory research frameworks and methodologies (Appendix 1; Hall 1979, Ferreira and Gendron 2011).

Our research included community members in all phases of the research process and created an open and transparent dialogue between scientific and traditional knowledge (Cruikshank 1981, Cornwall and Jewkes 1995). We prioritized *łeghágots'enetę* “learning together” and knowledge generation in an attempt to develop a richer, culturally respectful and relevant understanding of caribou variation. The principles and protocols governing the research were covered by a multiyear research license from the Aurora Research Institute (15217, 15443, and 15597), wildlife research licenses from ENR (WL500104, WL500307) and a University Ethics Protocol (J2012:202).

In December 2012, we held research planning meetings in Norman Wells, Fort Good Hope, Tulít'a, and Délı̄ne to discuss the project and plan for winter field work. Discussions facilitated the development of research priorities, research questions, and appropriate methods for the current and future monitoring of caribou populations. In January 2013, we held a series of RRC and public meetings to plan for winter sampling, build awareness for the program and train

community members in sampling techniques. We developed a Memorandum of Understanding with each RRC to confirm the governing principles of the research, budgets, research methods, intellectual property rights and administration of the project. Subsequent RRC meetings were held in each community (including the addition of Colville Lake) to continue to guide the research during the winters of 2013 and 2014.

In alignment with our approach of *łeghágots'enetę* “learning together” we prioritized opportunities that allowed for the establishment of collaborative relationships between an interdisciplinary group of community researchers, local experts, and academic researchers (discussed in more depth in Appendix 1). We promoted on-going communication with the public through outreach and relationship building in the communities. Local experts shared knowledge about caribou histories, movements and identities during formal and informal interactions on the land. The knowledge helped to guide sample collection and identified concepts and ideas that were discussed in depth at focus group meetings, with the advisory group, and among co-authors. All community participants received honoraria for their time.

Focus group meetings

We held focus group sessions (Agar and MacDonald 1995, Morgan 1996, Berman and Kofinas 2004) to build a comprehensive understanding of the origin, dynamic interactions and spatial structure of caribou in the Sahtú region. Workshops lasted between one and two days. Three to ten local experts, selected in partnership with the local RRCs, participated in five focus group sessions held in each of the communities (total 39 people) in April of 2013. Focus group participants had extensive firsthand knowledge of caribou populations in the region. Interpreters helped to develop appropriate metaphors to describe genetic concepts in ways that resonated

with community members. We found that simultaneous interpretation was often unsuccessful when explaining complex scientific topics. Instead, we more often used sequential interpretation which allowed more time for ideas to be heard and understood (many participants were bilingual). We also worked with community researchers and interpreters to build a robust understanding of Dene concepts and avoid back-translations from English. Focus group meetings included significant discussions in Dene language.

At meetings we provided an overview of the research process and described the methods and preliminary results. We documented information through word maps, flow charts, diagrams, geographic maps (Google Earth 7.1.5.1557) and note taking. We digitally audio-recorded meetings with participant consent. Consistent with the iterative nature of our research process, we concluded focus group meetings with a discussion of how the project could be improved. Key sections of the meetings were later translated and transcribed by local language specialists in English.

Genetic sampling

Community members, researchers, collaborators, and industry monitors collected caribou fecal pellets non-invasively during the winters of 2013 and 2014 by gathering frozen pellet piles found on the snow in plastic bags. In general, hunters and trappers collected samples while traveling on skidoo trails, winter roads, seismic lines, and traditional trails during normal on-the-land activities. The sampling area represented the range of all three types of caribou in the region. We encouraged community members to help with sample collection during outreach at public meetings, through promotional posters, regional newspaper stories, on local radio, and in Facebook posts. Community members received a \$25 gift card for gas at a local gas station for

each caribou fecal pellet sample they provided. The RRCs and Norman Wells ENR staff oversaw sample collection, data entry, and gift card distribution. Collaborations with industry partners also allowed for targeted sampling by helicopter to locate areas of caribou activity (tracks, cratering, etc.) during the winter of 2013. In April 2014, we spent an additional three days flying by helicopter with participants selected in collaboration with the RRCs of Fort Good Hope, Tulít'a and Délı̄në to collect scat samples and fill sampling gaps. We also collected muscle tissue samples and blood strip samples from hunted animals in collaboration with a caribou health monitoring study (Brook et al. 2009). Finally, we included caribou fecal samples collected in Nahanni National Park Reserve in the southern Mackenzie Mountains through collaborations with Parks Canada.

Microsatellite genotyping

We followed microsatellite genotyping protocols that had been established as part of a long term caribou genetic database to ensure the production of high quality genetic profiles (Ball 2007, Ball et al. 2010, Galpern et al. 2012b, Hettinga et al. 2012, Klütsch et al. 2012). To isolate DNA we swabbed and amplified the mucosal layer covering the caribou fecal pellets. We genotyped a panel of 9 microsatellite loci (BM848, BM888, MAP2C, RT5, RT6, RT7, RT9, RT24 and RT30; Bishop et al. 1994, Wilson et al. 1997, Cronin et al. 2005). In May 2013 swabbing took place in Norman Wells where we worked with local students and trained technicians to build capacity in the communities and to continue to foster collaboration during the research process. Subsequent genetic analysis took place at Trent University. Extraction protocol followed Ball (2007) and profiling procedures can be found in Galpern et al. (2012b) and Klütsch et al. (2016). Electropherograms were scored by at least two individuals with

GENEMARKER v. 1.9.1 (SoftGenetics, LLC) to determine allele sizes. Samples included in the final dataset had a minimum of eight successfully amplified loci. We used AlleleMatch 2.5 (Galpern et al. 2012a) to screen profiles for genotyping errors, remove duplicate profiles and identify the number of individual caribou sampled. Only one sample from each individual caribou was included in subsequent analysis.

Mitochondrial DNA (mtDNA) sequencing

Genetic analysis of nuclear and mtDNA (mitochondrial DNA), larger sample sizes and improved analytical methods have influenced our understanding of caribou taxonomy and evolutionary history in North America (McFarlane et al. 2009, Klütsch et al. 2012, Mager et al. 2013, Yannic et al. 2014). Specifically, analysis of mtDNA has revealed two distinct phylogenetic groups of caribou that represent separate northern and southern glacial refugia during the Pleistocene. Many of the boreal woodland caribou in the southern Canadian provinces originated south of the Laurentide ice sheet that covered most of present-day Canada (North American lineage; NAL), while barren-ground caribou likely originated in the northern unglaciated refugium of Beringia and the Canadian high arctic (Beringian-Eurasian lineage; BEL, McDevitt et al. 2009, Klütsch et al. 2012). To examine phylogeographic structure we amplified and sequenced a 429 bp mtDNA control region fragment using the primers: L15394:5' - AAT AGC CCC ACT ATC AGC ACC C - 3' and H15947:5' - TAT GGC CCT GAA GTA AGA ACC AG - 3' (Flagstad and Røed 2003). Only samples from individual caribou were sequenced. We followed lab procedures outlined in Klütsch et al. (2012). We used the program BioEdit 7.2.5 (Hall 1999) to check and align sequences. Mutations were manually double-checked and all newly identified haplotypes were re-sequenced to confirm their identity.

Genetic analysis

We used the program Structure 2.3.4 (Pritchard et al. 2000) to test for population subdivision and assign individual caribou to inferred subpopulations (Falush et al. 2003). We performed five runs with 1,000,000 burn-in iterations and 10,000,000 Markov chain Monte Carlo (MCMC) repetitions. We varied the number of K between 1 and 15 under the admixture model with correlated allele frequencies, and specified no *a priori* models of subpopulation structure. We plotted the mean and variance in likelihood per K using Structure Harvester v0.6.94 (Earl and vonHoldt 2012). We found the average individual membership coefficients across the five iterations using the programs CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) and DISTRUCT 1.1 (Rosenberg 2004). We mapped the structure output by interpolating the average probability assignment score using the inverse-distance-weighted interpolation in ArcGIS 10.1 (ESRI, Redlands, CA) and confining the interpolation to sampled locations (Twomey et al. 2014).

We assessed genetic diversity by calculating genetic indices of the structure informed populations with GenAlEx 6.501 (Peakall and Smouse 2006, 2012) and HP-Rare 1.1 (Kalinowski 2005). We tested for significant deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) per locus and population using GenePop 4.2 (Rousset 2008). We used SPAGeDi 1.5 (Hardy and Vekemans 2002) to test the microsatellite pairwise differentiation with F_{ST} and R_{ST} and used ARLEQUIN 3.5.2.2 (Excoffier and Lischer 2010) to test the mtDNA pairwise differentiation (Φ_{ST}) and analysis of molecular variance (AMOVA; see Klütsch et al. 2016 for further details).

Collaborative analysis

We analyzed information shared during focus group sessions using a combination of thematic analysis and modified grounded theory methods to identify important concepts and themes (Glaser and Strauss 1967, Bernard 2002, Berman and Kofinas 2004). We used the program NVivo (QSR International Pty Ltd. Version 10) to code meeting notes, transcripts, and other TK reports and publications. Hierarchical categories emerged through the process of coding and were developed into potential themes as the ideas became more concrete through repeated identification. To support a collaborative production of knowledge we facilitated a process for co-analysis of the TK and genetic data. With the help of RRCs, individuals were selected from all Sahtú communities for their expertise and interest in participating in an advisory group. The advisory group's role was to guide the project, ensure that Dene knowledge was properly and respectfully interpreted, and provide the TK context needed to help accurately interpret the genetic data. We discussed TK themes, language, and genetic results in two separate 3-day meetings to clarify and develop important concepts (Fig. A1-1 and A1-2). Our first advisory group meeting, held in June 2014, included 7 participants who helped plan and select additional elders to participate in a follow-up meeting. The meeting was transcribed and coded. The second meeting was held in February 2015 and included 11 participants.

We employed what we call a language-based methodology by working to elucidate conceptual Dene TK needed to ground the concepts and themes. Elders often requested to speak only in Dene language when discussing TK. Walter Bayha uses a translation of the teachings of his Shúhtagot'ine grandfather, Joseph Bayha, to explain this affinity, "Our history is written on the land. The language comes from the land." Dene knowledge holders stressed the importance of respecting dialect differences and were very careful to avoid making assumptions about how

speakers of other dialects would express a word or concept. The advisory group agreed that in general it is best to defer to Dene words in a dialect with a direct relationship to the caribou population being discussed. In this paper, we generally use Shúhta (S) dialect when referring to caribou in the mountains and Sahtú/Déłıne (D) dialect with respect to barren-ground caribou terminology. We also include K'áhsho (K) words where possible (Fig. 2-2).

The advisory group focused on key concepts and ideas from previous focus group meetings, TK literature, and publications. We used visual facilitation techniques to guide the advisors to expand on important topics and explain the genetic data. We paid special attention to clarifying Dene TK and descriptions of the types of caribou found in the Sahtú region as well as presenting our preliminary interpretation of the genetic data to help assess how appropriate our inferences were with respect to TK of caribou ecology in the region. Beyond the two formal meetings, several of the advisory group members have continued to guide the research, interpret genetic data, work on the details of Dene language translations, review drafts of manuscripts, co-present the research in schools and during public presentations, and co-author this manuscript.

Results

Traditional knowledge

During focus group meetings elders continually expressed their personal relationship with caribou as being crucial to understanding caribou knowledge. One example of this association was described by Alfred Taniton as bedélé t'á núzho (D) that translates to “we grew up with their blood” (Fig. 2-2). Alfred Taniton said, “We were raised with the blood from the caribou. In the past, the people have always survived because of the blood of the animals.” The intimate interaction between human and non-human animals highlights how many indigenous people

recognize the importance of their relationships with other beings on a daily basis. The concept behé ts'enézhq (D) “we grew up with them,” or as Walter Bayha translated, “we are people with them” – further illustrates how Dene people relate to caribou as unique entities – capable of intelligence, identity, perception, self-awareness, rationality, and intentionality.

When Dene people relate to non-human animals autonomously they follow important Dene laws regarding bets'erihchá (D) “respect” and łeghát's'eredı (D) “we give to each other.” Dene people recognize that individual animals have unique perspectives that allow them to gain knowledge and intelligence in distinctive ways (Legat 2012). Elders repeatedly state that caribou are their own bosses and cannot (and should not) be controlled by people. Rather, Dene laws provide guidance for mutual respect and honor that require that Dene take care of caribou so that caribou will reciprocally provide for them. As Gordon Yakeleya stated the following:

It's very important that we look after the animals, we have to have respect for them. There's a reason why they do what they do. They want to survive like we want to survive. It's the same thing. That's what my mom and dad always said: ‘Animals are like human beings.’ They do everything for a reason, just like we do. Like we go to store, they get food for the whole winter. They raise their young ones and teach their young ones. We do the same thing.

Fundamental to the Dene relationship with caribou is a profound knowledge of caribou morphology, behavior, and habitat preferences. Dene people identify three main types of caribou in the region: shúhta ʔepé (S) “mountain caribou”, ʔekwé/ʔedə (D/K) “barren-ground caribou” and tɔdzı “boreal woodland caribou” (Fig. 2-2). Participants describe tɔdzı as bekwı dezene (D) “darker colored/having a dark head,” larger and heavier than ʔekwé. Shúhta ʔepé are identified by their large size and close association with the mountains. The caribou types can also be distinguished based on their tracks (size, shape, and the encoded behavior) and their general

location. Though the ranges of t̥dzɪ and ʔekwé/ʔedə (D/K) overlap in many areas during the winter, knowledgeable hunters and elders are able to distinguish between the types. For example, Gabe Kochon of Fort Good Hope described a situation where he once saw a very large male t̥dzɪ (that was a dark color) in the center of a group of female barren-ground caribou during rut many years ago. Hunters have even reported being able to distinguish types by the taste of the meat. Interestingly, some Shúhtagot'ıne elders describe a fourth type of caribou called t̥nat'əa (S) “the fast runners” that live in the Mackenzie Mountains, migrate long distances, and are identified by particular morphological markings.

While there are dialect differences in the words used to refer to barren-ground caribou, the classificatory term t̥dzɪ “boreal woodland caribou” is shared across the region and mirrors the caribou population’s distribution. The word t̥dzɪ is also found in the T̥łch̥ language of central NWT and the second part of this word, dzɪ, is commonly associated with Athapaskan caribou words and is found in many related languages including T̥łch̥, Dene S̥ı́né, and languages of the Yukon, Alaska, and British Columbia. Further, in Déłıne the word ʔekwéwa (D) can be used when discussing different types of caribou and translates to “the real (or the original/prototypical) caribou” which links the language with the histories of the caribou. Gabe Kochon of Fort Good Hope also explained through translation that the “regular” caribou have always been in the north (living in the barren-land north of Fort Good Hope) whereas t̥dzɪ probably had a different origin.

Knowledge of differences in behavior between different caribou types is essential to successful hunts. Dene hunters describe how t̥dzɪ react much more strongly to the presence of humans than ʔekwé or shúhta ʔepé. Focus group participants explained that to successfully hunt t̥dzɪ it is necessary to anticipate the animal’s behavior. They used the Dene phrase goecha fehtə

(S) to describe a situation in which a t̥ɔdzɪ will loop back on his or her own trail so he/she can rest (lie down) in a sheltered area downwind from his/her path and thus be alerted to the scent of potential predators that might be following his/her tracks. The hunter must react by predicting the caribou's behavior and looping around behind to ensure that the animal can't smell the hunter before they can take a shot. In Dene, this can be described as goecha gots'anele (S) "to hunt from downwind." This behavior is also described for moose, but not ɤekwé or shúhta ɤepé.

Interestingly, a similar word is found in the placename Gocha Túé (D) that was first translated in the 1860s by French Oblate missionary Father Émile-Fortuné Petitot as Shelter Lake (and which he renamed Lac Ste-Thérèse/Lac Sainte-Therese; Petitot 1893). Walter Bayha was able to use Petitot's translation to uncover the obscured meaning of the placename through the word 'gocha' and the sheltered snowdrift-less characteristics of the lake where he spent time when he was young.

Monitoring caribou population fluctuations has been imperative to Dene survival for millennia (Beaulieu 2012). Over time, significant migrations and range-shifts have occurred between caribou groups. Dene descriptions of large-scale caribou movements help explain current caribou distribution, temporal patterns, and can be used to predict future movements. Uncommon movements of barren-ground caribou herds that winter around Great Bear Lake are often recalled and discussed because they can influence caribou health and hunting methods. For example, Gordon Yakeleya remembers how in the winter of 1988 barren-ground caribou migrated all the way down to K'áálq Tué (Willow Lake) near Tulít'a and displaced resident t̥ɔdzɪ. In Fort Good Hope, elders speak about a large herd of caribou that crossed the Dehcho and headed into the foothills of the mountains many years ago. Gabe Kochon said that they never

saw the entire herd return or migrate back across the river. He related the following in Dene language:

There was a lot of them, I have witnessed the caribou crossing ... ice, even though it was broken up, there was lots of them... Many years ago, the caribou crossed to the other side.... They have been gone a long time and people are saying that they have become lots again and they have been using that area for calving ... This is according to the elders and they also say that they will never disappear.

Microsatellites

We collected caribou scat samples from the Sahtú region and Nahanni National Park Reserve with the cooperation of ~100 community members and project collaborators including grade school and high school students, hunters, trappers, environmental monitors, researchers and industry partners. We obtained 1036 caribou fecal samples, 96 caribou tissue samples, and 16 caribou blood strips from localities across the Sahtú region and Nahanni National Park Reserve (Fig. 2-1). A subset of these samples were analyzed and 996 were successfully amplified at >8 loci and included in the analysis. We identified 555 individual animals (47% female, 41% male, and 12% unknown gender). Missing data in the microsatellite dataset was low (3.43%). Average number of alleles per locus was 20 across all individuals (Table A2-1). We did not find evidence for systematic deviations from HWE in specific populations (4/27 cases were significant after Bonferroni correction) or LD (no cases significant).

Structure analysis identified $K=2$ as the highest level of substructure (using the ΔK criterion) that corresponded to a boreal woodland group and a mountain/barren-ground group (Fig. A2-1). Further finer-scale structure of $K=3$ corresponded with an additional split between mountain and barren-ground (Fig. 2-3, Fig. A2-2). These partitions were largely concordant with the TK on caribou types in the region, supporting an ecological foundation for three inferred

groups that represent clusters of 1) barren-ground caribou; 2) boreal woodland caribou; and 3) mountain caribou (Fig. 2-3). The barren-ground population had the highest levels of allelic diversity and heterozygosity (Table 2-1). Pairwise comparisons between groups (F_{ST} and R_{ST}) indicated low levels of differentiation, though the boreal woodland group was the most differentiated from the other two types (Table A2-2, A2-3).

mtDNA

We identified 69 mtDNA control region haplotypes from 337 individual caribou (Table 2-2, Fig. A2-3). We fit the mtDNA data into the well-resolved phylogeny of NAL and BEL (see Klütsch et al. 2012, Klütsch et al. 2016). Unlike the nuclear markers (microsatellites) that showed intraspecific divisions between types at the regional scale – the phylogenetic mtDNA analysis revealed that caribou of the Sahtú belong predominantly to the BEL (96.7% Beringian). However, very few haplotypes ($n=12$) were found in more than one of the three clusters identified by structure (Fig. A2-3). Most haplotypes were non-overlapping, signifying long-standing diversification among the types. We identified only 3 NAL haplotypes (in 11 caribou) in the study area, most belonging to haplotype 50 ($n=9$ boreal woodland caribou) in the Sahtú region (Fig. A2-3). This was an especially surprising result and suggests that boreal woodland caribou in the northern extent of their range are distinct from more southern boreal woodland caribou that generally belong to the NAL (Klütsch et al. 2012). Pairwise comparisons using the mtDNA data (Φ_{ST}) were low but significant (Table A2-4) and showed the strongest differentiation between boreal woodland and mountain, and barren-ground and mountain which may suggest that the mountain group have been historically isolated. The AMOVA of the three

groups revealed that ~14% of the mtDNA genetic variation was found among populations (Table A2-5).

Caribou spatial diversity

Collection sites were distributed across the range of all types of caribou in the Sahtú region (Fig. 2-3) and were focused on; traditional hunting areas in the mountains (along the Begáádá “Keele” and Nóggha Chilne “Carcajou” Rivers, Tets’ehxe “Drum Lake,” and Canol Lake), Nahanni National Park Reserve, the boreal forest in the Mackenzie Valley, and the winter-ranges of the Bluenose West (area surrounding K’áhbamí Túé “Colville Lake,” Nılın Túé “Lac Belot” and Tashín Túé “Lac Des Bois”) and Bluenose East (ʔehdaḷa “Caribou Point” and around Délıne) barren-ground caribou herds.

Strikingly, the spatial distribution of the boreal woodland genetic cluster encompassed the known range of boreal woodland caribou and was restricted to the boreal forest of the Mackenzie valley (Fig. 2-3). While the geographic cohesion was strong there was overlap with the two other clusters that demonstrates at least some level of intergradation between the types. It is well known that barren-ground caribou herds often overlap in distribution with the much less numerous boreal woodland caribou in the winter. However, as described above, knowledgeable hunters are able to distinguish between the types and this was also demonstrated by the genetic results. In the winter of 2013, Wilbert Kochon, a Colville Lake hunter, killed three caribou, which he identified as t̄dzı, in an area where overlap with barren-ground animals was clearly occurring (based on tracks and reported sightings). Later, genetic analysis of tissue samples from the three caribou indicated they clustered with the boreal woodland group (average probability of assignment was 0.942 to the boreal woodland cluster). Interestingly, the few samples collected

along the Mackenzie River near Nahanni National Park Reserve also clustered most strongly with the boreal woodland group (Fig. 2-3).

The spatial boundaries between the barren-ground and mountain clusters were less distinct, however the two groups generally occur in the vicinity of Great Bear Lake and within the Mackenzie Mountains, respectively (Fig. 2-3). Admixture is apparent throughout the Mackenzie Mountains as well as in the winter-ranges of the barren-ground herds. Interestingly, genetic analysis of the 9 individual caribou sampled in the foothills of the mountains across from Fort Good Hope revealed that the group was genetically more similar to the barren-ground cluster than the mountain cluster. This coincides with the event described by Gabe Kochon about the historic movement of a large group of barren-ground caribou that crossed the Dehcho (Fig. A2-4).

Discussion

In this study, we used a participatory approach to examine the biological variation of caribou populations of the Sahtú region of the Northwest Territories. Our community-collaborative research engaged local indigenous experts in all stages of the project and generated results that united Dene TK and population ecology. The participatory framework and iterative methods generated space for the refinement of collaborative research questions and allowed for a rigorous knowledge co-production process. Our results provide evidence for genetic, linguistic, historical, phenotypic and behavioral differentiation among the caribou types in the region. By recognizing the lived experience and TK of indigenous people we were able to develop more profound understanding of caribou ecology through which we were able to more accurately interpret the population genetic results. The genetic subpopulation structure corresponded to

caribou types that are recognized and distinguished by Sahtú Dene and Métis people through their language. Detailed descriptions of t̥dzı “boreal woodland caribou,” ʔekwé (D) “barren-ground caribou,” and shúhta ʔepé (S) “mountain caribou” denote quantifiable characteristics that categorize caribou in the region.

Dene concepts reflect ecological processes and relationships that bring the complexity of dynamic biocultural systems to light. The consistency of the word t̥dzı across all Sahtú region dialects as well as the Tłıchǝ region may suggest stability of the boreal woodland caribou phenotype in the region (though more research is needed to understand the contrasting pattern of variability in barren-ground nomenclature). Interestingly, we found substantial genetic differentiation between t̥dzı and other caribou in the microsatellite genetic structure (Fig. 2-3). This is surprising because in other areas of North America where overlap among caribou types occurs, such clear delineation is not observed (Boulet et al. 2007, Klütsch et al. 2016, Pond et al. 2016). Thus, even in the face of extensive overlap and known mixing with barren-ground and mountain caribou populations (described by local Dene people), there are likely important adaptive traits that are necessary to retaining the behavioral and genetic characteristics of t̥dzı. Mechanisms that can produce intraspecific population structure across continuous habitats include isolation by distance, divergence with barriers, drift after expansion and local evolutionary adaptation (Puckett et al. 2015). In British Columbia, strong differentiation between wolf populations, that are capable of large dispersing movements, has been attributed to evolutionary adaptation to different ecological conditions (Stronen et al. 2014).

It is likely that the differentiation between t̥dzı and other types of caribou in the region is due in part to ecological divergence. Dene knowledge of the association between t̥dzı and the boreal forest is ubiquitous across the Sahtú region and was recorded as far back as the 1860s

when Petitot documented Dene language and culture during his travels as a missionary (Moir 1998). Petitot's writings include descriptions of woodland caribou as loners that lived in the forests (Petitot 1893). Knowledge about differences in behavior among the types of caribou that occurred in different habitats was crucial to Dene survival. Historically, some of the most renowned Dene hunters were those who could successfully hunt and kill the large and widely dispersed tōdzi.

The more closely people associate with non-human animals, the more intimate and detailed the knowledge becomes (Brightman 2002). As Fred Sangris, a Yellowknives Dene, said, "We learn by being in the field, by being with ekwó [barren-ground caribou] all the time" (Sangris 2012:77). The historic caribou movements only observed by people with intimate knowledge of the environment also played an important role in refining our questions and methods. Gabe Kochon's refined and detailed knowledge of historic caribou movements was crucial to our decision to collect samples from that specific region of the mountains. The information provided by the TK also allowed us to accurately interpret the genetic patterns that otherwise would have been difficult to understand, and supported the historic occupancy of distinct caribou groups in the region.

Likewise, Alfred Taniton's description of growing up with the blood of the animals demonstrates how Dene people's survival and ways of life are linked with wildlife. Historically, people traveled across the land to hunt caribou for essential food, clothing, and tools and these practices are part of the expression of their identity. The depth of Dene people's relationship with caribou is revealed within Dene language. Dene language includes numerous descriptors that help facilitate communication and improve hunting success. Language can also provide clues to the histories of the caribou through descriptions like ʔekwéwa "the original or prototypical

caribou” that is used in Délı̨ne to refer to barren-ground caribou and inform alternative ways of classifying the relationships between caribou types. While it is difficult to determine the exact time-frame reflected in the language, it is well established that Dene people have a substantial history with caribou, and barren-ground caribou in particular have been a crucial and relatively consistent resource for at least the last 8000 years (Gordon 2003, Gordon 2005, Andrews et al. 2012b, Beaulieu 2012).

The rich vocabulary of Dene caribou words points to the ease with which TK holders are able to describe complex behaviors and actions in Dene language that are difficult and unwieldy to depict in English. The use of words like goecha gots'anele in the context of hunting are understood by a relatively small portion of community members and require significant discussion in Dene language with elders, knowledgeable hunters and interpreters to capture the detailed nuances in English. Conducting work in both Dene language and English was a consistent challenge. However, the dialogue and back and forth that was required to refine terms and concepts allowed us to come to a common understanding and identify deeper ecological connections that might not be apparent on the surface. As Walter Bayha pointed out, “If I didn’t speak the language I wouldn’t be able to make these connections.” Thus, the examples we provide show that Dene language is deeply adapted to the environment that it evolved in and that a focus on Dene language, facilitated by the distinct disciplinary backgrounds of our research team, is one of the most important contributions of the collaborative work (see Appendix 1 for more information).

The complex nature of caribou substructure is further revealed by the differences between genetic marker types. Examining multiple markers concurrently can provide information about how phenotypic differences may be contributing to historical isolation and present patterns of

gene flow (Wood et al. 2014). In the case of t̥dz̥ in the Sahtú, the mtDNA haplogroups do not coincide geographically with the microsatellite markers. Similar divergence among markers has been shown in shovel-nosed snakes (Wood et al. 2014) and chipmunks (Good et al. 2008, Hird and Sullivan 2009). Surprisingly, results from the pairwise mtDNA analysis indicated that boreal woodland/t̥dz̥ and barren-ground appear to be more closely related than either are to the mountain group (Table A2-4). Recent research suggests that mtDNA can introgress quickly, even at low levels of gene flow, while other loci remain resistant to introgression (Chan and Levin 2005, Hird and Sullivan 2009). Thus, one possible explanation for the phylogenetic pattern present in t̥dz̥ is potential historic introgression with northern Beringian lineage animals. Alternatively, the boreal woodland caribou/t̥dz̥ phenotype may be an independent derivation from the Beringian lineage with little or no contribution from southern evolved boreal woodland caribou that carry NAL haplotypes. Analysis of competing evolutionary models will help identify and date divergence events and historical introgression between populations that have contributed to the current spatial genetic variation (e.g., Klütsch et al. 2016).

Variation below the species level is an important component of biodiversity because it provides the genetic variation required for incipient speciation and local genetic adaptation (Wood et al. 2014, Mee et al. 2015, Hamilton and Miller 2016). Cryptic intraspecific diversity, as is displayed between caribou ecotypes and subspecies (Pond et al. 2016), can be especially contentious because it is not always clear how to best identify, delimit or maintain genetic lineage diversity (Mace 2004, Wood et al. 2014, Fitzpatrick et al. 2015). Further, from a purely scientific perspective, there can exist multiple valid interpretations because rules for finding discontinuity in genetic or spatial ecological data are at some level arbitrary. Combining multiple knowledge systems can help to provide complementary criteria for designating distinct units for

conservation. We found this was the case in our study and used Dene TK to help us interpret the genetic statistical output (choosing $K=3$ as the most biologically relevant inference that was supported by both the statistical analysis and TK). In doing so we use multiple knowledge sources to guide the translation of data to understanding. Thus, through a pluralistic approach we were able to demonstrate the ways that linguistic, TK and genetic patterns corroborate each other and allowed us to identify criteria that can be used to identify and differentiate between groups of animals for biodiversity conservation.

Preserving evolutionarily significant diversity in caribou that is identified through the analysis of multiple genetic markers and TK is essential because caribou populations in the southern portions of their range face extirpation (Hebblewhite et al. 2010, Johnson et al. 2015). Further, recent research on loggerhead sea turtles (*Caretta caretta*) has shown that populations at the margins of the species range can be important reservoirs of genetic diversity and “contribute disproportionately to the adaptive potential and future viability of the population” (Stiebens et al. 2013:8). Thus, the genetic differentiation of t̄odz̄ı and the rich TK on the unique attributes of the type provide evidence for their prioritization as an irreplaceable component of Canada’s biodiversity. However, sustainable conservation strategies must find ways to maintain not simply the categorical entities (like subspecies) but rather the dynamic relations among peoples and species as the basis of bioculturally diverse systems.

The importance of supporting social-ecological relationships and processes is gaining momentum in conservation science (Gavin et al. 2015). Proponents of this viewpoint maintain that conservation priorities should be not be defined in relation to discontinuous species, but rather directed towards the protection of essential processes that create adaptive potential and sustain biological variation (Bowen 1999, Crandall et al. 2000, Moritz 2002, Eizaguirre and

Baltazar-Soares 2014). This viewpoint acknowledges the subjectivity of species categories and highlights the importance of conserving the dynamic nature of functioning ecosystems. Strategies for identifying units for conservation that integrate multiple biological criteria, acknowledge the dynamic nature of intraspecific diversity, respond flexibly to specific circumstances, and adapt to differing situations are needed to cultivate evolutionary potential in a changing environment (Fraser and Bernatchez 2001).

Similarly, ethnoecological explorations of the intrinsically adaptive nature of categorization systems place emphasis not on categorical entities (contents of categories such as species) but on defining elements of an ecosystem in relation to the other elements that surround them in time and space (Ingold 2011). As a consequence, more attention is given to an entity's function – its role in the larger spatial and temporal environment – rather than its intrinsic qualities which are devoid of context. Identifying important connections among ecosystem components allows the unpredictable emergent properties of a system to become apparent (Berkes et al. 2003, Ingold 2011) and can lead to improved conservation planning (Alcorn 1993, Fraser et al. 2006). For example, research suggests that TK classification systems can, in some cases, identify more taxa than science-based systems (Newmaster et al. 2007, Ragupathy et al. 2009) or be especially suited to identifying intraspecific diversity (Fraser et al. 2006). In the Sahtú, the description of a distinct group of caribou in the mountains known as ṭənat'əa warrants further study as they may harbor unique genetic diversity and could play an important role in intraspecific dynamics. Thus, the analysis of genetic variation in conjunction with the relationships indigenous people maintain with species has the potential to reveal complex patterns that would likely not be apparent when evaluated separately.

Conclusion

A renewed focus on interdisciplinary conservation frameworks demonstrates the importance of studying human and natural systems (social-ecological systems) in tandem (Liu et al. 2007, Collins et al. 2011, Bodin and Tengö 2012). By exploring indigenous people's relationships with caribou, which have been actualized through language, we developed new insights into the underlying processes that create structure and drive patterns of caribou biodiversity. We contend that indigenous languages provide an obvious place to ground research processes and build collaborations. Words can be used to strengthen people's relationship with local ecosystems and create appropriate and unifying dialogue. As Frederick Andrew affirmed, "The most important thing is to talk the old language and honor our ancestors that went before us." As a direct outcome of our research, the SRRB has made the decision to use the word *tòdzı* in all official correspondence relating to boreal woodland caribou. The process of changing vocabulary has the potential to allow for the development of common-ground from which new relationships can move forward (Stevenson 1998). By recognizing the validity of other knowledge systems it is possible to broaden the worldview of the listener (Gavin et al. 2015). In doing so the world "becomes richer as our ability improves to view it from a variety of angles" (Cruikshank 1981:86).

Through the process of *łeghágots'enetę* "learning together" we were able to embrace the synergies that come from the sometimes intangible process of knowledge expansion and develop comprehensive descriptions of caribou populations that reflect biodiversity. Our results point to the importance of assessing multiple criteria simultaneously when determining population boundaries and characterizing population structure. We found clear connections between Dene people's descriptions of caribou ecology and other domains of knowledge such as population

genetics where connectivity and delineation of groups are central themes. Utilizing multiple methods has the potential to strengthen evidence-based decisions with respect to range mapping as part of the boreal woodland caribou range and action plans (Environment Canada 2012) and environmental assessments in response to potential shale-oil development in the region. At the national scale, our results provide guidance on the delineation of DUs for caribou across Canada and suggest practical approaches towards the inclusion of TK in the development of policies related to SARA.

Interdisciplinary research broadens the scope of biological inquiry and recognizes the significant contribution that multiple knowledge sources provide (Gavin et al. 2015). By exploring multiple ways of organizing knowledge our research was able to forge the basis for cross-cultural collaboration. For example, by investing in cooperation from the outset, our project produced results that have been acknowledged from different world views, thus our research outcomes may be more broadly accepted. As Walter Bayha pointed out, “The future of research in the north will include more and more cases of science confirming the history of aboriginal people and thus add to the overall knowledge that has existed since time immemorial.” Likewise, as demonstrated by our research, TK also has the potential to inform and improve scientific methods, processes and outcomes. Through collaboration and *łeghágots'enetę* “learning together” our research outlines ways to respectfully draw upon indigenous knowledge and support relationships between people and wildlife. By working with local communities, combining methods from different disciplines, and establishing potential for transformative dialogue – we can generate new insights and assist managers in confronting the daunting conservation challenges of the future.

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Table 2-1. Genetic diversity estimates, averaged across 9 microsatellite loci, for the three major caribou groups identified by structure analysis: number of samples (N), number of alleles (N_A), allelic richness (A_R), private allelic richness (A_{RP}), observed (H_O) and expected (H_E) heterozygosity, F_{IS} estimates, and standard errors (SE) for each estimate.

Group	N	N _A	SE	A _R	A _{RP}	H _O	SE	H _E	SE	F _{IS}
Barren-ground	123	15.1	1.20	14.97	2.50	0.84	0.013	0.87	0.010	0.035
Boreal woodland	171	12.0	1.43	11.26	1.05	0.79	0.023	0.79	0.023	0.005
Mountain	260	17.1	2.93	14.38	2.29	0.82	0.014	0.84	0.011	0.031

Table 2-2. Haplotype (mtDNA) genetic diversity for the three major caribou groups identified by structure analysis: number of individual caribou samples analysed for mtDNA (N), number of samples assigned to the North American and Beringian-Eurasian haplogroup lineages (NAL_N and BEL_N, respectively), number of haplotypes in the NAL (NAL_H) and BEL (BEL_H) haplogroups, nucleotide diversity (π) and gene diversity (GD) with standard deviations (SD).

Group	N	NAL _N	BEL _N	NAL _H	BEL _H	π	SD	GD	SD
Barren-ground	93	1	92	1	37	0.0170	0.0090	0.9385	0.0165
Boreal woodland	110	9	99	1	12	0.0192	0.0100	0.8440	0.0195
Mountain	134	1	133	1	31	0.0213	0.0110	0.9174	0.0144

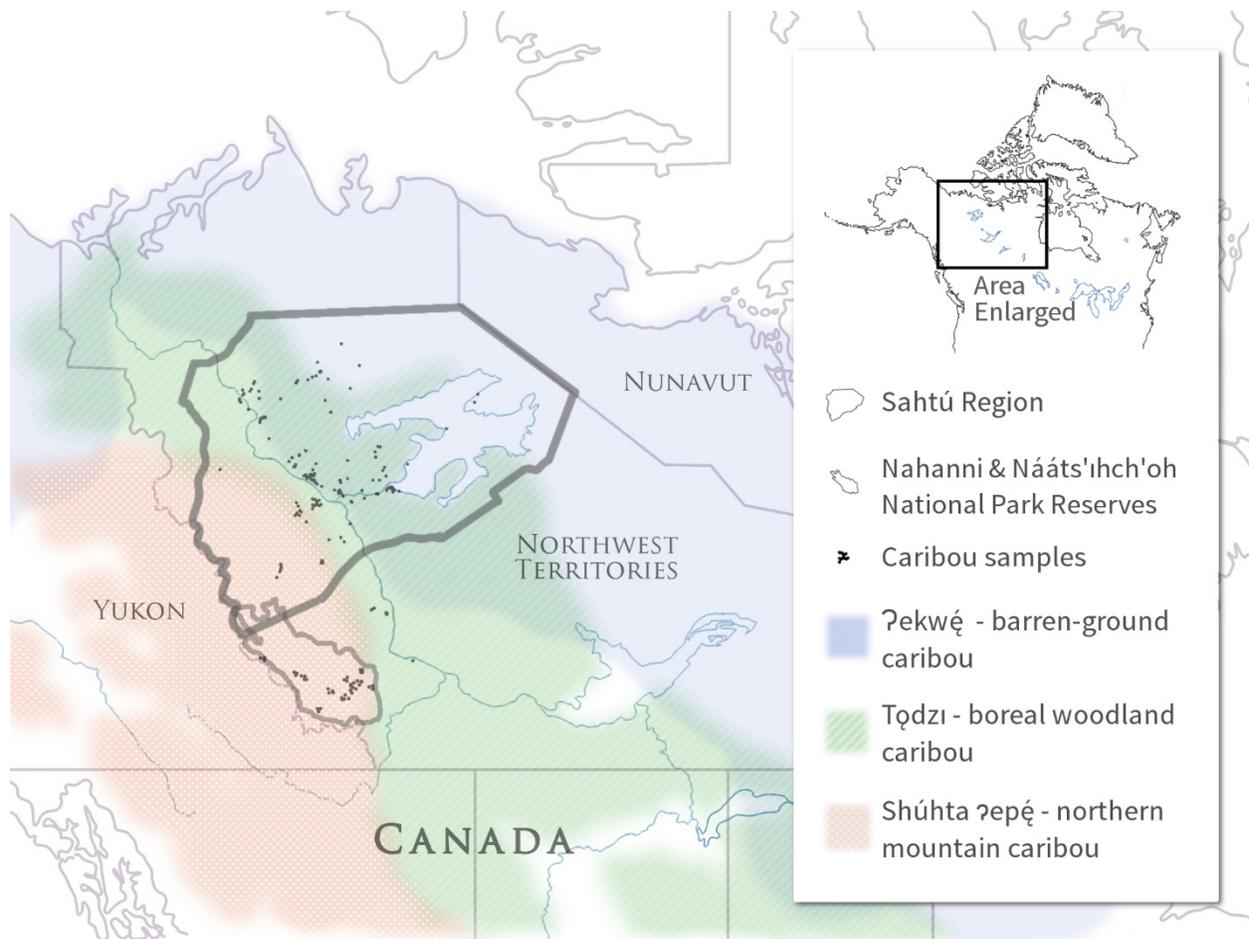


Figure 2-1. The Sahtú region of the Northwest Territories, Canada, includes the overlapping ranges of three types of caribou: t̄dzı (boreal woodland caribou; striped green), ʔekwé (barren-ground caribou; blue) and shúhta ʔepé (northern mountain caribou; stippled orange). Small black dots represent locations of caribou fecal, tissue and blood strip samples collected in the Sahtú Region and Nahanni National Park Reserve, Northwest Territories, Canada.

DENE WORD	DESCRIPTION
Bedelé t'á núzhq (D) be-delé t'á núzhq 3rd.person.possessor-blood; by means of, with; we grew up	We grew up with their blood
Behé ts'enézhq (D) be-hé ts'enézhq 3rd.person.object-with; we/one.grew	We grew up with them; we are people with them
Bekwi dezene (D); Befi dezene (K) be-kwi/be-fi dezene 3rd.person.possessor; it.is.black/dark	Darker colored
Bets'erihchá (D) be- ts'e rihchá 3rd.person.object; we, respect	Respect, things that belong to the creator we keep sacred; we respect, hold him/her/it in esteem
Gocha Tué (D) go-cha tué place-shelter; lake	Shelter Lake; Kotcha-t'oué/Lac Ste-Thérèse ¹ ; today known as Lac Sainte-Therese
Goecha fetə (S); ʔécha wetə (D) go-echa fetə place-leeward.side; 3rd.person.animate.subject.lies ʔécha wetə leeward.side; 3rd.person.animate.subject.lies	How an animal will rest downwind of his/her trail and you need to go around so the animal can't smell you
Goecha gots'anele (S) go-echa go-ts'ə a-ne-le place-leeward.side; place-from; thus-you.sg-do	To hunt from downwind
Leghəgots'enetə (D); ʔeleghəgotsenetə (S) le-ghá-go-ts'e-netə each.other-to-place-we-teach	We teach each other; learning together
Ləgháts'eredi (D); Eleghəzets'ededi (K) le-ghá-ʔe-ts'e-redi each.other-to-something-we-give	Giving to each other
Shúhta ʔepé (S) shúh-ta ʔepé mountain-among; caribou	Caribou among the mountains
Tənatl'əa (S)	Fast runner caribou that occur in the mountains, elders say they come from far away, possibly the ocean
Tədzı (S, D, K)	Boreal woodland caribou (dzi is found in many related languages)
ʔekwé (D); ʔepé (S)	Caribou (related to the term for flesh or meat)
ʔekwéwa (D) ʔekwé-wa caribou-prototypical	The real, original, or prototypical caribou
ʔeda (K)	Caribou (related to the term for horn or antler)

¹Petitot (1893)

Figure 2-2. Word descriptions and definitions in the Shúhta (S), Sahtú/Déłıne (D) and K'áhsho (K) dialects of the North Slavey language in the Sahtú region of the Northwest Territories, Canada.

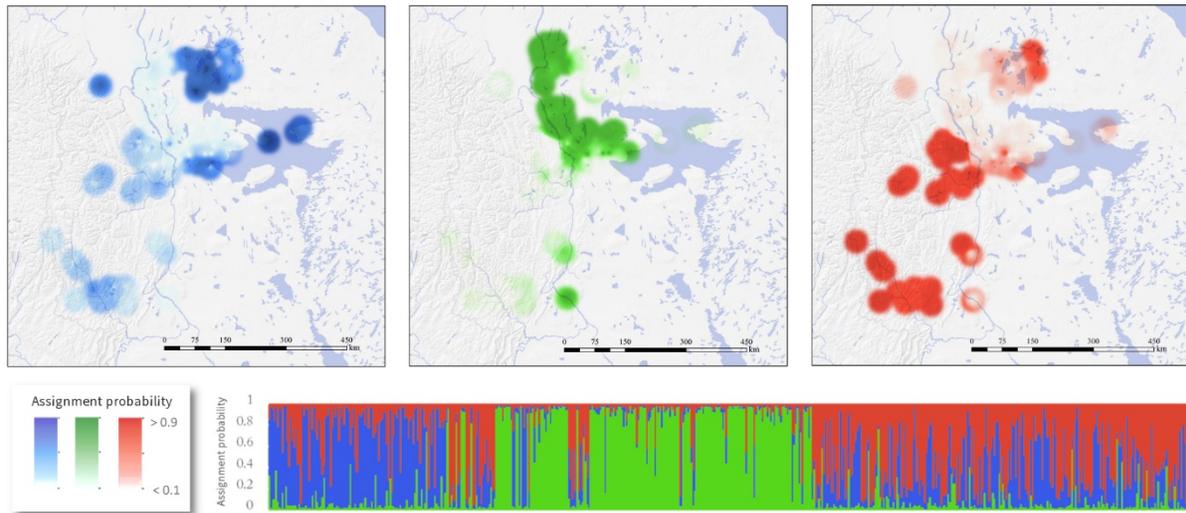


Figure 2-3. We analyzed microsatellite data from caribou genetic samples collected in the Sahtú region and Nahanni National Park Reserve of the Northwest Territories, Canada from 2012 to 2014. We used structure software to assign individual caribou to inferred genetic clusters. We found support for $K=3$ populations (shown in bottom bar) that coincided with clusters of 1) barren-ground (blue) 2) boreal woodland (green) and 3) mountain (red). Vertical colored bars indicate the probability that an individual belongs to a certain group. We mapped the structure output using the inverse-distance-weighted interpolation in ArcGIS and constrained the interpolation to the sampled locations.

CHAPTER 3: ANCIENT DIVERSIFICATION IN GLACIAL REFUGIA LEADS TO
INTRASPECIFIC DIVERSITY IN A HOLARCTIC MAMMAL[§]

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Abstract

Aim: Glacial-interglacial cycles influenced the contemporary genetic structure of many North American species. While phylogeographic lineage divergence among Pleistocene refugia has been proposed as a significant driver of subspecific and ecotypic differentiation, emerging evidence highlights the role of diversification within refugia in producing post-glacial variation. Caribou (*Rangifer tarandus*) exhibit significant morphological, ecological and behavioral phenotypic variation and occurred within Beringian and sub-Laurentide refugia. More specifically, the boreal ecotype of woodland caribou ranges from the southern regions of Canada to the Northwest Territories (NWT). Woodland caribou are generally accepted to have evolved south of the glacial extent, but the boreal ecotype in the northern part of their range co-occurs with caribou that have a Beringian origin. This proximity provides an opportunity to test whether woodland caribou colonized boreal habitats from a single southern refugial source or if independent evolution to a common ecotype resulted from diversification within refugia.

Location: Northwestern Canada.

Methods: We used approximate Bayesian computation to discriminate between alternate evolutionary histories of caribou belonging to boreal, northern mountain and barren-ground ecotypes using microsatellite and mtDNA markers.

Results: Our analysis indicates that unlike the southern-evolved boreal ecotype, the boreal ecotype of central NWT has Beringian origins and arose from a common lineage with barren-ground and mountain caribou. Importantly, the divergence of the lineage resulting in the boreal ecotype of central NWT significantly predates the Last Glacial Maximum.

Main conclusions: We demonstrate that independent evolutionary trajectories can converge on a similar phenotype and for the first time show that the boreal ecotype of caribou in North America

contains two phylogeographic assemblages. The ancient divergence suggests that diversification within Beringia could have resulted in ecological specialization. An eco-evolutionary focus will be essential to designing biodiversity conservation strategies for caribou that maximize genetic diversity and preserve adaptive potential in this intra-specifically diverse species.

Introduction

Intraspecific variation is recognized as a significant driver in the establishment and function of ecological dynamics including population persistence, competition, and responses to environmental change (Bolnick et al. 2011). However, the evolutionary processes that lead to the development and persistence of intraspecific variation, especially for vagile species in continuous habitats, can be difficult to identify (Fitzpatrick et al. 2015, Puckett et al. 2015). Glacial cycles during the Pleistocene have had a significant impact on species distributions and genetic diversity (Hewitt 2000). In North America, vicariant divergence associated with the North American Laurentide and Cordilleran ice sheets facilitated phylogeographic lineage diversification in several species (Dyke 2004, Weksler et al. 2010 and references therein). Subsequent isolation and divergent selection pressures in the physiographic conditions of refugia are commonly considered to influence intraspecific diversification through genetic drift and adaptive evolution (Richardson et al. 2014). However, recent research also points to the importance of divergence within single large refugia as a source of contemporary genetic variation and structure (Galbreath et al. 2011, Lanier et al. 2015).

Northern cold-adapted species experienced extensive range expansions, and in some cases increased population sizes during glacial periods (Flagstad and Røed 2003, Lorenzen et al. 2011). The extensive Beringian refugium, that stretched from eastern Siberia across the land bridge to Alaska and into the Yukon, fostered considerable genetic diversity and endemism (Weksler et al. 2010, Galbreath et al. 2011). Following glacial retreats, the reunification of divergent populations may have increased adaptive evolution through introgression, or alternatively, disrupted local adaptation and caused replacement or extinction of genealogical lineages (Lanier et al. 2015, Klütsch et al. 2016). During warm interglacial periods, the ranges of

cold-adapted species contracted as viable tundra and boreal habitat were redistributed, which contrasts with the pattern of expansion out of refugia displayed by many temperate species (Stewart et al. 2010). Molecular techniques provide an opportunity to reconstruct the population dynamics of cold-adapted species and predict how phylogeographic patterns influence contemporary population structure (Stewart et al. 2010, Galbreath et al. 2011, Espíndola et al. 2012).

In North America, caribou (*Rangifer tarandus*) persisted in both high and low latitude habitats over the course of the Pleistocene glaciations. The series of range oscillations and repeated demographic fluctuations associated with the expansion and retraction of continental glaciers produced conspecific populations with distinct morphological, ecological and behavioral traits (Flagstad and Røed 2003). The diverse spatial-temporal evolutionary histories that characterize caribou have made taxonomic clarity within the species challenging and are evident in extensive intraspecific genetic structure (Serrouya et al. 2012, Weckworth et al. 2012, Klütsch et al. 2016, Polfus et al. 2016). Genetic evaluations have attributed the most pronounced intraspecific split (first formally described as subspecies by Banfield in 1961) to two distinct mitochondrial DNA (mtDNA) phylogeographic lineages that originated south of the ice sheets (North American lineage; NAL) and north of the ice sheets (Beringian-Eurasian lineage; BEL, Flagstad and Røed 2003, Cronin et al. 2005, McDevitt et al. 2009, Klütsch et al. 2012, Weckworth et al. 2012, Yannic et al. 2014). Finer-scale subdivisions further classify North American caribou into ecotypes based on geography and natural history traits (regardless of genealogical relationships), however, naming conventions do not always correspond between jurisdictions and ecotype identification can be ambiguous (COSEWIC 2011, Pond et al. 2016).

Woodland caribou (*R. t. caribou*) belong predominately to the NAL and were isolated in habitats south of the Laurentide ice sheet during the Last Glacial Maximum (LGM: 26.5-19 thousand calendar years before present; kyr BP). Specifically, the boreal ecotype of woodland caribou are forest-dwelling animals known for their sedentary behavior, dark pelage, large body and long legs, small group-size, and low-population densities across their current range within the Canadian boreal zone (Fig. 3-1). The boreal ecotype is considered a Designatable Unit (DU; COSEWIC 2011) and is listed as threatened by the Canadian Species at Risk Act as a result of population declines that are generally attributed to extensive habitat loss and fragmentation (Environment Canada 2012).

In north-western Canada, at their northern range margin, the boreal ecotype co-occurs with barren-ground caribou (*R. t. groenlandicus*) that aggregate in large numbers to calve on the tundra and migrate to the boreal forest during the winter (Nagy et al. 2011) and the northern mountain ecotype (*R. t. caribou*) that occur throughout the mountains of the Northwest Territories (NWT), northern British Columbia, and Yukon Territory (COSEWIC 2011). However, even in the face of range overlaps and known mixing between the types, recent genetic analysis has shown that in central NWT, the boreal ecotype can be differentiated (Polfus et al. 2016). Likewise, indigenous Dene First Nation and Métis people of central NWT classify tódzi “boreal woodland caribou” based on identifiable physical features and behavioral traits, further supporting the boreal ecotype as a distinctive group in the northern extent of their range (Polfus et al. 2016).

Interestingly, the boreal ecotype in central NWT (hereafter NWT boreal) assigns predominately to the BEL based on mitochondrial patterns (Polfus et al. 2016), similar to sympatric barren-ground and northern mountain animals (Weckworth et al. 2012), and unlike the

boreal ecotype from southern provinces that assign to the NAL (Klüttsch et al. 2012). This proximity provides an ideal opportunity to test competing refugial hypotheses. If the boreal phenotype arose independently from distinct evolutionary lineages as a result of parallel phenotypic evolution, it would suggest that natural selection plays an important role in caribou intraspecific variation (Schluter et al. 2004, Elmer and Meyer 2011). In particular, ecological traits may be expected to converge in closely related genomes when certain environmental conditions strongly favor particular evolutionary outcomes (Rosenblum et al. 2014).

Alternatively, the boreal phenotype in central NWT may be a result of shared ancestry or historic introgression with NAL animals. Genetic drift may also be an important mechanism causing intraspecific differentiation in caribou, especially in small isolated populations (Serrouya et al. 2012, Mager et al. 2014).

Given signatures of significant BEL ancestry in central NWT caribou (Polfus et al. 2016), our goal was to test alternative evolutionary models to assess the origin of the boreal ecotype at the northern range margin. Specifically, we tested the following two alternative hypotheses: 1) the NWT boreal ecotype diverged from the BEL and converged to a boreal phenotype within Beringia; 2) the NWT boreal ecotype represents NAL woodland caribou that subsequently colonized the northern boreal zone following retraction of the ice sheets and experienced some level of introgression from BEL caribou at the northern range margin. To discriminate between these alternate evolutionary histories, we applied Approximate Bayesian Computation (ABC) of nuclear and mitochondrial genetic markers in contemporary caribou populations representing the boreal ecotype in central NWT, the barren-ground subspecies, the northern mountain ecotype, and the nearest population of boreal ecotype with NAL origins and little evidence of introgression from BEL (Table A3-3, Fig. A3-6). We also evaluated whether estimated

divergence times coincided with significant glacial events. Ultimately, we tested whether the boreal ecotype of woodland caribou evolved from a single refugial lineage or independently from two refugial lineages.

Materials and Methods

Study area and sample collection

A description of the central NWT study area and sample collection can be found in Polfus et al. (2016) and a description of central Saskatchewan (SK) can be found in Galpern et al. (2012b; Fig. 3-1). We assembled a dataset of caribou fecal and tissue samples from animals belonging to four major groups: 1) barren-ground caribou from the Bluenose East and Bluenose West herds of central NWT; 2) northern mountain ecotype from the Mackenzie Mountains, NWT; and two populations of boreal ecotype from 3) central NWT and 4) the Smoothstone-Wapeweka population, SK.

Microsatellite DNA genotyping

We followed protocols for microsatellite DNA extraction, amplification and genotyping that were developed as part of a long term caribou genetics database (Galpern et al. 2012b, Klütsch et al. 2012, Klütsch et al. 2016). We genotyped a panel of 9 microsatellite loci (BM848, BM888, MAP2C, RT5, RT6, RT7, RT9, RT24 and RT30; Bishop et al. 1994, Wilson et al. 1997). We used GENEMARKER 1.9.1 (SoftGenetics, LLC) to determine allele size. Two people evaluated all electropherograms and scores were compared on an online server. We used ALLELEMATCH 2.5 (Galpern et al. 2012a) to check for genotyping errors, remove duplicate

profiles, and identify individuals. Samples included in the final dataset had a minimum of 8 successfully amplified loci.

Mitochondrial DNA sequencing

We amplified and sequenced 429bp of the mtDNA control region using the primers L15394 and H15947 (Flagstad and Røed 2003) following Klütsch et al. (2012, 2016). We used BIOEDIT 7.2.5 (Hall 1999) to check and align sequences and DNASP 5 (Librado and Rozas 2009) to distinguish haplotypes.

Statistical data analysis

We tested each locus and population for significant deviations from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using GENEPOP 4.2 (Rousset 2008). We used STRUCTURE 2.3.4 (Pritchard et al. 2000) to identify population clusters (K) for $K = 1$ through $K = 15$ under the admixture model with correlated allele frequencies. We conducted five iterations for each K with 1,000,000 burn-ins and 10,000,000 Markov chain Monte Carlo repetitions on a high-performance computing cluster (www.sharcnet.ca). We summarized run statistics using STRUCTURE HARVESTER 0.6.94 (Earl and vonHoldt 2012). We used SPAGEDI 1.5 (Hardy and Vekemans 2002) to test microsatellite pairwise differentiation.

Approximate Bayesian Computation

We used ABC simulations to test competing evolutionary models. ABC analysis allows rapid tests of different scenarios by calculating summary statistics rather than exact likelihoods (Csilléry et al. 2010). Deviations between the simulated and observed summary statistics are

evaluated to measure fit for each model investigated (Lopes and Boessenkool 2010). We used the software DIYABC 2.0.4 (Cornuet et al. 2014) to explore whether the NWT boreal ecotype diverged from the BEL or the NAL. Alternative scenarios tested also included admixture between populations at various timescales. We divided the evolutionary scenarios into two major groups: 1) admixture models with divergence and admixture events (Fig. 3-2; scenarios 1-3) and, 2) split models with no admixture events (scenarios 4-5). First, we tested a set of split scenarios to identify the most likely candidates. The top three split models were added to a series of preliminary runs that included admixture models. We narrowed down the supported models to a top five (Fig. 3-2) and included them in a final run to test support with three datasets: microsatellites, mtDNA, and a combined dataset.

We initially set the mutation model parameters in DIYABC to a stepwise mutation model as identified by Klütsch et al. (2016) and then fine-tuned the parameters to the dataset. We used a uniform distribution and set the prior range for the split between the two phylogeographic lineages to $t_4 = 10 - 25,000$ generations. The prior range of the divergence events were set to $t_3 = 100 - 17,000$ and $t_2 = 10 - 10,000$ generations. The youngest event had a prior range of $t_1 = 10 - 3,000$ generations for the combined dataset. To convert time estimates to years we assumed a generation time of seven years for female caribou. We chose summary statistics (i.e., mean number of alleles, mean size variance of alleles, mean number of haplotypes, etc.) based on their success in previous analyses on caribou (see Klütsch et al. 2016). Approximately 3 million simulations were used to test scenarios on a high-performance computing cluster. We compared simulations through logistic regression and linear discriminant analysis in DIYABC. We used the model-checking option to assess the goodness-of-fit of model parameter posterior combination (Figs A3-1 and A3-2).

Results

Population structure and diversity

We amplified 655 samples (Table A3-1) from individual caribou. There was no evidence that certain loci deviated from HWE (6/36 cases significant after Bonferroni correction) or expressed LD (1/144 cases significant after Bonferroni correction). STRUCTURE analysis revealed $K=2$ (ΔK criterion) that corresponded to a NWT group and SK group. The mean likelihood also supported additional substructure at $K=4$ (all four groups showing differentiation; Figs A3-3 to A3-5). Pairwise comparisons (F_{ST} and R_{ST}) supported divergence among groups with the strongest differentiation found between the NWT boreal and the SK boreal (Table A3-2)

We sequenced 370 caribou at the mtDNA control region and found 79 haplotypes that fit into the well-resolved phylogeny of NAL and BEL (Klütch et al. 2012). Most haplotypes were non-overlapping between groups (Fig. A3-6). We found only 3 NAL haplotypes (in 11 caribou; 3.9%) in the NWT dataset, and only 1 BEL haplotype (in 3 caribou; 3.4%) in the SK dataset (Table A3-3).

ABC analysis

All top models identified through ABC analysis suggested that the NWT boreal ecotype has a BEL origin (Fig. 3-2). Scenario 1 was identified as the most likely evolutionary model for the microsatellite and combined dataset based on the posterior probability values, credible intervals, and logistic regression (Table A3-4, Fig. A3-7). Scenario 1 suggests that the NWT boreal ecotype diverged from the BEL ~60.5 kyr BP (CI: 19.5–109.2 kyr BP; combined dataset; Table 3-1). This model also estimates that the northern mountain ecotype arose relatively

recently at ~4.2 kyr BP (CI: 0.2–16.4 kyr BP; combined dataset) through admixture between two divergent populations that had initially split from the barren-ground and NWT boreal lineages of the BEL ~45.9 kyr BP (CI: 20.8–66.7 kyr BP; combined dataset). Models that included divergence of the SK boreal ecotype from the NWT boreal ecotype (or vice versa) were not supported. The most likely evolutionary model for the separate mtDNA dataset was scenario 4. This model suggests that both the northern mountain and the NWT boreal ecotypes diverged from the barren-ground lineage of the BEL at different time points. This result can be explained in part by the fact that NWT boreal caribou include primarily BEL haplotypes. In contrast, caribou mtDNA data from central Canada include more phylogenetically differentiated haplogroups and therefore, more haplotypic diversity (Klütsch et al. 2016). Since the majority of haplotypes in this analysis came from the BEL, the average number of mtDNA substitutions in this dataset was also lower than Klütsch et al. (2016), which could influence time estimates and model choice to a certain degree. Further, replacement events may have resulted in the loss of ancient haplotypes.

Discussion

The role of parallel evolution in intraspecific diversity

We show for the first time that multiple evolutionary routes can converge on a similar phenotype in an intra-specifically diverse Holarctic species. Our analysis points to the role of the Beringia refugium on genetic variation and structure in contemporary caribou populations. Boreal caribou of central NWT are specialized for survival in the boreal forest and are phenotypically and behaviorally similar to southern boreal ecotype animals (i.e., display sedentary behavior, dark pelage, and large body size; COSEWIC 2011). However, ABC simulations and mtDNA lineage assignment support a BEL origin for the NWT boreal ecotype,

distinct from the NAL of the boreal ecotype that diversified south of the ice sheets during the LGM. Because divergence between the Beringian derived barren-ground and boreal lineages extends to ~60.5 kyr BP, an alternative model is possible where the northern boreal lineage colonized southern habitats when the ice-free corridor between the Laurentide and Cordilleran first opened – ~14–15 kyr BP (Dyke 2004, Dixon 2015) – or perhaps even predating the LGM. However, our results show that the representative southern boreal ecotype from SK diverged before the Beringian derived barren-ground and boreal lineages. The order of divergence does not support a Pleistocene colonization model, but rather implies independent convergence to a similar boreal ecotype in separate refugia north and south of the ice sheets. Thus, caribou from distinct polyphyletic groups converged on a shared phenotype.

Our study suggests that natural selection has influenced the evolution of the boreal ecotype because a similar suite of traits evolved independently in association with the environmental pressures of the boreal forest. While we could not test the timing of ecological diversification compared to lineage divergence, we can infer that adaptation to Beringian microhabitat was likely an adaptive driver of this lineage. Further, although genetic drift is suspected to play a role in genetic diversification in caribou (Serrouya et al. 2012, Mager et al. 2014), genetic drift would not be expected to produce parallel phenotypic traits in multiple lineages in correlation with specific environments (Schluter et al. 2004). Thus, ecological variation and adaptive evolution may be significant drivers in caribou ecotype evolution to the extent that independent lineages converged to similar phenotypic outcomes.

Our results contrast with Banfield's classic *Rangifer* taxonomic interpretation, based largely on craniometrical measurements, that included western mountain and boreal ecotypes in the woodland subspecies (*R. t. caribou*) that originated in sub-Laurentide refugia. Rather, we

show that the mountain and boreal ecotype of central NWT are distinct groups with BEL origins. Our results support the intuition of Geist (2007), who, using pelage characteristics and taxonomic inferences, suggested that the mountain and boreal woodland caribou north of 60° latitude were more likely “splinter populations of barren ground caribou, which have adapted to a more sessile life style, increased in body size and assumed some ‘woodland mannerisms’.”

In fact, the NWT boreal ecotype may be similar to sedentary caribou that occur in the boreal zone of Alaska. In general, Alaskan caribou belong to the BEL, but have behavioral strategies that have been classified into migratory and sedentary ecotypes (Hinkes et al. 2005, Mager et al. 2014). However, the sedentary Alaskan caribou display significantly less genetic structure than we found in the NWT boreal ecotype. Using 19 microsatellites from caribou across the Alaskan mainland, Mager *et al.* (2014) found little genetic differentiation between migratory or sedentary herds that also ranged greatly in population size and used both forest and tundra habitats. Thus, local behavioral strategies may be relatively plastic within Alaska (Hinkes et al. 2005). Similarly, genetic evidence suggests that Eurasian forest reindeer (*R. t. fennicus*) arose from the large continuous population of BEL reindeer in the vast palaeo-tundra of Siberia and central Eurasia during the Pleistocene (Flagstad and Røed 2003). Thus, it is possible that the forest reindeer, the NWT boreal ecotype, and the Alaskan sedentary ecotype may have arisen through similar processes of parallel phenotypic evolution.

Among ungulates, caribou and reindeer display high levels of microsatellite heterozygosity (Côté et al. 2002, Boulet et al. 2007). The extensive standing genetic variability in *Rangifer* may be essential to the evolution of convergent phenotypes (Barrett and Schluter 2008, Elmer and Meyer 2011). Understanding the source of variation (selection on new mutations or pre-existing genetic variation) can help explain how intraspecific variation is maintained in

natural populations (Barrett and Schluter 2008, Espíndola et al. 2012). Parallel phenotypic evolution may be common in *Rangifer*. Genetic evidence suggests that Peary caribou (*R. t. pearyi*) and Svalbard reindeer (*R. t. platyrhynchus*) may have converged to a shared small-bodied, short-legged phenotype from two evolutionary lineages (Gravlund et al. 1998). The high arctic islands represent a severe and unpredictable environment with selection pressures that could have independently produced the phenotypically divergent characteristics of the Peary and Svalbard animals (Flagstad and Røed 2003).

Recent analysis suggests that mtDNA introgression (admixture of BEL and NAL) does not correspond to the presence of migratory behavior in caribou (Klüttsch et al. 2016). If ecotypic adaptations to different environments are a result of parallel phenotypic evolution then some behavioral traits, like migratory behavior, may not match patterns of neutral marker genetic structure (Pond et al. 2016). Further, unique phenotypes and behavioral adaptations are likely to be influenced by behavioral plasticity, pleiotropy, or interacting gene pathways (Réale et al. 2003, Kopp 2009). Cases of potential parallel evolution present an ideal opportunity for future genomic research to illuminate the genetic basis for adaptive traits (Elmer and Meyer 2011). For example, grey wolves (*Canis lupus*), like caribou, are highly mobile and display divergent ecotypic adaptations (Carmichael et al. 2001, Musiani et al. 2007). Recently, Schweizer et al. (2016) used single-nucleotide polymorphisms to examine phenotypic diversity in wolves and found patterns of selection on morphological genes that were correlated with environmental gradients suggesting that local adaptation is important to ecotype divergence. Genomic research in non-model species holds the promise of exposing synergies among intraspecific diversity, local adaptations, and population persistence, however, real world conservation applications are still speculative (Shafer et al. 2015).

Timing of divergence

Phylogeographic reconstructions provide context for current molecular patterns and allow for interpretation of the impact of past climatic cycles on caribou (Flagstad and Røed 2003, Klütsch et al. 2012, Røed et al. 2014, Klütsch et al. 2016). Our ABC analysis suggests that the BEL and NAL split ~135.8 kyr BP (CI: 68.6–173.6 kyr BP), which is comparable to Klütsch et al. (2016) at 97.3 kyr BP (CI: 44.6–135.8; combined microsatellite and mtDNA control region mtDNA). Our estimates are more recent than those predicted by Yannic et al. (2014) at 300 kyr BP (184–430 kyr BP) using *cyt b* sequences and significantly older than McDevitt et al. (2009) at 37.5 kyr BP (CI: 28.1–46.7 kyr BP) using mtDNA control region. However, the coalescence estimates reveal that it is important to consider multiple scales of cyclic climatic change, not just the LGM (Barnosky 2008). The interstadial periods of warm climate between the early, middle, and late Wisconsin glacial periods likely resulted in reunification and introgression between lineages (Fig. 3-3). In support of this assessment, an ancient caribou mtDNA sample dated to $29,775 \pm 564$ (IntCal09 years BP) recovered from the Yukon (Lorenzen et al. 2011), is ancestral to the NAL (western clade *sensu* Klütsch et al. 2012), and suggests that potential connections may have occurred prior to the LGM (Fig. 3-3).

Genetic diversification within refugia may be a source of post-glacial variation in cold-adapted species (Weksler et al. 2010). The palaeoenvironment of Beringia included pockets of low-elevation spruce forests (especially during interglacials and interstadials) among the extensive steppe-tundra and grass-dominated ecosystem (Zazula et al. 2007). The internal complexity of Beringia is thought to have influenced small mammal diversity (Weksler et al. 2010, Galbreath et al. 2011, Lanier et al. 2015), and could also have facilitated ecological divergence of caribou. For example, our results reveal that the split between the NWT boreal

ecotype and barren-ground caribou occurred prior to the LGM, which implies that genetic subdivision likely persisted within Beringia. While microgeographic adaptation to forested versus steppe-tundra habitats may have played a critical role in the development of caribou ecotypes during the Pleistocene, there is also the possibility that the ancient lineages of NWT boreal and barren-ground caribou experienced more pronounced geographical separation associated with the divide between the Eurasian and American landmasses.

The substantial sympatric phenotypic diversification in caribou suggests that some genetic signals can withstand contact zones. The Holocene has not been long enough for displacement or admixture to completely mask the genetic legacy of Pleistocene glacial vicariance in caribou. Interestingly, while overlapping ranges (Roffler et al. 2012, Mager et al. 2014) and large-scale merging between sedentary and migratory herds are common in Alaska (Hinkes et al. 2005), population merging between the boreal ecotype and barren-ground caribou is not presently common in the western Canadian boreal zone (Nagy et al. 2011). The genetic structure evident between barren-ground and the NWT boreal ecotype suggests that any mixing that does occur is not sufficient to prevent the perpetuation of distinct genetic signatures (Figs A3-5 and A3-6).

The clear microsatellite genetic structure across fine spatial scales in central NWT are likely a result of ancestral genetic signals and current ecological adaptations or behavioral mechanisms that promote reproductive isolation (Rundle and Nosil 2005). The relatively low genetic diversity in the modern NWT boreal ecotype may also suggest a recent expansion into the ice free region of central NWT and potential founder effects. Likewise, the behaviors associated with the boreal ecotype likely confer increased fitness in the boreal forest, especially since similar phenotypes are expressed by Eurasian forest reindeer and Alaskan sedentary

caribou. The genetic structure among neighboring caribou types suggests that microgeographic adaptation and its driving mechanisms could promote the persistence of local diversification (Rundle and Nosil 2005, Richardson et al. 2014). Future research is needed to understand how long periods of isolation need to exist for genetic differentiation to arise and remain divergent when contact is reestablished.

Similar to Weckworth et al. (2012) our results also contradict the inclusion of the northern mountain ecotype of western Canada in the woodland subspecies. Our analysis suggests that caribou in the Mackenzie Mountains arose ~4,000 years BP from ancient BEL populations. This corresponds to Letts et al. (2012) who found low mtDNA differentiation between ancient (up to 3,790 years BP) and modern mountain caribou (Fig. 3-3). However, weak microsatellite structure between the barren-ground and the northern mountain ecotype implies that historic exchange or incomplete lineage sorting is influencing differentiation between the groups (Letts et al. 2012, Polfus et al. 2016). In northern Alberta boreal ecotype caribou share BEL and NAL phylogeographic lineages (Weckworth et al. 2012) as do both boreal and mountain ecotypes in the central Rockies which suggest that zones of contact have occurred (McDevitt et al. 2009). Future ancient DNA approaches may provide more insight into the history of post-glacial contact and illuminate geographic events that influenced population persistence at transitional periods during the late Pleistocene and early Holocene.

Conservation implications

We demonstrate that the boreal ecotype of caribou in North America contains two phylogeographic assemblages that compose an irreplaceable component of Canada's biodiversity. Importantly, our results also show that southern boreal ecotype animals belonging

to the NAL represent an independent evolutionary unit of caribou. As was initially suggested by Geist (2007), protecting the “true woodland caribou” becomes even more critical if the group includes only NAL animals along the southern edge of caribou distribution. The southern extent of the boreal forest also faces threats related to anthropogenic disturbance, fragmentation, and shifting predatory-prey dynamics (Environment Canada 2012). Because the contiguous habitat of the boreal forest and the dispersal capabilities of caribou are likely critical components to the long-term persistence of the boreal ecotype, the genetic variation of the boreal ecotype of central NWT could help prevent the extinction of behavioral adaptations in declining southern populations through evolutionary rescue (Bell and Gonzalez 2009). Further, as managers consider reintroduction programs for declining caribou populations, our results indicate that attention must be paid to the evolutionary history of putative source populations.

Environmental change due to anthropogenic influence is an increasing threat to many species, especially cold-adapted species (Berteaux et al. 2004, Post et al. 2009). *Rangifer's* adaptation to a wide range of environments across the Holarctic and continuance through the glacial cycles of the Pleistocene suggests that a continuous geographic distribution and genetic mixing may be imperative to their success (Hinkes et al. 2005, Boulet et al. 2007, Lorenzen et al. 2011). In particular, caribou show substantial adaptive capacity and potential phenotypic plasticity that seem to make the species as a whole especially tolerant of changing conditions, however more information is needed to understand how caribou will respond to future environmental change (Yannic et al. 2014). Understanding the synergies between ecology and evolution may facilitate the design of biodiversity conservation strategies for caribou that prepare for future responses to restrictions on current interglacial climate refugia (Stewart et al. 2010). Dividing species into units (subspecies, ecotypes, or DUs) that confine policies to particular

groups in isolation, may misrepresent genetic histories and be an insufficient conservation approach. Rather, a focus on large-scale eco-evolutionary processes could provide a framework for maximizing genetic diversity and preserving adaptive potential.

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Table 3-1. Time estimates in calendar years before present for scenario 1 (found in Fig. 3-2) produced with Approximate Bayesian Computation for the combined dataset that includes caribou (*Rangifer tarandus*) microsatellite and mtDNA data from central Northwest Territories and central Saskatchewan, Canada.

Time point	Mean	Median	95% confidence interval	
t ₁	4193	2688	206	16450
t ₂	45920	46900	20790	66710
t ₃	60550	59360	19460	109200
t ₄	135800	141400	68600	173600

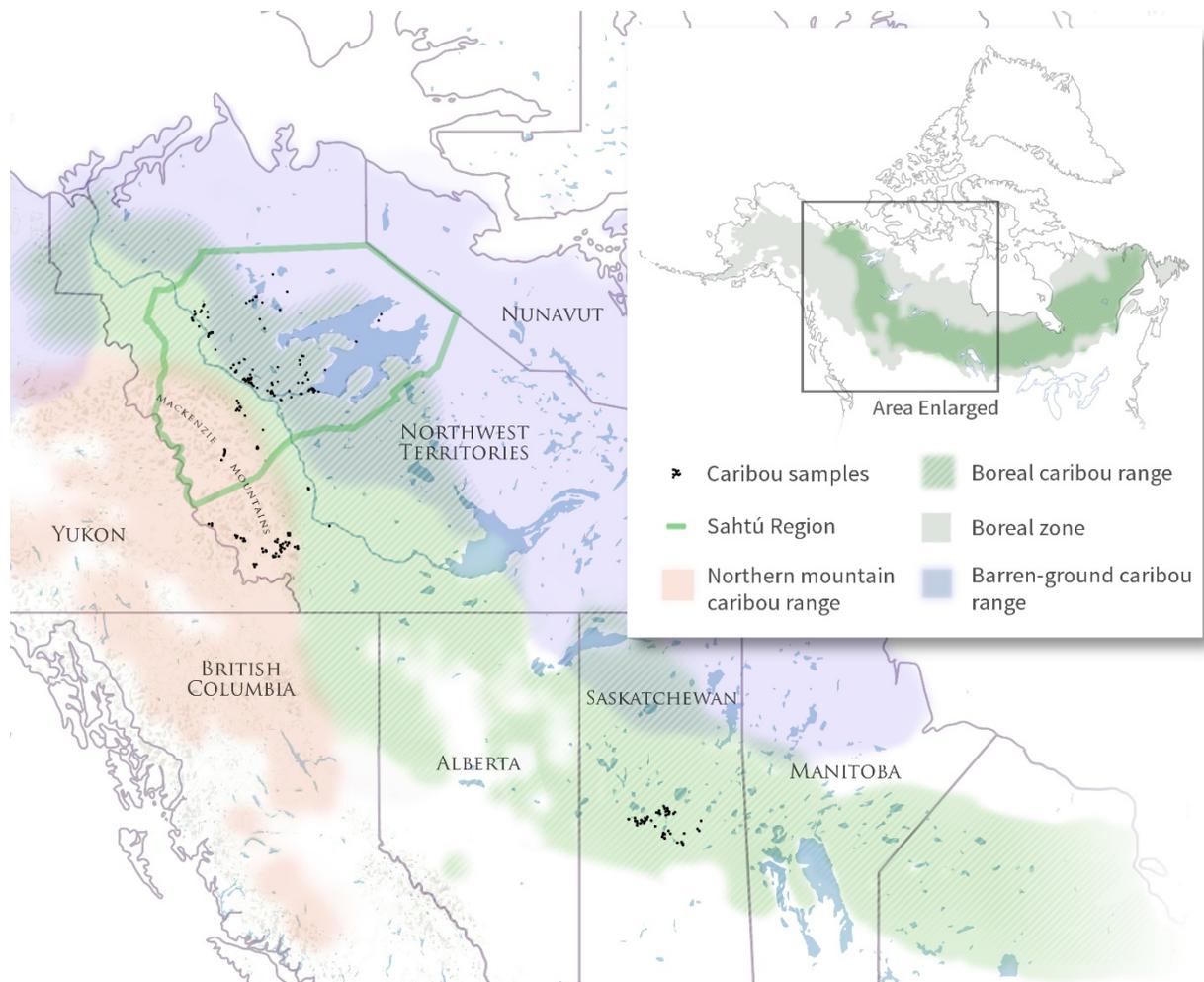


Figure 3-1. The range of the boreal ecotype of woodland caribou occurs within the boreal zone in Canada from the Northwest Territories to eastern Labrador (subset; Brandt 2009, COSEWIC 2011, Environment Canada 2012). Small black dots represent locations of caribou fecal, tissue, and blood strip samples collected in the Mackenzie Mountains (within the range of the northern mountain ecotype), the boreal forest of the Sahtú Region, central Northwest Territories (within the overlapping ranges of the boreal ecotype and barren-ground caribou), and the boreal forest of central Saskatchewan (Smoothstone-Wapeweka population of boreal ecotype).

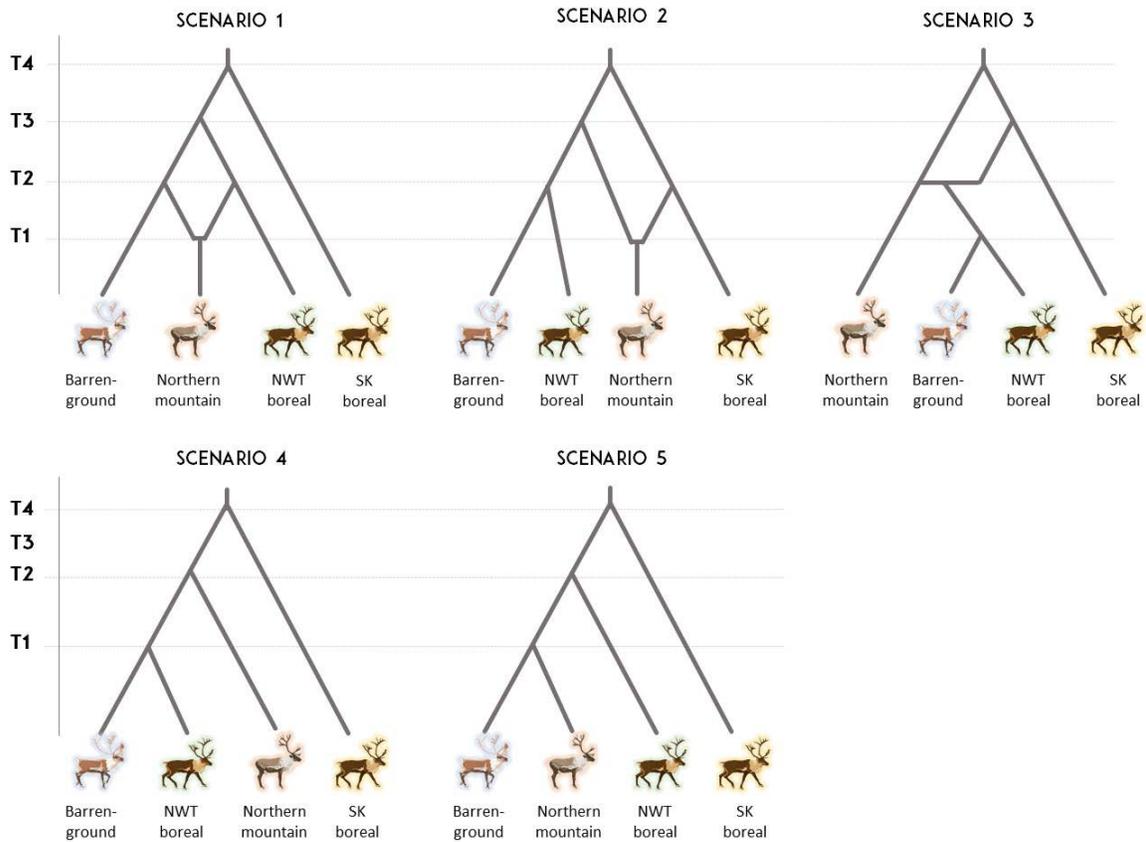


Figure 3-2. Top five Approximate Bayesian Computation (ABC) scenarios tested with DIYABC that model the evolutionary history of four contemporary caribou (*Rangifer tarandus*) groups: barren-ground caribou, boreal ecotype of central Northwest Territories (NWT), northern mountain ecotype, and boreal ecotype of central Saskatchewan (SK), Canada.

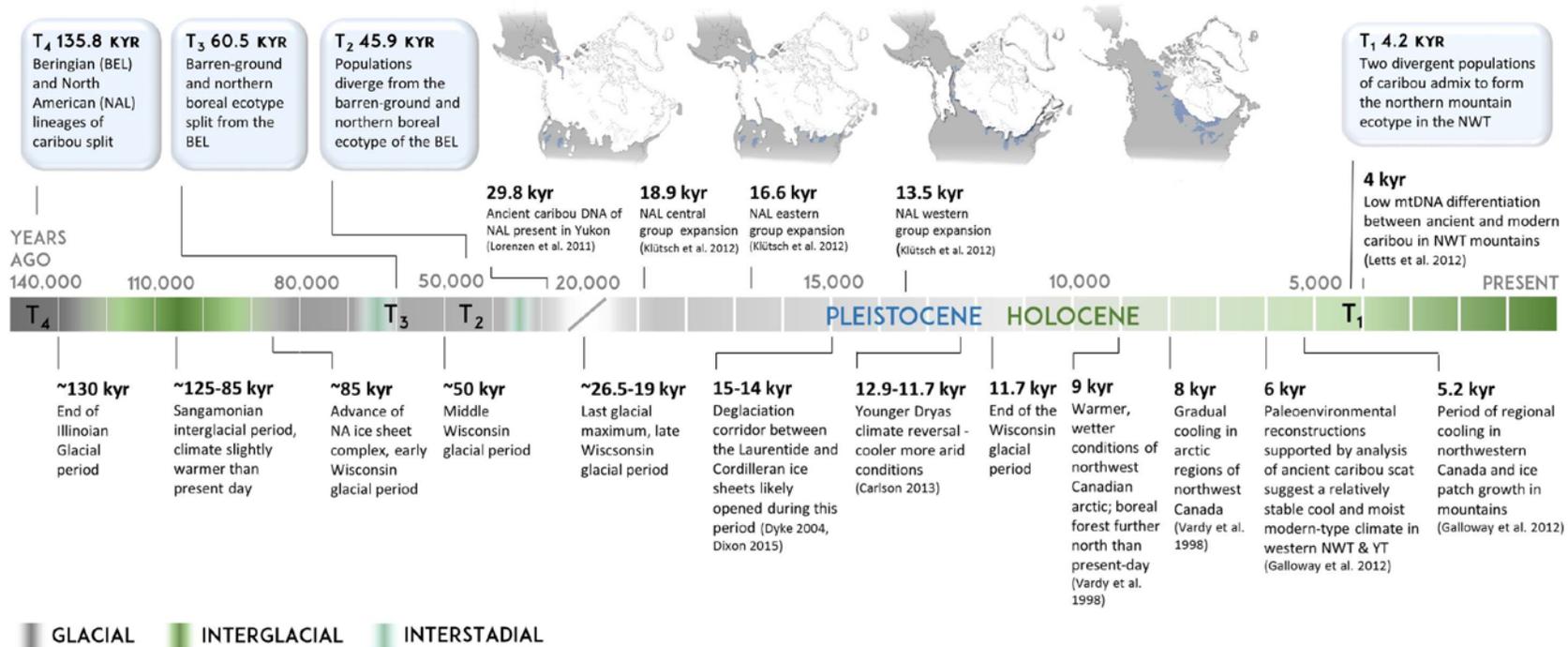


Figure 3-3. Timeline of last 140 thousand calendar years (kyr) before present. Blue bubbles represent the estimates (t1-t4) associated with the Approximate Bayesian Computation (ABC) scenario 1 (found in Fig. 3-2). The timeline includes associated caribou (*Rangifer tarandus*) histories in Canada (Lorenzen et al. 2011, Klüttsch et al. 2012, Letts et al. 2012), paleogeographic events (Carlson 2013, Dixon 2015), paleoenvironmental reconstructions (Vardy et al. 1998, Galloway et al. 2012) and glacial maps for North America (Dyke 2004). The scale of the timeline shifts from 10 kyr increments to 1 kyr increments around the last glacial maximum or at approximately 20 kyr before present. Abbreviations are: BEL – Beringian-Eurasian lineage, NA – North America, NAL – North American lineage, NWT – Northwest Territories, YT – Yukon Territory.

CHAPTER 4: CREATIVE CONVERGENCE: EXPLORING BIOCULTURAL DIVERSITY
THROUGH ART**

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Abstract

Interdisciplinary approaches are necessary for exploring the complex research questions that stem from interdependence in social-ecological systems. For example, the concept of biocultural diversity, which highlights the interactions between human diversity and the diversity of biological systems, bridges multiple knowledge systems and disciplines and can reveal historical, existing, and emergent patterns of variation that are essential to ecosystem dynamics. Identifying biocultural diversity requires a flexible, creative, and collaborative approach to research. We demonstrate how visual art can be used in combination with scientific and social science methods to examine the biocultural landscape of the Sahtú region of the Northwest Territories, Canada. Specifically, we focus on the intersection of Dene cultural diversity and caribou (*Rangifer tarandus*) intraspecific variation. We developed original illustrations, diagrams, and other visual aids to increase the effectiveness of communication, improve the organization of research results, and promote intellectual creativity. For example, we used scientific visualization and drawings to explain complex genetic data and clarify research priorities. Visual facilitation during meetings helped establish accurate representations of both cultural and biological diversity by externalizing heterogeneity and avoiding standardization. Group mind mapping enhanced collaborators' ability to visualize connections between Dene concepts, like *bets'erihchá* "respect" and caribou, and to recognize differences between knowledge systems that challenge translations and reduce the effectiveness of research outcomes. Collaborative visual products, like posters that represented different caribou types, allowed Dene partners to more clearly articulate subtleties within caribou intraspecific variation that are manifest through distinct dialects, place-based relationships, and cultural practices. Our results point to the potential for visual art to be used to improve communication, participation,

and knowledge production in interdisciplinary and cross-cultural research collaborations and to enhance the sustainable stewardship and protection of biodiversity.

Introduction

Art is increasingly recognized as a crucial component of interdisciplinary research. Visual art and design play a significant role in scientific communication, education, innovation, and public support for research (Curtis et al. 2012). Likewise, new scientific technologies continue to provide artists with contemporary methods of expression (Rieland 2014). Unfortunately, the entrenched and rigid structure of academic departments, designed to facilitate specialized research, has led to an artificial divide between art and the sciences that can limit creative reasoning, cross-fertilization of concepts, and intellectual creativity (Loehle 1990). The fields of art and science have not always been so polarized. Before the advent of photography and digital technologies for reproducing images, drawing was a necessary skill, taught as one of several standard academic subjects (Lerner 2007, Landin 2015). Naturalists, biologists, and specialists in many other fields have long recognized the importance of using visual aids to help communicate and decipher complex concepts (Nelkin and Anker 2004, Curtis et al. 2012). Recently, increased attention is being given to understanding how drawing and other data visualization techniques can be used to portray ideas, organize research results, improve comprehension, explain complex data, and transform public beliefs (e.g., TED talks, infographics, visual abstracts; Ainsworth et al. 2011, Hansen and Machin 2013).

In this paper, we examine the potential for visual art to aid in interdisciplinary social-ecological research that explores the dynamic relationships between human cultures, biota, and environments. In the early 1990s, social and natural scientists began to recognize the importance of identifying linkages between human cultural diversity (which may manifest, for example, in language and dialects, specific knowledge of the environment, and unique cultural practices) and the biological diversity of genes, species and ecosystems (Loh and Harmon 2005, Maffi and

Woodley 2010). The total variety of cultural and biological diversities, known as biocultural diversity, has the potential to reveal emergent patterns of variation, expose connections between forms of diversity, and provide insight into sustainable management and governance of complex unpredictable social-ecological systems (Kassam 2009, Pretty 2011, Gavin et al. 2015).

Engaging multiple knowledge systems through cross-cultural research with indigenous people is essential to sustainable biocultural research approaches that support equitable ecological decision-making and connect knowledge to effective actions (Pretty 2011). Language and practice ground indigenous people's association with biodiversity and encode place-based traditional knowledge of plants and animals (Hunn 2006). Culturally-ingrained knowledge of ecosystem processes and dynamics is constantly renewed through frequent interactions with the environment (Ingold 2000). Thus, collaborations with indigenous research partners have the potential to enable a more balanced understanding of complex human-ecological connections. However, communicating across language and knowledge systems within interdisciplinary collaborations can be challenging, leading to generalizations that compromise diversity and threaten the integrity of traditional knowledge (Jacobson and Stephens 2009). Effective biocultural research requires a diversity of approaches that can be enhanced by art to advance the interface between disciplines and knowledge systems.

Many important research tools and methodologies have been developed to enable cross-cultural collaborations and bridge knowledge systems (Berkes 2004, Tengö et al. 2014, Gavin et al. 2015, Rathwell et al. 2015). Among these, art and artistic processes have the potential to enhance collaborative research processes by improving the effectiveness of numerous social-ecological fields including occupancy mapping (Tobias 2000), complex systems science (Vervoort et al. 2014), social-environmental health and resilience (Castleden and Garvin 2008,

Rathwell and Armitage 2016), and ethnographic communication (Thomsen 2015), among others. Writing and oral communication have limited capacity to convey people's experiences with biodiversity and the complex patterns of the living world (Hunn 2006). Visual art can be effective in building dialogue within interdisciplinary teams and promoting research processes that acknowledge different knowledge bases and cultural contexts. Arts-based research attempts to develop "methodological pluralism" by combining traditional research methods with the creative and expressive approaches of the arts (Eisner 2006). Emergent methodologies, like participatory art, provide avenues for indigenous people to express important concepts and identify the context and details that ground their traditional knowledge (Castleden and Garvin 2008, Zurba and Berkes 2013). Similarly, art and "art making" can bridge knowledge systems and generate new knowledge through collaboration (Rathwell and Armitage 2016). New visualization technologies also enable researchers to tackle social-ecological complexity and to synthesize impacts, trends, patterns, and correlations (Hinke et al. 2004, Frankel and Reid 2008, Hampton et al. 2013, Vervoort et al. 2014).

In the Canadian north, biocultural diversity is often considered to be low due to the constraining effects of harsh ecological conditions that limit the number of species, human cultures, and linguistic groups. However, the regional biocultural diversity of the Arctic and Subarctic is apparent in the distinct practices of family and cultural groups, extensive dialects within languages, and subtle environmental variation that influence all life and can be difficult to quantify (Kassam 2009). Indigenous people's place-based knowledge can help reveal intraspecific diversities that are foundational to functioning systems (Fraser et al. 2006, Kassam 2009). In this paper we explore how visual art can be used in combination with scientific methods to examine the biocultural landscape of the Sahtú region of the Northwest Territories

(NWT), Canada. Our objective is to demonstrate how visual art can be used to synthesize and inform robust descriptions of indigenous cultural diversity and caribou (*Rangifer tarandus*) intraspecific variation.

Methods

Study area and context

The Sahtú region occupies 280,238 km² in central NWT, Canada. Dene people have lived in the area for thousands of years and maintain strong social-cultural connections to the land and wildlife (Andrews et al. 2012a, Andrews et al. 2012b, McMillan and Parlee 2013). There are currently five communities in the region; Délı̨ne, Tulı́'a, Norman Wells (Tłegóhı̨), Fort Good Hope (Rádelı̨ Kóé) and Colville Lake (K'áhbamı̨ Túé). While the communities share a common Athapaskan/North Slavey linguistic history, specific family roots and historic cultural relationships generate diversity that is evident in three main dialect groups (Fig. 4-1): 1. Shúhta (S) “mountain” dialect spoken in Tulı́'a, 2. Sahtú (D) “Bearlake” dialect spoken in Délı̨ne, and 3. K'áhsho (K) “Hare” and Dela dialects spoken in Fort Good Hope and Colville Lake. We use the abbreviations S, D, and K following Dene words in this paper to distinguish dialects. For a detailed description of the region's biocultural diversity see Polfus et al. (2016). The political and institutional structures of the Sahtú were defined by the Sahtú Dene and Métis Comprehensive Land Claim Agreement that concluded in 1993 and the Mackenzie Valley Resource Management Act of 1998. Management of renewable resources falls under the mandate of the ʔehdzo Got'ı̨ne Gots'é Nákedı̨ (Sahtú Renewable Resources Board; SRRB) and the five local ʔehdzo Got'ı̨ne (Renewable Resources Councils; RRCs). Recent initiatives by the SRRB and RRCs have sought

to re-frame approaches relating to natural resource research by focusing on innovative ways to include traditional knowledge and Dene laws in research and management (Polfus et al. 2016).

To facilitate these ambitious community objectives, we developed a community-collaborative research project (Tondu et al. 2014) to explore questions about biocultural diversity. An interdisciplinary approach was essential to conducting effective applied research, conservation, and management questions that addressed the interdependent complexity of northern social-ecological systems (Folke et al. 2007, Liu et al. 2007, Gavin et al. 2015, Rissman and Gillon 2016). Specifically, we were interested in describing and illuminating connections between caribou variation and the place-based traditional knowledge that is expressed in Dene and Métis people's relationships with caribou. The research drew heavily on participatory research frameworks and methodologies (Ferreira and Gendron 2011) as well as previous caribou traditional knowledge work carried out by the SRRB (Déḻṉe First Nation 2005, SENES Consultants Ltd. 2009, Sahtú Species At Risk Working Group 2013, 2014; and unpublished transcripts). A full description of the project's methods can be found in Polfus et al. (2016).

Focus group and advisory group meetings

We held a series of meetings in the Sahtú communities of Norman Wells, Fort Good Hope, Tulít'a, and Déḻṉe beginning in December of 2012. Our objectives were to plan the research, develop research questions and priorities, agree on methods, and share both scientific and traditional knowledge about caribou populations in the region. An initial set of focus group meetings were held in each community (including the addition of Colville Lake) during April of 2013. The information shared during the focus group meetings was analyzed and coded (NVivo; QSR International Pty Ltd. Version 10) to develop categories and themes (see Polfus et al. 2016

for further details). To best facilitate the collaborative production of knowledge and coanalysis of traditional knowledge and caribou genetic data we invited key individuals with an interest in the project to participate in what we initially called an advisory group. Advisory group members quickly became established as research partners and collaborators who informed the methods, ensured that Dene knowledge was interpreted accurately, and provided additional expertise in traditional knowledge and Dene language. The first three-day meeting was held in June 2014 and included 7 participants who helped select additional elders to participate in a follow-up meeting held in February 2015. All community participants received honoraria. Following the formal meetings, several of the research partners continued to work closely on the project by clarifying details of Dene language translations, presenting research results in schools and during public presentations, and reviewing and coauthoring project manuscripts (Polfus et al. 2016). The interdisciplinary nature of the research team (whose expertise also spanned knowledge and language systems) aided our ability to integrate tools and techniques from multiple disciplines, iteratively refine research questions, develop innovative methodological solutions, find and enhance connections with other ongoing research projects, and respond to community-based wildlife management needs.

Visual facilitation

We used visual aids to explain population genetic methods, depict the research process and collaborations, and help facilitate the ability of Dene people to share their own understanding about caribou with academic research collaborators. During meetings we used a mix of Microsoft PowerPoint presentations, whiteboard drawings, flip charts, large sticky notes, word maps, flow charts, diagrams, geographic maps (Google Earth 7.1.5.1557), and mind maps

to represent connections between themes and concepts. The lead author drew original artwork (both digitally and on paper) to represent animals, relationships, and ideas (Figs 4-2 to 4-5). We also teamed up with a cartoonist who had substantial experience drawing images related to northern resource management and indigenous cultures (Urquhart 2000, 2012). The cartoons inspired our use of bright colors and clear, simple illustrations to depict methods and research processes. For example, we used a simple visual flow chart to show the stages of the research process at every meeting (Fig. 4-2).

Prior to the first advisory group meeting we prepared several large flip charts of Dene concepts, caribou types, and Dene words. We also prepared a digital mind map to summarize and organize themes related to caribou genetics, relationships, behavior, language, and traditional knowledge that had been shared during the first set of focus group meetings. This visual information was used to prepare the meeting agenda and focus discussion on key research questions and concepts that required additional validation. To make visual facilitation more adaptive, the mind map was drawn using the open-source graphic editor GIMP v2.8 (www.gimp.org) so the lead author could modify it during the meeting (using a drawing tablet); modifications were projected, in real time, on a screen at the front of the room. This cumulative and iterative approach allowed us to refine initial categories and concepts to organize research themes with Dene language provided by participants. Before the second advisory group meeting the ideas, Dene words, and concepts from the initial advisory meeting flip chart sketches of the caribou types were digitally drawn, printed as large posters, and used as participatory tools to further refine concepts and research questions. In the second advisory group meeting, Dene elders and other collaborators annotated the poster illustrations, clarifying terminology and traditional knowledge of caribou subspecies diversity (Fig. 4-5).

Results

The process of using illustrations, diagrams, and other visual aids allowed research collaborators to expand on key research questions and underlying Dene concepts related to biocultural diversity. We discovered early in the research planning process that our explanations and presentations, specifically of population genetic methods, benefitted enormously from complementary drawings that used color and symbols to illustrate gene flow, population dynamics, and relationships between groups of animals (Fig. 4-3). Scientific visualizations and drawings helped community members understand and appreciate new, interesting, and sometimes complicated data – like mitochondrial DNA inheritance. However, our initial depictions did not always resonate with audiences that included Sahtú Dene and Métis elders with variable levels of formal western education and English language fluency. We worked closely with community researchers, an expert illustrator (Doug Urquhart), and interpreters to refine and adapt our approach to incorporate culturally appropriate symbols, humor, metaphors, and ecologically correct illustrations (Fig. 4-3). For example, we avoided stock imagery of caribou which we found often only includes images of large antlered males, and instead, the lead author drew illustrations to represent male and female animals of different age classes. These biologically representative illustrations more effectively conveyed practical information about gene flow to skilled traditional knowledge holders with substantial experience with caribou (Fig. 4-3).

We found that flip charts and images on the walls in the meeting space helped make esoteric and theoretical concepts more tangible. For example, it can be difficult to examine philosophical ideas, like respect, in a cross-cultural and multilingual setting. Challenging

translations and naive assumptions can derail dialogue or lead to fundamental misunderstandings. We found that when exploring definitions of Dene words, it can be just as important to ask “what does that look like?” as it is to ask “what does that mean?”. In our experience, strong visuals helped ground and center the discussion. At times, discussions involved sustained effort, including repeated explanations and work with sticky notes, flip charts and drawings on the white board, to reach consensus and understanding. The process of developing and agreeing to visual symbols that could be used to represent Dene concepts increased the ability of the research team to focus and refine ideas. We expand on two examples below that outline how images helped elucidate both cultural and biological diversity and led to increased clarity of our research questions.

Bets'erihchá “respect”

Dene concepts, understandings, and values are intricately related to representations of the political, cultural, and economic dimensions of biodiversity (Nazarea 2006). For example, the concept of respect is repeatedly brought up by indigenous people when talking about wildlife and the role of policies related to wildlife management (Délne First Nation 2005, Legat 2012). However, respect can have very different cultural connotations depending on who is using it and why it is being used. An all-encompassing interpretation of respect can also be difficult to identify across cultures because even within cultures, definitions and meanings are context specific and culturally diverse. From a western academic perspective, respect includes a sense of reverence or veneration toward a figure deemed to have especially admirable abilities or qualities. However, respect has other interpretations when used across age classes, to promote

cultural awareness, during political discourse, in relation to laws, or in the context of religion. Similarly, the interpretation of respect from a Dene perspective is contextual.

Dene conceptualizations of respect are non-prescriptive and linked to the very individual objective of “living in a good way.” Through our discussions we found it was impossible to separate the concept of respect from the series of practices that characterize Dene relationships with animals. The practical aspects of cultural diversity, such as family-specific behaviors related to how caribou are hunted, are explicitly linked to how individuals practice and conceptualize respect for caribou. Importantly, the distinct environmental conditions (specific habitats and lakes, rivers, mountains, etc.) experienced uniquely by different people across the Sahtú region (Fig. 4-1) have a strong influence on knowledge about specific caribou habitats and populations, how and why hunts occur, meat preparation techniques, and the language that is used to convey traditional knowledge. Thus, accurate representation of biocultural diversity requires a nuanced understanding of concepts like respect that portray the variation in knowledge that arises from diverse ecological contexts and avoids standardizing biodiversity (Kassam 2009).

When Dene and Métis people come together from across the Sahtú region there are important protocols for how knowledge is expressed and represented. Knowledge holders defer to individuals from specific sub-regions (at different scales as appropriate) in recognition that each cultural or family group has their own space and own cultural knowledge. As Walter Bayha explained, respect is “about being Dene, Dene ts'ı́ı, and then having that relationship with caribou. That's respect.” He continued, “Ası́ nezq bek'enedı (D) means you take care of them [caribou]. But, I think respect would go a lot further than that. See, this is the thing with even the word respect, [in Dene language] it's not even one word.” Frederick Andrew added, “Respect means bets'erı́hchá. When we respect caribou they know it, and in turn, they are there for us.

They are always there when we need them, and they provide us with food, clothes, and music.”

Another translation of *bets'erihchá* was expressed as “things that we hold sacred above all” and is related to Dene responsibility to care for animals as well as trusting that animals will provide Dene with the opportunity to survive. Thus, the essence behind the Dene language that is often translated into English as “respect” is deeply integrated with ideas of mutual compassion, trust, and empathy between Dene and caribou.

Dene concepts of respect are directly related to the idea that caribou are rational and self-aware beings that cannot (and should not) be controlled by humans. Dene elders in the Sahtú explain through stories that Dene *ʔekwé hɫé* (D) “Dene used to be caribou at one time.” The stories give agency to animals and explore the alternative perspectives of non-human beings. Dene ethics governing acceptable human impacts on caribou include the idea that to treat an animal with respect means to treat them as equals. Hunting is governed not solely by actions of Dene, but just as consciously by the decisions made by the caribou (for further discussion on this topic see Sharp and Sharp 2015). From a Dene perspective, individual caribou allow themselves to be killed to ensure Dene survival. In return Dene must respect caribou by following locally-acceptable practices, many of which promote *tɫch'ádú ts'ítsıwhıle* (D) “killing animals in the most humane and efficient way” and informal regulations, norms and social taboos that govern the treatment of animal remains.

We attempted to elicit distinct knowledge processes and externalize regional cultural diversity during meetings by working with visual representations of the language and dialects (Figs. 4-4 and 4-5). We found that abstract hierarchical concepts and themes (like key topics) did not necessarily translate easily, either visually or linguistically, between English and Dene perspectives. We spent significant time during our first advisory group meeting discussing the

organization and visual display of the main themes of the group mind map (Fig. 4-4). The thematic topics that emerged (1. ʔeʔah “Dene laws,” 2. Types of Caribou, 3. Así godí hé Dene ts’ı́łı “Relationships,” and 4. Caribou Behavior) evolved out of substantial dialogue and are significantly different than what was presented in the original version of the mind map. The concept of bets’erı́hchá “respect” was coupled with central concepts of ʔeʔah “Dene laws.” ʔeʔah relate to the ethics and cultural practices that necessitate “living in a good way” and, as discussed above, are contextual. A drum was used to symbolize the ʔeʔah portion of the mind map because caribou hide drums are critically important to the Dene way of life (Fig. 4-4). Frederick Andrew explained, “the drum brings us music, dancing, and hand games and makes you feel really good inside” and thus drums are a particularly venerated symbol of respectful cultural practices. Dene approaches to caribou and decision-making (and the often critical discussions of governance and policies related to caribou management in the region) also help explain the emphasis on ʔeʔah within the context of caribou research. Placing bets’erı́hchá near ʔeʔah in the mind map generated discussion about łeghát’s’eredı (D) “we give to each other” (symbolized by hands sharing food, Fig. 4-4) as well as a list of informal rules for the ethical treatment of animals. Łeghágots’enetę (D), which represents teaching, learning, and sharing the set of ethical practices with others, especially youth, is also tied closely with the concept of respect and was added to the conceptual model during discussions (symbolized by an image of a woman and child, Fig. 4-4).

Coming to consensus on organizational themes was difficult and we did not have enough time to develop Dene language-driven topics for “behavior” and “types of caribou” or identify adequate Dene imagery and symbols for every concept discussed. In fact, coming up with a Dene concept that encompassed the English word “relationships” (lower right quadrant of Fig. 4-4) also elicited four additional descriptions that differed dialectically and regionally across the

Sahtú. For the purpose of simplicity, we chose así godí hé Dene ts'łı, which translates more literally to “the being of all living things and people” in the collective sense. However, this term requires more discussion to adequately represent the cultural diversity of the concept.

As is the case in most multi-cultural and interdisciplinary research, the work could not be rushed. During meetings it was necessary to set priorities on the focus of discussions when dealing with complexity. We attempted to balance meeting agendas between academic research questions and compelling community-driven research priorities that were important to address at the time. Time and relationship building (within this project and through continued traditional knowledge explorations as part of the SRRB's broader research agendas) were critical to the success of our research processes. We anticipate continued work on Dene biocultural concepts and place-based biodiversity knowledge in future research initiatives.

Caribou biodiversity

Caribou are phenotypically diverse and are adapted to different habitats across their distribution. This variation is displayed in behavioral differences, numerous fur colors and patterns, size discrepancies, and specific life history traits. The inherent variation of caribou has made developing taxonomic categories for the species difficult, and many different iterations of subspecies, ecotypes, and populations have been proposed both internationally and within Canada (Flagstad and Røed 2003, COSEWIC 2011). Thus, collaborating with indigenous people who have extensive historic relationships with caribou has the potential to provide representations of caribou that acknowledge biodiversity and variation within a specific region, using criteria that may not always be identified by western-science-informed species taxonomies. An important component of our research project was to understand Dene conceptualizations and

language used to describe different types of caribou in the Sahtú region and synthesize how these types of caribou relate to population genetic differentiation (Polfus et al. 2016). To achieve this objective, we needed to address the biocultural landscape of the region and understand how variation is revealed through distinct place-based relationships and practices that Dene people have developed over millennia with caribou.

Initially, we found it challenging to clearly articulate Dene traditional knowledge and words specific to different types of caribou in the region. Dene language definitions of caribou were complicated by divergence among the three main dialects of the Sahtú region, the individual variation in caribou appearance (even within types), and each participant's specific life experiences. Thus, we found it was essential to create original illustrations to facilitate the development of robust traditional knowledge descriptions of caribou variation. Because particular types of caribou have also been defined by biologists, taxonomists, and government policies like the Canadian Species at Risk Act, it was also essential to avoid back-translating English concepts and names into Dene language. For example, through visual facilitation during advisory group sessions it became apparent that using the term gokwí (D) “barren-land or tundra” as a modifier to describe barren-ground caribou (gokwí ʔekwé (D), literally “barren-land caribou,” which had been used in some previous research projects) did not accurately reflect how Dene people used their language to convey meaning about caribou. Instead, Dene people have dialect-specific names for barren-ground caribou that vary across the region. The words are used in context and convey different meaning depending on who is speaking, what dialect is being used, what questions are being addressed, where on the land the speaker is located, and the dialect or background of the audience. Additional supporting information could be provided if

the speaker needed to make it clear that they were referring to a specific type of caribou or just speaking of all caribou in general.

Clear visual depictions of caribou helped participants come to agreement on overlap between caribou words and definitions for the three main types of caribou within the Sahtú region: 1. t̥d̥z̥ı (D,S,K) “boreal caribou,” 2. ʔekw̥é (D), ʔedə (K), n̥d̥ıl̥ə (S), ʔep̥é (S) “barren-ground caribou” and 3. shúhta ʔep̥é (S) “mountain caribou” (Polfus et al. 2016). Illustrations also provided a template for refining physical and behavioral characteristics recognized by Dene people as being representative of each type of caribou. We initially developed separate drawings on flip charts for each type of caribou that had been discussed in previous meetings (Fig. 4-5a,b). At the first advisory group meeting, we reviewed differences in caribou size, shape, color, and behavior and added Dene words and concepts to the initial draft of the illustrations. Participants slowly came to a consensus through this visually-facilitated discussion. Participants requested that the illustrations be turned into posters and used as teaching tools to help share caribou knowledge with youth. Dene partners realized that community-specific posters would be required to accurately represent regional dialects. At the second advisory group meeting, participants were invited to draw on the updated poster drafts, adding ideas and changing words or details as necessary (Fig. 4-5c,d).

Illustrations also helped us explore the question of how hunters could use caribou tracks to determine which type of caribou was present in an area. Initial sketches and discussion had resulted in two different shapes of tracks for ʔekw̥é (D) and t̥d̥z̥ı. However, when working closely with knowledgeable elders (who spoke several dialects) at the second meeting, we found that the word bek̥óg̥ə (K) or bek̥éǵı (D) referred to the space between the hooves (rather than hoof shape) that holds a gland called ʔéhtse (D; Fig. 4-5c). The insights into the Dene words for

hooves and tracks might not have been as clear without using drawings to depict the actual image of a hoof to the entire group. Participants agreed that identifying the type of caribou that left a track could be best established based on location, habitat type, group size, and size of the tracks. The illustrations gave participants the opportunity to more clearly understand research questions and compare specialized language about the different caribou types that is used by expert hunters and elders from different family groups. Similarly, the illustrations facilitated discussion and description of additional caribou features. For example, when presented with a poster of a caribou, elders were quick to add words and descriptions for the neck area, nose, stomach, antler beams, warble flies, caribou foods, scat and many other details that had not been discussed previously but demonstrated detailed knowledge of complex phenotypic differences among caribou types.

A visual approach to biocultural research enabled us to develop clear synergies between Dene traditional knowledge about caribou variation and caribou population genetics. Specifically, the three main types of caribou articulated through illustration by Dene people informed and corresponded with caribou genetic subpopulation structure identified through analysis of microsatellites and mitochondrial DNA from caribou fecal pellets (for full explanation see Polfus et al. 2016). Our research vividly illustrates the detailed knowledge that Dene people have about differences among caribou and, in doing so, demonstrates that Dene knowledge is a valid and essential platform for interpreting scientific (in this case genetic) data (Polfus et al. 2016). Understanding the more nuanced components of Dene traditional knowledge and language relating to caribou variation would have been much more difficult without the use of original illustrations and the visual participation of Dene collaborators. After being verified, the caribou posters will be presented to the communities as educational tools to help with

transmission of language, traditional knowledge, scientific knowledge, and the promotion of *bets'erihchá*.

Discussion

Our research project demonstrates the potential for visual art to increase communication and exchange of knowledge between interdisciplinary and cross-cultural research teams while at the same time illuminating and addressing biocultural diversity. Connections between Dene cultural diversity and environmental variation have shaped the ecological dynamics of the Sahtú region for millennia. Analysis of the multifaceted links between ecological and cultural diversity can provide insights into unique ecological histories and identify approaches for sustainable use of resources into the future (Maffi and Woodley 2010, Polfus et al. 2016). The first step to identifying and supporting local diversities is through a flexible and creative approach to research. Indigenous people's traditional knowledge describes biological variation that is interrelated with unique cultural identities and dialects. Research that generalizes people's knowledge stands to lose opportunities to understand how regional heterogeneity – in both culture and biodiversity – interact to produce patterns of biocultural diversity on the landscape (Kassam 2009). Art can illuminate the wide array of processes that cultures have developed to understand their environments. Thus, art offers researchers effective ways to identify, clarify, and convey biocultural concepts that are elicited from local people through different social-ecological methods. Biocultural diversity is not static, and, by acknowledging the dynamic nature of relationships with the natural world, it is possible to build more robust representations of social-ecological systems (Kassam 2009). In our research we used illustrations to identify, understand, and depict distinct Dene conceptualizations of relationships with caribou and the

caribou biodiversity that is identified through those relationships. Specifically, we found that visual methods enhanced communication, participation, and accurate representation of regional biocultural diversity.

Communication

Visual art is a powerful communication tool (Curtis et al. 2012). In many cases, the use of visualizations can reveal ideas that are difficult to comprehend through oral communication alone (Cornwall and Jewkes 1995, Hunn 2006). This is especially true when knowledge is represented within different knowledge systems and languages (Rathwell and Armitage 2016). When faced with increased levels of knowledge complexity during meetings, it can be difficult not to retreat to simplistic explanations which obscure critical details that are challenging to express orally (Sibbet 2010). Further, images can be used to quickly convey information to facilitate group discussions. For example, when Dene language is interpreted to English on the spot (as is often the case in multilingual meetings), clarity can be lost due to constraints on the interpreter's ability to instantly transform technical statements between languages. Visuals, like drawings of caribou, can aid in this type of interpretative context by increasing the level of detail available to the speakers and the audience. Phrases like "those caribou are darker" can be vague and lack contextual information required for shared understanding. Instead, multiple illustrations of caribou that depict the contrast between different shades of fur can instantly convey information which is cumbersome to express in words, especially across languages. Furthermore, short verb-based phrases in Dene language (for example descriptions of specific hunting techniques) transmit significant information to native-speakers, but lack resolution when translated into English. Drawing depictions of the hunting techniques on the white-board

illuminated technical Dene phrases that were difficult to translate because they encoded so much meaning (e.g., goecha gots'anele (S) “to hunt from downwind” described in Polfus et al. 2016).

Importantly, images can act as shared reference points that help to externalize private knowledge and enable effective dissemination of ideas (Ainsworth et al. 2011, Rathwell and Armitage 2016). The shared experience of perceiving an image allows for the establishment of a common level of understanding so that dialogue can advance to deeper and more complex topics. We found that the images of caribou and Dene concepts in our meeting space exposed shared knowledge and allowed the research team to advance more quickly to collaborative knowledge generation. For example, it is common in cross-cultural meetings for individuals to take turns providing statements of their own expert knowledge. This structure often includes repetitive elements, like generic descriptions of DNA inheritance or generic descriptions of caribou and respect. Providing a visual representation of this type of information allows both the presenter and their audience to demonstrate their understanding of baseline knowledge. Thus, artistic representations can produce a more dynamic form of back and forth communication and lead to deliberate and explicit analysis of specific research questions like caribou relationships or the diverse conceptualizations of respect. Visualizations allow interdisciplinary teams to develop group memory, organize background knowledge, and make alternative viewpoints accessible; all of which increase the exchange of information and the clarity of emergent ideas (Sibbet 2010, Ainsworth et al. 2011).

Art can also be an important tool for communicating research results to the general public (Curtis et al. 2012). There is growing recognition for the responsibility of scientists to reach beyond their disciplines and share their results more broadly (Baron 2010, Smith et al. 2013). Unfortunately, science communication is challenged by the pressures of modern academia and

funding agencies that reward publication in “high-impact” academic journals (Smith et al. 2013). Collaborative visual products that are part of the research process can also serve as ideal communication tools. During our meetings, community partners appreciated the chance to work on research outcomes, like the caribou posters, that had direct and identifiable use in the Sahtú schools. At the same time, academically situated members of our research team benefitted from the images for use in conference presentations and public outreach beyond the Sahtú region (Merkle 2016). Thus, a focus on visual art during the research process not only contributed to positive synergies among research priorities; art also helped us share research findings with those most impacted by potential research outcomes. Co-management authorities have used similar artistic products to help promote conservation and wildlife management initiatives in the region. For example, the book, “Remember the Promise,” used illustrations by our lead author and Dene language to describe how species are protected through the NWT Species at Risk Act and how species at risk policies sync with important Dene concepts and practices (Sahtú Species At Risk Working Group 2014). In this way, visual art can express traditional knowledge in new contexts that present opportunities to connect with youth and the public (Rathwell and Armitage 2016). Additionally, the book reminds non-Dene policy makers to integrate indigenous culture when developing legislation and management strategies.

Participation

Visual facilitation during meetings promotes active listening and participation because individuals’ contributions are acknowledged and recorded graphically (Sibbet 2010). In a media landscape that is saturated with photographs, original illustrations provide a refreshing and intriguing context. Featuring original artwork during meetings immediately improves group

engagement and promotes active listening (Valenza and Adkins 2009, Sibbet 2010). Engagement is essential to interdisciplinary collaborations, especially those that require input from all group members in order to produce output that is representative of cultural diversity. Art is also a medium that is open for critique from diverse and cross-cultural audiences, unlike academic manuscripts. For example, the posters featuring caribou illustrations allowed academic research partners to present preliminary results for review by Dene knowledge holders and elders in an accessible format. Asking participants to write and draw directly on the posters also elicited active participation in a shared research product (Fig. 4-5). By turning communication into a visual practice, rather than verbal, we provided a unique avenue for multilingual participants to demonstrate their knowledge.

Participatory art has been widely used to build collaborations between researchers and indigenous communities and empower participants to define their own visual representation that express connections between culture, environment, political systems, and community well-being (Castleden and Garvin 2008, Zurba and Berkes 2013, Zurba and Friese 2014, Rathwell and Armitage 2016). Further, participatory art can encourage collaborative processes that address important dimensions of social-ecological systems by bringing together people from different backgrounds to share in an inclusive dialogue around a piece of art (Zurba and Friese 2014, Rathwell and Armitage 2016). In fact, the creative processes and interactions that are required in participatory art projects can act as powerful tools for reconciliation and self-determination (Zurba and Friese 2014). While our project's initial goal was not to produce collaborative artwork, we were able to use participatory visualization approaches to effectively evoke specialized traditional knowledge (e.g., Dene words and names for different caribou anatomy that were added to the posters), build deeper understandings of research topics and themes, and

develop visuals useful for communicating social-ecological knowledge and biodiversity to local and broader audiences.

Participatory approaches also illuminate diversity within groups by confirming the legitimacy of multiple voices and points of view (Rathwell and Armitage 2016). For example, working with the mind map (Fig. 4-4) during our advisory group meeting allowed community research collaborators to expand on important cultural concepts and use Dene language to describe research themes. The visual representation of ideas within the mind map enabled nuanced reflection on the diverse experiences of different people and allowed cultural diversities to resonate more clearly among collaborators. Mind maps and other symbolic diagrams have been shown to enhance a group's ability to see connections between topics and find alternate ways to represent ideas, especially when concepts are bound closely with cultural ideologies and personal mental models (Sibbet 2010, Davies 2011). Highlighting multidimensional connections within mind maps during meetings can also allow interdisciplinary research teams to work together to recognize where important differences between knowledge systems exist (Winowiecki et al. 2011). Notably, these differences often occupy conceptual spaces where translations between languages can break down. Identifying disparities in how knowledge is organized and presented among cultures can be seen as an opportunity to: 1) open dialogue, 2) examine how different knowledge systems visualize the world, and 3) explore how approaches to problems may vary. In many cases these differences are a chance to learn together and generate new insights through collaboration.

The mind map developed for our research project was used to both organize traditional knowledge that had been shared in previous meetings and highlight priorities for further verification during the first advisory group meeting. Thus, while the mind map was adapted and

modified by the group during the meeting, the initial work on its organization was done in preparation for the meeting. Additional research will be able to address this limitation by initiating the creation of original mind maps during meetings. This type of participatory method can help academic researchers assume the role of facilitator and catalyst, rather than director (Cornwall and Jewkes 1995). Inclusive group facilitation techniques, like mind mapping, have the potential to provide better creative autonomy over projects and develop an even more representative picture of shared ideas (Winowiecki et al. 2011, Zurba and Friese 2014, Rathwell and Armitage 2016).

Representation

Our research benefitted enormously from the use of customized illustrations that we developed to increase clarity and communication during all phases of the research process. Importantly, these illustrations were often modified to represent updated information or address newly identified areas of confusion in an adaptive and applied way. Specific illustrations of caribou, Dene people, behaviors, and concepts – that also reflected Sahtú Dene and Métis cultural iconography – provided an important platform for discussions of cultural diversity and caribou variation. The unique illustrations that we developed specifically for the project also allowed academic research partners to establish credibility with skilled Dene knowledge holders. For example, depicting accurate caribou morphology demonstrated that traditional knowledge and teachings that had been shared previously were heard and recognized. Further, by carefully choosing culturally relevant imagery, like drums or caribou, we ensured participants were able to see their own identities represented during the research process, which helped build trust and relationships between research partners. By building our own visual aids and avoiding confusing

and non-specific images we were able to successfully engage with community partners on a deeper level.

Illustrations were essential because they allowed the advisory group to focus on the symbolic characteristics of each type of caribou. While photographs are powerful conduits of information, in many circumstances the extra information represented in a photograph can impede people's ability to isolate important characteristics (Monoyios 2011). For example, when presented with a photograph of a caribou, hunters will often ask for specific information about the location, time of year, and other clarifying details that would be important in the context of hunting. Skilled hunters also recognize that a photograph of a caribou represents just one individual, and individual caribou are known to show variation in physical features. On the other hand, a drawing can convey select information about spatial patterns and relationships quickly and clearly (Keller 2011, Monoyios 2011). A drawing is more easily seen as a generalized representation and allows important contrasts between various kinds of animals to be identified. Illustrations can also represent multiple ideas in a single image (e.g., overlays, diagrams to communicate processes, etc.) while at the same time eliminating distracting or superfluous details (Jennifer 2015).

One important consideration of our research was that almost all illustrations used in the project were generated by one researcher, the lead author, with the addition of a few early contributions by Doug Urquhart. Because symbols are culture-specific, the way that ideas are expressed visually will differ between people, languages, and knowledge systems. Our reliance on one artist's interpretation of the research process and results limits the ability of our images to represent alternative worldviews. Working with only one artist ensures a stylistically coherent body of images, which can also be valuable. Nonetheless, future research collaborations would

benefit from the perspectives of artists with diverse backgrounds who could develop Dene imagery for specific topics, like *bets'erihchá*. Future research should prioritize ways to help indigenous people use art to express their knowledge and improve collaborative and interdisciplinary social-ecological projects (Rathwell and Armitage 2016). In the conclusion we provide an example of how this approach is already being put into practice in the Sahtú region.

Conclusion

Strong visuals were essential to the successful communication and implementation of our community-collaborative research through all stages of the research process. Our approach builds on similar research that suggests that visual methods can improve communication, especially among knowledge systems and languages, and that artistic processes should be considered a fundamental component of interdisciplinary social-ecological research methodologies and practices (Rathwell and Armitage 2016). In collaborative research it is essential to draw upon the expertise of a diversity of people that span knowledge systems, language expertise, artistic abilities, and familiarity with specialized tools and techniques – from ecology, social sciences, and linguistics, to population genetics, visual design, and art (Gavin et al. 2015, Knapp et al. 2015, Pittman et al. 2016). Artistic ability can be fostered as a fundamental cross-cultural skill, and, much like humor, is a valuable contribution to collaborative teams that need to connect knowledge systems and develop sustainable solutions. We propose that investing in collaborations with artists is an effective way to enhance and improve biocultural or social-ecological research outcomes.

Art has the potential to act as a universal language and provides a platform for comprehensive analysis that can encompass multiple research elements simultaneously.

Interdisciplinary biocultural research must bridge not only distinct disciplinary barriers but also differing knowledge systems and languages. We demonstrate the potential for visual art to aid biocultural research processes and foster connections and understandings among academic researchers and indigenous community members. We found that refined visuals, such as illustrations, expanded the communication capacity of our diverse collaborative team. Art promotes creativity and enhances techniques that make it possible to co-develop research questions and collaboratively analyze research results.

Art can also be used to emphasize self-governance, indigenous stewardship, and local authority over biodiversity management while at the same time asserting cultural distinctiveness (Pretty 2011). For example, a local Dene artist was recently asked to attend a D  l  n   Caribou Working Group meeting focused on developing a community-driven caribou management plan. The artist listened to the ideas that were communicated and produced images that reflected the community stories shared during the meeting. The final artwork was used in the resulting plan and provided community ownership to the project in ways that were visually compelling and immediately apparent to everyone involved (D  l  n     ekw   Working Group 2016). Supporting cultural practices, dialects, and place-based knowledge presents opportunities for people to define their identity and assert the uniqueness of their perspective (Kofinas et al. 2000). By supporting diversity and encouraging creativity, through visual approaches, it is possible to facilitate a unique convergence of ideas across knowledge systems that enhance the sustainable stewardship of biodiversity (Teng   et al. 2014, Gavin et al. 2015).

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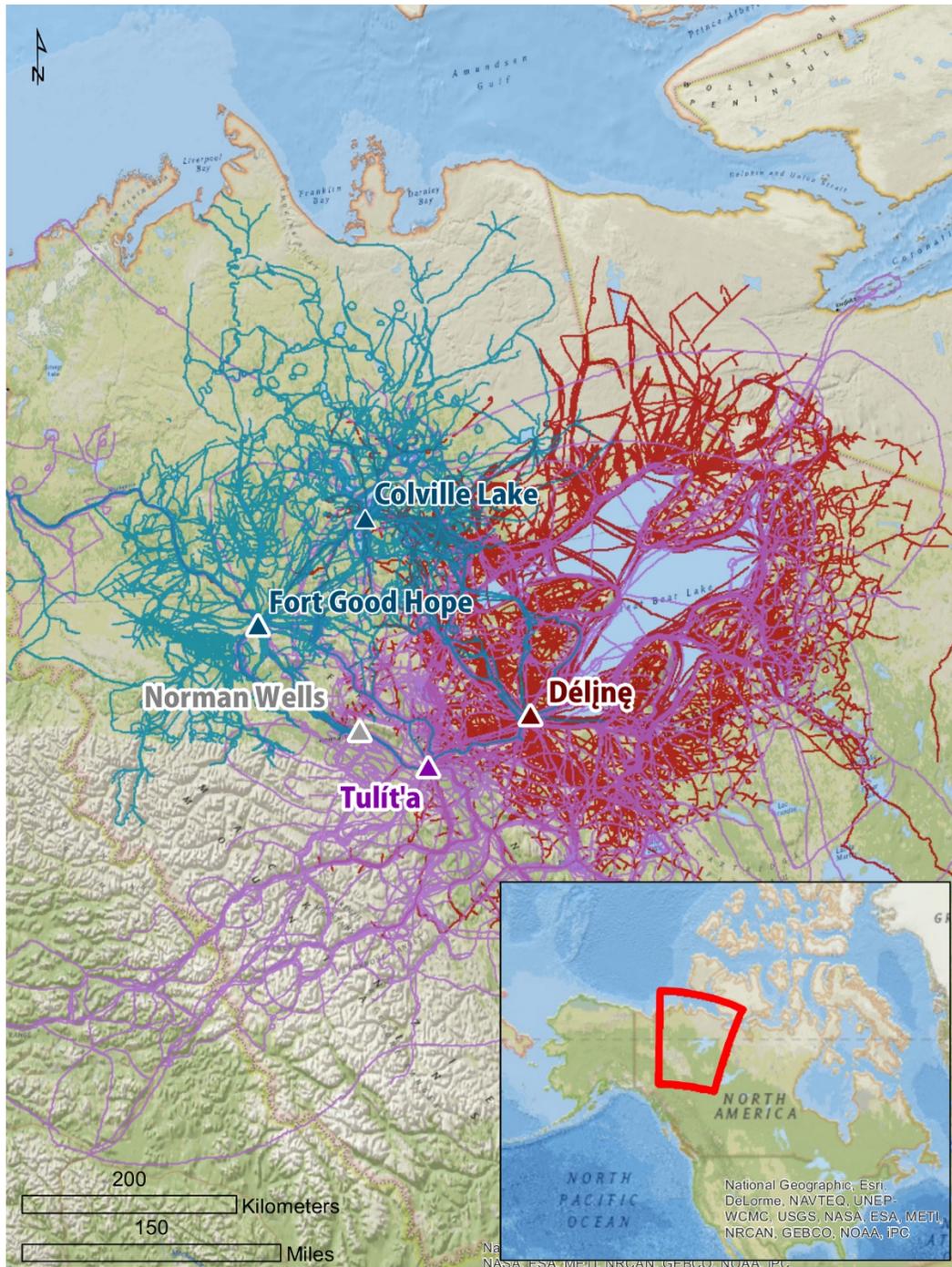


Figure 4-1. The Sahtú region of the Northwest Territories, Canada, currently includes five communities: Délı̄ne, Tulit'a, Norman Wells, Fort Good Hope and Colville Lake. Dene people have lived in the region for millennia and share a common Athapaskan/North Slavey linguistic history. However, cultural and linguistic variation between communities reflects historical

relationships between people, political agreements, and economic ties. Historic trail use displayed here by community helps to reveal, in general, the dynamic spatial patterns of the three main social-linguistic groups, as follows: 1. Tulít'a, including Shúhta Got'ine, K'áalq Got'ine, and Dəoga Got'ine (purple), 2. Dél'ine Got'ine (red), and 3. Fort Good Hope and Colville Lake, including K'áhsho Got'ine and Dela Got'ine (blue; unpublished data, Dene Nation, Dene mapping project 1900-1980).

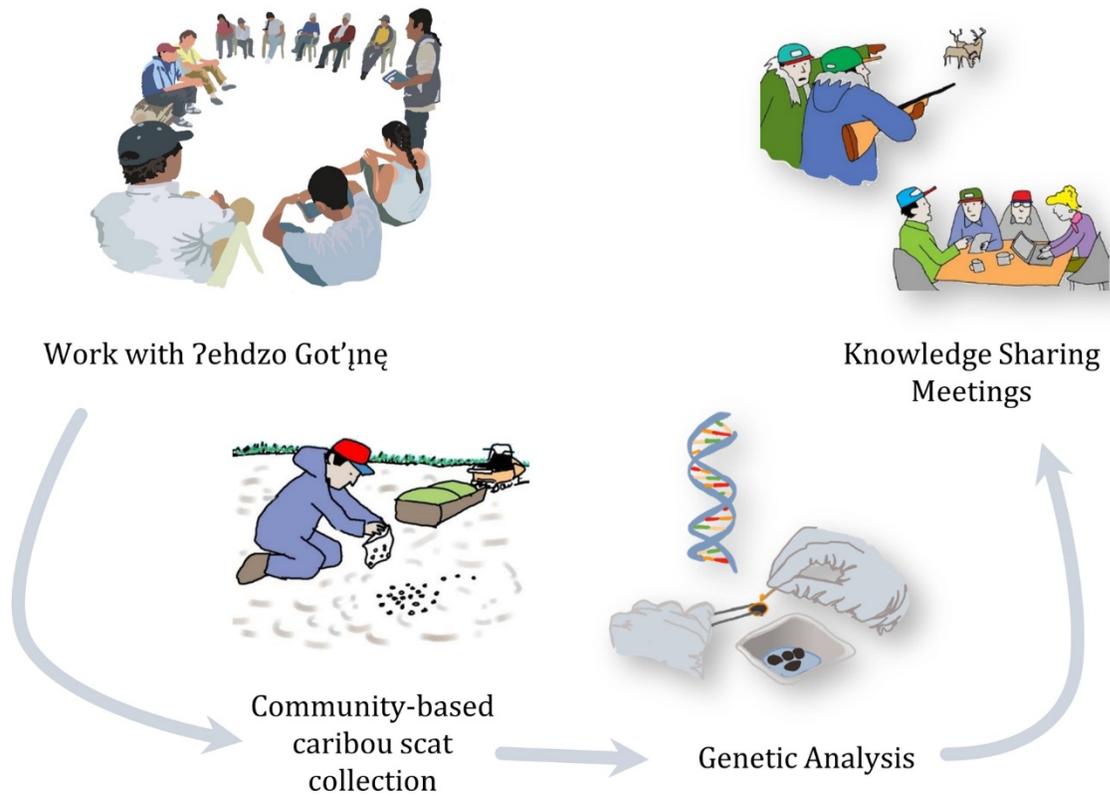
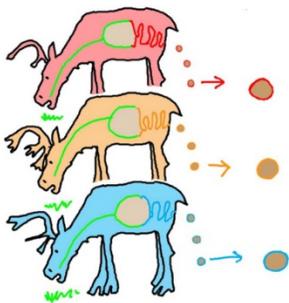


Figure 4-2. Diagram depicting the community-collaborative research process that was used during focus group meetings, advisory group meetings, and public presentations. The illustrations of the community-based scat collection and knowledge sharing meetings were developed and drawn by Doug Urquhart for the project and the other two illustrations were developed over the course of the project by Jean Polfus.

Methods

Population genetics allows scientists to understand how different groups of caribou are related to each other in much the same way humans are related to their extended families.



Each caribou has its own individual DNA that is found on the outside mucus layer on caribou scat (poop).

We are able to take DNA from the scat that is found frozen on the snow.



By analyzing the DNA from the caribou scat, we are able to identify how caribou are related to other caribou.

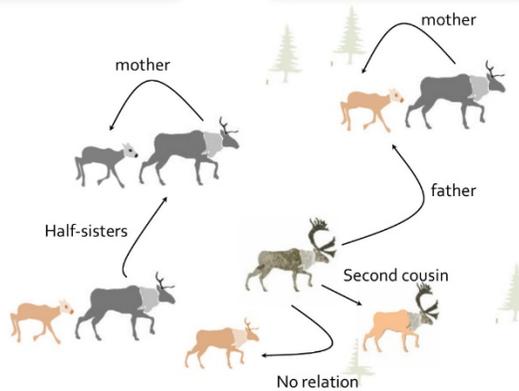


Figure 4-3. Diagram used in PowerPoint presentations and posters with visual description of genetic methods. The top two illustrations were drawn by Doug Urquhart and the caribou relationship drawing, photos, and overall design were developed by Jean Polfus.

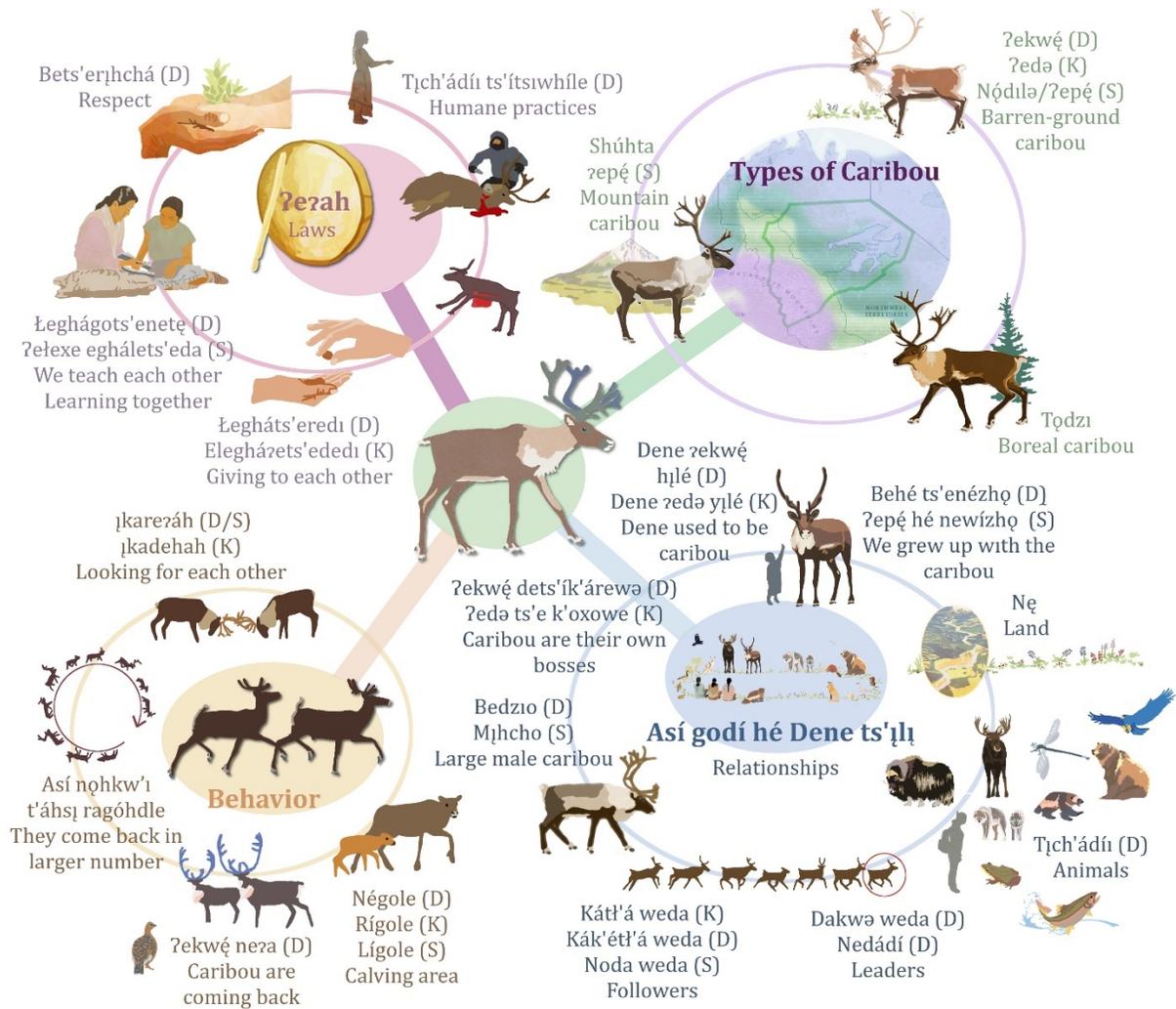


Figure 4-4. The research mind map diagram was developed to explore concepts and connections between Dene themes and research questions related to caribou with advisory group participants in June 2014. Thematic topics that were used to guide the agenda and focus discussions and where possible are represented with Dene concepts and Dene imagery. The topic areas are clockwise from top left: 1. ʔeʔah “Dene laws,” 2. Types of Caribou, 3. Así godí hé Dene ts'íłı “Relationships,” and 4. Caribou Behavior. Images were drawn by Jean Polfus.



a.



b.



c.



d.

Figure 4-5. Images from the advisory group meetings depicting various visual facilitation techniques: a. Jean Polfus adds key ideas to the white board (depictions of hoof shapes) and flip chart illustrations of the different types of caribou during the first advisory group session in June 2014; b. details of the flip chart illustration for Ɂekwé/Ɂedə/Ɂepé (D/K/S) “barren-ground caribou” and tódzi “boreal caribou” including notes with Dene language in the three main dialects of the Sahtú region; c. details from the draft of the large poster depicting further explanations and additional information added by participants of the second advisory group meeting held in February 2015; and d. participants of the second advisory group meeting work together on the large tódzi poster.

CHAPTER 5: CONCLUSION

Caribou biological diversity

The research in this dissertation bridges multiple disciplinary traditions to develop comprehensive and united representations of caribou biodiversity through an interdisciplinary exploration of population genetics, phylogenetics, traditional knowledge, language, and visual approaches. For the first time, we establish a broad scale description of the distribution, spatial organization, and the degree of differentiation of caribou populations in the Sahtú region of the Northwest Territories, Canada. Identifying caribou biodiversity (intraspecific diversity) is important because of the potential role of genetic diversity in population persistence, local adaptations, and incipient speciation (Mee et al. 2015, Hamilton and Miller 2016). Genetic analysis of material from caribou fecal pellets provided evidence for microsatellite genetic differentiation that corresponded to the caribou types recognized by Dene people: t̥d̥z̥ı̥ “boreal caribou,” ʔekw̥é “barren-ground caribou,” and shúhta ʔep̥é “mountain caribou.”

Our collaborative research approach revealed that caribou biodiversity does not exist in isolation, but rather is intrinsically and evolutionarily linked to cultural diversity and indigenous knowledge systems (Loh and Harmon 2005, Kassam 2009, Turnbull 2009). For example, Shúhta Got'ın̥ knowledge holders describe a distinct group of caribou in the mountains known as t̥nat'̥əa that likely represent an important component of caribou biodiversity not currently identified by scientific taxonomies. Information held in traditional knowledge categorizations may be especially suited to identifying this type of intraspecific heterogeneity (Fraser et al. 2006, Newmaster et al. 2007). Thus, including multiple knowledge systems and languages in environmental research is essential to defining appropriate descriptions of species variation that can be used to inform conservation strategies (Fraser and Bernatchez 2001). Future collaborative

work that includes Dene and Métis people's diverse place-based relationships with unique groups of caribou across the region has the potential to unveil synergies between ecological adaptations and life history mechanisms that promote the adaptive variation of caribou.

Molecular approaches to delineating intraspecific relationships among caribou are extremely valuable to increasing our understanding of population dynamics through time and space. The results of Chapter 3 support a growing body of literature that highlight the role of the Pleistocene glacial-interglacial cycles in shaping current patterns of caribou diversity (Flagstad and Røed 2003, McDevitt et al. 2009, Klütsch et al. 2012, Weckworth et al. 2012, Yannic et al. 2014, Klütsch et al. 2016). Specifically, in the Sahtú region we found that caribou that are recognized as the boreal ecotype of woodland caribou evolved independently from the northern Beringian lineage that also includes barren-ground and mountain caribou. Thus, the Sahtú t̥odzi have distinct phylogeographic origins that differ from the boreal caribou of southern Canada that belong to a lineage known to have persisted in sub-Laurentide refugia. This result demonstrates that two independent lineages of caribou have converged on a similar phenotype and suggests that natural selection plays an important role in caribou intraspecific variation (Schluter et al. 2004, Elmer and Meyer 2011). Intraspecific parallel evolution presents an ideal opportunity to test the genetic basis for adaptive traits (Elmer and Meyer 2011). New DNA markers and analytical tools, including forthcoming conservation genomic approaches, will help quantify adaptive loci and identify connections between gene complexes and specific adaptations to particular ecological conditions (Shafer et al. 2015). Future research into locally adapted caribou genomes will continue to increase our understanding of the complex intraspecific relationships that influence our definitions of species, subspecies, ecotypes, DUs, herds, and population units.

Phylogenetic research would also benefit from additional information held in Dene language and traditional knowledge of peoples' long-term relationships with caribou in the region. The historic knowledge captured in Dene stories depicts a unique understanding of caribou evolutionary history and demographic processes. For example, some Dene stories indicate that caribou originally came from the north. The detailed traditional knowledge of caribou movements has the potential to inform parallel genetic explorations of the origin and maintenance of caribou variation. Bringing together complementary knowledge systems can promote a more profound understanding of caribou population organization that will help focus resource management and biocultural diversity research in the future. Our results make it possible to refine forthcoming collaborative research questions related to caribou in the region and develop analysis approaches that will aid Sahtú communities in decision-making and community-based caribou management plans.

An interdisciplinary approach to conservation

An important contribution of this project was the development of a robust interdisciplinary community-based research process. An interdisciplinary approach to conservation is necessary to include the human dimensions of ecological systems in research and identify and protect both cultural and biological diversity (Pretty 2011, Bennett et al. 2016b). We acknowledged the interconnected structure of social-ecological systems from the outset of our research process and brought together a team of research partners and collaborators who represented diverse disciplines, knowledge systems, and languages. In doing so we embraced the opportunity for all collaborators to learn from each other through the process of *łeghágots'enetę* “learning together” (see Chapter 2 for more information). Non-Dene researchers benefited from

learning about the local ecology through the place-based traditional knowledge and language shared by Dene collaborators. Likewise, Dene research partners learned about genetic relationships between caribou and benefited from increased contact with “outsider knowledge” (Caine et al. 2007) that included access to information that was valuable for governance and conservation of local resources (see Appendix 1 for more information; Adams et al. 2014, Tondu et al. 2014).

Our collaboration was designed to meet the needs of a diverse group with different required research outcomes, from community-level capacity building to the completion of academic prerequisites. Our interdisciplinary approach utilized methods from both the natural and social sciences to overcome limitations imposed by each method used in isolation. This “methodological triangulation” allowed questions to be addressed from multiple perspectives, alternative solutions to emerge, and results to be verified by more than one source (Bennett et al. 2016a). By acknowledging the unique contributions of multiple knowledge systems we were able to increase the legitimacy and salience of potential conservation outcomes among community members and conservation practitioners. Furthermore, our approach built on other research that demonstrates how deliberate attention to art and other visual approaches can improve the effectiveness of interdisciplinary collaborations that bridge knowledge systems and languages (Rathwell and Armitage 2016). In particular, Chapter 4 highlights the importance of respecting and empowering the diverse skills of individual team members as part of an interdisciplinary social-ecological research process. This includes acknowledging the distinct cultural diversity that occurs across the Sahtú region and finding original ways to avoid standardizing important place-based knowledge and dialects. We found that visual techniques aided the research through all stages of the research process and made it easier to identify both

cultural and biological heterogeneity. Art also improved the research by clarifying communication, improving participation, and strengthening our representations of traditional knowledge and caribou diversity.

Conservation implications

Over the past 100 years caribou populations in North America have drastically declined following human-induced habitat loss, shifting predator-prey communities, altered parasite-host dynamics, and global climate change (Vors and Boyce 2009). Yet caribou remain one of the most evolutionarily successful cold-adapted ungulate species, occurring in habitats that vary dramatically in ecological and climatic conditions – from the high arctic to their southern fringes on small isolated islands along the north shore of Lake Superior. Caribou and reindeer are unique in their obvious intraspecific variation in behaviors, phenotypes, and neutral genetic markers. Interestingly, this variation, which has undoubtedly contributed to their successful circumpolar distribution and persistence over the glacial cycles of the Pleistocene, also poses unique challenges to conservation under the Canadian Species at Risk Act (SARA). Trying to apply targeted conservation policies to population units within the species quickly unveils dilemmas for species-based biodiversity conservation models (O'Brien and Mayr 1991, Fraser et al. 2006, Fitzpatrick et al. 2015). Developing a clear understanding of caribou diversity is the first step to successfully implementing a range of management policies, actions, and outcomes.

For example, in Canada caribou have been divided into various subspecies, ecotypes and most recently Designatable Units (DUs) by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), all of which stipulate classification schemes below the species level. All designations reveal that types can be distinguished based on multiple criteria, an idiosyncrasy

that reflects broader debates within the conservation community on how to prioritize units (subspecies, ecotypes, populations, or population components) within the assorted expanse of intraspecific diversity for conservation (O'Brien and Mayr 1991, Sites and Crandall 1997, Mace 2004, Crair 2015, Mee et al. 2015, Pond et al. 2016). Caribou conservation requires a clear understanding of the timing of genetic divergence and the reconstruction of population histories to identify biological diversity, establish conservation units, minimize the loss of genetic diversity, and implement effective recovery plans (Crandall 2009, Lopes and Boessenkool 2010, Klütsch et al. 2016).

At the national scale, our research results provide guidance on the appropriateness of using DUs to define caribou conservation units (COSEWIC 2011). Specifically, we demonstrate that the boreal ecotype of woodland caribou includes substantial biodiversity and is composed of two distinct phylogeographic assemblages, which calls into question the validity of treating the entire distribution of the boreal ecotype as one DU under SARA. The goal of the recovery strategy for boreal caribou is to achieve self-sustaining local populations (of which 57 were identified) throughout their distribution. However, as pointed out by Weckworth (2012) the local population unit “may be too fine scale to adequately protect the ecological and evolutionary integrity of the species.” Likewise, our results suggest that caribou conservation under COSEWIC and SARA may actually be hindered by treating caribou as separate DUs because intraspecific introgression (genetic exchange between populations, ecotypes or subspecies) may be evolutionarily critical to the persistence of the species as a whole (Hinkes et al. 2005, Lorenzen et al. 2011). Furthermore, reliably interpreting genetic or ecological criteria for designating DUs remains a subjective exercise. A more integrative conservation approach that takes into account meta-population dynamics, eco-evolutionary processes, and indigenous

knowledge may be better suited to conserving the diverse intraspecific variation inherent to caribou (Weckworth 2012).

Process-oriented conservation requires the protection of heterogeneous landscapes, biological diversity, and viable populations that contain the potential for selection to take place (Moritz 2002, Moritz and Potter 2013). The unique genetic and demographic history of caribou in North America (represented by multiple phylogenetic lineages and extensive standing genetic variability) implies that conservation initiatives may be better actualized by “preserving continuous environmental gradients across which selection and migration can interact to maintain population viability and (adaptive) genetic diversity” (Moritz 2002:238). It is possible that the contiguous habitat of the boreal forest is the catalyst for the origin of adaptations (specific ecotypes for example) and essential to maintaining adaptive potential, creating genetic variation, transferring important adaptations across the landscape, and promoting colonization and dispersal following extreme environmental events (i.e., fires). Thus, the successful conservation of the boreal ecotype of woodland caribou hinges on the protection of large, intact landscapes that allow eco-evolutionary processes, like evolutionary rescue, to occur (Bell and Gonzalez 2009).

Our research presents a foundational understanding of the biodiversity, spatial distribution, and connectivity among groups of caribou in the Sahtú. Current federal policies require that provincial and territorial governments develop caribou range and action plans (detailed local-level planning mandatory to guide implantation of recovery actions) to support the boreal caribou recovery strategy (Environment Canada 2012). Results from Chapters 2 and 3 will help managers better understand the genetic structure of caribou populations in the region and make informed decisions about range plans, population units, and trend-analysis. As caribou

genetic samples accumulate across Canada and the NWT in collaboration with other research projects, analysis techniques can be used to compare allele frequencies between ranges, monitor demographic histories, document dispersal and immigration patterns, and evaluate responses to anthropogenic activities (DeYoung and Honeycutt 2005). Further, our research provides baseline population structure data for caribou that will assist with Environmental Impact Assessments and enable managers to actively explore different land use scenarios, develop a cost-effective non-invasive sampling methods, and pursue recovery activities.

At the local level, a comprehensive understanding of historic gene flow and genetic lineages of caribou provide managers and Renewable Resources Councils with important insight into appropriate units for the management of boreal caribou populations in the Sahtú region. For example, the Government of the NWT requires the development of “comprehensive boreal caribou range management plans in areas where development may create significant access or loss of habitat” (Department of Environment and Natural Resources 2010). While it is understandable that subdividing large continuous populations into smaller management units may be required to facilitate recovery planning and management, it is essential that sufficient data, including traditional knowledge, be used to determine the borders because of the implications local population units have on recovery strategies (Zannèse et al. 2006). The baseline caribou genetic and traditional knowledge data collected in the Sahtú as part of this project can be used to identify fine-scale genetic structure within boreal caribou range and also has the potential to be used to monitor the impacts of localized industrial projects (especially structures like roads or shale-oil developments) on caribou population distribution (Ball et al. 2010, Galpern et al. 2012, Galpern et al. 2014). For example, the population genetic parameters identified in our research can eventually be used in simulations based on spatial network

connectivity analysis to assess the impact of different land use activities on gene flow (Galpern et al. 2014).

Including indigenous people in environmental research and conservation decision-making is legally required and crucial to the implementation of effective policy actions (Houde 2007, Adams et al. 2014, Housty et al. 2014). For example, the National Aboriginal Council on Species at Risk (NACOSAR) is mandated under SARA to consider the traditional knowledge of the indigenous peoples of Canada “in the assessment of which species may be at risk and in developing and implementing recovery measures.” However, inadequate funding and a lack of coordination has resulted in a limited range of opportunities for effective indigenous participation, engagement, and input into SARA-related decisions (Stratos 2006, Native Women's Association of Canada 2007). An approach to federal SARA policies that focuses on indigenous languages could be one potential avenue that would improve the inclusion of traditional knowledge in species assessments, recovery plans, action plans, and management plans. In Chapter 2 we establish that Dene traditional knowledge and language related to caribou are an important platform from which it is possible to aid in our understanding of the distinct intraspecific variation of caribou. Including indigenous languages in species at risk processes, for example, could create appropriate and unifying language that could be used for conservation unit prioritization under COSEWIC. For example, as a direct outcome of our research, the Sahtú Renewable Resources Board has begun to use the Dene word *tòdzı* in all official correspondence relating to boreal caribou.

Recent community-led conservation planning initiatives are reshaping governance and responsibilities for renewable resources in the Sahtú region (Délıne ʔekwé Working Group 2016). For example, the development of Délıne’s 2016 caribou management plan, *Belarewıle*

Gots'ę ʔekwę “Caribou for All Time” is based on Délıne ǵot'ıne ǵodı “stories” and ʔeʔa “laws and principles.” Our research aided in the community-driven management plan by supporting caribou traditional knowledge research and facilitating the role of community collaborators in specific language work related to caribou populations in the region. Connections between population genetic research, linguistic research, and historic data from the Dene Nation’s Dene Mapping Project have helped to identify the need for robust place-based traditional knowledge and cultural diversity research in the region. In fact, the research synergies that have occurred through collaborations among research projects have helped to inform the Sahtú Environmental Research and Monitoring Forum’s strategic goals for community-driven environmental research in the region. In Chapters 2 and 4 we illustrate that by supporting community-driven research we can give voice to important resource management priorities of the communities while at the same time building capacity and increasing the ability of community organizations to make the best information-based decisions about lands and wildlife.

Concluding thoughts

As the world braces for the global impacts of human-induced environmental changes that denote the Anthropocene, slowing the accelerating loss of biodiversity in the remaining resilient, functioning ecosystems is of critical importance (Caro et al. 2012, Corlett 2015). It is becoming increasingly clear that conservation practitioners must look beyond the field of ecology to find solutions to environmental problems (Mascia et al. 2003). The future of conservation will increasingly rely on successful interdisciplinary collaborations that draw on expert contributions among diverse fields to develop research, innovate new solutions, implement conservation plans, and work within complex institutional, political, and jurisdictional landscapes that characterize

social-ecological systems (Balmford and Cowling 2006, Leenhardt et al. 2015, Pittman et al. 2016). Further, Dr. Bill Adams of the Department of Geography in the University of Cambridge, suggests that:

We have to recognize that what we need in conservation are not inter-disciplinary teams, but inter-disciplinary people... Our real task is to create conservationists for whom these skills are innate, for whom the disciplinary boundaries so beloved of academic researchers are no constraint. (Adams 2007: 276)

This dissertation is a testament to the strength of an interdisciplinary education to foster the development of instinctive synergies among disciplines and knowledge systems.

The overlapping realms of human-nature interactions require integrated research processes that enable equality, legitimacy, and transparency during all stages of collaborative projects. More than ever the increase in collaborate approaches must also extend to cross-cultural research (Berkes 2004). Inclusive conservation recognizes the importance of supporting the diverse ways that nature is valued around the world and encouraging conservation scientists and practitioners from different cultures to engage in shared conservation action (Tallis and Lubchenco 2014). Conservation is fundamentally about people (Mascia et al. 2003, Ban et al. 2013, Bennett et al. 2016b). Thus, conservationists need to work as allies with indigenous people to influence successful conservation policy and practice. Only by including the voices of those people who are most directly impacted by management decisions will it be possible to produce sustainable conservation solutions, develop efficient and effective wildlife management policies, and ensure caribou remain an important part of the landscape (Kendrick and Manseau 2008, O'Flaherty et al. 2008).

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APPENDIX 1. COMMUNITY-COLLABORATIVE RESEARCH BACKGROUND

In northern Canada, landscapes, people and wildlife are inextricably and compellingly intertwined. Federal control over wildlife and the exclusion of indigenous people in wildlife management and decision-making for much of the 19th century has generated environmental, jurisdictional, and political conflicts revolving around natural resources (Sandlos 2011). For many years science-based wildlife conservation approaches often had negative impacts on the traditional harvesting practices of indigenous peoples. For example, concerns about declining populations led to legislative controls by the federal government in the early 1900s, prohibiting (and in some cases criminalizing) subsistence hunting of caribou and other large mammals and birds by Dene and Inuit hunters in the Northwest Territories (Sandlos 2011). Understanding the historical context of unequal power relations is an important part of developing new approaches to environmental research (Fletcher 2003, Nadasdy 2005, McGregor et al. 2010, Tobias et al. 2013).

In the 1970s researchers working in the north began to acknowledge the importance of indigenous people's knowledge and priorities in natural resource research (Cruikshank 1981). However, early traditional knowledge (TK) research focused mostly on collecting objective and quantifiable information that could be packaged and accessed within scientific frameworks (Stevenson 1998). This led to substantial misrepresentation and the appropriation of knowledge (Nadasdy 2005, Castleden et al. 2012). A more recent shift in the orientation of research advocates for collaborative processes that serve indigenous interests, provide ownership and control of research outcomes, and include local people in decision-making processes (Hall 1979, Simpson 1999, Smith 1999, Simpson and Driben 2000). For example, community-based

participatory research frameworks emerged in response to disrespectful and exclusionary approaches that concentrated research *on* people rather than *with* people (Simpson and Driben 2000, Fletcher 2003).

Participatory research (also including community-engaged, community-participatory, community-based, collaborative, cooperative; Ferreira and Gendron 2011) is intended to include people as active participants in all phases of the research process to “facilitate a more accurate and authentic analysis of social reality” (Hall 1979) and have been adapted in the fields of education (Hall 2005), public health (Christopher et al. 2011, Ferreira and Gendron 2011, Tobias et al. 2013), social science (Fletcher 2003), resource management (McKinley et al. 2012), and linguistics (Czaykowska-Higgins 2009) among others. The principles of participatory research include fostering a co-learning environment, answering relevant community-driven questions, focusing on co-capacity building and sustainable solutions, sharing decision-making responsibilities, and above all reflecting critically on the roles and power relations of those involved in the research process (Cornwall and Jewkes 1995, O'Fallon and Dearry 2002, Davidson-Hunt and O'Flaherty 2007)

In alignment with the principals of participatory research we brought together an interdisciplinary team of research partners and co-authors to build a solid foundation across diverse fields. Our research process was iterative and built on information and questions developed and refined over time. Significant knowledge exchange and *łeghágots'enetę* “learning together” between the co-authors and research partners occurred as ideas for the project were developed, at focus group meetings, during the selection of the field sampling sites, while collecting samples, and on the land during day trips, hunting trips and overnight trips to cabins.

The distinct disciplinary backgrounds of team members, who spoke different first languages, necessitated significant dialogue to come to common understanding for a project.

The commitment, interest and openness of community research partners in the Sahtú region was crucial to the collaborative research process. Michael Neyelle, Walter Bayha, Frederick Andrew, and Leon Andrew are all native Dene language speakers and have significant TK experience and knowledge from their personal experiences and their parents and ʔehts'éokə “grandparents.” They have worked in collaboration with the ʔehdzo Got'ineḡ Gots'é Nákedı (Sahtú Renewable Resources Board; SRRB) and other non-Dene researchers on various research projects over the years. Their interest in this research project, commitment to helping support the research, guidance on TK practices, and help with interpretation of the language, and their leadership positions within the communities allowed for new knowledge to be created and a common understanding to be reached. A focus on language during the research process was a means for Dene and non-Dene speakers to explore knowledge and understanding of the environment in more depth. For example, TK holders were able to unearth older knowledge that is not used every day. Non-Dene partners were able to explore the ways in which the words we use and the ideas we express influence the collaborative environment.

The project also included extended place-based research by non-Dene partners (Jean Polfus and Deborah Simmons live and work in the community of Tulít'a) that allowed for opportunities to participate in activities on-the-land and in the communities (thus learning was not restricted to research activities/agendas). Jean Polfus also traveled throughout the communities in the Sahtú to provide support for the ʔehdzo Got'ineḡ (Renewable Resources Councils), collect caribou fecal samples with community members, participate in hunting activities, meet with students at local schools and Aurora Colleges and coordinate sampling

efforts. The understanding required to respond appropriately to cultural cues and respectfully engage in *łeghágots'enetę* “learning together” is on-going, intangible and personal (for all research partners and co-authors) – but this exploration provides the necessary foundation needed to produce truly collaborative research.

Over time relationships were fostered that provided space for non-Dene researchers to learn important lessons regarding hunting traditions, on-the-land safety, and Dene *ɤekwé ɤeɤah* “caribou laws” required to demonstrate respect for the land and wildlife. Likewise, community members were also able to benefit from the collaborative relationship through increased contact with “outsider knowledge” (Caine et al. 2007), including expertise in wildlife biology, population genetics and linguistics, the chance to be involved in long-term natural resource management research and planning, and access to other resources that the non-Dene researchers could more easily acquire. The union of knowledge traditions can only be achieved through shared experiences, considerable time, and strong local and regional governance (McGregor et al. 2010). A large amount of knowledge was gained over time and cannot be readily summarized in a manuscript. The research process was organic and agreement on the interpretation of the results was gradual, forcing everyone to explore their own knowledge in depth, and in some cases leading to new questions and additional analysis.

Meeting the demands of academic requirements, funding agencies, and indigenous communities in the same process is fundamentally challenging and levels of participation, control and ownership of the research process and products often vary based on the complex constraints on each project (Cornwall and Jewkes 1995, Simpson and Driben 2000, Tondu et al. 2014). Our research benefitted considerably from the partnership with the SRRB. The board is a land-claim organization responsible for managing renewable resources. The SRRB’s

contributions to this project allowed our research to be firmly grounded in the communities needs and questions from the outset of the research because the project was built on past-experiences and related work. The SRRB also facilitated ongoing communication with the public and local research partners by developing connections between various research agendas and other co-occurring projects. The opportunity for long-term planning and stability in the research process (implemented through connections with multiple community-driven projects and long term institutional research strategies and programs) is an important contribution of collaborative interdisciplinary research and the SRRB's involvement was essential to the success of the long term collaborative project. Thus, we were able to produce research contributions that were deeper and more robust than could have been achieved by a single, stand-alone academic research project.



Figure A1-1. We discussed traditional knowledge themes, language, and genetic data with a local group of experts (advisory group, including co-authors) in two separate 3-day meetings to clarify and develop important concepts and themes related to caribou populations in the Sahtú region and Nahanni National Park Reserve of the Northwest Territories, Canada. Advisory group members June 2014 in Tulít'a, Northwest Territories: Gordon Yakeleya, Frederick Andrew, Michael Neyelle, Jean Polfus, Walter Bayha, Camilla Rabisca, Deborah Simmons, Michel Lafferty, and Judy Lafferty.



Figure A1-2. Advisory group members February 2015 at Deochah (Bennett Field), Northwest Territories: Back two rows – Jean Polfus, Gordon Yakeleya, Frederick Andrew, Richard Kochon, Jimmy Dillon, Walter Bayha, Deborah Simmons, Leon Andrew, Nicole Beaudry (ethnomusicologist), Michael Neyelle, and Lucy Jackson. Front row – Corrine Andrew (cook), Gabe Kochon, Maurice Mendo, and Hyacinth Kochon.

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APPENDIX 2. POPULATION GENETIC SUMMARY STATISTICS FOR CARIBOU GENETIC
 SAMPLES COLLECTED IN THE SAHTÚ REGION AND NAHANNI NATIONAL PARK
 RESERVE OF THE NORTHWEST TERRITORIES, CANADA FROM 2012 TO 2014.

Table A2-1. Summary of genetic diversity estimates for each microsatellite loci including allelic size range in base pairs, number of alleles (N_A), observed (H_O) and expected (H_E) heterozygosity, F_{IS} estimates and standard errors (SE) for caribou genetic data from the Northwest Territories, Canada. The original references for each loci are provided.

Microsatellite Locus	Allelic Range	N_A	H_O	SE	H_E	SE	F_{IS}	Source
BM848	356-386	16	0.819	0.0234	0.864	0.0150	0.053	Bishop et al. 1994
BM888	162-260	51	0.882	0.0041	0.865	0.0071	-0.019	Bishop et al. 1994
Map2C	89-115	16	0.824	0.0113	0.850	0.0232	0.030	Moore et al. 1992
RT5	88-116	15	0.768	0.0283	0.816	0.0373	0.058	McLoughlin et al. 2004 [†] , Wilson et al. 1997 [‡]
RT6	88-112	14	0.837	0.0122	0.833	0.0245	-0.005	Wilson et al. 1997
RT7	210-232	12	0.746	0.0242	0.772	0.0109	0.033	Wilson et al. 1997
RT9	100-128	15	0.840	0.0257	0.859	0.0077	0.022	Wilson et al. 1997
RT24	205-227	24	0.780	0.0497	0.786	0.0707	0.008	Wilson et al. 1997
RT30	183-211	19	0.829	0.0130	0.862	0.0242	0.039	Wilson et al. 1997

[†]Reverse primer

[‡]Forward primer

Table A2-2. Pairwise F_{ST} values based on microsatellites for the three major groups identified by structure analysis (below diagonal) and pairwise P values (above diagonal).

F_{ST}	Barren-ground	Boreal woodland	Mountain
Barren-ground	-	0.0000	0.0000
Boreal woodland	0.040	-	0.0000
Mountain	0.011	0.041	-

Table A2-3. Pairwise R_{ST} values based on microsatellites for the three major groups identified by structure analysis (below diagonal) and pairwise P values (above diagonal).

R_{ST}	Barren-ground	Boreal woodland	Mountain
Barren-ground	-	0.0303	0.0028
Boreal woodland	0.030	-	0.0269
Mountain	0.003	0.027	-

Table A2-4. Pairwise Φ_{ST} values based on mtDNA for the three major groups identified by structure analysis (below diagonal) and pairwise P values (above diagonal).

Φ_{ST}	Barren-ground	Boreal woodland	Mountain
Barren-ground	-	0.0000	0.0000
Boreal woodland	0.079	-	0.0000
Mountain	0.138	0.173	-

Table A2-5. Analysis of molecular variance (AMOVA) based on mtDNA haplotype data for the three groups identified by structure analysis. F_{ST} represents the variance within groups relative to the total variance.

Source of variation	d.f.	Variance components	% Variation	F	P
Among groups	2	0.63	13.9		
Within groups	334	3.91	86.1	$F_{ST} = 0.139$	0.0000

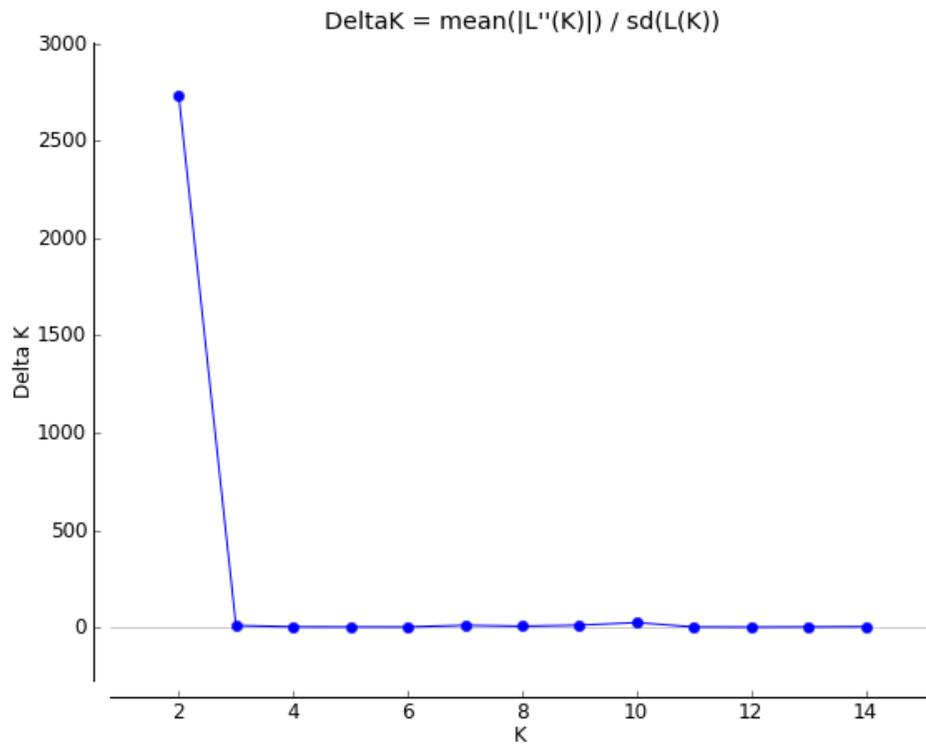


Figure A2-1. Most likely number of population clusters ($K = 2$) identified by the Evanno method (Evanno et al. 2005) using Structure Harvester v0.6.94 (Earl and vonHoldt 2012).

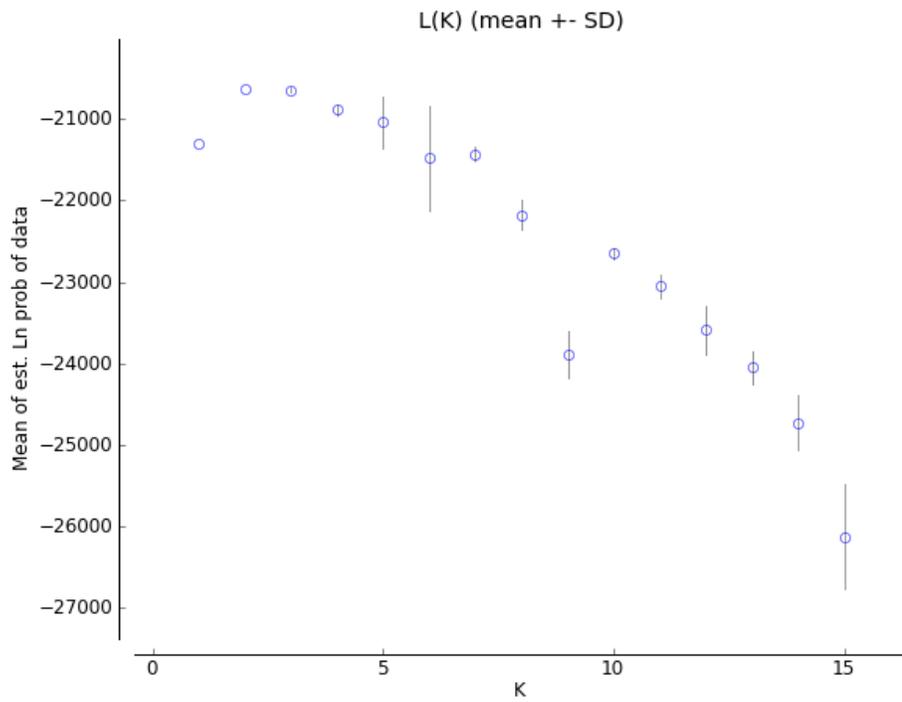


Figure A2-2. Mean likelihood for each K plus standard deviation as retrieved from Structure Harvester v0.6.94 (Earl and vonHoldt 2012).

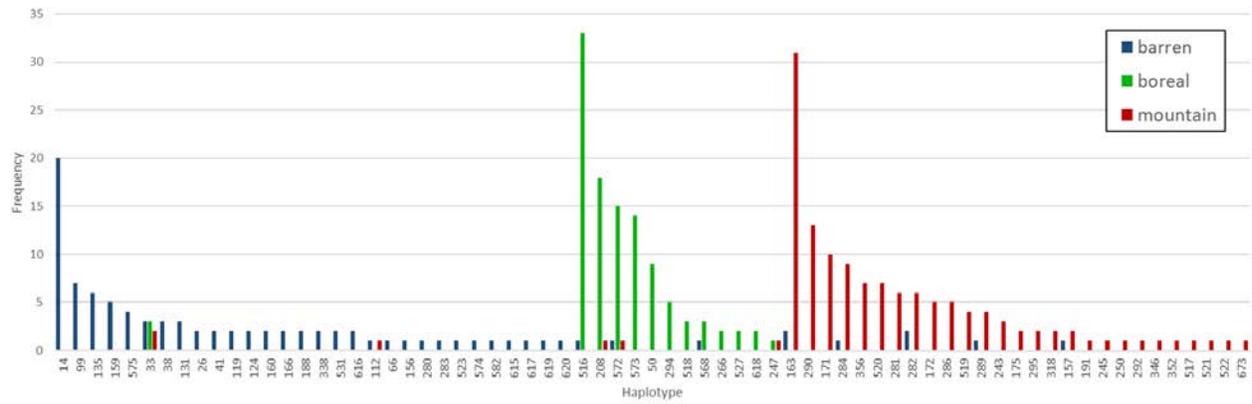


Figure A2-3. Frequency of mtDNA haplotypes for the three major groups identified by structure analysis: 1) barren-ground (blue), 2) boreal woodland (green), and 3) mountain (red). Three haplotypes belong to the North American haplogroup lineage (NAL): 50, 522 and 523, all other haplotypes belong to the Beringian-Eurasian haplogroup lineage (BEL).

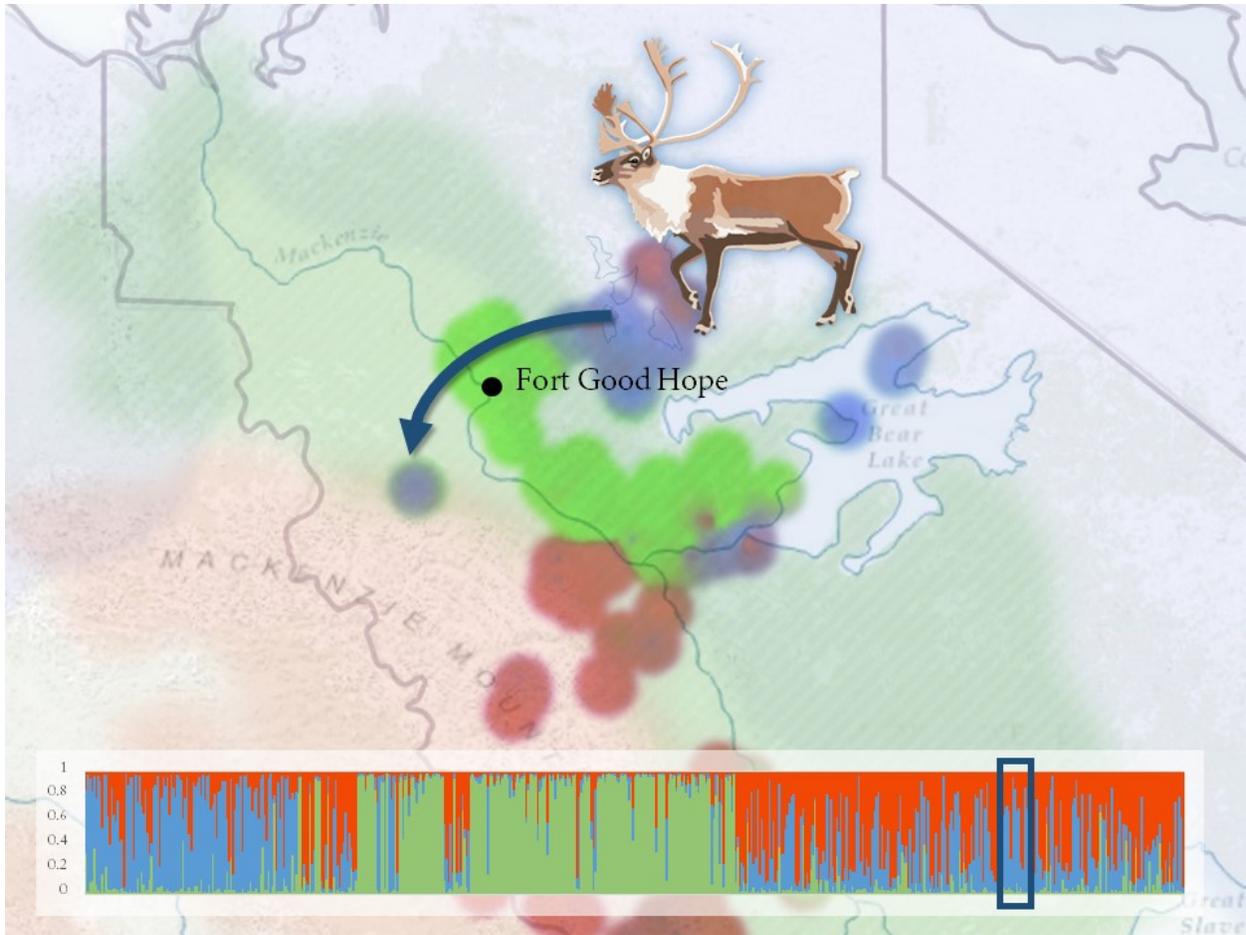


Figure A2-4. During a focus group meeting, Gabe Kochon of Fort Good Hope, Northwest Territories, Canada, described a historic event where a large herd of caribou crossed the Dehcho (Mackenzie River) and headed into the foothills of the mountains many years ago. We collected samples from the area identified by the arrow during our 2 April 2014 helicopter survey and identified 9 individual caribou from the site in subsequent genetic analysis. Structure analysis of these samples found a high probability of assignment (average 0.73) to the barren-ground caribou cluster (shown as blue in bottom bar and represented as blue on the map). Genetic structure analysis identified $k=3$ clusters of 1) barren-ground (blue) 2) boreal woodland (green) and 3) mountain (red).

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APPENDIX 3: POPULATION GENETIC SUMMARY STATISTICS AND ABC MODEL
EVALUATIONS FOR CARIBOU GENETIC SAMPLES COLLECTED IN NAHANNI
NATIONAL PARK RESERVE AND CENTRAL NORTHWEST TERRITORIES, CANADA
FROM 2012-2014 AND IN CENTRAL SASKATCHEWAN, CANADA FROM 2005-2008.

Table A3-1. Genetic diversity estimates, averaged across 9 microsatellite loci, for the four major caribou groups identified by structure analysis: barren-ground, central Northwest Territories (NWT) boreal ecotype, northern mountain ecotype, and central Saskatchewan (SK) boreal ecotype. The number of samples (N), number of alleles (N_A), allelic richness (A_R), private allelic richness (A_{RP}), observed (H_O) and expected (H_E) heterozygosity, F_{IS} estimates, and standard errors (SE) for each estimate are presented. We calculated genetic indices with GenAlEx 6.501 (Peakall and Smouse 2012) and HP-Rare 1.1 (Kalinowski 2005).

Group	N	N_A	SE	A_R	A_{RP}	H_O	SE	H_E	SE	F_{IS}
Barren-ground	106	14.7	0.91	14.4	1.84	0.84	0.011	0.87	0.009	0.030
NWT boreal	168	12.0	1.43	11.0	0.96	0.88	0.023	0.79	0.023	0.005
Northern mountain	217	16.7	2.77	14.0	2.24	0.81	0.016	0.84	0.012	0.033
SK boreal	164	10.7	1.13	9.94	0.93	0.68	0.042	0.72	0.030	0.055

Table A3-2. Pairwise F_{ST} values (below diagonal) and R_{ST} values (above diagonal) based on microsatellites for the four major groups identified by STRUCTURE analysis: barren-ground, central Northwest Territories (NWT) boreal ecotype, northern mountain ecotype, and central Saskatchewan (SK) boreal ecotype.

	Barren-ground	NWT boreal	Northern mountain	SK boreal
Barren-ground	-	0.0489	0.0180	0.0415
NWT boreal	0.0397	-	0.0211	0.0727
Northern mountain	0.0125	0.0411	-	0.0541
SK boreal	0.0780	0.0938	0.0924	-

Table A3-3. Haplotype (mtDNA) genetic diversity for the four major caribou groups identified by STRUCTURE analysis: number of individual caribou samples analysed for mtDNA (N), number of caribou assigned to the North American (NAL) and Beringian (BEL) haplogroup lineages (NAL_N and BEL_N , respectively), number of haplotypes in the North American (NAL_H) and Beringian (BEL_H) haplogroups. We used ARLEQUIN 3.5.2.2 (Exoffier and Lischer 2010) to calculate nucleotide diversity (averaged over loci; π) and gene diversity (GD) with standard deviations (SD).

Group	N	NAL_N	BEL_N	NAL_H	BEL_H	π	SD	GD	SD
Barren-ground	77	1	76	1	29	0.016	0.0084	0.921	0.0215
NWT boreal	108	9	99	1	12	0.019	0.0099	0.841	0.0202
Northern mountain	96	1	95	1	27	0.021	0.0111	0.910	0.0190
SK boreal	88	85	3	12	1	0.012	0.0064	0.841	0.0192

Table A3-4. Posterior probability and credible interval [CI] for the three ABC runs (microsatellite, mtDNA, and combined dataset). Scenario 1 was selected as the most supported model in the microsatellite and combined dataset while scenario 4 was chosen in the mtDNA dataset.

	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
Microsatellite dataset	0.959 [0.951 - 0.966]	0.002 [0.002 - 0.003]	0.001 [0.004 - 0.001]	0.001 [0.0001 - 0.001]	0.038 [0.031 - 0.045]
mtDNA dataset	0.032 [0.025 - 0.040]	0.093 [0.081 - 0.106]	0.291 [0.274 - 0.309]	0.572 [0.553 - 0.59]	0.011 [0.004 - 0.019]
Combined dataset	0.766 [0.729 - 0.802]	0.204 [0.085 - 0.322]	0.007 [0.000 - 0.153]	0.006 [0.000 - 152]	0.017 [0.000 - 0.191]

Figure A3-1a-c. Principal Component Analysis (PCA) pre-evaluation plots for the (a) microsatellite, (b) mtDNA, and (c) combined datasets generated by DIYABC v 2.0.4 (Cornuet et al. 2014). The large yellow dot represents where the observed data fits within a representative set (10,000 simulated datasets per scenario) of simulated datasets (small dots). Since all observed data fall within the cloud of simulated data this indicates that it is possible to produce summary statistics close to the observed summary statistics with the proposed scenarios in combination with the chosen prior distributions.

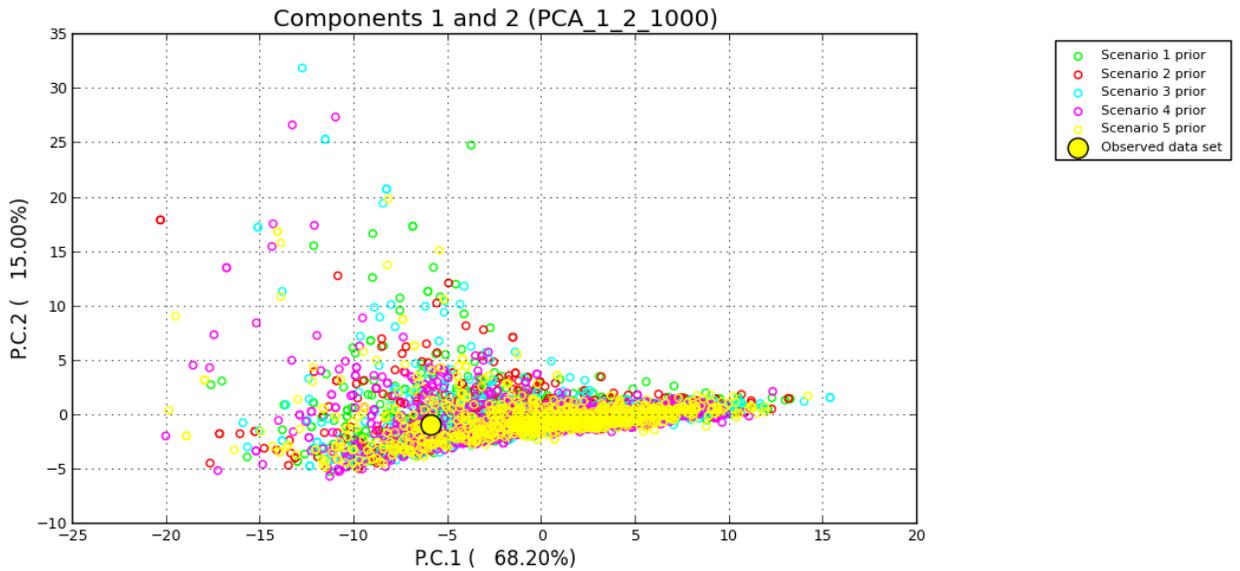


Figure A3-1a. Pre-evaluation of microsatellite dataset.

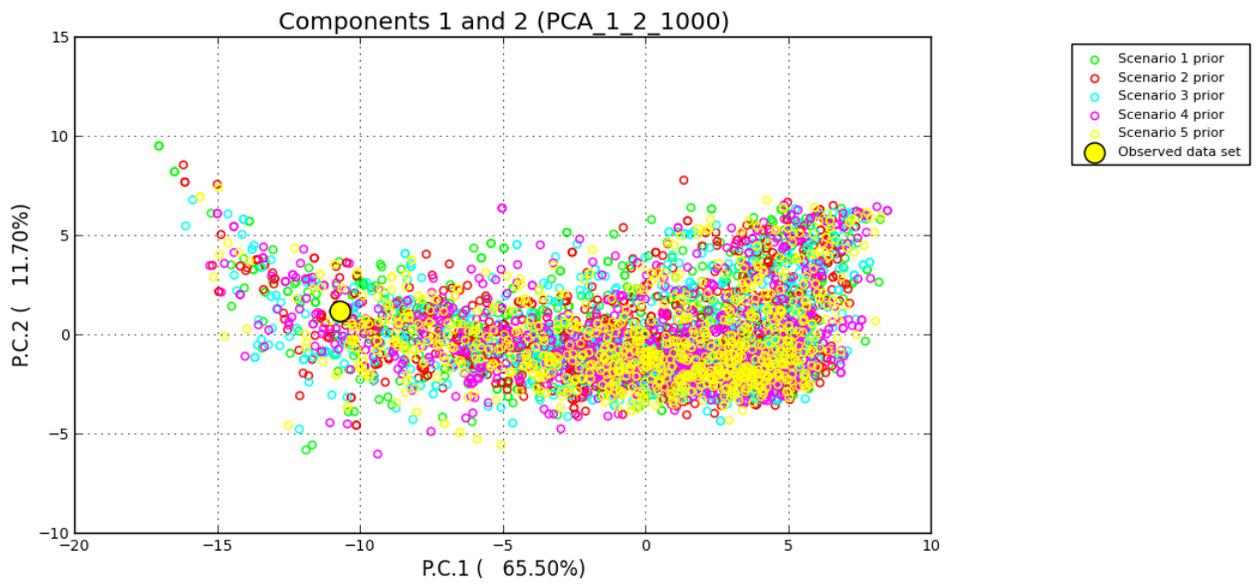


Figure A3-1b. Pre-evaluation of mtDNA dataset.

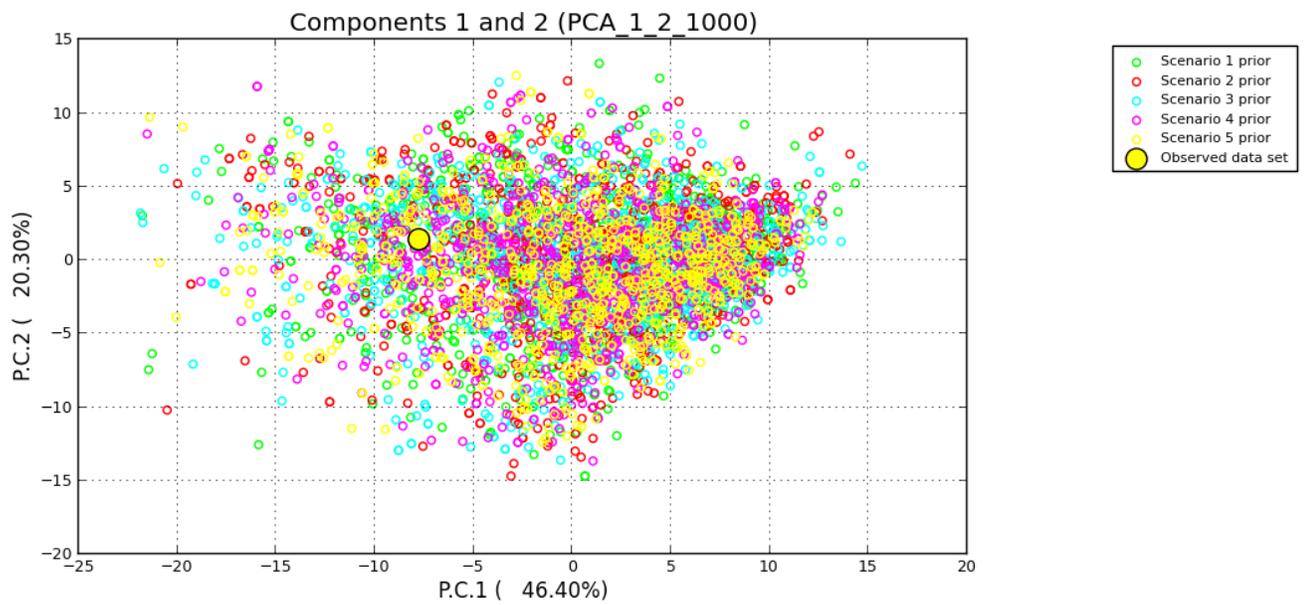


Figure A3-1c. Pre-evaluation of combined dataset.

Figure A3-2a-c. Model-checking evaluation for all three ABC analyses for the (a) microsatellite, (b) mtDNA, and (c) combined datasets generated by DIYABC v 2.0.4 (Cornuet et al. 2014). Large yellow dots represent how well the observed data fit the posterior predictive distributions (larger green dots).

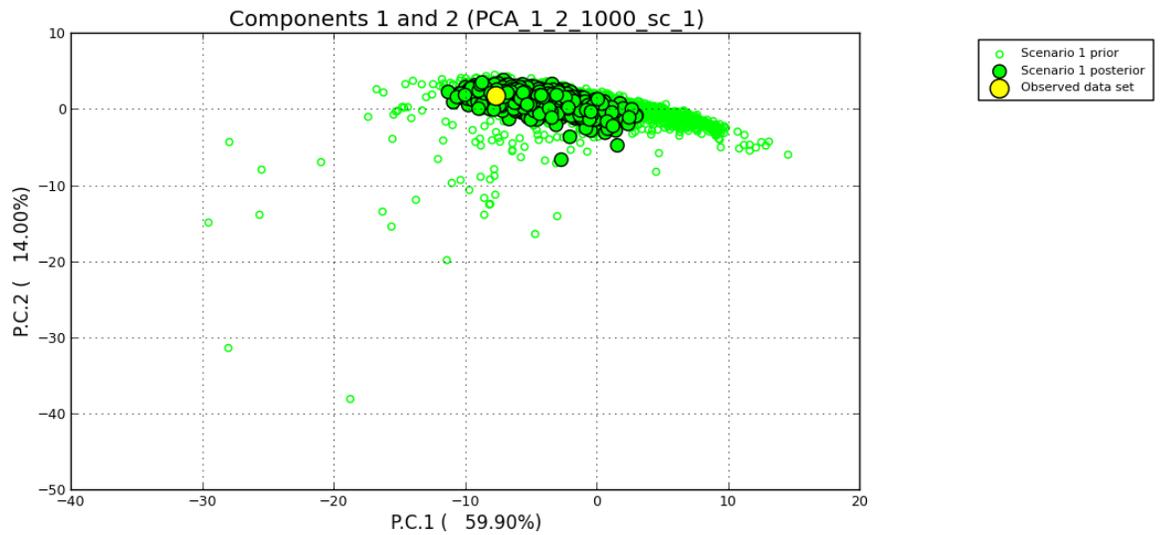
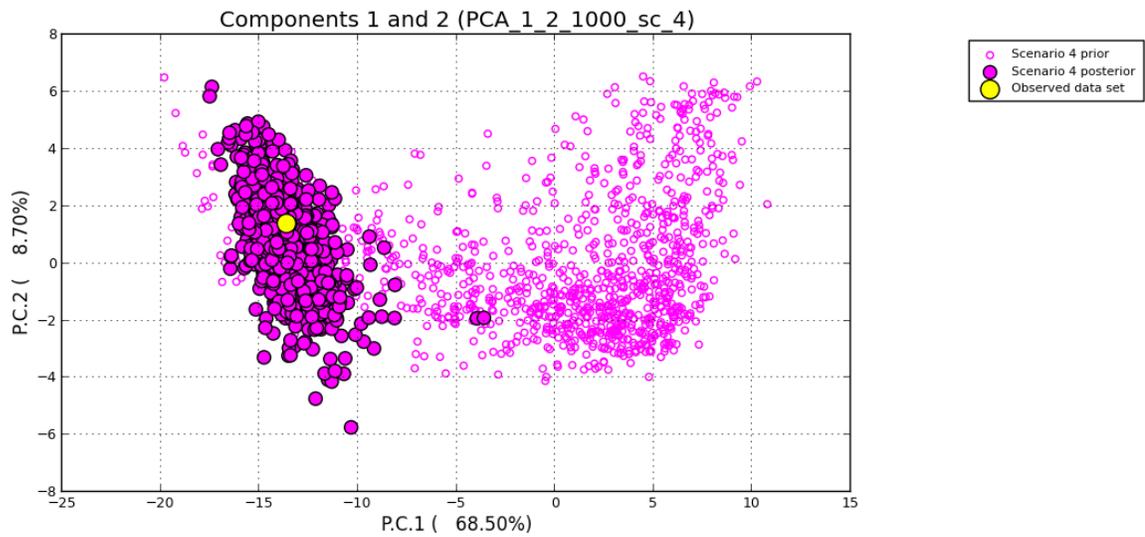
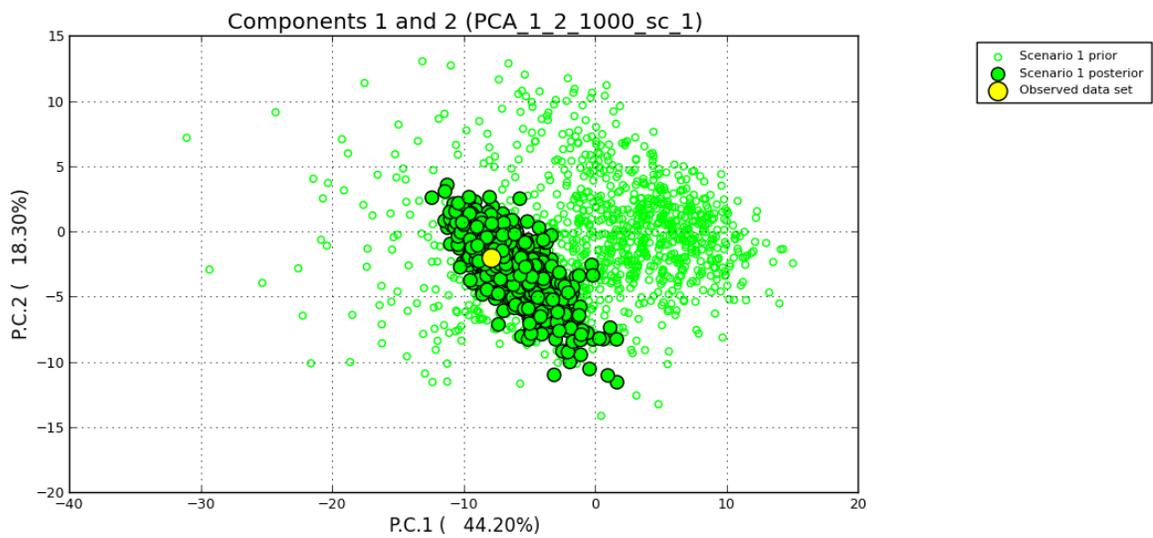


Figure A3-2a. Model checking evaluation for the microsatellite dataset



Figures A3-2b. Model checking evaluation for mtDNA dataset.



Figures A3-2c. Model checking evaluation for combined dataset

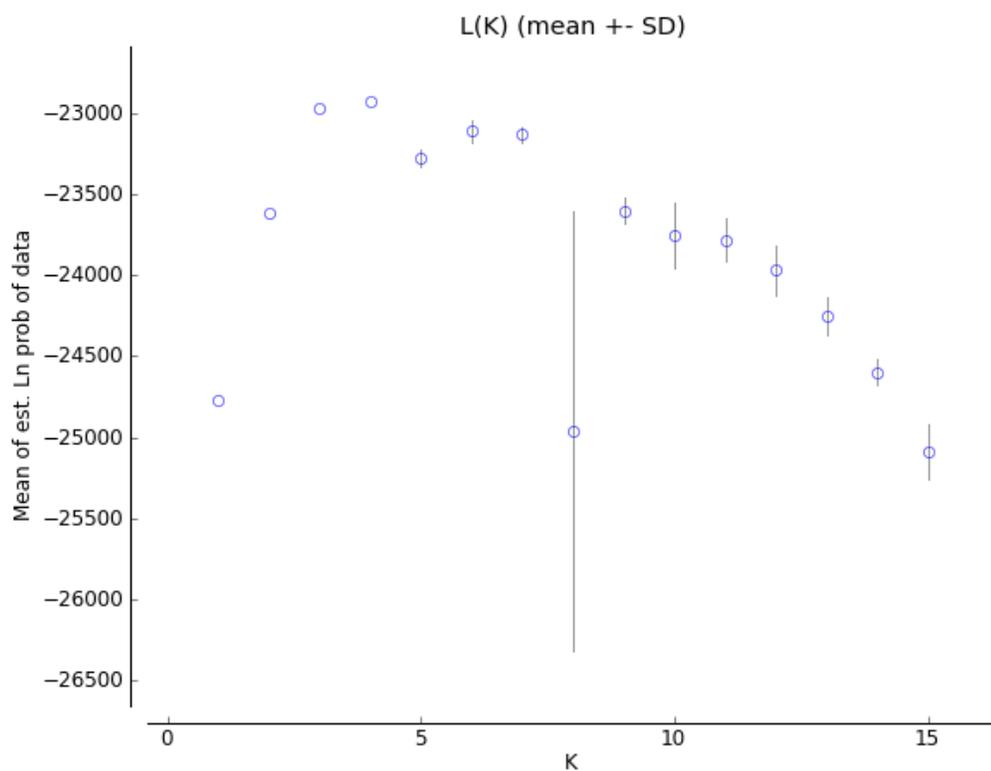


Figure A3-3. Mean likelihood for each K plus standard deviation as retrieved from Structure Harvester v0.6.94 (Earl and vonHoldt 2012).

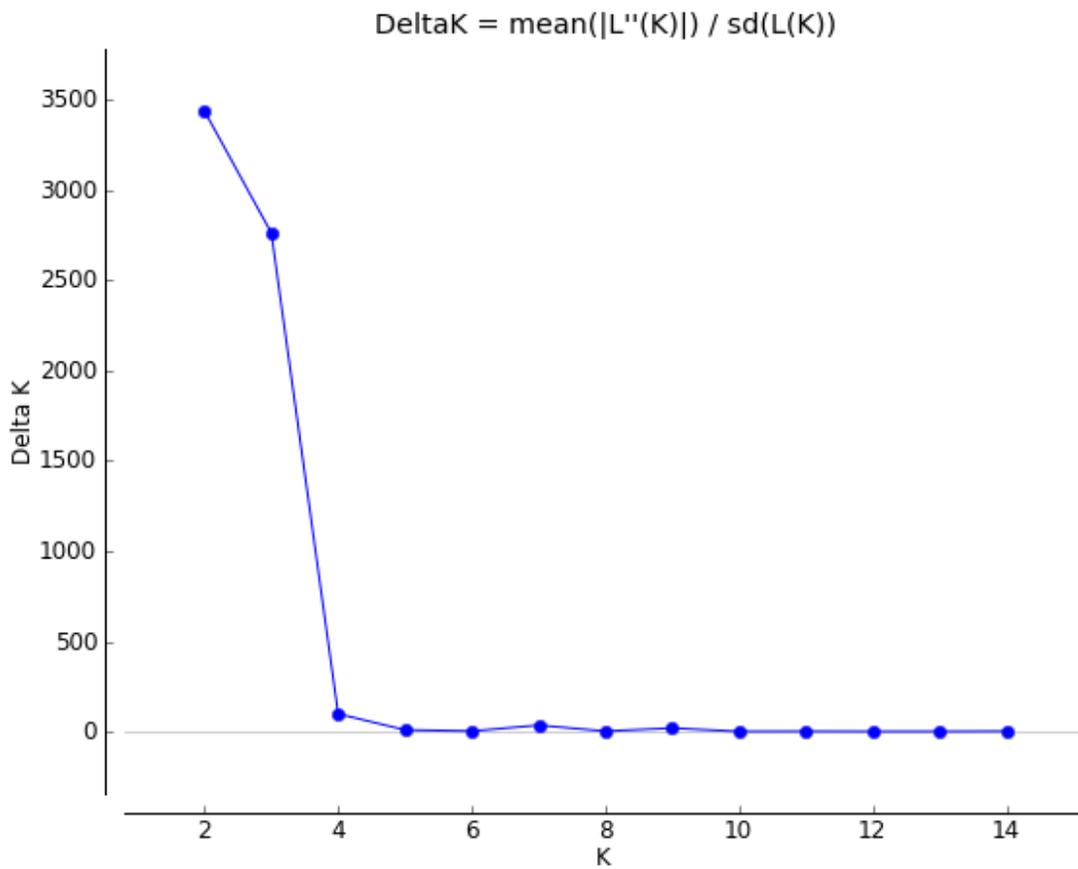


Figure A3-4. Most likely number of population clusters ($K = 2$) identified by the Evanno method (Evanno et al. 2005) using Structure Harvester v0.6.94 (Earl and vonHoldt 2012).

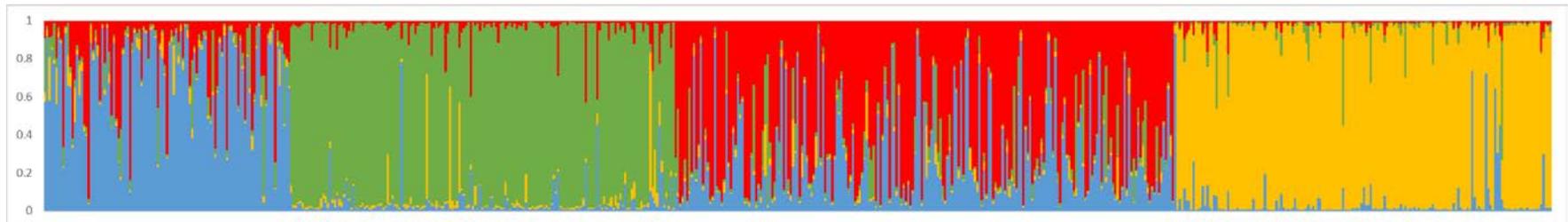


Figure A3-5. We analyzed microsatellite data from caribou genetic samples collected in central Northwest Territories (NWT) and central Saskatchewan (SK). We calculated the average individual membership coefficients across the five iterations using the programs CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007). We used STRUCTURE 2.3.4 (Pritchard et al. 2000) to assign individual caribou to inferred genetic clusters. We found support for $K=4$ populations that coincided with clusters of 1. barren-ground of central NWT (blue), 2. boreal ecotype of central NWT (green), 3. northern mountain ecotype of the Mackenzie Mountains, NWT (red), and 4. boreal ecotype of central SK (yellow). Vertical colored bars indicate the probability that an individual belongs to a certain group.

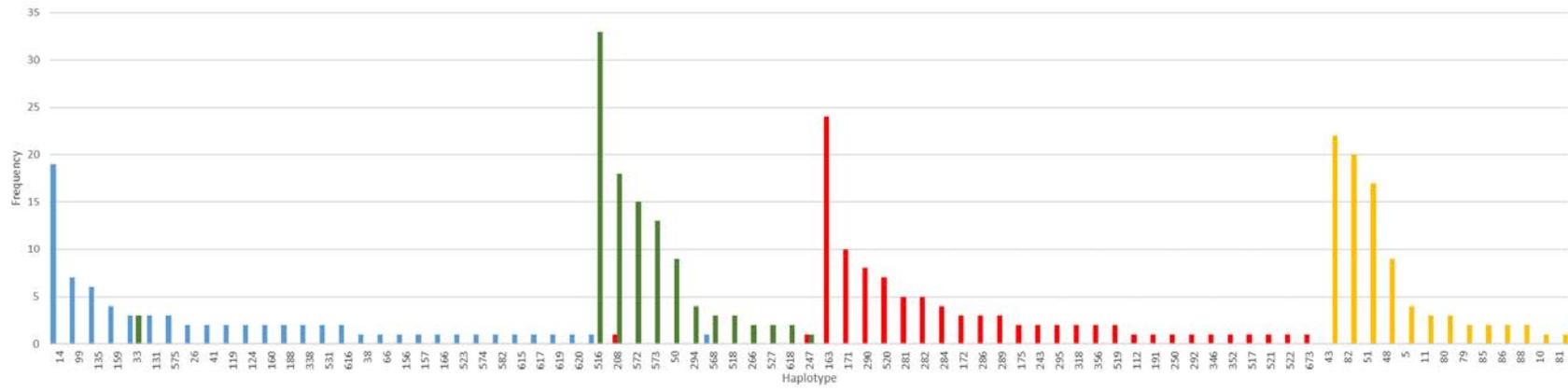


Figure A3-6. We analyzed mtDNA data from caribou genetic samples collected in central Northwest Territories (NWT) and central Saskatchewan (SK). Bars indicate the frequency of mtDNA haplotypes for the four major groups identified by STRUCTURE 2.3.4 (Pritchard et al. 2000) analysis: 1. barren-ground of central NWT (blue), 2. boreal ecotype of central NWT (green), 3. northern mountain ecotype of the Mackenzie Mountains, NWT (red), and 4. boreal ecotype of central SK (yellow).

Figure A3-7a-c. Comparison of ABC analyses the (a) microsatellite, (b) mtDNA, and (c) combined datasets ranking the posterior probabilities for each evolutionary scenarios tested with DIYABC v 2.0.4 (Cornuet et al. 2014) that model the evolutionary history of four contemporary caribou groups: barren-ground caribou, boreal ecotype of central Northwest Territories (NWT), northern mountain ecotype, and boreal ecotype of central Saskatchewan (SK).

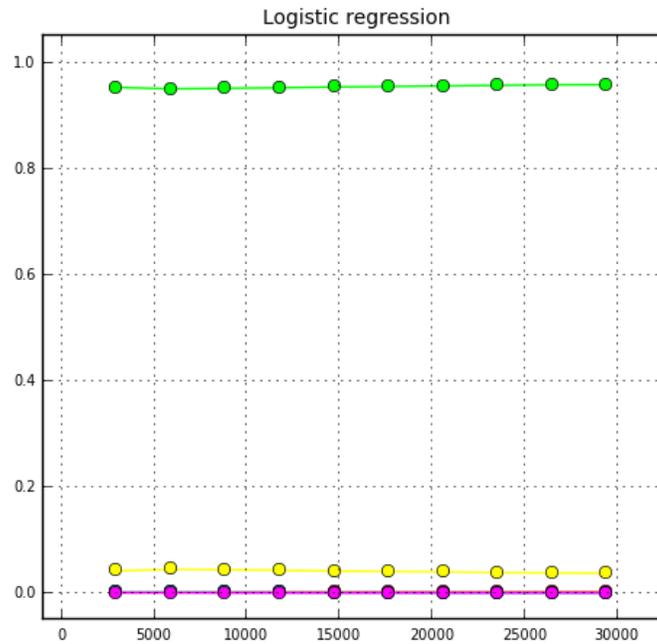


Figure A3-7a. Logistic regression for microsatellite dataset. Statistical support for each scenario is represented by colored lines. Green = scenario 1, red = scenario 2, turquoise = scenario 3, light purple = scenario 4, yellow = scenario 5.

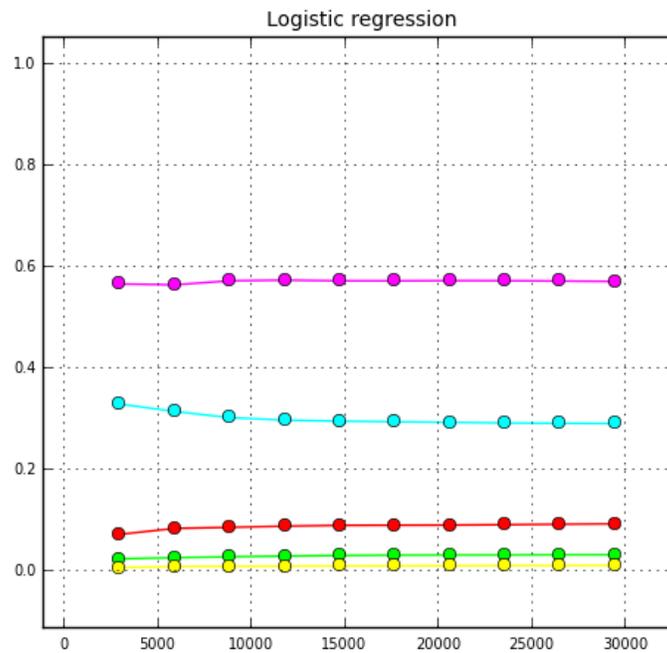


Figure A3-7b. Logistic regression for mtDNA dataset. Statistical support for each scenario is represented by colored lines. Green = scenario 1, red = scenario 2, turquoise = scenario 3, light purple = scenario 4, yellow = scenario 5.

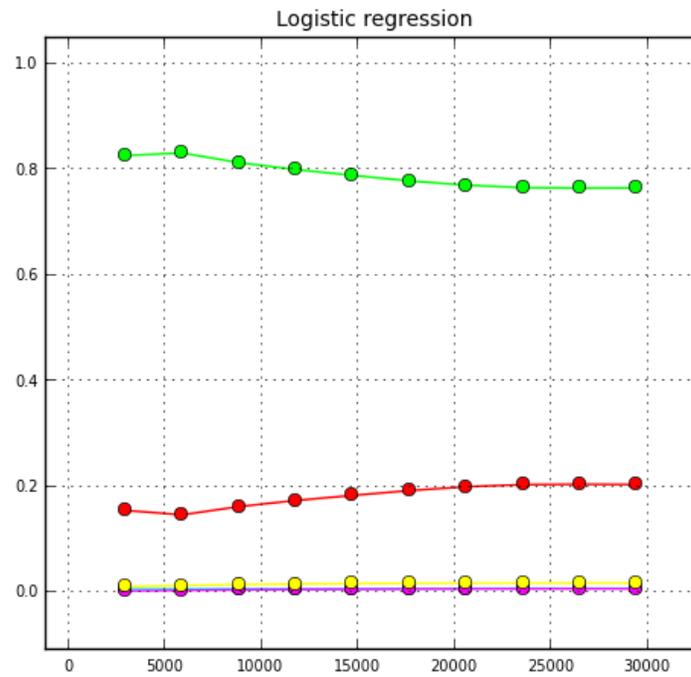


Figure A3-7c. Logistic regression for combined dataset. Statistical support for each scenario is represented by colored lines. Green = scenario 1, red = scenario 2, turquoise = scenario 3, light purple = scenario 4, yellow = scenario 5.

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