POPULATION STRUCTURE AND HYBRIDIZATION OF ALASKAN CARIBOU AND REINDEER: INTEGRATING GENETICS AND LOCAL KNOWLEDGE

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A

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**Abstract**

Alaskan caribou (*Rangifer tarandus granti*) are a valued game species and a key grazer in Alaska's terrestrial ecosystem. Caribou herds, defined by female fidelity to calving grounds, are management units. However, the extent to which herds constitute genetic populations is unknown. Historical fluctuations in herd size, range, and distribution suggest periods of contact and isolation between herds. Likewise, historical contact between caribou and introduced domestic reindeer (*R.t. tarandus*) created opportunities for hybridization, but its extent is not known.

I conducted an interdisciplinary study to understand how historical processes influence genetic identity and population structure of caribou and reindeer. Interviews with herders and hunters in Barrow, Alaska, revealed that many reindeer migrated away with caribou in the 1940s despite herder efforts to prevent mixing. Local observations of reindeer-like animals in caribou herds today suggest feral reindeer may survive and interbreed. Using genetic analysis of North Slope caribou and Seward Peninsula reindeer ($n$ = 312) at 19 microsatellite loci, I detected individuals with hybrid ancestry in all four caribou herds and in reindeer. Selective hunting of reindeer-like animals, along with herd size and natural selection, may remove reindeer from caribou herds over time.

I used genetics as well to describe caribou population structure and determine how it is influenced by geography, historical demography, and ecotypes. I found that Alaskan caribou from 20 herds ($n$ = 655) are subdivided into two genetic clusters: the Alaska Peninsula and the mainland. Alaska Peninsula herds are genetically distinct, while many mainland herds are not. I hypothesize that Alaska Peninsula herds have diverged due to post-glacial founder effects and recent bottlenecks driven by constraints to population size from marginal habitat and reduced gene flow across a habitat barrier at the nexus of the peninsula. I hypothesize that mainland herds have maintained genetic connectivity and large effective population size via range expansions and shifts over time. However, I find evidence that herds of different ecotypes (migratory, sedentary) can remain differentiated despite range overlap. Genetic evidence provides information for

herd-based management, while also demonstrating the importance of spatial connectivity of herds and their habitats over the long-term.

## Table of Contents

## List of Figures

Page

Page

## List of Tables

Page

## List of Appendices

Page

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# Chapter 1 General Introduction

## 1.1 Research Topic and Conceptual Framework

Wildlife conservation and game management rely on knowledge of population units and changes in their abundance, spatial distribution, and role in social-ecological systems over time. In the following chapters, I examine the history and population genetics of Alaskan caribou (*Rangifer tarandus granti*) and domestic reindeer (*R. t. tarandus*) to determine their historical interactions, potential hybridization, and genetic population structure. *Rangifer tarandus* is a widespread circumpolar species of deer distributed throughout boreal, arctic, and high-arctic areas of North America and Eurasia. Wild reindeer and caribou herds, and their domestic reindeer counterparts, are economically valued throughout the North and are central to many northern indigenous cultures. *R. t. granti*, hereafter referred to as caribou, is a wild subspecies native to Alaska and a valued game animal. Domesticated *R. t. tarandus*, hereafter referred to as reindeer, were introduced to Alaska in the late 19$^{th}$ century from Chukotka, Russia and are managed as free-ranging livestock. Both subspecies originate from a common, large, Beringian population (Flagstad and Røed 2003), but have diverged in isolation and through processes of domestication (Røed et al. 2008).

Alaskan caribou and reindeer provide a unique opportunity to understand behavioral interactions and hybridization among wild and semi-domestic subspecies recently brought into contact. It is known that large numbers of reindeer have joined the migratory Western Arctic caribou herd in the last 20 years (Dau 2000; Finstad, Bader, and Pritchard 2002; Schneider, Kielland, and Finstad 2005). However, little is known about prior reindeer-caribou interactions in other areas of Alaska and the extent to which reindeer and caribou have hybridized.

Caribou also provide a unique opportunity to understand evolutionary processes in abundant, migratory populations to inform their management. Caribou herds are defined on the basis of female philopatry to natal calving areas (Skoog 1968) and are the units of management for Alaskan caribou. While it is known that females of a herd show

strong fidelity to common calving areas, it is not known whether herds are genetically distinct. Population genetics is an essential source of information for designating management units for demographically independent populations (Moritz 1994; Palsboll, Berube, and Allendorf 2007; Taylor and Dizon 1999; Waples and Gaggiotti 2006). However, determining discrete units can be a challenge because boundaries are often fluid, reflecting ongoing evolutionary processes. Maintaining biodiversity and adaptive capacity over the long term relies on conservation of natural evolutionary processes (Mace and Purvis 2008), which can be revealed by determining how historical and geographic processes shape the genetic patterns of populations.

My goal in the following chapters is to improve understanding of the interactions and genetic structure of caribou and reindeer populations over time from the perspectives of caribou hunters and reindeer herders, population genetics, Alaskan geography, and herd-based management (Fig. 1.1).

## 1.2 Study System

The study system encompasses multiple reindeer and caribou herds throughout Alaska, and the people who hunt and herd them (Fig. 1.2). At a local scale, I studied the history of the Teshekpuk caribou herd (TCH) and Barrow-area reindeer herds that once grazed in the modern range of the TCH. At a regional scale, I examined reindeer-caribou hybridization in Northern Alaska, including four North Slope caribou herds and two Seward Peninsula reindeer herds. At a statewide scale, I described the genetic population structure of Alaskan caribou and the diverse landforms, habitats, and histories that have shaped genetic patterns in different parts of the state.

### *1.2.1 Background*

Biologists first noted year-round, resident caribou near Teshekpuk Lake in the late 1960s, and confirmed that the TCH was a distinct herd based on radio-collaring in the late 1970s (Burns 1990; Davis and Valkenburg 1978). At that time, the TCH was estimated to contain only 4,000 caribou, which used a relatively small area around Teshekpuk Lake

(Burns 1990; Davis and Valkenburg 1978). The first TCH census was 11,822 animals in 1984, and the herd grew to approximately 64,100 by 2008 accompanied by a range expansion (Parrett 2009). Though the herd continues to use the Teshekpuk Lake area for calving and summer range, annual movements vary greatly with some of the herd wintering on the coastal plain and others making long-distance migrations that overlap the ranges of other herds (Parrett 2009; Person et al. 2007). Little was known about the origins and history of the TCH, but its initially small size, erratic movements, and a history of reindeer herding in the area have generated speculation that the herd was recently formed as an offshoot of another North Slope herd or by feral domestic reindeer (Burns 1990).

The primarily Iñupiat communities of Barrow, Atqasuk, Nuiqsut, and several camps and historical settlements are located within the core range of the TCH. Caribou are a valued subsistence resource in the region, along with marine mammals, fish, and other terrestrial animals and plants. Caribou have been used throughout history for clothing and food (Brower 2008; Brower n.d.; Murdoch [1892] 1988; Toovak 2007), and remain economically and culturally valuable today with local communities harvesting 0.9 caribou per capita and a total of 6-8% of the TCH annually (Parrett 2009). The TCH is managed to sustain this valuable harvest, with the primary conservation concern centering on potential effects of increasing oil and gas development in the core range, most of which falls within the National Petroleum Reserve – Alaska (Bureau of Land Management 2008, 2011; Parrett 2009; Person et al. 2007).

Though caribou are abundant and locally hunted today, the abundance and distribution of Barrow-area caribou was very different in the past (Burch, in press; Skoog 1968). Caribou were scarce and inaccessible to Barrow-area hunters in the early 20$^{th}$ century (Matumeak 2010; Toovak 2007), and what is now the TCH range was used historically for introduced, domestic reindeer. Reindeer were brought to Alaska in 1892 to provide an additional food source for Alaska Natives, because many wild game populations were in decline (Stern et al. 1980), and to encourage Alaska Natives to transition from hunting to agriculture as a method of assimilation (Simon 1998). In 1898,

reindeer were driven to Barrow as part of a relief effort to provide food for stranded commercial whalers, and these formed the basis for subsequent Barrow-area reindeer herds owned and herded by Iñupiat (Brower, n.d.; Johnson 1942). Barrow-area herds were estimated to total over 35,000 reindeer by the mid-1930s, but by the early 1940s herds had severely declined and by 1950, Barrow's reindeer industry had come to an end (Sonnenfeld 1959).

Numerous potential causes for the reindeer decline have been described—poor management, predation by wolves, illegal killing by hunters, excessive slaughter by herders, severe weather, and mingling with caribou (Johnson 1942; Lopp 1939; Rood 1942; Sonnenfeld 1959; Zimmerman 1942). Local hunters and herders observed reindeer-caribou interactions in the past and report reindeer-like animals within caribou herds today, suggesting potential survival of feral reindeer and hybridization with caribou. However, little has been written about the role of caribou in the decline of reindeer, and the changes observed in caribou that may indicate hybridization with reindeer. No research efforts had yet been made to systematically document this history from hunter and herder perspectives.

Little was known, as well, about the potential impacts of reindeer introgression on caribou herds. Biologists have been concerned with the impact that domestic reindeer might have on caribou (Burns 1990; Jepsen, Siegismund, and Fredholm 2002; Klein 1980; Rausch 1951). However, differences in the morphology, behavior, and reproductive timing of caribou and reindeer would suggest that reindeer within caribou herds are more likely to suffer predation and less likely to reproduce, reducing their ability to persist in the wild (Finstad, Bader, and Prichard 2002; Klein 1980; Skoog 1968). Previous genetic studies of reindeer and caribou using mitochondrial DNA (mtDNA) and transferrin allele frequencies have concluded that reindeer alleles are not widespread within the Teshekpuk and other North Slope herds (Cronin, MacNeil, and Patton 2006, Røed and Whitten 1986). However, local observations suggested a need for further genetic investigation using a larger sample and more genetic markers than previously used.

Questions about the genetic identity of the TCH and other North Slope herds highlight a need to describe the population structure of North Slope caribou, given their uncertain history. Four North Slope herds—Western Arctic (WAH), Teshekpuk (TCH), Central Arctic (CAH), and Porcupine (PCH)—currently total an estimated 650,000 animals (Alaska Department of Fish and Game 2011a, 2011b; Lenart 2009; Parrett 2009). These large herds undergo long-distance annual migrations between seasonal ranges that may sometimes overlap. Females of a herd show strong fidelity to calving grounds and apparent dispersal is estimated to be relatively low, 6.9% from the TCH (Person et al. 2007). However, male dispersal is poorly understood and the extent to which herds interbreed when their ranges overlap during rut is unknown.

It is likely that North Slope caribou herds have had different patterns of spatial interactions in the past. The population sizes of North Slope herds have fluctuated by orders of magnitude throughout the last 150 years and are currently at relatively high numbers (Burch, in press; Caikoski 2009; Dau 2009; Joly et al. 2011; Lenart 2009; Parrett 2009; Skoog 1968). Population fluctuations in caribou are often followed by changes in range size and occasionally by range shifts, which may alter herd interactions and have potential demographic and genetic effects (Hinkes et al. 2005). The effect of these population fluctuations and range shifts on the genetic diversity and connectivity of large North Slope herds has not been well understood. Previous genetic studies (Cronin et al. 2003; Cronin, MacNeil, and Patton 2005) found no distinction among herds, but were limited by small sample sizes, potentially non-neutral markers, and markers of low variability. As the North Slope landscape is increasingly altered by industrial development, a pre-development genetic baseline would enable detection of future changes in genetic diversity and connectivity.

North Slope caribou comprise a majority of Alaska's caribou population, but only 4 of the 32 recognized herds (Alaska Department of Fish and Game 2009). Alaskan caribou herds range in size from less than 100 animals in the Galena Mountain herd to almost 350,000 in the Western Arctic herd (Alaska Department of Fish and Game 2009). They inhabit a diversity of landforms and habitats including arctic tundra, mountain

ranges varying in elevation and ruggedness, parts of the boreal forest, peninsulas, and islands. Different types of herds are classified by ecotype depending on their predominant habitat use (tundra or mountain) and strategies for spacing (dispersed or aggregated) and migration (sedentary or migratory; Bergerud 1996, Festa-Bianchet et al. 2011). Herds across Alaska are known to have fluctuated in population size, undergone range shifts, and experienced contact with reindeer (Burch, in press; Hinkes et al. 2005; Skoog 1968; Valkenburg and Davis 1986). However, like the TCH, many Alaskan herds were only recognized since the 1970s and their history is not well understood.

Caribou movement studies have revealed much about the differences and overlaps between various herds in the last 30 years (Alaska Department of Fish and Game 2009). However, a genetic study was needed to gain insight into the demographic histories of poorly understood herds and to understand the potential effects of past processes and geography on herds for which this information is available. Previous studies of some Alaskan herds suggested regional variations in the degree of genetic differentiation among herds (Cronin, MacNeil, and Patton 2005; Zittlau 2004). However, a comprehensive statewide study was needed to identify the extent to which herds, as management units, are genetically discrete and to describe the patterns of genetic structure at a statewide scale. Determining caribou population structure and its potential drivers has direct application to informing population-based management of Alaskan caribou.

### 1.3 Objectives, Methodology, and Outline

To address the questions and needs identified in the previous section, I developed a study around two overarching research questions:

1) How have historical interactions between Alaskan caribou and reindeer influenced their genetic identity?
2) How have landscape features, demographic fluctuations, and potentially divergent selective pressures influenced the diversity and connectivity of Alaskan caribou herds?

These questions have historical, genetic, ecological, and geographic components, requiring varying types of data and an interdisciplinary approach.

To document historical interactions between caribou and reindeer near Barrow, I drew upon the local knowledge of caribou hunters and former reindeer herders. Many hunters and herders develop expertise about animals through repeated observation over the course of their lifetimes. Local expert observations, as well as local theories about ecology and ethics of human behavior towards the animals, have made important contributions to wildlife ecology and management (Cruikshank 1998; Ferguson and Messier 1997; Huntington 2000; Nadasdy 1999; Skoog 1956; Thorpe 2004). I recorded semi-structured interviews with Barrow-area reindeer herders and hunters, and examined written archival documents, to gain a detailed understanding of reindeer-caribou interactions. Specifically, I sought to understand 1) changes in the abundance and distribution of Barrow-area caribou over time, 2) the role of caribou in the decline of the Barrow reindeer industry, 3) the specific contexts in which reindeer and caribou interacted, and their behaviors, 4) characteristics used by hunters and herders to distinguish caribou and reindeer, 5) evidence of reindeer-caribou hybridization and persistence in caribou herds, and 6) the implications of a cultural heritage with reindeer and caribou for Iñupiat identity and traditional knowledge. This research is presented in Chapter 2.

In Chapter 3, I examine the biological implications of reindeer-caribou interactions on North Slope caribou herds. Based on local knowledge, I predicted that caribou herds would contain individuals with hybrid ancestry resulting from historical interactions in the Barrow area and/or recent reindeer-caribou mixing on the Seward Peninsula, and that the TCH would show greater levels of introgression than other herds. I used population genetics techniques to analyze DNA from 312 caribou and reindeer at 19 microsatellite loci. Similar techniques have been used previously to detect hybridization between reindeer and caribou in Greenland (Jepsen, Siegismund, and Fredholm 2002) and between wild and domestic carnivores (Oliveira et al. 2008; Randi

and Lucchini 2002). I used insights from local knowledge and published biological literature to interpret the results.

To determine the influences of geography and demographic history on caribou herd connectivity, I analyzed the genetic population structure of caribou herds across the state. In Chapter 3, I described the population genetics of North Slope caribou herds to determine whether herds were distinct and how the population was structured over the landscape. In Chapter 4, I conducted a similar analysis of 20 herds at the statewide scale. Studies of caribou population structure in Canada over large spatial scales have found areas of genetic connectivity over large areas and instances of herd-based genetic differentiation, potentially linked to differences in ecotype (Boulet et al. 2007; Courtois, Bernatchez, and Ouellet 2003; Zittlau 2004). I aimed to determine 1) how the genetic structure of the North Slope compares to that in the Interior and Southwest regions of the state, 2) the number of populations and pattern of population subdivision statewide, and 3) whether herds constitute genetic units. I hypothesized four main factors to explain the genetic population structure at each of these spatial scales over evolutionary and historical time scales. Based on available historical, landscape, and behavioral data in the literature, I examined potential mechanisms by which these factors shaped the observed patterns of statewide and herd-level differentiation.

In Chapter 5, my objectives were to describe how I integrated local knowledge and genetics, compare my approach to other studies, and provide reflections and recommendations for the use of local knowledge in wildlife science. In Chapter 6, I summarize my findings from chapters 2-5 and seek to apply them to future scenarios of landscape change. In doing so, I focus on potential contributions to herd-based and population-level caribou management and on providing recommendations for future research.

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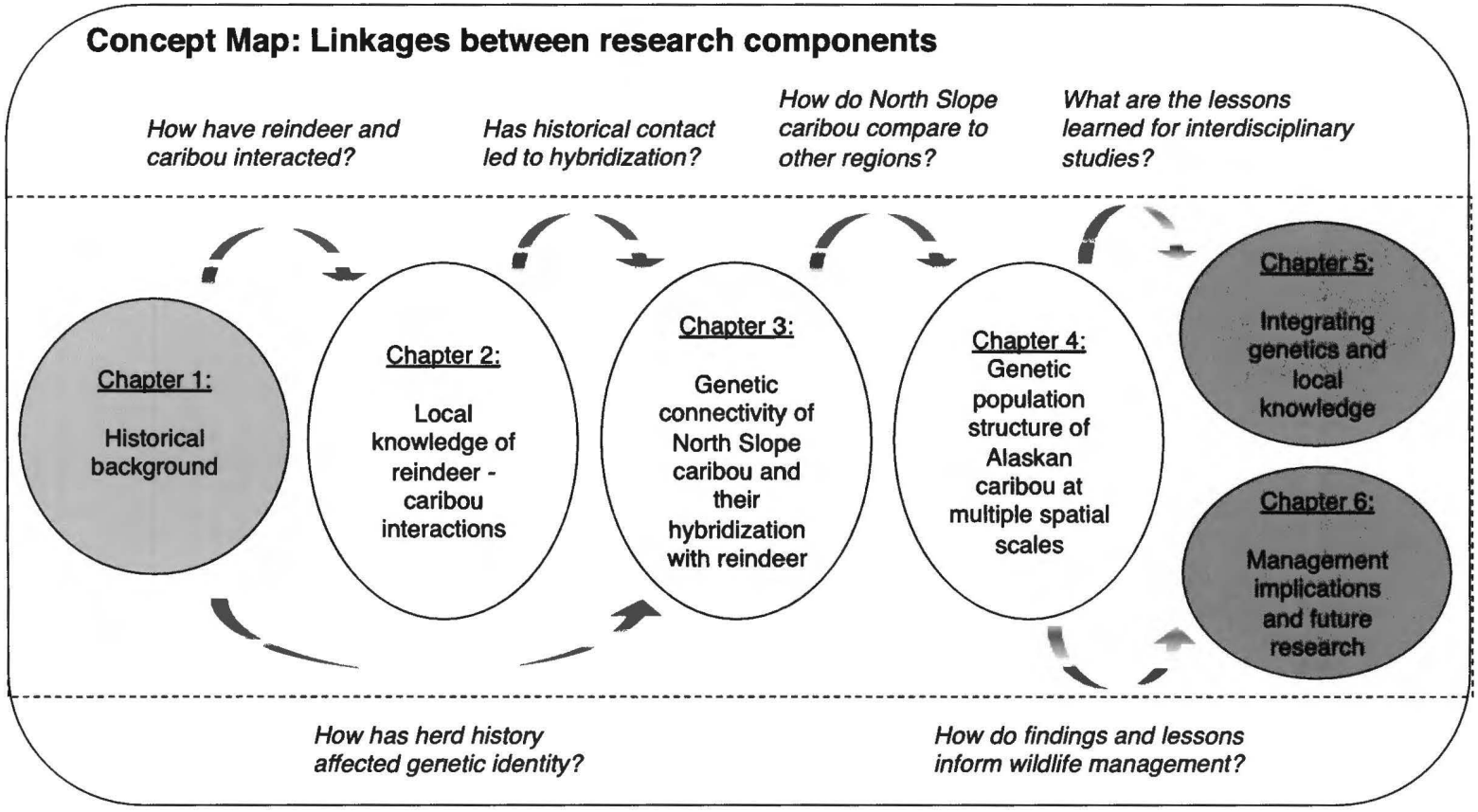


**Figure 1.1. Conceptual diagram of linkages between dissertation components**

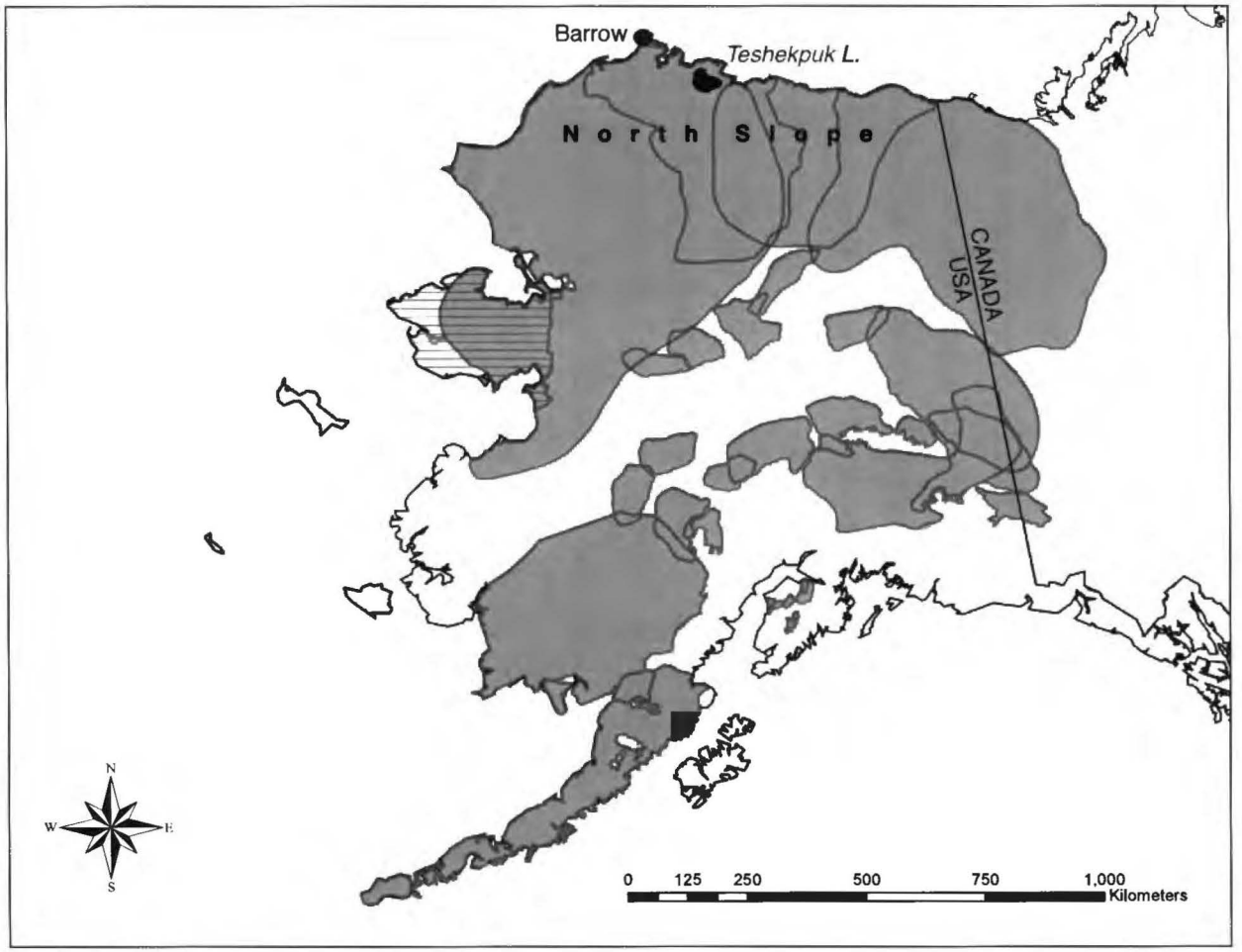


**Figure. 1.2. Map of Alaskan caribou herd ranges (grey) and Seward Peninsula reindeer ranges (lined) as of 2011.**

Outlines of the boundaries of individual herd ranges are shown to indicate where ranges overlap.

# Chapter 2 "I'd Be Foolish to Tell You They Were Caribou:" Local Knowledge of Historical Interactions between Reindeer and Caribou in Barrow, Alaska[1]

## 2.1 Abstract

During the period of domestic reindeer herding in Barrow, 1898-1951, changes in the abundance and distribution of caribou led to historical interactions between the native caribou and introduced reindeer. Herders remember losing their reindeer when the animals joined migrating caribou herds. This study aims to understand the role of caribou in the reindeer industry's decline and the fate of reindeer that joined caribou herds. Oral histories reveal a mismatch between herders struggling to prevent their reindeer from joining caribou herds and administrators who assumed that caribou problems could be eliminated through more careful herding. Hunter observations since suggest that some reindeer-like animals persist in caribou herds. These observations provide insights into the history of reindeer herding in the region, our biological understanding of how the two subspecies interact in the wild, and the influence of a heritage with reindeer herding on how Barrow people identify animals on the land today.

## 2.2 Dedication

Tiger Burch and I shared an interest in the history of Alaskan caribou herds, and after discovering each other's work, we exchanged ideas, sources, and critiques during the last two years of his life. We generally agreed on the ways in which oral histories and archival sources could be used to reconstruct changes in caribou herds, though we also had friendly debates. My research centered on the Barrow area with a focus on interactions between caribou and reindeer, while Tiger ambitiously (but not surprisingly) was writing a book on the history of all caribou herds in northern Alaska over the last 150

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years, including their interactions with wolves, reindeer, and people. Tiger's unfinished manuscript has been submitted for publication, but he never completed his research on reindeer and I never had the chance to share my final findings on reindeer-caribou interactions with him. This paper shares those findings from my research, and answers some of the questions Tiger and I both found so curious and compelling.

## 2.3 Introduction

The Iñupiat of Barrow, Alaska, have a heritage with domestic reindeer (*Rangifer tarandus tarandus*) herding and a tradition of wild caribou (*R. t. granti*) hunting. During the historical period of herding, changes in the abundance and distribution of caribou led to interactions between the native caribou and introduced reindeer. Herders remember losing their reindeer when the animals joined migrating caribou herds, but the fate of the animals and the impact of those losses on the local reindeer herders are not well understood. This raises the question: How has a history with both reindeer and caribou influenced the biology of the animals and the knowledge of local people today?

This paper describes historical interactions between caribou native to northern Alaska and introduced domestic reindeer, and seeks to understand how a heritage with reindeer influences the ways people identify caribou today. These issues are not well understood by biologists or historians, largely because the perspectives of people who spend the most time on the land with the animals—reindeer herders and caribou hunters—are not well represented in the literature. Interviews with herders and hunters in the Barrow area, conducted for this study, revealed a nuanced and detailed history of reindeer and caribou. Herders' stories revise our ideas about why reindeer herding ended in the Barrow area—namely, by explaining the role of caribou in that process. Barrow area people shot caribou in their reindeer herds in the past in attempts to protect their reindeer, and now they preferentially hunt reindeer-like animals among caribou found in their area today. By virtue of their heritage, they are well positioned to tell us about the history of the Barrow reindeer industry, the behavior and comparative biology of

interacting reindeer and caribou, and the cultural implications of a heritage with both herding and hunting.

Caribou are abundant near Barrow today and hunting them is culturally important, though access to caribou has varied over the years. In the late 1800s, Barrow Iñupiat hunted declining yet locally abundant caribou herds, but by the early 1900s, caribou were rare near Barrow and did not become common again until the 1940s (Brower n.d.; Burch, in press; Murdoch 1892; Smith 1883). Domestic reindeer were brought to Barrow in 1898 and herding by local Iñupiat began. As reindeer herds grew, herders began to graze them in the same areas that, until recently, had been used by caribou (Richardson 1916, Superintendent of Barrow 1911). Reindeer herding peaked in the 1930s, and by 1950, the industry had come to its end (Sonnenfeld 1959). Many factors—economic, cultural, ecological, and administrative—contributed to the demise of the Barrow reindeer industry (Johnson 1942; Lantis 1950; Sonnenfeld 1959). However, written accounts of the history tended to focus on the administrative and cultural challenges, rather than the ecological challenges. When ecological concerns are discussed, they often focus on range conditions and wolf predation with little discussion of caribou and are often presented as factors that herders should have been able to control.

Though mingling between native caribou and the domestic herds was rarely mentioned in administrative documents at the time, stories of reindeer-caribou interactions are remembered by Barrow residents today. Similar problems experienced recently on Alaska's Seward Peninsula, where thousands of reindeer joined the Western Arctic caribou herd since the 1990s and could not be recovered despite snowmachines, airplanes, and helicopters, demonstrate the impact caribou can have on a reindeer owner's ability to continue in the industry (Schneider, Kielland, and Finstad 2005). Barrow area herders recall the challenges they faced, without modern technologies, attempting to prevent their reindeer from joining caribou herds.

Little is known about the fate of the reindeer that joined caribou herds. Biologists have been concerned with the impact domestic reindeer might have on caribou (Burns 1990; Jepsen, Siegismund, and Fredholm 2002; Klein 1980; Rausch 1951), but also

reason that reindeer within caribou herds are more likely to suffer predation and less likely to reproduce[i], reducing their ability to persist in the wild[ii] (Finstad, Bader, and Prichard 2002; Klein 1980; Skoog 1968). However, there is little empirical research in the scientific literature about how domestic reindeer affect wild caribou. Few scientists have observed caribou and reindeer together in the wild to compare their appearance and behavior and to observe their interactions[iii]. The experience of herders and hunters who witnessed the two subspecies together may offer insights into how to differentiate caribou from reindeer and how local people identify reindeer-like animals in caribou herds today.

Memories of herding and observations of reindeer-caribou interactions are a part of the life experience of some of Barrow's Iñupiat elders[iv], most of whom have passed away since being interviewed for this project. As teenage herders[v], they moved their herds between coastal and inland ranges, learning to care for the reindeer and observing their responses to weather, forage, insects, predators, and caribou. Scholars have debated the extent to which the skills and knowledge required for pastoral reindeer herding were compatible with an Iñupiaq worldview and the traditional demands of the subsistence cycle, such as spring whaling (Lantis 1950, 1952; Sonnenfeld 1959). Reindeer were intended by the government to act as an agent of culture change, "a great step forward in lifting the native races of that boreal region out of barbarism and starting them toward civilization" (Harris 1890). However, in Barrow and elsewhere (Schneider, Kielland, and Finstad 2005; Simon 1998), reindeer were incorporated into society in ways that reinforced Iñupiat traditional values and identities. Herding is now part of Barrow's heritage as a livelihood that elders learned and knew well. Many former herders became leaders within the community and their stories contribute to cultural and ecological knowledge passed on to younger generations.

### *2.3.1 Background on Barrow Reindeer Herds*

Reindeer were brought to Alaska from Chukotka, Russia, in 1892 for two primary purposes: to provide what was perceived to be a stable food source for Alaska Natives because many wild game populations were in decline (Stern et al. 1980), and to

encourage Alaska Natives to transition from hunting to agriculture as a method of assimilation (Simon 1998:96). However, the reindeer driven to Barrow in 1898 were not intended for the Natives, but as a relief effort to provide food for stranded commercial whalers. The drive was successful, but the whalers were well supplied with game (including caribou) hunted by local Iñupiat. Because of this, and because the reindeer were in poor condition after the long drive, only 125 of the 400-500 reindeer were killed for food, and the rest formed the stock from which the Barrow area herds developed (Fig. 2.1; Brower, n.d.; Johnson 1942).

The early Barrow reindeer herd was supervised by Rev. H. R. Marsh, financed by Charles D. Brower, and herded by a chief herder, Takpuk, and several young Native apprentices (Johnson 1942). Administration shifted in 1908 to schoolteachers, who served as local reindeer superintendents under the regulations of the Alaska Reindeer Service (Acting Chief of the Alaska Division 1908). Herding apprentices earned ownership of live reindeer for their work, and by 1925, Barrow reindeer owners had established ten separate herds, including one near Wainwright and two near Barter Island (Johnson 1942). The other seven herds were kept in the area bounded by the Meade and Colville rivers, which will be referred to as the "Barrow area" throughout this paper (Fig. 2.2). At first, the herds were kept near coastal communities but as these grazing areas became depleted, herders moved their deer inland for at least part of the year.

In 1924, several Barrow area herds joined to form the Farthest North Reindeer Company, though the Brower and Cape Halkett herds remained separate. The herds continued to increase into the 1930s but exact herd sizes are uncertain because few complete counts were made (Sonnenfeld 1959). The Farthest North Reindeer Co. was estimated to own 30,000 reindeer in 1935, though the largest actual count was of 15,676 reindeer corralled in 1936 (Johnson 1942).

By the 1940s, Alaskan reindeer herds were severely reduced. Numerous potential causes for the decline have been described—poor management, predation by wolves, untended herds, illegal killing by hunters, excessive slaughter by herders for food, severe storms, and mingling with caribou (Johnson 1942; Lopp 1939; Rood 1942; Sonnenfeld

1959; Zimmerman 1942). Through some combination of these factors, Barrow area herds probably contained less than 5,000 deer by 1940 (Johnson 1942; Sonnenfeld 1959). The Farthest North Reindeer Co. was reorganized under the Northern Frontier Reindeer Company and, along with the small Brower and Halkett herds, persisted until the early 1950s when the Barrow area herds ceased to exist[vi]. This paper will focus on the experiences of reindeer herders during this period of decline.

## 2.4 Methods

Interviews were recorded with former reindeer herders and caribou hunters to: 1. Describe historical interactions between domestic reindeer and wild caribou witnessed by herders in the Barrow area during the 1940s; 2. Identify the physical and behavioral characteristics that hunters and herders use to distinguish reindeer from caribou; 3. Record local perspectives on the implications for today's caribou herds of reindeer-caribou interactions; 4. Understand how a heritage with reindeer herding and caribou hunting has influenced the ways in which Barrow people talk about the animals. The firsthand knowledge and richness of understanding offered by interview participants comprised the bulk of this study's information. However, written archival sources were also used to gain additional perspective on reindeer-caribou interactions, long-term trends in the caribou herds, and attitudes within the Reindeer Service administration.

### *2.4.1 Interview Participants and Procedures*

I interviewed 23 Barrow residents including 12 elders with direct herding experience and 11 individuals who were either caribou hunters or descendants of reindeer herders, or both (see Appendix 2.A). Herders were identified through a snowball sample—asking community members to identify former reindeer herders until no new names were added to the list. Most people who could remember working or living with reindeer herds have already passed away and I interviewed nearly all of those still living. Those elders primarily had memories of the Barrow, Brower, Cape Halkett, and Wainwright herds of

the late 1930s-1940s. To identify caribou hunters considered to be highly knowledgeable, community leaders and local wildlife management agencies were consulted. The hunters I interviewed represented a wide range of ages, and most were hunters in the Barrow area throughout their lives. Interview participants were not asked to identify their ethnicity or race but most referenced their Iñupiaq cultural identity during the course of the interview.

Audio-recordings were made for 21 of the 23 participants in interview sessions ranging from 1-3 hours. Some were interviewed in groups and in many cases family members were present. A translator was present for nearly all the interviews with elders. Most elders spoke Iñupiaq as a first language, though many were fluent in English as well. For younger participants, the interview questions were asked in English. I conducted follow-up interviews with five participants to ask for additional information and clarifications.

Interviews followed a semi-structured format. This provided space for participants to share the perspectives and stories of interest to them, including personal stories of time on the land, Barrow's history, or lessons about the intelligence of animals that provided context for other statements. Questions were used mainly to steer the conversation towards the research topic. Maps and historical photos were shared with some participants to spur conversation.

Audio-recordings were transcribed and coded using HyperRESEARCH software for qualitative data analysis (ResearchWare, Inc.). Because of the study's interest in the variety of observations and historical context of hunter and herder experiences, qualitative coding was used to organize and identify patterns in what participants said. The analysis followed a bottom-up coding procedure (Auerbach and Silverstein 2003:133)—flagging sections of text relevant to the research questions, thoroughly reading and coding passages with concepts important to the participant, re-coding ideas repeated in multiple interviews, and finally identifying themes and patterns within the group as a whole. This process identified areas of consensus, disagreement, and variable experience among participants, without diminishing the stories and unique voice of each participant. Because I used semi-directed interviews and bottom-up coding, the research

focus remained on the stories participants felt were most important to tell, which was important in determining the relative importance of reindeer-caribou interactions in their hunting and herding memories.

*2.4.2 Methodological Approach and Limitations*

To understand how reindeer-caribou interactions in the past influenced observations and dialogue about these animals today, we need empirical knowledge of the past as well as a range of perspectives and experiences that give rise to the conceptions of animal identity in Barrow today. I chose to favor oral histories over written sources regarding reindeer-caribou interactions because few Barrow Iñupiat with direct experience in historical herding and hunting have written about the subject (but see written life histories: Bodfish 1991; Brewster [ed.] 2004).

Accounts of experiences by native reindeer herders tell us how reindeer and caribou behaved on the range. They may provide different and more accurate accounts than the administrative documents of the Reindeer Service, most of which were written from a distance and focused on other issues such as the number of animals and incentives for herders. In his own work, Burch concluded, "information that is provided by people whom the Iñupiat consider competent historians should be regarded as true until proven false, no matter how extraordinary what they say may first appear" (Burch 1991:12-13). In reconstructing a part of Barrow's history, this study takes a similar approach. Corroboration among oral sources, and between oral and written sources, gives validity to the empirical history that is reconstructed. However, it is equally important to consider when stories and perspectives differ among interviewees as this may reflect the varied experiences of reindeer herders and a wider range of perspectives on caribou identity than have been documented to date.

Though I interviewed enough participants to provide a range of information and corroboration among sources, the history and understanding I derived are limited in several ways. After the passage of so many years and herders, this study was limited to

the memories of those who were children or teenage workers in the last years of the Barrow reindeer industry, a period when herds were in decline. The full range of hunter perspectives on animal characteristics may not be represented in this paper, as not all of the more than 30 hunters identified were interviewed. Finally, the true meaning of participants' statements may also have been obscured by linguistic and cultural misunderstandings on the part of the researcher.

### 2.5 Role of Caribou in the Barrow Reindeer Decline

"The caribou mingled with the reindeer herd, so the reindeers kind of took them, took the caribou away. Yeah, it happened to all...the villages in this area. That's how the reindeer diminished in this area, because of the caribou" (Whitlam Adams, interviewed July 3, 2008). Former reindeer herders in Barrow remembered frequent mixing between caribou and reindeer in the 1940s. In fact, incidences of mingling with caribou, and the subsequent loss of the reindeer herds, seemed to be some of the most significant memories for many herders. The herds they remembered losing numbered a few hundred to a few thousand, having declined or been re-started prior to their time as herders. However, Kenny Toovak, Sr. remembered the days of peak herd sizes, when he helped to corral and count an estimated 25,000 reindeer in Barrow in the mid-late 1930s. Those reindeer were subsequently lost—presumably to caribou although wolves were also a problem at the time—and Barrow then borrowed 3,000 reindeer from Wainwright in the late 1930s or early 1940s to re-start their own herd (Kenneth Toovak, Sr., interviewed August 3, 2007).

Though herders remember the 1940s as a time of particular conflict with caribou, interactions between caribou and reindeer occurred earlier as well. Bertha Leavitt, born in 1912, remembered the earlier days of the reindeer industry, growing up in a herding family (Fig. 2.3). She recalled times that caribou joined the reindeer, but said they were always shot for food and to protect the herd from straying (Bertha Leavitt, interviewed July 8, 2008). Some written sources from the time also describe the problem. As early as 1917, reindeer were reported lost in Barrow (Shields [ed.] 1917a). In response, Barrow

herders established a reward system for rounding up stray reindeer, and inland trappers helped to recover hundreds of strays. In one case, fifty-five reindeer with a single bull caribou were found and driven back to Barrow once the caribou was killed (Shields 1918). Despite these efforts, the lack of close herding after herds were reorganized into stock companies probably allowed more reindeer-caribou mixing to continue (Sonnenfeld 1959). In 1927, the trader Charles D. Brower wrote, "Reindeer scattered all over the country, no one herding them. Mixed in with caribou and many same as wild deer, without any marks" (Brower, n.d.:44). In the early 1930s, reindeer driven across the North Slope en route to Canada were lost to caribou herds along the Colville River southeast of Barrow (Morlander 1934). These reports make clear that problems with caribou existed all along, yet there are no accounts of major losses to migrating caribou herds near Barrow until the late 1930s–1940s.

Many former herders explained that in their youth there were few caribou near Barrow and hunters had to travel hundreds of miles to the foothills to find them. By the 1940s, however, herders observed an increase in the caribou. For the first time, they saw large herds of caribou coming all the way to the coast in the summer, seeking windy coastline for insect relief when the weather was warm. Warren Ovluaq Matumeak, Sr., described a common experience of herders in the 1940s: "The caribou kept coming. And finally, they come in larger numbers and during insect seasons and the reindeer start following them. And that's, that's when they get mixed up, mixed in with caribou... You could take care of them but these caribou, they start coming towards the coast in large numbers. They was, it was a bit hard to control the reindeer" (Warren Ovluaq Matumeak, Sr., interviewed June 5, 2010). Caribou came into contact with reindeer at a time of year when reindeer were difficult to herd. Alfred Shugluk explained, "In the springtime when it thaws out they want to move around to eat and we try to keep them together but it is hard. Wintertime it's easier to herd them. They don't wander as much" (Alfred Shugluk, interviewed July 7, 2008). Reindeer became even more difficult to control once they mixed with caribou and wanted to follow them.

*2.5.1 Reindeer Herder Responses to Caribou*

Herders responded to the caribou problem by trying to prevent interactions with caribou and recover lost reindeer. Most herders emphasized the need to be very protective of their reindeer: "If your timing is not in order, your herd could run away with the caribou. So we are very strict on that because we have 24-hour watch. That means we keep an eye on our reindeer for 24 hours a day" (Arnold Brower, Sr., interviewed July 2, 2008). In winter, reindeer had to be protected during the night from wolves. In summer, herders sometimes had to stay awake for days at a time to keep the caribou away (Samuel Nayukok, interviewed August 8, 2007). When the weather was bad, they would leave the reindeer for a few days and then had to find and retrieve them. Reindeer herders had to stay with the reindeer on foot during the summer, and their youthful physical condition enabled them to keep up. As Arnold Brower, Sr., (interviewed August 8, 2007) said, "I can't do it today. Those years I can run just like a fox and keep up with them." In nearly every case, herders who lost reindeer to caribou in the summer tried to catch up to them on foot, but couldn't. Samuel Nayukok remembers (as translated in the third person): "He just couldn't keep them away from the caribou herd. That's what hurt them. They tried catching them so they could try and get their reindeers back from the caribou herd. But it was just not possible. They chased the herd to try to get their reindeer back for days, but couldn't catch up with them" (Samuel Nayukok, interviewed August 8, 2007).

Herders used special areas, such as peninsulas and river gorges, as natural "corrals" to protect reindeer from caribou. Wesley Aiken kept his reindeer on a peninsula by the Kogru River. He told a rare story of losing his reindeer herd to caribou and getting them back.

> One time, we wasn't watching them in couple of days...and when we go check them after couple days, they were heading down towards the ocean. We find the tracks and we have to walk all the way down and find them. Took us day and night from here all the way down. It was in the summer. It was in July. We find them down there, maybe more than 10 caribous with them. I think they must have led them or get away from there, from that area....Yeah, we took the caribou

> back with us alright until we get close to our place over here and they just took off....We was going to kill them when we get close in there but they took off. (Wesley and Anna Aiken, interviewed July 9, 2008)

Several herders said it was necessary to kill caribou as soon as they mixed with the reindeer, if possible, and herders used the caribou they shot for food. However, despite herders' efforts to prevent losses to caribou, many reindeer from the Barrow area herds and across the North Slope joined the caribou and were never recovered. The Brower reindeer herd was the last to persist until it was finally lost, in 1951, when Navy vehicles "stampeded" the herd southward from its summer range and into the path of a migrating caribou herd (Thomas Brower, Sr. 1982).

*2.5.2 Fluctuations in Caribou Population Size*

To understand the magnitude of the "caribou problem" we have to understand how changes in the caribou herds led to the increased reindeer-caribou interactions that herders remember. Caribou populations can fluctuate in size by orders of magnitude and occasionally undergo geographic shifts. Today, four herds totaling approximately 650,000 caribou occupy Alaska's North Slope (Alaska Department of Fish and Game 2011a, 2011b; Dau 2009; Lenart 2009; Parrett 2009). The core range of the Teshekpuk caribou herd and some seasonal ranges of the other three herds encompass much of the region used historically by Barrow area reindeer herds (Fig. 2.2). However, the size and geographic distribution of those caribou herds were very different during the reindeer era, 1898-1950 (Burch, in press; Skoog 1968).

Caribou herds across northern Alaska crashed from the mid-1800s through early 1900s (Burch, in press:64). By the late 1800s, the Western Arctic caribou herd had severely declined and its contracted range (Burch, in press:138) was far inland from Barrow. However, caribou were "plentiful" near Barrow in the winter of 1897-1898 and hunters killed 1200 to feed shipwrecked whalers, before the reindeer drive intended to save them arrived that spring (Brower, n.d.). These were likely part of the historical Teshekpuk caribou herd (Burch, in press:130), which soon crashed, along with herds to

the east, by the early 1900s (Burch, in press:64). After the crash, caribou were far inland and difficult for Barrow residents to access. Herders remember the early days of reindeer herding, post-caribou decline, as a time when reindeer were needed for furs and meat.

Caribou in northwest Alaska had begun to increase by 1915 (Burch, in press:141) but still rarely came to the coast near Barrow (Skoog 1968:248). By the 1930s, large herds of caribou were noted to the west of Barrow (Andrews [ed.] 1937a) and to the east, where a trader returning from Barter Island observed, "there was a larger caribou migration this spring than ever before" (Rank 1936). Caribou near Barter Island migrated along the coast in summer and "occasionally...come as far west as the Meade River" near Barrow, but administrators noted that the caribou did not interfere with reindeer herding in the area (Daugherty and Rood 1936). It is worth noting that these reports are limited in scope, as few biologists studied North Slope caribou during the reindeer-herding period, with the exception of Olaus Murie (1935:64-66) who used information from traders and native hunters for his writings on the region. However, it is clear that by the late 1930s and throughout the 1940s, caribou were abundant on the coastal plain (Skoog 1968:249) due to an increase in population size, a range shift to the north, or both. For reindeer herders, this change was experienced as a sudden influx of caribou into the ranges of the Barrow area herds, leading to the problems and losses herders described.

### *2.5.3 Perceptions of Caribou in the Reindeer Administration*

Though herders described caribou as a major problem in the 1940s, caribou are hardly mentioned in written documents from the time. The few documents that do mention major losses to caribou (Forshaug 1940a, 1940b; Lopp 1939; Murie 1935:7) are based on correspondence with herders, and generally corroborate the stories shared by interview participants. U.S. Reindeer Service correspondence and the reindeer-focused periodical *The Eskimo* focus instead on administrative and economic challenges to the industry. When ecological factors affecting reindeer are discussed, they focus mostly on wolf predation and range degradation, not caribou. Caribou seem conspicuously absent from calculations of available range and stocking estimates in 1943 (Andrews [ed.] 1943),

despite the fact that rebounding caribou populations were foraging in many of the areas used by reindeer at that time. Why were caribou so rarely described as a problem by reindeer administrators while herders were experiencing problems with them? It appears that a lack of scientific studies and few administrators on the range talking with herders, coupled with a persistent perception that caribou were declining towards extinction and thoughts that caribou breeding could benefit reindeer, may have kept reindeer administrators from recognizing the increasing caribou population as a threat. When caribou problems were recognized, they may have seemed minor compared to other problems within the reindeer industry, especially because of the administrative belief that proper herding could prevent caribou problems altogether (Sonnenfeld 1959).

When reindeer were brought to Alaska, caribou were not perceived as a threat to reindeer. Rather, it seems likely that the man behind the introduction—U. S. General Agent of Education in Alaska, Sheldon Jackson—viewed reindeer as a replacement for disappearing caribou, which he was advised would go extinct by the turn of the century (Woolfe 1890). Even as caribou increased, dialogue continued about the replacement of caribou by reindeer. In 1937, *The Eskimo* reminded readers that, "When the reindeer work first was started in Alaska nearly all the caribou in Alaska had been killed out of N.W. Alaska....So the caribou were pretty well gone by 1900" (Andrews [ed.] 1937b). This perception may have persisted due to uncertainty about the caribou, which were not systematically studied at the time. After an aerial search for missing reindeer by Mr. Gubser, "Government Wolf Killer", *The Eskimo* published a quote and summary of his report, along with an editorial remark questioning his observation of a large caribou herd:

> 'Found herds notably missing. Saw no deer from Pt. Lay to Selawik. Was in air five hours covering Noatak, Kivalina, Pt. Hope, and Pt. Lay ranges without seeing signs of a single deer.' Reports in Kobuk near Cutler River flew for 25 minutes over an immense herd of caribou. Noted two spotted deer. (Remark; possibly all were reindeer and not caribou?). (Andrews [ed.] 1937a)

Perhaps uncertainty about whether the caribou population was really rebounding from perceived near-extinction, expressed in the above remark, partially accounts for why caribou were so rarely discussed as a threat to reindeer herds in administrative reports.

Ideas at the time that reindeer-caribou interbreeding was desirable may have also influenced perceptions of caribou. Though caribou tended to lead reindeer away, and were often shot by herders, efforts were also made to allow interbreeding. Caribou were experimentally bred with reindeer on Nunivak Island in 1925, though plans to move hybrid animals to the mainland were ultimately abandoned (Burdick 1940:8). On the mainland, attempts were made early on in the reindeer industry to "lure these hardy wild reindeer into the herds" because "the hardy caribou furnish the best possible new blood for the highly inbred domesticated deer" (Shields [ed.] 1917b). A caribou bull spent at least 6 months, including the rut, with the Noatak reindeer herd in 1917, but Wainwright was unable to keep caribou with their herd; and in Selawik, "a big caribou bull spent a week in Herd Number One during the rutting season. But he kept leading off bunches of females so he had to be shot" (Shields [ed.] 1917b). Perhaps, perceived advantages of caribou "blood" allayed concern about their contact with reindeer, though the lack of success in keeping caribou with reindeer herds foreshadowed the problems caribou would later cause.

For administrators, reports of caribou problems may have seemed minor compared to many other threats to the viability of the Barrow reindeer industry that concerned them more, including wolves, untended herds, and illegal or excessive slaughter (Andrews [ed.] 1939; Johnson 1942; Lopp 1939; Rood 1942; Zimmerman 1942). Economic and administrative changes affected herding practices by altering labor conditions and company organization, and the inadequate herding thought to result from such changes was blamed for "ecological" losses to wolves, caribou, storms, and poor forage (Sonnenfeld 1959). While incentives related to work and ownership certainly influenced the choices made by herders, it is striking that caribou posed challenges even after a protective herding style was re-adopted, with pay available for herders to tend the now smaller herds year round (Rood 1942).

Though Sonnenfeld (1959) suggests that a lack of herding in summer allowed losses to caribou, the former herders I interviewed witnessed those losses while out on the land with their reindeer and worked actively to prevent mixing and to recover their deer. While administrators felt that proper herding should prevent caribou problems, herder experiences suggest that preventing mixing with caribou was nearly impossible. Biologist Robert Rausch, who observed feral reindeer within caribou herds during his 1951 research in the Brooks Range, explained: "Great losses have occurred, when the unattended animals mingle with the wild caribou and migrate with them. Such losses are often attributed to wolf predation, since this is an explanation which is readily accepted, and which absolves the herder of any blame" (Rausch 1951:190). Though wolves were a major threat in some years according to herders, their real impact may have been overestimated in the written history (Burch, in press:72; Johnson 1942; Sonnenfeld 1959) and losses to caribou despite close herding were underrepresented.

The mismatch between written and oral histories on the topic of reindeer-caribou interactions reinforces the importance of herder perspectives in understanding what happened in the past. This is apparent even after caribou began to be acknowledged as a threat, as in a 1948 survey that asked reindeer herd operators across the state for their thoughts on what caused the decrease in reindeer. The survey report (Rouse, Montjoy, and Belcher 1948) summarized responses separately for natives and non-natives and, interestingly, natives listed "mixing with caribou" as a cause of reindeer decreases while non-natives did not[vii]. Wolves are listed as the primary cause of the decline statewide, though survey results from the Barrow area herds state that wolves caused few losses. Despite reporting losses to caribou in the Barrow herd (Rouse, Montjoy, and Belcher 1948:9), the report concludes, "Little difficulty from [caribou] has been experienced in the Barrow area" (Rouse, Montjoy, and Belcher 1948:14). Such a discrepancy between the written words of reindeer administrators and the oral testimony of herders emphasizes the value of first-hand observations by herders in the field, even when their experiences are remembered after many years rather than recorded at the time.

## 2.6 The Fate of Lost Reindeer and their Impact on Caribou Herds

Herders lost thousands of reindeer to mixing with caribou, and it is of interest to biologists and local people to know what happened to the reindeer, whether they hybridized with caribou, and if reindeer-like animals are still observed within caribou herds today. Experience with both reindeer and caribou gave herders and hunters knowledge of how to distinguish between them, and ways to identify potential hybrids.

To determine what participants meant when they described reindeer-like animals in caribou herds, it was important to first establish what criteria hunters and herders use to differentiate caribou and reindeer. Interview participants described a number of physical and behavioral characteristics they use to distinguish between caribou and reindeer. These encompass observations made over their lifetimes, both when caribou joined domestic reindeer herds in the past, and when reindeer were seen in caribou herds after reindeer herding ended.

### *2.6.1 Distinguishing Characteristics of Caribou and Reindeer*

There was quite a bit of agreement among interview participants in the distinguishing characteristics they use (summarized in Table 2.1), and clear memories of how different the animals looked side by side. Kenny Toovak, Sr. recalled, "when one caribou got in with the reindeer herd, boy you can see the difference. The reindeer about yea high, and the caribou would be taller. Longer legs, you know" (Kenneth Toovak, Sr., interviewed June 27, 2008). Leg length, fatness, and fur color were the most common aspects of animal appearance that hunters and herders noticed. Samuel Nayukok said, "[I] could point the reindeer at you, no problem. They have shorter legs than the caribou. And then they're, they have a plumy ass (laughter). And some of them have stripes, you know [in their fur]" (Samuel Nayukok, interviewed August 8, 2007). Many people noted the more variable coloration of reindeer pelage, including spotted and all white furs valued for clothing. Warren Matumeak (interviewed June 5, 2010) remembered that all white calves had an overbite and weren't able to suckle properly, so most of them died, while few of

those with a normal or spotted coat color had jaw problems. Differences between caribou and reindeer in the belly, nose, ears, and antlers were also noted (Table 1).

Herders and hunters noticed many differences in behavior between caribou and reindeer (Table 1), especially in their reactions to humans and human-caused disturbances. "When they see a dog team trail, real caribou he don't even cross that dog team trail. Real sensitive....They can smell and they won't get near to where there's a kind of strange smell" (Kenneth Toovak, Sr., interviewed June 27, 2008). Caribou were described as very vigilant: "Those caribous always watching around, you know, for something. They're easy to scare" (Wesley and Anna Aiken and David Leavitt, Sr., interviewed August 7, 2007). However, hunter Roy Nageak, Sr., noticed an exception: "When there's a lot of mosquitoes they couldn't care less if you're right next to them, they just want to get away from the mosquitoes. If you don't do anything drastic like go real fast or gun up your engine, they come right up" (Roy Nageak, Sr., interviewed June 4, 2010).

Reindeer, by contrast, were remembered as being "anxious to come back to the people...they come on their own when they see people" (Alfred Shugluk, interviewed July 7, 2008). Several herders said that their sled-pulling deer would come when called (Fig. 2.4). Tommy Pikok, Sr., fondly remembered, "reindeer are just like a pet when you stay with them after two, three months. They just like a family" (Tommy Pikok, Sr., interviewed July 9, 2008). As Toovak (interviewed June 27, 2008) described, "People have a kind of connection to the reindeer.... Pretty soon you just kind of pat their back, 'Hi, reindeer.' But you can't do that in a caribou."

### *2.6.2 Persistence of Feral Reindeer and Hybridization with Caribou*

Many herders and hunters used the same characteristics to distinguish caribou and reindeer, often based on repeated, direct observation of the animals. However, when it came to understanding what happened to reindeer after they joined caribou herds, and

whether they have persisted among caribou herds or interbred with them, their perspectives were much more varied.

Observations of reindeer-like animals in the wild led most hunters and herders to believe that some reindeer or their hybrid descendants are out on the land with caribou herds today. They have varying perspectives on the prevalence of reindeer within caribou herds, and the extent to which reindeer and caribou hybridized. Perspectives also varied about where the reindeer seen within caribou herds came from, with some discussing the possibility that reindeer observed recently had dispersed towards Barrow from Seward Peninsula reindeer herds that joined caribou within the last 15 years, instead of descending from historical Barrow herds.

After reindeer were lost to caribou in the 1940s, herders did not see whole herds of reindeer again. Former herder Tommy Pikok, Sr., (interviewed July 9, 2008) said the caribou "took the whole reindeer out inland somewhere. Since then we never seen too much of them." However, several people remember seeing a few reindeer in with the caribou in the years after reindeer herding came to an end, and some shared Pikok's view that "right now the reindeer are out there living with the caribou out there somewhere." Rausch wrote in 1951:

> The admixture of inferior reindeer bloodlines with the native caribou is serious. This has already occurred to a considerable degree, and it is hoped that proper control will be exercised if the reindeer industry is revived in Alaska. Ear-notched animals have been killed in the Anaktuvuk Pass country, and white reindeer have been seen running with the caribou. The number of unrecognized reindeer passing through could be great. (Rausch 1951:190)

Wesley Aiken (interviewed July 9, 2008) recalled, "some reported them, alright, to see [reindeer] way out here in the winter, but in the summer they don't show up." It seems possible that after joining caribou, some reindeer persisted far inland from where they were lost near the coasts.

In more recent years, many herders and hunters have seen or heard from others about reindeer in the wild. These include observations near Barrow, inland along the Meade, Chipp, and Ikpikpuk Rivers, to the east near Teshekpuk Lake, to the west towards Wainwright and Point Lay, and in the Brooks Range. A few hunters described seeing reindeer with caribou in the 1980s, long after herding ended in Barrow but before the major recent losses from the Seward Peninsula. Thomas Brower Sr. said in 1982, "I still up to this date see mother reindeer with mark bringing their young ones back to where the ranch is [at Alaktak] (Thomas Brower, Sr. 1982). In just the last five years, many people have seen reindeer in caribou herds near Barrow. Several people who had seen few reindeer themselves described hearing stories of reindeer from others, and it was clear that people were exchanging information, especially with family members but also between villages, about the animals they saw and hunted.

Though reindeer are seen near Barrow, it is unknown where they come from. Many people knew of hunters catching earmarked animals, likely from the Seward Peninsula, though a few people said they hunted very old animals from the historical Barrow reindeer herd, recognizable by their earmarks[viii]. George Edwardson (interviewed August 6, 2007) described flying over a group of feral reindeer from the Seward Peninsula in the mountains, but believed the reindeer seen in other regions originated from different historical herds: "when you catch reindeer near Peard Bay, that's part of Wainwright's herd. When you go over here to Admiralty, that's part of the Brower herd. The reindeer Nuiqsut gets, that's part of Takpak's herd over there". Some shared the view that the reindeer seen recently were descendants of the lost Barrow herds, while others thought the reindeer they saw in recent years had travelled from the Nome or Kotzebue area. Whitlam Adams (interviewed July 3, 2008) noted, "Just last year they got quite a few of these I think from Kotzebue area, those caribou, kind of small, short leg. They came from Kotzebue area, the reindeer with the caribou so people were catching reindeer last summer." While in the past people tried to eliminate caribou that came into the reindeer herds, now when they see a reindeer-like animal in a caribou herd it is a choice target. Several hunters expressed a preference for reindeer-like animals—as George

Edwardson (interviewed August 6, 2007) explained, "When we see them, that's the ones we'll go after because they're fat".

Though many people saw reindeer within caribou herds, there was little consensus on whether people were observing hybrids and whether interbreeding had influenced today's caribou herds. Some simply said they were uncertain about hybridization between caribou and reindeer, while others were more certain and explained their reasoning on the basis of their experience with the animals. Observations of unusual appearance and of odd behavior were used to identify hybrids. Kenny Toovak, Sr., explained:

> We fool you: 'Oh, I shot caribou yesterday about ten miles away.' I would be foolish to tell you they were caribou, you know, because they already got mixed up with reindeer....Because you can tell, like I was saying before, the caribou are real sensitive. They can smell and they won't get near to where there's a kind of strange smell. So today, when the wind is blowing and the herd are right there, when the snow machine come by, it make a lot of smell but that smell won't even disturb the animals that were there....[They are] half breed caribou and half breed reindeer, so I believe that. Fifty-fifty. Just like white people and native people got married together. Kind of half-breed. Same thing. So that's how I could explain the behavior of the animals today (Kenneth Toovak, Sr., interviewed June 27, 2008).

Whereas Toovak noticed broad changes in caribou over time, several hunters recalled seeing what Whitlam Adams (interviewed July 3, 2008) described as "strange looking caribou." Hunter Roy Nageak, Sr. listed several characteristics he has noticed in identifying animals as hybrids: "You could tell when they're mixed, mixed caribou-reindeer, by their legs. They're more stubby, lower to the ground. And their horns are a little bit out of place. Kind of weird horns....[The body is] not as dark as true caribou. And stubby. When you drop a caribou and their legs are stubby, 'alright'!, they're part reindeer. A juicier taste to it" (Roy Nageak, Sr., interviewed June 4, 2010).

*2.6.3 Cultural Implications of a Heritage with Reindeer and Caribou*

The observations shared by interview participants demonstrate the detail with which hunters and herders notice variability within animals and the value of assessing changes and unusual observations in the context of lifetimes of experience. Reindeer herding was a formative experience in the lives of many elders I interviewed. They remember their reindeer days as teenagers for both the hard physical labor, often without enough food or enough sleep, and the fun they had driving reindeer sleds, watching fawns play, and living out on the land. Time spent living on the land as herders gave them valuable skills and shaped aspects of their identity. Arnold Brower, Sr., remembered learning from his brother and from "old timers" while out with the reindeer: "I learned from them and I followed them around because it was interesting" (Arnold Brower, Sr., interviewed July 2, 2008). Later in life, herders shared stories about reindeer with family members and others.

Some of the hunters I interviewed remember being out on the land with former herders in their families and hearing stories about the reindeer. On the Seward Peninsula, the "generational and educational link between parents and grandparents who know herding and children who grow up in a herding environment" (Schneider, Kielland, and Finstad 2005) was important in re-establishing reindeer herding after a break in their families' involvement with reindeer. In Barrow, reindeer herds were never re-established, but elder reindeer herders' stories influence how younger generations today, who have never herded reindeer, understand the wild animals they observe.

Barrow's history with reindeer and caribou has influenced the ways in which people talk about the animals today, likely reflecting both changed biological conditions as a result of hybridization[ix] and changed understanding of the animals among people whose cultural heritage includes both herding and hunting. At times, hunters may see real hybrids and identify them as such, but they may also see real caribou and talk about them with reindeer in mind. Hunters without personal experience in reindeer herding use many of the same criteria as herders to differentiate between caribou and reindeer. Their ability to identify reindeer-like animals within caribou herds suggests the role of elder herders in

passing on observational skills and hunting expertise to younger generations. However, a heritage with reindeer may also influence how people understand natural variability among caribou by providing a comparison against which to describe how typical caribou look and behave. Very fat caribou, unusually colored caribou, or caribou acting in ways herders remember their reindeer acting, may be considered hybrids because hunters assess the animals with knowledge of both reindeer and caribou in mind. Though hunters clearly see reindeer-like animals within herds, we do not know with certainty that all the animals they see have reindeer ancestry. This does not make the observations any less valuable—they are useful to hunters in selecting animals to harvest and a valuable source of local knowledge about caribou and reindeer.

When reflecting on the loss of the reindeer and hybridization with caribou, some interview participants seemed to relate changes in the animals to social changes in their community. Describing hybrid animals often led interview participants to talk about multi-racial humans. Several people used metaphors, such as children of "tall African warriors and Pygmies," different species of eider ducks, or Iñupiat and white parents, to illustrate caribou-reindeer interbreeding. Herder Kenny Toovak joked with Ben Nageak, who joined the interview, "It's like, Ben married to a white lady." Both laughing, Toovak (interviewed August 3, 2007) explained: "In the family, you know for hunting, I use that for the people to understand what I mean. So, I think we call those caribou kind of mixed with the reindeer." Just as human metaphors were useful for explaining hybridization, some elders discussed the loss of the reindeer in the context of social change, identity, and control. Kenny Toovak, Sr. talked about what the loss of the reindeer herds means today:

> They have some herders to take care of those herds, keep them, trying to keep them in a group. But in that time of month, when the weather gets warm, kind of hard to control, so they come by, caribou come by, and then they disappear again. So that's where we end up. No caribou and no reindeer that we could claim today, you know. Wainwright even won't claim "Oh, that's my herd." No voice to claim when the herd come by. We call them caribou. Barrow people have no voice

> "Oh, that's my herd." We don't have no voice, that's why we just call them caribou. (Kenneth Toovak, Sr., interviewed June 27, 2008)

I am not sure I understand all of what Kenny is saying, but one interpretation is that village herds in the past were important representatives of community identity, and with the loss of the herds, Barrow simply has reindeer-like caribou. Alternatively, he may be explaining that the people of each community could recognize individual herds in the past, whereas today they can't be distinguished. Or, perhaps he is saying that in today's era, local people can no longer claim rights to the animals. Regardless, Kenny's statement is important because it demonstrates a link between village reindeer herds and the local investment that people have in the animals.

**2.7 Discussion**

Barrow reindeer herders shared memories of mixing between domestic reindeer and wild caribou and described the major role of caribou in reindeer herd declines in the 1940s. The reindeer that were ultimately lost to caribou were not recovered, and hunter and herder observations suggest that some feral reindeer and hybrids have existed in caribou herds ever since. These stories from herders revise our understanding of the decline in the Barrow reindeer industry by clarifying the ways in which caribou impacted reindeer herds, perspectives that are not described yet in the written history. In light of recent reindeer losses on the Seward Peninsula, where herders with motorized transport and other modern technologies were unable to prevent reindeer from joining caribou (Schneider, Kielland, and Finstad 2005), the challenges faced by Barrow herders attempting to recover lost reindeer on foot seem even more striking. While past research on the Barrow reindeer industry assumed caribou could be completely controlled by adequate herding labor (Lantis 1952; Sonnenfeld 1959), the experiences of former herders suggest that the reindeer industry may not have been able to persist through the influx of caribou even if economic incentives for recovering and sustaining herds had been more favorable.

Native herders no doubt informed reindeer administrators, as Unit Manager A.D. Johnson acknowledged: "Much valuable information has been and still is coming from the men who herd the deer, and who have spent their life living with the reindeer" (Johnson 1942). However, the words of the herders themselves are rarely found in historical documents, so their experience working with the reindeer may not have been fully represented. Unit Manager Jens Forshaug wrote candidly: "The Natives here have been misjudged at the office because of the type of men the Service is unfortunately burdened with...and who know how to write reports favorable to themselves. Facts can be used that distort the picture as a whole. Since coming I have found most of the theories prevailing in regard to local deer situation to be untrue (Forshaug 1940b). Forshaug suggests what this study demonstrates, that history as written by government administrators does not fully reflect the history that local people might tell.

This case illustrates the importance of oral histories told by local people in understanding the region's past. In doing so, it also provides a unique opportunity to understand the biological and cultural legacies that remain 60 years after reindeer herding came to an end. Researchers today increasingly acknowledge the value of local knowledge for understanding long-term environmental change (Berkes 1999; Cruikshank 1998; Huntington 2000; Krupnik and Jolly [eds.] 2002). In Alaska's North Slope, as for much of the Arctic, caribou herds began to be counted and monitored regularly only within the last 40 years. In contrast, Iñupiat have been observing, managing, and passing on knowledge about their local environments for many generations. Herders and hunters I interviewed offered new insight into the biology of both reindeer and caribou by describing their interactions, providing a consistent set of characteristics for identifying them, and documenting that reindeer and hybrids are seen in caribou herds today. By listening to people's stories and carefully reading historical documents, we better understand long-term changes in caribou populations and animal behavior.

Local knowledge of caribou and reindeer also reveals the cultural legacy left by reindeer herding, despite the fact that most herders have now passed away. Barrow's reindeer herding heritage and caribou hunting tradition both contribute to the pool of

cultural knowledge, which influences how people identify and selectively hunt reindeer-like animals in caribou herds today. Hunting and herding have been framed in the past as culturally incompatible, which is apparent in the assumption that reindeer could (or should) transform Alaska Natives into agriculturally-minded pastoralists (Harris 1890; Rood 1939, 1945; Townsend 1885), and that when efforts failed it was because the hunting worldviews intrinsic to coastal native cultures made them unable or unwilling to succeed at reindeer herding (Arnold and Cooley 1941; Burdick 1940; Lantis 1950, 1952; Sonnenfeld 1959). General Reindeer Supervisor, Sidney Rood, expressed his frustration with this perceived incompatibility in a letter to the Farthest North Reindeer Company in 1939: "You never tried to tame the caribou, to herd them...all you thought of was killing them. Today your people are treating their reindeer herd like caribou. If you keep on this way, you will have no herd" (Rood 1939). However, herders I interviewed were clearly able to manage the duality of pursuing animals while hunting and protecting them while herding. Kenny Toovak, Sr., (interviewed June 27, 2008) explained that people preferred to kill caribou rather than reindeer back in the reindeer herding days, because they had a relationship with the reindeer.

This study shows that hunting and herding practices were not entirely incompatible, and that reindeer herding was incorporated in conceptions of traditional Iñupiat culture. Lantis (1952:132) noted that hunters gain prestige by demonstrating skill and generosity, and questions what herding could offer them given that it is not as "spectacular." However, the stories shared by Barrow herders suggest that they demonstrated both skills and generosity as reindeer herders. The furs and meat that herders provided to the community were very important when caribou were far away and difficult to access. Several herders and hunters also recalled the story of herders Charlie and Eddie Edwardsen, and Arnold Brower, Sr., making visits to help an elderly couple in need while out on the land with their reindeer (see also Arnold Brower, Sr. 1982). These stories suggest that Barrow people enacted the Iñupiat values of sharing and subsistence skill whether hunting or herding.

Knowledge gained through reindeer herding seems to have persisted in Barrow because herding shaped the identity of future leaders—elders who perpetuated the oral tradition and taught hunting practices to younger generations. Recent research with herders on the Seward Peninsula describes how identity as a herder is retained after losing reindeer to caribou herds: "The heritage of herding through lean and plentiful times indicates that herding is an important resource, skill, and perceived possibility whether the herder has reindeer or not at any particular time. It is part of an identity, reinforced through the generational link with parents, and in some cases, grandparents, who were herders in good and bad times" (Schneider, Kielland, and Finstad 2005:47). After herding ended, many former reindeer herders in Barrow became known as experts within the community for their knowledge about animals. Arnold Brower, Sr., who was appointed a "Traditional Expert" by the Secretary of the Interior and known by many for his leadership as a whaling captain, continued to identify with reindeer herders throughout his life. He described a conversation with visiting Saami reindeer herders at a recent meeting: "So they come over here and knew right away that I was a reindeer herder. They know that, I mean, the big bosses of that tribe....We exchanged a lot of our habits and surviving with the reindeer: how we process the herd, the meat, the hide, and everything". He described how other Barrow elders with herding backgrounds began to listen to the conversation and eventually join in, and concluded the story saying, "You see how human beings would identify themselves" (Arnold Brower, Sr., interviewed July 2, 2008).

Herders valued the relationships they had with their reindeer. Their extensive experience with animals, including both caribou and reindeer, teaches us how the rise and fall of the reindeer industry and long-term fluctuations in caribou populations have influenced the animals today. As Arnold Brower, Sr., reflected, "You know, I grew up there (Fig. 2.5) and the animals knew me, I think. All of them knew me. Maybe they have a history and they can tell stories like we do. That's the way I look at it" (Arnold Brower, Sr., interviewed July 2, 2008). Animal histories interact with human histories and

understanding both is important. Certainly Tiger Burch believed, as do I, that those histories are worth telling.

## 2.8 Acknowledgments

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Time in the field with hunters and herders helped the author to grasp the complexity and tangible experience of the stories shared by participants. A boat trip to the historical reindeer corral at Alaktuk with Tom Brower III, helping to corral reindeer on the Seward Peninsula with the Ongtowasruk family from Wales, and conversations with Greg Finstad (UAF Reindeer Research Program) deepened my understanding of reindeer herding in practice. Fannie Akpik and Jana Harcharek invited me to join the 2008 Iñupiat Culture Camp, which was transformative in understanding how hunting, language, and sharing are integrated in a deep gratitude towards the animals and respect for their intelligence.

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## 2.9 Endnotes

[i] Reindeer may be more susceptible to predation than caribou because they have shorter legs and less migratory ability. Male reindeer may also be at a competitive disadvantage in mating, and reindeer calves may have lower survivorship because they are born earlier in spring than caribou.

[ii] The "wild" refers to conditions no longer under herder control, but it is a complex term in this case. It can be used to refer to reindeer that are on their range but not well protected, reindeer that have strayed off range but are not with caribou, or reindeer that have joined caribou herds and travelled with them on their migrations. The degree to which the "wild" differs from human control depends on the style of herding (how herders monitor, move, and handle their deer) and conditions in the environment (such as predators, parasites, forage, and weather). Domestics in the "wild" are sometimes referred to as "feral". Herders on the Seward Peninsula refer to reindeer that are uncontrolled and unmarked as "mavericks".

[iii] However, hunter and herder observations are reported in some scientific papers (Finstad, Bader, and Pritchard 2002; Jepsen et al. 2002; Rausch 1951).

[iv] Not all Barrow elders once herded reindeer. Youth living in population centers on the coast attended schools and learned to hunt from the sea, while others lived in relative isolation inland as trappers or herders for much of the year (Burch 1975:31). Barrow

people experienced a tension between life in coastal whaling communities with schools, versus herding and trapping livelihoods in remote inland areas, and adapted in a variety of ways to changing economic, environmental, and social conditions—an important part of the socio-economic history that is beyond the scope of this paper.

[v] Most of the herders I interviewed worked with reindeer as teenagers. By the 1940s, wage work in Barrow was a more lucrative option for married herders with families in town. One herder, Wesley Aiken, recalled learning to herd reindeer from a man who wanted to quit herding work so he could marry Wesley's sister. Many herders remember reindeer work with a mixture of fondness, for the animals and time on the land with friends, and wonder at their ability to do such challenging work and suffer extreme hardships in isolated living conditions. The experience of herders during Barrow's rapid socio-economic change in the 1940s is a fascinating story, but it is beyond the scope of this paper.

[vi] See Sonnenfeld (1959) for a figure summarizing the growth and decline of the Barrow herds.

[vii] Note that the Reindeer Act of 1937 made it illegal for non-natives to own reindeer. Thus, the non-natives surveyed in 1948 were probably administrators who spent less time with the deer.

[viii] Reindeer and caribou are not known to live so long (30 or 40 years old, as these hunters imply). It could be that some reindeer lost from the Seward Peninsula have earmarks that look like Barrow earmarks.

[ix] The author used genetic analysis to determine whether animals with hybrid reindeer-caribou ancestry are found within caribou herds today (see Chapter 3).

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**Table 2.1. Characteristics mentioned by interview participants for distinguishing wild caribou (CB) from domestic reindeer (RD).**

| Physical Characteristics | Behavioral Characteristics |
|---|---|
| RD legs are shorter than CB | CB more scared of people than RD |
| RD are fatter, especially in the hindquarter | CB are really sensitive to roads, pipelines |
| RD sometimes have spotted or white fur; CB never do | CB run off just from the smell of people; RD and CB both investigate by smelling |
| CB have a white neck/belly; RD are black | CB know the sound of snow machines |
| CB have a more tapered nose than RD | CB are always looking around, RD aren't |
| RD antlers are longer and more curved, "almost sideways" v. "almost straight up" in CB | RD sometimes come to people or come when called; they recognize people they know |
| CB have longer ears than RD | RD stop and look back after running away |
| RD have earmarks | Winter feeding areas differ: CB eat from areas with less snow, RD dig deeper craters |


**Figure 2.1. View of reindeer herd at edge of water with village of Barrow, Alaska in background.** Time period 1896 to 1913. AMRC-b65-18-574. Fred Henton Collection, Anchorage Museum at Rasmuson Center, Anchorage, Alaska.

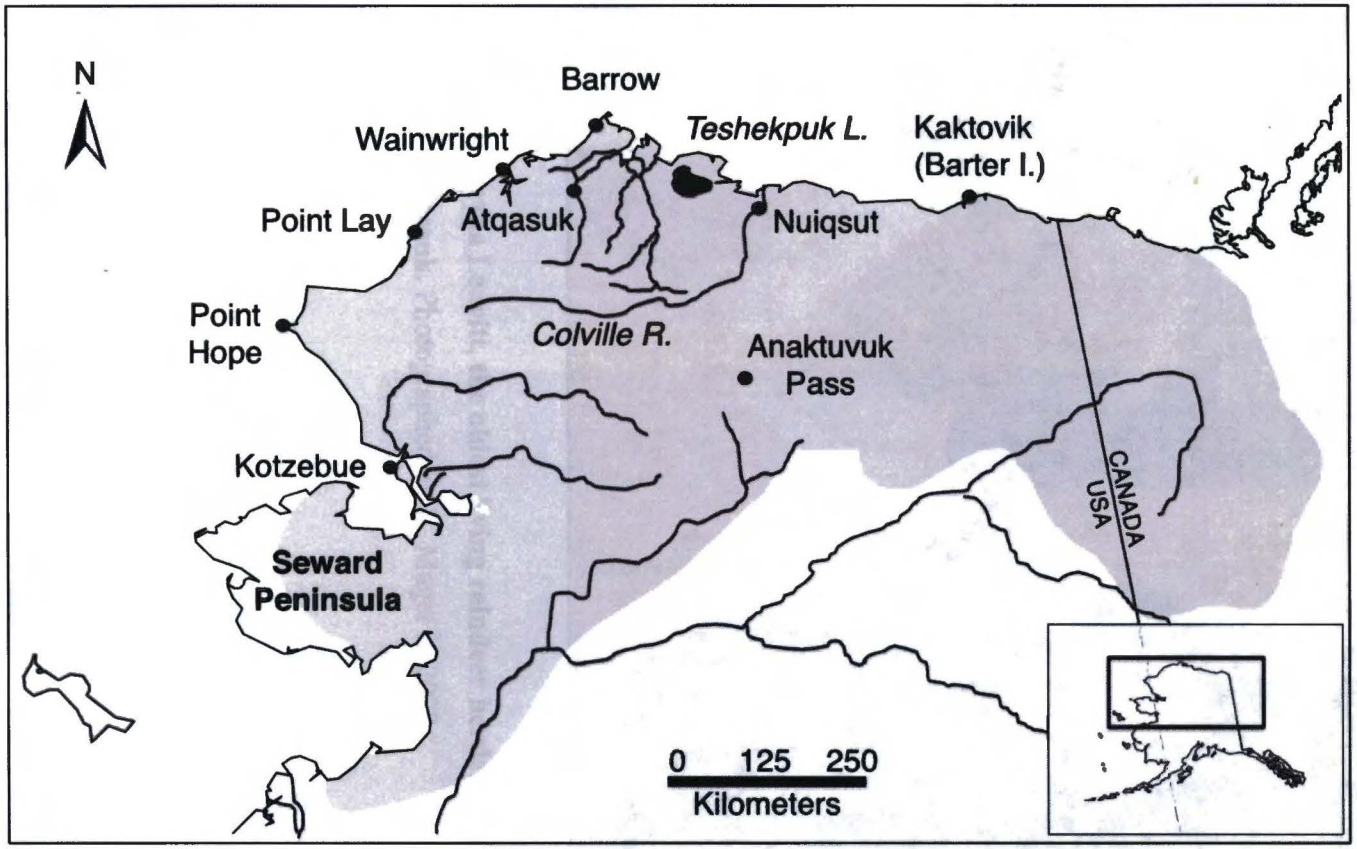


**Figure 2.2. Map of northern Alaska, including communities and landscape features referenced in the chapter.** Shading indicates the overall area used by North Slope caribou today. Reindeer herders interviewed for this paper had most experience on the land between Barrow, Atqasuk, and Nuiqsut, referred to in the paper as "Barrow area".

**Figure 2.3. Bertha Leavitt, the oldest living reindeer herder I interviewed, with Margaret Ahngasuk.** Photographed by K. Mager in 2008.

**Figure 2.4. Boys with harnessed sled deer.** Photo 94-02-024. Kramer Collection, 1922-1924. Iñupiat History, Language, and Culture Commission, Barrow, Alaska. Used with Permission.

**Figure 2.5. Remains of the Brower corral at Alaktuk.** Photographed by K. Mager in 2007, more than 50 years after reindeer herding came to an end. The corral was apparently taken apart in 1975 after caribou became trapped in it, but parts of it still stand.

## Appendix 2A

**Table 2A-1. Interview participants and details.** All interviews were conducted in Barrow, Alaska. People are listed as herders if they remember working, helping, or living with a reindeer herd. Interview recordings available to the public are archived with the Iñupiat History Language and Culture Commission (IHLC) in Barrow, Alaska.

| Name | Birth Year | Herder | Interview Date | Interviewer |
|---|---|---|---|---|
| Whitlam Adams | 1926 | Y | 7/3/2008 | KHM, MA |
| Jonas M. Ahsoak, Sr. | unknown | N | 6/9/2010 | KHM |
| Wesley Aiken and<br>Anna Aiken | 1926<br>1926 | Y | 8/7/2007,<br>7/9/2008 | KHM, MA |
| Arnold Brower, Sr. | 1922 | Y | 7/2/2008 | KHM, MA |
| Thomas C. Brower, III | unknown | F | 8/12/2007<br>6/9/2010 | KHM |
| Robert Edwardsen, Sr. | 1951 | F | 8/10/2007 | KHM |
| George Edwardson | 1947 | F | 8/6/2007 | KHM |
| Bertha Leavitt | 1912 | Y | 7/8/2008 | KHM, MA |
| David Leavitt, Sr. | 1929 | Y | 8/7/2007 | KHM |
| Warren Ovluaq Matumeak | 1927 | Y | 6/5/2010 | KHM |
| Ben Nageak | 1950 | F | 8/3/2007 | KHM |
| Roy M. Nageak, Sr. | 1951 | F | 6/4/2010 | KHM |
| Samuel Nayukok | 1930 | Y | 8/8/2007<br>7/7/2008 | KHM, RE, MA |
| Tommy Pikok, Sr. | 1930 | Y | 7/9/2008 | KHM |
| Alfred Shugluk | 1929 | Y | 7/7/2008 | KHM, MA |
| Dr. Kenneth Toovak, Sr. | 1923 | Y | 8/3/2007<br>6/27/2008 | KHM, BN |
| Brad Weyiouanna | 1979/80? | F | 6/8/2010 | KHM |
| Confidential A | 1931 | F | 7/10/2008 | KHM, MA |
| Confidential B | 1945 | F | 6/7/2010 | KHM |
| Confidential C | unknown | N | 6/10/2010 | KHM |
| Confidential D | 1920s | Y | 7/2/2008 | KHM, MA |
| Confidential E | unknown | N | 7/20/2008 | KHM |

Abbreviations: Y = yes, N = no, F = in the family, KHM = Karen H. Mager, MA = Margaret Ahngasuk, BN = Ben Nageak, RE = Robert Edwardsen, Sr.

# Chapter 3 Genetic Connectivity Between Caribou Herds and Hybridization with Domestic Reindeer in Northern Alaska[2]

## 3.1 Abstract

Defining genetic populations and detecting hybridization with introduced or domestic taxa are two major concerns for the conservation of population-level diversity. We studied the genetic population structure of the large, migratory caribou herds (*R. t. granti*) of Alaska's North Slope and examined the effects of contact with introduced domestic reindeer (*Rangifer tarandus tarandus*). We used a population genetics approach to determine: 1) whether the four caribou herds could be differentiated; 2) what factors appear to drive genetic population structure; and 3) how contact with domestic reindeer has affected the genetic identity of herds. Samples from caribou and reindeer ($n = 312$) were analyzed at 19 polymorphic microsatellite loci. We found that North Slope caribou are primarily isolated by distance, with no differentiation among herd pairs except for the most geographically distant herds. Overall, reindeer introgression has not broadly altered the genetic composition of caribou herds. However, we detected several recently admixed individuals within each of the herds. Our findings suggest that large caribou herds encounter few barriers to gene flow when their ranges overlap, while gene flow from reindeer is substantial but likely limited by natural and hunter selection.

## 3.2 Introduction

Empirical knowledge of population units benefits wildlife conservation and management. Understanding the impacts of history, landscape, and human activities on genetic diversity, population structure, and the integrity of local adaptations can aid conservation planning and active game management. Research efforts are often focused on small or fragmented populations of immediate conservation concern. However, maintenance of biodiversity over the long term depends on conservation of natural

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evolutionary processes (Mace and Purvis 2008), which are important to understand in large, intact populations as well.

*Rangifer tarandus* (North American caribou and Eurasian reindeer) is a widespread and highly mobile circumpolar species of deer found in boreal forest, arctic tundra, and high arctic islands. Two subspecies of *R. tarandus* are found in northern Alaska: Alaskan caribou (*R.t. granti*) and domestic reindeer (*R. t. tarandus*). Migratory caribou herds in Alaska's North Slope region—an estimated 650,000 animals as of 2010 (Alaska Department of Fish and Game 2011a, 2011b; Lenart 2009; Parrett 2009)—utilize a vast area of contiguous habitat during long-distance annual migrations to different seasonal ranges (Fig. 3.1; Table 3.1). Potential threats to the diversity and genetic identity of North Slope caribou have included historical fluctuations in herd size, contact with introduced domestic reindeer, and increasingly, potential habitat alteration due to industrial development and climate change (National Research Council 2003). Examining the effect of those threats on large, intact caribou populations may improve our understanding of the natural processes that either maintain or constrain diversity, gene flow, and local adaptations in healthy populations.

There are currently four herds of caribou on Alaska's North Slope——the Western Arctic Herd (WAH), Teshekpuk Herd (TCH), Central Arctic Herd (CAH), and Porcupine Herd (PCH). Alaskan caribou herds are defined by the strong fidelity of pregnant females to specific calving ranges (Skoog 1968), and herds constitute management units. However, the extent to which the herd concept approximates the genetic population structure is unresolved. Previous studies found no distinction among herds but were limited by small sample sizes, potentially non-neutral markers, and markers of low variability (Cronin et al. 2003; Cronin et al. 2005). The degree of genetic differentiation among herds, and the relationship between the herd concept and overall genetic population structure, are still unclear.

Fluctuations in population size can affect genetic diversity (Frankham 1996) and indirectly affect genetic connectivity (exchange of breeding individuals) by altering caribou seasonal ranges and distribution (Hinkes et al. 2005). Historically, North Slope

herds have fluctuated widely in size, range, and distribution (Burch 1972; Caikoski 2009; Dau 2009; Joly et al. 2011; Lenart 2009; Parrett 2009; Skoog 1968). Caribou in Northwestern Alaska decreased dramatically in the late 1800s, and began to recover by the 1920s (Burch 1972; Mager, submitted). The TCH and CAH herds were first described in the 1970s (Davis and Valkenburg 1978) when they were very small (estimated at 3,000 and 5,000, respectively), and scant evidence suggests they may have existed for at least 100 years prior (Burch, in press). All four North Slope herds have increased substantially since monitoring began in earnest in the late 1970s (Caikoski 2009; Dau 2009; Lenart 2009; Parrett 2009). The effect of those population fluctuations on the genetic diversity of North Slope caribou is unknown. Previous studies (Cronin et al. 2003, 2005) found lower allelic diversity and heterozygosity in North Slope caribou than that reported for studies of large, migratory herds in Northwestern Canada (Zittlau 2004) and Labrador (Boulet et al. 2007), though this may be due to differences in sample size and marker selection between studies.

Historically, changes in caribou herd size have corresponded with changes in total range area, and sometimes, with shifts in distribution (Ferguson et al. 2001; Hinkes et al. 2005). At current sizes, some North Slope herd ranges occasionally overlap, including during fall migration (Lenart 2009; Parrett 2009; Person et al. 2007) when breeding occurs (Lent 1965). Apparent dispersal of TCH caribou to neighboring calving areas has also been observed (Parrett 2009) at an apparent emigration rate of 6.9% (Person et al. 2007), though the birth locations (and thus herd identity) of the emigrants were unknown. There are few obvious barriers to gene flow among North Slope herds today, though the genetic connectivity of smaller, historical herds may have been more limited. Elucidating the spatial patterns of genetic variation in North Slope caribou could aid in understanding the effect of range shifts on genetic population structure.

Potential hybridization with introduced domestic reindeer may also influence the genetic identity of North Slope caribou herds. Globally, hybridization between native populations and introduced, formerly isolated, taxa is considered a major threat to biodiversity (Randi 2008; Simberloff 1996). Introgression from domestic animals has the

potential to degrade the local adaptations of wild populations (Randi 2008). Studies have detected hybridization between wild and domestic carnivores (Oliveira et al. 2008; Randi and Lucchini 2002) and between introduced reindeer and a native caribou herd near Nuuk, Greenland, where local hunters observed reindeer-like animals among caribou (Jepsen et al. 2002).

Reindeer were introduced to northern Alaska from Russia in the 1890s and multiplied to over 100,000 on the North Slope in the 1930s (Stern et al. 1980) before declining and ultimately disappearing by 1950 (Lantis 1950; Stern et al. 1980). Herders remember reindeer joining caribou herds as a primary reason for losing their domestic stocks in the 1940s (Mager, submitted; Rausch 1951), and recent contact between the WAH and reindeer on Alaska's Seward Peninsula in the past 15 years has resulted in further losses (Dau 2000; Finstad et al. 2002; Schneider et al. 2005). Feral reindeer survival and hybridization with caribou is expected to be limited due to differences in reproductive timing, behavior, and size (Finstad et al. 2002; Klein 1980). Genetic evidence of reindeer mtDNA haplotypes in 2.6% of North Slope caribou (Cronin et al. 2006) and differences in transferrin allele frequencies (Røed and Whitten 1986) suggest that reindeer alleles are not widespread within North Slope herds as a whole. However, local observations of reindeer-like animals within caribou herds (Mager, submitted; Rausch 1951) suggest that extensive historical contact may have permitted reindeer-caribou hybridization. Susceptibility to reindeer introgression may vary among herds based on differences in historical herd size and migration patterns. Those may affect the amount of interbreeding and the strength of selective pressures against non-native and hybrid traits in subsequent generations (Randi 2008).

In this study, we use population genetics to understand the effect of historical interactions and spatial distribution on the genetic identity and structure of caribou herds. Specifically, we seek to answer the following questions: 1) Are the four caribou herds genetically differentiated? 2) To what extent does the overall genetic population structure of North Slope caribou match the four-herd concept, and how does landscape affect population structure? and 3) Has recent and historical contact with domestic

reindeer led to full-blooded migrants, hybrids, or long-term introgression within wild caribou herds?

## 3.3 Materials and Methods

### *3.3.1 Genetic Sampling*

Fine-scale resolution of population structure requires a study design that provides adequate power to detect genetic differences among sub-populations, which depends upon both a large sample size and a large number of variable genetic markers (Ryman et al. 2006). To obtain adequate sample sizes, we used a minimum of 50 blood samples from each herd (Table 3.1). Whole blood from caribou was collected by biologists from the Alaska Department of Fish and Game (ADF&G), the North Slope Borough (NSB), the U.S. Fish and Wildlife Service (USFWS), and the Government of Yukon, Canada during handling and monitoring activities for each herd from 2008-2010. Archived blood from previous research with the CAH and PCH herds was also used to achieve desired sample sizes (Appendix 3A).

We collected blood and tissue samples from Seward Peninsula reindeer near the communities of Wales and Nome during summer corral handlings by the Ongtowasruk and Davis herd owners, respectively (Table 3.1). Because these reindeer come from the southwestern Seward Peninsula, close to the site of the original reindeer introduction and farther than other reindeer from the Western Arctic caribou herd, they are a reasonable proxy for historical North Slope reindeer herds. Samples were also collected by ADF&G from feral reindeer on Kodiak Island, a population founded by 54 reindeer brought to the island from the Alaska Peninsula in 1921 (U.S. Dept. of the Interior 1921). We also received tissue samples from a hunter who selectively hunts feral reindeer within the WAH when they are in the northeastern Seward Peninsula (Table 3.1).

Whole blood was collected in evacuated tubes with EDTA as a preservative and to prevent clotting. Blood and tissue samples were frozen at -80 °C. We extracted DNA using the DNeasy Blood & Tissue Kit (QIAGEN Inc.,Valencia, CA). Extracts were frozen at -20 °C.

*3.3.2 Geo-Spatial Data*

A landscape genetic analysis of a migratory species requires that location data be compared between individuals or populations in the same season. Blood samples were collected, however, during monitoring and handling activities in a variety of seasons (Appendix 3.A). Thus, we used blood samples from satellite- and radio-collared caribou when possible, and then obtained relocation data in calving and rutting seasons for each of those collared individuals. Specifically, we attempted to obtain one rutting season location and one calving season location for each individual in each year. For each individual/year, we used the closest available location to the approximate mid-date of rut (October 22) and one location during the peak of calving (first week of June; L. Parrett, personal communication). We also obtained the pregnancy status of each female located during calving, when available, because pregnant females show greatest fidelity to calving areas. For population-based landscape analysis we used seasonal ranges from ADF&G, which delimited total and summer range for all herds (T. Paragi, personal communication).

*3.3.3 Marker Selection and Genotyping*

To ensure we had an adequate number of variable markers to detect fine-scale differentiation, we amplified DNA at 19 polymorphic microsatellite loci, which were combined into three multiplexes: Multiplex 1 – RT6, RT27 and RT1 (Wilson et al. 1997), OheD and OheQ (Jones et al. 2000), NVHRT30 (Røed and Midthjell 1998), BM6506 and BM4513 (Bishop et al. 1994), and OARFCB193 (Buchanan and Crawford 1993); Multiplex 2 – RT9, RT7, and RT24 (Wilson et al. 1997); Multiplex 3 – RT10 and RT30 (Wilson et al. 1997), BL42 (Bishop et al. 1994), BMS745 (Stone et al. 1995), TEXAN4 (Holder et al. 1994), C89 (Jones et al. 2000), and BMS1788 (Stone et al. 1995). Markers were chosen for their ability to multiplex (D. Paetkau, personal communication) and their use in other studies.

We performed PCR amplifications in 10 μl reactions containing 5μl Qiagen Multiplex Master Mix®, 2.5 μl sterile water, 1 μl of the multiplex primer mix and 1μl

DNA template. Reactions were carried out in an MBS Satellite 0.2G thermal cycler: 30 cycles - 1 minute each at 94°C, 55°C, and 72°C. DNA fragment analysis was performed using an ABI 3730*xl* sequencer (Applied Biosystems, Inc., Carlsbad, CA) or using an ABI 3100 sequencer (Applied Biosystems). Data from the 3100 were calibrated to match the 3730.

Alleles were scored using Genemapper version 3.7 (Applied Biosystems). We checked for genotyping errors using Micro-Checker (Van Oosterhout et al. 2004) and found no evidence of null alleles or allelic dropout at any of our 19 loci. We found no evidence of linkage disequilibrium between all pairs of loci using FSTAT ver. 2.9.3 (Goudet 1995). We used a Hardy-Weinberg exact test in Genepop ver. 4.0.6 (Raymond and Rousset 1995, Rousset 2008) for each locus in each population. Markers out of Hardy-Weinberg equilibrium (HWE) were eliminated from population differentiation analyses that assume HWE.

*3.3.4 Statistical Analysis - Herd Differentiation and Diversity*

To quantify diversity, we calculated allelic richness and heterozygosity overall and for each herd using FSTAT ver. 2.9.3 (Goudet 1995). Allelic richness was standardized to a minimum sample size of 50 individuals using rarefaction. To determine whether the four caribou herds can be genetically differentiated from one another, we calculated two estimates of population differentiation. We calculated pairwise $F_{ST}$ with FSTAT ver. 2.9.3 (Goudet 1995) and pairwise Jost's $D$ with the DEMEtics package ver. 0.8-2 in R (Jueterbock et al. 2010). Recent studies have demonstrated the limitations of $F_{ST}$ for estimating true genetic differentiation among populations with high within-population heterozygosity (Jost 2008, Meirmans and Hedrick 2011), as in Alaskan caribou. Therefore, Jost's $D$ (Jost 2008) is more suitable for our study. We report $F_{ST}$ as well to allow direct comparison with past studies.

*3.3.5 Analysis of Genetic Population Structure*

To describe the overall genetic population structure of North Slope caribou and the extent to which it matches the four-herd concept, we used the clustering algorithm STRUCTURE version 2.3.3 (Pritchard et al. 2000) to determine the most likely number of population clusters within our total genetic dataset absent *a priori* population information and to assign individuals to clusters. We tested models ranging from a 1-population model to a 5-population model ($K$={1...5}). We ran 3 iterations of each model, with a burn-in of 75,000 followed by 200,000 MCMC replicates. We assumed admixture and correlated allele frequencies among populations. To determine the most likely number of clusters in our overall sample, we compared the likelihood of each model using the $\Delta K$ statistic (Evanno et al. 2005). Following the "hierarchical STRUCTURE analysis" method (described by Vähä et al. 2007) for detecting subtle genetic structure, the data were then partitioned into two groups based on the optimal $K$ and each group was run again in STRUCTURE using the same parameters

*3.3.6 Landscape Genetic Analyses*

To examine the effect of geographic distance on the genetic population structure of North Slope caribou, we performed a Mantel Test using Genodive ver. 2.0b21 (Miermans and Van Tienderen 2004) with $1x10^7$ permutations to test for significance. We used the geographic distance between the centroids of caribou herd summer ranges, calculated with GenAlEx ver. 6.4 (Peakall and Smouse 2006). Nei's $D$ was used as the measure of genetic distance between herd pairs.

To examine the overall landscape genetic population structure of the North Slope caribou, we analyzed combined spatial and genetic data using the Bayesian clustering algorithm in the software TESS (Chen et al. 2007). This program creates a spatial network from the geographical locations of genetic samples, assuming no *a priori* population membership, and then clusters individuals based on both genetic and geographic information. We analyzed three separate datasets: all individuals with rut locations, all individuals with calving locations, and pregnant females with calving

locations. The most recent location for each individual was used, and for females with known pregnancy status we used the most recent calving location in a year they were known to be parturient. We performed our TESS analyses using the CAR model, which assumes admixture. For each population model ($K$={2...4}), we performed 100 runs, each with a burn-in of 20,000 followed by 30,000 iterations. We used the $\Delta DIC$-values of each run to select from all models the 10% of runs with the highest likelihood.

*3.3.7 Hybridization and Reindeer Introgression Analysis*

To determine whether contact with domestic reindeer resulted in introgression of reindeer genes into North Slope caribou herds, we used STRUCTURE to detect individuals with hybrid ancestry under conservative and relaxed criteria (see Bohling and Waits 2011). First, we quantified the proportion of each individual's genotype assigned to the two clusters identified by STRUCTURE without *a priori* population info (as per Bohling and Waits 2011). Individuals with greater than 95% of their genotype assigned to either the reindeer or caribou cluster were considered "pure". Individuals with less than 95% (over 5% assignment to both clusters) were considered "unknown". We ran STRUCTURE a second time, with the "Use Population Information" setting, so that "unknown" individuals (POPFLAG = 0) would be assigned to clusters defined only by the allele frequencies of the "pure" reindeer and caribou (POPFLAG = 1).

Following Bohling and Waits (2011), we tallied the number of admixed individuals under both conservative and relaxed criteria. Under the conservative criterion, an individual is considered to be of hybrid ancestry if STRUCTURE has assigned it to two clusters and the 90% credibility interval (CI) around its proportion of assignment to each cluster does not encompass zero. Under the two relaxed criteria, an individual is considered admixed if it has at least 5% or at least 10% of its genotype assigned to both clusters, even if the 90% CI encompasses zero. These relaxed criteria are arbitrary, but commonly used (Bohling andWaits 2011; Neaves et al. 2009; Randi and Lucchini 2002); due to error in assignment it is possible that some "admixed" individuals have no hybrid ancestry. However, because at least 15 generations have passed since the period of initial

contact and potential hybridization between North Slope caribou and reindeer in the 1940s (though contact continues near the Seward Peninsula), some individuals with true hybrid ancestry may have low enough assignment to both clusters that they are not considered admixed. We therefore argue that this method is conservative.

## 3.4 Results

### *3.4.1 Herd Differentiation and Diversity*

Both reindeer and caribou herds showed high levels of genetic variation. Mean allelic richness ($AR$) and heterozygosity ($H_e$) were slightly higher in caribou herds ($AR$ = 12.28-13.15, $H_e$ = 0.86) than in reindeer ($AR$ = 10.06, $H_e$ = 0.75) (Appendix 3B).

Genetic differentiation among pairs of populations was greatest between domestic reindeer and caribou (Table 3.2). Pairwise estimates of genetic differentiation among caribou herds were very low, with only the WAH-PCH pair ($Fst$ = 0.003, $D$ = 0.023) being significantly different from zero (Table 3.2).

The WAH and PCH are the herds most geographically distant from one another, suggesting that patterns of differentiation between caribou herds could be due to isolation by distance. A Mantel test of isolation by distance indeed shows a strong correlation ($r$ = 0.965, $p$ = 0.04) between the geographic distance among herd pairs (measured as Euclidean distance between the centroids of summer ranges) and the genetic distance (Nei's $D$) among herd pairs (Fig. 3.2).

### *3.4.2 Overall Genetic Population Structure*

The program STRUCTURE found two population clusters within North Slope reindeer and caribou when all 312 samples were analyzed with no *a priori* population information. The two clusters corresponded closely to our two subspecies: reindeer and caribou (Fig. 3.3). The two-population model was clearly the most likely when compared to other models using the $\Delta K$ statistic (Evanno et al. 2005).

To further ensure that the distinct divide between reindeer and caribou was not masking more subtle population subdivision within caribou, we re-ran STRUCTURE

using only the samples in the reindeer cluster, then only the samples in our caribou cluster (following Vähä et al. 2007). For reindeer, this second analysis found the eight Kodiak Island individuals to be distinct from mainland Seward Peninsula reindeer. For caribou, the most likely solution for clustering North Slope herds was still a one-population model. The program TESS, which clusters individuals with no *a priori* population information using genotypic and location data, also grouped caribou from all four herds into one cluster. For each of our three analyses (rut locations, calving locations, and parturient females with calving locations), all individuals were assigned to a single cluster.

*3.4.3 Hybridization and Reindeer Introgression*

Though the two clusters identified by STRUCTURE correspond closely to our sample groups from caribou and reindeer, we found several admixed individuals presumed to have hybrid ancestry (Fig. 3.3). Under the relaxed criteria, we detected admixed individuals within all four caribou herds and both Seward Peninsula reindeer herds (Table 3.3). Overall, 50 individuals (16%) had greater than 5% of their genotype assigned to both clusters, and 26 (8%) had greater than 10% of their genotype assigned to both clusters (Table 3.3). Under the conservative criterion, the Central Arctic herd (CAH), Porcupine herd (PCH), and both Seward Peninsula reindeer herds contained individuals with hybrid ancestry (Fig. 3.4).

Seward Peninsula reindeer herds had the greatest percentage of admixed individuals, whereas Kodiak Island reindeer, isolated from caribou since the 1920s, had no admixed individuals (Table 3.3). Among caribou, the CAH had the greatest percentage of admixed individuals (Table 3.3). Proportions of assignment differed between caribou herds—the CAH, PCH, and WAH contained individuals with greater than 25% of their genotype assigned to both clusters whereas the TCH did not. Under relaxed criteria, however, the TCH and CAH had more admixed individuals with only a small percentage (5-20%) of their genotype assigned to the reindeer cluster than WAH and PCH (Fig. 3.3).

We also detected full-blooded migrants within both caribou and reindeer herds. Within Seward Peninsula reindeer, one individual was consistently assigned to the caribou cluster (Table 3.3). The individual, a female, was never tagged as a calf and was first handled as an adult when processed through the Ongtowasruk herd corral with several hundred reindeer in 2009. The three individuals hunted within a group of Western Arctic Herd caribou (D. Moto, personal communication) were also full-blooded migrants. The hunter who donated the samples visually identified the animals as feral reindeer, and their genotypic assignment to the reindeer cluster further supports his observations (Fig. 3.3).

## 3.5 Discussion

Our analysis of DNA from North Slope caribou showed little genetic differentiation among herds. All caribou were assigned to one cluster by STRUCTURE and TESS, though a strong correlation between genetic and geographic distance indicates herds are isolated by distance. Analysis of Alaskan reindeer showed them to be distinct as a group from caribou, but indicated several individuals likely to have hybrid reindeer-caribou ancestry.

### *3.5.1 Herd Differentiation*

Despite the strong observed fidelity of North Slope caribou herds to calving grounds, our results reveal that these herds are not four distinct genetic units. Recent studies of caribou distribution and movements support management of herds as demographically independent units (Person et al. 2007). Yet, the same studies also show some opportunities for gene flow among neighboring herds through range overlaps during rut and potentially through occasional dispersal to adjacent calving grounds (Person et al. 2007). Herds separated from one another by an intermediate herd (WAH and CAH; TCH and PCH) were not genetically differentiated, despite the fact that overlap among them is more rare than among neighbors (Lenart 2009; Parrett 2009). Geographically intermediate herds such as the TCH, which has an extensive fall and

winter range that can overlap either of its neighbors (WAH and CAH) during rut (Parrett 2009), may provide the mechanism for gene flow among more distant herds.

Because rates of genetic divergence among populations depend on both the number of migrants per generation (gene flow) and effective population size, we would expect the large North Slope herds to appear distinct only if gene flow among them is very limited (Waples 1998). Our results suggest gene flow has been ongoing over the long term at rates sufficient to counter divergence among the herds. However, we do not know how frequently gene flow occurs because we were unable to estimate the number of migrants per generation between herds with such low differentiation.

*3.5.2 Genetic Population Structure*

Though the North Slope herds are not distinct, we found strong evidence that herds are isolated by distance, demonstrating that weak genetic structure exists within North Slope caribou. The genetic distances among North Slope herds were clearly correlated with the geographic distances separating them (Fig. 3.2). Measures of differentiation (*Fst* and Jost's *D*) among neighboring herds were not significantly different from zero, consistent with the non-significant differentiation observed in barren-ground caribou herds in northwestern Canada (Zittlau 2004) and Labrador (Boulet et al. 2007). However, contrary to previous studies (Cronin et al. 2003, 2005), we found low but statistically significant differentiation among the most distant North Slope herds – WAH and PCH (Table 3.2). Findings from previous studies (Cronin et al. 2003, 2005) were limited by small sample sizes and low-variability markers, so the statistical power of our study likely enabled us to detect the subtle isolation-by-distance pattern structuring North Slope caribou.

Given the size and genetic diversity of the WAH and PCH, interbreeding between the two must be very low over the time scales relevant to wildlife management to allow detectable differences (Waples 1998). The four herds are not distinct, but neither are they simply one homogenous population, as previously found (Cronin et al. 2005). If distance, rather than herd identity, is the mechanism limiting demographic exchange across the

North Slope landscape, then considering spatial distribution of herds as a primary feature of caribou management is warranted.

*3.5.3 Reindeer-Caribou Hybridization*

Extensive historical contact between North Slope caribou and thousands of feral reindeer (Dau 2000; Mager, submitted; Rausch 1951) led us to predict that caribou herds today would show signs of introgressive hybridization. We found significant differentiation between reindeer and all four caribou herds. However, introgression is evident because 6% of the individuals sampled were determined to have hybrid ancestry under the most conservative criterion, and up to 16% under the relaxed criteria. A study comparing methods for detecting admixture among individuals of known ancestry showed that the conservative criterion (based on credibility intervals around assignment proportions from STRUCTURE) was overly conservative (Bohling and Waits 2011). Given the plausibility of introgression on the North Slope, we assume at least some of the admixture identified by relaxed criteria is real, and that some individuals with hybrid ancestry dating to the 1940s may have gone undetected. A lack of admixed individuals within the isolated Kodiak Island reindeer herd provides further evidence that admixture detected on the mainland is the product of recent hybridization, rather than ancestral similarities between the subspecies.

The presence of admixed individuals within North Slope caribou herds and Seward Peninsula reindeer demonstrates that reindeer are capable of surviving and breeding with caribou in the wild. Initial hybridization likely occurred during two periods of peak contact: between reindeer and caribou across the North Slope in the 1930s-1940s (15-20 generations ago) and between Seward Peninsula reindeer and WAH caribou from the late 1990s to present (0-4 generations ago). We can begin to understand how these events contributed to introgression in each herd by observing patterns in the spatial distribution and assignment proportions of admixed individuals, assuming that an individual's proportion of assignment ($q$) to the two clusters is a rough indicator of the generations since its hybrid ancestor. As a result of hybridization in the 1940s, we would

predict numerous individuals with low proportions of reindeer assignment across all herds, though our ability to detect them after so many generations would be influenced by the extent of hybridization at the time and selective pressures on hybrid descendents. As a result of hybridization on the Seward Peninsula in the 1990s, we would predict some individuals with greater proportions of reindeer assignment, mostly within the WAH.

We found full-blooded migrants, several apparent hybrids, and many individuals with a small proportion (5-25%) of their genotype assigned to both reindeer and caribou clusters. The range of admixture proportions suggests that hybridization occurred in both the 1940s and 1990s, however the herds in which those admixed individuals were found do not match our predictions. The CAH contains more admixed individuals than other caribou herds under both the conservative and relaxed criteria, which is puzzling given its distance from the Seward Peninsula (Fig. 3.1). Two CAH individuals have greater than 50% assignment to reindeer, suggesting they are F1 hybrids. One of those individuals was sampled in 1998, just after the greatest number of reindeer was lost from the Seward Peninsula in the winter of 1996-1997 (Schneider et al. 2005). It is possible, but unlikely, that those highly admixed individuals are descendents of reindeer lost over 15 generations ago in the 1940s, because we would expect a greater prevalence of reindeer genes throughout the CAH for such admixed individuals to be produced today. Therefore, we presume that highly admixed individuals in the CAH, PCH, and WAH, with > 25% assignment to the reindeer cluster are probably descendants of recently dispersing Seward Peninsula reindeer. Range maps indicate that parts of the central Brooks Range are used by all of these herds (Fig. 3.1), which may provide a mechanism for feral reindeer, without fidelity to particular caribou ranges, to move between herds. Hunters report observing feral reindeer in the Brooks Range and the Anaktuvuk Pass area, near this zone of potential overlap (Mager, submitted). Our results suggest long-distance dispersal of feral reindeer to the CAH and PCH ranges is plausible.

We did not find any highly admixed individuals within the TCH, which is somewhat surprising given their proximity to the Seward Peninsula in some winters. The TCH has experienced 6-8% harvest in recent years, the highest rate among the North

Slope herds (Parrett 2009). Many local hunters say they are able to visually identify reindeer within caribou herds, and express a preference for animals with reindeer-like phenotypes (Mager, submitted). Hunting may be a significant selective pressure removing highly admixed individuals with reindeer-like phenotypes from the TCH, and perhaps other herds like the WAH where many hunters have prior experience differentiating reindeer from caribou.

Interestingly, the TCH and CAH contain the greatest number of admixed individuals with only a small proportion (5-20%) of their genotype assigned to the reindeer cluster. This pattern—more individuals at low proportions of admixture—would be expected if reindeer ancestry were diluted over many generations since interbreeding in the 1940s. Biologists first described the TCH and CAH in the 1970s, when each contained only a few thousand animals (Davis and Valkenburg 1978). Oral and written histories indicate that both herds were smaller than today when they mixed with thousands of reindeer in the 1940s (Burch, in press; Mager, submitted). A greater ratio of reindeer to caribou on historical ranges may have permitted widespread interbreeding. Selective pressures on hybrid offspring may have differed between herds as well, if the migrations of the TCH and CAH were more limited at past small population sizes than they are today (Davis and Valkenburg 1978). Biologists have generally assumed that selection against reindeer is severe in large, migratory herds (Finstad et al. 2002; Klein 1980). However, a study in Greenland found significant introgression of feral reindeer into two small caribou herds (Jepsen et al. 2002). Though our interpretation of admixture proportions in the TCH and CAH is speculative, it supports the hypothesis that the size of a population can influence its susceptibility to long-term introgression (Skoog 1968).

Our results also show that caribou have influenced the identity of reindeer herds. Admixture in the Seward Peninsula reindeer herds—25% of all individuals, including one individual that appears to be a full-blooded caribou—is much higher than in any of the caribou herds. Despite herder efforts to protect reindeer from the encroaching WAH, which numbered over 400,000 caribou in the late 1990s, mixing appears to have had a proportionately larger effect on reindeer herds. It is also possible that hunting and natural

selection in the wild exert greater selective pressures on hybrids than reindeer owners do. Ordinarily, reindeer owners cull all animals with caribou phenotypes because they are more difficult to handle. However, decreased contact between herders and their reindeer, exacerbated by the economic hardships of reindeer losses to caribou (Dau 2000; Schneider et al. 2005) may allow more interbreeding and hybrid persistence than herders normally permit.

### *3.5.4 Constraints on Gene Flow and Hybridization in Large Populations*

Hybridization with introduced taxa and fluctuations in population size are major threats to small, fragmented populations, but less studied in large, intact mammal populations. This study is one of very few to document large-scale gene flow over vast areas in terrestrial mammals (see also: Lorenzen et al. 2008; Tammeleht et al. 2010). Despite historical fluctuations in population size, North Slope caribou retain high levels of diversity (Appendix 3B) when compared to boreal caribou populations at risk of extirpation (Ball et al. 2010; McDevitt et al. 2009). Large North Slope herds, despite extensive contact with reindeer, have also experienced less reindeer introgression than a small caribou herd in Greenland, where reindeer-specific alleles were found in 33% of individuals in one herd (Jepsen et al. 2002). Our results support hypotheses that population size and range size matter in maintaining gene flow and diversity, and limiting impacts from hybridization (Skoog 1968).

### *3.5.5 Conclusions*

We examined the potential effects of reindeer hybridization, herd identity, and landscape, on the genetic structure of North Slope caribou herds to inform their management and conservation. Designating management units for any wildlife species relies on multiple sources of information, including genetics, to define demographically independent populations (Moritz 1994; Palsboll et al. 2007; Taylor and Dizon 1999; Waples and Gaggiotti 2006). Currently, high population sizes and few landscape barriers permit overlap and movements among North Slope caribou herds, and our results suggest

genetic connectivity over the long term. The global loss of many large mammal migrations (Harris et al. 2009), and fragmentation of previously continuous mammal populations (Apps and McLellan 2006; Ashley et al. 1990; Keyghobadi 2007), emphasize the increasing uniqueness of populations like the North Slope caribou herds. If future landscape changes inhibit movement among herds, or future declines in herd size eliminate zones of overlap, our study may be used as a genetic baseline for detecting population fragmentation. Our results (Appendix 3B) show that North Slope caribou have comparable or higher genetic diversity than other migratory tundra herds (Boulet et al. 2007; Cronin et al. 2005; Zittlau 2004). This diversity could improve the ability of caribou to adapt to future changes, and future monitoring of allelic diversity and heterozygosity could inform conservation as well.

Our examination of historical interbreeding with reindeer identified factors that may influence hybrid persistence, such as historical herd size and hunting pressure. We detected animals with hybrid ancestry within a sample taken mostly from collared caribou in large herd aggregations. Further genetic analysis of potential resident caribou on the Seward Peninsula and hunter-collected samples, such as those identified as feral reindeer in this study, may provide further insights into reindeer-caribou interactions. Introgressive hybridization can degrade local adaptations, making it a primary threat to global biodiversity (Randi 2008; Simberloff 1996). Introgression is apparent in North Slope caribou, but instead of broadly impacting the genetic integrity of herds, it appears that caribou abundance relative to reindeer, natural selection, and selectivity by hunters and herders is effective in eliminating admixed individuals over time. However, the factors we identified should be considered if a reindeer re-introduction is planned in the future, especially if caribou are decreasing in population size or mobility at the time and unlikely to recover.

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**Table 3.1. Characteristics of sampled North Slope caribou herds and reindeer herds**

| Herd Name | Total Range ($km^2$) [a] | Estimated Population [b] (Year) | # DNA samples |
|---|---|---|---|
| **CARIBOU** | | | |
| Porcupine (PCH) | 224,385 | 169,000 (2010) | 60 |
| Central Arctic (CAH) | 114,995 | 67,000 (2008) | 66 |
| Teshekpuk Lake (TCH) | 114,787 | 64,100 (2008) | 52 |
| Western Arctic (WAH) | 377,465 | 348,000 (2009) | 67 |
| **REINDEER** | | | |
| Ongtowasruk from Wales, Alaska (ONG) | 2,425 | unknown | 43 |
| Davis from Nome, Alaska (DAV) | 3,875 | unknown | 13 |
| Kodiak Island feral reindeer (KOD) | unknown | 250-300 (2010) | 8 |
| Hunter-caught feral reindeer | n/a | n/a | 3 |

[a] Caribou range sizes from herd shape files, Sept. 2011 (from the Alaska Department of Fish and Game). ONG and DAV ranges were calculated based on grazing permit area. KOD feral reindeer utilize an unknown range area on the Southwest end of Kodiak Island.

[b] Population estimates are based on aerial counts of caribou herds conducted in the given year (Alaska Department of Fish and Game 2011a, 2011b; Lenart 2009; Parrett 2009) and on an estimate of total KOD reindeer population size after a minimum aerial count of $n$ = 64 (Cobb 2010).

**Table 3.2. Estimates of genetic differentiation among pairs of populations**: $F_{ST}$ (above diagonal) and Jost's $D$ (below diagonal). Abbreviations: Domestic reindeer (RD), Western Arctic Caribou Herd (WAH), Teshekpuk Lake Caribou Herd (TCH), Central Arctic Caribou Herd (CAH), and Porcupine Caribou Herd (PCH).

| | RD | WAH | TCH | CAH | PCH |
|---|---|---|---|---|---|
| RD | - | 0.0545* | 0.0482* | 0.0476* | 0.0497* |
| WAH | 0.2649* | - | 0.0003 | 0.0014 | 0.0032* |
| TCH | 0.2392* | 0.0012 | - | 0.0000 | 0.0018 |
| CAH | 0.2349* | 0.0072 | 0.0028 | - | 0.0005 |
| PCH | 0.2452* | 0.0226* | 0.0104 | 0.0063 | - |

* Indicates associated $P$-values were significant after Bonferroni correction for multiple comparison

**Table 3.3. The number of caribou, reindeer, and admixed individuals detected by STRUCTURE in each population sampled** (also shown as % of sample population). Individuals not assigned to their putative population are in bold italics. We report the number under both the conservative criterion (CI's around assignment proportion do not encompass zero) and under the relaxed criteria (based on proportion of assignment to each cluster). Note that we detect one full-blooded caribou in the Ongtowasruk reindeer herd under all three criteria. Abbreviations: "RD" denotes reindeer and "CB" denotes caribou.

| Sample Population | STRUCTURE – conservative (Use Pop Info setting) | | | STRUCTURE – relaxed (>0.10) (without Pop Info setting) | | | STRUCTURE – relaxed (>0.05) (without Pop Info setting) | | |
|---|---|---|---|---|---|---|---|---|---|
| | Caribou | Reindeer | Admixed | Caribou | Reindeer | Admixed | Caribou | Reindeer | Admixed |
| Kodiak RD | 0 (0%) | 8 (100%) | 0 (0%) | 0 (0%) | 8 (100%) | 0 (0%) | 0 (0%) | 8 (100%) | 0 (0%) |
| Davis RD | 0 (0%) | 9 (69%) | ***4*** (31%) | 0 (0%) | 11 (85%) | ***2*** (15%) | 0 (0%) | 9 (69%) | ***4*** (31%) |
| Ongtowasruk RD | ***1*** (2%) | 33 (77%) | ***9*** (21%) | ***1*** (2%) | 37 (86%) | ***5*** (12%) | ***1*** (2%) | 32 (74%) | ***10*** (23%) |
| Hunted RD | 0 (0%) | 3 (100%) | 0 (0%) | 0 (0%) | 3 (100%) | 0 (0%) | 0 (0%) | 3 (100%) | 0 (0%) |
| Western Arctic CB | 67 (100%) | 0 (0%) | 0 (0%) | 63 (94%) | 0 (0%) | ***4*** (6%) | 59 (88%) | 0 (0%) | ***8*** (12%) |
| Teshekpuk CB | 52 (100%) | 0 (0%) | 0 (0%) | 48 (92%) | 0 (0%) | ***4*** (8%) | 43 (83%) | 0 (0%) | ***9*** (17%) |
| Central Arctic CB | 63 (95%) | 0 (0%) | ***3*** (5%) | 59 (89%) | 0 (0%) | ***7*** (11%) | 55 (83%) | 0 (0%) | ***11*** (17%) |
| Porcupine CB | 58 (97%) | 0 (0%) | ***2*** (3%) | 56 (93%) | 0 (0%) | ***4*** (7%) | 52 (87%) | 0 (0%) | ***8*** (13%) |

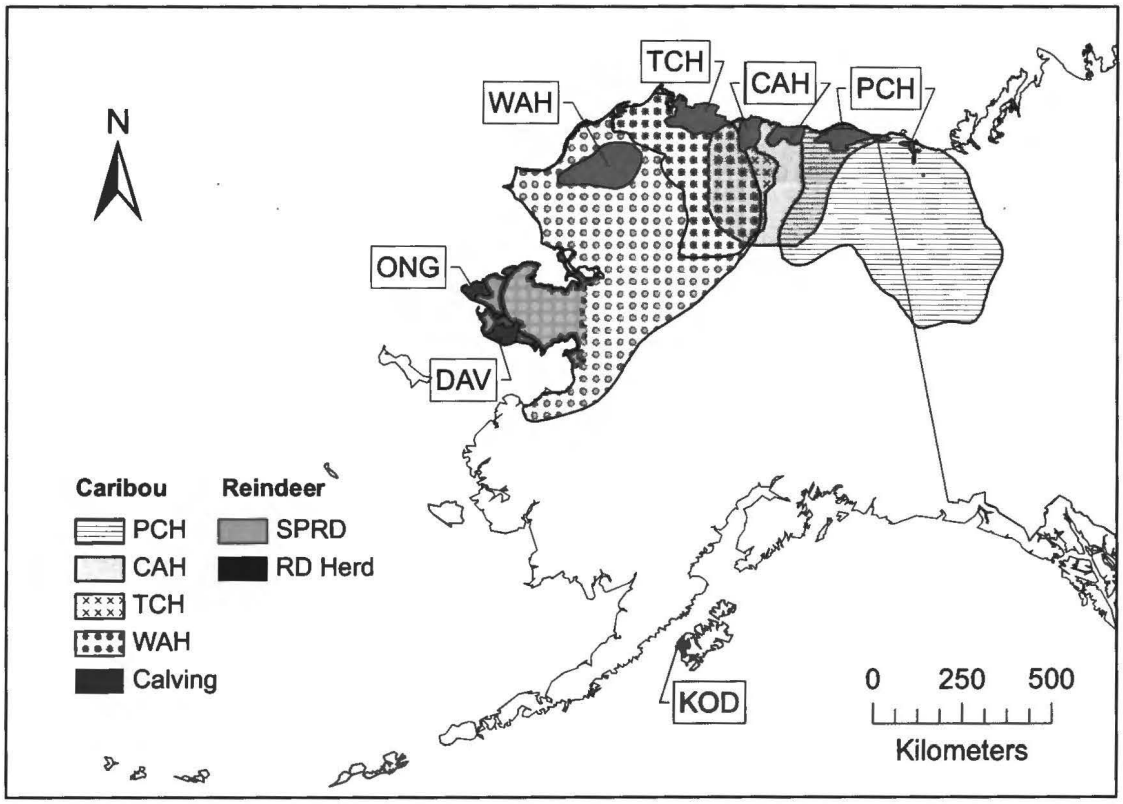


**Figure 3.1. Map of sampled caribou and reindeer herds.** Shown are the total ranges of the four caribou herds: Porcupine (PCH), Central Arctic (CAH), Teshekpuk (TCH), and Western Arctic (WAH), and the total range of the current Seward Peninsula reindeer grazing lands (SPRD). Dark gray shading (Calving) indicates calving areas for each of the four caribou herds. Black shading (RD Herd) indicates the specific reindeer herds we sampled: Ongtowasruk (ONG), Davis (DAV), and Kodiak Island (KOD).

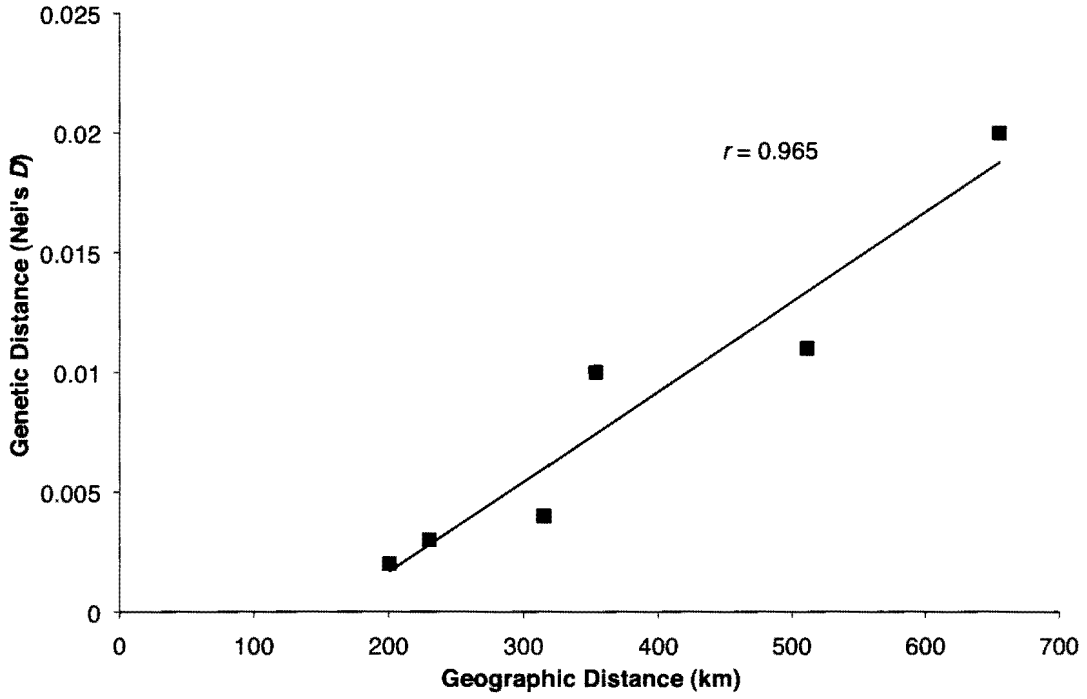


**Figure 3.2. Pattern of isolation by distance among North Slope caribou herds.** Note strong positive relationship ($r = 0.965$) between genetic distance (Nei's $D$) and geographic distance (measured as Euclidean distance between the summer range centroids of each pair of herds).

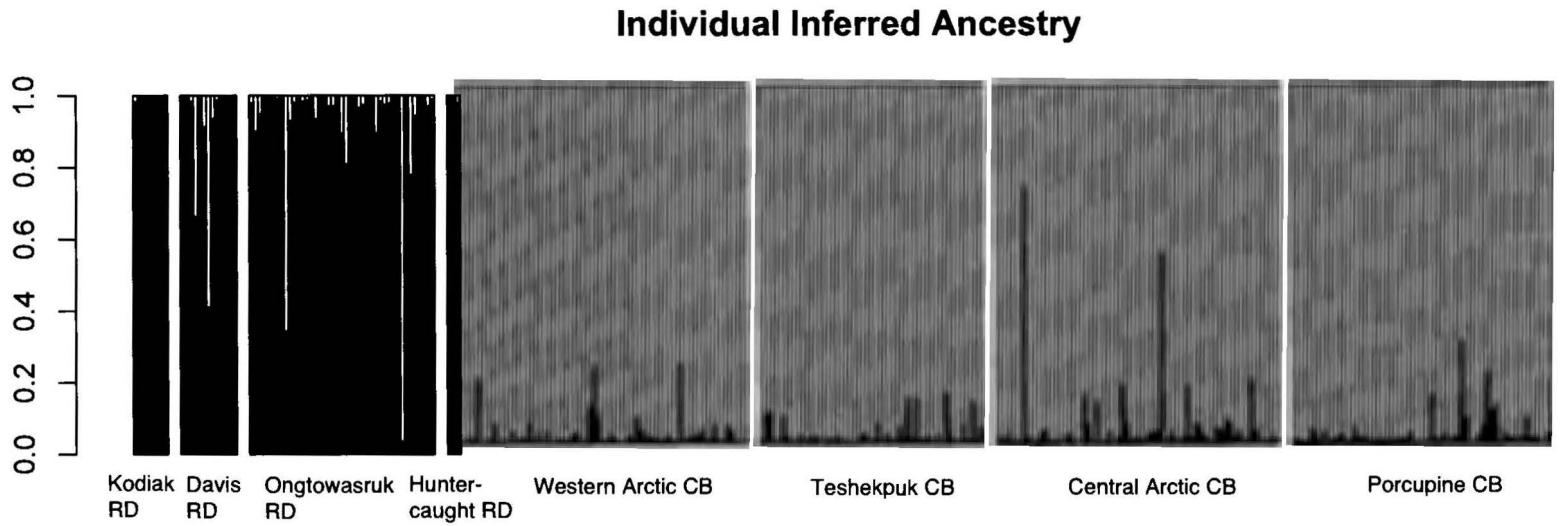


**Figure 3.3. Proportion of assignment of individuals in all populations to the two clusters identified by STRUCTURE.** Each vertical bar represents one individual and shows the proportion of the individual's genotype that is assigned either to the black (reindeer-dominated) cluster or to the white (caribou-dominated) cluster. Abbreviations: Reindeer (RD), Caribou (CB)

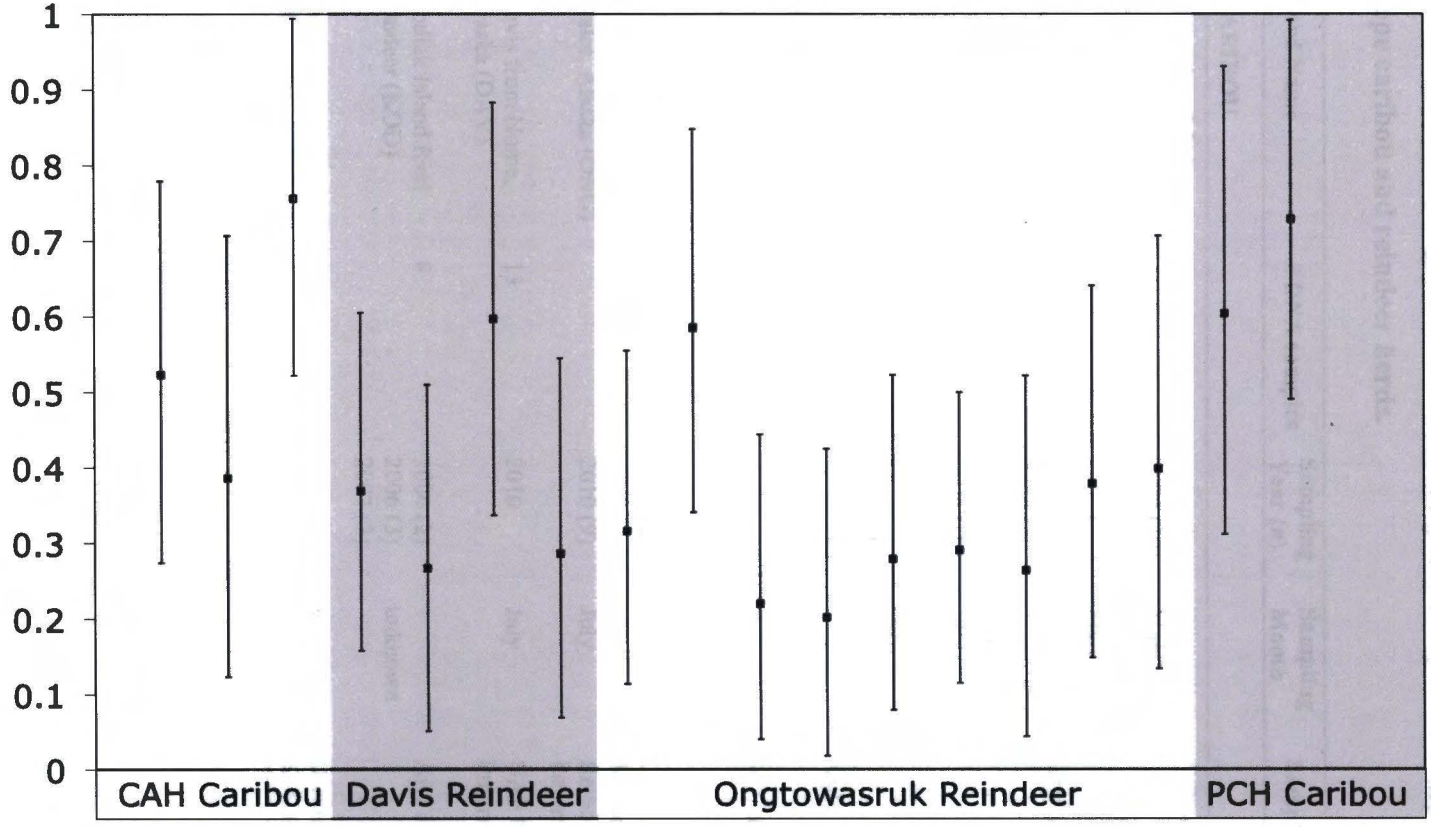


**Figure 3.4. Admixed individuals identified using the STRUCTURE-conservative criterion** (credibility intervals of individuals do not encompass zero). Position along the y-axis shows the proportion of assignment to the caribou cluster, where 1 indicates full assignment to caribou and 0 indicates full assignment to reindeer.

## Appendix 3A

**Table 3A-1. Sampling year, month, and agency for genetic samples from North Slope caribou and reindeer herds.**

| Herd Name | # DNA samples | Sampling Year (*n*) | Sampling Month | Sampling Agency |
|---|---|---|---|---|
| **CARIBOU** | | | | |
| Porcupine (PCH) | 61 | 1988 (7)<br>2004 (10)<br>2008 (19)<br>2009 (25) | June<br>March<br>March<br>March | Yukon Govt; USFWS |
| Central Arctic (CAH) | 66 | 1998 (16)<br>2000 (4)<br>2001 (9)<br>2008 (16)<br>2009 (10)<br>2009 (3)<br>2010 (10) | June<br>June<br>July<br>July<br>April<br>June<br>April | ADF&G |
| Teshekpuk Lake (TCH) | 52 | 2008 (36)<br>2009 (16) | June<br>June | NSB; ADF&G |
| Western Arctic (WAH) | 67 | 2008 | Sept. | ADF&G |
| **REINDEER** | | | | |
| Ongtowasruk from Wales, Alaska (ONG) | 43 | 2009 (34)<br>2010 (9) | July<br>July | Mager, K.; UAF Reindeer Research Program |
| Davis from Nome, Alaska (DAV) | 13 | 2010 | July | UAF Reindeer Research Program |
| Kodiak Island feral reindeer (KOD) | 8 | 2004 (2)<br>2006 (3)<br>2007 (3) | unknown | ADF&G |
| Hunter-caught feral reindeer | 3 | 2009 | winter | Dickie Moto, Kotzebue/Deering, AK |

## Appendix 3B

**Table 3B-1. For each locus in each population: Number of Alleles (A), Allelic Richness (AR), Observed Heterozygosity (Ho), and Expected Heterozygosity (He).**

| Pop | | RT6 | ObeD | ObeQ | NVHRT30 | RT27 | RT1 | FCB193 | BM6506 | BM4513 | RT9long | RT7 | RT24 | RT10 | RT30 | BMS745 | TEXAN4 | C89 | BL42 | BMS1788 | Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| RD | A | 11 | 10 | 16 | 9 | 12 | 11 | 10 | 12 | 13 | 11 | 10 | 8 | 12 | 12 | 5 | 4 | 10 | 14 | 13 | 10.684 |
| | AR | 10.115 | 9.46 | 14.583 | 8.562 | 11.227 | 10.538 | 9.421 | 10.85 | 12.503 | 10.553 | 9.287 | 7.779 | 11.496 | 11.704 | 4.992 | 4 | 9.458 | 13.495 | 12.295 | 10.122 |
| | Ho | 0.719 | 0.734 | 0.797 | 0.641 | 0.672 | 0.794 | 0.688 | 0.641 | 0.841 | 0.781 | 0.719 | 0.820 | 0.766 | 0.844 | 0.651 | 0.578 | 0.734 | 0.703 | 0.781 | 0.732 |
| | He | 0.787 | 0.727 | 0.807 | 0.708 | 0.741 | 0.816 | 0.722 | 0.738 | 0.863 | 0.837 | 0.767 | 0.830 | 0.772 | 0.773 | 0.738 | 0.624 | 0.727 | 0.883 | 0.748 | 0.769 |
| WAH | A | 13 | 14 | 20 | 10 | 14 | 14 | 14 | 15 | 17 | 13 | 8 | 18 | 8 | 15 | 7 | 4 | 14 | 16 | 12 | 12.947 |
| | AR | 12.202 | 13.91 | 18.376 | 9.998 | 13.715 | 13.677 | 13.22 | 14.151 | 15.783 | 12.661 | 7.995 | 16.845 | 7.999 | 13.665 | 6.937 | 3.996 | 13.91 | 15.16 | 11.239 | 12.392 |
| | Ho | 0.848 | 0.955 | 0.940 | 0.866 | 0.910 | 0.896 | 0.896 | 0.864 | 0.877 | 0.836 | 0.761 | 0.803 | 0.806 | 0.761 | 0.716 | 0.582 | 0.955 | 0.866 | 0.836 | 0.841 |
| | He | 0.860 | 0.882 | 0.901 | 0.853 | 0.899 | 0.880 | 0.863 | 0.860 | 0.897 | 0.872 | 0.775 | 0.884 | 0.851 | 0.866 | 0.803 | 0.596 | 0.882 | 0.899 | 0.869 | 0.852 |
| TCH | A | 12 | 13 | 19 | 13 | 14 | 15 | 12 | 13 | 13 | 13 | 9 | 16 | 12 | 16 | 7 | 4 | 13 | 15 | 13 | 12.737 |
| | AR | 11.958 | 12.998 | 18.805 | 12.885 | 13.959 | 14.922 | 11.922 | 12.923 | 13 | 12.959 | 8.96 | 15.921 | 11.885 | 15.769 | 6.999 | 4 | 12.998 | 14.883 | 12.921 | 12.667 |
| | Ho | 0.846 | 0.846 | 0.904 | 0.904 | 0.904 | 0.904 | 0.846 | 0.808 | 0.820 | 0.827 | 0.827 | 0.750 | 0.846 | 0.827 | 0.750 | 0.596 | 0.846 | 0.904 | 0.769 | 0.828 |
| | He | 0.864 | 0.834 | 0.909 | 0.853 | 0.870 | 0.901 | 0.828 | 0.833 | 0.898 | 0.839 | 0.770 | 0.885 | 0.844 | 0.884 | 0.781 | 0.671 | 0.834 | 0.895 | 0.895 | 0.847 |
| CAH | A | 14 | 16 | 20 | 14 | 16 | 14 | 12 | 16 | 14 | 12 | 10 | 16 | 12 | 14 | 7 | 4 | 16 | 21 | 13 | 13.737 |
| | AR | 13.337 | 15.172 | 18.505 | 13.438 | 15.236 | 13.967 | 11.511 | 15.072 | 13.697 | 11.933 | 9.74 | 15.061 | 11.4 | 13.201 | 6.984 | 4 | 15.172 | 19.661 | 12.516 | 13.137 |
| | Ho | 0.818 | 0.924 | 0.864 | 0.879 | 0.712 | 0.864 | 0.848 | 0.938 | 0.909 | 0.788 | 0.682 | 0.828 | 0.788 | 0.727 | 0.758 | 0.682 | 0.924 | 0.894 | 0.846 | 0.825 |
| | He | 0.868 | 0.850 | 0.889 | 0.855 | 0.873 | 0.896 | 0.860 | 0.862 | 0.906 | 0.861 | 0.767 | 0.857 | 0.855 | 0.872 | 0.765 | 0.644 | 0.851 | 0.919 | 0.886 | 0.849 |
| PCH | A | 13 | 15 | 19 | 11 | 13 | 14 | 12 | 16 | 17 | 14 | 10 | 17 | 11 | 14 | 7 | 4 | 15 | 17 | 11 | 13.158 |
| | AR | 12.473 | 14.657 | 17.632 | 10.666 | 12.803 | 13.673 | 11.807 | 15.412 | 16.497 | 13.586 | 9.776 | 16.278 | 10.639 | 13.801 | 6.973 | 3.996 | 14.657 | 16.438 | 10.973 | 12.776 |
| | Ho | 0.933 | 0.883 | 0.867 | 0.917 | 0.817 | 0.932 | 0.867 | 0.833 | 0.966 | 0.867 | 0.717 | 0.767 | 0.833 | 0.883 | 0.767 | 0.583 | 0.883 | 0.867 | 0.817 | 0.842 |
| | He | 0.862 | 0.879 | 0.864 | 0.864 | 0.881 | 0.904 | 0.882 | 0.857 | 0.907 | 0.867 | 0.718 | 0.880 | 0.859 | 0.896 | 0.795 | 0.601 | 0.879 | 0.902 | 0.889 | 0.852 |
| All | A | 16 | 17 | 26 | 15 | 16 | 16 | 15 | 20 | 19 | 17 | 12 | 24 | 16 | 17 | 8 | 4 | 17 | 22 | 17 | 16.526 |
| | AR | 12.652 | 14.195 | 18.054 | 11.502 | 14.414 | 13.927 | 11.897 | 14.597 | 14.652 | 12.855 | 9.769 | 16.257 | 12.466 | 13.659 | 7.191 | 3.998 | 14.191 | 16.649 | 12.751 | 12.930 |
| | Ho | 0.835 | 0.871 | 0.876 | 0.841 | 0.800 | 0.880 | 0.832 | 0.817 | 0.881 | 0.822 | 0.738 | 0.795 | 0.807 | 0.810 | 0.728 | 0.599 | 0.871 | 0.849 | 0.812 | 0.814 |
| | He | 0.855 | 0.841 | 0.882 | 0.833 | 0.858 | 0.888 | 0.838 | 0.839 | 0.902 | 0.863 | 0.765 | 0.875 | 0.844 | 0.866 | 0.783 | 0.631 | 0.841 | 0.908 | 0.868 | 0.841 |

# Chapter 4 Genetic Population Structure of Alaskan Caribou (*Rangifer tarandus granti*) at Multiple Spatial Scales: Influences of Geography, Demography, and Ecotype[3]

## 4.1 Abstract

We examined genetic variation in Alaskan caribou to describe the population structure of the subspecies on multiple spatial scales and to understand the influence of geographic, demographic, and behavioral factors on this structure. Using 19 microsatellite markers, we analyzed genetic diversity and differentiation in 655 caribou from 20 herds across Alaska. We found, at the coarsest scale, that caribou are grouped in two geographically distinct population clusters—one on the Alaska Peninsula, the other encompassing all caribou on the mainland. At the finest scale, the herd, we found that some herds are more distinct than others. In different regions of the state, patterns of genetic structure (herd differentiation) and diversity vary. Herds from southwest Alaska are distinct genetic units, while most herds on the mainland (with the exception of the White Mountains herd) are not. We hypothesize four drivers of genetic structure in Alaskan caribou related to geography, habitat, demographic bottlenecks, and habitat selection by different ecotypes. We discuss evidence that southwest Alaskan herds have diverged due to a combination of bottlenecks and geographic constraints. We also discuss potential causes of differentiation among sympatric herds of different ecotypes. These results have implications for caribou management by demonstrating that some herds are genetically distinct while, for others, genetic exchange over the long-term may be important in maintaining diversity and adaptive capacity.

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## 4.2 Introduction

Nearly 800,000 caribou (*Rangifer tarandus granti*) are distributed across Alaska in multiple herds, each completing an annual migration through seasonal ranges of variable size and terrain (Alaska Department of Fish and Game 2009a). Caribou are a valued game species across Alaska and the circumpolar North, and one of few ungulates with intact, long-distance migrations (Harris *et al.* 2009). Though abundant and ubiquitous in Alaska at present, caribou populations can fluctuate greatly in size over the span of decades and centuries, often accompanied by changes in range size and spatial distribution (Skoog 1968; Messier *et al.* 1988; Bergerud 1996; Ferguson *et al.* 2001; Gunn 2003; Hinkes *et al.* 2005). Range expansions and contractions, along with occasional range shifts and dispersal events, alter spatial patterns of herd connectivity (Ferguson *et al.* 2001; Hinkes *et al.* 2005; Person *et al.* 2007). The effects of those changing spatial patterns on caribou diversity and population connectivity, however, are largely unknown. Previous genetic studies of some Alaskan caribou herds (Cronin *et al.* 2003; Zittlau 2004; Cronin *et al.* 2005; Roffler *et al.* in press; Mager *et al.* submitted; Colson *et al.* in prep) suggest populations are structured differently in different regions of the state. However, no comprehensive description exists of the subspecies-wide genetic population structure, which could inform coordinated management of populations and subpopulations across the state. Nor has there been any comprehensive study of factors driving the development of population structure in Alaskan caribou.

Alaskan caribou herds have been identified on the basis of their calving grounds, to which females return each summer to give birth (Skoog 1968). Throughout the rest of the year, however, herd ranges may sometimes overlap (Fig. 4.1; Skoog 1968; Hinkes *et al.* 2005, Roffler *et al.* in press). Biologists find evidence that herds may constitute closed populations (Valkenburg *et al.* 2002), subpopulations with occasional exchange of individuals (Skoog 1968), components of metapopulations over some temporal scales (Hinkes *et al.* 2005; Boulet *et al.* 2007; Roffler *et al.* in press), and/or geographic entities that together constitute a single population (Cronin *et al.* 2003). Some authors have

proposed higher-order population concepts beyond the herd scale for Alaskan caribou based on their use of space and patterns of movement (Skoog 1968; Hinkes *et al.* 2005).

Heterogeneity in geography, habitat, and predation risk may result in diversified strategies of space use (Bergerud 1996), which can induce variability in the relative size and isolation of different caribou subpopulations, potentially influencing their genetic structure. Biologists recognize several ecotypes of caribou in North America based on broad habitat classifications (tundra, mountain, boreal forest, and high arctic Peary caribou; Festa-Bianchet *et al.* 2011), migration (migratory and sedentary; Bergerud 1996; Festa-Bianchet *et al.* 2011), and spacing strategies for predator avoidance (aggregated and dispersed during calving; Bergerud 1996). Ecotypes have been proposed as an ecology-based classification alternative (Festa-Bianchet *et al.* 2011) to the morphology-based subspecies (Banfield 1961), which on the basis of mtDNA do not appear to reflect the species' phylogeography (Flagstad & Røed 2003). Ecological classification by ecotype has been argued to be more practical than subspecies for management purposes, because herds with similar habitats face similar conservation threats (Festa-Bianchet *et al.* 2011).

Ecotypes have also been proposed as a useful descriptor of environmental factors that may influence differentiation between herds of the same subspecies. Three recognized ecotypes of the Woodland subspecies (*R. t. caribou*) in eastern Canada are genetically differentiated, though gene flow between them has been documented (Courtois *et al.* 2003, Boulet *et al.* 2007). However, Alaskan caribou have been observed to shift between sedentary and migratory ecotypes in response to changes in density or contact with neighboring herds of a different ecotype (Hinkes *et al.* 2005). Increased density (> 2 caribou /km$^2$) seems to drive changes in their use of space, including range expansions and shifts, changed movement patterns, and the formation of new herds or assimilation of existing herds (Skoog 1968; Hinkes *et al.* 2005). As such, it seems that caribou population dynamics are both a response to the constraints of available space and a driver of changes in space use.

Though it seems fairly straightforward to define a herd as a group of caribou sharing a common calving ground, long-term changes in space use may mean changes in the locations of calving grounds (Valkenburg & Davis 1986; Hinkes *et al.* 2005;), shifts in spacing strategy from aggregated to dispersed calving (Bergerud 1996), or the use of a single calving area by two previously separate herds (Hinkes *et al.* 2005; Nagy *et al.* 2011). The tendency for females to travel together to the same calving areas has been consistently observed in migratory caribou (Schaefer *et al.* 2000), and females continue to show spatial affiliation even as they shift calving grounds and overlap with other herds (Nagy *et al.* 2011). However, because herds are the units of management for caribou in Alaska, long-term changes in space use present practical challenges to wildlife managers, especially regarding spatially explicit land management.

Recognizing demographically independent herds on the basis of spatial affiliation becomes more challenging when one herd appears to join another and ceases to be an independent unit, or when new herds are formed (Hinkes *et al.* 2005). Understanding the frequency and cause of such changes is difficult due to a lack of long-term studies. Reconstructed herd histories based on historical documents indicate some herds have persisted over the long term, while others such as the historical Bering Seacoast and Seward Peninsula herds have disappeared (Skoog 1968; Burch, in press). Many herds were only formally recognized within the past 30-40 years, including two—Teshekpuk and Central Arctic—that have grown to become some of the larger herds in the state. Most of these recently "discovered" herds probably existed long prior to being described by biologists, but some may have formed only recently. Some small resident herds are currently found within the ranges of larger herds but are not recognized, despite utilizing separate calving grounds (Hinkes *et al.* 2005).

Based on historical accounts and movement data, it is known that caribou herds change in size, space use, and identity over time. However, it is not known how these processes are related to patterns of genetic subdivision at larger and smaller scales, or whether herds retain demographic independence over time. Genetic data are needed to understand the influence of such changes on caribou populations to determine, for

example, how population declines influence genetic diversity important for adaptability, or whether novel contact between herds will be important in maintaining diversity or be detrimental to local adaptations. Skoog (1968) proposed a framework for population subdivision in Alaskan caribou. He hypothesized that Alaskan caribou comprise one genetic population divided into six genetic subpopulations that "have been more or less discrete entities over the past 100 years and somewhat isolated as well". He suggests that each subpopulation occupies a specific geographic region, with a "center of habitation" encompassing the best habitat in the region and supporting continual occupation by caribou despite fluctuations in population size. Over time, if caribou increase in density, they extend their movements and expand their range into more marginal habitat. When a caribou population subsequently declines, its range contracts back to the center of habitation, leaving small "remnant herds" behind. Thus, each region can contain several herds, each with its own calving area.

Skoog (1968) used extensive historical research and field study to construct this concept; however, changes in the abundance and distribution of caribou since then may have revised the boundaries of the regions he proposed. Expansion and a southwestward shift of the Mulchatna herd have caused it to overlap more with Alaska Peninsula caribou in Southwest Alaska (Hinkes *et al.* 2005) than with Denali caribou herd as Skoog (1968) proposed. Overlap between the Denali, Delta, Nelchina, and Fortymile herds of Interior Alaska suggest greater connectivity across that region than Skoog observed. Finally, the recognition and growth of the Teshekpuk and Central Arctic herds suggests connectivity across Alaska's North Slope. Genetic studies conducted within each of these three regions suggest different patterns of genetic population subdivision within each of them. In the North Slope, four large migratory caribou herds are genetically diverse and show little differentiation over vast distances, with the slight variation following a pattern of isolation by distance (Cronin *et al.* 2005; Mager *et al.*, submitted). In Southwest Alaska, by contrast, herds are genetically distinct and decline in allelic richness along the Alaska Peninsula with increasing distance from the mainland (Colson *et al.*, in prep). Many more caribou herds, however, reside between these two regions in the Interior—a region

containing a diversity of topography and habitat inhabited by herds of widely varying size. Zittlau (2004) analyzed some Interior herds and found them to be variable in their connectivity to other Alaskan and Canadian woodland and barren-ground (*R. t. groenlandicus*) herds, but generally less differentiated than herds in Southwest Alaska. However, a comprehensive study is required to describe the population structure in the Interior, to compare the three regions to one another, and to determine patterns of connectivity and diversity within the subspecies.

We use a population genetics approach to describe the genetic structure of caribou at multiple spatial scales: the herd, the region, and statewide. Specifically, we make several predictions based on the work of Skoog (1968) and others: 1) Alaskan caribou comprise a single genetic population; 2) several somewhat discrete subpopulations exist as geographically distinct, containing multiple herds with adjacent or overlapping ranges; 3) within regions, herds at the "center of habitation" have greater genetic diversity than nearby "remnant" herds; 4) herds thought to share a recent common origin will be genetically similar; 5) herds known to have fluctuated greatly in population size will show evidence of genetic bottleneck(s).

We aim to understand patterns of genetic diversity and genetic differentiation among caribou herds today in relation to several factors hypothesized to influence effective population size and genetic connectivity (gene flow) over evolutionary and historical time periods. Because extant Alaskan caribou range across the state in great numbers, are highly mobile, and are thought to descend from a single, large Beringian population (Banfield 1961), we might expect few opportunities for divergence among them. We hypothesize that any herds or regional groups of herds found to be genetically distinct have undergone divergence driven by some combination of four main factors: 1) Geographic barriers to movement or constraints to population size caused by the shape and topography of landforms; 2) Barriers or constraints due to the spatial distribution of suitable habitat, which may change rapidly (e.g., due to fire, overgrazing, climate change, human development, and hunting access); 3) Differential habitat use or social organization (ecotypes) resulting in divergence due to selection; 4) Historical bottlenecks

or persistently small population size which, together with limits to gene flow, increase the speed of divergence due to genetic drift.

## 4.3 Methods

### *4.3.1 System Description and Genetic Sampling*

Alaskan caribou are found across much of the state, with the exception of Southeast Alaska and most maritime islands (Fig. 4.1). There are 32 recognized herds in Alaska, currently ranging in size from less than 100 individuals in the smallest herd to approximately 350,000 in the large Western Arctic herd (Alaska Department of Fish and Game 2009a). One herd along the Alaska-Canada border, the Chisana herd, is classified as *R. t. granti* in Alaska and *R. t. caribou* in Canada (Zittlau 2004; Chisana Caribou Herd Working Group 2010). Three ecotypes of Alaskan caribou are currently recognized: migratory tundra, migratory mountain, and sedentary mountain caribou (Festa-Bianchet *et al.* 2011). It is worth noting, however, that both subspecies and ecotype classifications have been vaguely defined and frequently changed in nomenclature (Banfield 1961; Bergerud 1996; Mallory & Hillis 1998; Courtois *et al.* 2003; Couturier *et al.* 2010; Festa-Bianchet *et al.* 2011). Regardless of classifications, all Alaskan caribou are somewhat migratory (Skoog 1968), utilizing specific seasonal ranges for each of the "caribou seasons": calving, post-calving, mosquito harassment, mosquito and oestrid fly harassment, late summer, fall migration and rut, winter, and spring migration (Person *et al.* 2007).

We sampled 655 caribou from 20 caribou herds throughout the subspecies range (Fig. 4.1), including all herds in the North Slope region and the Southwest region, and most herds in the Interior (see Table 4.1 for herd abbreviations and details). These regions are adjacent and without clear boundaries in places. However, they differ in general ways from one another in geography and habitat characteristics that could be expected to influence caribou range sizes, movements, and potentially life history traits.

- *North Slope*—Alaska's North Slope is home to approximately 650,000 caribou, which comprise four large herds of the migratory tundra ecotype (Alaska

Department of Fish and Game 2009a; Festa-Bianchet *et al.* 2011). The region is the vast coastal plain extending north from the Brooks Range to the Chukchi and Beaufort Seas. Much of the region is above treeline, regardless of elevation, though tundra habitat types vary in vegetation and hydrology at both landscape and micro-climatic scales (CAVM Team 2003).

- *Interior*—The Alaskan Interior contains many herds of the mountain ecotype, some migratory and some sedentary. For the purposes of this paper, the Interior encompasses all the herds that do not range along the coast. The area is bounded by the Brooks Range to the north, the Chugach and Wrangell-St. Elias ranges to the south, and the deltas of the Yukon and Kuskokwim Rivers to the west. Several Interior herds span the Alaska-Canada border to the east. The geography of this region is heterogeneous and includes the large Alaska Range, several smaller mountain ranges, and boreal forest. Generally in the Interior, higher elevations are characterized by alpine tundra, with boreal forests and muskegs at lower elevations (in contrast to much of the North Slope). We have divided this region into three subregions—the Northern Interior includes herds north of the Yukon River; the Central Interior includes herds found between the Yukon and Tanana River valleys; and the Southern Interior includes herds south of the Tanana, most of which are located in or near the Alaska Range with the exception of the Chisana herd.
- *Southwest*—Southwestern Alaska includes the Alaska Peninsula and adjacent coastal areas of the mainland, south of the Yukon-Kuskokwim Delta. This region is bounded to the west and south by coast, and is separated from the North Slope by a large swath of the Yukon-Kuskokwim Delta, which has no recognized caribou herds at present but contained caribou historically (Skoog 1968; Burch, in press). The boundary to the east is less defined, as five small caribou herds (not sampled) inhabit the area between the southwest-region Mulchatna herd and the interior-region Denali herd. We divide the Southwest region into the mainland subregion, comprised solely of the large Mulchatna herd, and the peninsula

subregion, which in addition to the two Alaska Peninsula herds includes Unimak Island close to the tip of the peninsula and the Nushugak herd transplanted from the Alaska Peninsula in the 1980s.

We sampled all large herds and most small herds from these three major regions. Herds not sampled in this study include 5 small herds between the Denali and Mulchatna ranges, the Mentasta herd near the Canadian border, and the small transplanted herds on the Kenai Peninsula and Adak Island.

Other regional concepts have been proposed for Alaskan caribou. Skoog (1968) described 6 caribou regions, based on the centers of habitation for caribou at that time and in recent history. We consider Skoog's regions in this study (Table 4.1), but based on changes in the size and distribution of herds since 1968, and improved knowledge of caribou movements gained from subsequent studies, we feel the regions and subregions we use are more discrete at present.

*4.3.2 DNA Extraction and Genotyping*

To examine genetic variation on the scale of each herd, each region, and statewide, we sampled 20 herds distributed across the state. We aimed to analyze at least 20 individuals per herd to adequately represent within-herd genetic diversity, however 5 herds with a smaller number of samples ($n$ = 4-17) were included in the study. Whole blood, tissues, and hair were collected from 655 caribou (Table 4.1) by biologists from the Alaska Department of Fish and Game, U. S. Geological Survey, U. S. Fish and Wildlife Service, Yukon Government, and U. S. Bureau of Land Management. Samples were stored frozen at either -80 °C or -40 °C. DNA was extracted using either the DNeasy Blood & Tissue Kit (QIAGEN Inc.,Valencia, CA) or the MOBIO UltraClean DNA BloodSpin Kit (MoBio Laboraties, Inc., Carlsbad, CA), and extracts were stored frozen at -20 °C.

We amplified DNA at 19 microsatellite loci using PCR, scored alleles by fragment length, and checked for genotyping errors (for details see Mager *et al.*

submitted). We found no evidence of linkage disequilibrium between any pairs of loci using FSTAT ver. 2.9.3 (Goudet 1995). Fifteen loci met assumptions of global Hardy-Weinberg equilibrium (HWE), based on a Hardy-Weinberg exact test in Genepop ver. 4.0.6 (Raymond & Rousset 1995, Rousset 2008) for each locus in each population. Three markers out of HWE were eliminated from population differentiation analyses that assume HWE, and one additional marker was removed from analyses assuming stepwise mutation.

*4.3.3 Spatial Data*

For landscape genetic analyses, we used estimates of herd ranges, including total range and some seasonal ranges, compiled by Alaska Department of Fish and Game as of 2009. Updated ranges, as of August 2011, were used for the four North Slope herds. ArcMap ver. 10 (ESRI, Redlands, CA) was used to calculate range centroids, distances between pairs of herds, and areas of range overlap.

*4.3.4 Statistical Analysis for Genetic Diversity*

To estimate various measures of genetic diversity, we used Genodive ver. 2.0b21 (Miermans &Van Tienderen 2004) to calculate the number of alleles, observed heterozygosity ($H_O$), expected heterozygosity ($H_S$), and $G_{IS}$, and FSTAT version 2.9.3 (Goudet 1995) to calculate allelic richness. To compare genetic diversity between herds, we calculated the rarefacted allelic richness of each herd based on a minimum sample size of $n = 4$. We used linear regression, implemented with the Analysis ToolPak add-in for Excel, to examine the hypothesized relationship between current herd size (log-transformed) and allelic richness. We also used linear regression to determine whether a herd's allelic richness could be explained by its distance from the Porcupine herd, which we consider a proxy for a large ancestral population as it has the highest allelic richness in the state and has shown connectivity to other Alaskan herds (Mager *et al.* submitted) and some Canadian *R. t. caribou* and *R. t. groenlandicus* herds (Zittlau 2004) thought to

be at least partially derived from the same large Beringian population (Flagstad & Røed 2003).

To determine whether genetic diversity was influenced by past demographic bottlenecks, we calculated the M-ratio for each herd. The M-ratio compares the number of alleles at a locus to the allelic range (number of possible alleles) based on the assumption that under a dramatic population decline, loss of alleles causes the number of alleles to decline more rapidly than the range in allele size (Garza & Williamson 2001). For calculating herd-specific critical values for the M-ratio, we used a two-phased mutation model (90% stepwise mutation model, 10% infinite alleles model) with a variance of 12, parameters that have performed well in a variety of taxa (Garza & Williamson 2001; Hundertmark & Van Daele 2010). Values of the M-ratio were evaluated by comparison to published threshold values and to population-specific critical values calculated using Critical_M.exe (Williamson 2007).

*4.3.5 Statistical Analysis for Genetic Differentiation*

We estimated two measures of genetic differentiation between herds: $F_{ST}$ and Jost's D, which is a better estimator of differentiation in populations with high heterozygosity (Jost 2008). Pairwise $F_{ST}$ was calculated using FSTAT version 2.9.3 (Goudet 1995). Pairwise Jost's *D* was calculated with DEMEtics package ver. 0.8-2 in R (Jueterbock *et al.* 2010), and we calculated *P*-values based on 1000-fold bootstrap re-sampling. We identified pairwise differentiation significantly different from zero at a *P*-value (0.00858) calculated using the Benjamini-Yekutieli correction for multiple comparisons (Benjamini & Yekutieli 2001; Narum 2006).

To determine how genetic variance is partitioned among different scales of organization (individuals, herds, regions, and statewide), we used AMOVA. We performed this analysis in Genodive (Miermans & Van Tienderen 2004) on three different conceptual models of regional organization—Main Regions, Subregions, and Skoog's Regions (see Table 4.1)—to determine which regional model best explains

hierarchical population structure by minimizing differences within groups and maximizing differences between groups.

*4.3.6 Analysis of Hierarchical Population Structure*

To describe the genetic population structure of caribou statewide, we used program STRUCTURE version 2.3.3 (Pritchard *et al.* 2000) to determine the number of populations within the state and to assign individuals to populations. We examined 1-cluster to 20-cluster models ($K$={1...20}) for population subdivision of the 655 individuals sampled. Three iterations of each model were run, with a burn-in of 100,000 followed by 500,000 MCMC replicates and the assumptions of admixture and correlated allele frequencies among populations. We compared the 20 models using mean log likelihood (Pritchard *et al.* 2000) and the $\Delta K$ statistic (Evanno *et al.* 2005).

Because fine-scale population structure may be masked by higher-level population subdivision, we also used STRUCTURE to perform hierarchical partitioning (following Vähä *et al.* 2007). After determining the most likely $K$ in our first STRUCTURE run, we partitioned the sample by placing individuals in the cluster to which they had at least 0.50 assignment. These clusters were then re-run as separate datasets to look for any additional subdivision within each cluster, using mean log likelihood (Pritchard *et al.* 2000) and the $\Delta K$ statistic (Evanno *et al.* 2005) to select the most likely model. Three iterations each of models $K$={1...10} were run, with a burn-in of 200,000 followed by 800,000 MCMC replicates. Clusters were repeatedly partitioned, using only individuals with at least 0.50 assignment to one cluster, until no additional subdivision could be resolved.

*4.3.7 Analysis of Spatial Arrangement of Genetic Populations*

To examine the association of geographic distance between pairs of herds to the genetic distance between herds, we implemented Mantel tests in Genodive (Miermans & Van Tienderen 2004) using $1\times10^7$ permutations to calculate $P$-values. We used Nei's D

as a measure of genetic distance, and correlated it with several measures of geographic distance. We used Genodive to measure the distance between the centroids of each herd pair's total ranges and summer ranges. Summer range was not available for HOD, so we used the total range centroid for that herd. However, because caribou herd ranges vary in size, the distance between the outer extents (or edges) of herd ranges may more accurately reflect the probability of contact among herds. To encapsulate the wide variability in total range size and potential for range overlap, we calculated the distance from one herd's range centroid to the nearest location along the edge of the other herd's range using ArcGIS. For the Mantel test, we used the mean of the two distances (e.g. Distance = (AB+BA)/2, where AB = distance from Herd A centroid to Herd B edge and BA = distance from Herd B centroid to Herd A edge).

## 4.4 Results

### *4.4.1 Genetic Diversity*

Alaskan caribou were polymorphic at all 19 loci, ranging from 5 to 26 alleles per locus. Mean allelic richness (rarefacted for sample size $n = 4$) varied between herds, with the Unimak Island Herd (UCH) at the lowest (3.749) and the Porcupine Herd (PCH) at the highest (5.295; Table 4.2). A positive relationship between log herd size and allelic richness was highly significant ($p = 0.0002$; Fig. 4.2a). Two herds that deviated most from predicted values include UCH and SAP, whose allelic richness is less than expected for their herd size (though both herds are small). We also found a highly significant negative relationship between allelic richness and geographic distance from the PCH (Fig. 4.2b), indicating a decline in diversity in herds located further from large, connected herds on a continental scale.

M-ratios of two herds, SAP (0.64) and UCH (0.57), indicate they have gone through recent bottlenecks. Both herds had M-ratios below the generic critical value suggested by Garza and Williamson (2001), and below the herd-specific values assuming a pre-bottleneck theta < 50, which is very plausible for those two herds. Four additional herds—DENA, NAP, NELC, and RMC—had M-ratios below calculated herd-specific

values, assuming theta < 5. This scenario seems plausible though not likely based on the size of those herds at present. However because the mutation rate is unknown, we have little certainty in assessing a scenario of theta < 5.

*4.4.2 Genetic Differentiation of Herds*

Pairwise genetic differentiation varied greatly between herd pairs, with $F_{ST}$ values ranging from 0 – 0.23 and Jost's D values ranging from 0 – 0.69 across the 190 pairwise comparisons (Table 4.3). Jost's D values were noticeably higher than $F_{ST}$ for most herd pairs, and they are probably more accurate given the high heterozygosity within Alaskan herds. Jost's D was greater than 0.10 for 122 herd pairs out of 190. Seven herds were significantly differentiated from all other herds—CHI, GMC, MCH, NAP (not differentiated from NUSH transplant), SAP, UCH, and WMC (Table 4.3). It is worth noting that this includes all Southwest herds with $n \geq 17$ (Fig. 4.3). Outside the southwest region, only the WMC is significantly differentiated from all other herds (as are CHI ($n$ = 8) and GMC ($n$ = 5), but their small sample sizes limit inference about herd differentiation; Fig. 4.3). The degree of herd differentiation varied between regions. North Slope herds were not differentiated within their region, whereas within the Interior, the patterns are more variable. Herds in the Alaska Range (southern Interior) were generally not differentiated from one another, whereas some of the small herds to the north (WMC, GMC, WOLF) appear to be fairly distinct.

Some herds were more differentiated from those within their region than from those in other regions. The MCH was more similar to Interior and even North Slope herds than it was to herds on the Alaska Peninsula. Three herds in the northern and central Interior subregions (40CH, HOD, and RMC) were not differentiated from some North Slope herds, but demonstrate low levels of differentiation from DENA and other Interior herds. Four herds for which we had small sample sizes (CHI, GMC, NUSH, WOLF) had many pairwise comparisons with relatively high $F_{ST}$ values, but several of those were not statistically significant (Table 4.3). Those with larger sample sizes are compared in Figure 4.3.

*4.4.3 AMOVA*

We found the AMOVA method was not particularly useful for comparing models of regional organization, because so little of the variance was generated among regions. Most of the variance (96%) was within individuals. Our model that classified herds into 6 sub-regions was the best at maximizing the variance among regions (0.011%) and minimizing variance among herds within regions (0.017%). However, the other models were similar ("3 main regions" model variance was 0.005% among regions, 0.022% within regions; "Skoog's 6 regions" model variance was 0.008% among regions, 0.019% within regions).

*4.4.4 Subspecies-wide Population Structure*

Despite the fact that the 655 individuals sampled came from 20 different herds, *a priori* clustering with program STRUCTURE indicates a two-population model (K = 2) is the most likely solution based on the $\Delta K$ statistic (Evanno *et al.* 2005), with K = 5 as another likely possibility for further subdivision (Fig. 4.4). When evaluating the models based on mean log likelihood (Pritchard *et al.* 2000), three to five populations (K = 3–5) appear most likely (Fig. 4.4). The solution K = 2 seems to delimit the highest order of population subdivision, separating mainland herds from Alaska Peninsula herds. Although broad patterns of further subdivision are revealed as the number of clusters increases, few individuals have their whole genotype assigned to any of these populations beyond K = 2 (Fig. 4.4). When STRUCTURE was re-run excluding small herds ($n < 17$) to examine for the influence of uneven sample sizes, we did not see any major change in the results, though MCH and WMC appeared slightly more distinct.

Using a hierarchical partitioning method to examine subdivision beyond the K = 2 level, we examined structure within each of the 2 main clusters independently. For Cluster 1, which includes 527 individuals mostly from mainland Alaska (with 5 from NAP), there was no clear solution. Two options indicated as likely based on $\Delta K$ are K = 4 and K = 9 but neither provides neat clustering of whole individuals, though K = 4

separately clusters some herds (Fig. 4.5). This four-population model for Cluster 1 (mainland herds) appears similar to the assignment of those herds in the K = 5 solution for the full dataset (Fig. 4.5). Six herds (CHI, GMC, HOD, WOLF, WMC, MCH) had greater than 0.50 assignments to a single cluster, consistent with significant pairwise differentiation in those herds, indicating some basis in true population subdivision. However, because so many individuals had less than 0.50 assignment to any one cluster, we did not subdivide Cluster 1 for further hierarchical partitioning.

Cluster 2 included all of NUSH, SAP, and UCH; most of NAP; and a few individuals from MCH ($n$ = 3), PCH (1), RMC (1), TCH (2), and WAH (2). Based on $\Delta K$, a two-population model was the most likely. The UCH and all but one SAP formed the first cluster, whereas the NAP and NUSH along with the few individuals from mainland herds formed the second cluster (Fig. 4.5). When we divided the sample into separate datasets for each cluster and re-ran STRUCTURE on each of those, UCH and SAP grouped neatly in separate clusters (Fig. 4.5), while the NAP-dominated group resolved for K=1.

*4.5.5 Spatial Analysis*

Mantel tests indicated a significant isolation-by-distance pattern within Alaskan caribou (Fig. 4.6a), though the fit of the correlation varied between regions (Fig. 4.6b). Geographic and genetic distances were tightly correlated within the North Slope and Southwest regions, whereas the correlation for Interior herds was more noisy. For the statewide analysis, all three measures of geographic distance were significantly correlated with genetic distance but the center-to-edge distance was most strongly correlated: total range centroids ($r$ = 0.534, $P$ = 0.00048), summer range centroids ($r$ = 0.509, $P$ = 0.00085), center-edge ($r$ = 0.594, $P$ = 0.00009; Fig. 4.6).

To further examine the influence of range overlap, we examined all herds within 200 km of one another (mean center-edge distance) and compared the mean genetic distance (Nei's D) of non-overlapping herds to overlapping herds. The mean genetic

distance of non-overlapping herd pairs (Nei's D = 0.118) was greater than for overlapping herds (Nei's D = 0.067) but the difference was not significant ($P = 0.186$).

## 4.6 Discussion

### *4.6.1 Statewide Genetic Population Structure*

Our findings reveal surprisingly little genetic population structure within caribou distributed throughout the vast Alaskan mainland, with the exception of the Alaska Peninsula herds. Skoog (1968) suggested that Alaskan caribou constitute one genetic population comprised of 6 subpopulations each containing multiple herds. We find instead that the 20 caribou herds sampled statewide belong to two predominant population units: one large group on the mainland, including 5 of Skoog's 6 subpopulations, and one distinct group on the Alaska Peninsula, defined by Skoog as a single subpopulation with one primary center of habitation (Fig. 4.5). The Alaska Peninsula population contains discrete herds (Fig. 4.5), whereas the mainland pattern is less clear—the spatial distribution of genetic variance is not entirely random, yet none of our *a priori* models seems to fully explain this variance, as some herds follow an isolation-by-distance pattern more closely than others (Fig. 4.6b) and only two of the mainland herds with large enough sample sizes for interpretation are somewhat genetically discrete (Fig. 4.3). These patterns are consistent with results from Zittlau (2004), who found distinct herds on the Alaska Peninsula, but little differentiation among *R. t. granti* herds along the Alaska-Yukon border. By sampling most Alaskan herds across the state for this study, we can now say definitively that the area of greatest change in genetic variance statewide occurs at the nexus of the Alaska Peninsula and the mainland.

Isolation by distance explains part of the statewide pattern, especially when range overlap between herds is considered (Fig. 4.6a). Lack of differentiation among herds with overlapping ranges has also been observed in Canadian *R. t. caribou* and *R. t. groenlandicus* herds (Zittlau 2004; Boulet *et al.* 2007; McDevitt *et al.* 2009), though many herds without overlap are also genetically similar (Zittlau 2004; McDevitt *et al.*

2009), consistent with our study. Range overlap and distance appear to be important; however, there is notable variation between regions in the strength of those correlations and the rate at which genetic differentiation increases with increased geographic distance (Fig. 4.6b). This suggests that different, additional processes are at work in different regions of the state.

*4.6.2 Regional Patterns of Genetic Diversity and Differentiation*

The statewide population subdivision described herein does not match the three main geographic regions or the subpopulations proposed by Skoog (1968). Still, those regions describe observed patterns of spatial connectivity at present, and examining differences in the genetic characteristics of regions can help us to understand the relationship of evolutionary processes to the patterns observed today.

North Slope herds are known to lack differentiation (Cronin *et al.* 2003; Cronin *et al.* 2005; Mager *et al.,* submitted), with a highly correlated pattern of isolation by distance associated with the minor genetic differentiation among them (Mager *et al.,* submitted). When compared against the remainder of the subspecies, this study reveals that North Slope herds are among the least differentiated in the state (Table 4.3). The North Slope herds were also the four most diverse herds in the state, consistent with Canadian studies that found the greatest diversity in large migratory tundra herds (Courtois *et al.* 2003; Zittlau 2004; Boulet *et al.* 2007). Alleles per locus and heterozygosity ($H_S$) for North Slope herds were similar to migratory tundra *R. t. groenlandicus* herds in northwest Canada (Zittlau 2004) and slightly higher than migratory tundra *R. t. caribou* herds in Labrador, with more alleles in Alaskan herds at each locus in common between this study and Boulet *et al.* (2007).

Herds in the Southwest region, by contrast, are relatively genetically discrete (Zittlau 2004; Colson *et al.* in prep) with declines in diversity and increased differentiation associated with distance away from the mainland along the Alaska Peninsula (Colson *et al.* in prep). Compared to the remainder of *R. t. granti*, we find that Alaska Peninsula herds are the most discrete herds in the state (Figs. 4.3 and 4.5). They

also appear the most likely to have experienced recent bottlenecks, and this may have influenced their genetic diversity. Among Alaskan herds with adequate sample sizes, Southwest herds had the lowest allelic richness with the exception of a single Interior herd (WMC; Table 4.2).

The Interior region was the least understood prior to this study, and we find its genetic patterns are somewhat intermediate between those of the North Slope and Southwest, but much less clear. Levels of differentiation among Interior herds are generally low though significant (Table 4.3). Within the southern Interior, adjacent herds in the Alaska Range are not genetically differentiated from one another. In fact, DEL and DENA was the only herd pair in the state that showed zero differentiation based on both Jost's D and $F_{ST}$. By contrast, the small sample from the Chisana herd in the southern Interior appears genetically differentiated from other herds as expected, although the sample size ($n = 8$) is too small to make those results conclusive. In the northern Interior, HOD and RMC lacked differentiation from some Interior and North Slope herds, whereas GMC and WOLF appeared differentiated from all other herds, though extremely small sample sizes ($n = 4, 5$) makes any reasonable interpretation difficult. Within the central Interior, the 40CH and WMC were very different despite historical and current range overlap, and a hypothesized recent common origin (Durtsche & Hobgood 1990). The 40CH showed little differentiation from herds across the state (Fig. 4.3), whereas WMC was differentiated from all herds including 40CH (Fig. 4.3) and had the lowest diversity of all Interior herds (Table 4.2).

Potential pathways of inter-regional connectivity between Interior herds and those to the North and Southwest may mediate gene flow across the state, leading to the observation of statewide isolation by distance. Several Interior herds (40CH, HOD and RMC) could not be significantly differentiated from North Slope herds (Table 4.3), likely due either to historical common ancestry or recent observations of range overlap during North Slope population highs. The MCH herd to the southwest, though differentiated from most Interior herds, was generally more similar to Interior herds than to herds within its own region, suggesting greater connectivity to the Interior over the long-term

despite its recent range overlaps with the NAP and NUSH. Because the STRUCTURE results clustered all mainland herds together, while the herd-scale pairwise comparisons demonstrated differentiation among a majority of herd pairs, it appears that connectivity of each herd to just a few other herds is sufficient to maintain the inter-regional connectivity suggested by the STRUCTURE results.

*4.6.3 Herds as Genetic Units*

Sixteen herds had adequate sample sizes to draw conclusions about whether herds constitute genetic units and of those 16, five were significantly differentiated from all other herds: UCH, SAP, NAP, MCH, and WMC (mean pairwise differentiation ranging from: $F_{ST}$ = 0.03 - 0.08 and Jost's D = 0.15 - 0.44). Interestingly, those five herds also had the lowest allelic richness and heterozygosity in the state, implying that their relative distinctiveness may be associated with processes that decrease diversity, such as bottlenecks or prolonged isolation. Three additional herds with small sample sizes appeared to be distinct (CHI, GMC, and WOLF), but further study is needed to confirm this. Other Alaskan herds were not significantly differentiated from their neighbors or, sometimes, from herds long distances away. Though a majority of herd pairs were significantly differentiated, the degree of differentiation among herds in the North Slope and many in the Interior was low ($F_{ST}$ < 0.02). These results answer the question of whether herds are distinct units by showing that some herds may be distinct genetic units, while others are components of larger metapopulations.

*4.6.4 Genetic Variation in a Circumpolar Context*

The various patterns of genetic differentiation observed in Alaskan caribou at multiple spatial scales are intriguing when viewed in a circumpolar context. Herds from Alaska's North Slope are genetically differentiated from the SAP and UCH herds (pairwise $F_{ST}$ values 0.063 - 0.100) of the same subspecies, whereas the PCH (a North Slope herd) shows little differentiation from *R. t. groenlandicus* herds across Canada ($F_{ST}$ = 0.0007 - 0.016) despite its classification as a separate subspecies (Zittlau 2004). $F_{ST}$

values greater than those found by Zittlau (2004) are observed even between the WMC and PCH, whose range edges are only ~100 km apart and both overlap the 40CH. The pairwise differentiation between PCH and WMC ($F_{ST}$ = 0.022) is greater than all the values of pairwise differentiation between the PCH and several, much more distant, Canadian barren-ground herds (Zittlau 2004).

Previous studies have found dissimilarities between the genetic population structure of caribou and their morphologically determined subspecies designations based on variation in microsatellites (Zittlau 2004) and mtDNA (Flagstad & Røed 2003). Those results were somewhat unexpected, as mtDNA is thought to reflect evolutionary divergence in isolated glacial refugia, whereas microsatellites reflect more recent patterns of population connectivity (McDevitt *et al.* 2009). An alternative hypothesis for genetic structure is differences in ecotype, such that herds with similar migratory behaviors, habitat use, and seasonal aggregations, are expected to be more genetically similar regardless of subspecies. Within *R. t. caribou* of Eastern Canada, herds with different ecotypes (montane, woodland, barren-ground) are genetically differentiated from one another (Courtois *et al.* 2003), though genetic exchange has also been observed (Boulet *et al.* 2007). However, this does not explain the patterns of differentiation in the Alaskan subspecies, as North Slope herds of the migratory tundra ecotype are not differentiated from several mountain herds in the Interior, and ecotypes appear to be plastic within Alaskan herds in response to changes in density (Skoog 1968; Hinkes *et al.* 2005). Across North America, it appears that lack of genetic differentiation is a common feature among large migratory herds with overlapping ranges, regardless of their subspecies (e.g. North Slope *R. t. granti*, continental *R. t. groenlandicus*, and Labrador *R. t. caribou*). Smaller herds of the same ecotype or subspecies may be more genetically differentiated (e.g., Alaska Peninsula), suggesting influences such as effective population size, range size, habitat, and geography are important in structuring populations regardless of their subspecies or ecotype.

*4.6.5 Drivers of Genetic Structure in Alaskan Caribou*

We hypothesize four potential drivers of the genetic population structure (or lack thereof) observed in extant Alaskan caribou herds, which are thought to descend from a single, large Beringian refugial population (Banfield 1961). These factors include (1) geographic barriers to gene flow and constraints to population size, (2) habitat barriers and constraints, (3) adaptive divergence in life history traits, (4) and demographic bottlenecks coupled with isolation. Alaska's geographic landforms, relatively unchanged in shape and topography since the deglaciation and sea level rise at the end of the Pleistocene (Mann & Hamilton 1995), may influence caribou population structure by limiting and directing movements (e.g. in peninsulas and glaciated mountains) and by constraining the size of available ranges (e.g. on islands or isolated alpine areas within boreal forest), thereby limiting effective population size and gene flow. Alpine and tundra habitat availability, considered necessary for the long-term persistence of Alaskan caribou herds in any given area (Skoog 1968), may change rapidly in quality and spatial distribution (e.g. due to fire, overgrazing, climate change, human development, and hunting access), influencing gene flow and constraining range sizes on shorter time scales than geographic landforms. Topography and habitat heterogeneity may also lead different caribou herds to adopt divergent strategies for habitat utilization and predator avoidance (e.g., by constraining caribou density, thereby determining whether or not caribou aggregate and migrate; Bergerud 1996; Hinkes *et al.* 2005), which may result in adaptive divergence if herds using different strategies (learned or genetically-based) are behaviorally isolated from one another in breeding. Finally, historical demographic bottlenecks and/or persistently small population sizes cause rapid genetic divergence, relative to large stable populations, as long as gene flow is somewhat limited.

We propose that the interaction of some or all of these factors can explain why some herds and geographic regions are more genetically distinct than others. This, in turn, may assist wildlife managers in predicting the impacts of future changes in demography and landscape on caribou herds, and in designing studies to monitor the effects of such changes on the adaptive capacity of caribou. We use these four hypotheses

to interpret two interesting genetic patterns observed in this study—the subspecies-wide analysis clustering mainland herds separate from peninsula herds, and the herd-level analysis demonstrating notable differences in diversity and differentiation between the spatially overlapping 40CH and WMC herds.

*4.6.6 Hypothesized Drivers at the Subspecies Scale*

The predominant feature of subspecies-wide genetic population structure is an apparent genetic boundary at the nexus of the Alaska Peninsula, which separates the large, diverse, and relatively homogenous mainland population from several small, discrete herds with reduced diversity on the Alaska Peninsula. Isolation by distance cannot adequately explain this pattern, as genetically differentiated Alaska Peninsula herds are actually much closer together at the edges of their ranges than many mainland herds that cannot be differentiated. Several factors—varying shapes and glacial histories of landforms, a barrier to gene flow created by undesirable habitat, historical bottlenecks, and perhaps adaptations to local forage availability—may explain statewide structure instead.

During the Pleistocene, Beringian habitats supported a population of caribou in what is now mainland Alaska, whereas the Alaska Peninsula was entirely covered by glaciers (Mann & Hamilton 1995). Expansion of caribou into the recently deglaciated peninsula after the last glacial maximum may have decreased the diversity of ancestral Alaska Peninsula herds through founder effects, caused by the limited number of individuals that could be supported on the peninsula. Founder effects may have been compounded by successive colonization events down the peninsula, and by range constraints imposed by glacial re-advances as recently as 9500 BP (Mann & Hamilton 1995). The shape of the peninsula may further constrain herds by limiting the potential for population expansions and range shifts, and by constraining gene flow to a linear pathway. By contrast, herds on the mainland are able respond more dynamically to increases in density through range expansions and shifts, which may help to maintain high effective population size and gene flow with surrounding herds. Thus, the Alaska

Peninsula with isolation by distance over significantly differentiated subpopulations may best conform to a one-dimensional stepping-stone model of gene flow, whereas herds on the mainland with weaker differentiation and isolation by distance conform more to an island metapopulation model of gene flow.

Alaska Peninsula caribou, limited in their ability to disperse to new areas, may be more apt to experience severe reductions in population size when habitat quality (much of which is considered "marginal"; Skoog 1968) declines due to periodic volcanic eruptions (Skoog 1968). Additionally, market hunting may have caused a recent bottleneck in the once "exceedingly abundant" UCH, which was "greatly reduced" by hunting in the 1800s (Allen 1902). Bottlenecks can accelerate divergence through random genetic drift (Nei *et al.* 1975), though this may be counteracted over time by gene flow from neighboring populations. However, mainland herds recovering from bottlenecks are more likely to experience gene flow than Alaska Peninsula herds. Skoog (1968) described several features that can serve as barriers to movement (thus limiting gene flow) between herds on the Alaska Peninsula, including glaciers, rocky mountainous areas, open ocean, and volcanic cinders. The habitat surrounding Lake Iliamna and the Kvichak River, where the Alaska Peninsula joins the mainland, is also not ideal caribou habitat. Within the last century, forest fires (Skoog 1968) and overgrazing of the area by domestic reindeer (Leopold & Darling 1953) apparently caused caribou to abandon their use of the area. Skoog (1968) stated, "no movement across this border has been recorded since prior to 1900", though MCH and NAP have both utilized the area in the last 20 years (Hinkes *et al.* 2005) and through the 1800s caribou are thought to have moved between the peninsula and the large Bering Seacoast herd that once existed on the mainland (Banfield 1961). By contrast, all other potential boundaries between caribou regions on the mainland (especially forested river valleys that support high predator densities and moist coastal areas with extensive snow fall) are noted to be permeable and occasionally used by caribou (Skoog 1968), an assertion supported by movement data in recent years (Alaska Department of Fish and Game 2009a).

Given the differences in historical and spatial dynamics between the mainland and peninsula populations, and their isolation from one another, adaptive divergence is also a plausible explanation. *R. t. granti* was originally described from Alaska Peninsula specimens (Allen 1902), and Banfield (1961) noted a gradation in size from the larger-bodied Alaska Peninsula caribou to the small North Slope caribou, such that caribou in northern Alaska could not be separated from *R. t. groenlandicus* in northern Canada or *R. t. granti* on the Alaska Peninsula. However, the greatest change in size seems to occur between herds of the North Slope and herds to the south (including Interior and Alaska Peninsula herds; Banfield 1961) rather than between peninsula and mainland populations. Based on observed changes in the morphology of transplanted caribou, it seems that environmental conditions may have a greater influence on morphological gradients in Alaskan caribou than differences in genetics (Skoog 1968). However, the potential for divergence to be driven by adaptive differences between mainland herds and peninsula herds cannot be ruled out.

*4.6.7 Hypothesized Drivers at the Herd Scale – Sympatric Ecotypes*

Understanding how our four hypothesized drivers of genetic differentiation operate at the herd scale is important because it allows us to go beyond the question of whether herds are distinct, by enabling us to examine what causes some to be more distinct than others. The most intriguing example of this in Alaska is the case of the Fortymile (40CH) and White Mountains (WMC) herds, which share a portion of their range but differ greatly in their genetic diversity and connectivity to other herds.

The 40CH was thought to be the largest herd in Alaska and the Yukon Territory in the earlier part of the 20$^{th}$ century, estimated at over 500,000 in the 1920s (Murie 1935). At that time, the 40CH had its primary calving area in the White Mountains (Murie 1935, Skoog 1956). The herd continued to use the White Mountains calving area throughout a sharp population decline in the 1930s and a subsequent rebound to ~50,000 by the 1960s (Valkenburg & Davis 1986). In 1950s-60s, however, the 40CH shifted its calving distribution to areas to the southeast (Valkenburg & Davis 1986) that are still

used today (Gross 2009). The 40CH continues to utilize parts of the White Mountains during summer and early fall (Durtsche & Hobgood 1990). It currently numbers approximately 40,000 (Gross 2009). Based on the 40CH herd's extensive historical range and more recent observations of range overlap with several herds (Fig 1), including use of common wintering areas with the PCH (Valkenburg & Davis 1986), it is likely that extensive opportunities have existed for gene flow with other herds. Its lack of genetic differentiation from most other herds on the Alaskan mainland (Table 4.3) suggests long-term genetic connectivity.

Less is known about the history of the WMC, as it was only confirmed to be a separate herd with its own calving area in the 1970s (Selinger 2001). The herd was estimated at only ~150 individuals in 1978, but grew to ~900 in 1992 (Selinger 2001) before declining to 600-700 by 2007 (Seaton 2009). Based on common range use by 40CH and WMC, and the suitability of the area's terrain and habitat for caribou, there is no evidence of geographic or habitat barriers to gene flow between the WMC and the 40CH. Instead, their differentiation may be explained by different strategies of habitat utilization. The 40CH has occurred at high densities in the past and is considered to belong to the migratory mountain ecotype (Festa-Bianchet *et al.* 2011). The WMC, by contrast, is a low-density herd (Selinger 2001; Seaton 2009) that fits the description of the sedentary montane ecotype. In contrast to barren-ground herds that are aggregated during calving and other parts of the year, the WMC often occurs in small groups within forested areas (Selinger 2001) and is dispersed during calving (Durtsche & Hobgood 1990, Seaton 2009) in treeless high-elevation areas (Selinger 2001).

The differences in genetic diversity between the 40CH and WMC are consistent with differences in their population sizes; however, differences in ecotype do not make the mechanism or temporal scale of their genetic differentiation immediately clear. Durtsche and Hobgood (1990) considered the WMC a "remnant" of the 40CH from its last population high, and predicted that animals would disperse between the two herds when the 40CH re-expands into WMC range in the future. However, genetic data do not support this view and instead suggest that the WMC existed prior to the declines and

range shifts of the 40CH within the last century. Genetic differentiation between the 40CH and WMC is not large at first glance ($F_{ST}$ = 0.0196, Jost's D = 0.1024), but given the lack of differentiation between the 40CH and others herds in mainland Alaska, it is surprising. For perspective, it is worth noting that measures of 40CH-WMC pairwise differentiation are comparable to those between 40CH and NAP (*Fst* = 0.0189, Jost's *D* = 0.1163), which occur 1,080 km apart. In order for the observed levels of differentiation between WMC and 40CH to have developed within the last 100 years (approx. 25 generations), the WMC would need to have experienced a severe bottleneck when it split from the 40CH. However, we find no evidence of bottlenecks in the WMC (M-ratio = 0.83). Furthermore, though the herd is very small and has lower allelic richness than other mainland herds, it has not been geographically isolated from contact with the 40CH. Despite this opportunity for gene flow recently, and presumably historically, genetic differentiation suggests that interbreeding and dispersal may be uncommon. Thus, data suggest that the 40CH and WMC have remained differentiated despite being sympatric for some time.

Caribou herds are defined on the basis of fidelity to common calving areas, so it is intriguing that 40CH and WMC likely existed as different herds while the 40CH was utilizing calving areas in the White Mountains. Though little historical information is available about the WMC, a few observations provide evidence that the WMC shared a common calving area with 40CH but used a separate winter range, prior to the shift in 40CH calving areas away from the White Mountains in the 1950s. Skoog (1956) cites several observations by H. Bucholtz, a long-time resident on Beaver Creek in the heart of the WMC range, that are consistent with migratory patterns of the WMC. Bucholtz observed bulls remaining on Beaver Creek in the winter of 1944-45, and noted a "fall movement westward across Beaver Creek" and that a "run of cows and young animals moved east across Beaver Creek to calving grounds" (Skoog 1956). Murie (1935) also noted more generally that small groups were scattered throughout the 40CH migratory range in winter, including "some localities harboring only a few small bands". It seems unlikely that caribou from the large, historical 40CH would have used completely

separate calving areas from the WMC when both calved in the White Mountains. Indeed, Durtsche and Hobgood (1990) cite writings by Olson who in 1956 reported 40CH caribou calving on the upper ridges of Bear Creek and Quartz Creek drainages, some of the exact same locations used by WMC today.

To retain genetic differentiation despite range overlap and historical use of a common calving ground, some mechanism must exist to limit gene flow between WMC and 40CH. Based on our knowledge of caribou ecology, retaining a distinct herd identity and genetic differentiation would seem to require strong fidelity of both WMC and 40CH to social groups and/or seasonal ranges (thereby minimizing immigrations and emigrations when the herds mingle), coupled with either a lack of contact or herd-specific mate selection during the rut (thereby minimizing gene flow). If fidelity of either herd were not strong, 40CH caribou could remain with WMC for the winter (perhaps unlikely based on the observed "migratory urge" of aggregated caribou; Skoog 1956) or WMC caribou could join the 40CH and migrate away. It is possible that this has occurred, but that some WMC caribou have retained range fidelity. A recent study of location data in Canadian herds found that strong spatial affinity of females maintained demographically separate subpopulations even during calving area shifts and, most notably, when two subpopulations shared a calving area (Nagy et al. 2011). In the WMC and 40CH, spatial affinity based perhaps in a migratory tradition among each group of females (Skoog 1968) may have been important in maintaining the use of separate winter areas despite a common calving ground.

It is unclear what mechanism limits gene flow over the long-term between 40CH and WMC during the rut, though differences in habitat selection or mate selection seem two likely hypotheses. There is inadequate information to evaluate either of these. Both 40CH and WMC breed during fall migration between summer and winter ranges. At present, 40CH rut in areas to the south and southeast of the White Mountains (Gross 2009), whereas WMC ruts while on northwestward movements through the White Mountains area to their winter range in open black spruce forests (Durtsche & Hobgood 1990). The 40CH and WMC probably have not overlapped during the rut at least since

the 1980s (J. Herriges, personal communication). It is possible that subpopulation density drives divergent approaches to habitat selection during fall and winter, creating ecologically driven allopatry during the breeding season. It is also possible that inherited predispositions for rutting behavior limit gene flow despite the opportunity for contact. Biologists have observed larger body size in WMC caribou and potential differences in antler morphology (J. Herriges, personal communication), which could plausibly provide some basis for assortative mating. This would be surprising in Alaskan caribou, as biologists have observed rutting associations to be very fluid even over the course of a day within the 40CH and North Slope herds (Skoog 1956; Lent 1965). However, Lent (1965) predicts, "in populations showing migratory behaviour during the rutting season there is a decreased emphasis on the maintenance of rutting groups", implying that sedentary herds may be more likely to recognize individuals and maintain rutting groups.

Bergerud (1996) predicted that both migratory (aggregated) and sedentary (dispersed) ecotypes should be found in areas with plateaus adjacent to rugged topography. This has been observed in southwest Alaska (Hinkes *et al.* 2005) and seems suitable to explain the co-existence of the WMC and 40CH (though the topography is rolling hills and mountains, not flat plateaus). Hinkes *et al.* (2005) observed that the transplanted NUSH herd utilizes a dispersed strategy in treeless terrain despite originating from the migratory NAP herd and that the montane Kilbuck herd used a dispersed strategy until it came into contact with the migratory MCH and was subsumed by that herd. It is not clear why the NUSH did not join the MCH, as it also mingled with that herd (Hinkes *et al.* 2005). These observations lead Hinkes *et al.* (2005) to describe ecotypes within *R. t. granti* as a choice of strategy made by caribou herds, rather than a genetically predisposed trait. By contrast, ecotypes of Canadian *R. t. caribou* may have some genetic basis (Courtois *et al.* 2003). A study of *R .t. caribou* in the Canadian Rocky Mountains, where a contact zone occurs between mtDNA haplotypes from northern and southern glacial refugia, found evidence of greater migratory tendencies within individuals with northern haplotypes (McDevitt *et al.* 2009). Alaskan caribou are thought to originate from a large northern refugia and this basic similarity may mean that

divergent ecotype strategies do not have separate evolutionary roots. However, we cannot determine whether genetic variation in the neutral markers used for this study indicates any genetic predisposition for ecotypes. Other sedentary herds examined in our study (CHI, GMC, WOLF) appear to be genetically differentiated from neighboring herds, but sample sizes were small ($n$ = 4 - 8) and additional work is needed to confirm those results. Though we propose potential hypotheses that drive population genetic patterns within Alaskan caribou, further research is needed to determine whether Alaskan ecotypes differ in other aspects of behavior (including rutting behavior and mate choice, dispersal, and spatial or social fidelity) or in mtDNA and functional genes.

*4.6.8 Conclusions and Management Implications*

Using microsatellite data from 20 herds of Alaskan caribou, we showed that population structure is organized in multiple spatial scales—two main population clusters (one large mainland population and one smaller Alaska Peninsula population), and 20 herds (management units) of which 5 were genetically distinct from all others, and 4 could not be interpreted due to small sample size. Similar patterns are found in other highly mobile and widely distributed species. African wildebeest (*Connocheates spp.*) are known, like caribou, for their long-distance migrations in large herds. Despite the recent isolation of South African Blue Wildebeest (*C. taurinus*) on game ranches, analysis of protein-coding loci indicates very little differentiation among populations (pairwise $F_{ST}$ > 0.0021; Grobler & Van der Bank 1993). The Plains Zebra (*Equus quagga*) is distributed throughout arid regions of sub-Saharan Africa in 6 subspecies displaying great phenotype variability (Lorenzen *et al.* 2008). However, genetic analysis using mtDNA and microsatellites found high variation and low differentiation across several thousand kilometers (Lorenzen *et al.* 2008), similar to Alaskan caribou.

Patterns of genetic variation in several migratory birds also show parallels with caribou. Adelie penguins (*Pygoscelis adeliae*) number more than 10 million animals and, like caribou, show natal philopatry to colonies that vary widely in size (Røeder *et al.* 2001). Røeder *et al.* (2001) found high genetic diversity but little genetic differentiation

(pairwise $F_{ST} < 0.02$) between colonies, which they suggest is due to the slow speed of genetic drift within the large population. Canada Geese (*Branta canadensis*) in Alaska fall into two genetically and morphologically discrete groups. Subspecies in the small-bodied group are found mostly in Southwest Alaska and the North Slope, while subspecies in the large-bodied group are found mostly in Interior, Southcentral and Southeast Alaska. However, genetic differentiation among populations and subspecies within these two groups varied greatly, suggesting some recent and ongoing gene flow within large regions, as with caribou. The marbled murrelet (*Brachyramphus marmoratus*), a sea bird found in Alaska, has few barriers to dispersal, philopatry to breeding areas, and differential habitat selection in different parts of the state (Congdon *et al.* 2000). Only murrelet populations at the extreme edges of the range in the Aleutian Islands were genetically differentiated; those on the mainland (including the Alaska Peninsula) were not (Congdon *et al.* 2000). The authors consider multiple evolutionary hypotheses for this pattern and conclude that small populations at the extremes the species' range may diverge through drift alone (Congdon *et al.* 2000), an analogy relevant perhaps to Alaska Peninsula caribou.

The patterns of population differentiation we observe have relevance to population-based management of Alaskan caribou and, perhaps, to other abundant and mobile species such as those profiled above. Caribou herds sharing a common calving ground constitute management units, yet knowledge about their demographic independence has been limited mostly to studies of female movements and dispersal. Based on our study, we now know that some of those herds are fairly genetically distinct while others are not. Demographic bottlenecks and geographic isolation likely explain why Alaska Peninsula herds are distinct. On the mainland, the White Mountains herd (WMC) is differentiated from the large migratory herd with which it overlaps in range. Though divergence due to genetic drift is more rapid in small herds like the WMC, we find no evidence of recent bottlenecks, suggesting differences in habitat selection and potentially in rutting and calving behavior have enabled the two herds to remain differentiated while sympatric. This may be the case for other sedentary herds within the

ranges of larger herds in Alaska, though further study is needed. More research on rutting behavior, dispersal, and functional genes is needed to understand whether the divergent strategies of Alaskan caribou ecotypes are evidence of adaptive divergence or behavioral plasticity.

Most herds we examined were not genetically distinct, suggesting gene flow among them. A lack of genetic differentiation indicates a lack of demographic independence over the long term. However, the historical patterns of gene flow reflected in genetics may not match current patterns of dispersal and gene flow within a given region if equilibrium between gene flow and genetic drift has not been achieved (Hutchison and Templeton 1999). Various models of isolation-by-distance (IBD) can indicate whether populations within a region are at migration-drift equilibrium (Hutchison and Templeton 1999). Alaskan caribou are isolated by distance ($r = 0.6$), but the residuals of the IBD relationship show no association with distance ($r = 0$) and thus do not meet the second equilibrium model assumption that IBD weakens as distance increases (Hutchison and Templeton 1999).

When regional patterns of IBD are compared to Hutchison and Templeton's (1999) models, it appears that Southwest herds, which conform to the stepping-stone model of IBD ($r = 0.88$); (Case I in Hutchison and Templeton 1999), may be at migration-drift equilibrium. By comparison, North Slope herds exhibit IBD ($r = 0.97$) but show very little genetic differentiation over large distances, suggesting gene flow may be more influential on their population structure than genetic drift (Case II in Hutchison and Templeton 1999). Indeed, this is to be expected in large populations like the North Slope herds where divergence due to drift is very slow, suggesting even a small number of migrants between them may be effective in countering genetic divergence. Interior herds exhibit the weakest association between distance and genetic differentiation ($r = 0.53$), suggesting the region, as a whole, may not be at migration-drift equilibrium. This is logical, given that fluctuations in herd size and range extent on the mainland are likely to result in variable patterns of genetic connectivity over time, consistent with the dynamics expected in a metapopulation. The great variation in herd size in this region may also be

influential, such that drift has a disproportionate effect on small herds relative to larger herds.

Therefore, genetic findings indicate long-term average gene flow among herds but may not reflect current patterns of dispersal between herds. In determining units for population management, combining genetic data with information on inter-herd dispersal will most accurately reflect demographic relationships among herds. Additional research on male dispersal and rut interactions between herds may be needed to understand the extent to which our genetic findings reflect current demographics. However, the fact that herds are likely not at equilibrium suggests our genetic findings may overestimate gene flow. In other words, mainland herds have experienced more gene flow than peninsula herds over time, but their lack of differentiation does not necessarily indicate substantial exchange of individuals at present.

It is also important to realize that two herds may be demographically independent (i.e. nearly all individuals remain with their natal herd) *and* exchange genes. Caribou are thought to have open and tenuous associations during the rut (Lent 1965), therefore interbreeding between herds may occur when they overlap during the rut, even if individuals return to their own calving area the next spring. Therefore, population dynamics within each herd may be independent over the time scales relevant to management, even if they experience substantial gene flow from other herds. The fidelity of caribou to seasonal ranges implies that migratory traditions are an important feature of caribou ecology and are an important unit of management regardless of their genetic distinctiveness. Maternally inherited genes (e.g. mtDNA) may reflect female philopatry in caribou, and show greater genetic differentiation, than nuclear markers such as microsatellites used for our study (Roffler *et al.* in press).

We recommend that, in addition to herd management, caribou habitats be managed to allow continued gene flow to occur naturally between genetically similar herds over the long term. Maintaining large effective population sizes is important for retaining the substantial genetic diversity in caribou, which is essential to adaptive capacity (Frankham 1996). Given that range expansions and shifts appear to be an

important response of caribou to environmental change, managing for large effective population size and gene flow will require maintenance of migratory pathways and potential future ranges, in addition to critical seasonal habitats. Maintaining the capacity of the subspecies to undergo range expansions and shifts over the long term will help it to retain genetic variability needed for adaptation and enable behavioral plasticity, an important response to environmental variability. Variability in the terrestrial environments of Alaska may necessitate variability in caribou movements compared to migratory birds or sea mammals (Lent 1965). Caribou have the mobility to react to change but require space to do so and, as such, researchers have suggested that the conservation of large and spatially heterogeneous areas is important to long-term caribou management (Bergerud *et al.* 1984; Hinkes *et al.* 2005; Mårell & Edenius 2006, Person *et al.* 2007). The results of this study confirm large-scale spatial connectivity between caribou herds and support coordinated management of herds at a statewide scale.

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**Table 4.1. Caribou herds sampled and their characteristics** (page 1 of 3)

| Herd | Pop. Size | Range Size ($Km^2$) [F] | Range Overlaps | ($Km^2$) | Region | Subregion | Skoog's Region [H] | Ecotype [I] | Sample Size |
|---|---|---|---|---|---|---|---|---|---|
| Fortymile (40CH) | 38364 [A] | 70866 | NELC<br>PCH<br>WMC | (16497)<br>(171)<br>(1318) | Interior | Central | V | A [J], M | 25 |
| Central Arctic (CAH) | 66772 [A] | 114995 | PCH<br>TCH<br>WAH | (36648)<br>(47802)<br>(37062) | North Slope | n/a | IV | A, T | 66 |
| Chisana (CHI) | 766 [A] | 6700 | none | | Interior | Southern | VI | D [N], M | 8 |
| Delta (DEL) | 2985 [A] | 12159 | NELC | (1794) | Interior | Southern | VI | A [J], M | 25 |
| Denali (DENA) | 2070 [B] | 16250 | NELC | (66) | Interior | Southern | II | A or D [M], M | 29 |
| Galena Mountain (GMC) | 93 [C] | 5487 | WAH | (1417) | Interior | Northern | III* | D, M [N,0,P] | 5 |
| Hodzana Hills (HOD) | 1107 [D] | 7626 | PCH<br>RMC | (265)<br>(911) | Interior | Northern | IV* | U [N], M | 20 |
| Macomb (MAC) | 1305 [A] | 3339 | none | | Interior | Southern | VI* | U [N], M | 24 |
| Mulchatna (MCH) | 30000 [A] | 135875 | NAP<br>NUSH | (4094)<br>(53) | Southwest | Mainland | II | A, M | 77 |
| Northern AK Pen. (NAP) | 2250 [A] | 52315 | MCH | (4094) | Southwest | Peninsula | I | A [Q], M | 72 |

**Table 4.1 continued. Caribou herds sampled and their characteristics** (page 2 of 3)

| Herd | Pop. Size | Range Size ($Km^2$) [F] | Range Overlaps | ($Km^2$) | Region | Subregion | Skoog's Region [H] | Ecotype [I] | Sample Size |
|---|---|---|---|---|---|---|---|---|---|
| Nelchina (NELC) | 33288 [A] | 66783 | 40CH<br>DEL<br>DENA | (16497)<br>(1794)<br>(66) | Interior | Southern | VI | A, M | 22 |
| Nushugak Pen. (NUSH) | 556 [C] | 2365 | MCH | (53) | Southwest | Peninsula [G] | I* | D [Q], M | 5 |
| Porcupine (PCH) | 169000 [E] | 224385 | 40CH<br>CAH<br>HOD | (171)<br>(36648)<br>(265) | North Slope | n/a | IV | A, B [K] | 60 |
| Ray Mountains (RMC) | 1850 [A] | 10067 | HOD | (911) | Interior | Northern | III* | A or D [R], M [N] | 23 |
| Southern AK Pen. (SAP) | 700 [A] | 8387 | none | | Southwest | Peninsula | I | A or D [N], M | 30 |
| Teshekpuk (TCH) | 64106 [A] | 114787 | CAH<br>WAH | (47802)<br>(103514) | North Slope | n/a | III* | A, T | 52 |
| Unimak Island (UCH) | 350 [A] | 4108 | none | | Southwest | Peninsula | I | U [N], M | 17 |
| Western Arctic (WAH) | 348000 [F] | 377465 | CAH<br>GMC<br>TCH<br>WOLF | (37062)<br>(1417)<br>(103514)<br>(512) | North Slope | n/a | III | A, T | 67 |
| White Mountains (WMC) | 620 [A] | 8093 | 40CH | (1318) | Interior | Central | V* | D [S], M | 24 |
| Wolf Mountain (WOLF) | 400 [C] | 6696 | WAH | (512) | Interior | Northern | III* | D [N], M | 4 |

**Table 4.1 continued. Caribou herds sampled and their characteristics** (page 3 of 3)

Population size estimates are the most recent available estimates from management reports: [A] Alaska Department of Fish and Game 2009a; [B] Adams 2011; [C] Alaska Department of Fish and Game 2009b; [D] Tim Craig, pers. comm., based on 2005 count; [E] Alaska Department of Fish and Game 2011a; [F] Alaska Department of Fish and Game 2011b. Methods for population estimation vary, and are indicated by formatting of superscript text: *minimum estimates from aerial census*, total estimates derived from various data, and *other exact counts*. When estimates were reported as a range, the mean was used. For specific information on the methods of each herd size estimate, please consult the original management reports.

[F] Range area ($Km^2$) was calculated for each herd from herd shape files as of 2009 with the exception of the 4 North Slope herds, which were calculated from total range polygons updated August 2011 (all shape files from Alaska Department of Fish and Game). Areas of overlap between these herd total ranges were calculated in $Km^2$ for herds that overlap geographically. Note that herd ranges are the total annual ranges, delineated based on multiple years of observation. Therefore, range overlap between two herds does not signify whether actual overlap of animals occurs in any given season or year.

[G] NUSH formed in the 1980s from animals transplanted from the northern Alaska Peninsula. Thus, it is designated a peninsula herd despite its current location on the mainland.

[H] Regions defined by Skoog (1968) around "centers of habitation" for Alaskan caribou. *These were not yet recognized as independent herds at the time of Skoog's work (1968), so they have been assigned to the region they predominantly occupy.

[I] Ecotypes have been defined variously on the basis of calving density, migratory behavior, and range habitat characteristics (Bergerud 1996, Hinkes *et al.* 2005, Festa-Bianchet *et al.* 2011). For each herd, we denote two ecotype characteristics: Calving density and Range characteristics. Calving density is either aggregated (A) usually in migratory herds or dispersed (D) usually in relatively sedentary herds, following Bergerud (1996). Herds are also categorized either as tundra (T) or mountain (M) ecotypes after Festa-Bianchet *et al.* (2011). Some herd ecotypes are undetermined (U) based on information available in the published literature.

[J] Bergerud 1996; [L] Chisana Caribou Herd Working Group 2010; [M] Adams and Dale 1998; [N] Alaska Department of Fish and Game 2009; [0] Stout 2001; [P] Robinson 1991; [Q] Hinkes et al. 2005; [R] Jandt 1998; [S] Durtsche and Hobgood 1990, Seaton 2009, and Selinger 2001

**Table 4.2. Genetic diversity of Alaskan caribou herds**

| Herd | A | $A_4$ | $A_{16}$ | Ho | Hs | Gis |
|---|---|---|---|---|---|---|
| 40CH | 10.158 | 5.106 | 9.129 | 0.806 | 0.853 | 0.055 |
| CAH | 13.737 | 5.241 | 10.014 | 0.825 | 0.856 | 0.036 |
| CHI | 6.211 | 4.544 | n/a | 0.836 | 0.797 | -0.048 |
| Del | 10.316 | 5.116 | 9.271 | 0.829 | 0.850 | 0.025 |
| DENA | 9.895 | 5.040 | 8.778 | 0.848 | 0.844 | -0.004 |
| GMC | 4.421 | 3.977 | n/a | 0.684 | 0.704 | 0.028 |
| HOD | 10.158 | 5.102 | 9.445 | 0.796 | 0.849 | 0.063 |
| MAC | 9.526 | 4.898 | 8.720 | 0.789 | 0.827 | 0.046 |
| MCH | 11.684 | 4.816 | 8.517 | 0.790 | 0.820 | 0.036 |
| NAP | 10.579 | 4.819 | 8.354 | 0.825 | 0.822 | -0.003 |
| NELC | 9.368 | 4.862 | 8.579 | 0.837 | 0.830 | -0.009 |
| NUSH | 5.158 | 4.551 | n/a | 0.811 | 0.793 | -0.022 |
| PCH | 13.158 | 5.295 | 9.940 | 0.842 | 0.859 | 0.020 |
| RMC | 9.368 | 4.865 | 8.629 | 0.817 | 0.825 | 0.010 |
| SAP | 7.263 | 4.077 | 6.492 | 0.717 | 0.752 | 0.046 |
| TCH | 12.737 | 5.213 | 9.835 | 0.828 | 0.855 | 0.032 |
| UCH | 5.579 | 3.749 | 5.540 | 0.692 | 0.708 | 0.023 |
| WAH | 12.947 | 5.263 | 9.796 | 0.841 | 0.859 | 0.021 |
| WMC | 9.105 | 4.761 | 8.268 | 0.782 | 0.813 | 0.038 |
| WOLF | 4.632 | 4.632 | n/a | 0.763 | 0.827 | 0.077 |

A = mean number of alleles per locus

$A_4$ = rarefacted allelic richness (min. sample $n = 4$)

$A_{16}$ = rarefacted allelic richness (min. sample $n = 16$)

Ho = observed heterozygosity

Hs = expected heterozygosity

Gis = inbreeding coefficient

**Table 4.3. Genetic differentiation among pairs of herds.** $F_{ST}$ values above diagonal and Jost's $D$ below diagonal. Negative values have been converted to zeros. Values in ***bold italics*** are significantly different from zero based on a critical value ($p$ = 0.00858) corrected for multiple comparisons using the modified false discovery rate of Benjamini and Yekutieli (2001). Out of 190 total herd pairs, 155 were significantly differentiated using $F_{ST}$ and 164 were significantly differentiated using Jost's $D$.

| | 40CH | CAH | CHI | DEL | DENA | GMC | HOD | MAC | MCH | NAP | NELC | NUSH | PCH | RMC | SAP | TCH | UCH | WAH | WMC | WOLF |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **40CH** | | 0.0011 | ***0.0192*** | 0.0043 | ***0.0059*** | ***0.0904*** | ***0.0067*** | 0.0052 | ***0.0068*** | ***0.0189*** | 0.0054 | ***0.0192*** | 0.0026 | 0.0022 | ***0.0743*** | 0.0011 | ***0.1088*** | ***0.0040*** | ***0.0196*** | ***0.0368*** |
| **CAH** | 0.0137 | | ***0.0235*** | ***0.0045*** | ***0.0066*** | ***0.0857*** | 0.0076 | ***0.0108*** | ***0.0104*** | ***0.0159*** | ***0.0073*** | 0.0211 | 0.0006 | 0.0036 | ***0.0639*** | 0.0000 | ***0.0956*** | 0.0017 | ***0.0198*** | 0.0315 |
| **CHI** | ***0.1069*** | ***0.1344*** | | ***0.0295*** | ***0.0241*** | ***0.1171*** | ***0.0411*** | ***0.0368*** | ***0.0382*** | ***0.0540*** | ***0.0296*** | ***0.0731*** | ***0.0262*** | ***0.0377*** | ***0.0925*** | ***0.0293*** | ***0.1286*** | ***0.0232*** | ***0.0425*** | ***0.0565*** |
| **DEL** | 0.0277 | ***0.0316*** | ***0.1605*** | | 0.0000 | ***0.0885*** | ***0.0096*** | 0.0042 | ***0.0142*** | ***0.0234*** | 0.0057 | 0.0226 | 0.0026 | ***0.0079*** | ***0.0671*** | ***0.0066*** | ***0.1126*** | ***0.0054*** | ***0.0232*** | 0.0319 |
| **DENA** | 0.0345 | ***0.0444*** | ***0.1160*** | 0.0000 | | ***0.0897*** | ***0.0088*** | ***0.0069*** | ***0.0104*** | ***0.0234*** | 0.0053 | ***0.0309*** | ***0.0071*** | ***0.0064*** | ***0.0804*** | ***0.0076*** | ***0.1153*** | ***0.0081*** | ***0.0149*** | ***0.0421*** |
| **GMC** | ***0.3192*** | ***0.3093*** | ***0.3599*** | ***0.3006*** | ***0.2891*** | | ***0.0573*** | ***0.0864*** | ***0.1015*** | ***0.1075*** | ***0.1022*** | ***0.1313*** | ***0.0929*** | ***0.0884*** | ***0.1663*** | ***0.0858*** | ***0.2294*** | ***0.0876*** | ***0.1272*** | 0.0763 |
| **HOD** | ***0.0474*** | ***0.0488*** | ***0.2092*** | ***0.0574*** | ***0.0547*** | ***0.2069*** | | ***0.0158*** | ***0.0213*** | ***0.0234*** | ***0.0203*** | ***0.0303*** | 0.0082 | 0.0099 | ***0.0778*** | ***0.0074*** | ***0.1138*** | ***0.0097*** | ***0.0346*** | 0.0239 |
| **MAC** | 0.0299 | ***0.0715*** | ***0.1946*** | 0.0319 | ***0.0462*** | ***0.2547*** | ***0.0954*** | | ***0.0166*** | ***0.0318*** | 0.0019 | ***0.0359*** | ***0.0093*** | ***0.0126*** | ***0.0944*** | ***0.0150*** | ***0.1338*** | ***0.0162*** | ***0.0250*** | 0.0347 |
| **MCH** | ***0.0365*** | ***0.0557*** | ***0.1792*** | ***0.0744*** | ***0.0510*** | ***0.3064*** | ***0.1047*** | ***0.0887*** | | ***0.0220*** | ***0.0163*** | ***0.0297*** | ***0.0140*** | ***0.0085*** | ***0.0870*** | ***0.0120*** | ***0.1260*** | ***0.0177*** | ***0.0313*** | ***0.0545*** |
| **NAP** | ***0.1163*** | ***0.0965*** | ***0.2750*** | ***0.1398*** | ***0.1243*** | ***0.3796*** | ***0.1312*** | ***0.1810*** | ***0.1198*** | | ***0.0303*** | 0.0000 | ***0.0176*** | ***0.0193*** | ***0.0439*** | ***0.0190*** | ***0.0865*** | ***0.0249*** | ***0.0409*** | ***0.0640*** |
| **NELC** | 0.0323 | ***0.0504*** | ***0.1596*** | 0.0357 | 0.0260 | ***0.3462*** | ***0.1153*** | 0.0098 | ***0.0857*** | ***0.1570*** | | ***0.0376*** | ***0.0125*** | ***0.0155*** | ***0.0884*** | ***0.0134*** | ***0.1317*** | ***0.0121*** | ***0.0248*** | ***0.0448*** |
| **NUSH** | ***0.1198*** | ***0.1183*** | ***0.3261*** | ***0.1261*** | ***0.1427*** | ***0.4261*** | ***0.1930*** | ***0.1767*** | ***0.1584*** | 0.0020 | ***0.1747*** | | 0.0215 | ***0.0153*** | ***0.0345*** | 0.0208 | ***0.1062*** | ***0.0294*** | ***0.0540*** | ***0.0768*** |
| **PCH** | 0.0154 | 0.0070 | ***0.1433*** | 0.0177 | ***0.0447*** | ***0.3455*** | ***0.0470*** | ***0.0680*** | ***0.0719*** | ***0.1076*** | ***0.0825*** | ***0.1084*** | | ***0.0069*** | ***0.0633*** | 0.0017 | ***0.0985*** | ***0.0044*** | ***0.0219*** | 0.0341 |
| **RMC** | 0.0126 | 0.0265 | ***0.1972*** | 0.0385 | ***0.0371*** | ***0.2814*** | ***0.0469*** | ***0.0748*** | ***0.0463*** | ***0.1115*** | ***0.0940*** | 0.0724 | ***0.0382*** | | ***0.0707*** | 0.0014 | ***0.1006*** | ***0.0100*** | ***0.0230*** | 0.0392 |
| **SAP** | ***0.3624*** | ***0.3224*** | ***0.3855*** | ***0.3199*** | ***0.3534*** | ***0.5937*** | ***0.3710*** | ***0.4287*** | ***0.3905*** | ***0.2063*** | ***0.3767*** | ***0.1448*** | ***0.3116*** | ***0.3230*** | | ***0.0640*** | ***0.0675*** | ***0.0698*** | ***0.0958*** | ***0.1019*** |
| **TCH** | 0.0166 | 0.0001 | ***0.1616*** | ***0.0478*** | ***0.0470*** | ***0.3135*** | 0.0398 | ***0.0953*** | ***0.0695*** | ***0.1149*** | ***0.0921*** | ***0.1189*** | 0.0101 | 0.0138 | ***0.3212*** | | ***0.0958*** | 0.0003 | ***0.0215*** | ***0.0424*** |
| **UCH** | ***0.4382*** | ***0.4084*** | ***0.4376*** | ***0.4518*** | ***0.4535*** | ***0.6934*** | ***0.4569*** | ***0.5227*** | ***0.4731*** | ***0.3350*** | ***0.5030*** | ***0.3664*** | ***0.4143*** | ***0.3851*** | ***0.2143*** | ***0.3960*** | | ***0.1015*** | ***0.1272*** | ***0.1609*** |
| **WAH** | 0.0263 | 0.0082 | ***0.1237*** | ***0.0383*** | ***0.0504*** | ***0.3297*** | ***0.0542*** | ***0.0997*** | ***0.0892*** | ***0.1408*** | ***0.0837*** | ***0.1594*** | ***0.0311*** | ***0.0601*** | ***0.3320*** | 0.0014 | ***0.4116*** | | ***0.0260*** | ***0.0446*** |
| **WMC** | ***0.1024*** | ***0.1180*** | ***0.2172*** | ***0.1256*** | ***0.0801*** | ***0.3859*** | ***0.1805*** | ***0.1190*** | ***0.1534*** | ***0.2074*** | ***0.1157*** | ***0.2397*** | ***0.1199*** | ***0.1372*** | ***0.3966*** | ***0.1276*** | ***0.4689*** | ***0.1513*** | | ***0.0659*** |
| **WOLF** | ***0.2115*** | ***0.1726*** | ***0.2625*** | ***0.1472*** | ***0.1963*** | ***0.1800*** | ***0.1408*** | ***0.1675*** | ***0.2163*** | ***0.3333*** | ***0.2349*** | ***0.3828*** | ***0.1668*** | ***0.1315*** | ***0.4467*** | ***0.2261*** | ***0.5519*** | ***0.2348*** | ***0.2730*** | |

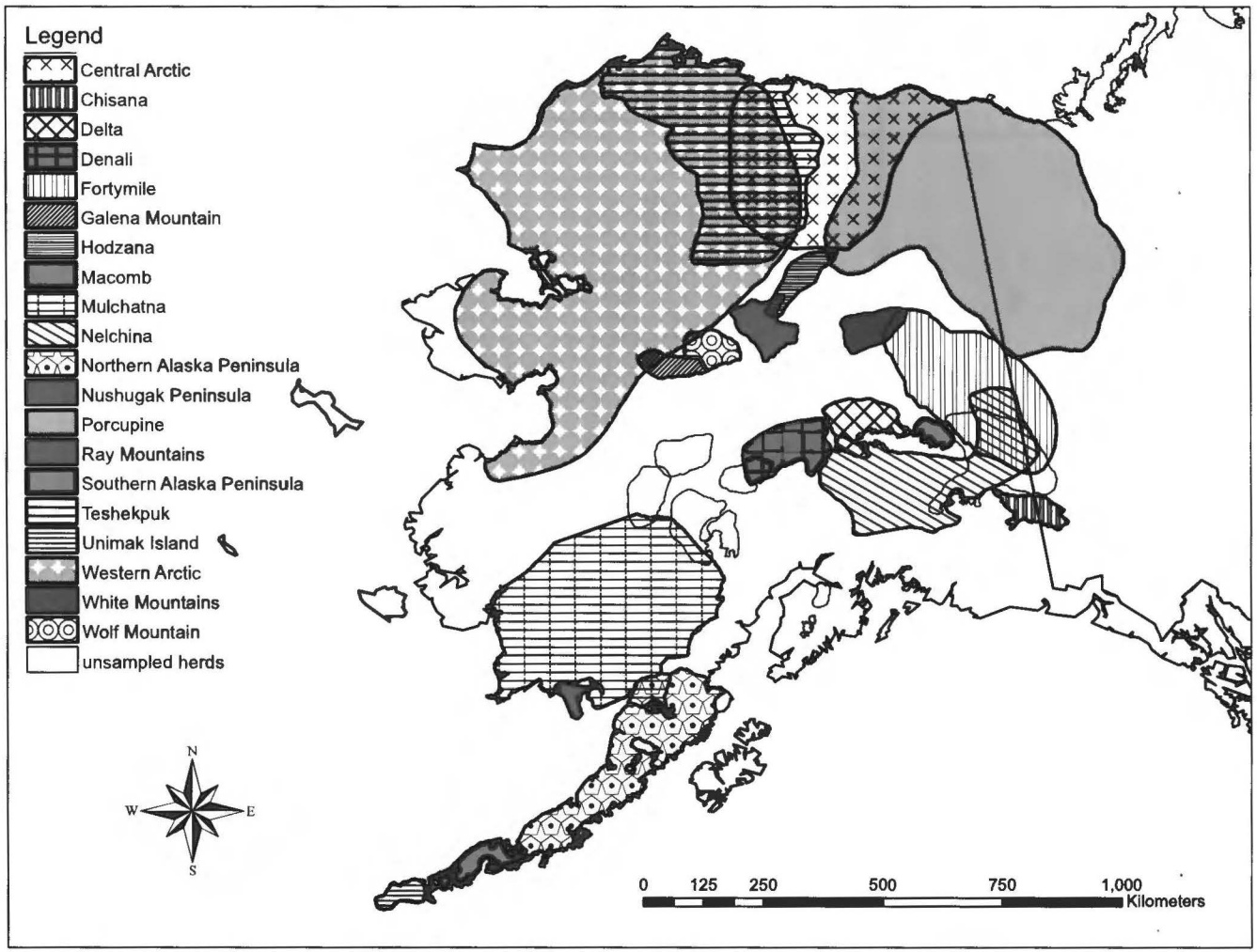


**Figure 4.1. Map of Alaskan caribou herd ranges.**

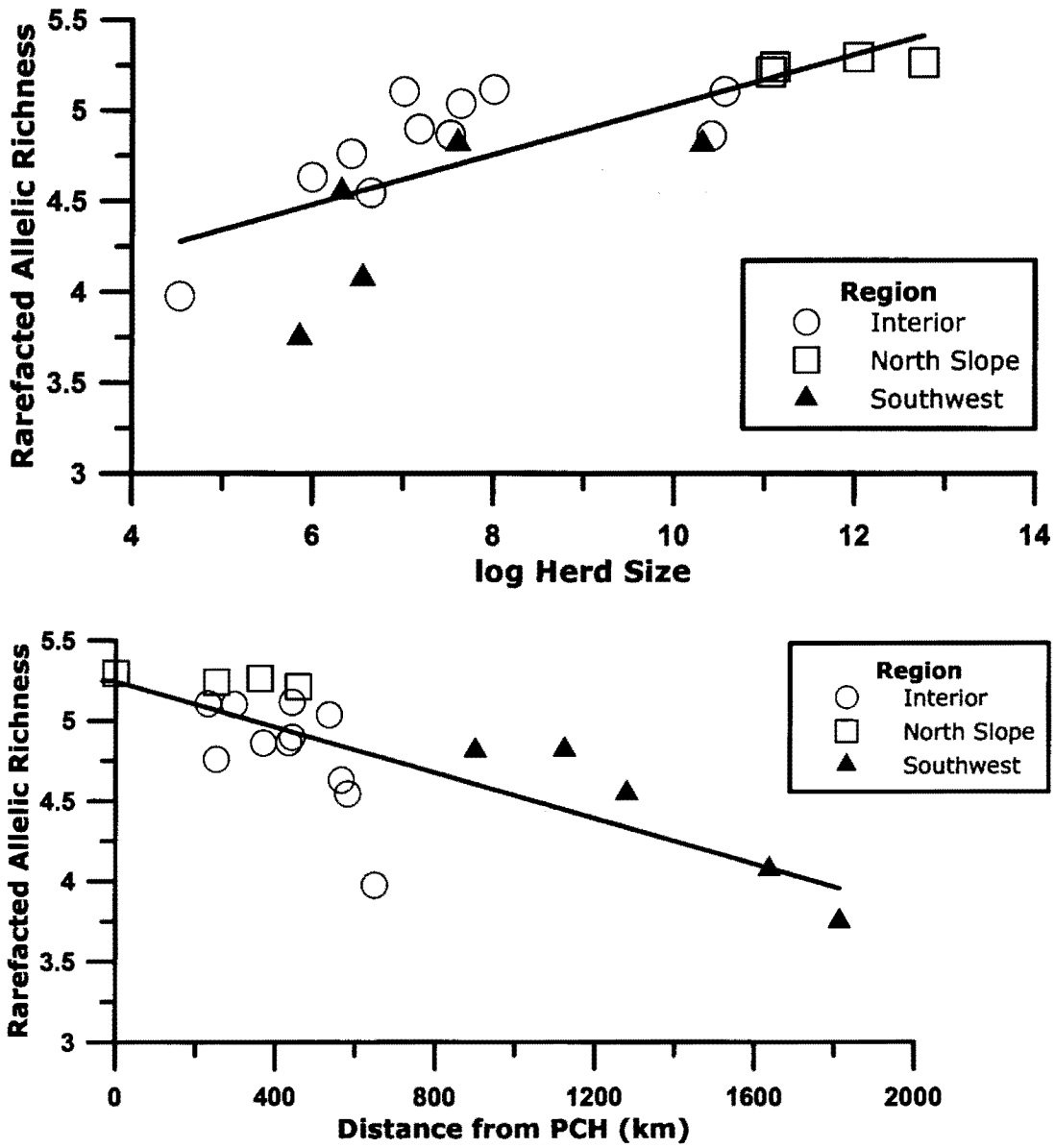


**Figure 4.2. Relationship of allelic richness to current and ancestral population size.** 2a. Positive relationship of herd size to allelic richness ($p = 0.0002$); 2b. Negative relationship ($p$ = highly sig.) between allelic richness and distance from the Porcupine Herd (PCH), which we use as a proxy for the presumed large ancestral population for northwest North American caribou, based on its lack of genetic differentiation from herds across Northern Alaska (this study) and Canada (Zittlau 2004), and its high allelic richness in Alaska.

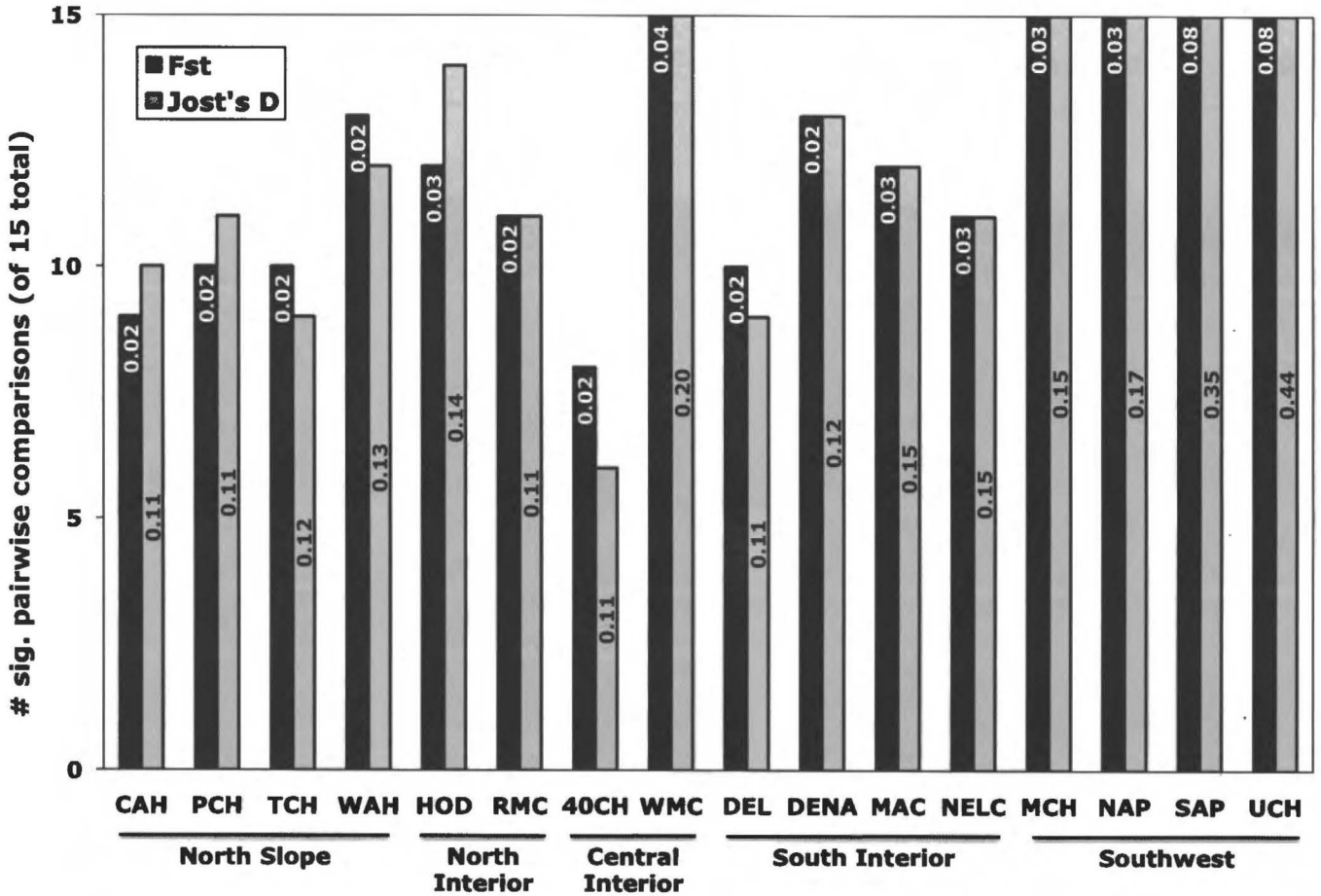


**Figure 4.3. Relative genetic distinctiveness of Alaskan caribou herds determined by pairwise differentiation** (herds with $n < 17$ excluded; pairwise comparisons in Table 4.3). Bars indicate the number of herds (y-axis) from which each herd (x-axis) shows genetic differentiation significantly different from zero (based on $p$-values for pairwise $F_{ST}$ and Jost's $D$). Mean amount of differentiation ($F_{ST}$ and $D$) across all pairwise comparison is shown within each bar. Geographic regions shown below.

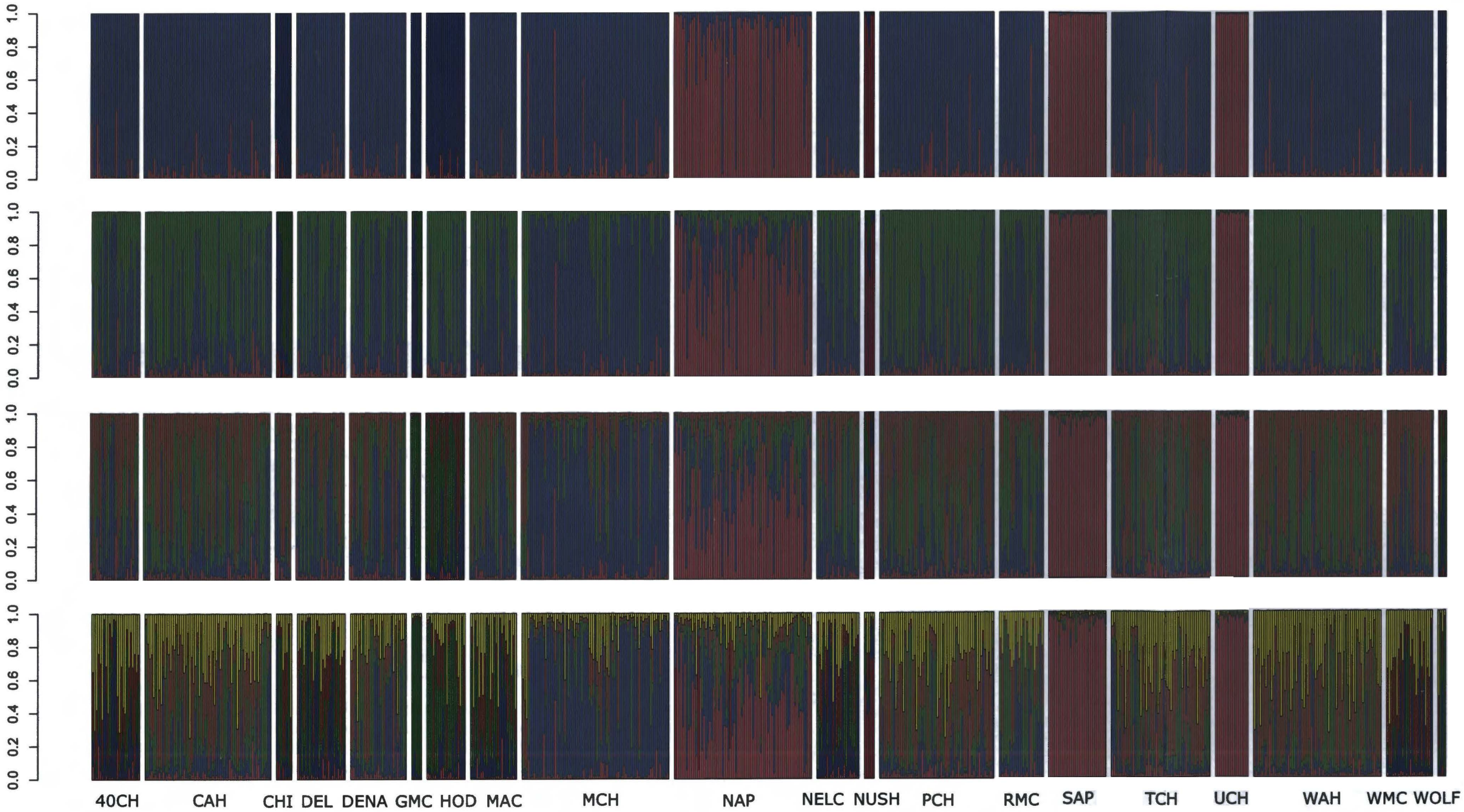


**Figure 4.4. STRUCTURE assignment of 655 Alaskan caribou to population clusters under successively more subdivided population models ($K = 2…5$).** Each vertical bar is an individual, and the colors within each bar represent clusters to which that individual is assigned. Individuals are grouped by herd (for abbrev. see Table 1). Mean log likelihood and $\Delta K$ for these and other models ($K = 1…20$) are visualized in Fig. 4.5.

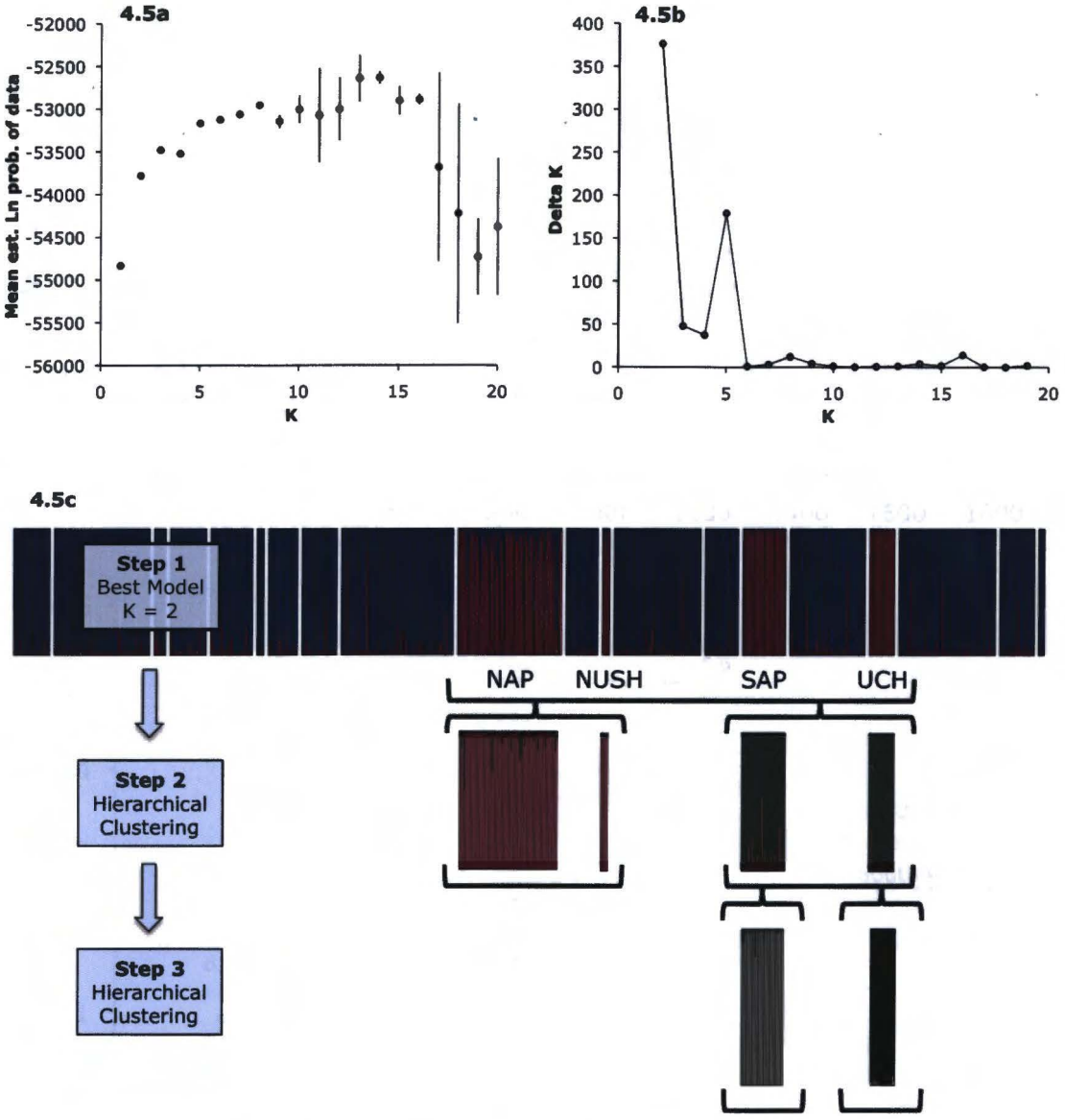


**Figure 4.5. Likelihood that Alaskan caribou ($n$ = 655) are clustered in one to twenty population units ($K$ = 1…20).** 4.5a. Asymptote of mean log likelihood indicates $K$ = 2…5. 4.5b. $\Delta K$ indicates population models $K$ = 2 and $K$ = 5 have the highest likelihood. 4.5c. The most likely model ($K$ =2) was partitioned for hierarchical STRUCTURE analysis. Cluster 1 (mainland) resolved for $K$ = 1, while Cluster 2 (Alaska Peninsula) resolved into 3 clusters by herd (NAP & NUSH; SAP; and UCH).

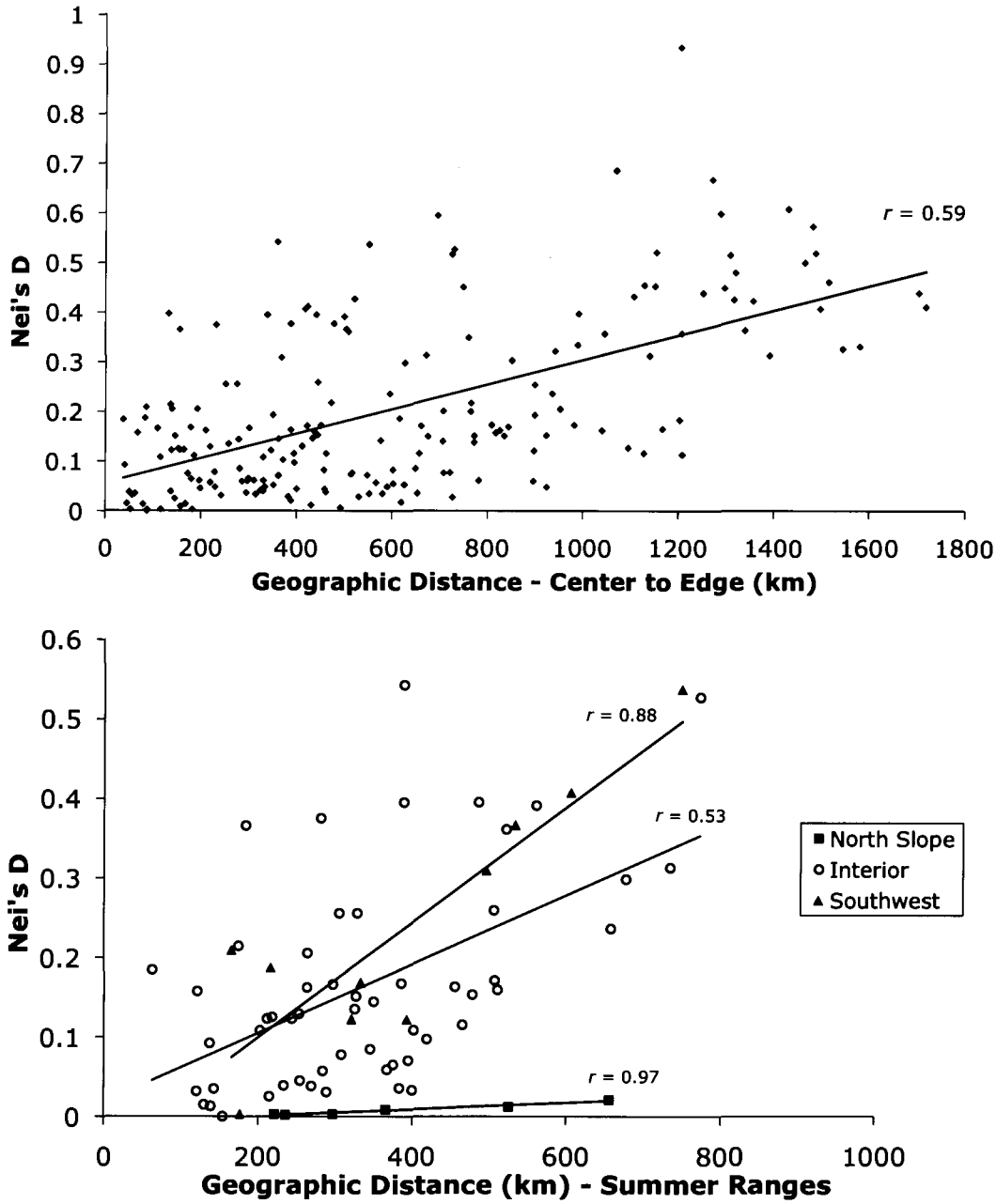


**Figure 4.6. Correlation between geographic distance and genetic distance.** 4.6a. Correlation ($r = 0.594$, $p = 0.000085$) between pairwise Nei's $D$ and geographic distance, measured as the mean distance from the centroid of each herd's range to the edge of the other herd's range; 4b. Correlations among herds within each region. Note the tight correlations in the North Slope ($r = 0.972$, $p = 0.042$) and Southwest ($r = 0.881$, $p = 0.017$) regions, as compared to the Interior ($r = 0.525$, $p - 0.0057$).

# Chapter 5 Synthesis: Integrating Genetics and Local Knowledge to Understand Reindeer-Caribou Interactions

Researchers increasingly recognize a need to integrate local knowledge with scientific research, but often question how to do so (Huntington 2000, 2005). In this chapter, I describe how I integrated local knowledge and genetics, compare my approach to other studies, and reflect on the benefits and lessons learned from the process. I examined historical interactions between reindeer and caribou near Barrow, Alaska, using methods in oral history to record local knowledge and methods in population genetics to detect hybridization. Few biologists directly studied caribou in the Barrow area during the reindeer-herding period, whereas local caribou hunters and reindeer herders have observed and developed expertise about the animals over their lifetimes.

There is much debate in the academic literature about the definitions and scope of local and traditional knowledge, and to what extent they differ from Western scientific knowledge (Agrawal 1995; Houde 2007; Johnson 1992; Tester and Irniq 2008; Turnbull 1997; Wenzel 1999, 2004; Wright 2005). Social and natural sciences have always relied on the knowledge of local people (Agrawal 1995; Brewster 1997; Krupnik 2002; Wenzel 1999). However, this type of research has become increasingly recognized as Alaska Native and Canadian Aboriginal land claims proceedings have urged and sometimes mandated integration of traditional knowledge into wildlife management (Caulfield 1988; Freeman 1976; Houde 2007; Tobias 2000).

There are many benefits to using local and traditional knowledge in science and management (Huntington 2000) but many challenges as well. Documenting traditional knowledge, for example through oral recordings and mapping, can be valuable to local communities by making elders' stories available to younger generations and by providing documentation for land claims and environmental assessments (Huntington 2000; Johnson 1992; Tobias 2000). However, because knowledge systems are adaptive and most relevant in a local context, researching local knowledge using the criteria of science

may cause its meaning and performative value in different contexts to be lost (Agrawal 1995; Cruikshank 1998; Nadasdy 1999; Nazarea 2006).

Caribou biologists in Alaska have long used local knowledge (Murie 1935; Rausch 1951; Skoog 1956, 1968), though it has not always been referred to as such and methodologies for collecting and using the information were not always explicit. Since the emergence of explicit local knowledge research, several studies have used local knowledge to understand long-term population dynamics in caribou, though their methods of doing so have varied (Berkes 1999; Cruikshank 1998; Ferguson and Messier 1997; Ferguson, Williamson, and Messier 1998; Kofinas et al. 2002; Padilla 2010; Parlee, Manseau, and Lutsël K'é Dene First Nation 2005; Schneider, Kielland, and Finstad 2005; Stewart, Keith, and Scottie 2004; Thorpe 2004). By reflecting on my approach, and comparing it to other studies, I hope to highlight some of the practical aspects of integrating social science methodologies into biological research.

## 5.1 Choosing Different Methodologies for Different Sources

To address the question of how historical interactions between caribou and reindeer have influenced their genetic identity, I determined that genetic data, local knowledge of hunters and herders, and historical documents were the primary sources available. However, each source required different methods or different theoretical assumptions and needed to be treated differently at each stage of the research process. The benefits of researching each source "on its own terms" were one of the lessons of this project.

### *5.1.1 Local Knowledge Methods*

Local knowledge, in this study, is defined as the expertise possessed by caribou hunters and reindeer herders based on lifetimes of experience with the animals. This knowledge is contained in people's memories and enacted when people recount stories and practice hunting and herding activities. It encompasses their observations, their understanding of relationships derived from repeated observations, the stories they have heard, and their beliefs regarding how to act. Many hunters and herders have extensive empirical

knowledge about the animals, but communicating this knowledge is not as simple as entering facts into a database. The things people say are usually qualitative, often subjective, and may be influenced by memory or personal motives on the part of the knowledge holder, and by issues in translation and comprehension on the part of the researcher (Schneider 2011). Because of this, I chose to use ethnographic methods developed primarily within the social sciences for the local knowledge research. I conducted semi-structured interviews with hunters and herders, allowing me to discover what was most significant in each person's memory and to better grasp the nuances of the information they shared.

Though my instinct as a biologist was to meticulously ask for the specific years, places, dates, and numbers associated with each story, I quickly learned that doing so did not always yield helpful answers and often derailed the interviewee's train of thought. Instead, by allowing interviewees to tell their full stories, I gained extra information I might not have known to ask about. For example, if I had directly questioned each participant on the exact places and dates where reindeer and caribou interacted, I would have learned they mixed together along ocean coasts during the summers of the 1940s. However, by listening to people's stories, I learned additionally about the role of seasonal behaviors in those interactions—that the tendency of reindeer to spread out in summer for foraging and insect relief made them especially difficult to control for herders, who were challenged as well by traveling with the reindeer on foot over moist tundra (Chapter 2). In some cases, the meaning of an interviewee's story was not immediately clear. However, working with translators and participating in hunting, herding, and an Iñupiaq culture camp revealed practical and cultural perspectives on human-animal relationships that improved my understanding.

I attempted to interview all living reindeer herders in Barrow, which had the advantage of revealing the experiences common to all of them or unique to some individuals. Determining whether interviewees were reliable was important. However, achieving agreement among all sources was not. Understanding the variations in the experience of each reindeer herder provided a more full and complex view of the

influences caribou had on reindeer and the ability of herders to respond. Thus, by using ethnographic methods rather than more quantitative techniques typical of biological research, I believe I gained a deeper biological understanding of reindeer and caribou.

*5.1.2 Written Archival Methods*

Written primary sources from throughout the past 125 years were also useful for understanding how caribou and reindeer interacted. These sources preserve the exact words of an observer as written at the time, but often without context or the ability to ask questions of the observer about their motives for writing what they did. The writings of non-biologists provide some of the only written biological information on reindeer and caribou from certain points in history. However, to attempt to minimize errors in reconstructing history based on those sources, I used methods of source criticism based in the discipline of history to assess their reliability and validity (Barber and Berdan 1998). Rather than taking facts at face value, I compared historical accounts to one another and to oral sources and attempted to understand the purpose for which documents were written, the motivations of the authors writing them, and the ability of authors to know what they claimed to know, to understand how these factors influenced the information that was presented. By doing so, I discovered several potential reasons for the mismatch between the writings of Reindeer Service administrators, who seemed to discount caribou problems, and the testimony of Iñupiaq herders who remember major problems with caribou (Chapter 2). Because I attempted to scrutinize sources using the methods of a historian, I learned more about what happened when reindeer and caribou interacted in the past and why accounts of that history vary.

*5.1.3 Population Genetics*

I used genetics to determine whether interbreeding between reindeer and caribou was extensive and persistent enough to influence the identity of caribou herds today (Chapter 3). The DNA of an animal sampled today will reflect its ancestry and can reveal if a recent ancestor was a caribou-reindeer hybrid. I used population genetics techniques to

analyze repeating segments of non-coding DNA (microsatellites) whose allele frequencies vary in different populations due to the interplay of mutation, gene flow, and genetic drift, thus reflecting the historical patterns of long isolation followed by recent contact between the two subspecies. DNA is a highly objective "measure" of an animal's ancestry, but because the conclusions I draw are based on the assignment of an individual to one or more populations, how I sample those populations becomes very important. Using representative sample sizes, informative genetic markers, and recognizing biases in when and where animals are sampled, can improve confidence in results. Because of this, I chose to sample at least 50 individuals from each population, to use a large suite of polymorphic genetic markers, and to include samples from reindeer isolated from caribou (Kodiak Island) and animals in caribou herds with reindeer phenotypes (hunter-donated samples). However, caribou herds are large and it is possible that more hybrids could be found in small groups separate from those sampled by caribou biologists. Genetic analysis is objective and quantifiable, with few sources of measurement error, making it a good tool for determining the outcome of reindeer-caribou interactions.

### 5.2 Iterations Between Natural and Social Sciences

Integrating natural and social sciences meant not only using different methods to analyze different sources, but also allowing insights from genetics and local knowledge to inform one another throughout the process (Fig. 5.1). This iterative process was especially important in determining which research questions to ask, in making predictions, and in interpreting results. I was motivated to ask Barrow residents about historical reindeer herding in the area after talking to biologists curious about the possible role of reindeer in the history of the Teshekpuk caribou herd. My initial interviews with reindeer herders revealed that reindeer and caribou had interacted in the past (Chapter 2), and this inspired genetic investigations (Chapter 3). Further local knowledge research suggested several possible sources for the reindeer-like animals observed within caribou herds today, and this detailed local knowledge generated specific genetic predictions: that herds contain individuals with hybrid ancestry resulting from interbreeding during and after the 1940s,

that herds contain feral reindeer and hybrids who have dispersed from existing herds on the Seward Peninsula, and that the Teshekpuk herd in the Barrow area has experienced substantial introgression from domestic reindeer.

Local knowledge helped to inform the research questions I asked and enabled me to better interpret the proportions and spatial distributions of hybrids I detected using genetics. For example, I did not initially expect to find similar levels of hybridization in all four North Slope caribou herds because many more reindeer were herded, and lost, in the vicinity of the Teshekpuk and Western Arctic herds. However, interviews made clear that hunters had observed reindeer-like animals in a wide range of areas across the Arctic Coastal Plain and Brooks Range. Interviews also made clear that hunters were exchanging information among villages—many mentioned hearing from people in other villages as far east as Kaktovik about ear-notched reindeer seen there. These particular observational details provided some support for my genetic findings.

The genetic findings, in turn, helped me to think more carefully about the meanings and motivations behind the stories hunters and herders shared. Genetic detection of reindeer-caribou hybrids provided support for hunters' claims that the unusual looking animals they hunted might be hybrids. Genetic analysis also confirmed that animals with reindeer phenotypes hunted within the Western Arctic herd were genetically reindeer. By drawing the link between known genetic identity and known hunting preferences, I learned that targeted hunting of reindeer-like animals by expert hunters is a potentially significant selective pressure that is removing reindeer from caribou herds.

Genetic analysis did not find evidence that the Teshekpuk herd had been swamped by reindeer introgression, implying that changes in caribou behavior, such as decreased vigilance, that herder Kenny Toovak attributed to the influence of reindeer, may instead be due to other causes. Though genetics do not confirm Toovak's interpretation, his observations still contribute to biological knowledge of long-term changes in caribou, demonstrating that considering both local knowledge and genetics can be useful even when they do not appear to agree.

### 5.3 Comparison to Other Studies of Local Knowledge of Caribou

Several other researchers have studied local and traditional knowledge of long-term changes in caribou populations from the perspective of wildlife science. Ferguson and Messier (1997) estimated long-term cycles in caribou population size on Baffin Island by conducting directed interviews with 43 Inuit observers and comparing them to aerial survey data to create an abundance index (Ferguson, Williamson, and Messier 1998). Because their interview questions were structured and their goal was to create a single, quantitative index, they treated inconsistencies among Inuit and non-Inuit written sources as signs of inaccurate reporting or research errors in compiling Inuit knowledge (Ferguson and Messier 1997). Communities in the Arctic borderlands share local knowledge with one another to document ecological change in the region, such as the influence of hydrology on caribou movements (Kofinas et al. 2002). Padilla (2010) used interviews with elders and others who hunt the Porcupine Caribou Herd to document a variety of concepts for caribou leadership behavior. Others have used oral histories related to specific places on the landscape to better understand caribou movements (Parlee, Manseau, and Lutsël K'é Dene First Nation 2005; Stewart, Keith, and Scottie 2004).

Though my research is most interested in what oral histories can teach us about wildlife biology, several researchers have described the significance of local knowledge about caribou to conveying hunting ethics and cultural histories in local communities. Thorpe (2004) compiled traditional knowledge about caribou hunting in the Bathurst region of Canada to create a "caribou code" meant to govern ethical behavior towards caribou as a means of community-driven wildlife management. Berkes (1999) also described how Chisasibi Cree elders shared their traditional knowledge of caribou cycles at a community gathering to encourage ethical hunting behavior. They reminded hunters of a prediction their elders had made—that the caribou herds, which ceased returning to the area in the 1910s after hunters were disrespectful, would return one day but stay only if hunters were respectful towards them. Schneider, Kielland, and Finstad (2005) described elders' warnings to reindeer herders on the Seward Peninsula that caribou

would return after more than 100 years absence, and demonstrated the strong regard herders had for the elders' knowledge when they reflected on those warnings after caribou indeed returned in the 1990s. Cruikshank (1998) described the historically and mythically complex stories told by Southern Tutchone elder Mrs. Ned in response to questions by a caribou biologist about long-term changes in caribou, to illustrate how focusing only on the biological "data" in her story would misrepresent its greater meaning and Mrs. Ned's intention.

It is important to note the range of meanings and performative values that local knowledge can have. The concept of local and traditional knowledge is broad; researchers with particular objectives seek aspects of local knowledge that interest them, and thus use different research approaches (Huntington 2005). I focused on biological observations and behavioral understandings of the animals. However, the oral recordings I made preserve many other messages interviewees shared about how to hunt ethically or about Barrow's history. Each study of traditional knowledge about long-term changes in caribou differs not only due to the goals of the researchers and the methods they used (Huntington 2005) but also due to the goals of local knowledge holders and the information they offer. I aimed to use hunters' knowledge to better understand the identity and interactions of the animals over the long term, and while hunters and herders I interviewed were happy to teach me, they were also motivated by creating recordings about their life experiences for family members and cultural archives. My semi-structured approach to recording hunter and herder observations, as part of the stories they wished to tell, differed from that of Ferguson and Messier (1997). By using qualitative analysis of semi-structured interviews, I was able to document a wide variety of observations about reindeer-caribou interactions, characteristics, and potential hybridization. Enabling people to share their stories in full provided a much more detailed picture of what they had observed than a directed interview would have, while also allowing me to assess areas of consensus between many interviewees and perspectives unique to others.

### 5.4 Lessons from an Interdisciplinary Approach

Insights from this and other interdisciplinary studies suggest several benefits of incorporating local knowledge into biological studies by using social science methods. Doing so may improve the accuracy and relevance of biological research at each step in the research process. For example, it may:

- Provide historical and ecological context for the research question
- Help to pose the research question in relation to the desired outcome (e.g. is the goal to advance ecological theory, address local user concerns, or inform management decisions?)
- Guide exploratory research in under-studied fields
- Provide an empirical basis for making specific predictions
- Characterize the sample population to improve research design
- Validate research findings
- Explain outliers in the data
- Increase certainty that results are biologically meaningful
- Interpret unexpected patterns or surprising results
- Reveal ways in which local people influence the ecosystem, and vice versa
- Discover the language and perceptions of local users, to improve the ability of scientists, users, and managers to communicate

Ideally, biologists would have the theoretical grounding, available literature, and detailed field knowledge necessary to understand such nuances at each stage in their research. However, in practice, this is not usually the case and partnering with knowledgeable local observers can often provide those insights when they are needed.

Ultimately, my ability to interpret my findings and make sense of their significance relied on the diverse set of knowledge and perspectives gained from multiple sources. Local knowledge helped me to better understand what our genetic data told us about patterns of historical interactions, interbreeding, and selection against reindeer traits. Without the local knowledge, my interpretation of the genetic data would have been much more speculative. Likewise, genetic data helped me to better understand what

people said about the animals. I believe that using different methodologies for each source, while integrating insights from each along the way, was the key to meaningful integration. It is important to note that I did not use the genetic data to evaluate the reliability of the local knowledge, or vice versa. I assumed that my sources were reliable and my methods were sound while following research procedures appropriate to the sources and the nature of their observations. Because I recognized those inherent differences, I received more information.

By describing the interdisciplinary process I used, I hope to have demonstrated that integrating natural and social sciences can create synergies for both disciplines and advance the research as a whole. Both oral histories and genetics provided evidence of reindeer-caribou interbreeding. However, the added value of a combined approach was what I learned about the people and animals in addition to that. One of those added values was learning how the genetics of the animals and the hunting and herding practices of local people influence one another. The interactions between caribou and reindeer have influenced how people hunt, because hunters use their knowledge of reindeer and caribou characteristics to selectively hunt reindeer-like animals. Selective hunting by knowledgeable hunters likely has some effect on the genetic composition of caribou herds by removing reindeer genes from the population.

An interdisciplinary approach also reveals that, although local knowledge is consistent with genetic findings, hunters and herders may talk about the animals in very different ways than biologists might. A cultural heritage with both caribou and reindeer has influenced the ways in which people evaluate and describe the animals today. Iñupiat hunters' particular attention to unusual individuals, to social behavior, to changes over long periods of time, and to particular places best suited to hunting desirable animals, comprises a body of knowledge that is not always expressed using the language and metrics of professional wildlife management. Though comparing the theoretical models and worldviews of Iñupiat and North American wildlife management was beyond the scope of this thesis, my interviews suggest that engaging in cross-cultural research may

improve wildlife management by increasing mutual understanding between scientists, managers, and hunters.

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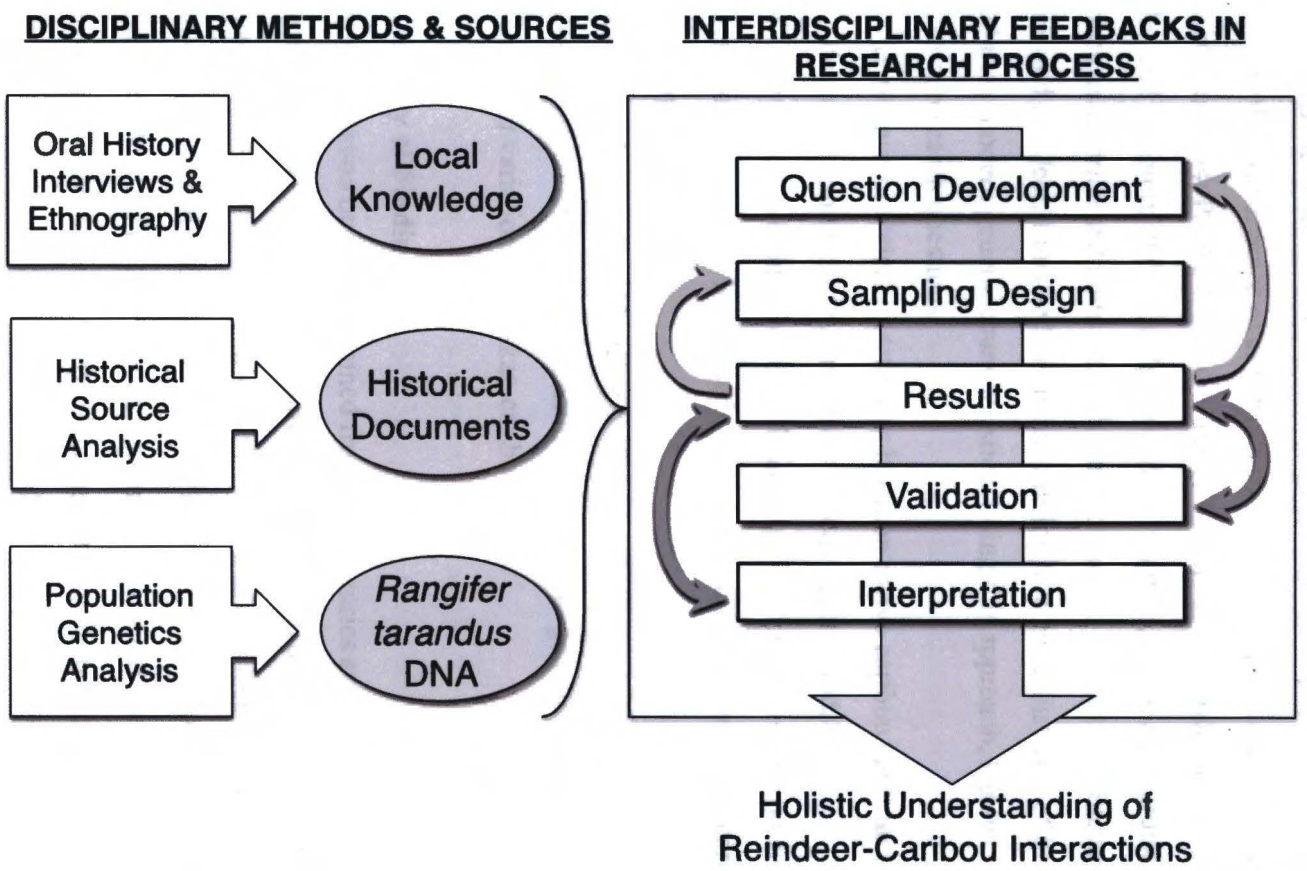


**Figure 5.1. Conceptual diagram of interdisciplinary process used to research reindeer-caribou interactions.** Arrows represent interdisciplinary feedbacks (e.g. local knowledge results inform genetic question development). For detailed methods and results, see chapters 2 and 3.

# Chapter 6 General Conclusions and Future Recommendations

A key problem in wildlife conservation is identification of population units and factors influencing their divergence over various spatial and temporal scales (Mace and Purvis 2008; Moritz 1994; Palsboll, Berube, and Allendorf 2007; Taylor and Dizon 1999; Waples and Gaggiotti 2006). In the preceding chapters, I used an interdisciplinary approach to describe and understand drivers of genetic population structure in Alaskan caribou and reindeer. I focused on understanding how local histories of herds have shaped their modern genetic characteristics. Using this approach, I answered two integrative research questions:

1) How have historical interactions between native caribou herds and introduced domestic reindeer influenced their genetic identity today?
2) How have landscape features, demographic fluctuations, and potentially divergent selective pressures influenced the diversity and connectivity of caribou herds today?

Both questions have a direct bearing on the adaptive capacity of caribou in the future, by revealing potential environmental, anthropogenic, and genetic drivers of morphological and behavioral variation in Alaskan caribou herds.

## 6.1 Summary of Findings

To answer question one, I determined from oral histories and written sources that reindeer joined caribou herds near Barrow in the 1940s, despite reindeer herder attempts to protect and recover their animals. In the years since reindeer herding ended, many hunters have observed and often selectively harvested reindeer-like animals within caribou herds, leading us to predict that hybridization would be apparent in the genetic composition of caribou herds today. Using genetic analysis I found animals with hybrid ancestry in all four North Slope caribou herds and in Seward Peninsula reindeer, demonstrating that reindeer can survive and successfully breed in wild caribou herds. Three animals visually identified by a hunter as feral reindeer and selectively harvested

within the Western Arctic caribou herd were confirmed through genetic analysis to be full-blooded reindeer. Surprisingly, I did not find the greatest proportion of hybrids in the Western Arctic and Teshekpuk herds, which have had the most contact with reindeer. Selective hunting of reindeer-like animals, natural selection against maladaptive reindeer traits, an uneven ratio of caribou to reindeer in breeding, and lack of hybrid detection after many generations of backcrossing, may explain why these herds contain fewer hybrids than expected.

To answer question two, I used genetic analysis to determine that there is substantial variation in the genetic population structure of caribou in different regions of the state. At a statewide scale, Alaskan caribou herds clustered into two primary populations—one on the Alaska Peninsula and the other on the Alaskan mainland. Herds on the Alaska Peninsula in southwest Alaska were genetically distinct, while most North Slope and Interior herds on the mainland were not. I discuss potential mechanisms by which geographic barriers and constraints to population size and gene flow, demographic fluctuations, and differences in ecotypes, could explain genetic patterns at both of those spatial scales.

### 6.2 Response of Caribou to Future Change

I examined the impact of historical processes on the genetic structure of caribou populations, which may aid in considering future scenarios of change for Alaskan caribou. With knowledge of history, this provides the opportunity to view the species' biology, its role in the ecosystem, its use by people, and present management issues within a historical perspective. Historical information makes it possible to identify whether novel phenomena are within the realm of historical experience or not, to understand the outcomes of past processes, and to develop more informed predictions about the potential influence of climate change and industrial development on caribou.

Northern social-ecological systems are changing rapidly as a result of global climate change (Hinzman et al. 2005) and increasing industrial development (National Research Council 2003). Climate change may influence caribou populations by altering

forage access and quality through extreme weather events, changes in forage plant phenology, and forest fires (Cebrian, Kielland, and Finstad 2008; Joly, Chapin, and Klein 2010; Vors and Boyce 2009); by increasing interspecific competition and predation through changes in species overlap (Vors and Boyce 2009); by altering timing and severity of insect harassment (Bali, n.d.; Weladji, Holand, and Almøy 2006); and by causing shifts in migration and habitat use associated with changes in the spatial distribution of seasonal habitats (Sharma, Couturier, and Côté 2009). Industrial development may also influence caribou through habitat alteration, potential barriers to movement from infrastructure, changes in habitat use due to human disturbance, and increased hunting associated with road development (Bergerud, Jakimchuk, and Carruthers 1984; National Research Council 2003; Parlee, Manseau, and Lutsël K'é Dene First Nation 2005). If caribou populations respond to these changes as they seem to have responded to past changes in habitat and predation risk—through range expansions and contractions, altered movements, and shifts in ecotype (Hinkes et al. 2005; Skoog 1968)—they may retain their genetic diversity and connectivity or they may change as a result of new habitat constraints.

This study demonstrates how past population declines, reindeer-caribou interactions, gene flow among herds, geographic barriers and constraints, and divergent selective pressures have shaped the genetic diversity, differentiation, and identity of caribou herds today. Those characteristics provide the genetic basis for adaptation to future changes. Genetic variation provides the raw material on which natural selection acts, and populations with greater genetic diversity may have greater adaptive capacity (Frankham 1996). Inherent phenotypic plasticity may also be an important adaptation to a stochastic environment, through which caribou respond to change by altering movements (Adams, Dale, and Roffler 2005), strategies of habitat use and predator avoidance (Bergerud 1996; Hinkes et al. 2005), body size (Couturier et al. 2010), and reproduction (Adams 2005). Specific local adaptations may enable populations to better respond to some changes in their environment, while proving disadvantageous to other rapid changes. Thus, my genetic findings have implications for the adaptive capacity of caribou

to future change and for understanding the potential effects of future landscape change on genetic diversity and connectivity.

### 6.3 Implications of Findings for Future Reindeer Herding in Alaska

My study has some application to the future of reindeer herding in Alaska. Former reindeer herders in Barrow lost their reindeer when they joined migratory caribou herds despite efforts to protect and recover their deer (Chapter 2). The caribou problem was a major factor in the demise of Barrow's reindeer industry (Chapter 2) and in recent reindeer losses on the Seward Peninsula (Schneider, Kielland, and Finstad 2005), demonstrating the challenges of sustaining an economically viable reindeer industry in the presence of large, migratory caribou herds. I found evidence that contact between caribou and reindeer has resulted in hybridization, but instead of broadly impacting the genetic integrity of herds, it appears that caribou abundance relative to reindeer, natural selection, and selectivity by hunters and herders is effective in eliminating hybrids over time (Chapter 3). Reindeer herders have been concerned as well about caribou introgression in their herds. I found hybridization was more widespread in reindeer herds than in caribou (Chapter 3), suggesting caribou have had a genetic impact on domestic herds despite reindeer herder efforts to remove caribou-like animals.

Hybridization can threaten populations by degrading local adaptations (Randi 2008; Simberloff 1996), but there is no reason to believe it has negatively impacted caribou populations thus far. If a reindeer re-introduction is planned near caribou ranges in the future, I suggest that plans to prevent reindeer-caribou contact, consideration of the caribou population size relative to reindeer, and determination of potential future caribou ranges be considered to minimize potentially negative impacts from hybridization.

### 6.4 Implications of Findings for Herd-Based Management of Caribou

A key question in determining units for management is: what is a population? Caribou herds constitute management units, yet the extent to which they comprise distinct genetic populations was previously unknown. I found that some caribou herds were genetically

distinct, while others were not (Chapter 4). The two most genetically distinct herds are Unimak Island and Southern Alaska Peninsula. The Northern Alaska Peninsula (with Nushagak Peninsula), Mulchatna, and White Mountains herds were also significantly differentiated from all other caribou herds in the state. Results also indicate the Chisana, Galena Mountain, and Wolf Mountain herds are likely distinct, though larger sample sizes are needed to confirm those results. The remaining 11 herds (Fortymile, Central Arctic, Delta, Denali, Hodzana, Macomb, Nelchina, Porcupine, Ray Mountain, Teshekpuk, Western Arctic) each lacked differentiation from at least one other herd. This connectivity likely explains why all mainland herds form a single genetic cluster despite significant differentiation among a majority of herd pairs.

Those geographic patterns of genetic structure—an Alaska Peninsula cluster containing distinct herds and a mainland cluster comprised of somewhat connected herds—suggest different population concepts are appropriate for managing herds in these two regions. Alaska Peninsula herds show substantial genetic differentiation likely resulting from genetic bottlenecks coupled with long-term isolation. Those herds are demographically independent and may have evolved herd-specific adaptations, suggesting that population viability be maintained by intrinsic factors, when possible, to avoid disrupting local adaptations (see Appendix C). Most mainland herds, by contrast, demonstrate genetic connectivity suggesting they have experienced gene flow from other herds over the long-term. Movement data has shown that females have strong fidelity to their natal herds, however genetic data suggest those herds are components of a larger metapopulation over the long term.

Currently, many caribou herds are managed for a target range in herd size (Alaska Department of Fish and Game 2009), which may be confounded by immigration and emigration. Understanding whether herds are demographically independent over the short term is, therefore, important. Though genetic differentiation indicates demographic independence over evolutionary time scales, it is necessary to consider several factors including migration-drift equilibrium, mechanisms of gene flow, and dispersal data to assess whether genetically similar herds lack demographic independence over the time

scales relevant to wildlife management. Alaskan caribou herds may not be at migration-drift equilibrium (see Chapter 4), meaning historical patterns of gene flow and isolation reflected in genetics may not be representative of those relationships today. For large herds, in particular, genetic data may overestimate gene flow because a small number of migrants can be sufficient to counteract divergence due to genetic drift, which is very slow in large populations.

It is also important to realize that caribou herds may exchange genes without exchanging individuals. Two mechanisms for gene flow—overlap between herds during the rut and dispersal of individuals from one herd to another—have similar genetic effects but different impacts on herd size. Individuals of different herds may breed when together during the rut but then remain with their own herds, such that no dispersal occurs. When dispersal is the mechanism, it may be male-biased such that herds lack differentiation in bi-parentally inherited neutral markers (such as microsatellite used in my study) but retain a signature of independence in maternally inherited markers (e.g. mtDNA). For example, in a recent study, microsatellite data for the Nelchina and Mentasta herds indicated no differentiation between them, but differentiation in mtDNA and strong fidelity to calving grounds indicated that females of each herd are independent—a revelation not reflected in the microsatellite data (Roffler et al., in press).

Because different mechanisms of gene flow have such different demographic consequences, continued radio-tracking of females and increased monitoring of male dispersal are needed to assess whether dispersal is currently occurring between genetically similar herds. When dispersal data is not available, genetic data alone may be used, with caveats, to assess whether two herds are demographically independent. However, it is important to do so with the knowledge that genetics reflect long-term average gene flow, not the amount of dispersal between herds that could be expected over the span of decades.

Several Alaskan herds are genetically differentiated, and others lacking differentiation may still be demographically independent over the shorter time scales relevant to management. These results support continued herd-based management of

caribou. Additionally, connectivity among mainland herds suggests a higher-order metapopulation concept is also important for caribou conservation over the long term. Caribou naturally fluctuate in population size on the time scale of decades and centuries. Those fluctuations often result in range expansions, contractions, and shifts that influence patterns of contact and isolation among herds and, occasionally, may cause herds to join together or allow new "remnant" herds to be created. These dynamics maintain connectivity among herds in the metapopulation, maintaining the large effective population size and substantial genetic variation that enhance the adaptive capacity of caribou to environmental change. Enabling spatial connectivity not only has genetic consequences; it may also be important for caribou abundance and for harvest opportunities by providing caribou populations the capacity to shift to new areas or adopt new strategies rather than decline. For these reasons, I recommend that caribou habitats be managed to allow for continued gene flow between genetically similar herds as a part of natural ecological processes.

### 6.5 Implications of Findings for Management of Caribou Habitat

Managing caribou for long-term metapopulation connectivity across such a vast area has implications for management of caribou habitat. Climate change may alter the spatial distribution of caribou habitat in Alaska (Murphy et al. 2010). Range expansions and shifts appear to be an important response of caribou to changes in habitat and population size (Hinkes et al. 2005; Skoog 1968) and over time may be an important mechanism maintaining gene flow between herds. Habitat fragmentation has been shown to cause genetic isolation and reduced genetic diversity in wild populations (Keyghobadi 2007), and the cumulative effects of industrial development and land cover change may cause fragmentation of caribou habitats (Apps and McClellan 2006; National Resource Council 2003). Industrial development leases have stipulated conservation of critical habitats of caribou herds (Bureau of Land Management 2008), and while these measures are important in the short term, continued development around herd ranges may impede the

mobility and adaptive capacity of caribou in the long-term if potential future ranges and migratory pathways between herds are not also conserved.

Several other researchers have suggested that the conservation of large and spatially heterogeneous areas is important to long-term caribou management (Bergerud et al. 1984; Hinkes et al. 2005; Mårell and Edenius 2006; Person et al. 2007). Mobility enables caribou to react to environmental change in the short term, and the genetic diversity maintained by this spatial connectivity may be important in enabling adaptive responses to change over the long term. *Rangifer tarandus* is unique as one of few remaining land mammals to undergo long-distance migrations in such large aggregations (Harris et al. 2009). My findings confirm that caribou show genetic connectivity at a spatial scale observed in few other ungulates (cf. Lorenzen, Arctander, and Siegismund 2008). These findings imply that coordinated management of caribou and their habitats over large spatial scales may be important.

## 6.6 Recommendations for Future Research

### *6.6.1 Future Research Questions*

The results of this study raise many additional questions about caribou ecology. Several of these questions surround mechanisms of gene flow between herds. Though females are known to show strong fidelity to calving areas, more research on male dispersal is needed to determine if gene flow is sex-biased in caribou. There are logistical challenges in tracking male movements over the span of a lifetime, however doing so would help to answer this question. Genetic analysis of mitochondrial DNA (mtDNA), which is maternally inherited, could reveal whether female fidelity to calving grounds has caused herds to be more genetically discrete using mtDNA than microsatellites. Additional studies of rutting behavior are also needed to determine whether rutting groups or mate selection could be related to herd identity, to determine factors influencing interbreeding when herds overlap during the rut. Similarly, studies of caribou and feral reindeer on the Seward Peninsula during the rut could reveal more about the situations in which reindeer and caribou interbreed. Genetic analysis of resident caribou on the Seward Peninsula

could also be useful to determine whether these animals are caribou, feral reindeer, or hybrids. DNA extraction from pre-20th century caribou and from Chukotkan reindeer could establish a pre-reindeer baseline for caribou and reindeer genetics, to which modern samples could be compared.

Several other questions raised by this study relate to the link between phenotypic and genotypic variation in Alaskan caribou. Researchers have hypothesized that strategies of habitat selection and predator avoidance (ecotypes) may change as a result of changes in density (Hinkes et al. 2005). However, my findings suggest that the genetic distinctness of small herds in Alaska may possibly be linked to differences in ecotype. Additional genetic research on small Interior herds and on suspected sedentary groups within larger herds may help to resolve this question. Including both Alaskan herds and Canadian montane and woodland caribou populations in a single study would be especially informative. A comprehensive effort is also needed to determine the ecotypes of all Alaskan herds, either through field studies or by surveying regional biologists to characterize the spacing strategies, habitat use, seasonal fidelity and migratory behavior of each Alaskan herd. Determining the extent to which ecotypes reflect plasticity or genetic adaptations will be useful in determining how changes in population size and habitat may impact different herds.

Understanding phenotypic and genotypic variation in caribou and other wildlife may also be achieved through collaborative research with hunters. Exploratory research to document local expert observations of within-species variation may yield new research questions and useful data for documenting variability. Use of hunter-collected samples in future genetic research would provide a means to explore phenotypic and genotypic variation by linking hunter observations of the individual animal's characteristics to genetic characteristics and other quantitative measures of variability.

### *6.6.2 Genetic Monitoring*

Genetic monitoring has numerous applications in wildlife conservation (Schwartz, Luikart, and Waples 2006), including the potential to detect loss of diversity and changes

in gene flow over time. This study was the first to document measures of genetic diversity and differentiation in Alaskan caribou herds across the state and thus may serve as a baseline against which future population genetic results may be compared. A comparative genetic analysis could be used to detect whether population declines or habitat fragmentation have caused reductions in genetic variation. Genetic analysis may also be used to detect dispersers between genetically differentiated herds and to study processes of divergence or hybridization if distinct herds were to split or merge. I used genetic markers that were highly variable, and using the same markers in future studies could enable direct comparisons. However, more informative techniques using SNPs or even genomics may yield greater insights into caribou population structure as they become feasible and cost-effective in the future.

### *6.6.3 Local Knowledge*

This study demonstrates several benefits of incorporating local knowledge into biological research (for a detailed discussion see Chapters 2 and 5). Wildlife managers and scientists have limited resources and cannot study all aspects of caribou ecology and behavior at any given time. Hunters and local observers of caribou may contribute useful information to researchers at all stages of the research process: determining what questions to study, providing insight on how to sample, contributing observational data and theoretical concepts, and interpreting research results. The observations of expert hunters over the span of a lifetime provide a long-term view of changes in caribou and other wildlife populations, exceeding the time span of most biological research projects. Local knowledge may not always appear to agree with biological results, but exploring the reasons for disagreement may yield new research questions and increased cross-cultural understanding. Wildlife management relies upon management of human behavior (e.g. hunting) as well as management of the animals and their habitat. Research that documents the knowledge and values of hunters, in their own words, may aid wildlife managers by revealing how hunters decide which animals to harvest, what characteristics they value, and the words they use to communicate about the animals. I suggest that

collaboration with local knowledge-holders on wildlife research can improve wildlife science and management.

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# Appendix A

## IRB Approval for Human Subjects Research

UAF
UNIVERSITY OF ALASKA FAIRBANKS

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**Institutional Review Board**
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

July 20, 2007

To: William Schneider, Ph.D
Principal Investigator

From: Bridget Stockdale, Research Integrity Administrator
Office of Research Integrity

Re: IRB Protocol Application

Thank you for submitting the IRB protocol application identified below. I have administratively reviewed this protocol and determined that it meets the requirements specified in federal regulation for exempt research under 45 CFR 46.101(b)(2). Therefore, I am pleased to inform you that your protocol has been approved.

| | |
|---|---|
| Protocol #: | 07-46 |
| Title: | *North Slope residents' knowledge of caribou herd structure and identity, and of the history of reindeer husbandry on the North Slope.* |
| Level: | Exempt |
| Received: | July 9, 2007 |
| Approved: | July 20, 2007 |

*Exempt research does not require annual continuing review, but please submit any modifications or changes to this protocol to fyirb@uaf.edu for administrative review. Modification Request Forms are available on the IRB website (http://www.uaf.edu/irb/Forms.htm). Please contact the Office of Research Integrity if you have any questions regarding IRB policies or procedures.*

# Appendix B

## IACUC Approval for Reindeer Research

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**Institutional Animal Care and Use Committee**
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 1, 2009

To: Kris Hundertmark, PhD
Principal Investigator

From: Erich H. Follmann, PhD
IACUC Chair

Re: IACUC Assurance Application

The University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC) reviewed the following Assurance at their February 19, 2009, meeting. This Assurance was approved pending receipt of a revised assurance addressing the committee's questions. The assurance received on May 21, 2009 was determined to be satisfactory; therefore I am pleased to issue approval.

Protocol#: 09-08

Title: *Identity and History of the Teshekpuk Caribou Herd*

Received: February 12, 2009 (orig)
May 21, 2009 (revisions)

Approved: June 1, 2009

Review Due: June 1, 2010

*The PI is responsible for acquiring and maintaining all required permits and permissions prior to beginning work on this assurance. Failure to obtain or maintain valid permits is considered a violation of an IACUC assurance, and could result in revocation of IACUC approval.*

# Appendix C

## Report on Southwest caribou for Alaska Department of Fish and Game

Kevin Colson, Karen H. Mager, and Kris J. Hundertmark

### Introduction

Defined populations are important units in the demographic and genetic management of species, but the question as to how to recognize population boundaries has long been difficult to address. Tools that assign individuals to populations without *a priori* knowledge of population groupings have become available within the last decade, allowing managers to approach the more vexing problem of delineating boundaries in what appear to be uniform assemblages of individuals (Pritchard et al. 2000; Corander et al. 2003). However, in genetically diverse or highly mobile species, this may be difficult, as $F_{ST}$ values may be small and therefore population boundaries difficult to detect (Latch et al. 2006; Schmidt et al. 2008). Recent developments in genetic statistics may allow us to correct for high levels of diversity and more accurately describe population genetic structure (Hedrick & Goodnight 2005; Jost 2008).

Barren ground caribou (*Rangifer tarandus granti*) are managed on the basis of herds, which are defined by female fidelity to a calving ground (Skoog 1968). However, herd ranges may shift, herds may split into two separate areas, join with other herds, or herds may collapse entirely (Skoog 1968; Hinkes et al. 2005; Joly et al. 2011). Additionally, how sound the caribou herd is, as a construct, remains unclear, as authors have documented both short-term mixing (Hinkes et al. 2005) and long-term genetic homogenization (Cronin et al. 2003) in wild Caribou populations. However, there is also additional evidence that in many cases, Caribou herds represent demographically important units, and would therefore represent the appropriate grouping for wildlife conservation and management (Valkenberg 2002). Our objective is to apply genetic analyses to a set of relatively well studied caribou herds in southwest Alaska and on the

Alaska Peninsula (AP) to document long term population identity, interconnectivity, and to test for the signal of specific demographic events within select herds.

The AP has been considered marginal caribou habitat due to the severe icing conditions and ash fall from frequent volcanic eruptions (Skoog 1968). Nonetheless, there are two recognized herds on the peninsula (Figure C-1) – Northern Alaska Peninsula caribou herd (NAP) and the Southern Alaska Peninsula caribou herd (SAP) – as well as Unimak caribou herd on Unimak Island at the southern terminus of the peninsula. Recently, caribou herds on the AP have demonstrated considerable population fluctuations, with estimates fluctuating from 2000 caribou to 20,000 in the NAP (Butler 2007a) and between 500 and 10,000 in the SAP (Butler 2007b). The Unimak caribou herd has varied somewhat less in magnitude, from 500 to 5000 caribou (Butler 2007c). Between the early 1980s and the mid to late 1990s the nearby Mulchatna caribou herd recovered from a population low, and in doing so expanded into the adjoining Kilbuck caribou herd. Previous work suggests that there may be some degree of population structure among southwestern caribou herds (Zittlau 2004), however work using radio collars instead suggested considerable mixture between herds (Hinkes et al. 2005). Whether these extreme fluctuations in population size among the NAP, SAP, and Unimak caribou herds have caused an appreciable loss in diversity is an open question. Additionally, whether there is long-term population structure among all the southwestern herds, and the extent to which there is population connectivity between herds, remains unclear.

Reindeer (*Rangifer tarandus tarandus*) are a Eurasian subspecies that has been separated from North American *Rangifer* following the flooding of Beringia after the last glacial maximum (Flagstad et al. 1999; Flagstad & Roed 2003). While in Eurasia, populations of reindeer were thought to have been independently domesticated on at least three occasions (Roed et al. 2008). Sheldon Jackson transplanted reindeer from domestic Siberian herds in 1891 in an attempt to introduce an alternate food source and pastoralism to the Alaska Natives on the Seward Peninsula (Stern et al. 1980). Reindeer were

subsequently re-transplanted to a variety of locations, including introductions to Kodiak Island, Umnak Island, Nunivak Island, Atka Island, Cantwell, and other locations (Skoog 1968; Klein 1980; Stern et al. 1980). Reindeer herding in Alaska underwent a subsequent decline through the 1940s, with domesticated herds experiencing mixing with wild animals, and a general collapse of the industry except on the Seward Peninsula (Stern et al. 1980).

Previous research has suggested that introgression of reindeer genes into Caribou herds would generally be limited in time, would be swamped by Caribou genes, and would be purged through selection (Skoog 1968; Klein 1980; Stern et al. 1980; Roed & Whitten 1986; Finstad et al. 2002). However, reindeer mitochondrial haplotypes have been detected within northern Alaska caribou herds (Cronin et al. 2005; 2006), suggesting that the potential for introgression from reindeer was somewhat realized. Wild caribou populations in Nuuk, Greenland also appear to show evidence of introgressive hybridization with domesticated reindeer (Jepsen et al. 2002). The introgression that has been documented has thus far have been from herds where the number of Caribou at the time of the collapse of herding was thought sufficiently large to swamp potential introgression, as was potentially the case on the Alaska Peninsula (Skoog 1968). We sought to quantify the level of introgression of reindeer genetic material into Caribou herds in our study sites, partly because an analysis of population structure would be incomplete without accounting for domestic introgression. However, potential introgression is of its own importance, as introgression from domesticated stock has the potential to impact adaptation to local conditions by native populations (Randi 2008).

**Methods**

We extracted DNA using the DNeasy Tissue Kit (Qiagen Inc. Valencia, CA) from the blood or tissue of 297 individuals, comprising 67 reindeer and 230 caribou. The caribou sample comprised the Denali caribou herd (n = 29), Mulchatna caribou herd (n = 77), Northern Alaska Peninsula caribou herd (n = 72), Nushagak Peninsula caribou herd (n =

5), Southern Alaska Peninsula caribou herd (n = 30), and Unimak Island caribou herd (n = 17). Reindeer samples come from the Ongtowasruk herd (n = 43), the Davis herd (n = 13), a feral reindeer herd on Kodiak Island (n = 8) and earmarked reindeer found by hunters within the Western Arctic Herd's wintering grounds (n = 3). DNA was stored at -80°C until analysis.

We used 21 microsatellites in three multiplexed PCR reactions. Multiplex 1 contained RT6, RT27, and RT1 (Wilson et al. 1997), OheD and OheQ (Jones et al. 2000), NVHRT30 (Roed & Midthjell 1998)), BM6506 and BM4513 (Bishop et al. 1994), FCB193 (Steffen et al. 1993), and OARFCB193 (Buchanan & Crawford 1993). Multiplex 2 contained RT9, RT7, and RT24 (Wilson et al. 1997), NVHRT16 (Roed & Midthjell 1998), and CRH (Moore et al. 1992). Multiplex 3 contained RT10 and RT30 (Wilson et al. 1997), BL42 (Bishop et al. 1994), BMS745 and BMS1788 (Stone et al. 1995), TEXAN4 (Holder et al. 1994), and C89 (Jones et al. 2000). Markers were selected based upon ability to effectively multiplex with other markers as well as known polymorphism in *Rangifer*. RT9 was modified to improve PCR characteristics by lengthening the primer pair (D. Paetkau pers. com.). Our PCR reactions were 10 µL total, consisting of 5 µL Qiagen Multiplex Master Mix®, 1 µL of the multiplex primer solution, 1.5 µL DNA template and 2.5 µL sterile water. Each reaction was incubated at 95°C for fifteen minutes, before undergoing 30 cycles of 30 seconds of 94° C, 30 seconds of 57° C, and 1 minute of 72° C. The 30 cycles were followed by a 30 minute extension at 72° C, followed by a hold at 4° C.

Reactions were analyzed using either an ABI 3100 Genetic Analyzer or an ABI 3730*xl* (Applied Biosystems, Foster City, California), using a 500bp size standard. Each sample was amplified twice for each multiplex, with electropherograms being scored through GENEMAPPER 3.7 software® (Applied Biosystems, Foster City, California). Repeat samples were run on both analyzers, to ensure the intercompatability of results.

Samples were examined for deviations from Hardy-Weinberg equilibrium (HWE) expectations on a per-population, per-locus basis using the program GENEPOP v4.0 (Raymond & Rousset 1995). Markers with significant deviations from HWE were excluded for all subsequent analyses except where specifically noted. Markers were also examined for the presence of null alleles using MICRO-CHECKER v2.2.3 (van Oosterhout et al. 2004). We computed observed heterozygosity ($H_O$), subpopulation expected heterozygosity ($H_S$), subpopulation inbreeding coefficient ($G_{IS}$) and number of alleles (A) in GENODIVE (Meirmans & Van Tienderen 2004), and rarefacted allelic richness ($A_5$) across all loci as well as examining for linkage disequilibrium among loci using FSTAT v2.9.3.2 (Goudet 1995).

We examined population subdivision by computing $G_{ST}$ for each herd pair using the program GENODIVE (Meirmans & Van Tienderen 2004), and the R package DEMETICS (Gerlach et al. 2010) to compute Jost's D (Jost 2008). Jost's D appears to be a more accurate measure of population subdivision in high diversity species (Gerlach et al. 2010), but $G_{ST}$ may yield some information on migration under the finite-island model (Ryman & Leimar 2009; Leng & Zhang 2011), and is included for comparison to previous studies (Ryman & Leimar 2009; Leng & Zhang 2011). The significance values for both Jost's D and $G_{ST}$ were Bonferroni corrected (Rice 1989). We examined for isolation by distance using GENODIVE (Meirmans & Van Tienderen 2004) to perform the Mantel test (Mantel 1967) on a matrix containing Euclidian distance between herd calving grounds centroids (T. Paragi pers. com.) and Nei's genetic distance (Nei 1972) with $1\times10^4$ permutations to test for significance. Reindeer were excluded from this analysis because their presence in Alaska is not the result of natural processes. Additionally, we hypothesize that the distance from populous sources of genetic diversity is linked with declining herd diversity through barriers to dispersal or potential serial founding events. To test this, we examined whether diversity declined with increasing distance from the Denali herd, a herd with a large number of adjoining herds in the center

of Alaska. We used linear regression as implemented in the program R (Ihaka & Gentleman 1996).

To assess the rate of long-term exchange between herds, we employed the program MIGRATE-N 3.2.15 (Beerli & Felsenstein 1999; 2001) to calculate effective migrants per generation, $4N_em$. We used the Bayesian inference strategy, allowing mutation rates to vary among loci, and a uniform prior distribution of $\theta$ and $M$. In the long chain we recorded $3.5\times10^4$ steps with a sampling increment of 100 steps after a $5\times10^4$ step burnin, and the results were averaged across four runs. We repeated the analysis to check for convergence, and repeated the analysis with changed settings to examine for dependence of results on the priors. The Nushagak herd was excluded from this analysis due to low sample size, and reindeer were not included as any potential introgression would have been a one-time event for each population (Stern et al. 1980), and not due to long-term connectivity with reindeer herds. We considered populations to exhibit evidence of connectivity if the posterior estimate's 2.5 percentile did not encompass 0.

We tested for the presence of population subdivision using the program STRUCTURE v2.3.3 (Pritchard et al. 2000) using the admixture model and correlated cluster allele frequencies. All loci were included in these analyses. We used a burnin of $1\times10^5$ iterations, followed by $7\times10^5$ MCMC repetitions after burnin. Number of clusters K was simulated between 1 and 10 six times each, where we compared the maximum likelihood K solution to the solution with the highest second order rate of change (Evanno et al. 2005) as implemented in STRUCTURE HARVESTER (Earl 2011).

We further examined the data using a hierarchical STRUCTURE analysis (Vaha et al. 2007) to account for high-level structure in our data corresponding to the sub-specific divide. Individuals were divided into groups corresponding to their maximal assignment from the best solution of K, and were re-analyzed separately in STRUCTURE using the same parameters as the initial run, but only varying K between 1 and 5. Individuals without $q >$

0.5 to any cluster were discarded for subsequent rounds of analysis. K was assigned in subsequent rounds using the ΔK method in conjunction with the absolute ln $P(X \mid K)$.

Previous work has indicated that there may be differences in performance between Bayesian assignment packages, and that running and comparing the results of multiple methods may be informative (Latch et al. 2006). For this reason, we also performed the clustering analysis in the program BAPS (Corander et al. 2003). We performed 10 analyses in BAPS, using a maximum K of two times the sampling sources, or K = 14. For the admixture analysis we used a minimum number of 5 individuals per cluster, $5\times10^4$ iterations, 25 reference individuals from each cluster, and $1\times10^3$ iterations for reference individuals. Additionally, we performed k-means clustering as implemented in the program GENODIVE (Meirmans & Van Tienderen 2004), clustering by within-individual allele frequency using $1\times10^6$ simulated annealing steps varying K between 1 and 10. We evaluated the most likely number of clusters using both pseudo-F (Calinski & J Harabasz 1974) and Bayesian information criterion. To examine for admixture between reindeer and caribou, we used K = 2 with the same model and settings but a burnin of $5\times10^5$ and $1.5\times10^6$ subsequent MCMC repetitions after burnin. We constructed a table of the percent of individuals in each caribou herd above arbitrary values of proportions assigned to the cluster corresponding to reindeer, including generalized thresholds found through simulative study (Pritchard et al. 2000; Vaha & Primmer 2006).

To examine the potential presence of past demographic bottlenecks within individual caribou herds, we examined the data using the M-Ratio (Garza & Williamson 2001). In order to evaluate the significance of the M-Ratio value, we compare our resultant herd M-Ratios to both a recommended critical value, as well as calculating a herd-specific critical value ($M_C$) of $\alpha = 0.05$, using the program CRITICAL_M.EXE (Garza & Williamson 2001). For CRITICAL_M.EXE, we used a conservative two-phased model (Di Rienzo et al. 1994; Garza & Williamson 2001), consisting of 90% single-step mutations (Kimura & Ohta 1978) and 10% multi-step assuming a variance in size of multi-step

mutation ($\sigma_g^2$) of 12. Given that pre-bottleneck θ ($4N_e\mu$) is an unknown parameter in our populations, for CRITICAL_M.EXE we varied θ between 0.1, 0.25, and 0.5, as well as ×10 and ×100 the base values, to encompass θ spanning 3 orders of magnitude. The Nushagak herd was excluded from these analyses due to low sample size.

**Results**

MICROCHECKER did not find any loci with significant signs of null alleles. Of the 21 loci, 6 were globally out of HWE: RT27, FCB193, NVHRT16, CRH, and BL42. When these loci were removed, no herds deviated from HWE expectations. There was no significant linkage disequilibrium after Bonferroni correction was applied. Diversity was generally high, with an average $H_S$ of 0.79, and $A_5$ varying between 3.95 and 5.62, with an across-population $A_5 = 5.67$ (Table C-1). No population had a value of $G_{IS}$ significantly different from zero. Mantel's test also found that herds exhibit a strong pattern of isolation by distance ($r = 0.70$, $P = 0.019$; Figure C-2). Allelic richness also declines with herds located further down the Alaska Peninsula ($P = 0.016$; Figure C-3).

Pairwise values of Jost's D were considerably higher than those for $F_{ST}$, varying between 0 and 0.472 (Table C-2). However, for both $F_{ST}$ and Jost's D, all pairwise values were significant except for the NAP-Nushagak pair, which was zero for both statistics. The apparent lack of differentiation between the two herds must be interpreted with caution, however, given the low sample size in the Nushagak caribou herd. The G statistic showed an identical pattern of differentiation, with all pairwise combinations being significant ($P < 0.001$) except for the NAP-Nushagak pair ($P = 0.517$). Results from MIGRATE-N suggest that most herds have some limited form of population exchange, with the exception of Unimak and SAP, whose effective migrants rate to or from the herds could not be distinguished from 0 (Table C-3).

Structure found similar signals of population subdivision, with K = 4 being most favored for the first round of assignments. This generally represented reindeer, Mulchatna and

Denali, NAP and Nushagak, and SAP and Unimak herds as clusters (Figure C-4a). Subsequent iterations of Structure found that the SAP-Unimak cluster could be decomposed further into two clusters, and the primarily reindeer cluster could be decomposed into a Seward Peninsula reindeer component and a Kodiak Island reindeer component (Figure C-4b). While the cluster primarily comprising Mulchatna and Denali herds did not decompose in a way that met our criteria for having hierarchical structure, K = 2 showed signs of structuring between the two (MCH assignment to $q_1 = 0.401$ $q_2 = 0.599$, Denali $q_1 = 0.743$ $q_2 = 0.257$) and the difference in likelihood between K = 1 and K = 2 was 44.9. The primarily NAP cluster could not be further decomposed.

BAPS solved for an optimal K = 5 clusters largely corresponding to Seward peninsula reindeer, Kodiak Island reindeer, Mulchatna and Denali, NAP and Nushagak, and SAP and Unimak (Figure C-5). Population structure was considerably more distinct, and few individuals showed signs of admixture with other clusters. However, 4 individuals were assigned some membership to another cluster by BAPS. The K-means clustering analysis implemented in GENODIVE found the best solution according to pseudo-F (Calinski & J Harabasz 1974) was K = 2, corresponding to the reindeer and caribou subspecific designation, with 89.4% of variation being within clusters. However, the best solution according to Bayesian Information Criterion was K = 4 (Figure C-5). Both K = 5 and K = 3 had considerable support ($\Delta$BIC < 2).

Using a conservative of $q_{\text{reindeer}} \geq 0.2$ proportional assignment as a criteria for identifying admixed individuals, our admixture analysis identified 3% of total caribou as containing admixture (Table C-4). Denali showed the highest over-all assignment to the reindeer cluster (6.9%), while Nushagak, SAP and NAP contained no individuals of 20% $\leq$ proportional assignment to the cluster corresponding to reindeer. Only one caribou, in Mulchatna, had a $q_{\text{reindeer}}$ with a lower credibility interval that did not encompass zero. At 5% $\leq$ proportional assignment, all herds identified punitive introgressed individuals except NAP and Nushagak.

The M-Ratio varied between 0.52 (Unimak) and 0.82 (reindeer). Two populations, SAP and Unimak, had M-Ratios less than the generic critical value indicating that populations have gone through substantial reductions in effective population size in their past (Garza & Williamson 2001). Using CRITICAL_M.EXE to find an appropriate critical value, we find that Denali would have had a pre-bottleneck $\theta < 10$ for it to currently show significant signs of having undergone an effective population reduction. SAP and NAP require $\theta < 100$, while Mulchatna and Unimak require $\theta < 2.5$, and reindeer require $\theta < 1$. Mulchatna and the reindeer ancestral populations doubtlessly exceed these values of $\theta$, while it is plausible that Unimak has a pre-bottleneck ancestral $\theta$ less than 2.5

**Discussion**

Our analyses support the existence of strong genetic population structure among southwest Alaskan caribou herds that corresponds to the existing herd designations. The only herd pair that showed no sign of genetic structure between them is NAP and Nushagak (Table C-2). This may be due to the low sample size in Nushagak, and so results including that herd must be interpreted with caution. However, it is also worth noting that Nushagak was artificially created by the Alaska Department of Fish and Game in 1988 from 146 caribou captured in NAP range (Paul 2009). Such a large and successful transplant would invariably capture a large portion of the diversity, and therefore reduce the genetic identity of the resultant herd (Frankham et al. 2009). Alternatively, migrants from NAP could erode any genetic identity that Nushagak may develop. However, given the time since the transplant and the large number of animals involved, we favor the former interpretation.

The next smallest value of Jost's D is 0.059 between Denali and Mulchatna. The low level of differentiation between the two herds, as evidenced by STRUCTURE's inability to resolve the herd pair (Figure C-4a), may stem from exchange between the two herds via the intermediary herds, the Rainy Pass caribou herd and Beaver Mountain caribou herd,

or it may reflect that since divergence, each herd has retained a sufficient effective population size to retain much of their diversity in a manner similar to ancestral composition. However, the value of Jost's D is expected to increase faster than $F_{ST}$ and related metrics in the matter of divergence from high heterozygosity ancestral populations, such as caribou (Leng & Zhang 2011). Indeed, the remainder of the herds show high values of Jost's D, indicating strong genetic structure, and results from MIGRATE-N supporting strong differentiation from low migration rates (Table C-3). Migration rates appear to decline with distance, indicating that although caribou are capable of very long distance migration between populations (Cronin et al. 2005), in this system distance is more isolating than one would expect given the level of dispersal found in other regions (Figure C-2).

These results support initial genetic findings in the region (Zittlau 2004), but are in stark contrast to recent studies using radio telemetry to track population exchange (Hinkes et al. 2005). It is likely that radio telemetry studies reflect short-term processes, perhaps only occurring at specific population sizes or range conditions. Alternatively, it is possible that the high rate of exchange seen by Hinkes et al. (2005) reflects real, long-term processes, but that migrants may suffer barriers to reproductive success. Under this scenario, migration need not be fitness reducing, so long as migrants achieve larger reproductive success in their new herds than in their source population, while having less lifetime reproductive success than individuals from the recipient population. It is of interest to note that populations with no discernable interchange (Table C-3) align with anecdotal observations that those herds generally do not receive migrants (Skoog 1968) whereas those with non-zero $N_e m$ correspond to populations where interchange has been implicated (Hinkes et al. 2005).

Population bottlenecks, especially on the AP, could exacerbate low rates of population exchange in establishing strong population structure in the region through winnowing of herd genetic composition that has a low probability of recovery from outside sources. It

has been suggested that the M-Ratio may reflect longer-term processes (Hundertmark & van Daele 2010). All three Alaska Peninsula herds show signs of historic population reductions from the M-Ratio. Historic sources report periods of regional non-occupation and population lows on the AP, as well as isolation from non-peninsular herds due to adjacent reindeer herding (Leopold & Fraser 1953; Skoog 1968), which are supported by the decline in diversity with increasing distance from the center of the state (Figure C-3). This, combined with the strong signal of population bottlenecks found in all three AP herds, suggests that the modern population fluctuations observed within AP herds (Butler 2007a, Butler 2007b, Butler 2007c) may be due to large variance inherent to caribou ecology on the AP and not due to more modern causes. As diversity declines due to reoccurring population bottlenecks, it may be difficult for herds to recover due to immigration, especially in those located furthest south along the AP.

In light of current conservation concerns surrounding the extremely female biased sex ratio and the low population estimate for Unimak island (Service 2010), our analysis supports Unimak Island caribou herd as being a distinct population with little population exchange with adjoining herds (Table C-2). It is experiencing or has recently undergone a reduction in effective population size, and it contains the lowest diversity of any of our studied herds (Table C-1) or previously studied herds in Alaska (Cronin et al. 2003; Zittlau 2004). Given its long term persistence (Skoog 1968), and morphological (Banfield 1961) and genetic character (this study), it may possess some degree of adaptation to local conditions, which would make it a priority for conservation in the region. Jost's D is lowest between Unimak Island caribou herd and SAP; the next closest population, NAP, has a considerably higher divergence from Unimak, and shows signs of experiencing extensive domestic introgression, whereas SAP does not. Therefore, we strongly recommend that in the event of translocating individuals for supplementing the Unimak population, they be sourced from SAP.

The relative performance of assignment methods has been of some interest as the number of assignment packages increases. Here, we found that differing assignment methods seem to resolve differentiation between herds in quite dissimilar manners. STRUCTURE found K = 4 as the best solution both through ΔK (Evanno et al. 2005) and through maximum likelihood (Pritchard et al. 2000). However, this solution failed to resolve the presence of the Unimak caribou herd, the Mulchatna caribou herd and the Denali Caribou herd as separate demes, and the Kodiak Island reindeer as a separate deme (Figure C-4a). BAPS appropriately recognized the existence of Kodiak Island reindeer as a separate deme, but failed to recognize the distinctiveness of the Unimak caribou herd, the Mulchatna caribou herd, and the Denali Caribou herd (Figure C-5). Traditional metrics successfully resolved all caribou herds, but there was no indication of the Wahlund effect (Frankham et al. 2009) within the reindeer samples, so the presence of the Kodiak Island reindeer as a separate deme went unrecognized. Although Mulchatna is recognized to have recently merged with the Kilbuck herd (Hinkes et al. 2005), there is no evidence of Kilbuck's genetic signature among our samples at the time sampling occurred. This may be because Mulchatna and Kilbuck had a similar genetic composition before merging, or because Mulchatna has completely subsumed Kilbuck's signature via gene swamping.

When we employed the hierarchical STRUCTURE analysis (Vaha et al. 2007) we were able to resolve substantial structure within clusters, successfully identifying all herds except for Denali and Mulchatna caribou herds, likely due to the low $F_{ST}$ between the pair (Figure C-4b). K-Means clustering appeared to identify the same population structure as STRUCTURE, however there was substantially more co-membership of herds within clusters than the more model driven packages. We would also recommend employing multiple methods in elucidating population structure with less prior information. We also would strongly recommend that in the case of species with a strong signal of phylogenetic separation in initial STRUCTURE runs, future analyses use the hierarchical STRUCTURE analysis method to resolve lower-level structure.

The results from STRUCTURE also provide supporting evidence for the introgression of domestic genes from reindeer to caribou as a consequence of the collapse of reindeer herding. The pattern of percent assignment (Table C-4) appears to follow patterns similar to the pattern of reindeer herding in the region (Stern et al. 1980). Cantwell contained a reindeer herd of 1437 reindeer in 1922 until 1928 when herding activities ceased due to constant problems with caribou mixing with reindeer (Stern et al. 1980). Similarly, the region around Bethel, Alaska was a major hub for reindeer herding outside the Seward Peninsula, with the first herd being established in 1901, with considerable head of reindeer until ca. 1949, when it was reported as having likely strayed from herders (Lantis 1950; Stern et al. 1980). Reindeer herding in the Alaska Peninsula area collapsed before 1940 at a time where wild caribou were reported at a population low of ca. 2,000 (Skoog 1968). Unimak island contained reindeer ca. 1940 (Burdick 1940), though the exact number is not clear. The low extent of possible introgression suggests either few reindeer were released, or that contact between caribou and reindeer was limited, however (Table C-4). The southern Alaska Peninsula was somewhat protected from the presence of reindeer, although there were nearby reindeer at Port Moller (Skoog 1968).

Although previous work suggested limited introgression in Alaskan herds (Roed & Whitten 1986), here we document what appears to be wide-spread but low levels of domestic introgression into wild herds. Higher density markers such as, single nucleotide polymorphisms, are needed to most accurately elucidate the extent of domestic introgression within wild herds, along with new tools to more accurately quantify low levels of admixture where pure reference populations may not be available. Credibility intervals as currently implemented in STRUCTURE appear to underestimate admixture, as despite the presence of several quarter admixed or greater individuals, only one caribou had a credibility interval that didn't encompass zero admixture. To deal with this in a less ad-hoc manner, we have attempted to design a rigorous method for determining which admixture is not derived from error in assignment, but given it identifies two individuals in Unimak as potentially admixed individuals, there may be room for improvement.

**Conclusions**

Here we have identified genetic population structure in the southwestern Alaskan caribou herds, and assessed long-term migration between them. Given the correspondence between herds and distinct populations, and the low rate of effective migrant exchange, we suggest that for long time horizons, a metapopulation is not a completely accurate model of herd structure in this area, as it fails to anticipate barriers to effective migration between herds. Status quo, herd-based management units appear to align neatly with regional structure, unlike caribou on Alaska's North Slope (Cronin et al. 2005).

Our comparison of various individual based assignment methods has revealed potential problems for datasets containing both high and low level genetic structure. Normal implementations of STRUCTURE and BAPS appear to have failed to subdivide clusters appropriately, instead focusing on high-level splits such as the one between subspecies. It was only through the hierarchical STRUCTURE analysis that finer scale divisions between more closely related populations became apparent. This underscores the need to separately reexamine clusters for population structure that was missed in initial analyses, a task that is too often ignored.

The analyses of this study also suggest that three herds appear to have undergone significant population contractions in their history. As management of AP caribou herds becomes a large issue, it is important to understand the role of past bottlenecks in understanding the ecology of the herds. Additionally, an understanding of population structure and relatedness allows for more informed management decisions in undertaking population rescue, especially with special respect to the translocation of individuals. Finally, our data suggest that caribou herds in southwestern Alaska carry a burden of domestic introgression from historic reindeer herding. The hybridization of domestic animals with wild animals is of global concern, and the long-term impact of such hybridization in caribou is not fully understood. Further work is needed to develop better tools for detecting introgression in situations where reference populations are not

available, so the issue may be fully explored. These findings also suggest that future reindeer herding activity in caribou range should be carefully managed to avoid potential genetic impacts on wild caribou.

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**Table C-1. Sample size and genetic diversity of reindeer and caribou herds.**

| | Sample Size | $H_S$ | $H_O$ | A | $A_5$ | $G_{IS}$ |
|---|---|---|---|---|---|---|
| Denali Caribou Herd | 29 | 0.84 | 0.86 | 9.63 | 5.62 | -0.02 |
| Mulchatna Caribou Herd | 77 | 0.81 | 0.78 | 11.44 | 5.29 | 0.04 |
| Nushagak Peninsula Caribou Herd | 5 | 0.81 | 0.85 | 5.25 | 5.25 | -0.06 |
| Northern Alaska Peninsula Caribou Herd | 72 | 0.82 | 0.83 | 10.56 | 5.39 | -0.01 |
| Southern Alaska Peninsula Caribou Herd | 30 | 0.75 | 0.72 | 7.31 | 4.53 | 0.04 |
| Unimak Island Caribou Herd | 17 | 0.69 | 0.67 | 5.44 | 3.95 | 0.03 |
| Domestic Reindeer | 67 | 0.77 | 0.74 | 10.63 | 4.78 | 0.04 |
| Overall | 297 | 0.79 | 0.78 | 14.44 | 5.67 | 0.01 |

$H_S$ – Expected subpopulation heterozygosity, $H_O$ – observed subpopulation heterozygosity, A – Average per-locus number of alleles, $A_5$ – Average per-locus mumber of Alleles rarifacted for a sample size of 5. $G_{IS}$ – subpopulation inbreeding coefficient.

**Table C-2. Pairwise genetic differentiation between sampled herds**: $F_{ST}$ (below diagonal) and Jost's D (above diagonal). Herd Abbreviations: Denali Caribou Herd (DENA), Mulchatna Caribou Herd (MCH), Nushagak Peninsula Caribou Herd (NUSH), Northern Alaska Peninsula Caribou Herd (NAP), Southern Alaska Peninsula Caribou Herd (SAP), Unimak Island Caribou Herd (UCH) and Reindeer (RD).

| | DENA | MCH | NAP | NUSH | SAP | UCH | RD |
|---|---|---|---|---|---|---|---|
| DENA | - | **0.059** | **0.141** | **0.136** | **0.363** | **0.472** | **0.296** |
| MCH | **0.012** | - | **0.129** | **0.154** | **0.373** | **0.466** | **0.296** |
| NAP | **0.028** | **0.024** | - | 0.000 | **0.196** | **0.318** | **0.314** |
| NUSH | **0.030** | **0.029** | 0.000 | - | **0.154** | **0.370** | **0.384** |
| SAP | **0.085** | **0.086** | **0.044** | **0.038** | - | **0.171** | **0.458** |
| UCH | **0.123** | **0.126** | **0.085** | **0.110** | **0.059** | - | **0.418** |
| RD | **0.064** | **0.065** | **0.068** | **0.091** | **0.119** | **0.124** | - |

**Bold** values indicate *P*-values significant after Bonferroni correction for multiple comparisons. Negative values are converted to zero.

**Table C-3. Effective migrants between herds**. Values are in 4 times effective migration rate per generation ($4N_e m$). Column axis represents source herd for migrants, row axis represents recipient herd. See Table 2 for herd abbreviations. We consider any value that does not encompass zero at the 2.5 percentile as showing significant evidence for herd connectivity.

| | DENA | MCH | NAP | SAP | UCH |
|---|---|---|---|---|---|
| DENA | - | **15.9** | **11.3** | 1.2 | 0.5 |
| MCH | **30.8** | - | **27.0** | 2.4 | 0.6 |
| NAP | **46.5** | **54.1** | - | 2.6 | 0.9 |
| SAP | 7.4 | 8.6 | 7.2 | - | 0.6 |
| UCH | 5.9 | 2.9 | 4.0 | 0.9 | - |

**Bold** values indicate that the posterior distribution for the parameter does not encompass zero at the 2.5 percentile.

**Table C-4. Caribou herd admixture.** Overall values represent the proportion of assignments to the primarily reindeer and the primarily caribou clusters ($q$). P > $q_{reindeer}$ is the proportions of individuals within a population with assignment to the reindeer cluster greater than the threshold for that column. 0.043 is the calculated critical level for admixture. See Table 2 for herd abbreviations.

| | Overall | | P > $q_{reindeer}$ | | | | | |
|---|---|---|---|---|---|---|---|---|
| | $q_{reindeer}$ | $q_{caribou}$ | 0.04 | 0.05 | 0.10 | 0.15 | 0.20 | 0.25 |
| DENA | 0.043 | 0.957 | 0.345 | 0.276 | 0.103 | 0.069 | 0.069 | 0.034 |
| MCH | 0.037 | 0.963 | 0.208 | 0.156 | 0.078 | 0.065 | 0.039 | 0.039 |
| NAP | 0.015 | 0.985 | 0.056 | 0.028 | 0.014 | 0.014 | 0.014 | 0.014 |
| NUSH | 0.011 | 0.989 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| SAP | 0.006 | 0.994 | 0.033 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| UCH | 0.015 | 0.985 | 0.118 | 0.118 | 0.000 | 0.000 | 0.000 | 0.000 |

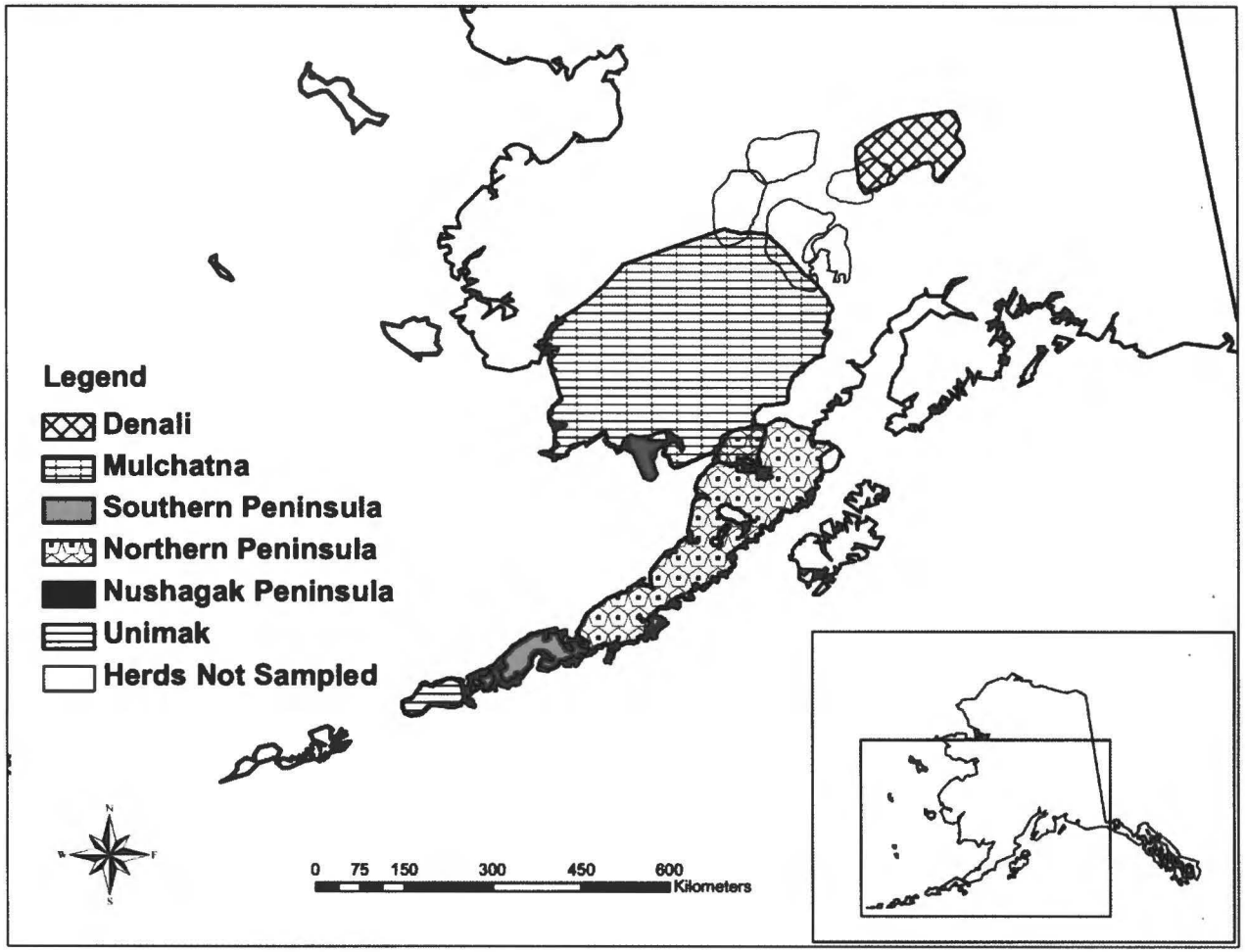


**Figure C-1. A map of caribou sampling localities and nearby unsampled herds.**

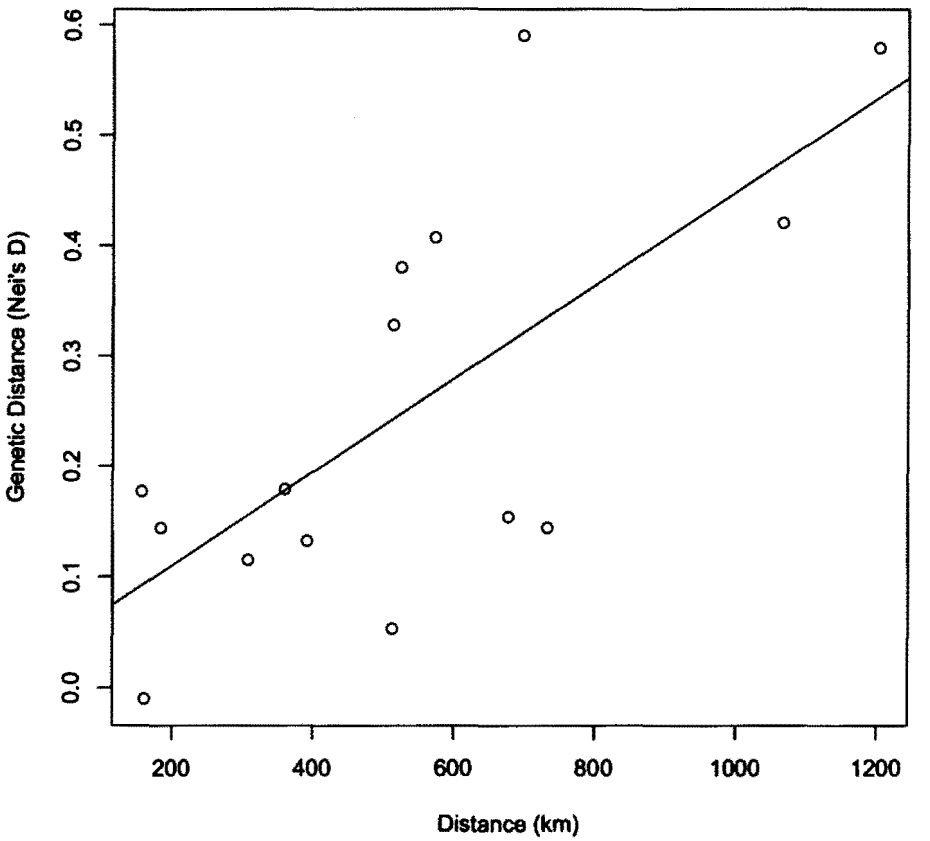


**Figure C-2. Relationship between pair-wise genetic distance and Euclidian geographic distance between herds.** Solid line represents the fitted relationship among all herds ($r = 0.70$, $P = 0.019$).

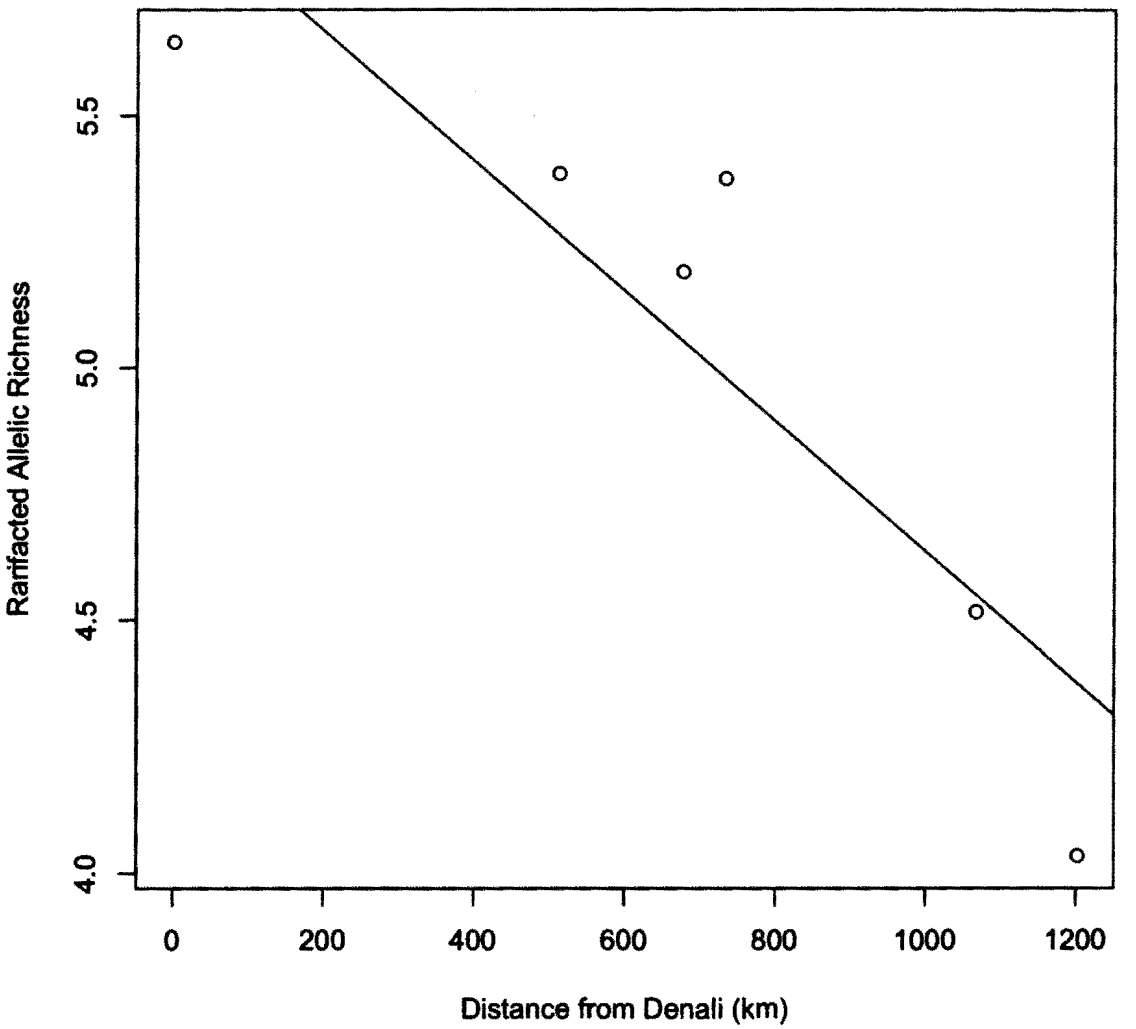


**Figure C-3. Genetic diversity declining with distance from other central caribou herds.** The distance from interior caribou herds is represented by Euclidian distance from the Denali caribou herd. The over-all relationship (dark line) between distance from Denali caribou herd and rarifacted allelic richness was significant ($P = 0.016$).

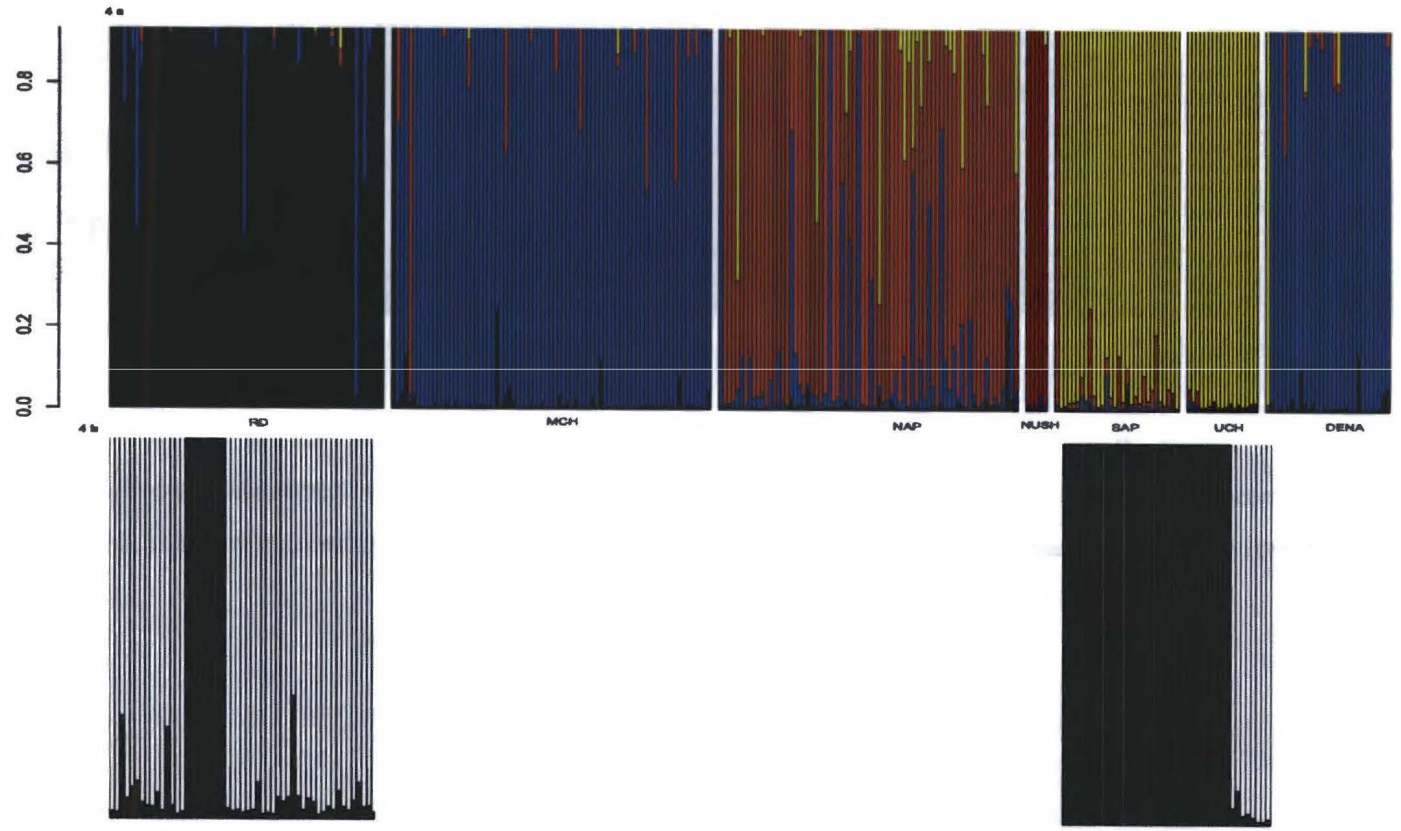


**Figure C-4. Population structure as estimated through STRUCTURE using the hierarchical structure method.** Each line represents a single individual partitioned into K colored segments representing assignment to a corresponding cluster. 4a represents the best solution of K = 4 for the initial set of STRUCTURE results, where reindeer, Denali and Mulchatna, NAP, and SAP and Unimak are distinguished as clusters. 4b represents results from subsequent analyses of clusters using the hierarchal structure method, whereby two clusters (reindeer, as well as Unimak and SAP) are found to have solutions at K = 2. For reindeer, this distinguishes Kodiak reindeer from Seward Peninsula reindeer; for Unimak/SAP, this approximately distinguishes the two herds.

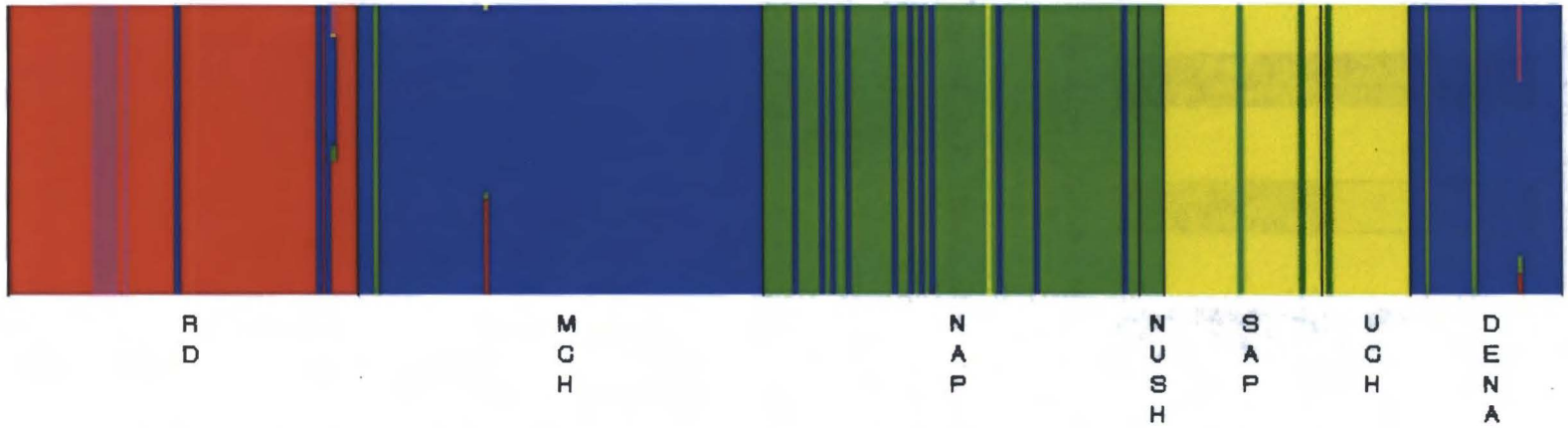


**Figure C-5. Population structure as estimated through the program BAPS.** Each individual is represented by a solid bar divided into K colors representing proportional assignment to inferred clusters. K = 5 was best solution found by BAPS, and is shown here.

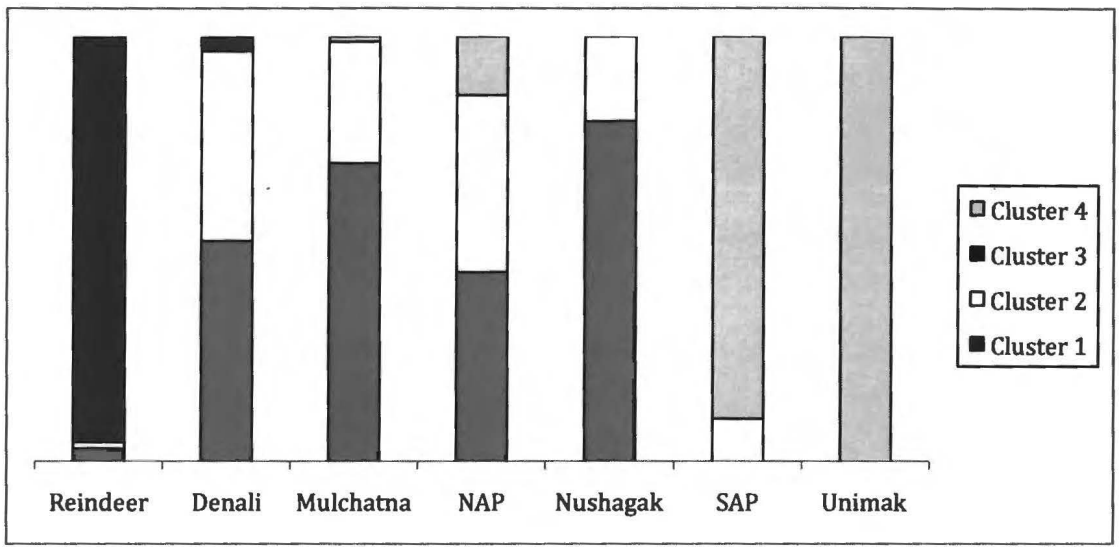


**Figure C-6. K-Means clustering results.** Each population is represented by a bar divided into 4 colors, with each color representing over-all proportional assignment of that population to a cluster.