Migration: On the Move in Alaska

Alaska Park Science

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Cover photo: Caribou migration through Onion Portage, Kobuk Valley National Park.
NPS/Kyle Joly

Migration: On the Move in Alaska

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Dead Tufted Puffin and Short-tailed Shearwater found in Bering Land Bridge National Preserve, 2017.
NPS /Stacia Backensto

The far north provides both challenges and benefits to the people and animals that live here. In summer, Alaska is teeming with life, providing abundant food and resources. In the winter, however, darkness and bitter cold require Alaska's inhabitants to use a variety of strategies to survive. Some animals, like collared pika (*Ochotona collaris*), collect and store food in their summer homes to last them the winter. Many animals move across the landscape to winter ranges that may be across the next valley or across the globe.

Migration encompasses a variety of movements between two areas (Dingle and Drake 2007) and Alaska is well known for some spectacular examples of the phenomenon. Arctic Terns (*Sterna paradisaea*) nest and raise young in Alaska each summer and then in the fall undergo the longest known animal migration, flying about 15,000 miles (over 24,000 km), to wintering areas in Antarctica (McKnight et al. 2013, Egevang et al. 2010). Caribou (*Rangifer tarandus*) in northern Alaska perform the longest over-land migration of any terrestrial animal on the planet traveling over 2,000 miles (3,200 km) annually between summer calving grounds and wintering areas where their preferred winter forage, lichen, is plentiful (Fancy et al. 1989, Joly and Cameron

2017). Millions of salmon return from the ocean to the rivers of Alaska each year to spawn, providing a critical food resource for wildlife and people. While these astonishing movements exemplify migration in Alaska, smaller movements of animals on the landscape are equally important to an individual's survival as well as the integrity of ecosystems.

The daily and seasonal movements of the smallest animals support the function of marine ecosystems in places like Glacier Bay National Park and Preserve. These migrations do not meet the traditional definition of migration as exemplified by long-distance migratory birds, but are similar in function. Tiny marine invertebrates collectively referred to as zooplankton support much of the life in the oceans as prey to fish, whales, and seabirds. Zooplankton exhibit a daily vertical migration within the water column, ascending to shallower waters at night and descending to deeper waters during the day, to avoid some of their many predators (Stich and Lampert 1981). Small forage fish feed primarily on zooplankton and their seasonal movements indicate areas of high plankton productivity as well as important spawning areas. Migratory patterns may change from year to year because of the changes in ocean waters such as temperature, salinity, and freshwater inputs. These changes, in turn, can result in cascading effects within seabird and forage fish populations.

Changes in patterns of seasonal movements—at large spatial scales or more localized—have far-reaching affects throughout the ecosystem.

For example, with less sea ice, the dark open ocean absorbs more heat from the sun. Warm ocean waters are poor habitat for forage fish that are critical to the survival of seabirds.

Alaska's largest seabird die-off occurred in the Gulf of Alaska in 2015-2016, affecting hundreds of thousands of Common Murres. The birds had starved because forage fish were largely absent. The forage fish (like capelin, herring, and juvenile pollock) feed on zooplankton, abundant in cold waters.

In the fall of 2017, dead birds washed up on the shores of the Bering and Chukchi seas. Among them were Short-tailed Shearwaters that migrate 9,000 miles (14,400 km) to Australia from Alaska, Northern Fulmars, kittiwakes, murres, auklets, and puffins.

While we don't know the cause of the recent die off, this is the fourth consecutive year the Bering and Chukchi seas have been exceedingly warm. Warm waters can also trigger toxic algal blooms, which are suspected in some marine mammal deaths in recent years.

Arctic Terns have the longest known migration, traveling between the Arctic and Antarctica each year.
NPS/Jared Hughey
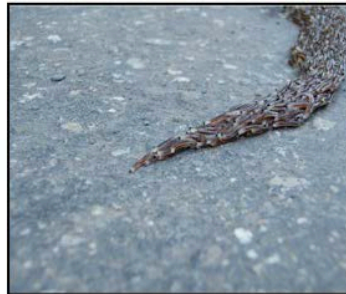
Migrations in the Microwilderness

Jessica Rykken, National Park Service

While we don't know of any Alaska insects that undergo long-distance migrations, the larvae of some fungus gnats (family Sciaridae) have a remarkable method of traveling *en masse* to reach their pupation sites. Each larva is small, less than half an inch (about a centimeter) long, but they congregate in columns of up to a thousand or more individuals to form long, snake-like bands up to an inch (several centimeters) across and yards (meters) in length. The writhing column also has depth because larvae are stacked on top of one another, each secreting a layer of mucus that allows the upper larvae to slide forward over the lower ones, with those in the rear rising to the top layer, much like a conveyor belt. In this manner, the column of fly larvae (maggots) can advance an inch (several centimeters) per minute, leaving a trail of mucus behind it.

Fungus gnat larval aggregations have been observed to travel up to 32 feet (ten meters). The exact reasons behind these mass maggot migrations are still somewhat of a mystery, but it's hypothesized that the mature larvae are seeking drier ground in which to pupate. One of the migrating

ONE OF TWO MASS MICRO-MIGRATIONS OF CATERPILLARS OBSERVED ON THE EXIT GLACIER PAVED TRAIL AT 0705 HOURS ON 07-30-2011.

LOOKED ALMOST LIKE A STICK A FIRST GLANCE.

NOTE THE RESIDUE TRAIL AT THE TAIL END OF MIGRATION.

fungus gnat species inhabiting Alaska is *Sciara militaris*, also known as army worms or snake worms. Visitors at Kenai Fjords National Park have been fortunate to observe this migratory phenomenon on multiple occasions on the paved trails at Exit Glacier.

Across a landscape as vast and sparsely populated as Alaska, our understanding of the ecology and movement patterns of many species that live here is limited. This is particularly evident in invertebrates, some of which undertake long-distance migrations as observed in well-known insects such as monarch butterflies (*Danaus plexippus*), though we do know of some very interesting smaller scale insect migrations. Another challenge is piecing together ancient movements of animals now extinct such as investigating the colonization of Alaska during periods when the Bering Land Bridge was present.

In this issue of *Alaska Park Science*, readers will learn how scientists discover the stories of animals' movements across Beringia in "Duck-billed Dinosaurs, Ancient Environments, and Cretaceous Beringia," and "Pleistocene Megafauna in Beringia." People also travelled across Beringia and developed specialized methods for hunting Pleistocene megafauna like steppe bison (*Bison priscus*) and caribou. "A Survey of Human Migration through Time" describes the movements of the first Alaskans over thousands of years. A more recent human migration is described in "The Klondike Gold Rush."

Many Alaskans still rely on migratory animals to support subsistence lifestyles. Caribou and salmon have figured prominently in Alaska Native culture for thousands of years. "History, Purpose, and Status of Caribou Movements" and "Future Challenges for Salmon and Freshwater Ecosystems" discuss how changes in the populations (of caribou and salmon respectively) may affect today's Alaskan residents. As seasonal ice conditions change with climate warming, longer periods of ice-free water during the year has implications for the marine mammals using Pacific Arctic ecosystems. "Seasonal Sea Ice and Arctic Migrations of Beluga Whale" discusses the impacts of these changes. Similar reductions in ice associated with the retreat of tidewater glaciers impact the

movements of seals as described in "Influence of Spring Prey Pulses on the Seasonal Distribution and Migrations of Pinipeds."

As incredible migration is at many scales and across many taxa, birds are still the stars of long-distance migration. Over 80% of more than 300 resident birds connect Alaska to six continents through their migrations (Gibson et al. 2018). While Arctic Terns fly the farthest, birds like Bar-tailed Godwits (*Limosa lapponica*) and Bristle-thighed Curlews (*Numenius tahitiensis*) exhibit astounding non-stop flights of 2,500-6,000 miles (4,000-10,000 km) across open ocean (Gill et al. 2005, Marks and Redmond 1994). Or the Pacific Golden-Plover (*Pluvialis fulva*) that can cover its 3,000-mile (4,800 km) migration in as little as three days at speeds of up to 185 miles/hour (Johnson et al. 2011). The coastal areas of Northwest Alaska provide staging areas where tens of thousands of shorebirds congregate during migration to gorge on invertebrates before continuing their long flights across the globe (Alaska Shorebird Group 2008). Bird migrations highlighted in this issue include, "Statewide Movements of Non-territorial Golden Eagles in Alaska During the Breeding Season" and "Connecting Taiga to Tropics: Swainson's Thrush as a Model for Nearctic-Neotropical Migration in Alaska."

Alaska's national parklands, encompassing nearly 54 million acres (22 million hectares), play an increasingly important role in conserving migratory animals as human development continues to fragment the landscape outside protected areas. However, as detailed in this issue, animals do not recognize park boundaries and face ever-increasing threats to their ability to complete their migratory journeys. Migration at all scales, from local to hemispherical, are a fundamental part of Alaska's landscape. Read more about this in "Bridging the Boreal" about landscape linkages and "Migration's Foundation" about ecological intactness.

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A Survey of Human Migration in Alaska's National Parks through Time

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Ancient hunter-gatherers of the Arctic and Subarctic regions were nomadic people that moved camp regularly with the seasons. Ethnographic data show Native Alaskan populations typically limited their residential moves within familiar territories (e.g., Burch 2006); however, the archaeological record demonstrates there were times in prehistory when humans spread from their homelands to new areas, sometimes lands where humans had never lived before. Archaeologists most commonly use the term *migration* to refer to long-distance moves with the intention of residing in a new location permanently. Archaeologists reserve the term *colonization* for those migration events of the first people into a new area. The timing and causes of these major population resettlements remain a major topic of archaeological interest, and understanding the nature of human migrations is a fundamental step toward interpreting the archaeological record. This article describes human migrations into and through Alaska over the past 14,000 years to provide a better understanding of who created the archaeological sites found within Alaska's national parklands.

To tell the story of human migration in Alaska's national parklands, we must consider the archaeological record of the entire state and the neighboring regions in Canada and Russia.

Archaeologists have come to learn that the first Alaskans did not just arrive 14,000 years ago and stay in one place, but rather, people have been coming and going, adapting and mixing with each other ever since humans first arrived to Beringia (Potter 2010). In fact, current research demonstrates that native Alaskan populations in prehistory show signs of growth and decline, regional abandonment, and recolonization of depopulated areas (Mullen 2012, Potter 2008, Tremayne and Brown 2017). Some regions of Alaska show population and cultural stability over vast time-periods, while others indicate rapid and frequent change (Tremayne and Winterhalder 2017). Using observable changes in artifact types, styles, and designs, archaeologists have constructed a detailed culture history for Alaska (Figure 1). However, many questions about the origins and relatedness of the people that created these materials remain unanswered.

Recognizing human migration in the archaeological record is complicated. In fact, the evidence can often be equivocal and difficult to decipher. For example, some changes in material culture are due to *in-situ* cultural evolution, where environmental changes or interactions with neighbors promoted new adaptations and technological innovations, leading to gradual changes over time. In these cases, the artifacts (i.e., material culture) produced by people from later periods no longer resemble those from their early ancestors despite being part of the

same biological population. For example, people in northwest Alaska stopped using microblade technology and adopted ceramics around 3,000 years ago, yet many of their tools remained unchanged. Based on this observation, archaeologists believe the changes were within the same population. In other cases, cultural continuity is not demonstrable and the younger artifacts show no relationship to the earlier culture indicating population replacement. In these instances, archaeologists look to neighboring regions for clues to the origins of the new arrivals. Such evidence does not come from a single artifact or site, but rather from a comparative analysis of hundreds or even thousands of archaeological sites, assemblages, and radiocarbon dates. While our understanding of human migration into Alaska is still developing, archaeologists have identified at least four major cultural transitions over the past 14,000 years (Figure 1) and numerous minor developments. Some of these cultural transitions represent traces of physical migration of people, while others probably constitute the diffusion of ideas or internal adaptive change.

One method to differentiate between migration and in-place change is to use many lines of evidence, including the archaeological record (e.g., artifact types and styles, radiocarbon dates), biological data (e.g., skeletal morphology, dental records, genetics), and linguistic relationships. Each line of evidence is fraught with complications, but also
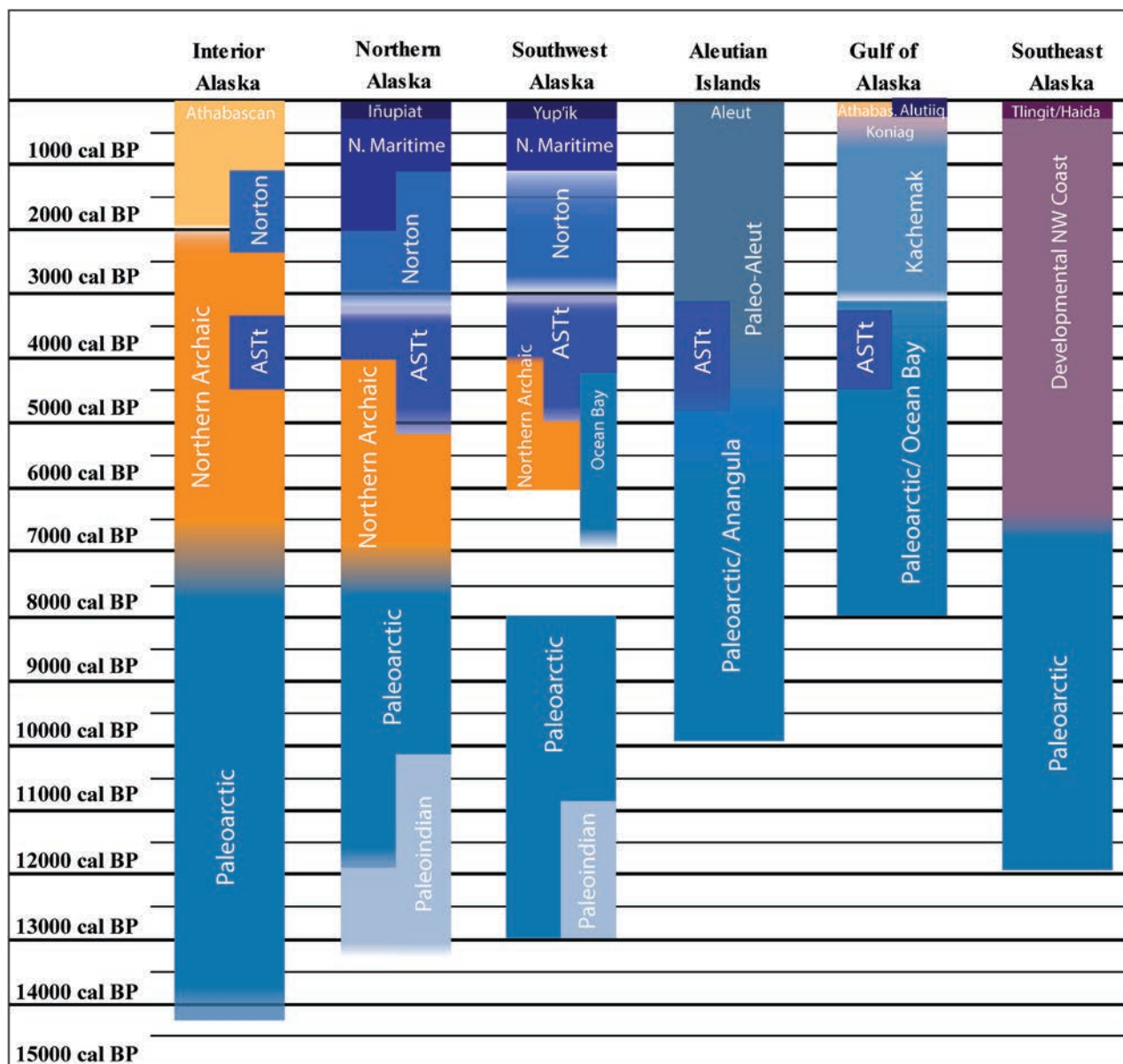
Arctic hunters travel to a new camp near the sea.
Frank and Frances Carpenter collection, Library of Congress

Figure 1. A timeline by region of the major archaeological traditions of Alaska. Timeline is calendar years before present.

the only source of information we have to work with. With archaeological data, we can only trace the distribution of a cultural tradition and, in ideal cases, track its spread into a particular region at a given point in time. Without associated biological remains, we cannot be certain that it was population replacement and not cultural diffusion (sharing of ideas and technologies). Historical linguistics can also provide compelling clues towards cultural and biological affinities, but we must exercise caution when assigning prehistoric cultures and genetic lineages to a linguistic family, as researchers have long known that languages can spread and evolve independently. Additionally, the further back in time we go, the less confidence linguists have in language reconstruction. As such, archaeologists typically use linguistics relationships as a complementary line of evidence when searching for historical relationships. With that said, it is fair to assume that it is more likely than not that genetic populations, their associated material cultures, and languages correlate with each other (Potter 2010). Taken together, material culture, skeletal remains, genetics, and linguistics can help archaeologists trace the movement and spread of particular prehistoric populations. Based on this data, the following provides a short summary of the current hypotheses for major human migrations and culture change in Alaska prehistory.

The First Migration into Alaska and the Americas (and Back Again)

Archaeologists interested in the peopling of the Americas have long looked to Alaska for evidence of the colonizing population. During the Last Glacial Maximum (LGM) 24,000-15,000 years ago, glaciers locked up so much water on land that sea levels were at least 120 meters lower than today exposing a land bridge between Alaska and Asia. Researchers refer to this area as Beringia (Figure 2). The glaciers at this time were so large that they effectively cut

off Alaska from the rest of North America, making it geographically and ecologically part of northeast Asia. There is broad consensus in the scientific community that humans spread into Beringia during the LGM and dispersed into the Americas from there (Hoffecker et al. 2016, Potter et al. 2017). However, significant debate persists about the timing and route of the colonizers moving south from Alaska (e.g., Braje et al. 2017, Potter et al. 2018).

The traditional interpretation, known as the *Clovis-First* model, was that the first Americans passed through Alaska and migrated south through an ice-free corridor into mid-latitude North America (Meltzer 2009). Others contend that there were people south of the great ice sheets many thousands of years before Clovis (Dillehay 1997) and that the ice-free corridor would not have been open early enough for people to pass through that route (Pedersen et al. 2016). Proponents of the coastal migration hypothesis argue the first Americans must have taken a coastal route from Alaska south at time prior to the opening of the ice-free corridor (e.g., Braje et al. 2017; Figure 2). The source population then would have been a maritime-adapted group that lived on the shores of Beringia. Evidence for these coastal migrants, of course, would now be under water. Still, many archaeologists question this hypothesis based on the lack of hard evidence and alternate interpretations for the "pre-Clovis" sites in the Americas hang on the timing for the opening of the ice-free corridor (Potter et al. 2018). A single discovery of pre-Clovis site on the coast or within the interior would be very significant.

While these archaeological debates continue, the field of ancient population genetics has begun to make significant contribution toward our understanding of prehistoric relationships between North America and greater Beringia. Proponents of what is termed

Figure 2. The distribution of radiocarbon dated Paleoarctic and Paleoindian sites in Alaska around 14,000-10,000 years ago (site data from the Alaska Historic Resource Survey 2017). The arrows indicate the directionality of the proposed first migration to Alaska across Beringia and the back migration of Paleoindians through the ice-free corridor around 12,000-13,000 years ago. Glacial extent estimated from Potter et al. (2017). National parklands are outlined in green.

the *Beringian Standstill* hypothesis found that populations in Alaska and the rest of North America were all descended from a northeast Asian or Beringian population that was genetically separated/isolated from their Asian ancestors for thousands of years before colonizing the Americas (Hoffecker et al. 2014, Tamm et al. 2007). To date, investigators have yet to discover conclusive archaeological evidence of this hypothetical population. However, recent work

by University of Alaska, Fairbanks archaeologist Ben Potter and colleagues discovered that the DNA of 11,000 year old humans from the Upward Sun River site shows the first Alaskans are genetically distinct from all other Native American populations, confirming the existence of a "Beringian" population (Moreno-Mayar et al. 2018).

While the earliest sites of the Beringian Standstill population remains undiscovered, our knowledge of the first archaeological culture in Alaska is increasing with each new field season. So far, the oldest undisputed site in Alaska, Swan Point located in the Tanana Valley, dates to around 14,000 years old (Potter et al. 2017). Archaeologists refer to the material remains of the oldest archaeological sites in Alaska as the *Paleoarctic tradition* (see Figure 1). Researchers define the Paleoarctic tradition by the presence of microblade technology and unique bifacially worked stone tools, as exemplified by sites such as found at Onion Portage in Kobuk Valley National Park (Anderson 1988). However, by about 12,000–8,000 years ago, some of these people began exploiting resources in coastal contexts developing a tradition sometimes referred to as *Paleomarine* (Davis 1990, Potter 2010). Interestingly, the Alaskan Paleoarctic does not resemble Paleoindian or Clovis material culture from mid-continent North America; instead, it shares closest resemblances to the Diuktai Culture of Asia, demonstrating a migration west to east across Beringia (Potter 2010; Figure 2), as archaeologists have long suggested.

To complicate the picture, researchers have also discovered evidence for Paleoindians at multiple sites in Alaska (including in both Bering Land Bridge and Noatak national preserves), that contain both fluted and tapering-base spear points similar to those of mid-continental North America (Goebel et al. 2013, Rasic 2011). What is notable about these discoveries is that all of the fluted point sites post-

date Clovis by 1,000 years or so, prompting some researchers to propose a "back-migration" into Alaska from Paleoindian populations from the south (Goebel et al. 2013; Figure 2). If the fluting technique originated in Alaska, we would expect to find the oldest "Clovis" sites here. To date we do not, but this does not mean their origins are not ultimately from Beringia, especially considering some of the tapering-base lanceolate points such seen in Sluiceway Complex at sites in the Noatak National Preserve have radiocarbon dates contemporaneous with Clovis (Rasic 2011). More work is needed to sort out these ancient relationships, but a story of the first migrations in Alaska is beginning to emerge.

Based on these competing models, the expectations are that two biologically and culturally distinct populations came to inhabit Alaska by the close of the Pleistocene 11,000 years ago: the Paleoarctic culture and the Paleoindian culture. While we lack genetic data from Paleoindians in Alaska, mitochondrial DNA (mtDNA) from two Paleoarctic sites predating 10,000 years ago (Lindo et al. 2017, Tackney et al. 2015) provides compelling evidence in support of the Beringian Standstill hypothesis, but also that the genetic diversity of the Pleistocene population within Alaska is complex and varied. For example, the DNA sequences of two infants from 11,500-year-old burials at Upward Sun River revealed mtDNA haplogroups B2 and C1b, which are rare in modern populations from northern North America, but are found today primarily in Native American populations in the mid-latitude North and South America (Tackney et al. 2015) suggesting ancient biological affinities. At On Your Knees Cave site, from the southeast Alaska Island of Prince of Wales, the 10,300-year-old Shuká Káa man revealed mtDNA D4h3a, which is the same as Anzick-1, a Clovis skeleton from Montana (Lindo et al. 2017). An analysis of the complete genome of Shuká Káa man along with other DNA samples
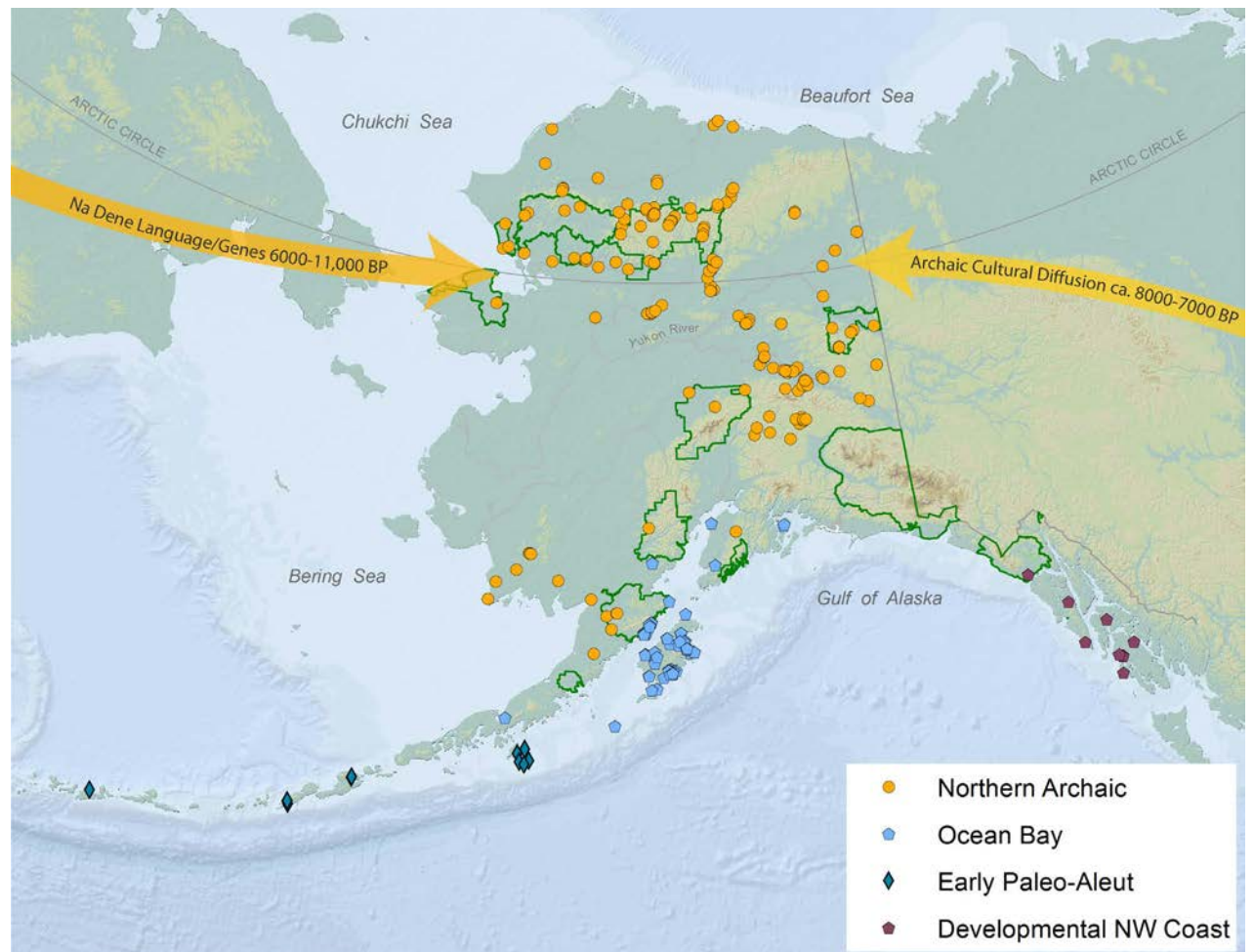
from the region shows genetic continuity through to modern populations of the Northwest Coast region, while the Clovis individual shares greater affinities to Native Americans in Central and South America. Even more recently, Moreno-Mayar et al. (2018) sequenced the nuclear genome of the 11,000-year-old Upward Sun River babies, demonstrating the people who possessed a Paleoarctic culture have a distinct, but related, genome from all other Native Americans. In fact, the current study shows that the oldest genome in Alaska is a unique, newly discovered genetic group that existed during the late Pleistocene/early Holocene, but has no living descendants today in the Americas. This discovery suggests a genetic split between Paleoarctic and Paleoindian people happened while Beringia was still dry land. The implications of these findings on the migration(s) into the Americas is that the hypothetical source population from Beringia was more genetically diverse than once thought, and that Paleoarctic and Paleoindian archaeological cultures represent related, but distinct biological populations.

The Spread of the Northern Archaic and the Origins of Athabaskans

As the early Holocene conditions continued to warm and rising waters inundated the Bering Land Bridge, Paleoarctic people persisted in Alaska by diversifying and adapting to regionally specific ecological niches and maritime habitats. However, archaeologists recognize the appearance of a new culture in Alaska around 6,500-7,000 years ago, demarcated by a suite of new artifact types, in particular the notched dart point, referred to as the Northern Archaic tradition (Anderson 1968, Esdale 2008). Archaeologists have documented Northern Archaic sites across Alaska and they are common in most of Alaska's national parklands (Figure 3). Some representative Northern Archaic sites include Palisades in Cape Krusenstern National Monument

(Giddings and Anderson 1986), Onion Portage in Kobuk Valley National Park (Anderson 1988), and Agiak Lake in Gates of the Arctic National Park and Preserve (Wilson and Slobodina 2007). It is still unknown if the origin of this new tradition represents the spread of ideas and new technologies into the Paleoarctic populations or if it represents the physical immigration of a new group of people that displaced their indigenous contemporaries. Based on persistent use of some artifact types, namely microblade technology, Potter (2010) argued for continuity between the Paleoarctic tradition people and the Northern Archaic with minor diffusion of ideas from Canada and mid-latitude North America. However, the genetic study of the Upward Sun River burials (Moreno-Mayar et al. 2018), indicates an influx of new genes into Alaska must have occurred at some point following the existence of the Paleoarctic tradition. Perhaps the Northern Archaic people brought in the new genes. The question remains: where did this new group of people come from?

Many researchers consider the Northern Archaic people to be direct ancestors of Na Dene speaking Athabaskans (e.g., Esdale 2008, Potter 2008). Interestingly, historical linguistic analysis suggests the origins of the Na Dene language family is in central Asia (Kari and Potter 2010). This would indicate, as others have argued before (e.g., Greenberg et al. 1986), that a second migration wave from Asia occurred many thousands of years after the arrival of the first Beringians. Others have pointed out the notched point technology originated first in the mid-latitudes of North America (Anderson 1968, Esdale 2008), proving the Northern Archaic technology arrived from the east, not Asia. Ancient DNA from a Northern Archaic individual could help answer these questions, but to date archaeologists have yet to discover human remains from these sites, so we have no genetic data available to test these competing hypotheses. However, recognizing that the Athabaskan DNA does not match the Paleoarctic genetic signatures, we can assume there was an influx of genes that occurred with the arrival of Northern Archaic people. When and where they came from remain important questions for archaeologists to work out. Since there are so many Northern Archaic sites on NPS managed lands, our program can play an important role in helping solve this mystery.

Figure 3. The distribution of archaeological cultures around 5,000-7,000 years ago (site data from the Alaska Historic Resource Survey 2017). The arrows indicate hypothetical movement of ideas or language into the existing biological population, which we assume to be ancestors of the Northern Archaic tradition and coastal Paleomarine cultures. National parklands are outlined in green.

The Arctic Small Tool Tradition Migration

While the Northern Archaic people were dominating the Alaska interior 5,000 years ago, and coastal Paleoarctic descendants continued to thrive in southern Alaska, another group of people located in eastern Siberia was poised to embark on a new migration that would ultimately result in the colonization of the entire North American Arctic from Alaska to Greenland. The Arctic Small Tool tradition (ASTt), as defined by William Irving (1957), represents a stone tool technology employed by a hunter-gatherer culture that originated during the Siberian Neolithic sometime before 6,000-7,000 years ago (Mochanov and Powers 1969). Archaeologists have discovered dozens of ASTt sites in Alaska national parklands and these sites are particularly common in our northern parks (Figure 4). Most of the information we have about the ASTt comes from their ancient camps found at Cape Krusenstern National Monument (Giddings and Anderson 1986), Bering Land Bridge National Preserve (Tremayne 2015), Onion Portage in Kobuk Valley National Park, and at numerous lakeside sites in the Brooks Range best exemplified by the Matcharak Lake site in Gates of the Arctic National Park (Tremayne 2011). National Park Service archaeologists working at Kuzitrin Lake in Bering Land Bridge National Preserve discovered an ASTt site with the oldest dates ever reported at 5450±320 (Harritt 1998). In Southwest Alaska, Don Dumond (2005) defined the southern ASTt at Brooks Camp in Katmai National Park and Preserve, and recently traces of this group were documented in Lake Clark National Park and Preserve, as well (Rogers et al 2013). The fact that so many of our national parks in Alaska have ASTt sites, including possibly the oldest ever found, demonstrates the importance of our mission in telling this story.

Figure 4. The distribution of archaeological cultures around 3,500-5,000 years ago (site data from the Alaska Historic Resource Survey 2017). The arrows indicate the proposed directionality of the ASTt migration into Alaska and across the Arctic. National parklands are outlined in green.
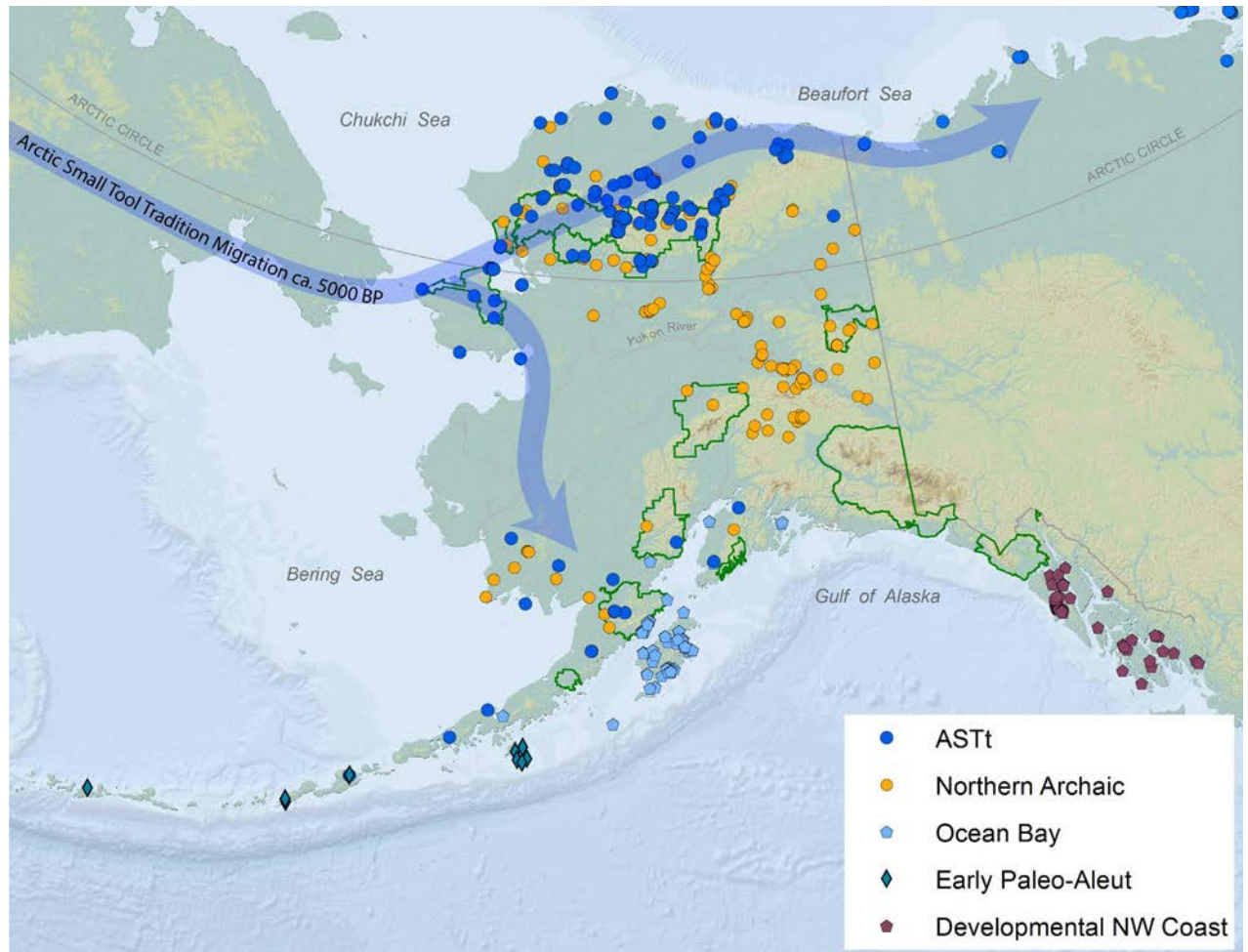
Based on stone tool forms the ancestors of the ASTt people appear to be descendants of Siberian Paleoarctic cultures (Mochanov and Powers 1969). Archaeologists assume that the ASTt people crossed the Bering Strait around 5,000 years ago, presumably by boat, spreading first along the coastal areas of Alaska, south to Bristol Bay and Cook Inlet, and northeast to the Chukchi Sea, into Canada, and eventually to Greenland (Figure 4; Tremayne and

Winterhalder 2017). Over the next two millennia, the ASTt population grew rapidly, moving into both coastal and tundra ecoregions of Arctic and western Alaska, displacing the Northern Archaic groups that once occupied these territories. Currently, there is very little archaeological evidence for mixing between ASTt and Northern Archaic populations; their archaeology sites are very distinct and distinguishable from each other. Where they overlap geographically, the ASTt is always younger than the Northern Archaic occupations, providing the evidence for population replacement rather than gene flow and cultural transmission. In southwest Alaska on the other hand, particularly the Aleutians and Kodiak, there is strong evidence for the transmission of culture, and probably genes, between ASTt people and the Paleoaleut of the Aleutian Islands (Davis and Knecht 2010, Gilbert et al. 2008) and Ocean Bay people living in Kodiak (Steffian and Saltonstall 2005; Figure 4).

The discoverers of the ASTt, referred to the makers as *Paleoeskimos*, which implied there was a direct relationship to modern Eskimo people, today referred to by their chosen names Iñupiat, Yup'ik, and Inuit people. While there is limited archaeological evidence of cultural continuity from Paleoeskimo to Neoeskimos (discussed below), the biological relationship is less certain. Currently, we lack genetic data from ASTt people in Alaska, but researchers published the results of a fully sequenced genome from a 4,000-year-old Saqqaq ASTt man from Greenland (Rasmussen et al. 2010). Remarkably, this ancient ASTt DNA sequence showed that the closest living populations to this individual were not Inuit from Greenland or Canada, but people from Chukotka, Russia and the Aleutian Islands (Gilbert et al. 2008, Rasmussen et al. 2010). A subsequent analysis of 169 mitochondrial ancient DNA sequences from prehistoric Arctic populations

clearly demonstrated that ASTt people and their descendants are distinct from modern Inuit and Iñupiat. In fact, it looks increasingly like another migration event from Alaska to Greenland 1,000 years ago led to the extinction of the ASTt descendants, known as *Dorset*, in the east (Raghavan et al. 2014). The fate of ASTt people in Alaska, however, remains a mystery. Archaeologists generally agree that the people of the ASTt reconfigured their economy to adapt to new conditions as climate changed. A new emphasis on coastal resources and marine mammal hunting resulted in the development of the Norton culture from the late ASTt people. The Norton culture dominated coastal Alaska from around 2,800-2,000 years ago in northwest Alaska and to 1,000 years ago in southwest Alaska. By 1000 A.D., this long-lived tradition disappeared from the record. What happened?

The Great Thule Migration

Beginning around 2,000 years ago, another new culture appears in the Bering Strait region that was in direct competition with the Late ASTt/Norton people discussed above. Archaeologists refer to this culture as the *Northern Maritime* tradition (Collins 1964). Researchers recognize the Northern Maritime tradition by their extensive use of ivory, elaborate artistic engravings on hunting equipment and ritualistic objects, and their near-total reliance on marine resources for subsistence. We find the oldest Northern Maritime sites on St. Lawrence Island in the Bering Sea region, and evidence of connections with Chukotka are well established. The question remains, were the people of the Northern Maritime tradition directly descended from the ASTt and Norton people or were they instead part of another newly arrived biological population from Asia that we have yet to identify?

There remains many questions about the origins of Northern Maritime tradition, but what is clear is that by 1000 AD they morphed into a group that is widely referred to as the *Thule* tradition, often called *Neoeskimos* in the literature. Archaeologists and geneticists agree the Thule people are the direct ancestors of Inuit, Iñupiat, and Yup'ik people (Raghavan et al. 2014). Importantly, the Thule are genetically distinct from ASTt people demonstrating once again the arrival of a new biological population. Once the Thule culture reached maturity, this group rapidly spread across the Arctic, from northwest Alaska, south to Bristol Bay and northeast to Greenland, culturally and biologically replacing and/or assimilating all of the late ASTt people they encountered (Figure 5). In the eastern Arctic, the replacement appears to be complete. In Alaska, there are indications that ASTt genes have survived into the modern populations, however in very low frequencies (Raff et al. 2015). By 800-700 A.D., the Thule tradition became so dominant that it also overtook the indigenous populations on Kodiak Island and along the coast of the Gulf of Alaska, where previously populations that probably retained some of the genes from Paleoarctic people still existed. Some of the most important Thule sites that have been studied are found in Alaska's national parks, including on the beach ridges of Cape Krusenstern National Monument (Giddings and Anderson 1986) and Cape Espenberg in Bering Land Bridge National Preserve (Alix et al. 2017). Today we find Thule sites everywhere that Iñupiat and Yup'ik people live, suggesting cultural continuity for at least 1,000 years.

Interestingly, the Thule never penetrated far into the interior of Alaska, presumably because the Athabaskan people continued to control these territories. The result of this last great migration resulted in the cultural and linguistic boundaries of Alaska Native populations that Russian, European
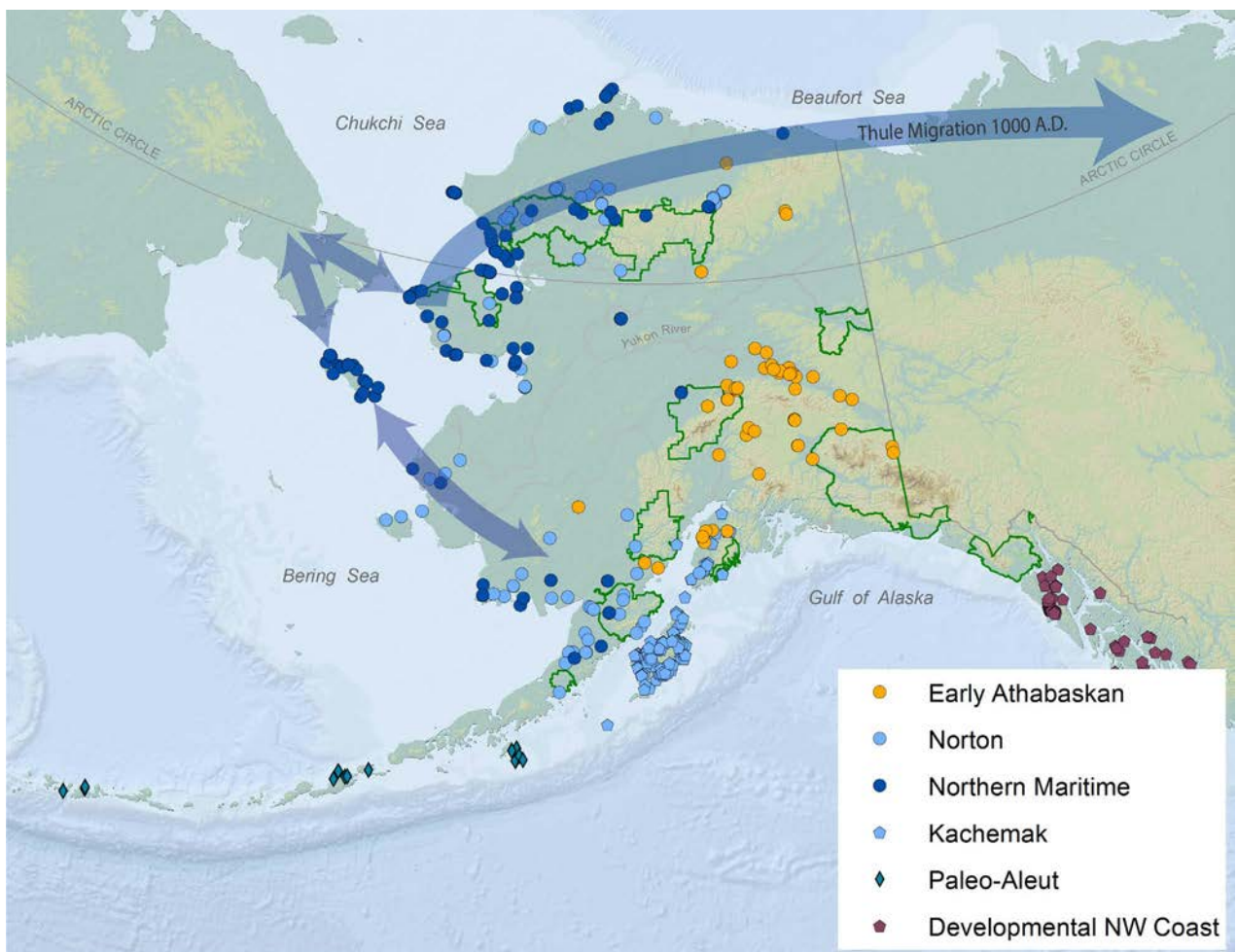
Figure 5. The distribution of major archaeological traditions known from the last 2,000 years (site data from the Alaska Historic Resource Survey 2017). Arrows indicate the proposed directionality of the Thule migration, which began around 1000 A.D. National parklands are outlined in green.

Summary

In this article, I have discussed a multitude of evidence for at least four major migrations to and from Alaska since the arrival of the first people over 14,000 years ago. The pace at which we are acquiring new information about prehistoric genetic variability, biological relationships, migrations, and population dynamics is accelerating. We still have a great deal to learn and new questions emerge with each new study. Alaska's national parklands contain many of the key sites that have defined the traditions and archaeological cultures discussed and the National Park Service is mandated to preserve the sites that tell these stories. The efforts of National Park Service archaeologists, other staff, and outside researchers are integral to fulfilling our mission to protect and interpret archaeological resources on our public lands. Ultimately, the discoveries made by National Park Service archaeologists transcend the park boundaries and are relevant for understanding the prehistory of all of Alaska, for the first people that roamed these lands knew nothing of the boundaries modern people would impose upon the land. The first Alaskans and their descendants went where they needed and left traces of the migrations across the entire state. It is our mission to discover, manage, and protect the sites that preserve this record and to share these stories for the benefit of all.

and American explorers first documented beginning in the 18th century. Hundreds, maybe even thousands, of Thule and late prehistoric sites are found in Alaska's national parklands. Our goal is to continue to study and protect these sites so that we can better understand their biological and cultural origins and to share the story of survival and adaptation in Alaska.

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Excavations of a Northern Maritime tradition house feature at Cape Espenberg, Bering Land National Preserve are providing new insights into the Thule culture, part of the last great migration across coastal Alaska.
NPS/Andrew Tremayne

Duck-billed Dinosaurs (Hadrosauridae), Ancient Environments, and Cretaceous Beringia in Alaska's National Parks

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Beringia is a concept that was originally proposed for an hypothesized ice-free corridor between northeastern Asia and northwestern North America, a corridor that served as a refugium for plants during the Quaternary Epoch (Hultén 1937). More specifically, Hultén (1937) recognized floral similarities between these two areas of land and proposed the name Beringia for the presumed landmass that resulted from a sea level drop due to glacial advance. Since this first definition, the concept has grown, changed, and been used to explain the movement and distribution of many mammals across these same continents during the periodic existence of the land bridge (e.g., Repenning 1987, Hopkins 1967 and 1996, Hopkins et al. 1982, Guthrie 1982 and 2001).

Recent exploration of dinosaur faunas across these same two continents has shown similar broad features (e.g., bidirectional faunal exchange, complex system of vegetative zones, gregarious keystone species) in the Cretaceous Period as observed by these workers of Quaternary deposits (Fiorillo 2008). These newer perspectives on dinosaur biogeography

across this region (e.g., Russell 1993, Cifelli et al. 1997, Sereno 2000, Fiorillo 2008) have increased our understanding of Beringia in deep time starting at least 110 million years ago, during the Cretaceous Period, when tectonics moved geologic plates into a configuration that allowed for a Beringian land bridge to first occur (Lawver et al. 2002). It was during the Cretaceous when dinosaurs roamed freely around what we now call Alaska. Here we present new information from Aniakchak National Monument and Preserve on the Alaska Peninsula, that, when compared to time-equivalent rock units elsewhere in Alaska, sheds light on the likely ancient environment that allowed the migration of one group of dinosaurs, the hadrosaurs (duck-billed dinosaurs), across Beringia during the Cretaceous.

Evidence of Cretaceous Dinosaurs in Alaska's National Parks

Though the first technical description of Alaskan dinosaurs came from discoveries in northern Alaska (Roehler and Stricker 1984), the first dinosaur discovery in an Alaska park occurred in Aniakchak National Monument and Preserve (Fiorillo and Parrish 2004). Additional work in other parks has shown that Late Cretaceous rocks found within Denali National Park and Preserve (Fiorillo et al. 2007, 2009, 2011, 2014a, 2015; Fiorillo and Adams 2012, Fiorillo and Tykoski 2016, Tomsich et al. 2010), Yukon-Charley Rivers National Preserve (Fiorillo et al. 2014b), and Wrangell-St. Elias National Park

and Preserve (Fiorillo et al. 2012) provide some of the most significant opportunities to examine in detail a mosaic of ancient high-latitude terrestrial ecosystems that supported dinosaurs. Examining the latest Cretaceous rocks within Denali and along the Colville River in northern Alaska has provided a more thorough understanding of not only dinosaurs, but associated fauna, environments, and the climate in which they lived. This regional ecosystem contained a rich dinosaurian fauna as well as other fossil vertebrates including mammals, birds, and fishes. The floral component of this paleoecosystem was similarly diverse and included a variety of angiosperms (flowering plants), gymnosperms (seed- or cone-bearing plants), and ferns (Fiorillo et al. 2010a, Tomsich et al. 2010, Flaig et al. 2013).

There is increasing evidence from older Cretaceous rock units such as the Nanushuk Formation of northern Alaska (Fiorillo et al. 2010b) as well as rocks along the middle and lower Yukon River (May et al. 2014) that Alaska has a rich dinosaur record even within the origin of Beringia. The age of these earlier rock units tells us, for example, that early members of the ceratopsians (horned dinosaurs; Fiorillo et al. 2010b), and hadrosaurs (duck-billed dinosaurs; Cifelli et al. 1997) were among the first to exploit ancient Beringia by moving across this land bridge from Asia into North America (Fiorillo et al. 2010b). The Cretaceous rocks of Alaska, and particularly within Alaska's national

An interpretation of the Chignik area in the Cretaceous Period in what is now Anaiakchak National Monument and Preserve.
Artwork courtesy of Karen Carr

parks, are potentially full of intellectually stimulating discoveries regarding the timing of migration for different dinosaurs across Beringia.

Examining the fossil bone deposits that are approximately 70 million years old within the Prince Creek Formation of northern Alaska, a rock unit now recognized as the most abundant source of polar dinosaur bones in the world (Rich et al. 2002), provides insight into the environmental preferences of different types of dinosaurs. By using a multi-disciplinary approach that included vertebrate paleontologic, sedimentologic, and paleobotanical data, Fiorillo and others (2016) showed that hadrosaurs preferred the wetter, lower delta plain environments, while the ceratopsians preferred habitat that was the more proximal, slightly elevated, and drier upper coastal plain (Fiorillo et al. 2016). Not surprisingly, predatory dinosaurs were not confined to a single ecosystem, but followed food resources in whatever ecosystems they could be found (Fiorillo et al. 2016).

New Insights from Aniakchak National Monument and Preserve

We have now discovered dozens of dinosaur tracks from exposures of the Cretaceous Chignik Formation in Aniakchak National Monument and Preserve a rock unit that was deposited at approximately its current latitude, which is almost 57° N (Hillhouse and Coe 1994). Tracks were photographed, measured (Figure 1), coordinates recorded, and molds were made of select representative tracks. Tracks were found in cross-section within the face of cliffs (Figure 2) or in planar view either on *in situ* bedding planes (Figures 1 and 3) or on isolated eroded blocks that had fallen from the cliff face.

The tracks are primarily footprints of hadro-saurian dinosaurs, identified by the presence of three

Figure 1. Measuring duck-billed dinosaur footprints on a bedding plane. This is also an example of one of the larger *in situ* bedding planes found.
All photos courtesy of Anthony Fiorillo

Figure 2. Example of large duck-billed dinosaur footprint in cross-section eroding out from cliff face.
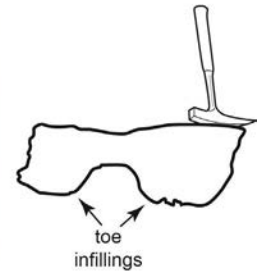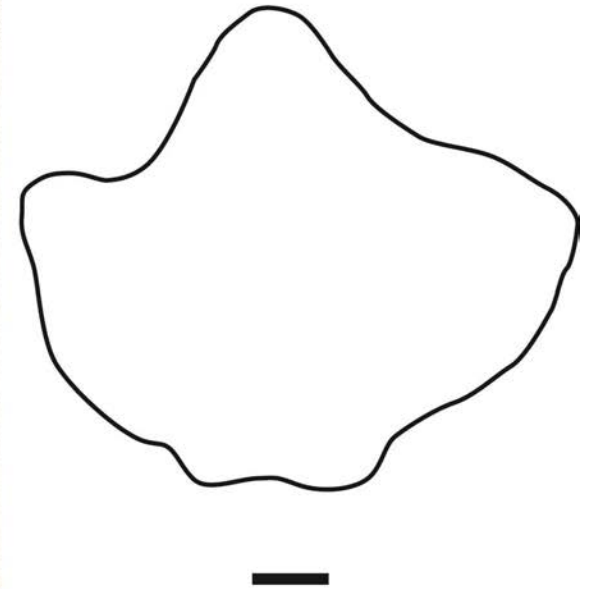

Figure 3. Planar view of a large duck-billed dinosaur footprint. Note the three large rounded toes.

elongated toes with rounded tips and a bi-lobed heel (Figure 3). The hadrosaur tracks range in size from those made by likely full-grown adults to juveniles. Tracks attributable to ankylosaurs (armored dinosaurs) are currently uncommon in frequency, while trace fossils left by birds and the fin rays of bony fishes are rare. Further, we documented a rich fossil flora that includes upright conifer tree trunks and numerous horizons with angiosperm leaves (Figures 4 and 5).

Previously there had been only three track sites recorded within the Chignik Formation (Fiorillo and Parrish 2004, Fiorillo et al. 2004, Fiorillo 2018), and only one track site recorded from the older (Jurassic) Naknek Formation (Druckenmiller et al. 2011), a rock unit that crops out extensively along the Alaska Peninsula, including in Aniakchak National Monument and Preserve, and Katmai and Lake Clark national parks and preserves. The recent work in Aniakchak that includes re-evaluating the potential fossil resources of the Chignik Formation has now revealed over 50 new track sites, dramatically increasing the dinosaur record from not only Aniakchak National Monument and Preserve, but the entire Alaska Peninsula. It also makes Aniakchak the second-most important park in Alaska, after Denali, for studying dinosaurs, their ecosystems, and the climate in which the dinosaurs lived.

What these Findings Tell Us about Migration

The discovery of dinosaurs so far north initially puzzled researchers and one of the early ideas was that they must undergo large-scale migration to cope with the high-latitude environment. While it is no longer thought that hadrosaurs survived the winter using seasonal migrations like those of modern caribou (Fiorillo and Gangloff 2001), evidence does suggest that dinosaurs migrated between what is now modern Asia and North America through Alaska during the Cretaceous.

Figure 4. Carbonized upright conifer tree trunk found in place in Aniakchak. The tree trunk is nearly vertical and is best seen above the geologic rock hammer. The white arrows point to the top, middle and bottom of the exposed tree trunk. The blue handle of the rock hammer is resting on the root mass.

The modern depositional environments in the distal part of the Aniakchak River as it makes its way into Aniakchak Bay provide a superb modern analog for the Late Cretaceous Chignik Formation (Figure 6). Overall, the Chignik Formation is a cyclic succession of sedimentary rocks representing shallow marine environments in the lower part and predominantly non-marine environments in the upper part (Fairchild 1977, Detterman 1978, Detterman et al. 1996). The part of the section measured in detail in

Figure 5. Angiosperm leaf from the Chignik Formation of Aniakchak. Scale bar is in cm.

2016 represents primarily non-marine deposition on an ancient alluvial-deltaic coastal plain (Figure 7). There is also evidence of tidal influence on some of the distal deposits, including tidal flats as well as marginal marine beach and estuarine deposits. The Cretaceous coastal plain was dominated by sinuous meandering fluvial channels, with abundant crevasse splays, small lakes and ponds, and a few thin peat swamps.

The partially correlative and well-known dinosaur remains of the Prince Creek Formation 870-930 miles (1,400-1,500 kilometers) farther north in Alaska partially overlap in age with these discoveries in the Chignik Formation (see Fiorillo and Parrish 2004, Flaig et al. 2014). Preliminary results of this similar interdisciplinary study in the Chignik Formation seem to corroborate the habitat preference model

Figure 6. View of Aniakchak River estuary which is a modern analog to the Cretaceous Chignik Formation of Aniakchak National Monument and Preserve.

Figure 7. Coastal exposure of the Chignik Formation of Aniakchak National Monument and Preserve. These rocks represent a variety of non-marine, beach, and estuarine sedimentary environments.

for Cretaceous high-latitude hadrosaurs proposed for the hadrosaurs of the Prince Creek Formation. That is, hadrosaurs preferred areas that included lowland deltas and other tidally influenced habitats. This understanding of hadrosaurs' habitat preference allows specific questions on how that habitat might change through time and space. Continued fine-tuning of our understanding of the details of these habitat preferences will not only illuminate the potential causal mechanisms for non-recurrent migration in Cretaceous Beringia, but also tell us something about large-scale ecosystem processes through deep geologic time.

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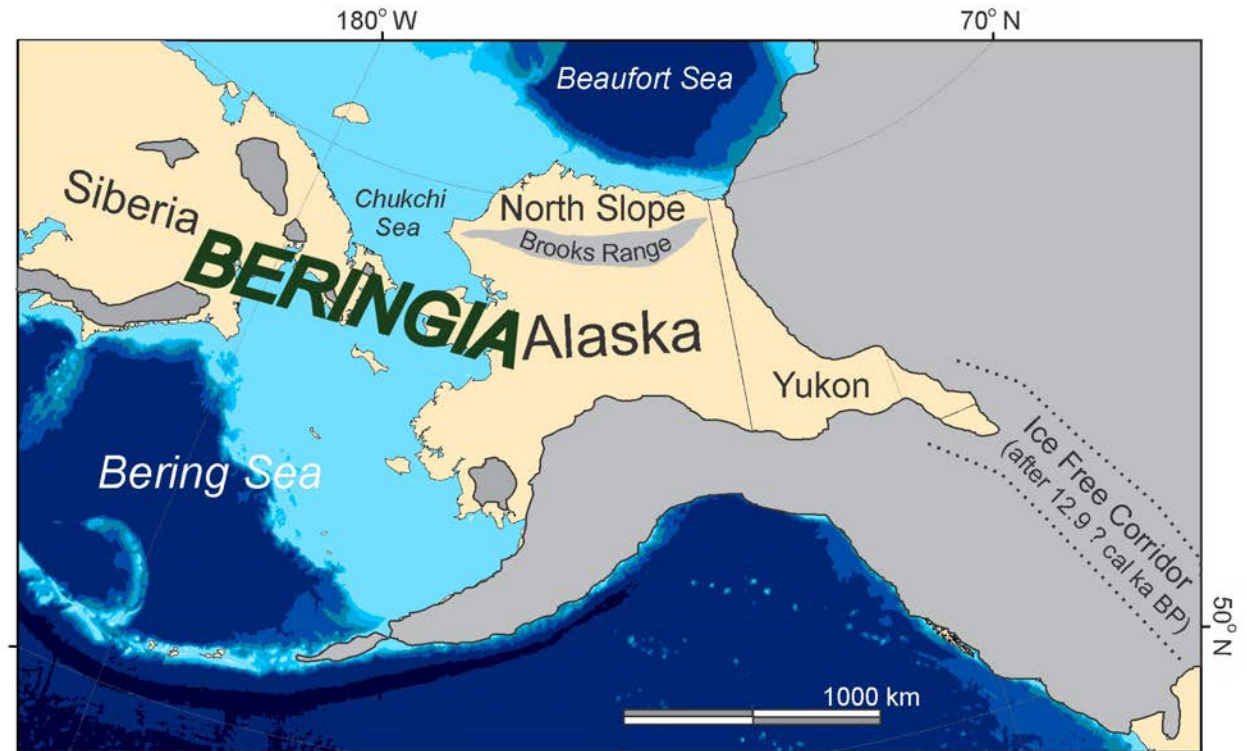
The Chignik Formation today in Anaiakchak National Monument and Preserve.
Photo courtesy of Anthony Fiorillo

Pleistocene Megafauna in Beringia

Pamela Groves, University of Alaska

At the peak of the last ice age, 20,000 years ago, when most of northern North America was covered by massive glaciers, much of Alaska was ice-free and home to a diverse assortment of large mammals. This unglaciated region, which extended from the Yukon Territory in Canada west across to eastern Siberia, is called *Beringia*. Because so much of the planet's water was locked up in glaciers, sea level was much lower than it is now, and Alaska and Siberia were connected by the Bering Land Bridge (Figure 1).

Beringia's ice-age (Pleistocene) iconic mega-fauna (mammals >100 lbs or 45 kg) included the mastodon (*Mammut americanum*), woolly mammoth (*Mammuthus primigenius*), woolly rhino (*Coelodonta antiquitatis*), lion (*Panthera spelaea*), and short-faced bear (*Arctodus simus*), all of which are now extinct. Quite common were horses (*Equus* spp.), similar to but smaller than our modern horses (*Equus caballus*), and a species of bison, the steppe bison (*Bison priscus*), that is now extinct but was the ancestor to our modern plains bison (*Bison bison*). Cattle similar to the modern yak (*Bos grunniens*) grazed in Siberia and interior Alaska. Finally, there were species that are still alive today including muskox (*Ovibos moschatus*), caribou (*Rangifer tarandus*), mountain sheep (*Ovis dalli* and *nivicola*), saiga (*Saiga tatarica*), brown bears (*Ursus arctos*),

Figure 1. Beringia 20,000 years ago. Tan areas are unglaciated Beringia. Light blue shows extent of Bering Land Bridge, gray areas are glaciers (from Mann et al. 2015).

and wolves (*Canis lupus*). Moose (*Alces alces*), elk (*Cervus elaphus*), and humans (*Homo sapiens*) were not present in eastern Beringia until the ice age was waning, perhaps 14,000 years ago.

Ice Age Beringia was very different from modern Beringia. The Arctic is depauperate of megafauna today. Estimates of Pleistocene megafaunal biomass are about 100 times greater than today's (Zimov et al. 2012, Mann et al. 2013). If one were to wander around Beringia today, one might observe some caribou, or a few moose, sheep in the mountains, and wolves and bears. Muskoxen seen on the tundra

An artist's interpretation of ice age fauna.
Image courtesy of Mauricio Antón

Figure 2. Siberian mammoth baby mummy "Yuka" (left, photo courtesy of A. Kharlamova); Interior Alaska steppe bison mummy "Blue Babe" (center, photo courtesy of the University of Alaska Fairbanks Museum); and Northern Alaska steppe bison skeleton skull "Bison Bob" held by Dan Mann (right, photo courtesy of the Bureau of Land Management, P. Groves).

today are descendants of muskoxen reintroduced in the 1930s and 1970s, decades after the last indigenous muskoxen of Beringia died off in the 1800s.

Given such dramatic changes, there are some questions to ask about Ice Age Beringia: How do we know those megafauna lived there? When did they live there? Why did they live there? And what happened to all of them?

How do we know all those animals lived there?

Being so far north, Beringia is its own deep freezer and has preserved the remains of many of its former inhabitants. The most dramatic finds have been in western Beringia, in Siberia, where mummies and skeletons of extinct Pleistocene mammals have been discovered (Figure 2). Mummies and skeletons are not as common in eastern Beringia, but in the 1980s, a steppe bison mummy was found near Fairbanks (Guthrie 1990). The mummy, named Blue Babe, is now on display at the University of Alaska Museum (Figure 2).

Far more common are individual bones of these mostly vanished animals. These bones are not mineralized fossils like most dinosaur remains, but are still bone, sometimes with marrow inside. Because the bones have been frozen, they tend to be well-preserved and are suitable for various isotopic and DNA analyses. Miners across Beringia routinely expose bones of Pleistocene megafauna in their search for mineral treasures. Some rivers also expose bones as they meander back and forth across their valleys. Bering Land Bridge National Preserve in northwestern Alaska and other parks in Alaska have been the sources of many Pleistocene bones. Most of these bones are disarticulated, individual bones, although rarely skeletons are found such as "Bison Bob" in northern Alaska in 2012 (Figure 2). Over decades, many of these bones have been collected and deposited in museums where they are studied by paleontologists.

By simply identifying the bones, we can learn what species were present and relative abundance of those species across different environments. From this it is immediately apparent that Beringia was not one vast homogenous ecosystem, but was made up of diverse ecosystems. For example, during the late Pleistocene (about 45,000-11,700 years ago) in Siberia, caribou was the most common species followed by horse and bison, whereas in northern Alaska, the horse was most common followed by bison and caribou, and in interior Alaska, bison dominated the landscape followed by horse and mammoth (Figure 3; Guthrie 1968, Zimov et al. 2012, Mann et al. 2013).

When did they live there?

There are two main ways of determining when an animal lived. Remains may be found embedded in layers of undisturbed geologic sediments. Some of these layers, such as volcanic ash, are very distinctive and their ages can be established, and thus those of the remains as well. For bones not in stratigraphic context, we can analyze small pieces of bone using
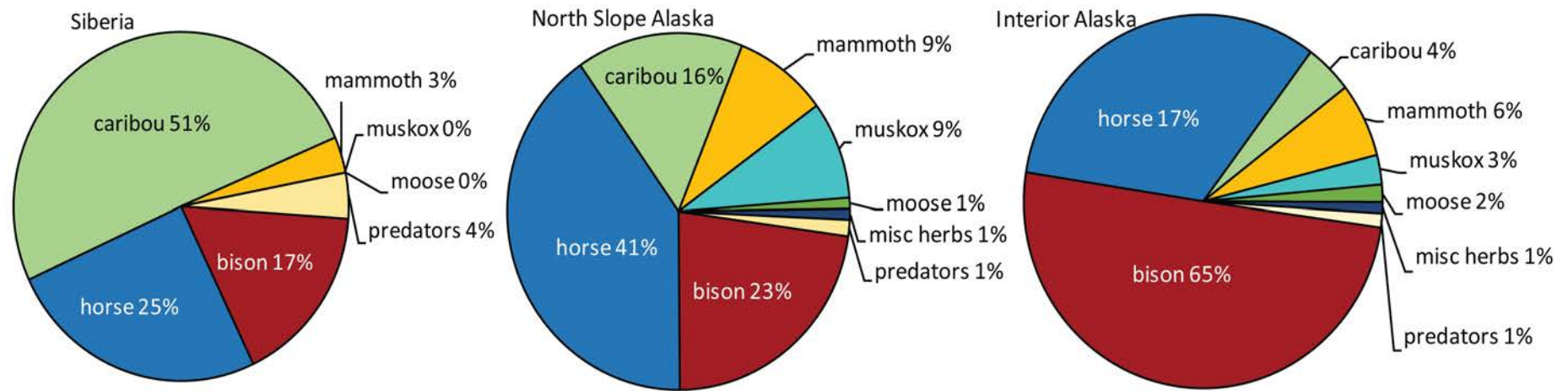
Figure 3. Relative abundance of late Pleistocene megafaunal species from three regions of Beringia. Data are from Zimov et al. 2012 (Siberia), Mann et al. 2013 (North Slope of Alaska), and Guthrie 1968 (Interior Alaska).

radiocarbon (^{14}C) analysis to measure the amount of carbon 14 isotopes in bones and estimate how long ago the animal died. This ^{14}C analysis is effective for bones up to about 45,000 years old; older bones do not retain enough carbon to be dated using this method. Unfortunately, there are no effective techniques for dating bones older than this. Not all bones collected have been dated, because ^{14}C analysis costs hundreds of dollars per sample.

Almost all the dates obtained on Pleistocene-era Beringian remains are from disarticulated bones and thus are from ^{14}C analysis. Consequently, most of our information on ages of Beringian megafauna is from the late Pleistocene. Hundreds of ^{14}C-dated bones from northern Alaska show that in addition to being spatially diverse, relative abundances of different species changed over time. In particular, the relative numbers of horse and bison changed throughout the last 45,000 years (Figure 4) suggesting that climatic and environmental fluctuations differentially favored some species over others (Mann et al. 2015).
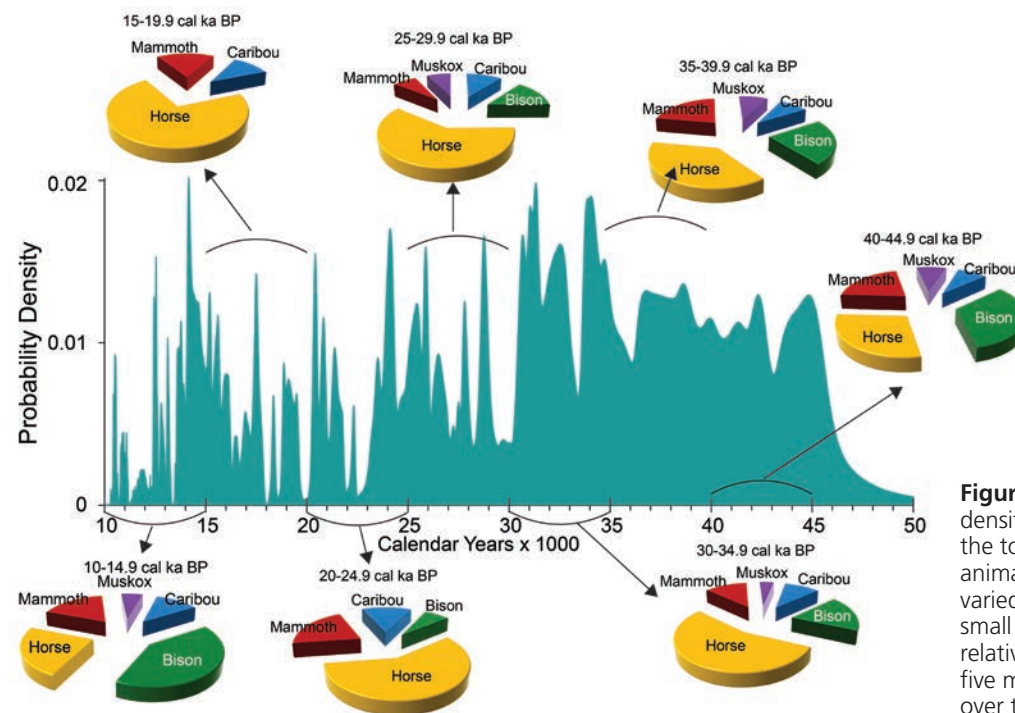

Figure 4. The probability density graph shows that the total numbers of animals in northern Alaska varied widely over time. The small pie charts show the relative abundances of the five main herbivore species over time. Data from Mann et al. 2015.

Bering Land Bridge

The Bering Land Bridge was episodically open throughout the Pleistocene until about 13,000 years ago. A corridor was created by falling sea levels that provided an opportunity for Asian species including mammoths, bison, muskoxen, caribou, lions, brown bears, and wolves to move into North America. One American species, the horse, dispersed westward across the land bridge to Asia. One iconic Pleistocene species, the woolly rhino, never made the journey east into Alaska, while short-faced bears never ventured west to Siberia.

Interestingly, DNA evidence suggests that despite its vast area, the land bridge was not a busy highway with populations moving back and forth between the continents. While the distribution of woolly mammoths extended from Europe, across Siberia into North America, the genetic evidence suggests after colonizing North America, there was minimal gene flow back west across the land bridge (Chang et al. 2017). It is possible that some eastern Beringian males dispersed westward long distances, just as modern male elephants do, but female mammoths mostly stayed on just one side or the other of the land bridge. Pleistocene bison also had a wide distribution and had two major dispersals into North America from Asia. But DNA analysis shows a fair amount of genetic separation of Pleistocene bison from east and west Beringia suggesting there was only limited movement of bison back west over the land bridge (Shapiro et al. 2004, Froese et al. 2017).

Since the Land Bridge is now flooded by the Bering Strait, we have no way of knowing if megafauna actually inhabited that region and what the landscape was like there during the Pleistocene. The Bridge would have been low-lying land and closer to the ocean than the continental Mammoth Steppe. There is some evidence from the edges of the land bridge that when exposed, it was dominated by shrub vegetation and had a mesic (wet) climate (Elias and Crocker 2008). These

Woolly rhino (top; image by Charles Knight, 1914) and short-faced bear (above; image courtesy of Sergio d'la Rosa).

characteristics would have made it a barrier to the grazing species adapted to well-drained grasslands. Movements of megafauna across the land bridge may have been limited to narrow windows of time when the conditions were more favorable.
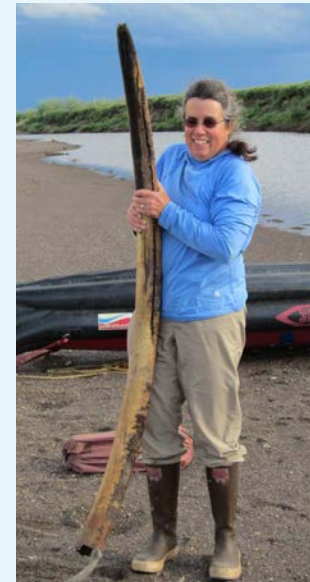
Mastodons and Mammoths

Despite the superficial resemblance, mastodons were distinct from mammoths. Mastodon were shorter and stockier than mammoths with shorter, straighter tusks. Mastodons were wood browsers and their molars have pointed cones specially adapted for eating woody browse. Mammoths were grazers, their molars have flat surfaces for eating grass.

Recent evidence suggests that mastodon inhabited Beringia during a previous warmer episode, or interglacial, when there were trees or shrubs, probably >75,000 years ago along with Jefferson's giant ground sloth (*Megalonyx jeffersonii*), giant beaver (*Castoroides ohioensis*), western camel (*Camelops hesternus*), and even a peccary (*Platygonus compressus*), another species adapted to warmer woodland environments (Zazula et al. 2014).

Mastodons and woolly mammoths overlapped in Beringia during the early to mid-Pleistocene with mastodons thriving in the warmer interglacial periods and mammoth favoring the colder glacial epochs. Mammoths survived in eastern Beringia until about 13,000 years ago (Guthrie 2006), while the very last mammoths in Alaska appear to have survived on the Pribilof Islands until about 6,000 to 8,000 years ago (Guthrie 2004, Veltre et al. 2008). The very last woolly mammoths lived in northern Siberia on Wrangel Island until about 4,000 years ago (Vartanyan et al. 2008)!

Mastodon tusks (above left; photo courtesy of Daniel Mann) were shorter and straighter than mammoth tusks, which were longer and curved (above right; photo courtesy of Pam Groves).
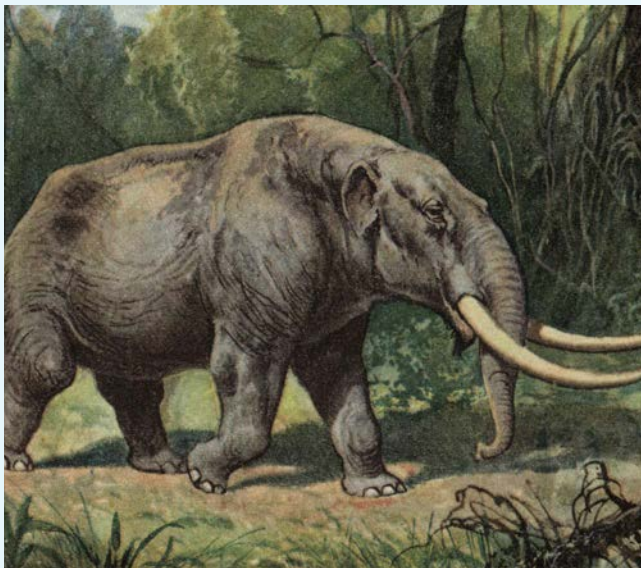
Mastodon (above left; photo courtesy of H. Harder) were browsers and mammoth (above right; photo courtesy of Mauricio Antón) were grazers. You can see the difference in their molars (far right) with mastodon molars having cones and mammoth molars being flat (photo courtesy of Daniel Mann).

Why did the megafauna live there?

Modern Beringia is covered by vast expanses of permafrost, peat, spongy tundra vegetation, and boreal forests of mostly coniferous trees. Much of it is buried in snow over half the year and during the cool, wet summer, it swarms with mosquitoes. This modern ecosystem supports a fraction of the animals that lived there during the Pleistocene. So, what was different? Not surprisingly, the climate was generally colder and drier during most of the Pleistocene, which would seem to make it less hospitable to megafauna. Because sea level was so much lower, the land mass of Beringia was larger and included the expansive Bering Land Bridge. This resulted in a more continental climate with little precipitation and clear skies: conditions that produced a unique biome called the Mammoth Steppe (Guthrie 1990), unlike anything found in Beringia now. The climate was too cold for trees and the dry conditions favored steppe-like grasslands, which provided abundant food for grazing megafauna; the late-Pleistocene megafauna were grazers and not browsers (or wood-eaters). The dry grasslands and low snow levels also provided a firm substrate that was easy for the hooved animals to walk over throughout the year.

The Mammoth Steppe was a complex biome that changed over time and across the region. This resulted in a mosaic-like ecosystem that varied in response to a constantly changing climate. During the Pleistocene, the climate changed much more dramatically than it has during the last 10,000 years, the period known as the Holocene, a remarkably stable climatic period compared to the preceding million years or so. The unstable climate of the Pleistocene caused rapid changes in the plant communities and thus forage for megafaunal herbivores. Abundance and distributions of these animals would have varied in response to the changes. Being large, the megafauna would have been able to move across the landscape tracking favorable patches of habitat both seasonally and over longer time scales.

Because of low snow levels and clear weather, green-up would have been earlier than now so the Mammoth Steppe growing season was probably longer. The clear skies of a continental climate may have allowed warmer temperatures during the growing season than occur with modern cloudier weather (Guthrie 2001). Mammoth Steppe soils were therefore dryer, warmer, and more fertile than now (Young 1982, Walker et al. 2001). This would have enhanced plant productivity and megafauna, that could graze around the clock, and could grow larger during the summer. With the nutritious plant growth, the megafauna also would have been able to consume enough in the summer to put on reserves to help them survive the long, cold winter.

This was a complete ecosystem of megafauna with herbivores and the predators that consumed them. Like most ecosystems, there were many more herbivores than carnivores. The giant short-faced bears may have mostly scavenged already-dead herbivores (Matheus 1995), but brown bears, lions, and wolves undoubtedly hunted and killed their prey. Radiocarbon dates suggest the lions may have specialized in hunting horses (Mann et al. 2013).

What happened to all of them?

The Mammoth Steppe ecosystem vanished at the end of the Pleistocene. Some experts argue that humans are responsible for the megafaunal extinctions (Alroy 2001), but across Beringia, we know that humans co-existed with the extinct species for long periods. Documented ^{14}C dates show that humans in Alaska overlapped with horse, bison, and lions for >1,000 years and also probably with mammoths, and we lack evidence of overhunting of these animals (Mann et al. 2013). The region of Beringia is vast and the early human population was small. A more likely explanation for the extinctions is that the prolonged warming at the end of the Pleistocene caused environmental changes that did not favor the Mammoth Steppe megafauna.

When the climate warmed, it became wetter. Shrubs would have invaded the region and replaced the grasslands. Many shrubs have chemicals that protect them from herbivore browsing and they are not suitable food for grazing animals. As the glaciers melted and sea level rose, the climate would have become more maritime, with increased precipitation and cloud cover. Despite the overall warming trend, the summer growing season would have been wetter, shorter, and probably cooler due to decreased sunshine (Guthrie 2001). As these changes persisted, peat would have spread across the landscape and negatively affected megafauna. Peat is not a nutritious food and it insulates the ground promoting the spread of permafrost, creating a waterlogged, inedible substrate.

The spongey substrate and deeper winter snows would have negatively impacted the megafauna. Most megafauna would have had difficulty walking through deep snow or over spongey ground because of their small feet relative to heavy body weight (high foot loading). They would have had to expend more energy walking at the same time that food resources were becoming scarcer. The megafaunal herbivores that disappeared from Beringia had high foot loadings, whereas caribou and muskox that survived the changes to the modern climate have low foot loadings, making it easier for them to move across the present landscape. Moose and humans who moved into the region as the shrubs invaded also have lower foot loadings than the extinct megafauna (Guthrie 1990; Figure 5).

The changing vegetation would have meant the diets of the grazers would have changed. Analyses of

nitrogen and carbon isotope ratios in bones reflect the diet and amount of moisture the animal was consuming. By comparing isotope values in bones over time, it is possible to detect changing patterns in diet. A survey of bone isotope values at the peak of the ice age shows that bison, horse, and mammoth were consuming a different diet from caribou and muskox that were selecting plants that favored warmer and wetter environments. The dietary difference became more pronounced as the climate warmed (Mann et al. 2013; Figure 6). Species that survived the end of the ice age had probably selected plant communities that would thrive in the post-Pleistocene climate throughout the ice age. It is interesting to note that caribou and muskoxen not only had a diet that favored the changing environment, but they had low foot loadings, which also favored the new environment.

Thus, as the climate continued to remain warm, Pleistocene megafauna would have been confronted with food scarcity and increasingly difficult travel due to the boggy ground during summer and deep snow conditions during winter. These environmental changes would have been compounded by shorter growing season and rising sea level culminating in the closing of the Bering Land Bridge and a reduction in grazing area. The disappearance of herbivores affected the specialized predators—short-faced bears and lions. DNA evidence indicates that Pleistocene Beringian wolves also became extinct (Leonard et al. 2007). Wolves currently inhabiting Alaska are genetically distinct from those that lived here during the Pleistocene.

The changes at the end of the Pleistocene were not negative for all species. Caribou, muskox, sheep, and brown bears continued to inhabit the region. The establishment of shrubs prompted by the warming allowed wood-dependent species such as moose, elk, and humans to colonize Beringia. Moose
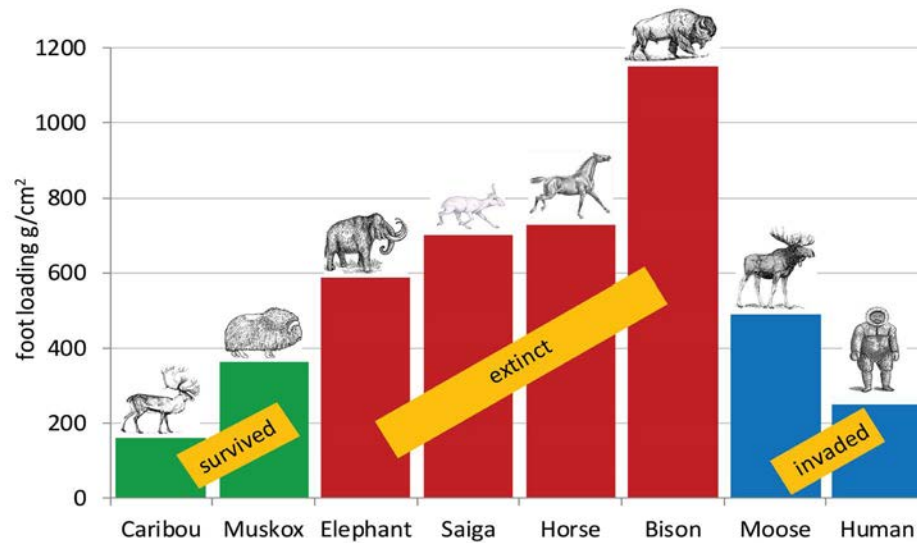

Figure 5. Foot loading of megafauna herbivores (data from Guthrie 1990).
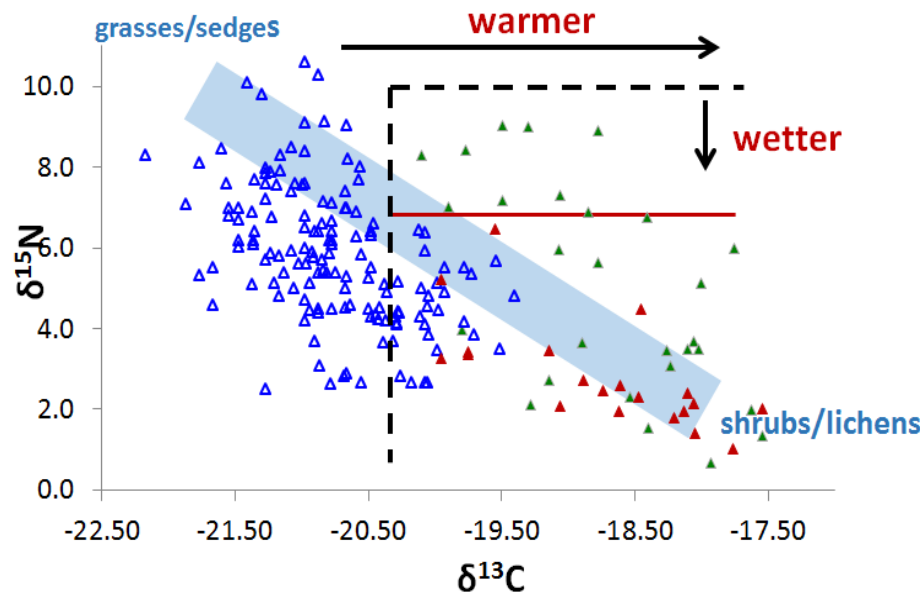

Figure 6. Differences in diets among species over glacial and post-glacial time periods based on ratios of nitrogen and carbon isotopes (Mann et al. 2013).

and elk are browsers and require woody plants for their diets. The early humans in Beringia depended on wood both for fuel and as a building material.

Modern Beringia is inhabited by a small subset of the Pleistocene megafauna adapted to survive in this altered landscape. Diversity and abundance of these animals is lower in today's Beringia, which is now dominated by peat, boreal forests, permafrost, and extreme seasonal weather.

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Species common near the end of the ice age.
Image courtesy of Mauricio Antón

PACKERS ASCENDING SUMMIT OF CHILKOOT PASS.
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The Klondike Gold Rush: A Search for the Archaeological Traces of an Historic Migration Event

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People have been migrating into and through Alaska for over 14,000 years (Tremayne 2018). The last major migration into Alaska began with the Russian colonialism in the mid-late 18th century and intensified with the arrival of Euro-American traders, missionaries, and prospectors in the mid-late 19th century. The Klondike Gold Rush from 1896-1899 was a particularly intense, but brief, wave of migration that would forever change the course of history for Alaska. Klondike Gold Rush National Historical Park, located in southeast Alaska in the town of Skagway (Figure 1), was founded with the mission to preserve and interpret the story of the prospector's lives, including the routes and modes of transportation by which the men and women took to get to the gold fields.

As part of its mission, National Park Service (NPS) archaeologists routinely survey the park to inventory and assess the condition of the resources. In 2016 and 2017, park archaeologists initiated a project to assess the cultural resources preserved along the Chilkoot Trail, one of the primary routes prospectors used to access the gold fields. By necessity, migration requires the transportation of goods and supplies. While new discoveries were limited, this project documented a handful of artifacts that preserve the various transportation methods into Alaska including foot power, pack animals, tramways, and even boats.

Historical Background

The Klondike Gold Rush began in August 1896 when Skookum Jim Mason, Dawson Charlie, and George Washington Carmack discovered gold in a tributary of the Klondike River in Canada's Yukon Territory. From 1897 to 1898, thousands of stampeders poured into southeast Alaska with dreams of gold and riches across the mountains in the Klondike (Neufeld and Norris 1996). Between 1890 and 1900, the United States Census showed a dramatic increase in the Alaska population, which grew from 32,035 to 63,592 in less than ten years (Ducker 1994). This population boom resulted in the establishment of mines, trading posts, homesteads, and boomtowns, which dramatically increased interactions between Alaska Natives and immigrants.

With the sudden arrival of thousands of men, the small tent cities of Skagway and Dyea grew to be prosperous outposts. Dyea boomed at the foot of the Chilkoot Trail just as Skagway did at the foot of the White Pass Trail, two of the primary transportation routes to the gold fields. According to historians, most of the prospectors were young men from the western United States and Canada, but there were foreign-born immigrants from as far away as Scandinavia and China drawn to the region (Ducker 1994). Wealthier entrepreneurs, including supply outfitters, saloon owners, entertainers, and others in the service industry, also arrived *en masse* ready to capitalize on the needs of the miners (Neufeld and Norris 1996).
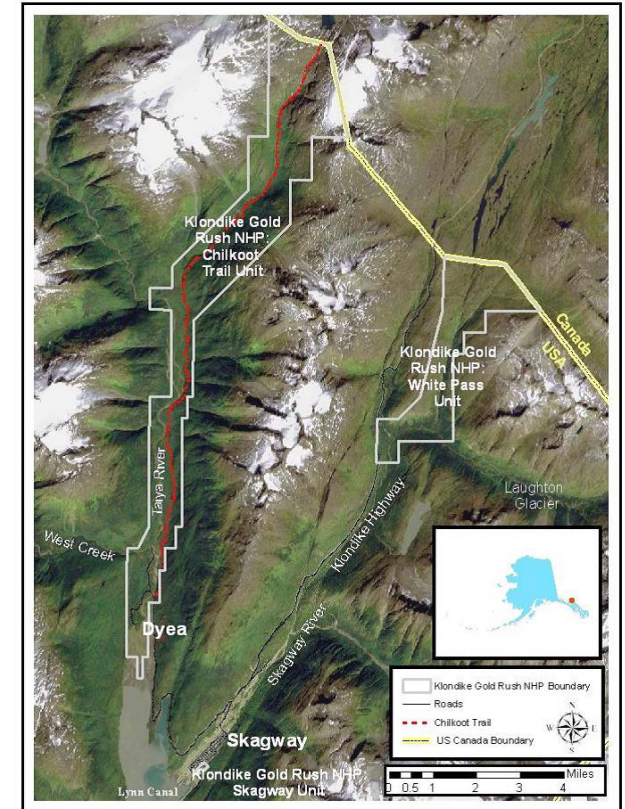
Figure 1. Klondike Gold Rush National Historical Park map.

The Chilkoot trail, beginning at Dyea, is a 33-mile-long route that climbs 3,500 feet into the mountains over a pass into the Yukon Territory of Canada (Figure 1). The Tlingit people had used this trail and other passes in the region for thousands of years as a way to get from the coast to the interior to

From 1897-1899 the Chilkoot Trail had thousands of eager prospectors transporting supplies across the pass to embark upon their journey in search of riches.
NPS /Library of Congress, USZ62-28477

trade with Athabaskans (Neufeld and Norris 1996). The presence of obsidian sourced to Mount Edziza in British Colombia from a 10,000-year-old coastal site in southeast Alaska (Dixon 2001), indicates coastal people must have exploited such routes to the interior as soon as the glaciers retreated at the end of the ice age. As the Chilkoot Pass is not a particularly hospitable location for a village, the expectations are that most of the pre-contact site types reflect short-term, ephemeral camps and hunting stations. Historic era sites, on the other hand, preserve objects related to mining and the transportation of goods through the pass.

In 1898, hopeful prospectors literally marched in single file lines up the long pass, making many trips to haul the thousands of pounds of supplies they needed to outfit their expeditions; for once they made it over the pass, these men still had to build boats to float down the Yukon River to get to the gold fields. A number of the wealthier stampeders sent their outfits over by tramway, a major engineering feat for its time. Others of more humble means used pack animals to haul their loads on the journey from Dyea to Lake Bennett in the Yukon; however, many simply carried their gear on their backs. At times, their burdens became too great to bear, for man and beast, and wearied travelers jettisoned gear and left their exhausted pack animals behind.

In the Prospectors Steps

The prospectors hiked through the Chilkoot Pass as quickly as possible. One-hundred and twenty years later, archaeologists with the National Park Service hiked the pass slowly to carefully scour the trail for traces of this historic migration. In spite of the thousands of people that traversed the Chilkoot Pass, historic debris does not litter the trail. Instead, artifacts are rare and often concealed, requiring a careful eye and attention to detail to locate them.
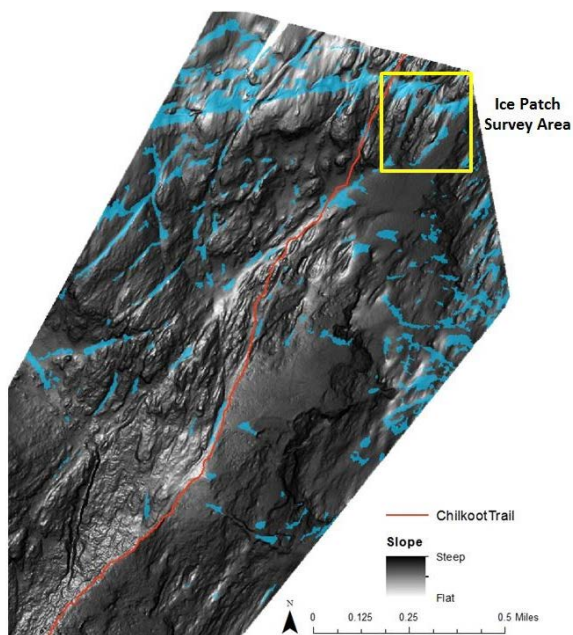

Figure 2. Location of the ice patch survey area along the Chilkoot Trail. The team of NPS archaeologists surveyed ice patches in the Coast Mountains, directly south of the border with Canada.

Over a century of harsh weather, vegetation growth, and sediment deposition has a way of breaking archaeological materials down and obscuring artifacts that were once on the surface.

The survey area for the 2016-17 project focused on ice patches and lichen-free zones from recently melted ice patches located in the alpine environment of the Chilkoot Pass south of the Canadian border (Figure 2). Ice patch archaeology from the Yukon and Alaska has already provided a great deal of information on subsistence hunting and prehistoric weaponry (Dixon et al. 2014, Hare et al. 2004). Ice patches are widely known for preserving ancient hunting tools because hunters would target caribou and other animals that used ice patches to gain respite
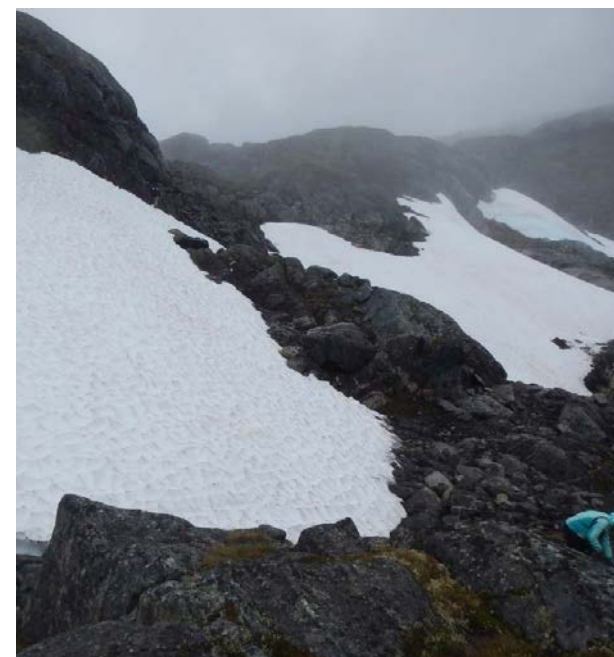
Figure 3. Snow patches located in the Chilkoot Pass. NPS archaeologists found preserved Klondike Gold Rush-era artifacts thawing from the margins of some of these snow patches.
NPS/Corrine Michel

from heat and insects (VanderHoek et al. 2012). One of the goals of the project was to determine if historic artifacts related to the Klondike Gold Rush would likewise be well preserved thanks to the deep snowpack and ice.

The survey methods involved teams of archaeologists scouring the ground for any objects that were not part of the natural environment. Once in the pass, the team explored the margins of melting snow patches for preserved organic artifacts (Figure 3). If an artifact was located, the archaeologists recorded the precise locations with GPS devices, took photographs, and wrote down notes to document the setting and objects found (Rankin et al. 2017). The team also revisited known sites to assess the

condition of artifacts. One goal of park cultural resource management is to preserve *in situ* historic objects along the Chilkoot Trail. When threats or disturbances at sites are noted, park archaeologists seek solutions for ways to mitigate the damage.

Survey Results and Interpretations

The results of the Chilkoot Trail survey included the discovery of three new historic archaeology sites, one possible pre-contact site, and the condition assessment of one well-known, historic site (Rankin et al. 2017). The known site is unique and somewhat strange, for this site preserves the remains of wood and canvas supplies to build a number of "knock-down boats" (Figure 4A) that one prospector had hauled to the top of the pass only to abandon once he got there. We do not know the reason for the remains of the boats at the summit. However, there are several theories, the most plausible being that crews hauled them to the top of the pass for the "Flowers, Smith and Company" only to be abandoned once they reached the summit (Norris 1983). It is likely that Canadian officials refused their entry into the country due to safety concerns of these boats breaking up and killing their passengers during the journey over the Yukon River (Norris 1983). These wood planks, still wrapped in canvas at the top of Chilkoot Pass, are a tangible reminder of the importance placed on water transportation to move their supplies to Whitehorse, Dawson, and into Alaska, but also that sometimes the project failed even before making it to the rivers.

At one of the newly discovered sites, the archaeology team recorded heavy chains and hardware (Figure 4B) related to a trail-length tram used to haul supplies up the pass (Neufeld and Norris 1996). The tram system, one of five built in the region, was erected in 1894. (It should be noted that people were using the pass and moving into the Yukon prior to the 1896 discovery at Bonanza Creek. As such, the hauling of gear across the pass was big

Figure 4. (A) Abandoned remains of "knock-down boats" at summit of Chilkoot Trail. (B) A gold miner's shoes, chains, and tools left behind for unknown reasons. (C) Skeletal remains of an ox that died while crossing the pass. (D) A modified wood implement, possibly part of an ice probe left behind by pre-gold rush explorers.
NPS/Shawn Jones

business even before the main thrust of the Klondike Gold Rush occurred). Prior to the construction of the trams, many companies employed Tlingit men and women to carry loads on their backs through the pass, but by the end of 1898, the tramway and pack animal caravans caused most of these jobs to disappear (Neufeld and Norris 1996).

At this same site, the team discovered a worn-out pair of shoes, presumably lost by a prospector (Figure 4B). Articles of clothing are typically rare to find in the archaeological record and are interesting for many reasons. Every person required good shoes for their journey, but some failed to make it to their ultimate destination. What happened to the owner

of these shoes? Did they simply drop an extra pair, or did the owner meet a more tragic fate? Many of the prospectors died in the pass, including nearly 70 people in a single avalanche (Neufeld and Norris 1996). We can only speculate about the individual who owned these shoes, but the presence of this historic artifact inspires us to imagine what that individual's life must have been like.

As noted above, stampeders used horses, mules, and even oxen as pack animals to haul supplies through the Chilkoot Pass (Neufeld and Norris 1996). The steepness and ruggedness of the Chilkoot Trail took its toll on some of the animals and they were shot and left behind. This project discovered the bones of one oxen—that apparently met its fate at this time—scattered among some boulders in the pass (Figure 4C). As with the old, worn-out shoes, there is little monetary value in finding the bones of a long-dead animal, but the story that these bones verify is that the journey into the gold fields could be perilous for both men and beasts alike. Additionally, the bones provide a concrete link to the past events, preserving the empirical evidence that allows us to revisit this historical event from a more personal, individualistic perspective.

In addition to the Klondike Gold Rush-era sites that were discovered and revisited, the NPS crew also discovered a wooden artifact (Figure 4D), most likely an ice probe for travel over glaciers and snow, which was radiocarbon dated to 140 years before present. The date suggests Tlingit or Athabaskan people probably left it behind a few decades prior to the Gold Rush. This artifact is an excellent reminder that the prospectors of 1898 were not the first people to pass through this area, but there were people that had long used this route to travel between territories. More work is needed doing ice-patch surveys in adjacent areas to document the prehistoric sites that surely must exist here.

Conclusions

While a great deal of archaeological work has documented the historic camps at Skagway, Dyea, and in the Yukon Territory (Neufeld and Norris 1996), archaeologists have completed only a small portion of possible survey and documentation of historic resources related to the Klondike Gold Rush in the Chilkoot Pass itself. Each new survey, including this project that focused on areas in the pass where thawing ice patches are present, results in the discovery of some preserved artifacts and new evidence with which to interpret this historic migration event.

Considering the nature of the artifacts in the Chilkoot Pass within the theme of migration, we can discuss at least four lines of evidence for mobility: foot power, pack animals, tramways, and boats. Each tells a story about transportation and mobility. Most men walked (and sometimes lost their shoes), others used pack animals or transported goods using tramways, and almost all relied on boats to haul gear down river into the Yukon and Alaska. Considering the location of these artifacts and features high on the Chilkoot Pass, it drives home the point that this was a difficult and arduous journey.

For many immigrants to the Yukon and Alaska, the Chilkoot Pass was the gateway to their new homeland. To cross the pass signified the departure from the familiar and the entry into a new land where untold fortunes awaited. The reality of the harsh climate and the competition with hordes of prospectors racing to the gold fields crushed many a stampeders' dreams, but ushered in the era of colonialism that would eventually affect the lives of all Alaskans, indigenous or migrant. While many of the prospectors were transient, others stayed behind to create the trading outposts, hotels, restaurants, and taverns. Many of the Gold Rush boomtowns are today major Alaskan

and Canadian cities, while others, such as Skagway, are living museums, preserved for the enjoyment of tourists. The Chilkoot Trail remains a challenging hike. Today, about 2,000 adventurous hikers a year experience its grandeur and history (compared to the gold rush peak when the trail was used by 1,000 people each day). For those who go, there is still opportunity to discover some of the objects left behind by the Stampeders and it is the goal of the National Park Service to preserve and share this amazing story of migration.

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Future Challenges for Salmon and the Freshwater Ecosystems of Southeast Alaska

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Mass animal migrations are awe-inspiring sights. Every summer and fall, residents and visitors to Alaska can witness one of the great underwater migrations: Pacific salmon returning from the ocean to their home streams, rivers, and lakeshores to spawn. Hundreds of millions of salmon return to Alaska's freshwaters annually (Stopha 2018). These anadromous fish are born in freshwater, migrate to saltwater to accrue the majority of their mass, and then return to their natal stream to spawn and die. The diversity of habitats used by Pacific salmon is staggering: large lakes, beaver ponds, icefields, wetlands, and waterfalls all play important roles in the salmon's web of life (O'Neel et al. 2015). Some individuals will fight strong flows for hundreds of miles to spawn in the tributaries of massive international watersheds like the Yukon River, while some will effortlessly slip several yards up one of the hundreds of tiny creeks lining the Alexander Archipelago in Southeast Alaska.

Naturalists have known since the 16th century that salmon typically return to their place of birth to spawn (Quinn 2005). This unique aspect of their life cycle continues to provide coastal and interior Alaskan communities with dependable sustenance year after year. The importance of salmon to Alaska cannot be understated. Salmon fisheries have the greatest economic impact on the Alaskan seafood industry, providing thousands of jobs to residents every year (McDowell Group 2017). In 2016, The Nature Conservancy conducted a poll showing that 96% of Alaskans believe salmon are essential to their way of life. For a group of species this important to society, it is imperative for scientists to continue learning more about the various salmon species residing in Alaskan waters and anticipate future challenges for their populations. Fluctuating ocean survival and harvest strategies undoubtedly play an important role in regulating salmon populations (Mantua et al. 1997, Mundy 1997), but in this article I concentrate on freshwater ecosystems, where the habitat provided by national parks plays a large role in the salmon life cycle.

The five primary species of semelparous (spawning once before dying) Pacific salmon each have their own unique life histories (Table 1), but all generally require cool, clean rivers with shallow water for spawning and deep pools for holding and migrating upriver. While ocean and estuary environments play critical roles in salmon growth and survival, changes in the abundance of salmon in rivers may indicate shifts in the habitat characteristics of freshwater ecosystems and potentially broader changes to park natural resources and visitor experience.

Salmon benefit the freshwater ecosystems they return to, transporting energy and nutrients gained from the ocean (Gende et al. 2002) and directly

Visitors viewing salmon in the Indian River at Sitka National Historical Park (top); pink salmon enter the Indian River in large numbers every August (above).
NPS photos

A char with a group of spawning sockeye salmon.
Photo courtesy of J. Armstrong

Table 1. Common names, scientific names, and notable life history characteristics of the five major species of semelparous Pacific salmon in Southeast Alaska. These descriptions are generally accurate, but exceptions exist. The unique life cycle of each species presents different combinations of research and management considerations. These descriptions are adapted from the Alaska Department of Fish and Game species profiles, which also include photos, videos, and links to other research.

Species	Scientific Name	General Life History
Chinook	*Oncorhynchus tshawytscha*	• After hatching, remain in freshwater up to one year • Spend one to five years feeding and growing in the ocean • Often found rearing and spawning in the mainstems of larger systems such as the Taku and Stikine Rivers
Chum	*Oncorhynchus keta*	• After hatching, migrate to the ocean within days • Spend several months in estuaries before ocean migration • Spend three to four years in the ocean • Often spawn in lower river reaches
Coho	*Oncorhynchus kisutch*	• After hatching, remain in freshwater for one to three winters • Use side-channels or beaver ponds to avoid floods • Spend approximately eighteen months in ocean • Spawn in small to large river systems
Pink	*Oncorhynchus gorbuscha*	• Have a predictable two-year life cycle • After emerging from gravel, migrate to ocean • Spend approximately eighteen months in ocean • Present in large rivers, but more commonly spawn in smaller coastal streams and intertidal zones at stream mouths
Sockeye	*Oncorhynchus nerka*	• After hatching, remain in freshwater for one to four years • Many juveniles spend significant time rearing in lakes • Spend one to three years in ocean • In addition to rivers, will also spawn on lakeshores

feeding more than fifty species of animals (Willson and Halupka 1995). This is not news to most Alaskans, but what is surprising is that scientists continue to learn more about the current and future challenges threatening this important group of species. Here, I describe some recent salmon research in Southeast Alaska and touch on future issues of concern in the region's three national parks: Glacier Bay National Park and Preserve, Klondike Gold Rush National Historical Park, and Sitka National Historical Park.

Climate Change Influences Salmon Migration Patterns and River Habitat

Whether it is a new river channel formed by a large landslide or completely new watershed sitting at the foot of a retreating glacier, salmon have adapted their migration pathways and timing to a constantly shifting habitat mosaic for thousands of years. The coming decades present new challenges and it is unclear if salmon will be able to keep pace with them. In Southeast Alaska, climate models predict rising air temperatures, increasing annual precipitation, and decreasing precipitation falling as snow (Shanley et al. 2015). Increased winter flooding due to higher precipitation amounts will promote active downstream transport of sediment and likely decrease the survival of salmon eggs buried in gravel during winter (Shanley and Albert 2014). The future timing of upriver migration to spawn and deposit eggs will play an important role in each population's continued success. The extent to which increased flooding will affect important habitat characteristics such as the presence of deep pools, streambank stability, and the density of large embedded trees that help form and maintain these features is understudied in this region. Changing streamflow patterns and subsequent impacts to salmon populations were major topics of discussion in 2012, when National Park Service staff, other agency representatives, and local and tribal leaders met in Juneau for the
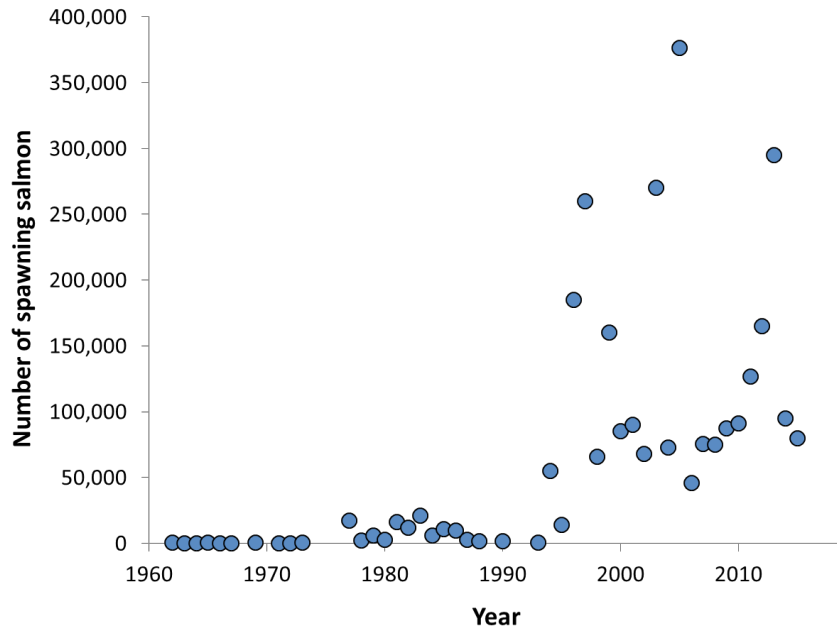
Figure 1. The approximate peak number of pink salmon present in the Indian River each year since aerial surveys began (adapted from Stopha 2015). The Sheldon Jackson Hatchery, which is adjacent to the mouth of the Indian River and Sitka National Historical Park, began annual releases of pink salmon fry in 1975. From 2013-2015, hatchery stray salmon rates ranged from 0-62% depending on the time of year surveyed (S. Gende/NPS, unpublished data).

Southeast Alaska Climate Change Scenario Planning Workshop (Winfree et al. 2014).

Even though total annual precipitation and frequency of winter floods are likely to increase in Southeast Alaska, decreasing snowpack will decrease the amount of water available for spawning salmon in the summertime. Rain- and snow-dominated watersheds without glaciers will see minimum summer flows continue to shrink during periods of low precipitation, often during periods overlapping with peak salmon spawning migrations. Recent water quality monitoring data from the Indian River in Sitka National Historical Park have demonstrated that low streamflow can combine with high salmon abundance to create low dissolved oxygen (hypoxic) events that lead to resident stream fish and salmon mortality, even in relatively cold streams that have the capacity to hold a lot of oxygen (Sergeant et al. 2017). In other words, many salmon breathing at the same time in a slow-moving river can create hypoxic conditions, which can lead to delayed upstream migration and even premature death.

Humans Magnify the Effects of Salmon Migration on Freshwater Ecosystems

Human-driven activities such as river water diversion and straying hatchery salmon (salmon that return to streams instead of their intended hatchery of origin) further increase the probability of hypoxic events by crowding more fish into smaller volumes of water. Recent straying rates in the Indian River have ranged as high as 62%, while other southern Alaska streams have approached 100% at times (Figure 1; Brenner et al. 2012, Piston and Heinl 2012, Hollowell et al. 2016). The extent that hatchery salmon impact wild salmon populations and their recovery has been debated for decades in the Pacific Northwest (Brannon et al. 2004, Mobrand et al. 2005). This is likely to become a more common debate in Alaska in the coming years. Additionally, escaped Atlantic salmon from aquaculture net pens may potentially compete with native Pacific salmon stocks by colonizing stream habitat; this remains a concern along the northwestern coastline of North America.

Watershed Characteristics and Salmon Combine to Influence Freshwater Contaminants

In contrast to most watersheds in the Pacific Northwest, Southeast Alaska watersheds have significant glacial and wetland coverage, and these two landscape features play important roles in contaminant transport. As glaciers continue to diminish (Loso et al. 2014), they may release contaminants previously deposited from the atmosphere and locked in ice. Sulfate-reducing bacteria in wetlands efficiently convert atmospheric mercury to methylmercury, a more toxic and bioavailable form of mercury that is dangerous to humans and other animals (Nagorski et al. 2011). Salmon returning to spawn may also act as biovectors that transport marine-derived contaminants to freshwaters. Thus, the combination of glacier, wetlands, and dense salmon populations increases the possibility that freshwater contaminants will be a continuing concern in this region. But for mercury accumulation, the role of salmon as biovectors in some streams may be counter-intuitive.

Many stream-dwelling fish, such as Dolly Varden (*Salvelinus malma*), have evolved to closely track the spawning migrations of salmon to gorge on their eggs and gain an important energetic boost before the lean feeding times of winter (Sergeant et al. 2015). Because salmon eggs are naturally low in mercury, recent research in Klondike Gold Rush and Sitka national historical parks demonstrated that Dolly Varden that feed on abundant salmon eggs actually have lower mercury concentrations than their cohorts residing in areas above migration barriers where salmon eggs are not available (Cyr et

al. 2016). It remains unknown whether Dolly Varden foraging on salmon eggs influences the patterns of concentration of other contaminants.

Conclusion

Scientists continue to gain a more nuanced view of the roles of salmon in the freshwater ecosystems of Southeast Alaska. We know from studies at Glacier Bay National Park and Preserve that salmon colonize new habitat and adapt to changing conditions (Milner et al. 2011, Scribner et al. 2017). This flexibility in habitat choices and migration timing in response to local changes is often called "plastic" behavior. An important question is whether the plasticity of salmon can keep pace with rapid change brought about by the climate and human development (Crozier et al. 2008).

One thing is certain, though: salmons' roles are hard to generalize and are very species- and river-specific. For example, many sockeye salmon populations in Southeast Alaska are migrating later than they have historically, while pink, chum, and coho salmon are migrating earlier (Kovach et al. 2015). From a National Park Service natural resource conservation and visitor experience perspective, it will be important to study the unique characteristics of salmon populations within each park and track population abundance and spatial distribution of juveniles and adults to understand future change. Basic monitoring of the number of juvenile salmon migrating downstream to the ocean and the number of adults migrating upstream to spawn is missing for most park rivers. In order for natural resource managers to have a more accurate perspective of trends in salmon abundance and distribution, parks should maintain long-term data collection where it already exists and strive to consolidate existing data sets to assess the ranges of variability and rates of change in populations.

The expansive and wild character of Alaska parklands creates many field challenges. While traditional aerial survey escapement counts and weirs will likely play a role in these efforts, newer technology such as Dual-frequency Identification Sonar (DIDSON), which uses sound to image underwater migrating salmon, or aerial drones may be important technology to consider, as well. Moving into the future, Alaska parks will need to elevate the importance of salmon to the health of freshwater resources, promote fisheries conservation efforts, create or maintain salmon-based interpretive opportunities for visitors, and advance freshwater ecosystem monitoring in priority streams and rivers.

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History, Purpose, and Status of Caribou Movements in Northwest Alaska

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Caribou (*Rangifer tarandus*) are thought to be a species of Eurasian descent (Osborn 1910). While the species is known for having high fidelity to their calving grounds, the establishment of new calving grounds was essential to allow the species to expand its distribution, which now spans the Arctic globally. Flexibility in this behavioral trait allowed for eastward expansion, hundreds of thousands of years ago, across the now-submerged Bering Land Bridge (Banfield 1962, Guthrie and Matthews 1971).

People followed caribou across the land bridge much more recently, perhaps some 15,000 years ago. These first Alaskans relied on caribou for food, clothing, and tools, and the species has played a prominent role in Alaska Native culture for thousands of years (Anderson 1968, Burch 1972). People who depend on caribou are keenly aware of their movements and have needed to be mobile and flexible enough to move to where the caribou are or were heading. As Noorvik elder Clarence Jackson recalls, he would "hunt way up to the head of the Noatak River, stay there ten days to two weeks until they had enough caribou to bring home" (Betcher 2016). Entire families would work together to drive caribou toward waiting hunters during migration. These community caribou drives are no longer conducted for numerous reasons, including the

adoption of new technologies, such as the use of firearms and motorized transportation (Burch 2012). However, Alaska Natives continue to harvest caribou during their migrations by anticipating and then intercepting their movements at strategic locations using knowledge that has been passed down through generations.

Migration is a distinctive behavioral trait of caribou. Caribou display the longest terrestrial migrations anywhere on the planet. In northwest Alaska, caribou travel up to 2,737 miles (4,404 km) per year (Joly and Cameron 2017). One of the main purposes of migration is to minimize exposure to predation, especially during calving when young animals are particularly vulnerable (Fryxell and Sinclair 1988). Migratory barren-ground caribou tend to aggregate during calving and calve synchronously (most females giving birth within a week of each other). The hypothesized purpose of this phenomenon is to "swamp" or overwhelm the finite number of predators that exist within a relatively limited amount of space and time.

For the Western Arctic Herd (WAH), which ranges over all of northwest Alaska, calving has taken place in the Utukok uplands, north of the Brooks Range, for at least a century (Figure 1; Lent 1966, Joly et al. 2011, Burch 2012). Another critical purpose of migration is to track the availability of abundant high-quality forage (Fryxell and Sinclair 1988). Green vegetation emerges this far north (69°N

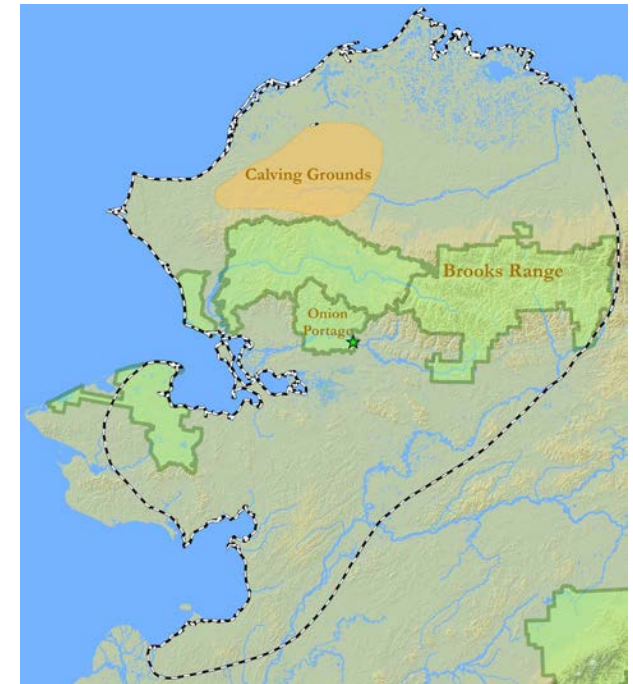**Figure 1.** Range of the Western Arctic Herd (black and white dotted line). Their calving grounds (orange polygon) are north of the Brooks Range. Lands managed by the National Park Service are in green. Onion Portage (green star), a traditional location to hunt caribou for thousands of years, lies within Kobuk Valley National Park.

Caribou in April on their northward migration to their calving grounds.
NPS /Kyle Joly

A small band of female caribou and newborn calves on their calving ground in northwest Alaska.
NPS/Kyle Joly

Thousands of caribou on the tundra along the Wulik River.
NPS/Kyle Joly

latitude) soon after calving and provides nutritious forage high in protein. Caribou need this high protein intake to fill nutritional deficits accumulated over the winter, produce milk, and gain body mass during the short summer months. Summer months are not easy on caribou; swarms of mosquitoes, biting flies, and other insect parasites harass caribou incessantly and are the primary driver of caribou movements during this time. Movement rates are greatest during this time of the year as caribou seek out cool and windy places for relief. It is at this time of year that the spectacular congregations of caribou occur, with groups numbering in the tens or even hundreds of thousands of individuals.

After insect harassment subsides, caribou disperse and can be found throughout the Brooks Range and the North Slope of Alaska. With the arrival of fall, most, but not all, caribou start to migrate south through the mountains. Commonly, caribou still cross the Kobuk River at Onion Portage, within Kobuk Valley National Park, during fall migration as they have done for ten thousand years (Anderson 1968, Joly and Cameron 2017). As forage quality decreases in vascular plants with the onset of fall, caribou begin to rely more heavily on lichens. Lichens dominate the winter diets of caribou and are much more abundant south of the Brooks Range (Joly et al. 2015), which may be an important factor driving the fall migration. Mid-winter is the time of energy conservation for caribou and is when movement rates are lowest. Depending on weather and snow conditions, caribou begin their northward spring migration in early April (Joly and Cameron 2017), back toward the calving grounds.

Caribou distribution, movements, and migratory patterns are known to be related to herd size (Messier et al. 1998, Ferguson and Messier 2000). Overgrazing of winter range may be a factor in this relationship. For example, as northwest Alaska elder

Nelson Greist observes "if caribou numbers are too high, they over eat" and "when caribou over eat, they need to change" where they go. The size of the WAH naturally oscillates at the decadal scale (Joly et al. 2011). The herd hit a low of 75,000 animals in 1976, but quickly rebounded, reaching nearly 500,000 by 2003 (ADFG 2011). From 2003, the herd steadily declined to 201,000 caribou in 2016 (ADFG 2016), but again increased to 259,000 caribou in 2017 (ADFG 2018). As herd size increases, there is a tendency for its range to expand; as herd size decreases, its range often contracts. The combination of decreasing abundance and diminishing range size can produce extreme hardships for rural subsistence users that rely on caribou, particularly those at the edge of the herd's range. As the WAH has declined, areas that often saw caribou in the past, such as Unalakleet, have not seen them for 15 years. As lichen abundance has declined on the eastern side of the Seward Peninsula, caribou have migrated out to the western Seward Peninsula to overwinter (Joly et al. 2007, Joly and Cameron 2017). Even annual shifts in migratory patterns can have profound impacts on communities in northwest Alaska that can experience large year-to-year swings in caribou availability even when the overall herd size is steady or growing.

On a global scale, long-distance, terrestrial migrations by large mammals are an imperiled phenomenon (Berger 2004). Encroachment of humans on the vast ranges used by migratory animals is one of the primary reasons for their endangerment. There has been relatively little development of northwest Alaska and thus caribou migrations continue to occur relatively unimpeded. A 50-mile- (80-km) long industrial road connecting a mine to its port site does intersect the western-most fall migration corridor of the WAH. The migration of some caribou traveling this route has been delayed by an average of 30 days (Wilson et al. 2016). Vehicular traffic stirs up dust along the road, which impacts vegetation and may alter caribou movements (Hasselbach et al. 2004, Chen et al. 2017). Other proposed development projects, like the 200-mile- (320-km) long road to the Ambler Mining District, could further constrain caribou movements in the area. Roads can have numerous impacts in addition to altering migratory movement, such as increasing vulnerability to vehicle collisions, predation, and hunting. Typically, it is not a single road or development that jeopardizes long-distance migrations, but the cumulative effects of many such projects. While caribou avoid dense vegetation, rough terrain, and wide sections of major rivers during their fall migration southward, current levels of sport hunting activity by people from outside the region does not appear to hinder migration (Fullman et al. 2017). However, many rural residents, such as Noatak elder Eugene Monroe, suggest that sport hunters that arrive by aircraft "disrupt the migration of the caribou" (Betcher 2016). Weather, climate change, and predators are other factors that may impact caribou movements. For example, hunter Lee Ballot, Sr. notes that caribou do not migrate when "it's just too warm, that's what triggers them to move, it is the cold" (Betcher 2016). Much additional research is required, but local knowledge can guide and enhance western-based scientific inquiries.

Large migratory caribou herds, such as the WAH, require vast spaces. While caribou are tolerant of some levels of development, vigilance, caution, and conservation are required to help maintain one of the greatest migratory spectacles in the world; if not just for its own existence, then for the people of northwest Alaska who are inextricably tied to caribou.

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Caribou in fall migrating to their winter grounds.
NPS /Kyle Joly

Influence of Spring Prey Pulses on the Seasonal Distribution and Migrations of Pinnipeds in and Adjacent to Alaska's National Parklands

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Central to understanding the migration of organisms is an understanding of *why* they move. Explanations for migratory behavior may include reducing the risk of predation, enhancing access to breeding opportunities, or enhancing access to aggregations of high-quality food or shifting patterns of food abundance (Alerstam et al. 2003, Milner-Gulland et al. 2011).

Each spring in the marine waters of the northeast Pacific Ocean, spawning aggregations of forage fish provide an episodic influx of energy to coastal and nearshore regions that cascades throughout marine ecosystems. The spawning aggregations of forage fish are an example of a resource pulse (e.g., Yang et al. 2010) that provides a "moveable feast" and short-term burst of prey availability for numerous invertebrates, fish, seabirds, and marine mammals (Willson and Womble 2006). The predictable prey pulse provided by spawning aggregations of forage fish including eulachon (*Thaliechthys pacificus*), capelin (*Mallotus villosus*), and herring (*Clupea pallasii*), supplies a significant source of calories (e.g., Surma et al. 2018) prior to the energetically demanding pupping and breeding season of pinnipeds, including Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina richardii*;

Womble et al. 2005). These marine mammals inhabit the nearshore coastal waters of the northeast Pacific Ocean and the marine waters in and adjacent to Alaska's parklands. Changes in the distribution and seasonal migrations of these pinnipeds have been documented and linked to the availability of high-quality prey that varies both temporally and spatially (Womble et al. 2008, Womble and Gende 2013, Sigler et al. 2017).

The annual cycle of pinnipeds is composed of reproductive, non-breeding, and migration periods that may vary in timing and location. Although periods of the annual cycle may be separated geographically by hundreds or thousands of miles, they are fundamentally linked as conditions encountered during the non-breeding season may directly influence the reproductive season (e.g., Marra et al. 2015). This is particularly true for *capital breeders*, those species that rely primarily upon stored energy reserves acquired prior to the reproductive season to fuel energy costs associated with reproduction and other critical life-history phases (Jönsson 1997). Most phocids, (Family Phocidae comprised of true seals) including harbor seals, have largely separated feeding from reproduction (Costa 1991) and rely primarily on stored energy to fuel the brief lactation period that typically ranges from 4-45 days (Bowen et al. 1985, Oftedal et al. 1987). For example, the extensive migrations of northern elephant seals (*Mirounga angustirostris*) from

California to the mesopelagic zone of the northeast Pacific Ocean demonstrate the extreme separation between pupping/breeding sites and foraging areas (LeBoeuf et al. 2000, Robinson et al. 2012). In contrast, the otariids (Family Otariidae comprised of sea lions and fur seals) are *income breeders* and rely upon intermittent foraging throughout an extended lactation period during which adult females provision their young, and are dependent upon local prey availability (Boyd 1998).

The seasonal energy pulse provided by spring aggregations of forage fish undoubtedly provides a significant energy influx for pinnipeds prior to the pupping and breeding season with likely implications for reproduction and survival for both capital and income breeders. Numerical responses, shifts in distribution, and shifts in the diet of pinnipeds provide evidence that the influx of the seasonal prey aggregations is important for both harbor seals and Steller sea lions (Sigler et al. 2004, Womble et al. 2005, Womble and Gende 2013). Herein, examples of seasonal migrations of harbor seals and Steller sea lions are described in relation to the influx of spawning aggregations of forage fish in and adjacent to the marine waters of Alaska's national parklands.

Harbor seals are primarily capital breeders and are the most widely distributed pinniped in the northern hemisphere. In Alaska, harbor seals come ashore at terrestrial sites and also use icebergs in tidewater glacier fjords to pup, breed, and molt (Mathews and

A harbor seal pops up in Glacier Bay National Park and Preserve.
NPS photo

Pendleton 2006, Womble et al. 2010). Tidewater glacier fjords host some of the largest seasonal aggregations of harbor seals in Alaska; however, a satellite telemetry study conducted in Glacier Bay National Park and Preserve demonstrates that harbor seals travel widely outside of the reproductive season (from September to April) with some harbor seals migrating over 560 miles (900 kilometers) away. Juvenile and adult female harbor seals traveled extensively both within Glacier Bay and throughout much of northern southeast Alaska, the eastern Gulf of Alaska, Prince William Sound, and to other tidewater glacier habitats in Disenchantment and Icy bays adjacent to Wrangell-St. Elias National Park and Preserve. Harbor seals departed Johns Hopkins Inlet, the primary glacier ice site in Glacier Bay, between September and November and began to return the following year in April. Although harbor seals traveled widely during the post-breeding season, they exhibited a high degree of fidelity back to Glacier Bay the following pupping season (May-June; Womble and Gende 2013).

There was a high degree of individual variability in post-breeding season migration patterns of harbor seals from Glacier Bay and several lines of evidence suggest that some harbor seals migrated to take advantage of seasonal aggregations of forage fish. For example, one adult female seal (PV08GB21) traveled from Johns Hopkins Inlet in Glacier Bay and spent >200 days in the eastern Gulf of Alaska and made several extended forays to an area near the continental shelf edge approximately 60 miles (95 km) offshore. Beginning in February through mid-May, the adult female seal moved to the mouth of the Alsek River, near Dry Bay, where eulachon, an energy-rich forage fish, spawns during spring. In mid-May, the adult female seal traveled from the Alsek River back to Johns Hopkins Inlet in Glacier Bay where she was tagged the previous autumn
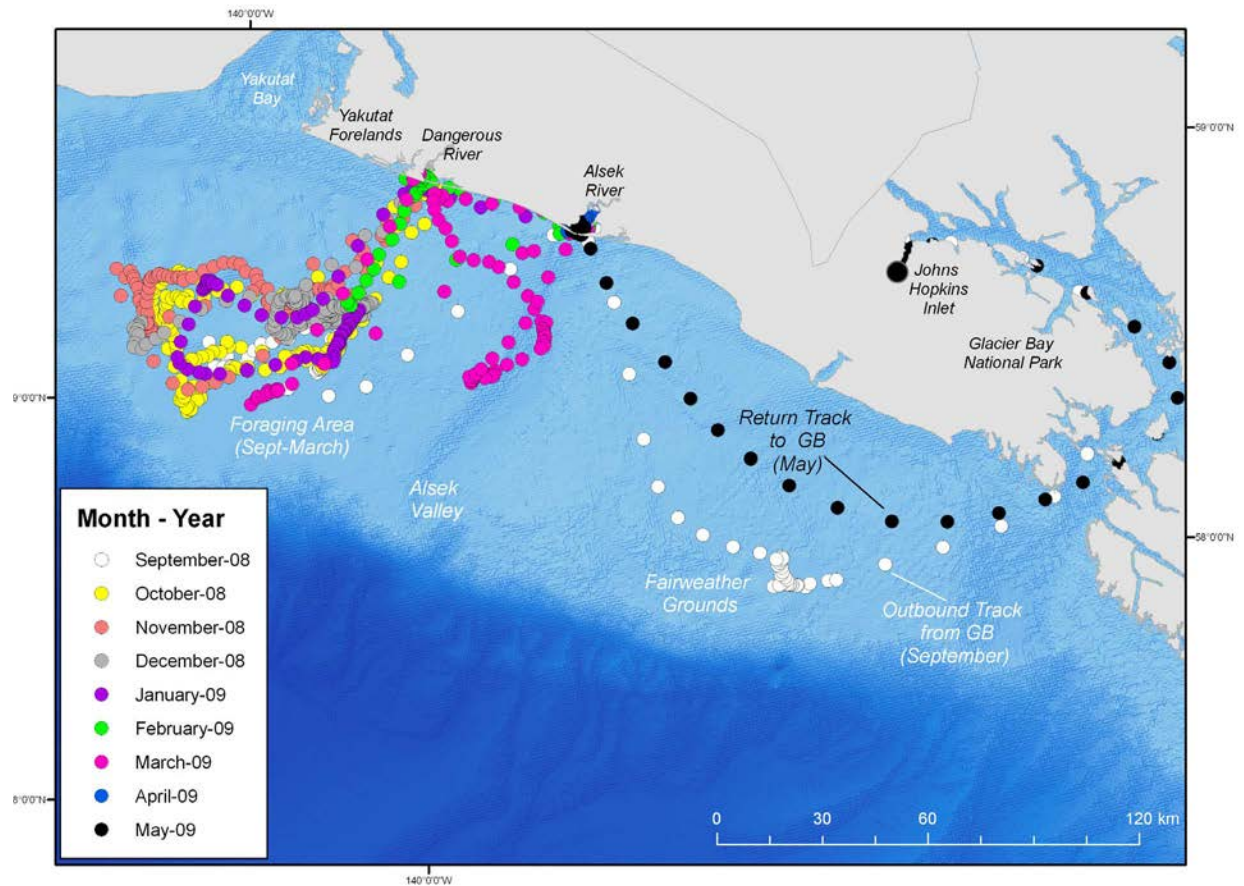

Figure 1. Track of adult female harbor seal (PV08GB21) that was tagged with a satellite-linked transmitter in Johns Hopkins Inlet in Glacier Bay National Park. The seal traveled to the eastern Gulf of Alaska and spent time near Dry Bay, at the mouth of the Alsek River during spring.

(Womble and Gende 2013; Figure 1). Aggregations of harbor seals have also been observed hauled out (>900 seals) and foraging in the Alsek River (Figure 2; Jamie Womble, personal observation, April 2013). Similarly, three harbor seals from Glacier Bay also traveled to estuaries in Chilkat Inlet and Lutak Inlet in northern Lynn Canal when eulachon, capelin, and herring were spawning.

The distributions and seasonal migrations of Steller sea lions are also influenced by the availability of spring-spawning forage fish in many regions throughout Alaska in and adjacent to Alaska parklands. Over 2,000 Steller sea lions regularly aggregate at Dry Bay near the mouth of the Alsek River, along the border of Glacier Bay National Park and Preserve (Figure 3) and at several other rivers

Figure 2. Harbor seals resting on sand bar in the Alsek River during eulachon aggregation in April.
NPS/Jamie Womble

Figure 3. Steller sea lions at the mouth of the Alsek River during the spring eulachon run.
NPS/Jamie Womble

along the Yakutat Forelands during spring when eulachon (Figure 4) are spawning (Womble et al. 2008, Mathews et al. 2011). Steller sea lions from haulouts and rookeries throughout southeast Alaska make seasonal migrations to the Alsek River during spring to take advantage of this high energy, densely aggregated prey resource. In fact, several Steller sea lions that were marked in southeastern Alaska have been observed at Dry Bay (Rehberg et al. In revision).

Steller sea lions also aggregate in response to spring-spawning fish in other areas in and near Glacier Bay National Park and Preserve including Adams Inlet, Tarr Inlet, and the estuaries and lower reaches of the Dixon River and the Excursion River. Steller sea lions respond to spring-spawning aggregations of eulachon in the estuary at the mouth of the Taiya River near Klondike Goldrush National Historical Park. Similarly, Steller lions aggregate and forage on spring-spawning herring in Sitka Sound (Figure 5) near Sitka National Historical Park (Womble et al. 2005).

California sea lions (*Zalophus californianus*), a pinniped that is not particularly common in Alaska (Maniscalco et al. 2004), also seasonally migrate to the Alsek River in spring when eulachon are present. For example, the carcass of a male California sea lion that was marked on the Columbia River in Astoria, Oregon, and had previously traveled to San Miguel Island in California (Bryan Wright, Oregon Department of Fish and Wildlife, personal communication, June 2016), was documented south of the Alsek River in 2016.

Collectively, these examples demonstrate the influence of aggregations of spring-spawning forage fish on the distribution and migrations of pinnipeds in and adjacent to Alaska's national parklands. The importance of the connections between spawning forage fish and far-ranging marine vertebrates,

Figure 4. Eulachon in the Akwe River along the Yakutat Forelands.
NPS/Jamie Womble

Figure 5. Steller sea lions in Sitka Sound during herring spawning aggregation in spring.
NPS/Jamie Womble

such as pinnipeds, demonstrates the importance of ecological connections in marine food webs regardless of management boundaries. Ultimately, variability in the scale and extent of aggregations of spawning forage fish may have significant implications for direct and indirect energy transfer throughout Alaskan marine ecosystems.

Acknowledgements

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Seasonal Sea Ice and Arctic Migrations of the Beluga Whale

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Each spring to early summer, the continental shelves of the Chukchi and Beaufort seas north of Alaska emerge from a cloak of winter sea ice. Such seasonal phases of sea ice break-up in the spring and sea ice freeze-up in the fall govern the accessibility and productivity of Alaska's Arctic Ocean for several migratory marine species. Open water in spring serves as a welcome mat for beluga whales (*Delphinapterus leucas*) and bowhead whales (*Balaena mysticetus*) that transit the Pacific's only gateway into the Arctic through the narrow Bering Strait. Each year, these Arctic whales pass the coastal boundaries of Bering Land Bridge National Preserve and Cape Krusenstern National Monument, dispatched from their winter haunts in the Bering Sea. After passing through the Bering Strait each spring, they enter the southern Chukchi Sea, one of the most seasonally productive regions of the global oceans (Grebmeier 2012). Some belugas and most bowhead whales continue on their >1,500 mile (>2,500 km) migration north of Alaska to the Canadian Beaufort Sea for the summer.

For beluga whales, recent cooperative research has provided deeper insights into the relative distribution, movements, and behavior of two distinct populations. The Eastern Chukchi Sea and Eastern Beaufort Sea beluga populations ("Chukchi" and "Beaufort" populations) return each summer to the nearshore regions of Kasegaluk Lagoon in northwest Alaska and the Mackenzie River Estuary, Canada, respectively (Figure 1). A mixture of large, white adults and dark grey calves arrive around June-early July, presumably for an annual molt of their skin in the warmer, less saline coastal water (St. Aubin et al. 1990). These coastal regions also provide a more protected area to nurture their young. Scientists working collaboratively with local communities have tagged beluga whales from the Chukchi and Beaufort populations with satellite-linked transmitters since 1993.

Location data from the transmitters reveal extensive movements around the Chukchi and Beaufort seas and deep (1.9 miles, or more than 3,000 m) Canada Basin, with some animals ranging to nearly ~80°N latitude (Richard et al. 2001, Suydam et al. 2001). Two decades of tracking data, combined, in some cases, with data on underwater diving behavior, help clarify why these populations use the Pacific Arctic as well as when and where they may overlap. Chukchi and Beaufort belugas are spatially segregated during July and August. However, both populations use the Alaskan Beaufort Sea and overlap during September when Beaufort belugas rapidly shift their distribution from the Canadian Beaufort Sea to the western Chukchi Sea, a month ahead of the Chukchi population's westward
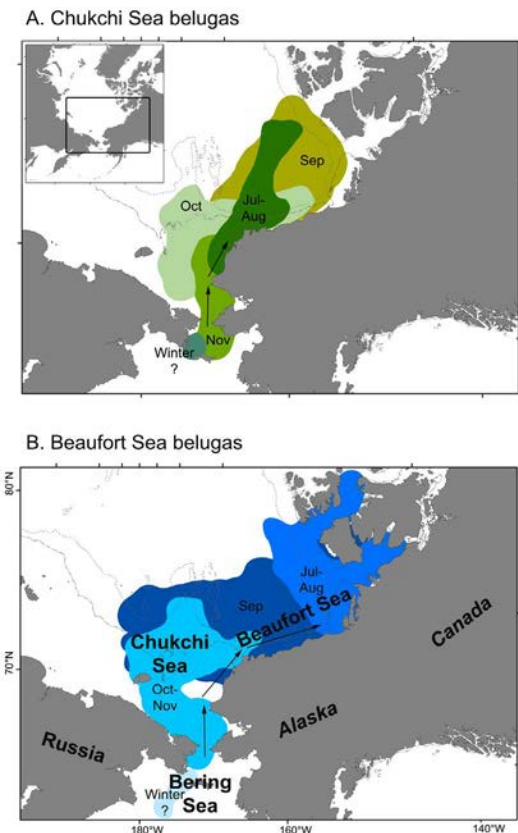

Figure 1. Schematic of seasonal ranges of (A) Chukchi Sea and (B) Beaufort Sea beluga whales, based on telemetry locations and home ranges (Richard et al. 2001, Suydam et al. 2001, Hauser et al. 2014). Winter locations are uncertain, based on the small number of tags transmitting past November (Hauser et al. 2015, Citta et al. 2017). Black arrows indicate potential spring migration routes for Chukchi (May-June) and Beaufort belugas (April-June), based on historic sightings (Lowry et al. 1987, Frost and Lowry 1990, Frost et al. 1993), acoustic detections (Garland et al. 2015) and few tagged whales (P. Richard, R. Suydam, unpubl. data). Figure modified from Hauser (2016).

Beluga whale pod in the Chukchi Sea.
Photo courtesy of Laura Morse, National Oceanic and Atmospheric Administration, Marine Mammal Permit #782-1719
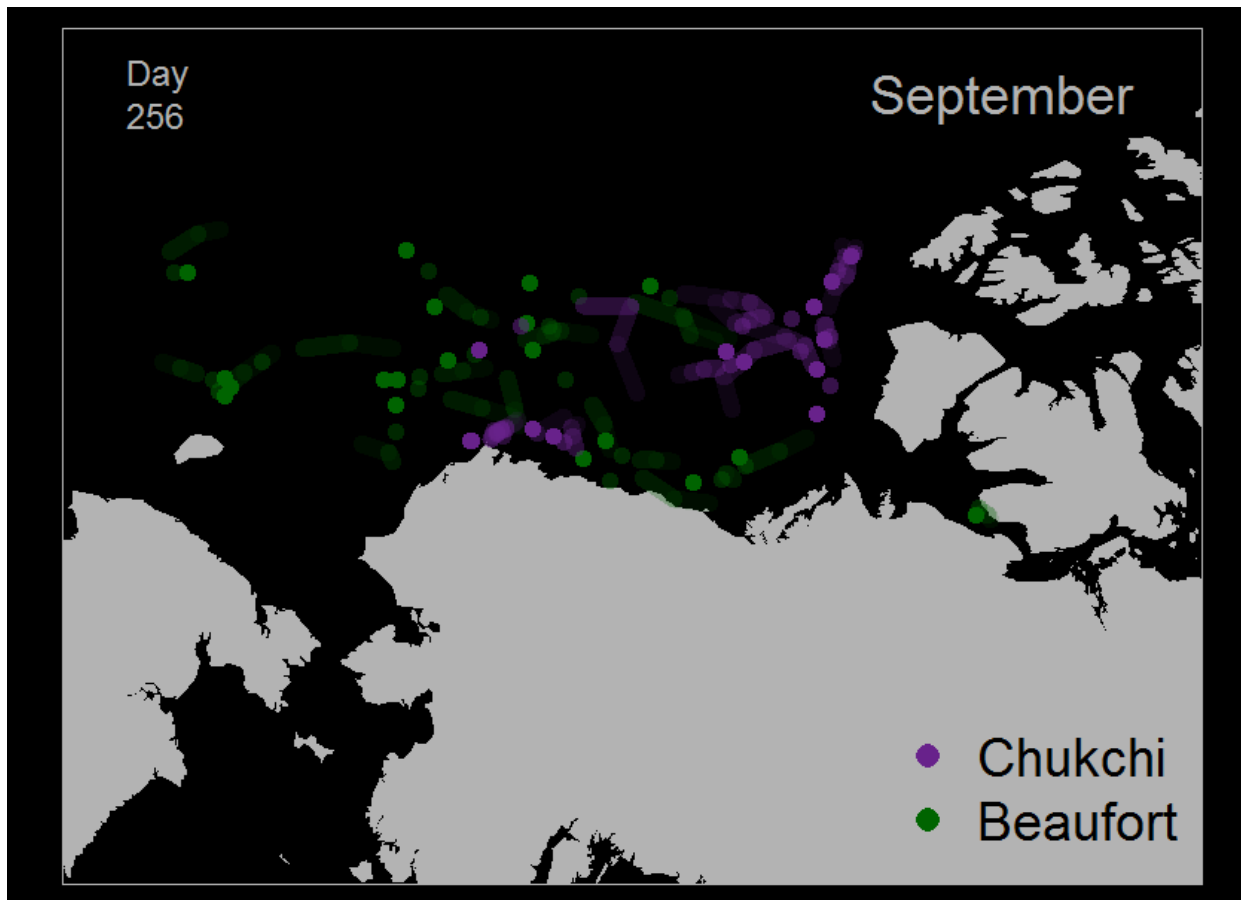
Figure 2. Screen shot from an [animation] of daily locations from Chukchi Sea ('Chukchi': purple dots) and Beaufort Sea ('Beaufort': green dots) beluga whales tagged from 1993-2007. Data were collected in collaboration with the Alaska Beluga Whale Committee, North Slope Borough, Village of Point Lay, Alaska Department of Fish and Game, National Marine Fisheries Service (for Chukchi Sea belugas) as well as Fisheries and Ocean Canada, Fisheries Joint Management Committee, and Hunter and Trapper Committees of villages in the Inuvialuit Settlement Region (for Beaufort Sea belugas). See Hauser et al. (2014) for more details and additional acknowledgements of the individuals, organizations, and funding sources that supported tagging and analysis efforts.

migration (Figure 2; Hauser et al. 2014). There is also limited spatial overlap in fall months in the Chukchi Sea. Adult males generally separate from females during summer and use deeper water, farther from shore, and denser sea ice concentrations (Hauser et al. 2017a).

These complicated seasonal distributions beg the question of why migrate and what factors influence their movements? Belugas have encountered this highly seasonal and ephemeral sea ice environment since at least the Late Miocene (Harington 2008), so their population-specific fidelity to distinct summer

areas, sexual segregation, and offset migration timing are presumably shaped by seasonal fluctuations in summer to fall conditions and sea ice in particular. Beluga philopatry (site fidelity) and migration patterns are also culturally transmitted, passed down from their mothers (O'Corry-Crowe et al. 2016). Belugas mediate their behavior to respond to patchily distributed prey, as illustrated by variations in diving behavior among Pacific Arctic regions. For example, both beluga populations dive to depths and portions of the water column that would presumably optimize foraging opportunities, based on the available information of prey distributions as well as oceanographic properties that concentrate prey (Hauser et al. 2015). Therefore, beluga distribution, movements, and behavior are ultimately driven by combined effects of genetic, social, and environmental influences.

Beluga Migrations in the Face of a Changing Pacific Arctic

The Arctic is undergoing rapid and unprecedented change, with warming twice as fast as the rest of the planet (AMAP 2017). The Pacific Arctic ecosystem is transforming with an expanded open-water summer season, increased wind-forcing and upper-ocean heat content, more freshwater, and upwelling (Wood et al. 2015). How are belugas and other Arctic marine mammals mediating these changing conditions, and to what extent, given tradeoffs in social versus environmental forcing?

Tagging data are again useful in helping assess beluga responses to shifts in their environment. The annual spring ice break-up in both the Chukchi and Beaufort seas now occurs earlier while fall freeze-up has shifted later, meaning that the overall duration of the open-water season has increased (13-15 days/decade during 1979-2013; Laidre et al. 2015). Comparing tagging data from 1998-2002 to 2007-

Table 1. Changes in fall migration timing between early (1993-2002) and late (2004-2012) years in which Chukchi and Beaufort beluga whales were tagged. Significant changes in migration shifts are shown in **bold**. Modified from Table 1 in Hauser et al. (2017b).

Migration Passage Location	Median Migration Day of the Year in Early, Late Periods	Days Between Median Dates (Late - Early)
Eastern Chukchi Sea belugas (tagged 1998-2002 and 2007-2012)		
Exit Beaufort Sea (first day west of 157°W)	6 Oct, 8 Nov	**+33**
Commence southward migration (last day north of 70°N)	22 Oct, 12 Nov	**+21**
Enter Bering Sea (first day south of Bering Strait, 65.9°N)	11 Nov, 25 Nov	**+14**
Eastern Beaufort Sea belugas (tagged 1993-1997 and 2004-2005)		
Exit Canada (first day west of 141°W)	8 Sept, 2 Sept	-6
Exit Beaufort Sea (first day west of 157°W)	17 Sept, 9 Sept	-8
Commence southward migration (last day north of 70°N)	16 Oct, 18 Oct	+2
Enter Bering Sea (first day south of Bering Strait, 65.9°N)	None tagged, 10 Dec	N/A

2012 (when sea ice cover significantly declined), Chukchi belugas delayed fall migration to allow for a prolonged presence in the Beaufort Sea as sea ice freeze-up also occurred later (Table 1; Hauser et al. 2017b). These results support the hypothesis that Chukchi belugas are coping with a changing Pacific Arctic environment by shifting migration timing. In contrast, there were few examples where migration timing of Beaufort belugas changed between the 1990s and 2000s, nor was there evidence that freeze-up timing cues migration for the Beaufort population. Rather, Beaufort beluga migration timing appears to be somewhat "pre-programmed" for a particular time each fall. More research is needed to determine how the migration strategies of Chukchi and Beaufort belugas affect their population dynamics, vital parameters, or potential for persistence. In the case of Pacific Arctic bowhead whales, current sea ice and oceanographic conditions seem to support enhanced foraging opportunities that have improved recent body condition and population growth (George et al. 2015), which may also be the case for belugas. However, later migration from the Beaufort Sea in the fall may expose Chukchi belugas to more variable freeze-up patterns and the potential for fatal ice entrapments. Ultimately, it seems that beluga responses to changing sea ice conditions vary among populations, which not only complicates predictions for future conditions, but also suggests some beluga populations may be more likely than others to persist in a changing climate.

In the face of sea ice loss, belugas and other Arctic marine mammals are also likely to experience increased anthropogenic activities and changes in the marine mammal community. For example, Arctic marine mammals and the subsistence communities that rely on them are vulnerable as sea ice loss expands the navigability of Arctic sea routes (Huntington et al. 2015) and possibilities for oil and gas development (Reeves et al. 2014). An increasingly ice-free Pacific Arctic may also affect the more temperate marine mammal species that ply Alaska's northern waters on a seasonal basis. Some baleen whales, such as fin and humpback whales (*Balaenoptera physalus* and *Megaptera novaeangliae*), are more commonly sighted now in the Chukchi Sea north of Bering Strait. This is either the result of a lack of sea ice or simply reflects the recovery of North Pacific populations following the cessation of commercial whaling (Clarke et al. 2013). Killer whales (*Orcinus orca*), a relatively novel Arctic predator, are also increasingly observed in the Pacific Arctic, similar to the Eastern Arctic. Overall, additional research is needed to understand the impacts of sea ice loss on Arctic marine mammals (Laidre et al. 2015).

For More Information

Beluga research in Alaska (North Slope Borough): http://www.north-slope.org/departments/wildlife-management/studies-and-research-projects/beluga-whale

Video on beluga whale migratory responses to sea ice loss: https://science360.gov/obj/video/3e608ad2-68aa-4374-b81a-fe5226bc0278/nsf-science-now-episode-49

Bowhead whale research in Arctic Alaska: http://www.adfg.alaska.gov/index.cfm?adfg=marinemammalprogram.bowhead

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A dark grey beluga whale calf with its mother during spring migration past Utqiaġvik (formerly Barrow).
Photo Courtesy of Kate Stafford

Statewide Movements of Non-territorial Golden Eagles in Alaska During the Breeding Season: Information for Developing Effective Conservation Plans

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In his foundational book of 1954, *The Natural Regulation of Animal Numbers*, renowned ecologist Dr. David Lack (Lack 1954) stated: "In a migrant species, reproduction and the main mortality may occur in regions several hundred miles apart. This greatly complicates the study of the factors influencing numbers." Lack's statement exemplifies the challenges of studying the population ecology of migratory animals, but it also understates the difficulties of studying and conserving migratory species that move thousands of miles across their annual cycle. As of January 2018, 521 naturally occurring species of birds had been recorded in Alaska (Gibson et al. 2018). Many of these are international migrants that move at continental and hemispheric scales during their annual cycle. The conservation of Alaska's migratory birds, including Golden Eagles (*Aquila chrysaetos*), requires identifying how events across their annual cycles influence their survival and reproduction (Sillett et al. 2000). To develop and implement effective and efficient conservation and management plans for migratory birds, National Park Service (NPS) and U.S. Fish and Wildlife Service (USFWS) managers need to know how, where, and when they travel and how conditions across their range affect their ability to survive and to produce young. However, there is limited information about the suite of conditions driving key demographic parameters of most species of migratory birds, including Golden Eagles, which nest or are raised in Alaska's national parklands.

Effective conservation of migratory birds also requires understanding how their age and social status influence seasonal movements. This is particularly important for longer-lived species that may exhibit different behaviors and movement patterns during different stages of their life cycle. For example, during the breeding season in Alaska, the behavior and movements of Golden Eagles depend on whether or not they are part of the breeding population. Eagles that are members of the breeding population have obtained a nesting territory and are defined as territorial eagles. Territorial eagles occupy and defend nesting territories, attempt to raise young when conditions allow, and focus their movements within and near their territories during the breeding season (Figure 1). In contrast, eagles that are not members of the breeding population and have not obtained a nesting territory are defined as non-territorial eagles. Non-territorial eagles do not occupy or defend nesting territories, do not attempt to raise young, and their movements are not focused within or near their territory (Figure 1; McIntyre et al. 2008). Non-territorial eagles can be separated into two categories: individuals that are actively seeking entry into the breeding population and individuals that are not. Migratory individuals that are actively seeking entry into the breeding population usually return to Alaska about the same time as territorial eagles, from late February through March. In contrast, migratory individuals that are not actively seeking entry into the breeding population usually return to Alaska much later, from mid-April to late May.

This article focuses primarily on second- and third-year Golden Eagles that are not actively seeking entry into the breeding population. These younger eagles represent the future generations of the breeding populations, but a large data gap exists regarding their role in population growth and stability (Watson 2010). Overall, very little is known about the natal dispersal of Golden Eagles (Watson 2010).

The classic definition of *natal dispersal* in birds is the dispersal from the natal nest to the site (location) of first reproduction (Greenwood and Harvey 1982). Many raptor ecologists agree that the natal dispersal stage of a Golden Eagle's life can span many years and that many individuals may spend a substantial portion of their lives waiting for opportunities to enter the breeding population (Watson 2010). What we've learned is the breeding-season movements of non-territorial eagles that are not attempting to enter the breeding population are strikingly different than those of members of the breeding population and most likely from non-territorial eagles that are
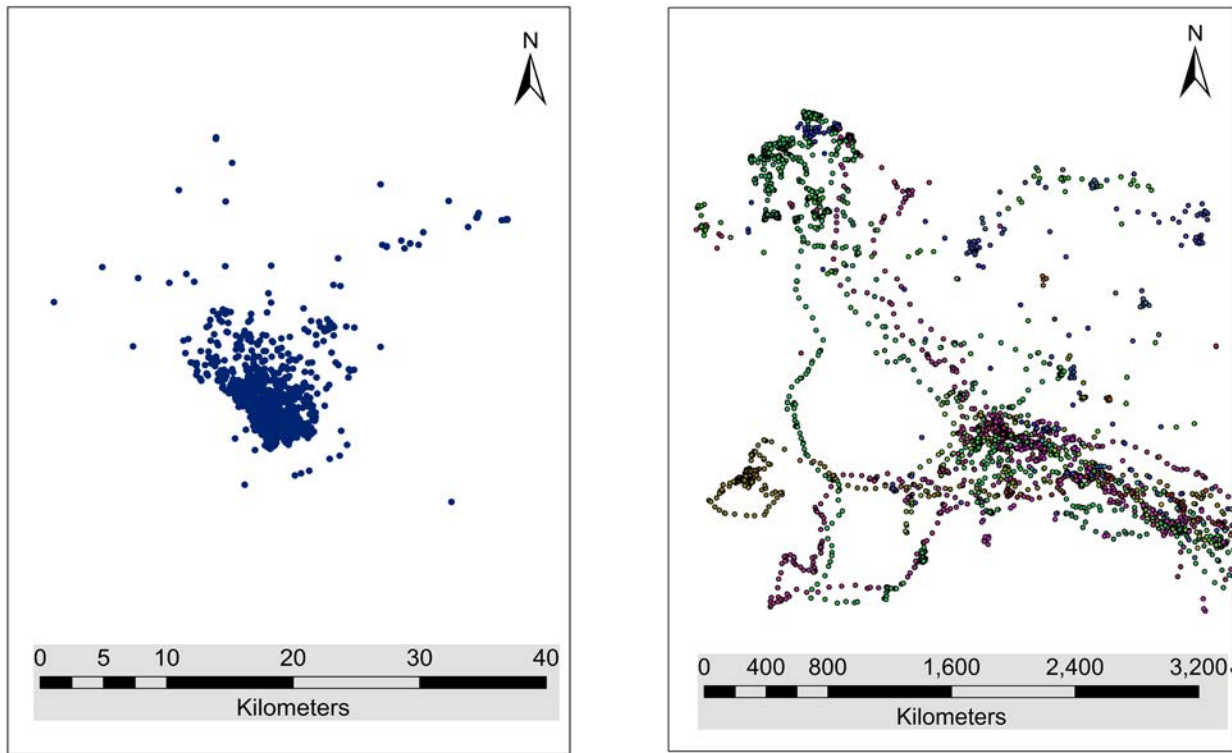
A Golden Eagle soaring above Denali National Park and Preserve.
NPS photo

Figure 1. Relocations of Golden Eagles captured in Denali National Park and Preserve, 2014-2016. Movements of territorial Golden Eagles, shown by relocations of a territorial adult male in the left panel, during the breeding season in Alaska are focused on their nesting territories. In contrast, movements of non-territorial, second- and third- year Golden Eagles, shown by relocations of 20 telemetered eagles in the right panel, are distributed across much of Alaska and portions of northwest Canada. Note scale of the map at the bottom of each panel.

Golden Eagles is not well-studied because it has been very difficult to monitor individuals over the time and space during the natal dispersal period. Some of these challenges have been overcome with the advent of lightweight telemetry tracking units.

In recent years, Golden Eagles have emerged as a conservation concern in the United States (Katzner et al. 2012, Millsap et al. 2013, Collopy et al. 2017). In response, the USFWS, the agency responsible for managing the species in the United States, has expanded their efforts to learn more about Golden Eagle ecology (USFWS 2016). Across their range, there are new concerns about the demographic resiliency of Golden Eagles (Millsap et al. 2013) particularly in relation to increases in anthropogenic sources of mortality, including habitat loss, electrocution on power distribution lines, contaminants, collisions with vehicles, and illegal shooting (Collopy et al. 2017). Overall, there is a growing need to identify management and conservation practices that reliably reduce or mitigate factors limiting the population and support management and conservation of the species at local, regional and continental scales (Collopy et al. 2017). For Alaska's migratory Golden Eagles, this requires new studies to document their movements and sources of mortality for all age-classes across their annual cycles.

In this article, we provide some historical perspective on Denali's Golden Eagles, highlight some of the findings from our studies of non-territorial second- and third-year Golden Eagles in Alaska during the breeding season, and use our tracking data (relocations) to demonstrate the usefulness of a landscape-scale conservation strategy for protecting and preserving Golden Eagles in Alaska.

actively seeking entry into the breeding population. These differences in movement and resource use are important to consider when developing management and conservation plans, particularly because the needs of non-territorial eagles may be considerably different than that of territorial eagles. If conservation plans for Golden Eagles in the United States rely heavily on information based on breeding eagles or nesting territory locations (Murphy et al. 2017), it is plausible that they are not adequately addressing the needs of non-territorial eagles. Further, areas used during natal dispersal are usually unknown for

most long-lived species and consequently these areas are usually less protected than breeding territories, which may lead to increased risk of mortality for the dispersing individuals (Penteriani et al. 2005).

Further, understanding the needs of non-territorial migratory Golden Eagles is important because their survival may be relatively more important for population persistence than it would be in a non-migratory population because migration may affect risk of mortality (Katzner et al. 2006). Across their range, the ecology of non-territorial

A Bit of History about Denali's Golden Eagles

In 2017, the NPS celebrated the 100th anniversary of the establishment of Mount McKinley National Park. This area was expanded and renamed Denali National Park and Preserve (Denali) in 1980 with the passage of the Alaska National Interest Lands Conservation Act. Denali's centennial celebrations included recognizing the accomplishments of many of the scientists and naturalists whose efforts resulted in protecting this region and increasing awareness of its wildlife, including Golden Eagles.

Charles Sheldon, Joseph Dixon, and Adolph Murie are some of the most celebrated naturalists and scientists in Denali's history. All three recognized that the northern foothills of the Alaska Range (now within Denali) supported a large concentration of nesting Golden Eagles (Sheldon 1930, Dixon 1938, Murie 1944, 1963). Dixon (1938:47) referred to Golden Eagles as "one of the outstanding avian citizens" of the area and recommended that the species be "preserved as an integral part of the native fauna." Murie (1944) recognized that Denali's Golden Eagles were migratory and understood the link between their survival and the "many new hazards in the south" (Murie 1963:3). Sheldon, Dixon, and Murie's studies provided the inspiration to start Golden Eagle studies in Denali in 1987 (McIntyre et al. 2006a).

During the earlier years of our study (1987-1996), we banded many Golden Eagle nestlings with aluminum leg bands. The recovery of some of these eagles showed that their migration corridors and wintering areas covered a vast area of western North America (McIntyre et al. 2006a, McIntyre 2012). Further, the recovery of eagles killed by electrocution, shooting, and collisions with vehicles showed how events thousands of miles away from their protected breeding areas in Denali affected their survival (McIntyre 2012).

In 1997, we started studying the movements and survival of juvenile, second year, and third year Golden Eagles from Denali across their annual cycle. These studies were made possible by the availability of lightweight satellite telemetry tags that would allow us to track the movements of eagles across their year-round range. Using satellite telemetry, we provided some of the first estimates of survival and continental-scale movements of migratory Golden Eagles in North America (McIntyre et al. 2006b, McIntyre et al. 2008). For example, once juvenile eagles left Denali on their first autumn migration, they traveled across western North America and overwintered from the grasslands of central Alberta to the high deserts of central Mexico. These non-breeding-season movements were impressive, but not surprising since we had already recovered eagles banded in Denali in some of these areas (McIntyre 2012).

What did surprise us, and many others, were the extensive movements of the eagles when they returned to Alaska the next summer (McIntyre et al. 2008). For example, many of our radio-tagged eagles spent most of the breeding season hundreds of kilometers away from Denali, often in the Brooks Range or on Alaska's Arctic Coastal Plain. For decades, other scientists working on a variety of wildlife species noted immature or subadult Golden Eagles in these areas (Mauer et al. 1985, Ritchie et al. 2003, Stehn 2013, Ritchie 2014, Shook and Ritchie 2017), but until our earlier telemetry studies (McIntyre et al. 2008), none of them suspected that some of the eagles they observed were raised in Denali, hundreds of miles to the south.

Expanding on Our Historical Studies

Our more recent tracking studies, a collaborative effort with NPS, USFWS, U.S. Geological Service, and Alaska Department of Fish and Game (McIntyre 2015), are building upon our work in the late 1990s, providing new information and reinforcing some of our earlier findings. Pooling data from deployments in the late 1990s and from 2014-2016, we noted a great deal of variation in the timing and movements of our telemetered eagles in Alaska and northern Yukon during the breeding season. Some individuals wandered for most of the breeding season, never settling in one area for very long. Others wandered extensively for part of the breeding season and then settled into a general area for extended periods of time (Figure 2). For example, four eagles settled into areas in northwest Alaska for much of June, July, and August, including areas within the western National Petroleum Reserve-Alaska (NPR-A; Figure 3). This included eagles tagged in the late 1990s and in 2015, thus showing repeated use of this area by Denali's Golden Eagles over a long time period.

Many individuals move great distances in Alaska during the breeding season. For example, at least two individuals tagged in Denali in 2015 moved over 3,100 miles (5,000 km) each during the 2016 breeding season (Figure 4). Interestingly, these eagles were relocated in similar areas in southwestern Alaska, but during different times of the breeding season. One eagle traveled through the area in May, right after it returned to Alaska. The other traveled through the same area in September, right before it started autumn migration. Individuals also used different areas between years (Figure 5). Both eagles were located again in the NPR-A in 2015 and 2016.
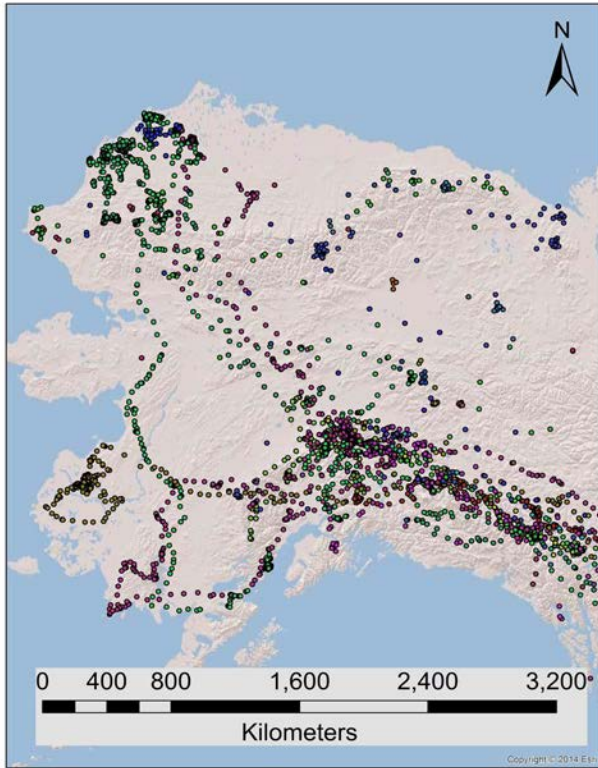
Figure 2. Relocations of 20 non-territorial Golden Eagles during the breeding season in Alaska and Yukon. Different colored circles represent individual eagles.
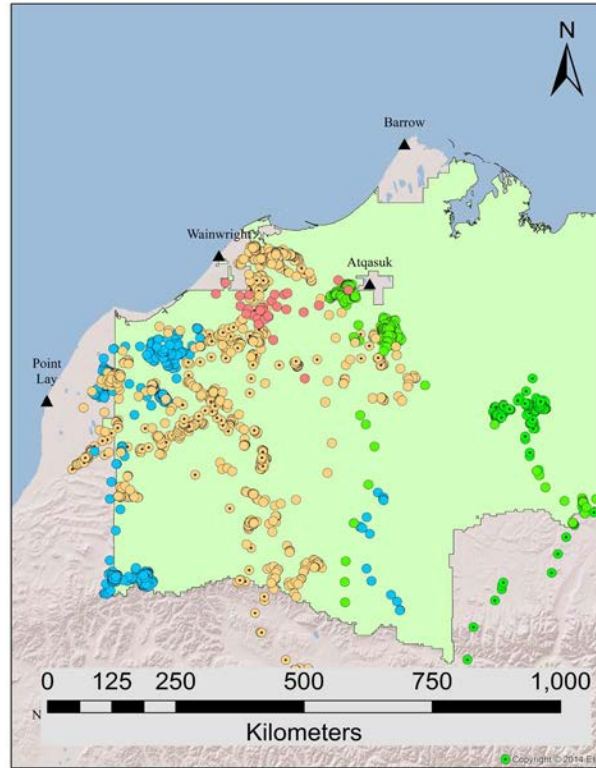

Figure 3. Relocations of four non-territorial Golden Eagles in the National Petroleum Reserve-Alaska during breeding seasons. The eagles were telemetered as fledglings in Denali in 1999, 2014, and 2015. Circles with the same color but with a black dot in the center represent the same eagle in different breeding seasons.
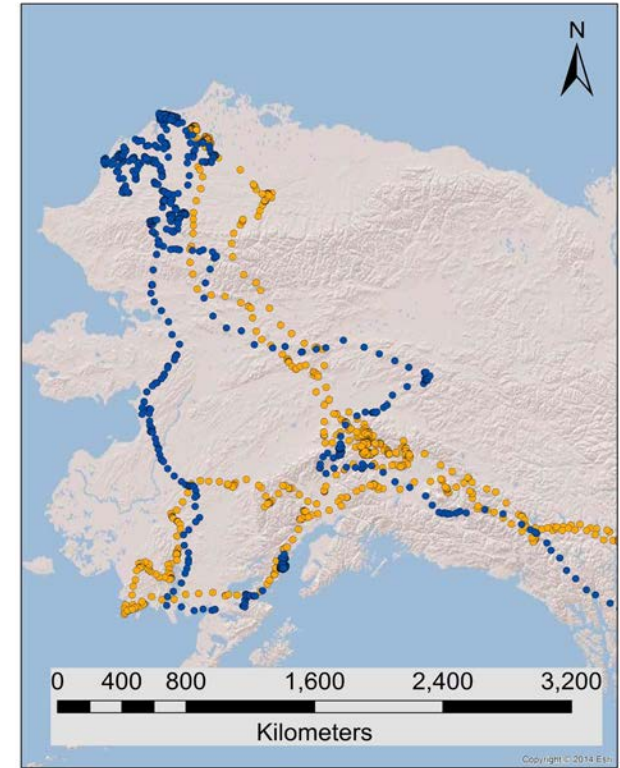

Figure 4. Statewide breeding season movements of two non-territorial second-year Golden Eagles from April through September 2016.

Additional Insights on Non-territorial Golden Eagles from Other Areas

We also tracked two non-territorial Golden Eagles that may have originated in natal areas outside of Denali, but who were both captured in NPS areas in Alaska. We telemetered one of the eagles along the southern slopes of the Mentasta Mountains in late March 2015 during spring migration and another near an occupied nesting territory in Denali in early April 2015. These eagles also exhibited Alaska-wide movement, spending time in places where we had not yet documented non-territorial Golden Eagles from Denali, including the Seward Peninsula in western Alaska (Figure 6).

Connections with Federally Managed Areas

In addition to the NPR-A, our telemetered eagles were relocated in 27 other federally managed areas in Alaska and three federally managed areas in the Yukon during the breeding season in years after the fledging year (Table 1, Figure 7). Many of these lands serve as a cornerstone of conservation and management and play a critical role in maintaining biological diversity and ecosystem services (Chape et al. 2008). Individual eagles were relocated at as many as 2 to 17 federally managed areas during the breeding season (Table 2). This is not too surprising, since Alaska contains more federally managed public lands than most other states. In some cases, the eagles were moving through these areas during migration, such as the Tetlin National Wildlife Refuge (NWR), or while traveling between areas within the breeding season. Others spent extended periods of time in
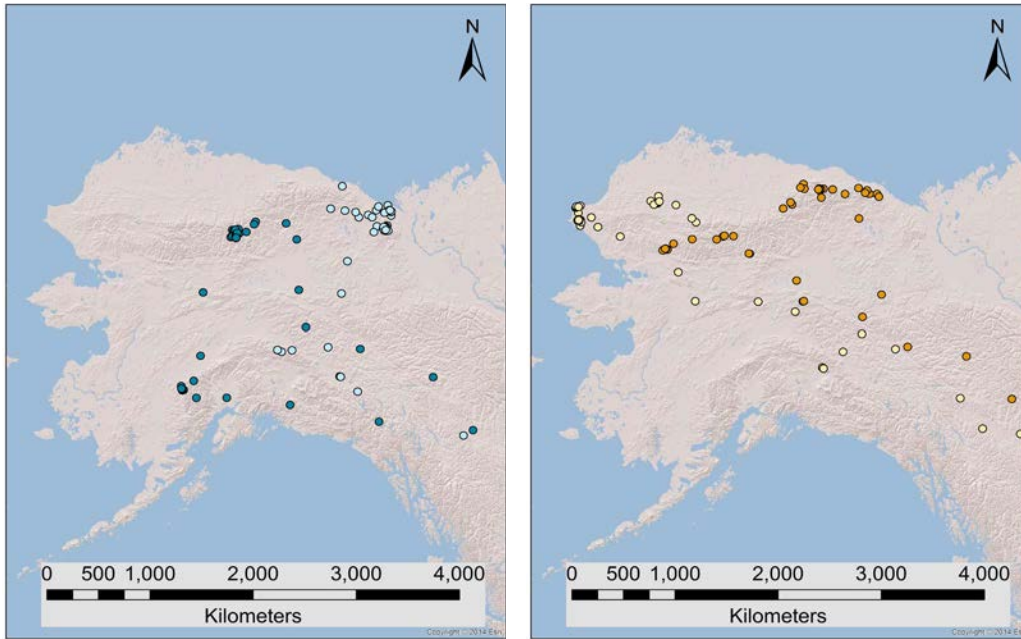
Figure 5. Relocations of two non-territorial Golden Eagles during two breeding seasons. Each panel represents an individual eagle in consecutive years. In each panel, the darker color represents second-year movements and the lighter shade represents third-year movements.
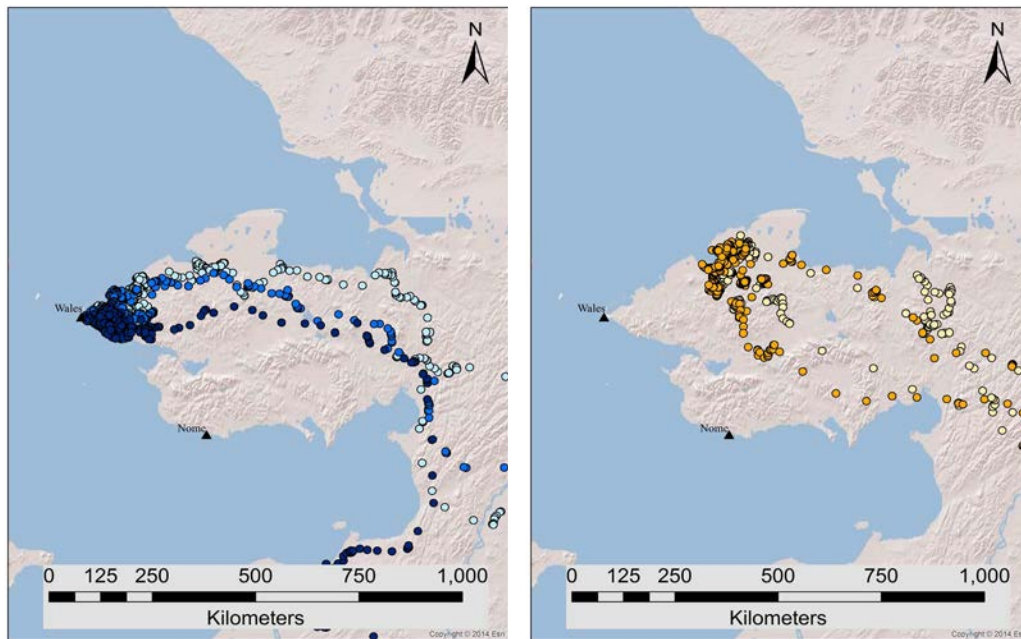

Figure 6. Relocation of two non-territorial Golden Eagles that were telemetered as After-Second Year individuals in late March in Wrangell-St. Elias National Park and Preserve, Alaska (left panel) and in early April in Denali National Park and Preserve, Alaska (right panel) from April through September. The different color circles represent different years for each eagle.

Table 1. List of federally managed areas where non-territorial second- and third-year Golden Eagles telemetered in Denali and Wrangell-St. Elias were relocated during the breeding season in Alaska.

| **Federally Managed Area** |
| --- |
| Admiralty Island National Monument |
| Alaska Maritime National Wildlife Refuge |
| Arctic National Wildlife Refuge |
| Bering Land Bridge National Preserve |
| Delta Wild and Scenic River |
| Denali National Park and Preserve |
| Fortymile Wild and Scenic River |
| Gates of the Arctic National Park and Preserve |
| Glacier Bay National Park and Preserve |
| Gulkana Wild and Scenic River |
| Innoko National Wildlife Refuge |
| Katmai National Park and Preserve |
| Kobuk Valley National Park |
| Lake Clark National Park and Preserve |
| National Petroleum Reserve-Alaska |
| Noatak National Preserve |
| Nowitna National Wildlife Refuge |
| Selawik National Wildlife Refuge |
| Steese National Conservation Area |
| Togiak National Wildlife Refuge |
| Tongass National Forest |
| White Mountains National Recreation Area |
| Wrangell-St. Elias National Park and Preserve |
| Yukon-Charley Rivers National Preserve |
| Yukon Delta National Wildlife Refuge |
| Yukon Flats National Wildlife Refuge |
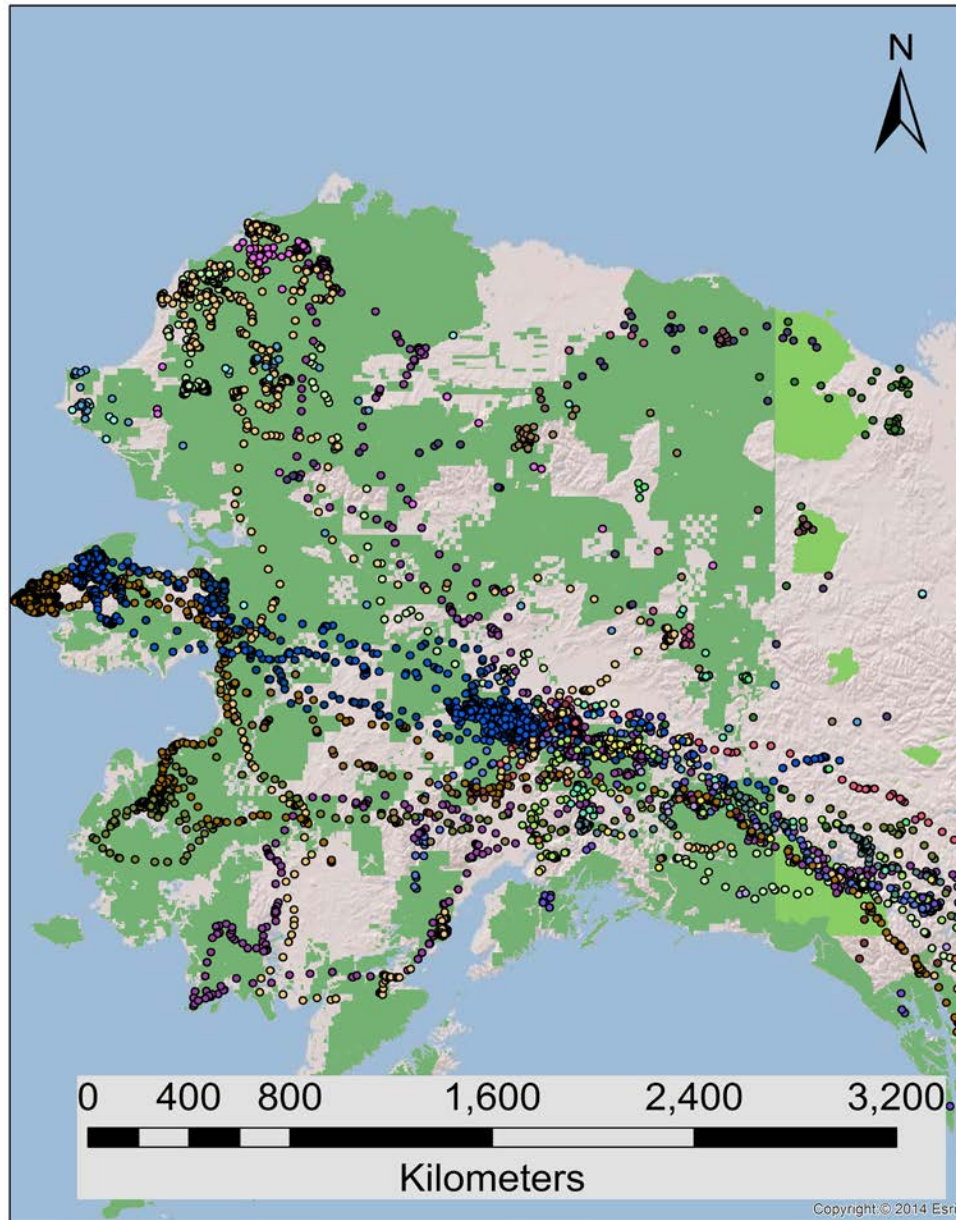
Figure 7. Relocations of non-territorial Golden Eagles telemetered as fledglings in Denali National Park and Preserve or as non-territorial migrants in Wrangell-St. Elias National Park and Preserve and Denali in relation to Federally Managed Lands (shown in green) during the breeding season in Alaska. Different colored circles represent individual eagles.

Table 2. Number of federally managed areas used by non-territorial Golden Eagles, and the proportion of their relocations within these areas during the breeding season, April through September, in Alaska.

Eagle[a]	Federally Managed Areas	Proportion of Relocations in Federally Managed Areas	Number of Relocations in Alaska through June 2017
1403	*6*	*0.39*	*1,814*
1502	*6*	*0.26*	*5,291*
1503	*5*	*0.70*	*4,782*
1505	*6*	*0.45*	*2,901*
1506	*11*	*0.44*	*2,828*
1507	*17*	*0.52*	*2,864*
1602	*4*	*0.61*	*490*
1605	*2*	*0.11*	*467*
2632	5	0.24	29
2635	6	0.65	54
2636	2	0.38	47
2641	2	0.26	19
2647	2	0.11	19
2657	2	0.32	19
2670	4	0.41	54
2681	3	0.10	69
2685	3	0.11	158
2689	2	0.12	25
2692	5	0.17	136
2697	10	0.38	136

[a] Eagles in italics were telemetered in 2014-2016 and telemetry unit duty cycle provided 12 relocations every day. In contrast, eagles with prefix "26" were telemetered in late 1990s and telemetry unit duty cycle provided relocation data every three to five days.

the breeding season in the Arctic NWR, Bering Land Bridge National Preserve, Denali National Park and Preserve, NPR-A, and the Yukon Delta NWR (Table 1 and 2). In Alaska, federally managed areas may comprise a relatively large portion of the areas used by non-territorial Golden Eagles during their extended dispersal process. This has direct conservation implications since implementing conservation actions directed toward Golden Eagles on federally managed lands may be less complicated than on private lands.

Of specific interest are six eagles that spent at least part of the breeding season in the western half of the NPR-A on Alaska's North Slope. The NPR-A is managed by the Bureau of Land Management (BLM) and is an area of increasing interest for oil and gas extraction. Four Denali eagles spent over 35% of the breeding season in the NPR-A (range 36.6-53.7%). These eagles arrived on the NPR-A from early to mid-June and remained there until late August and early September. Two others arrived in mid-June, but only remained for two to three weeks. We know of at least one other second-year Golden Eagle tagged on the wintering grounds in Montana that also spent an extended amount time in the NPR-A during the 2014 breeding season (Harmata, pers. comm., July 2014). Further, observers recorded 32, 33, and 30 Golden Eagles flying near or perched on bluffs in this area in 2012, 2013, and 2016, respectively (Shook and Ritchie 2017). In 2012 and 2013, at least 75% of these were subadult plumaged eagles and in 2016, at least 90% were subadult plumaged eagles (Shook and Ritchie 2017). While we do not yet know the fate of some of these eagles, our telemetry relocations and observations by Ritchie et al. (2003), Ritchie (2014), and Shook and Ritchie (2017) suggest that some of the NPR-A provides important resources for non-territorial Golden Eagles, including those raised in Denali. We believe that this importance should be acknowledged in conservation and management actions on the NPR-A and in statewide Golden Eagle management plans.

Statewide Movements Call for a Statewide Conservation Strategy

Every telemetered eagle tells an important, and unique, story. Our telemetry studies continue to provide new information on the movements of non-territorial Golden Eagles in Alaska during the breeding season, expanding our understanding of the ecology of this species. This information should be useful for developing effective management and conservation strategies for this species in Alaska. While limited by sample size, our studies clearly show that many second- and third-year Golden Eagles use resources across much of interior and northern Alaska during the breeding season. Thus, a statewide conservation strategy is necessary to preserve the resources needed by these eagles. While our data are restricted primarily to the eagles we tagged in Denali, our results raise interesting and important questions about the movement patterns and resource use of non-territorial Golden Eagles during the breeding season in Alaska.

Collaboration is Essential for Conservation

The dispersed movements of non-territorial Golden Eagles from Denali during the breeding season suggests that individuals are exposed to different drivers of population change across this part of their annual cycle. For example, individuals that summer in interior Alaska experience different events and conditions than those that summer in northwest Alaska. Conserving these wide-ranging eagles requires a landscape-scale approach, reaching far beyond the boundaries of Denali (Finch et al. 2017) during the breeding season and across the rest of their annual cycle. The recent emphasis on annual-cycle studies of birds (Marra et al. 2015) must be matched by the implementation of annual-cycle conservation strategies. For wide-ranging species, including Denali's Golden Eagles and many other migratory birds, this will require close and active collaboration among all the agencies and organizations that manage the lands and resources used by these birds (Runge et al. 2014).

New Research on Golden Eagles takes Flight

We will be tracking dozens of Golden Eagles in Denali and other Alaska national parklands in the next five years as part of our ongoing collaborative studies among the NPS, USFWS, U.S. Geological Survey, and Alaska Department of Fish and Game (McIntyre 2015). The GPS-GSM telemetry units we will be using have the potential to provide data for many years because they use solar-rechargeable batteries and highly efficient software and programming (M. Lanzone, pers. comm., March 2018). This affords us new opportunities to quantify seasonal and age-specific survival, natal dispersal, lifetime reproductive success, and breeding dispersal for migratory Golden Eagles, all of which increase our ability to identify and understand factors affecting their populations. This information is critical for developing effective conservation strategies for these wide-ranging eagles.

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Connecting Taiga to Tropics: Swainson's Thrush as a Model for Nearctic-Neotropical Migration in Alaska

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The Swainson's Thrush (*Catharus ustulatus*) is a medium-sized songbird renowned for a beautiful spiraling flutelike song and an affinity for mature dense forests. Twice a year, the Swainson's Thrush connects the boreal forests of North America to the tropical forests of Central and South America through its flight across the Western Hemisphere. About 200 bird species, primarily songbirds such as thrushes and warblers, are considered Nearctic-Neotropical migrants that fly thousands of miles annually between breeding and wintering areas. But why would an animal undertake such a perilous and energetically costly journey? Ultimately, long-distance migration exists because it increases a bird's fitness which is the ability to raise young over its lifetime (Alerstam et al. 2003).

Alaska's unique position on the globe, far north at the extremities of North America and the Pacific Ocean, and encompassing much of historical Beringia, provides the state with a fantastic diversity of birds. These birds must incorporate a wide variety of strategies to survive and successfully breed at latitudes greater than 60°N (Kessel and Gibson 1978). Most of Alaska's 300 annually occurring bird species (Gibson et al. 2017) leave the state in the fall to overwinter further south. Where they go and how they get there evolved over time with changing climate and geography. Northern bird populations

were thought to be particularly influenced by glacial cycling during the Pleistocene that shaped migratory pathways and created divergence in species (Avise and Walker 1998, Lovette 2005). In Alaska, we can trace the migratory routes of many songbirds to the recolonization of expanding northern forests by birds with the retreat of ice sheets (Pielou 1991).

The Swainson's Thrush is an excellent model to illustrate post-glacial colonization of Alaska by migratory birds wintering in the New World tropics. Recent research has begun to paint a more complete story of the Swainson's Thrush's annual trip across continents. While observations and recovery of banded birds previously sketched an outline of the distribution of the two subspecies of Swainson's Thrush throughout the year, application of new genetic, isotopic, and tracking methodologies across a large part of its breeding range has made this songbird's migration one of the better understood in North America.

The two subspecies of Swainson's Thrush, the "russet-backed" group (*C. u. ustulatus*) that breeds along the Pacific Coast of North America and the "olive-backed" inland group (*C. u. swainsoni*) that breeds in boreal forests across Canada and the United States, are distinguished by their plumage characteristics as well as by differences in migration routes, wintering areas, breeding habitat, and vocalizations (Mack and Yong 2000). Notably, banding data and observations during migration

suggested that inland populations of Swainson's Thrush made a long and circuitous flight east across North America before heading south, unlike their coastal cousins that take a direct route south to their wintering grounds in Central America (Brewer et al. 2000).

Genetic researchers began to investigate the divergence of the two subspecies of Swainson's Thrush in depth in the early 2000s (Ruegg and Smith 2002, Reugg et al. 2006, Ruegg 2007). They found that the migratory pathway of the inland *swainsoni* group mirrors the post-glacial expansion of boreal forests and that subspecies likely diverged when ice sheets isolated populations during the last glacial maximum (Ruegg 2007). Where the two subspecies meet along the crest of the Cascade and Sierra Nevada Mountain Ranges, researchers found hybrid individuals that show physical and genetic traits that transition from *usulatus* to *swainsoni* along a gradient between coastal and interior ecosystems (Ruegg 2007). This research provided compelling evidence for the evolution of migratory pathways and the development of subspecies in songbirds through glacial cycling at northern latitudes; however, the complete story of the Swainson's Thrush's annual cycle were not known until tracking devices small enough to be deployed on songbirds were developed in the last decade.

Light-level geolocators have revolutionized research on small migratory birds (McKinnon et al.

The light-level geolocator fitted on this Swainson 's thrush will record light levels in relation to time allowing researchers to calculate latitude and longitude when they recapture the bird and recover the device the following summer.
NPS photo

2013). Previous tracking technology such as satellite and GPS transmitters were too heavy to deploy on smaller birds like thrushes, so the exact routes and wintering areas of specific breeding populations have been unknown. At less than a gram, geolocators are archival light-recording devices that record light levels in relation to time allowing researchers to calculate latitude and longitude based on day length and sun elevation angle (Hill 1994). Geolocators must be recovered to download the data, so they rely on the ability to recapture birds in subsequent years and therefore, sample sizes are generally low. Combined with genetic and isotope data, these units provide powerful empirical support for defining annual movements at a population level.

Researchers have deployed geolocators on Swainson's Thrush at a number of sites across their western range including Point Reyes National Seashore in California, coastal and inland sites in British Columbia, Rocky Mountain National Park in Colorado, and most recently Denali National Park and Preserve in Alaska. The resulting location data confirmed the direct and cross-continent migration paths of the coastal and inland populations as well as the intermediate routes of hybrid and rocky mountain populations (Delmore et al. 2012, Cormier et al. 2013, Delmore and Irwin 2014, J. Beason [Bird Conservancy of the Rockies] unpublished data, NPS unpublished data). In addition to better outlining migratory pathways, geolocator data also helped define wintering areas for the various populations. Wintering areas ranged from western Mexico to central South America and showed strong migratory connectivity, or links between breeding and wintering locations, for populations in California, Coastal British Columbia, and Alaska (Figure 1, Comier et al. 2013, NPS unpublished data).

The ability to define specific wintering areas for breeding songbird populations has huge implications

Figure 1. Researchers deployed geolocators on Swainson's Thrush at a number of sites across their western range including Point Reyes National Seashore in California, coastal and inland sites in British Columbia, Rocky Mountain National Park in Colorado, and most recently Denali National Park and Preserve in Alaska. The resulting location data confirmed the direct and cross continent migration paths of the coastal and inland populations and also helped define wintering areas for the various populations (Delmore et al. 2012, Cormier et al. 2013, Delmore and Irwin 2014, J. Beason (Bird Conservancy of the Rockies) unpublished data, NPS unpublished data).

for conservation and protection since these birds spend more of each year in the tropics than in their northern nesting grounds. While widespread declines in Nearctic-Neotropical migratory bird populations have been reported in the literature since the 1980s (Rappole and McDonald 1994), current research has

highlighted how complex the population dynamics of migratory birds may be as populations respond temporally and spatially to various factors at breeding and wintering areas as well as during migration (Faaborg et al. 2010). Managers of migratory birds have to know what habitats these wide-ranging birds

are using throughout the year to really understand what factors might be driving population declines. For the Swainson's Thrush, we now know that factors driving population trends in birds breeding in Rocky Mountain National Park will likely be very different than those affecting Denali National Park and Preserve's thrushes since the areas used by each population overlap very little across the year. To protect Swainson's Thrushes and other migratory birds, National Park Service managers will need to collaborate with national and international partners responsible for the conservation of specific habitats used by different breeding populations throughout their annual cycle. A greater understanding of where birds go when they leave park boundaries is critical to their conservation.

Acknowledgements

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Bridging the Boreal: Landscape Linkages Connecting the Federal Conservation Estate in Alaska

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Migration, like other ecological functions and processes, depends on connected landscapes. Alaska's vast forests, river valleys, and mountain ranges provide wildlife with diverse habitats and the ability to move between them as conditions require. In this article, we review why landscape connectivity is important and how to plan for connectivity given climate change. We describe "Bridging the Boreal" as a collaborative, multi-jurisdictional strategy to maintain landscape connectivity between protected areas in the Northwest Boreal Region with implementation examples from ongoing planning projects.

Ecologically, Alaska is relatively intact, but the region is changing quickly (Chapin, III et al. 2004, Saura et al. 2017). The climate associated with current biomes is changing and we can no longer expect them to be stable into the future (Murphy et al. 2010). Spruce forests are in the process of converting to hardwood, while glacier retreat is rerouting entire rivers in boreal Canada (Shugar et al. 2017). In addition to climate change, land development fragments and degrades habitats (Forman 2014). Alaska has a vast network of federally managed conservation lands. As development occurs, these protected areas could become isolated islands surrounded by other, perhaps incompatible, land

uses. By applying landscape connectivity practices, land managers can support the flow of individuals and genes across the landscape to maintain healthy populations (Belote et al. 2016). In the future, as investment in infrastructure increases, there will be fewer options to provide for landscape connectivity between conservation lands. Once lost, it's politically and financially difficult to restore and reconnect isolated islands of habitat (Morrison and Boyce 2009).

Alaska's decision makers have an opportunity to proactively design landscape linkages to ensure that connectivity between protected areas is maintained into the future (Chapin, III et al. 2004). Many management strategies can be used to maintain landscape connectivity, from road-crossing structures to greenways that facilitate the movement of people and other species to compensating landowners to manage their lands for wildlife movement.

Landscape Connectivity Matters

Landscape ecologists have empirically described a robust pattern of land-use conversion and habitat fragmentation that coincides with western economic development and increasing human population size (Forman 2014). In less than thirty years, from 1973 to 2000, developed areas in the contiguous United States increased by 33% and the conversion rate is accelerating (Sleeter et al. 2013). Alaska's protected areas are currently in connected landscapes, but

Alaskans should anticipate an increasing anthropogenic footprint as global economies and increasing human populations shape northern regions (Chapin, III et al. 2004, Saura et al. 2017).

Species diversity is higher in landscapes that have historically been connected (Lindborg and Eriksson 2004). A connected network of conservation lands increases the likelihood that animal populations will persist because immigration between sub-populations allows for recolonization and decreases inbreeding and other problems associated with small, isolated populations. Large carnivores, such as brown bears (*Ursus arctos*), wolves (*Canis lupus*), and wolverine (*Gulo gulo*), have been extirpated from portions of their range due to land-use conversion and the resulting habitat loss, degradation, and fragmentation (Ceballos and Ehrlich 2002, Yackulic et al. 2011). Roads and other linear, anthropogenic features can also isolate animal populations. For example, sub-populations of desert bighorn sheep (*Ovis canadensis nelsoni*) in California became genetically isolated and lost genetic diversity after a highway bisected adjacent habitat areas (Epps et al. 2005). Highways and infrastructure in Anchorage, Alaska correspond with genetic subdivision in moose (*Alces alces*) that is likely due to reduced gene flow (Wilson et al. 2015). Many animals depend on annual migrations across large regions to survive (Newton et al. 2017). Moreover, connected lands allow for populations to migrate to new areas as climate change

Several different enduring features are visible on the slopes of the Arctic Divide near Anaktuvuk Pass in Gates of the Arctic National Park and Preserve.
NPS/Sean Tevebaugh

Definitions of Connectivity Terms

Connectivity
is generally defined as the ease with which species can move through a landscape (Kindlmann and Burel 2008). Connectivity has been characterized in terms of landscape structure and function (Baguette et al. 2013).

Structural connectivity
measures the physical characteristics (i.e., distance) between and among habitat patches.

Functional connectivity
considers the behavioral responses of animals to landscape structure.

Corridors
are strips of habitat that a species can use for movement between habitat patches (Forman 2014).

Landscape linkage
is a general term for areas that increase animal movement or the continuity of ecological processes at regional scales (Bennett 1999).

alters current habitats and makes novel habitats more suitable for individual species (Schneider 2002). Connectivity is crucial for a natural change in species distributions (as opposed to more intensive active relocations) and thus, increases the resilience and adaptive capacity of the landscape substantially.

To deal with the problem of conservation lands becoming isolated from anthropogenic land-use change, landscape ecologists and restoration ecologists began planning for landscape connectivity. In this paper, we present a strategy to plan for landscape linkages between established protected areas.

Often, efforts to increase connectivity are based on identifying corridors using current habitat use information from a single species. In many cases, corridor design focuses on restoring movement between isolated habitat patches in urbanizing regions. In more-intact regions, designing and implementing corridors for many species independently is not practical. Landscape connectivity can be more generally assessed using measures of ecological intactness (Belote et al. 2016). Another approach is to base planning for connectivity on underlying landscape characteristics that will not change, these are called *enduring features* (Reid et al. 2017). Enduring features are less dynamic than species composition or land cover that change over the course of years or decades. Protecting the diversity of enduring features, or *geodiversity*, has also been suggested as a strategy for conserving biodiversity.

Connectivity and Climate Change

Wildlife are already moving in response to climate change and will continue to do so (Parmesan 2006). For example, moose in Alaska are moving further north and west into the Arctic following the expansion of riparian shrub habitat (Tape et al. 2016). Climate change will only increase the need for connected landscapes so that species can move to access needed habitat (Heller and Zavaleta 2009, Galatowitsch et al. 2009). Species are expected to respond individually and not together as a cohesive ecosystem. Therefore, we can expect new ecological communities to form as species redistribute with changing climate conditions (Hobbs et al. 2013, Williams and Jackson 2007).

Landscape planning efforts need to incorporate changing habitat conditions into planning and management approaches (Stein et al. 2014). In other words, corridors based on current habitat conditions may not be well suited for future conditions. Modelling can be used to understand where species may move as the climate changes, but these forecasts are highly uncertain (Brost and Beier 2012). Furthermore, habitat suitability may not represent dispersal and migration pathways well (Keeley et al. 2017). Enduring features provide a climate-resilient solution to designing landscape linkages since as the climate changes, the current habitats and how species will use them over the course of their lifecycles will not be stable (Beever et al. 2015). Topographic features, such as elevation, slope, and aspect, influence ecological processes and therefore, structure habitat conditions (Beier and Brost 2010). The idea is that similar enduring features with similar topography (for example, places that are steep, high-elevation, with sunny slopes) can host similar species and community assemblages. As the climate changes, the composition of species and ecosystem type on a given enduring feature will change, but we expect that similar enduring features will have the capacity to host similar species assemblages. Using these enduring features and providing connectivity for all geodiversity types should allow all species to reshuffle where they occur on the landscape given the new climate conditions. In other words, connecting geodiversity will allow

species to adapt and find new habitat. However, it is difficult to determine the long-term ecological results of using enduring features for connectivity in Alaska where landscapes are currently largely intact. We will not have empirical evidence of how well linkages perform until future land-use changes landscape permeability. Maintaining connectivity is a key strategy for maintaining biodiversity in the future (Lawler et al. 2015).

Bridging the Boreal with Proactive Planning: An Opportunity in the North

With the Alaska Native Lands Conservation Act (ANILCA; PL 96-487), Congress established a vast network of protected areas that provides essential habitat for boreal species like caribou (*Rangifer tarandus*), lynx (*Lynx canadensis*), and moose. Fifteen National Park System and 12 National Wildlife Refuge System units were identified resulting in 120 million acres of core protected lands managed by the National Park Service and U.S. Fish and Wildlife Service. The lands between protected areas (another 100 million acres) are multijurisdictional including other federal agencies such as the Bureau of Land Management (BLM), Department of Defense, and U.S. Forest Service with mandates for multiple use; Alaska Native Corporations; and the state of Alaska.

There is an opportunity to proactively maintain landscape connectivity between the ANILCA conservation system units before development occurs to avoid the high economic costs of retroactively restoring connectivity once it is lost. The idea is not to add more lands to Alaska's vast protected areas network, but to find creative solutions to maintain connectivity between them. In this way, we are leveraging the federal conservation estate to allow for development and other uses while keeping the lifestyle enjoyed by Alaskans. Linking these large protected areas is a cost-effective strategy because

these investments maintain animal populations and therefore do not carry the large costs associated with avoiding extinction after a species has declined (Drechsler et al. 2011). Currently, the land between the ANILCA protected lands is permeable, so animal movement is not constrained (Saura et al. 2017). It may seem strange to overlay linkages on an intact landscape, but the key is to consider the future value of these planned linkages when land-use change is more of an issue. Proactive conservation, or conservation action that plans for future changes, rather than reacts to historic or current impacts, is the opportunity of the north (Schmiegelow et al. 2014). Anticipating future changes and getting ahead of them is more cost effective and arguably more ecologically effective to maintain natural systems and processes. Landscape-scale connectivity clearly requires deliberate collaboration in land-use and natural resource planning as no one landowner or agency has the jurisdiction or responsibility for lands outside its own boundaries.

This scale of collaborative conservation often requires a bridging organization to provide a neutral platform, build trust among agencies and landowners, and orchestrate key alignments in planning and decision making. Landscape Conservation Cooperatives (LCCs) can fill that role. LCCs are "an international conservation network of organizational entities that facilitate adaptive co-governance by offering a much needed structure and process for analytic deliberation; refinement of perspective based on exposure to new information and social learning; coordination of information generation, conservation planning, and delivery; and leveraging of resources to improve conservation at a landscape scales" (Jacobson and Robertson 2012: 335). Each organization, agency, and landowner has different mandates, responsibilities, and management authorities. The Northwest Boreal LCC is comprised

of over 30 federal and state/provincial agencies, non-governmental organizations, Tribes and First Nations, and research institutions in the boreal zones of Alaska and Northwest Canada. Maintaining landscape connectivity has emerged as one of three central goals for the partnership and it is working on aligning strategies among these organizations to achieve measurable outcomes. These landscape linkages can also provide for human movement and support the subsistence lifestyle that is highlighted in ANILCA and valued by Alaskans.

Implementing Bridging the Boreal

The BLM is considering management decisions in their planning alternatives that would leverage the acreage of these conservation lands to increase the conservation value of the entire planning area via connectivity while providing for other landscape uses and values. Because the Northwest Boreal LCC stakeholders determined that a strategy of maintaining connectivity between protected areas is important, we were able to offer this problem framing and supporting analysis to regional planning efforts. The BLM's Resource Management Plan (RMP) process provides an example of where the Bridging the Boreal strategy is being considered in a planning process for implementation.

The BLM is currently engaged in two planning processes in Alaska. The BLM's Central Yukon (CY) Planning Region is 59 million acres with 13.1 million acres of BLM-managed public lands and the Bering Sea Western Interior (BSWI) planning area is over 62 million acres with 13.2 million acres of BLM-managed public lands. Both planning areas are multijurisdictional landscapes with multiple values and uses. Approximately 74 million acres of lands in the conservation estate occur within or directly adjacent to the planning area. This includes Gates of the Arctic and Denali national parks and
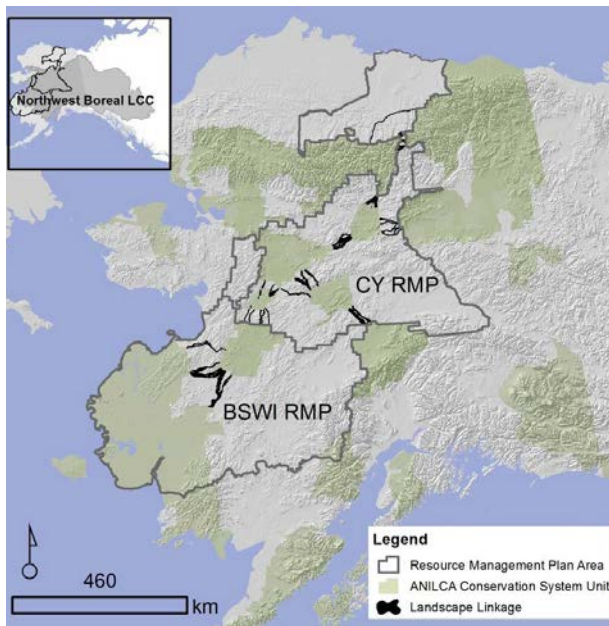
Figure 1. Modeled corridors among large conservation areas in two BLM planning areas demonstrates the potential application of landscape linkages to provide connectivity.

preserves managed by the National Park Service and eight national wildlife refuges managed by the U.S. Fish and Wildlife Service. In addition, Noatak National Preserve and Kobuk Valley National Park are contiguous and therefore, provide another 8 million acres that would benefit from landscape connectivity in the planning areas. We modelled landscape linkages between protected areas based on a least-cost path between enduring features (Brost and Beier 2012, Magness et al. 2018; Figure 1). The least-cost pathway is the pathway with the lowest resistance and shortest distance between geodiversity termini (Magness et al. 2018). There are stunning opportunities to connect protected areas. For example, managing as little as 87,025 acres would ensure connectivity for approximately 50 million acres of conservation lands; essentially maintaining connectivity for the majority of the Brooks Range.

In the CY RMP, linkages constituting as little as one percent of the study area could connect over 64 million acres of existing conservation lands.

Conclusion

Planning for landscape connectivity at this scale requires extensive collaboration as Northwest Boreal LCC partners put in place the management structures, decisions, and policies that are necessary to maintain connectivity in this region. While future habitat and climate are difficult to project, connecting large protected areas through linkages based on geodiversity can allow species to adapt to a changing landscape. It is a clear and quantifiable case study for the effectiveness of LCCs, or bridging organizations in general, in aligning management goals and objectives for multiple agencies, organizations, and landowners at a very large scale.

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Migration's Foundation: Ecological Intactness of Alaska's Ecosystems

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Actors upon a stage, aptly describes the relationship between migratory species and the landscapes through which migration occurs.

Migrating species bi-annually travel from breeding grounds to wintering grounds, sometimes across great distances. Many factors influence the success of a migration—habitat quality on breeding and wintering grounds, ample time to accumulate energy reserves needed to make the trip, and a suitable landscape across which migration can occur with minimal hindrances to movement (we use landscape herein because we will focus on terrestrial systems and non-avian migrations, but the general concepts equally apply to seascapes, airscapes, and aquatic systems). The more difficult it is to move through landscapes, the more energy reserves are expended and the less likely migration will be successful. This makes understanding landscape permeability very important. Landscape permeability, usually defined as "the quality of a … landscape to provide passage of animals," provides "…a broad measure of resistance to animal movement…" (Singleton 2002:2). Permeability differs by species and their sensitivity to specific hindrances (human activity, for example), by locomotion strategy (e.g., wind dispersal versus walking, flying, or swimming), and other factors. While these factors are important for species-specific management, our interest here is not to describe the permeability of landscapes at the species level, but to provide an overall assessment of landscape permeability on a sub-continental scale—the entire state of Alaska.

In more developed regions, including across much of the lower-48 United States, landscapes are highly fragmented in comparison to the sparsely populated northern latitudes. Fragmentation, due to urbanization (e.g., building highways, industrial roads, and shopping malls) or land-use conversion (e.g., forests and prairies becoming cornfields or golf courses), increases resistance to movement and decreases permeability for many species. A recent review of movement data for 57 mammal species found that in areas with a relatively high human footprint (more fragmented) a species' extent of movement was reduced by one half to one third on average compared to areas with very low human footprint (more intact). This was due, in part, to the loss of species with long-range movements no longer found in areas with higher human impact (Tucker et al. 2018). Such changes in movement patterns and species composition impact species themselves, the region's ecology, as well as human users who may no longer be able to access a species (e.g., decreased hunting opportunity).

In fragmented systems, conservation biologists and planners typically use the patch-corridor-matrix model of landscape ecology (Forman 1995) for assessing and restoring habitat connectivity. In this conservation model, *patches* are isolated areas of habitat, *corridors* are landscape connectivity features that support movement of species between patches, and the *matrix* is a heterogeneous background with various levels of resistance to movement, often relatively inhospitable to focal species. Attempts to ensure migration opportunity typically focus on connectivity between patches of similar habitats on a local scale, or between conservation areas regionally. For decades, most landscape conservation attention has been devoted to enhancing migratory capacity in the continent's mid-latitudes by re-connecting fragmented landscapes (e.g., Belote et al. 2017). Without the appropriate connectivity, a landscape becomes impermeable (where "appropriate" depends on the targeted species).

In large, relatively unfragmented landscapes, as commonly found in northern latitudes around the globe, assessments of connectivity are less informative than assessments of *landscape intactness*. The very limited human-development footprint is isolated to relatively small patches in a matrix of heterogeneous, contiguous habitat across large geographies (on the order of many hundreds of miles in all directions). At these broad scale, metrics

The large and contiguous protected areas in the Brooks Range provide intact and connected landscapes that support the migratory behavior of caribou and other animals.
NPS photo

of landscape intactness—"quantifiable estimate[s] of naturalness measured on a gradient of anthropogenic influence across broad landscapes or ecoregions" (Carter et al. 2017:55) are thus also informative about landscape permeability.

Intactness is an indicator of "the absence of human modification of the habitat" (Theobald 2013: 1859). Landscapes with high levels of intactness are considered to have higher retention of (historical) ecological structure, composition, and function (Hak and Comer 2017). In other words, highly intact regions are also commonly assumed to have high *ecological integrity* (Theobald 2013).

Here we summarize recent work providing the first quantitative assessment of intactness for Alaska as a whole and for each of its 32 ecoregions (Figure 1) as defined by Nowacki and colleagues (2001). This assessment provides a quantitative foundation for discussions of landscape-scale planning and management in Alaska, as well as highlights the potential for a more detailed assessment of climate connectivity (McGuire et al. 2016). We also discuss the conceptual limitations of intactness metrics in their failure to capture major climate-driven changes in landform and ecological processes in northern systems.

The Intactness Metric

Landscape intactness was assessed using the Landscape Condition Model (LCM) methodology (Hak and Comer 2017) modified to better represent the effect of human development on systems in Alaska (Trammell and Aisu 2015). The LCM measures intactness by first quantifying the direct impact (called the *impact score*) and the indirect impact (called the *decay distance*) of each of a variety of types of human modifications on the landscape then combining the resulting scores into a single measure of intactness at each pixel or grid cell.
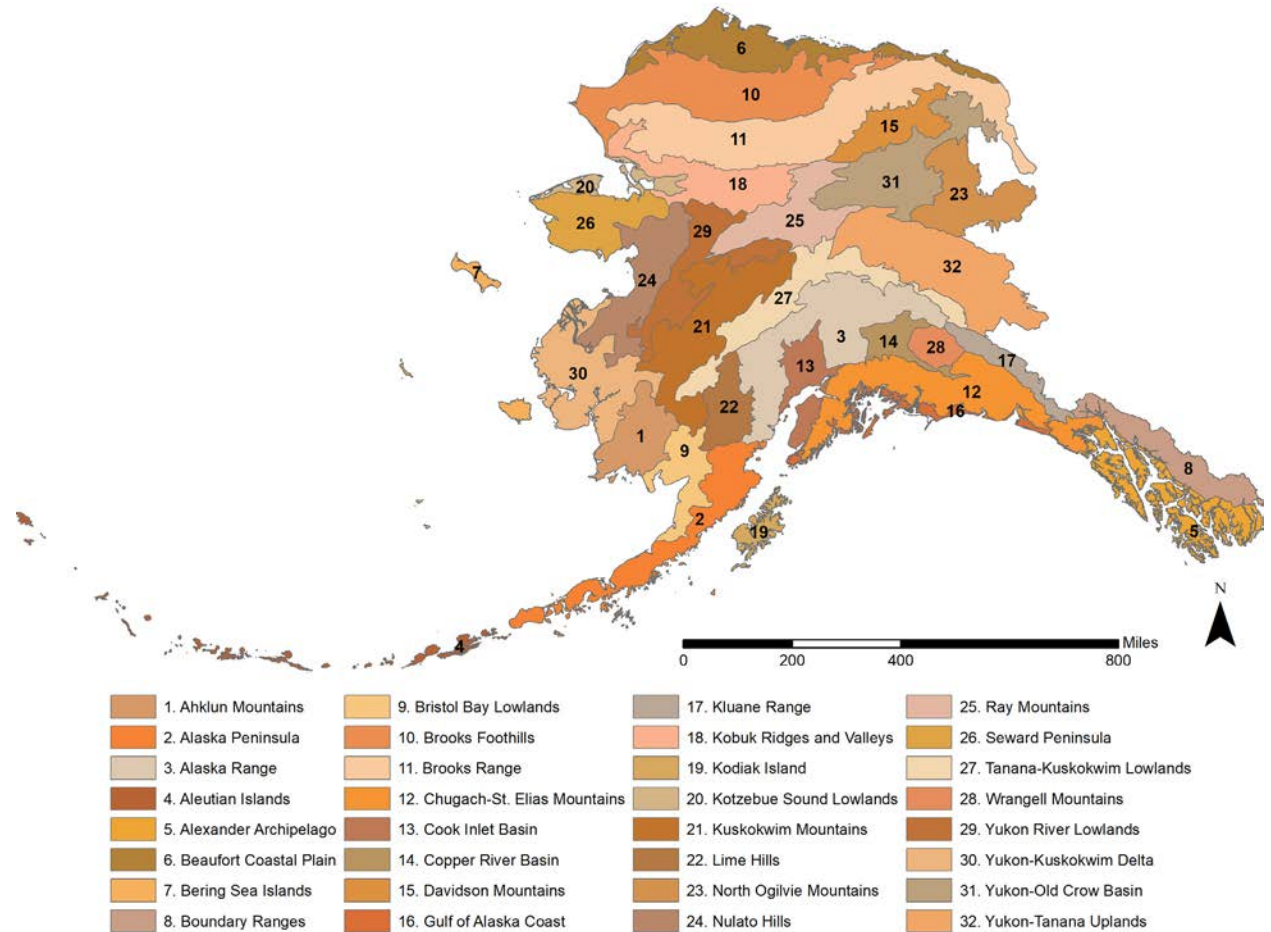

Figure 1. The ecoregions of Alaska (based on Nowacki et al. 2001).

Each type of human footprint is assigned a site impact score that varies from 0.05 for major highways and high-density urban development to 0.9 for areas recently logged but returning to natural forest. These impact scores are a relative measure; they are not focused on any particular ecological resource (species or habitat), but rather represent a scaled measure of the overall impact of a human activity on the landscape. Values range from 0 (lowest condition landscapes, limited function) to 1 (highest condition landscapes, fully functioning).

Using a geographic information system (GIS), these direct and indirect impacts are combined to calculate an intactness score to each 0.3 mile x 0.3 mile cell (500 meter on a side; one-quarter km²) of a statewide grid, creating a continuous map of landscape condition (Trammell 2014, 2015).

Human Footprint Types and Data Sources

The LCM was originally developed for the contiguous U.S. and was modified for use in Alaska. A complete table of direct and indirect impact scores can be found in Trammell and Aisu (2015),

and additional information on methods, limitations, and other uses of the LCM in Alaska can be found in Trammell (2014, 2015). Table 1 lists the types of human footprints accounted for and the best available (at the time) datasets used to represent them statewide.

We report LCM summary statistics for the whole state and for each ecoregion (as defined by Nowacki et al. 2001). The composite data layers and final LCM data are available from the Alaska Center for Conservation Science (accs.uaa.alaska.edu).

Alaska Scores Very High in Intactness

Statewide, there are approximately 12,500 miles (20,000 km) of major roads and over 22,900 miles (37,000 km) of trails (Figure 2). Additionally, there are approximately 5,000 square miles (1,300 square kilometers) of urban development (Trammell and Aisu 2015). In terms of modeled landscape condition, over 95% of the state is considered "very high" in intactness (LCM composite scores ≥0.80). Approximately 3% is "high" or "moderate" intactness, while less than 0.5% is classified as "very low" in intactness (Figure 2).

When assessed at the ecoregion scale, all ecoregions have some evidence of physical human disturbance (Figures 2 and 3). However, even the most impacted ecoregion (Cook Inlet Basin) still has a mean LCM score of 0.86, classified as "very high" intactness (Figures 2 and 3).

Not surprisingly, the large majority of Alaska's landscapes are very highly intact (Trammell and Aisu 2015) as they have not been directly modified as measured by the selected indicators and data sources (Table 1). This limited human footprint means most of the state has landscape condition values far in excess of even the most undeveloped regions of the lower-48 states (see Hak and Comer 2017).

Table 1: List of datasets used to compile comprehensive human footprint estimate for Alaska.

Dataset	Source	Description
Pipe Lines	ADNR	All industrial pipeline activity
Power Lines	ADNR	All power lines for Alaska
Telephone Lines	ADNR	All known telephone lines in Alaska
AKEPIC	AKNHP	Invasive species database, accessed January 2015
BLM Trails	BLM	RS2477 trails linear features
Ice and Rolligon Roads	BLM	Seasonal winter roads, based on permits
Major Rivers	ADNR	Derived from the National Hydrography Dataset
Transportation	ADNR	Includes highways, secondary roads, current and historical four-wheel drive roads, major trails (like Iditarod) as well as foot trails
Mining	USGS	Slightly outdated estimate of current mining activity, limited to point data
Logging	USFS	Current estimate of logging operations
National Land Cover Database	USGS	Used for high-, medium-, and low-density urbanization, as well as agriculture

ADNR = Alaska Department of Natural Resources, BLM = Bureau of Land Management, AKNHP = Alaska Natural Heritage Program, USGS = U.S. Geological Survey, USFS = U.S. Forest Service. From Trammell and Aisu (2015).

These landscape conditions are the fundamental stage supporting the migratory behavior of many of Alaska's species.

Clearly, the landscape model that best describes intactness in Alaska is "reverse" of the model appropriate for most of the contiguous United States and the world. Alaska is best described by the reverse matrix or conservation matrix model where the human footprint occurs in patches within a background of intact and functioning ecosystems, rather than as patches of habitat with interconnecting corridors within a matrix of fragmented and modified landscapes (Schmiegelow et al. 2006).

All Alaska ecoregions exhibit some human footprint—there are no pristine ecoregions—and some ecoregions have relatively high development and, thus, low intactness (e.g., Cook Inlet and Copper River Basin; Figure 3). Yet, even the most developed regions of the state are well described by the reverse matrix model and surrounded by highly intact landscapes providing an opportunity to ensure maintenance of important migration corridors and other ecosystem services to nearby communities (Trammell and Aisu 2015).

These intact, permeable landscapes support the seasonal migration and wide-ranging behaviors of many important terrestrial species. Though
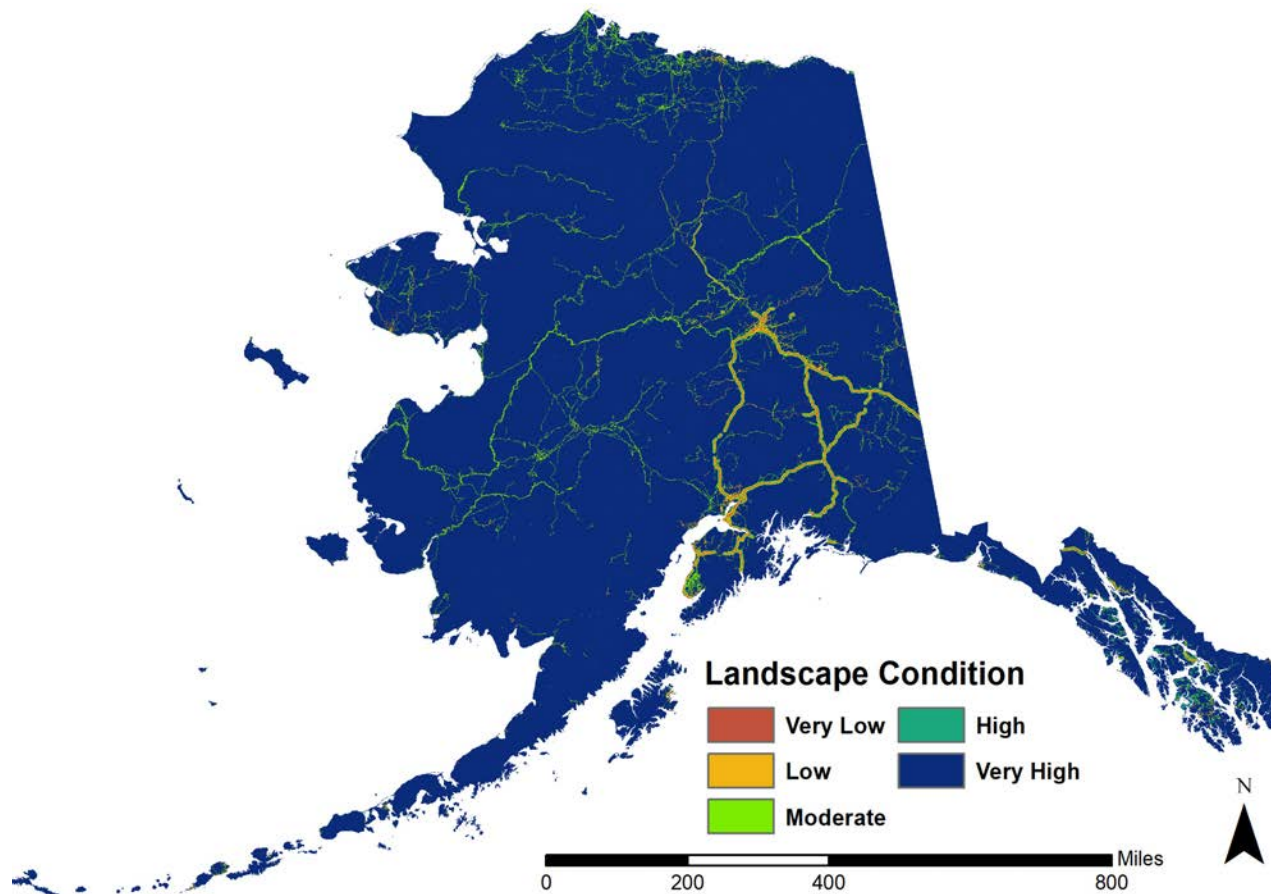
Figure 2. Landscape intactness, as modeled by the landscape condition model (LCM; Hak and Comer 2017), for Alaska. Categories represent relative intactness according to the LCM score.

not addressed here, Alaska's very limited human modification also underpins the connectivity of the state's freshwater systems, which support the seasonal migration and movement patterns of many important aquatic species (e.g., anadromous fish).

Although Intact, the Changing Climate Threatens Alaska's Ecological Integrity

In interpreting these intactness values, it is important to distinguish between the concepts of landscape integrity, as measured by intactness, and ecological integrity. Landscape integrity is a function of the structure of the landscape; the intactness

measure employed here specifically focuses on physical modification of the land surface by humans (or the lack thereof). Structure is just one component of ecological integrity, along with composition and function (Dale and Beyeler 2001, Tierney et al. 2009) and, in some conceptions, ecological processes (Wurtzebach and Schultz 2016). High intactness directly implies high retention of ecological structure. The very high levels of intactness found in Alaska are commonly interpreted as also implying high retention of ecological composition, function, and process. Thus, high intactness is often interpreted as equivalent to high ecological integrity (Theobald 2013).

The equivalence breaks down and can become misleading when other drivers of landscape-scale change, such as climate change impacts, become prominent (IUCN 2017). Specifically, the assumption that "intactness implies ecological integrity" is breaking down in Alaska where, arguably, the dominant driver of ecosystem change is not direct human modification of the landscape, but instead the rapidly changing climate (Chapin, III et al. 2014).

While a statewide focus masks regional differences, Alaska's statewide annual climate warmed twice as rapidly as the contiguous U.S. in the last 60 years (ibid). The statewide average winter temperature (December, January, February) increased from 1949 to 2012 by over 6°F (3.7°C; Bieniek et al. 2014), with all of the state's regional climate divisions exhibiting average increases of at least 3°F (1.7°C) except the Aleutians, which increased relatively little (the state's 13 climate divisions are defined by Bieniek et al. 2012). These warming trends are projected to continue (Chapin, III et al. 2014), with winter extreme temperatures expected to continue warming much faster than other climate extremes (such as summer maximum temperatures; Lader et al. 2017). In conjunction with the greatly increased

precipitation expected throughout Alaska, freezing temperatures and frozen precipitation are expected to be "… increasingly less frequent by late century" (Lader et al. 2017:2407).

Among other important observed and projected impacts of changes in climate are:

- shorter snow season and river and lake freeze-up periods, which impact seasonal migration of birds and other animals, and the northerly range expansions of species (Chapin, III et al. 2014);

- longer and drier growing seasons, with implications for shifts in major vegetation community composition and distribution, and more large fires (ibid); and

- rapidly warming (and thawing) permafrost (>56% of Alaska is underlain by permafrost vulnerable to subsidence upon thawing due to the magnitude of its ice content; ibid), leading to potentially major restructuring of landscapes due to thermokarst, subsidence, and related landform processes, including relatively rapid changes in lake and wetland spatial and size distributions (ibid).

Even in the absence of human development pressures, these climate-driven changes are impacting and will continue to impact ecosystem structure, function, and composition (ecological integrity) while not affecting intactness as typically measured. Among other effects, these changes are likely to modify landscape resistance, and therefore permeability, for many species and, ultimately, habitat suitability, undermining the interpretation of intactness as a surrogate for permeability. This highlights the need to be cautious in over-intepreting what can be inferred from high levels of intactness, and to develop measures of habitat suitability and
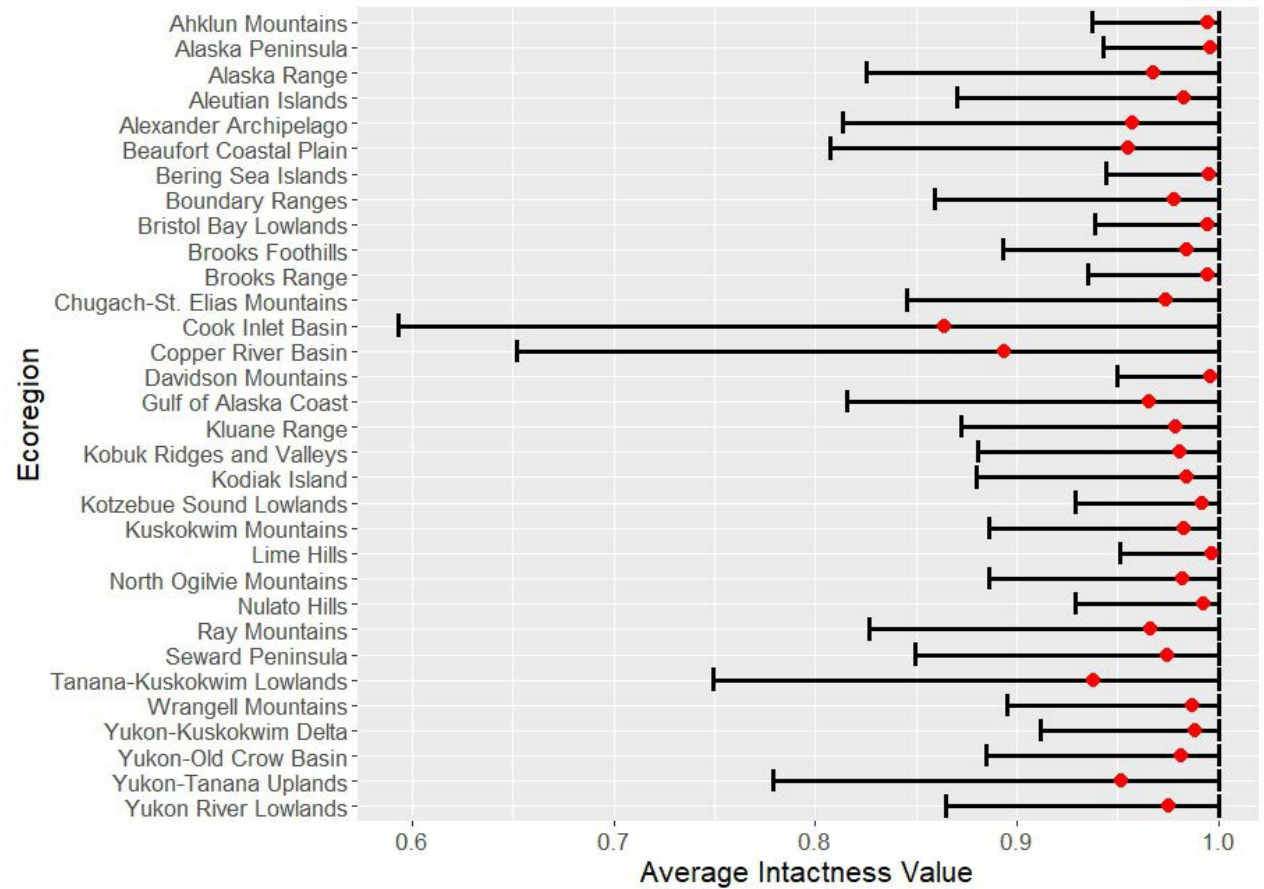

Figure 3. Average intactness, by ecoregion, as measured by the Landscape Condition Model method over a grid of cells 0.3 mile (500 meter) on a side. The dots denote the average value for all cells in an ecoregion; the lower bar denotes the standard deviation of intactness across all grid cells in the ecoregion (the upper bar is limited to not extend beyond the maximum feasible score of 1.0). All ecoregions had cells with values of 0.05 (highly modified) and some with values of 1.0 (no human modification).

permeability that account for more than just direct (and permanent) anthropogenic modifications of the landscape; for example, changes in freeze/thaw cycles, habitats shifts, and landform in part due to permafrost loss.

So while Alaska is, and will likely remain, very highly intact (as commonly measured), this provides limited understanding of variables likely to change landform processes that, in turn, are likely to increase landscape resistance and the state's future capacity to support migratory and wide-ranging behaviors of Alaskan species, let alone the state's future ecological integrity. Understanding the rate and scale of climate impacts on migration and species movements may be provided by assessing climate-connectivity potential that accounts for both landscape structure and projected rates and magnitudes of climate change (e.g., McGuire et al. 2016). While meaningful, having been developed in patch-corridor-matrix landscapes, these ideas have to be modified for relevance to the "reverse matrix"' landscapes of Alaska and other northern latitude systems (e.g., Barber et al. 2015). Developing tools for these landscapes, and the impacts on them of changing climate, is a focus of a number of active discussions among land management agencies (e.g., National Park Service, Bureau of Land Management, U.S. Fish and Wildlife Service), boundary organizations (e.g., the Landscape Conservation Cooperatives), non-governmental organizations, and university partners in Alaska and Canada.

The future of migration in Alaska depends on the capability of landscapes to support it. While we are still working to characterize the cumulative changes expected in the region's physical, ecological, and human landscape, it is clear current landscape permeability and ecosystem integrity will change. It is also clear, however, that intactness of habitats in Alaska provides an enviable foundation for ensuring

successful adaptation to those changes. It is apt that such systems are being referred to as "landscapes of opportunity" (F. Schmiegelow, pers. comm., August 19, 2017).

Fore More Information

See the Alaska Department of Fish and Game's Crucial Habitat Assessment Tool (CHAT), which uses the LCM. http://www.adfg.alaska.gov/index.cfm?adfg=chat.main#map_layers

For additional uses of and description of the LCM in Alaska, see the Bureau of Land Management Rapid Ecoregional Assessments (REAs) at: https://landscape.blm.gov/geoportal/catalog/REAs/REAs.page or http://accs.uaa.alaska.edu/landscape-ecology

For additional information on the upcoming session at the North American Congress for Conservation Biology discussing *Landscapes of Opportunity: Conserving Large Functioning Systems in Northern Canada and Alaska*, see: https://www.xcdsystem.com/scbna/program/3Rny03X/index.cfm?pgid=451

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A Golden Eagle comes in to land in Denali National Park and Preserve.
NPS photo

Alaska Park Science