The Science and Challenges of Conserving Large Wild Mammals in 21st-Century American Protected Areas

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Introduction

Five centuries ago—when Italian Cristoforo Colombo and his three Spanish ships touched the shores of the New World—bison (*Bison bison*), grizzly bears (*Ursus arctos*), and wolves (*Canis lupus*) were found from Mexico to Alaska. Cougars (*Felis concolor*) occurred throughout what would become the contiguous United States, and wolverines (*Gulo gulo*) inhabited Michigan, California, Colorado, and New Mexico. Such wildlife grandeur occurs no more. As an ecological player, bison are absent. Wolves and grizzly bears are so geographically restricted south of Canada that they are seen most frequently only within the confines of three American parks, although they do roam beyond park boundaries. Still, the days when these species commanded awe across unbridled lands are gone. The causes are obvious.

Today more than 320 million people are within the contiguous United States. Lands are crowded. Species inimical to people or to economies or requiring large spaces are not well tolerated. As protected areas become increasingly isolated, and habitats within and beyond them change, future conservation of large mammals will become progressively difficult. Enhancing knowledge and putting it into practice will require not only understanding science but understanding and then changing human behavior. On the science front, there are many unknowns, including how climate modulates population dynamics and species persistence. Coupled with such uncertainty is the reality that animals move and park boundaries do not, an onerous combination that creates conflict when lands are crowded with people. Notwithstanding the depth of ecological knowledge about systems or species, human choices determine conservation outcomes. It’s
unlikely that effective conservation structures can ever be placed without a focus on people.

In this chapter, I address three contemporary conservation challenges confronting wild mammals in US national parks—insularization, long-distance migration, and climate change. I use large mammals to underscore interest by park visitors, they play large ecological roles, and they have an uncanny ability to inspire while serving as ambassadors for conservation and biodiversity.

Specifically, I ask how conservation can be achieved given what we know empirically and what we do not know. I focus on parks within a mosaic of lands differing in public and private ownership, human population densities, and remoteness. Because of the inevitable expanding human population, I begin in the contiguous United States where a plethora of scientific studies reveals much about effects of isolation on animal population structure. Parks in more crowded environs are increasingly insular. Consequently, we find that many large mammals experience difficulties to disperse, which causes increased levels of inbreeding, reduced migration, and exacerbated conflicts with humans at or beyond park boundaries. Where immediate conservation goals are to enhance prospects for near-term population viability, changes in land use and the loss of open space are more likely to outstrip climate issues in urgency. I then shift to what is known about the reality of reconnecting populations, and use a case study about long-distance migration to illustrate building bridges across fragmented lands that vary in statutory jurisdictions and stakeholder input. Finally, I concentrate on climate challenges in protected areas of Arctic Alaska where uncertainties are great and, in contrast to the contiguous 48 states, where human populations are extraordinarily low.

Consequences of Insularization of Parks on Large Mammals

Backdrop

The US National Park Service (NPS) manages a total of more than 360,000 km², an area in size just smaller than Montana. More than half the area is in Alaska, with the remaining aggregate dispersed primarily across the conterminous United States. Together, this remaining land is approximately the combined size of Missouri and Florida.

From the perspective of large mammals, large spaces are unavailable because most parks are small. An inverse relationship exists between the
number and size of parks, with few parks sufficiently large to sustain landscape-level natural processes (fig. 9.1), as noted over the past 80 years (e.g., Wright, Dixon, and Thompson 1933; Leopold et al. 1963; Colwell et al. 2012). The mosaic of surrounding land uses has resulted in habitat degradation, loss, and fragmentation (Hilty, Lidicker, and Merenlender 2006). As a consequence, calls have been repeated for management of external events beyond protected area boundaries because these events can have dramatic effects on processes and species within parks (Keiter 2010; Austen 2011).

Concerns about park size and animal movements have been expressed since the establishment of Yellowstone National Park, even in the absence of a large number of people living nearby. In 1893, Arthur Hague commented, “Let Congress adjust the boundaries in the best interests of the Park . . . clearly defining them in accordance with the present knowledge of the country, and then forever keep this grand national reservation intact.” Two decades later, William Hornaday (1913) said, “The 35,000 elk that summer in the Park are compelled in the winter to migrate to lower altitudes in order to find grass that is not under two feet of snow. In the winter of 1911–12, possibly 5,000 went south into Jackson Hole and 3,000 north into Montana.” Today’s concerns still focus on conflicts around park
borders, but they have broadened to include the dynamics of ecological change and population viability.

Conservation evolves, and the issues of last century—overharvesting, poaching, and predator control—will not be the most pressing issues of the future. For instance, while there are 12 native ungulates that reside in NPS units, there are more than twice as many nonnative ungulates on NPS lands (Plumb et al. 2013). Invasive species, shifting communities of animals and plants, emerging diseases, and unforeseen changes will arise, just as global climate change did toward the end of the 20th century. Nevertheless, the twin threats of habitat loss due to expanding human land uses and climate change will likely be two key drivers affecting large mammals into the foreseeable future.

Management issues will always persist for parks embedded in a mosaic of private, state, and public lands. When a population becomes disconnected from other populations, its individuals often tend to suffer from the effects of isolation. Two case studies are illustrative; the first involves cougars in a dense array of human-dominated environs, and the second examines the situation facing the largest land mammal of the Western Hemisphere, the bison.

Short- to Long-Term Effects of Impermeable Landscapes

Cougars have the widest distribution of any land mammal in the New World, having once occurred across all of the contiguous United States. Populations have become isolated in different ways, but two are notable for the lessons they connote about the consequences of past persecution and modern congestion, both of which result in reduced gene flow.

About 100 years ago, the Florida panther (also called cougar) was reduced to ∼30 individuals in southern and central Florida, including Everglades National Park; the nearest neighboring population was situated in the Louisiana-Texas region (Roelke, Martenson, and O’Brien 1993). Because of high levels of mating between closely related animals, inbreeding in the Florida population resulted in spermatozoan defects, cryptorchidism, and enhanced susceptibility to infectious diseases (Roelke, Martenson, and O’Brien 1993; Culver et al. 2008). Elsewhere, cougars have similarly suffered reduced gene flow as a result of increased urbanization and the inability to cross major roadways. Populations from California’s Santa Ana and Santa Monica Mountains are relatively more isolated than elsewhere (Ernest et al. 2014). The former was characterized by a genetic
bottleneck 40–80 years ago, and now—in common with Florida panthers—each of these semi-isolated California subgroups has low genetic diversity. Kinked tails (fig. 9.2), thought to be a manifestation of inbreeding depression, have been found in both Florida and Santa Ana pumas (Roelke et al. 2003; Ernest et al. 2014).

Bison, however, are probably the best example of challenges to conserving large, wide-roaming species. Today, they occupy less than 1% of their historic range, an area stretching from northern Mexico to boreal Canada and from the Atlantic seaboard to Oregon and Washington (Sanderson et al. 2008). In Badlands and Wind Cave National Parks, bison are confined by fencing. In places like Yellowstone National Park, the fencing is virtual. When animals move beyond park boundaries for very long, they are often rounded up or shot (Plumb et al. 2009). The effect is identical to being entirely fenced.

Bison are managed as closed herds (Berger and Cunningham 1994; Halbert et al. 2007), and reproductive isolation will continue until migration is induced. Nowhere other than the contiguously situated Yellowstone
and Teton National Parks is it possible for interpopulation bison movements. Bison face the near impossibility of a reconstituted metapopulation. However, management plans to move individuals across more than a dozen federal reserves were suggested more than 20 years ago (Berger and Cunningham 1994) and are now being designed to achieve gene flow by exchange, or supplementation, of individuals (G. E. Plumb, unpublished data), as is done in zoos.

With respect to isolated populations, both cougar and bison show broadly similar responses when disconnected for generations. Cougars in California and Florida had morphological anomalies manifested by kinked tails or undescended testicles (Ernest et al. 2014), whereas bison in highly inbred lineages and in the absence of new mating partners for at least 75 years had striking limb deformities (Berger and Cunningham 1994) (see fig. 9.2), a situation that would carry strong fitness costs had predators been present. The bison condition is further complicated since cattle DNA is evident in most NPS bison populations, with the exceptions of the Yellowstone and Wind Cave herds (Halbert and Derr 2008). The body of evidence is robust—when metapopulation structure is fractured, populations increase in demographic risk (Crooks and Sanjayan 2006).

Conservation Challenges in Impermeable Landscapes and Beyond

Implementation of conservation is onerous because the human dimension is complicated and often independent of science. Experience involving wild animals—digitally or on the ground—greatly affects perceptions and tolerance. Cougars, for example, are often tolerated locally despite real dangers to people, livestock, and pets. Bison are also considered dangerous, yet they are less endured. They have potential to harm people and property (e.g., fences) and to transmit disease to livestock. The disease issue is local, as only bison in the Greater Yellowstone ecosystem carry brucellosis (Berger and Cain 1999; Plumb et al. 2009). The other issue—danger—is serious, as people have been killed by bison. Moose (Alces alces) are also dangerous, have killed more people (via attacks and collisions with cars), and are far more abundant, yet they are tolerated. In comparison, human deaths by horses and cattle in the United States average about 40 per year (Forrester, Holstege, and Forrester 2012). Now, of course, if there were more bison free roaming, perhaps there might be more frequent deaths. Nevertheless, while science dictates connectivity as a means to thwart the growing impermeability of crowded landscapes, the reality is that percep-
tions, not necessarily the facts, about species dictate what is acceptable to society.

Opinions about animal movements across both soft and hard park boundaries into porous landscapes will be further influenced by the imminent threat of danger and the size of a species, as well as its life history and status (i.e., abundant, rare, or endangered). Large carnivores like cougars or black bears (*U. americana*), or smaller carnivores such as coyotes (*C. latrans*), navigate arrays of congested private lands, roads, and other impediments including cities like Los Angeles and Chicago. Once landscapes become pervious to dispersers, the biological problems described above disappear.

As is the case with bison, large mammal movements beyond protected areas will push the limits of tolerance in some circles and will remain an issue for human dimensions, but not one lacking in ecological dimensions. While fortunately no one has died in the United States because of wolf reintroduction, livestock are killed, big game populations reduced, and some individuals feel their liberties have been abrogated. As in the bison case, perception and reality create issues when landscapes become crowded.

When little tolerance remains for ecological challenges, such as connectivity, two additional consequent challenges will grow from the insularization of large mammals. First, ungulates will attain relatively high density, especially in small NPS units where large carnivores are absent. When this occurs, vegetation structure, composition, and density are strongly affected, which can have important secondary and tertiary effects on a multitude of organisms including insects and birds (Ray et al. 2005; Ripple et al. 2015). Second, where populations remain small, vulnerability to stochastic events will increase proneness to extinction, a process exacerbated by climate change (Epps et al. 2006). Constraints associated with park size will continue to force consideration of management alternatives (Colwell et al. 2012; Plumb et al. 2013).

Corridor development continues to be suggested as a way to increase connectivity, but appreciable knowledge deficits remain and corridors will never be the panacea to enhance passage. Migratory species, like all species, can carry disease, and these in turn may increase disease risks to park resources or export them beyond park boundaries (Hess 1996). On the other hand, creating or increasing the efficiency of corridors can be a useful strategy to combat climate change by enhancing accessibility to habitats that may become suitable in the future (Beier and Gregory 2012; Hilty, Chester, and Cross 2012).
Future Prospects

Continuing pressures have further capacity to isolate populations. Energy exploration is one such pressure. On average, 50,000 new energy wells per year have been built across central North America since 2000, a pattern likely to remain (Allred et al. 2015). Another pressure emanates from expansion of human populations. While cities and towns are distributed heterogeneously and mean densities are less in the intermountain region of the United States (\(\sim 10/km^2\)) than elsewhere (22/km\(^2\) for the Pacific region, 90/km\(^2\) in New England) (US Census Bureau 2013), lands are increasingly occupied and less permeable. The conflation of roads, infrastructure, and habitat loss will continue to jeopardize abilities to ensure metapopulation structure.

A Disappearing Phenomenon—Long-Distance Migration—Requires Solutions That Meld People and Engage Stakeholders

Backdrop

Among ecological processes collapsing at a global scale is long-distance migration (Harris et al. 2009). Areas the size of the Arctic National Wildlife Refuge (78,051 km\(^2\)) and Serengeti National Park (14,763 km\(^2\)) are insufficient to capture the full range of movements of caribou (\textit{Rangifer tarandus}) and wildebeest (\textit{Connochaetes taurinus}). Smaller protected regions, including many of the national parks within the contiguous United States, fail to encompass the seasonal ranges for migrants. Pronghorn (\textit{Antilocapra americana}) are a striking model. Pronghorn occur in more than 14 NPS units, yet not one is large enough to contain their normal movements throughout an annual cycle.

The largest protected area network in the contiguous United States, the 100,000 km\(^2\) Greater Yellowstone Ecosystem, is composed of two national parks, four national wildlife refuges, and seven national forests. Yet the migrations of elk, mule deer (\textit{Odocoileus heminous}), pronghorn, and bison have been either compromised or totally lost (Berger 2004). While migrations are still being discovered and refined in this comparatively wild region (Copeland et al. 2014; Sawyer et al. 2014), the scale of collapse of these ungulate migrations across most landscapes beyond the Greater Yellowstone Ecosystem is unprecedented.
The Public Face and the Park Face

Given economic realities, serious obstacles exist to protecting ample space to ensure migration and to connect seasonal ranges or populations, including competing and growing demands on public lands and the juxtaposition of private lands in and around NPS units. If parks are to function ecologically in a coupled natural-human system, collaborative networks have to be placed across broad landscapes that are already human dominated (Machlis, Force, and Burch 1997; Colwell et al. 2012). A cadre of stakeholders readily exists when parks are embedded in crowded landscapes (Hamin 2001), and among them may be varied sectors of public and park patrons, industries, homeowners, hunters, and recreation associations, as well as nongovernmental organizations (NGOs) and state and federal managers.

There are staggering impediments to conserving broad-scale migrations, some resulting from internal NPS forces and others from externalities. No parks have inventoried the bulk of their migratory species, although much is known about ungulate migrations. Nevertheless, even on a park-by-park basis, let alone under a broader NPS umbrella, numerous pragmatic questions will need to be asked, and answered, if serious attempts will be undertaken to conserve migrations.

There are many questions about migrations relevant to the NPS (Berger et al. 2014). What should be conserved—the phenomenon of migration itself, or perhaps abundant migrations only, or maybe just the rare ones? Can lost migrations be restored? Should they? Are some NPS units more important than others to focus efforts to retain migrations? From a social perspective, how should partners be identified? Do they need to be adjacent landowners or agencies? Can they be geographically distant? How will they be involved? What role should they play?

At a smaller scale and in an area of low human population density, colleagues and I coordinated many stakeholders to facilitate the creation of the Path of the Pronghorn, the popular moniker for America’s first federally protected migration corridor, established in 2008 (Berger and Cain 2014) (fig. 9.3). Rather than focus on the science, we strategically addressed conservation needs, some of which first came forth by building partnerships and trust between government and private interests, and by enhancing interest in migratory phenomena across landscapes differing in political interests and economic bases (Berger and Cain 2014).

The creation of the Path of the Pronghorn ensured safe passage along an invariant route used by pronghorns for at least 6,000 years and through
9.3. The Path of the Pronghorn in the western United States. The federally protected portion of the corridor is on US Forest Service (Bridger-Teton) lands between Grand Teton National Park and private and Bureau of Land Management properties. Map courtesy of Steve Cain, from Berger and Cain (2014).
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three narrow topographical bottlenecks between summer ranges in Grand Teton National Park and less snowy wintering areas far south of NPS statutory authority. Impediments to the migration include fencing and energy development on crucial winter habitat (Beckmann et al. 2012), which also occurs for other ungulates reliant on portions of the same route (Sawyer et al. 2013). The entire round-trip distance for pronghorn migrating from the park and back exceeds 700 km, although most animals move shorter distances (Berger, Cain, and Berger 2006).

The Path of the Pronghorn resulted from public meetings and formal and informal collaborations involving industry, cattlemen associations, and NGOs, as well as discussions with county commissioners, the business community, and transportation departments, along with quiet support from state and some federal agencies. Ultimately, a 70 km long by 2 km wide pathway was protected by amendment of the US Forest Service Land Management Plan (Hamilton 2008), for which nearly 20,000 public comments were received by the federal government (Berger and Cain 2014). Related approaches have also been successful, including conservation easements where private lands may be disassociated from federal ones (Pocewicz et al. 2011).

**Future Prospects**

Among the central issues facing the future conservation of large mammals will be how to ensure adequate population sizes given their large spatial needs. The above subsection used one particular case study in which the human milieu and migration phenomena were juxtaposed and the conservation outcome was positive. Part of the success may have derived from Wyoming’s low population density (<2.5/km²), but other contributing factors include the availability of public land and the willingness of stakeholders to focus on common goals.

If migrations are to be conserved, whether in settings with an admixture of public acreage of relatively low human density or in more human-dominated areas with hard boundaries, lands will fall under diverse ownership and management, and successes will only derive from collaboration and bottom-up approaches. Failing this, however, other options remain. Animals can be shot when troublesome and beyond park borders. They can be trucked between areas where connections to suitable habitats have been severed. Migratory phenotypes can be selected against, and animals can be artificially sustained with food enhancements to reduce free-roaming be-
behavior. Many would argue that these solutions lack creativity or imagination. They might be correct. Conservation means creating participation and investment, building consensus, and adopting an ideology that biodiversity matters.

**Can a Cold-Adapted Mammal Persist in Arctic Parks Given Climate Change?**

**Backdrop**

Neither producers of musk nor members of the ox family, the misnamed muskoxen’s closest North American relatives are mountain goats (*Oreamnos americanus*). Muskoxen (*Ovibos moschatus*) are the largest extant ungulate whose modern distribution is exclusively Arctic (Lent 1999) (fig. 9.4). Caribou, moose, and Dall sheep (*Ovis dalli*) also occur regionally in some sectors of the lower Arctic, but their distributions also transition into sub-Arctic. In the 19th and 20th centuries, moose and caribou were widespread, occurring from temperate Canada to parts of the contiguous United States from Maine to Idaho. By contrast, muskoxen are limited to permafrost, a restriction that points to a limiting role of abiotic factors in their modern

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9.4. Muskoxen defensive formation with adult males (pictured *left* and *right*, with thicker horns) and adult female (*middle*); the young are not visible (*center*). Photo by J. Berger.
distribution. This is relevant for understanding possible limits to the maintenance of biodiversity in Arctic parks.

Key changes associated with polar environments include temperatures warming at two to three times the rates found elsewhere on Earth, which has changed ice and snow regimes, phenology of plant flowering and animal migrations, ecological community structure, species ranges, species life histories, and vital rates (Brodie, Post, and Doak 2012). Specific effects of abiotic factors on muskoxen are not well known; yet in both Greenland and northern Canada, population stability is more likely to occur when climate is cold and dry, in contrast to lower survival and population decline when climate is wet and warm (Vibe 1967). There has been an increase in rain-on-snow events, which encase vegetation in ice and cause population declines in wild reindeer (*R. tarandus*) (Tyler 2010). Biotic factors, such as disease predation or competition, may also play prominent, but as of yet undetermined, roles on population dynamics.

Muskoxen are probably the least studied ungulate of North America in part because research in remote, cold, and roadless areas is logistically complex and expensive. The species was extirpated from Alaska by the late 19th century owing to harvest, and population restoration commenced with reintroductions into the 1970s (Lent 1999).

Unlike some of the issues confronting large mammals in the contiguous United States, those in the Arctic differ in both kind and scale. Human population density is 0.5/km², 20 times less than the intermountain region of the United States with its relatively large national parks. Neither fenced boundaries nor insularization are issues likely to affect large mammals in Arctic parks, but climate change is, especially for species like polar bears (*U. maritimus*) and other ice-dependent obligates such as seals and walrus. Other increasing threats outside and within NPS statutory boundaries include roads and energy infrastructure. Conflicts between federal and states’ rights perspectives will likely continue to have impacts on biological diversity in Alaskan parks. For the largest Arctic ungulate, only now are we beginning to understand the direct and indirect challenges.

*Maintaining a Species as Ecological Conditions Deteriorate When the Science Is Uncertain*

Like in most species, muskoxen demographic patterns frequently vary; in xeric climes, hot or cold events, like drought or icing, can severely affect Arctic wildlife population growth (Hansen et al. 2013). Alaskan musk-
oxen populations differ in their population dynamics (Schmidt and Gorn 2013), and a central question is why. Understanding the relative role of humans versus that of a warming Arctic with its suite of climatic-associated factors—increased growing season length, more rain-on-snow events, and enhanced warm temperatures—will be important in designing conservation strategies. A starting point is documenting when and where population trajectories differ, and then asking what is known of possible drivers of these differences.

Muskoxen were reintroduced in the 1970s and 1980s to three sites—the Arctic National Wildlife Refuge, the Seward Peninsula, and Cape Thompson. Muskoxen numbers increased rapidly at the first two sites, and after a few years apparently did so at Cape Thompson. Trajectories diverged widely thereafter. Across a 15-year span, the Arctic National Wildlife Refuge population dropped from about 425 animals to less than 5. The massive decline apparently occurred because of dispersal beyond the boundaries of the vast 78,000 km² refuge and from predation by grizzly bears (Reynolds, Reynolds, and Shideler 2002). The extent to which weather and/or food limitation played roles in this decline was unclear.

The other two sites were established as NPS units in 1980. Neither Cape Krusenstern National Monument (CAKR) nor Bering Land Bridge National Preserve (BELA) were locales of original muskoxen reintroduction, but were colonized on their own. The CAKR population is contiguous to the north to Cape Thompson and has increased very slowly over several decades. On the Seward Peninsula, muskoxen increased for over three decades, averaging 15% per year, and the population approached ~3,000 animals, of which a portion are within the 10,916 km² BELA. This positive growth has been reversed locally, and the population has declined 4%–12% annually for a decade (Schmidt and Gorn 2013).

Given that muskoxen occur within a mosaic of state, borough, and federal lands with different management statutes, conservation efforts will require understanding (1) likely causes of population change and whether they stem from threats within or beyond NPS boundaries, (2) the extent to which potential drivers of change are locally manageable (e.g., mining or harvest versus climate), and (3) which, if any, NPS actions can facilitate persistence of this iconic cold-adapted representative of biodiversity.

In 2008, I initiated a project with Layne Adams on causes of variation in population growth trajectories in two broad locales: the Cape Thompson to CAKR region and the BELA region on the Seward Peninsula. The population from the former region had not grown rapidly and has been stagnant to declining. My present efforts with those of colleagues from 2008 to 2015
are intended to provide a basis for dialogue that crosses the bridge from science to conservation by understanding why populations differ in vital rates.

**Sources of Variation in Muskoxen Population Dynamics: From Climate to Biological Interactions**

Several interrelated drivers might explain why demographic rates at BELA and CAKR differ, including nutrition, stress, extreme climate events, parasites and disease, and predation. For instance, if food is limiting, the stagnating population (CAKR) should be characterized by individuals who are smaller, lighter, and less fecund, with other factors equal. Moreover, this population might be characterized by higher levels of glucocorticoid concentrations which signal chronic physiological stress (Sapolsky 1992; Wingfield and Romero 2001). Here the focus is on testing a food hypothesis, and I examine predictions about resource limitation based on the strong relationship between nutrition and individual growth rates in juvenile muskoxen (Peltier and Barboza 2003). An absence of differences between the BELA and CAKR animals would suggest either intersite variation in weather drivers, or perhaps biological interactions involving other community members.

Specifically, I assess muskoxen head size as a response variable and its change across different juvenile and subadult groups, pregnancy rates, and body mass because such traits are mediated by nutrition (Stewart et al. 2005). Data were derived primarily from three approaches: (1) tagging or radio-collaring more than 215 juvenile and adult females with associated measures of body mass, concentrating on areas in and adjacent to CAKR and BELA (L. Adams, unpublished data); (2) noninvasive techniques including photogrammetry (Berger 2012), from which I generated more than 700 measures of head size of one-, two-, and three-year-olds, and pregnancy and stress levels based on fecal metabolites to assess glucocorticoids (Cain et al. 2012; J. Berger, unpublished data); and (3) potential weather-related effects explored through vegetation greenness and other climatic variables. Density estimates of potential carnivore predators were unavailable.

Despite lacking pertinent information on predators and muskoxen density, the data do allow assessment of the potential role of food and

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weather—both anticipated either individually or jointly—to account for population-level variation and vital rates. A metric related to nutrition, head size, was not statistically different between the CAKR and BELA sites. Additionally, had food quality varied substantially between sites, differences in adult pregnancy rates should have occurred. Furthermore, if chronic stress induced by nutritional inadequacies or other factors (e.g., predators, inclement weather) affected one population more than the other, fecal cortisol levels should have consistently differed. None of these measures differed between populations, nor were temperature, precipitation, and NDVI (normalized difference vegetation index) associated with head sizes. These findings suggest that both populations responded similarly to weather, or that weather effects were minimal (table 9.1).

Juvenile recruitment can have strong effects on population growth, especially for species in which adult survival varies little (Mills 2012). In the western Arctic, recruitment of juvenile muskoxen was inversely related to skewed adult sex ratios, and ratios decreased 4%–12% per year across 10 years (2002–2012), as subsistence and trophy hunters harvested more males (Schmidt and Gorn 2013). While hunting by humans is legally permitted in and around both CAKR and BELA, harvest is more heavily concentrated on the Seward Peninsula including in BELA. Young animals are not taken, however, so hunting can be excluded as a direct source of the variation in juvenile survival. So, too, can the differential production of offspring, since pregnancy rates were similar in CAKR and BELA. If predation pressures, especially by grizzly bears, have changed and affect juvenile survival, they may arise as an indirect consequence of the removal of adult males (Schmidt and Gorn 2013), a hypothesis in need of testing.

What is the evidence that biological interactions might play a greater proximate role than weather in affecting growth in the CAKR and BELA populations? While weather and climate have dramatic effects on northern ungulates (Post et al. 2008; Hansen et al. 2013), including localized persistence of muskoxen (Vibe 1967; Darwent and Darwent 2004), during the period for which our data exist, population trends reversed across just a few years. Alteration of sex ratios by harvest of adult males was negatively correlated with juvenile survival. For several ungulates and primates living in mixed-sex groups, adult males are associated with defense and deterrence of predatory approaches (van Schaik and Hörstermann 1994; Fischhoff et al. 2007). Whether this is the case for muskoxen is unknown. Investigation of this hypothesis using playback models in Arctic NPS units continues, and it will enable clarification of the extent to which biologi-
Table 9.1  Summary of population change in muskoxen at two NPS sites (CAKR and BELA) and at Arctic National Wildlife Refuge, and five response variables to test a food limitation hypothesis

<table>
<thead>
<tr>
<th>Trajectory</th>
<th>Cape Krusenstern (CAKR)</th>
<th>Bering Land Bridge (BELA)</th>
<th>Arctic National Wildlife Refuge</th>
<th>Years sampled</th>
<th>Comment: CAKR-BELA contrasts</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st three decades&lt;sup&gt;a&lt;/sup&gt;</td>
<td>~8% increase/yr</td>
<td>~15% increase/yr</td>
<td>Increase, then stable</td>
<td>~15 yrs</td>
<td></td>
</tr>
<tr>
<td>Last decade&lt;sup&gt;b, c&lt;/sup&gt;</td>
<td>Stable to decline</td>
<td>Decline</td>
<td>Harsh decline</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Response Variable</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult female mass&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Similar</td>
<td>Similar</td>
<td>NA</td>
<td>4 (2009–2012)</td>
<td>Only 2009 differs p &lt; 0.05</td>
</tr>
<tr>
<td>Juvenile head size&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Similar</td>
<td>Similar</td>
<td>NA</td>
<td>7 (2008–2014)</td>
<td>No statistical differences</td>
</tr>
<tr>
<td>Subadult head size&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Similar</td>
<td>Similar</td>
<td>NA</td>
<td>7 (2008–2014)</td>
<td>No statistical differences</td>
</tr>
<tr>
<td>Stress level&lt;sup&gt;f&lt;/sup&gt;</td>
<td>Similar</td>
<td>Similar</td>
<td>NA</td>
<td>5 (2008–2012)</td>
<td>No statistical differences</td>
</tr>
<tr>
<td>Pregnancy rates&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Similar</td>
<td>Similar</td>
<td>NA</td>
<td>5 (2008–2012)</td>
<td>No statistical differences</td>
</tr>
</tbody>
</table>

Note: All populations stem from 31 founders established on Nunivak Island in 1935–1936. Descendants reintroduced to the three mainland sites between 1969 and 1981. NA = not available.

<sup>a</sup> Schmidt and Gorn (2013) and references therein; Reynolds (1998)

<sup>b</sup> USFWS, unpublished data

<sup>c</sup> J. Berger, unpublished data; NPS, unpublished data

<sup>d</sup> USGS, unpublished data

<sup>e</sup> Methods described in Berger (2012); Cain et al. (2012); J. Berger and C. Hartway, unpublished data

...cal interactions involving bears may be affecting muskoxen population dynamics independent of weather.

**Future Prospects**

Does a cold-adapted Arctic-obligate mammal have a strong possibility to persist as climate changes? Evidence so far suggests that, despite low human densities, harvest regimes may be playing an indirect role in muskoxen population declines, primarily through offtake of adult males concentrated outside NPS units. The extent to which warming temperatures and variable precipitation, as mediated by rain-on-snow events, may govern long-term survival of muskoxen is unclear. Past evidence from northern Canada and Greenland suggests warm, wet periods are challenging (Vibe 1967). If cur-
rently changing temperature and precipitation regimes are strong determinants of persistence, then immediate management may matter little.

The broader issue here is not about muskoxen per se, though their persistence as an icon of Arctic biodiversity in NPS units is of unquestionable relevance. The key matter concerns science and what we don’t know, and how one might configure a plan for long-term conservation given uncertainty about biological interactions and other factors that affect species.

Despite difficulties in predicting long-term population and climatic trends, conservation of large Arctic ungulates and carnivores, including wolves, brown bears, and wolverines, requires consideration of time frames longer than half a century and suitable habitats far beyond the boundaries of existing protected areas (Klein 1982, 1992), especially given changing fire regimes, time for vegetation recovery, and broad alteration of habitat productivity (Ferguson and Messier 2000). Where not harassed, muskoxen, caribou, and other species can flourish in areas with human infrastructure including oil pipelines and wind turbines, though these areas are perhaps less appealing from aesthetic perspectives. The challenges that large mammals face in these lightly human-populated lands in the Arctic differ from those in the contiguous United States, a place where research has added amply to understanding and resolving some of the challenges associated with large mammals in parks.

Science and Conservation Challenges as Human Populations Grow

Three decades ago key tenets of conservation biology were set forth (Soulé 1986). They included protecting multiple large areas, maintaining them with buffer zones, and connecting them when and where additional land cannot be acquired. Science gives us unassailable evidence about the often negative consequences of isolation, both through experimental and field studies. Much is known about genetics and demography. We are less confident about possible effects of climate change, although knowledge accumulates rapidly.

In the case of Arctic species, there is much uncertainty on how and where cold-adapted species may persist. Polar bears are an obvious example of an ice-dependent species in serious trouble, and where currently existing protecting areas have little to do with sustaining them at contemporary levels far into the future. Climate change here is the issue for which we as individuals may have little immediate control, a situation that dif-
fers markedly from wolves. Wolf persistence beyond the boundaries of protected areas is about human dimensions and not science per se.

The polar muskoxen case study differs substantially from our other examples in the contiguous United States, and is illustrative of how and why knowledge of biological interactions is pertinent for prudent management. Despite unfettered NPS landscapes along the Chukchi Sea and associated low human densities, human subsistence and trophy hunters may be having an important indirect effect on juvenile muskoxen survival, as mediated by the loss of large males for herd protection against predators. Conjecture, however, far outstrips empiricism in this system.

On the other hand, we know that real-world complexities—many of which involve our consumptive lifestyles and our growing human populations—prevent uniform approaches to conservation. Within the more crowded landscapes of the contiguous United States, biological corridors offer effective ways to connect populations and facilitate gene flow. Science and science communication are important, and they serve as a first step in formulating conservation planning. The critical questions need not be about our resolve, the importance of biodiversity, or human dimensions, but what we want of our future landscapes. Parks have diverse missions and one is about enjoyment for future generations.

Science is, of course, relevant to scientists, but in a complex world with more than seven billion people, it is but a single currency, and rarely is it the final arbiter in decision making. When science is fused with policy, conservation practices can be furthered. In the end, however, it is education and experience that will shape and inevitably change human values. Conservation means people. If we as scientists want conservation, we need to have parks that are relevant to people.

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