

Causes, Consequences, and Conservation of Ungulate Migration

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Abstract

Our understanding of ungulate migration is advancing rapidly due to innovations in modern animal tracking. Herein, we review and synthesize nearly seven decades of work on migration and other long-distance movements of wild ungulates. Although it has long been appreciated that ungulates migrate to enhance access to forage, recent contributions demonstrate that their movements are fine tuned to dynamic landscapes where forage, snow, and drought change seasonally. Researchers are beginning to understand how ungulates navigate migrations, with the emerging view that animals blend gradient tracking with spatial memory, some of which is socially learned. Although migration often promotes abundant populations—with broad effects on ecosystems—many migrations around the world have been lost or are currently threatened by habitat fragmentation, climate change, and barriers to movement. Fortunately, new efforts that use empirical tracking data to map migrations in detail are facilitating effective conservation measures to maintain ungulate migration.

1. INTRODUCTION

Animal migration—the seasonal movements between distinct, nonoverlapping ranges—has long fascinated ecologists and naturalists alike. Scientific investigations into the ecology of ungulate migration began over a half century ago. In the 1950s, Pruitt (1959) quantified how snow conditions prompted the movements of barren-ground caribou (*Rangifer tarandus*) across the Arctic tundra. Pennycuik (1975) was among the first to map the iconic migration of Serengeti wildebeest (*Connochaetes taurinus*) using aerial surveys to estimate seasonal movements on a 10-km² grid throughout the ecosystem. Subsequent work by McNaughton (1976) linked these large-scale, coordinated movements to vegetation phenology. Likewise, Fryxell & Sinclair (1988) mapped the seasonal movements of white-eared kob (*Kobus kob leucotis*) in Boma National Park, connecting their migration to seasonal variation in water and forage. Around the same time, studies on elk (*Cervus canadensis*) migrations in the Greater Yellowstone ecosystem were conducted using colored neckbands, allowing for individual identification throughout the year (Craighead et al. 1972). Later, the advent of radiotelemetry permitted frequent relocation of elk via triangulation from ground or air (Rudd et al. 1983) (**Figure 1**).

Today, ecological studies of migratory ungulates are burgeoning, and discoveries are accumulating rapidly. Heretofore-undescribed migrations are being revealed, particularly for ungulates that do not form conspicuous aggregations. For example, a mule deer (*Odocoileus hemionus*) in southern Wyoming, USA, exhibited a 242-mile long one-way migration across the Greater Yellowstone ecosystem (Kauffman et al. 2020). Additionally, the study of ungulate migration is generating broad ecological insights on topics including cultural transmission of movement tactics (Jesmer et al. 2018), ecosystem dynamics (Geremia et al. 2019), and impacts of climate change (Aikens et al. 2020a).

Recent discoveries made possible by modern tracking methods suggest that ungulate movements are more diverse, complex, and critical to their life histories than has been recognized (Aikens et al. 2017, Geremia et al. 2019, Joly et al. 2020, Nandintsetseg et al. 2019). At the same

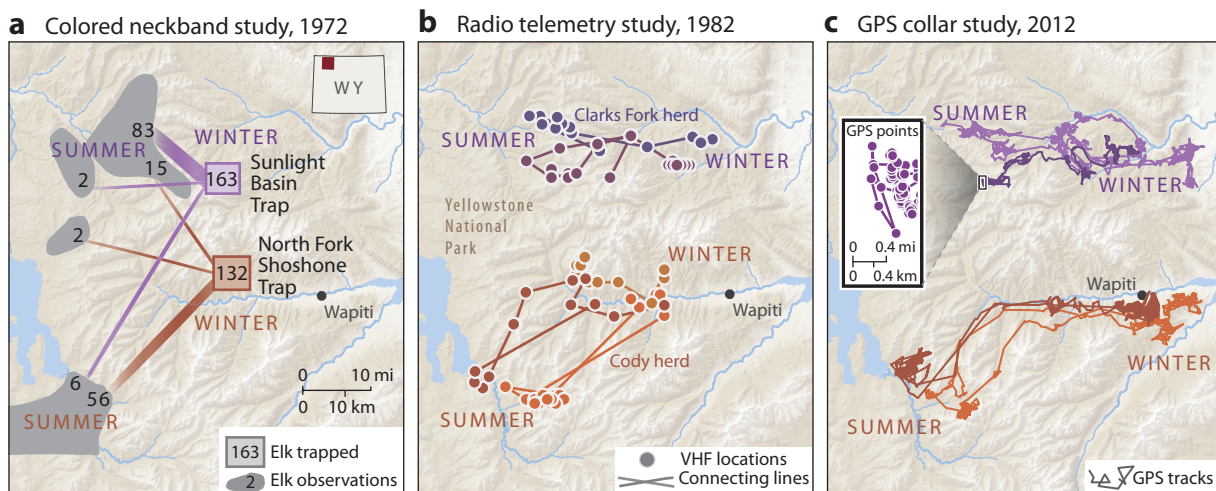


Figure 1

Advances in tracking technology have allowed migrations to be mapped with increasing precision. (a) The migration of the Clark's Fork elk herd in the Greater Yellowstone ecosystem was first mapped via resighting of colored neck bands by Craighead et al. (1972) nearly a half century ago. (b) In the 1980s, the same population was mapped via triangulation of telemetered animals, which showed approximate migration corridors (Rudd et al. 1983). (c) GPS tracking in 2012 provided a detailed depiction of the migration, including migration routes and stopover areas (Middleton et al. 2013). Abbreviations: GPS, Global Positioning System; VHF, very high frequency. Figure adapted with permission from Kauffman et al. (2018).

time, the detailed movement data for individual animals that modern tracking studies generate, combined with an enhanced capacity to quantify resources via remote sensing, have created a powerful means of studying migration ecology (Kauffman et al. 2018). Additionally, because migrating ungulates must plod hoof by hoof across increasingly human-impacted landscapes, their conservation status can serve as an early warning signal for the erosion of wildlife habitats and their functional connectivity (Middleton et al. 2020).

In this review, we seek to describe our current understanding of migration across ungulate taxa. We begin by discussing the diversity of movement strategies that fall under a broad conceptualization of migration, followed by an effort to relate movement strategies to variation in ungulate morphology, physiology, and life history. Next, we explore contemporary theories that explain why ungulates migrate, a question that has guided research for over a half century. Here, detailed tracking data are facilitating new research into the navigation mechanisms that underpin these seasonal movements. As researchers have better understood the benefits of migration, the myriad ecosystem benefits of migratory populations also are becoming clear. Amid growing recognition of their importance, many migrations around the world are in peril as the human footprint expands. Although the factors causing decline of migration are strikingly consistent across global landscapes, new research and analytical methods hold promise for catalyzing a broad range of science-based conservation efforts.

2. UNGULATE TAXA AND THEIR MIGRATIONS

We follow a traditional convention of defining ungulates as mammals that bear weight on modified nails (hooves) and thus exhibit unguligrade or (in the case of elephants, hippos, and rhinos) graviportal locomotion. This definition of ungulates is paraphyletic, including three

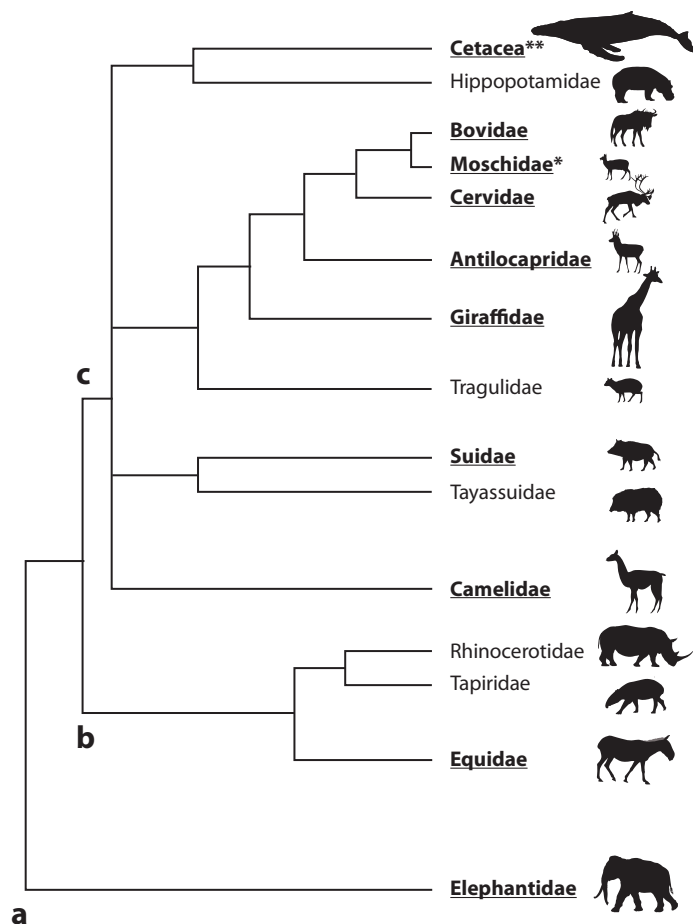


Figure 2

Phylogeny of ungulates among mammalian orders and families. Three orders are represented: (a) Proboscidea, (b) Perissodactyla, and (c) Artiodactyla. The clade containing Artiodactyla, Hippopotamidae, and Cetacea has been variably referred to as an order, a superorder, and a monophyletic clade. Families that are underlined and in bold contain species known to migrate. It is unknown whether Moschidae (asterisk) contains migratory species. Typically, Cetacea (double asterisk) is classified as an infraorder, and it contains many migratory species. Species in this group are not typically regarded as ungulates. Figure adapted from Spaulding et al. (2009) (CC BY 3.0 US). Silhouettes of Moschidae, Cervidae, Antilocapridae, and Camelidae reproduced from PhyloPic.org (<http://www.phylopic.org>) (CC0 1.0).

orders of mammals—Artiodactyla, Perissodactyla, and Proboscidea—thereby establishing that the unguligrade mode of terrestrial locomotion evolved independently on multiple occasions (Figure 2). While migrations are most pronounced in the Bovidae (hollow-horned ruminants) and Cervidae (antlered ruminants), members of the families Antilocapridae (pronghorn), Equidae (horses and relatives), Camelidae (camels and relatives), Elephantidae (elephants), Giraffidae (giraffes), Suidae (pigs), and perhaps Moschidae (musk deer) have been reported to migrate (reviewed in Wilson & Mittermeier 2011).

2.1. Movement Strategies

A diversity of strategies for migration and other long-distance movements are exhibited by extant ungulates (**Figure 3**). These are not mutually exclusive, such that populations—and even individuals—can exhibit different patterns in different seasons, years, or life stages (Aikens et al. 2020b, Estes 1966).

2.1.1. Range residency. Individuals reside in home ranges that are small relative to the range of the population. This strategy is fairly common in small-bodied (<15 kg) species that occur in forests or other dense habitats [e.g., chevrotains (family Tragulidae), duikers (subfamily Cephalophinae), dwarf antelopes (Tribe Neotragini), pudu (*Pudu* sp.)] (Wilson & Mittermeier 2011). Range-crossing times are typically short (hours or days), and there is no clear delineation of seasonal ranges.

2.1.2. Dispersal. As with most mammals, ungulates move from natal ranges to new areas, in which they establish residency, mature, and reproduce. In contrast to seasonal movements, dispersal most typically occurs only once (or a few times, at most) during an individual's lifetime.

2.1.3. Classic migration. Individuals exhibit regular movements to and from discrete seasonal ranges. Such movements are often made back and forth on the same route, but they also can occur

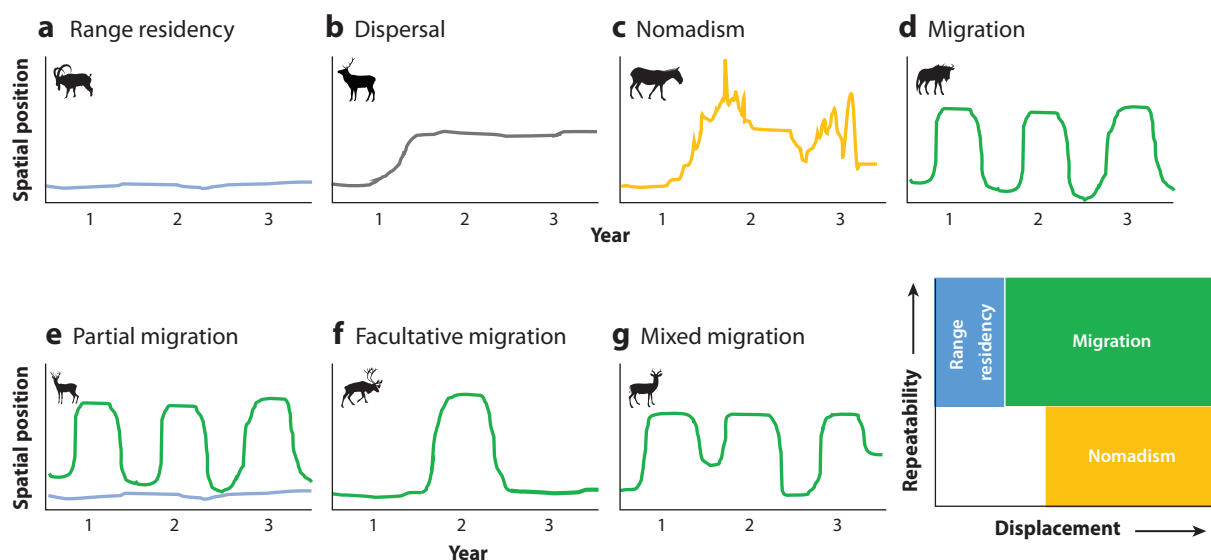


Figure 3

Typical movement patterns of ungulates. Examples include (a) range-resident Alpine ibex (*Capra ibex*), (b) male elk (*Cervus canadensis*) that exhibit dispersal movement (*Cervus elaphus*), (c) nomadic onager (*Equus hemionus onager*), (d) migratory wildebeest (*Connochaetes taurinus*), (e) partially migratory mule deer (*Odocoileus hemionus*), (f) facultatively migratory Svalbard reindeer (*Rangifer tarandus platyrhynchus*), and (g) mixed migratory white-eared kob (*Kobus kob leucotis*). Movement strategies of ungulates can be characterized along two axes: repeatability, or the predictability of movement in space and time, and displacement, measured as the movement distance. Range residency and migration are both characterized by predictable patterns of space use, but migration differs from range residency in that migrants move between spatially distinct seasonal ranges, often resulting in large annual displacement. Nomadism also results in large annual displacement but is characterized by unpredictable movements across space and time. Panels a–d adapted with permission from Teitelbaum & Mueller (2019). Elk silhouette reproduced from PhyloPic.org (<http://phylopic.org/>) (CC0 1.0).

along discrete outbound and inbound paths [e.g., wildebeest and plains zebra (*Equus burchelli*) of the Serengeti-Mara ecosystem]. Migration can occur along linear, narrow corridors or across broader expanses (Berger 2004, McNaughton 1976).

2.1.4. Long-distance migration. The most well-known form of migration in ungulates, long-distance migration occurs over hundreds of kilometers. Examples include caribou and Tibetan antelope (*Panthalops hodgsonii*) (Joly et al. 2020, Schaller 2000).

2.1.5. Altitudinal migration. Especially in more mountainous regions, ungulates move across comparatively short spatial scales, where seasonal ranges are composed of different habitats (e.g., forest versus alpine) but are in close proximity. Altitudinal migration is exemplified in wild goats (*Capra*) (Schaller 1977).

2.1.6. Facultative migration. When individuals switch between migration and range residency between years, migration is categorized as facultative. Many pronghorn (*Antilocapra americana*) populations are facultative migrants (Jakes et al. 2018a).

2.1.7. Mixed migration. Individuals migrate different distances across years or groups of individuals migrate different distances within a year. Mixed migration strategies can also occur in populations where not all individuals always migrate the same distance, as in the case of mule deer in Wyoming, USA (Aikens et al. 2017).

2.1.8. Partial migration. Many populations exhibit a mixture of migratory and resident strategies, which individuals adhere to over the course of their lifetimes. Partial migration can arise when only one sex migrates (Schaller 2000) or when migratory tendency is density dependent (Mysterud et al. 2011).

2.1.9. Nomadism. Like migration, nomadism often leads to long-distance movements that facilitate resource acquisition, but movements are unpredictable and often lack seasonality. Nomadism is usually observed in landscapes with unpredictable phenology or in response to stochastic events (e.g., fire, winter storms). Mongolian gazelle (*Procapra gutturosa*) make nomadic movements (Nandintsetseg et al. 2019).

2.2. Ungulate Life History, Adaptations, and Diversification

Frequently, ungulates are categorized along a browser-grazer spectrum. Pure browsers include species whose diets are composed of >90% fruits (duikers), forbs [e.g., bushbuck (*Tragelaphus scriptus*), klipspringer (*Oreotragus*)], or the foliage of trees and shrubs [e.g., gerenuk (*Litocranius walleyi*), giraffe (*Giraffa camelopardalis*), moose (*Alces alces*)]. Pure grazers typically are unselective and exhibit diets characterized by >90% monocots [e.g., American bison (*Bison bison*), plains zebra]. Many ungulates are mixed feeders and range from eating predominantly grass [grazer-browsers, e.g., impala (*Aepyceros melampus*)] to predominantly forbs and woody plants [browser-grazers, e.g., eland (*Tragelaphus (Taurotragus) oryx*), Thomson's gazelle (*Eudorcas thomsonii*), pronghorn]. These categorizations are most valuable as heuristics, because interpopulation variability in diets means that many species of ungulates do not neatly conform to such classifications (Gordon & Prins 2008, Kartzin et al. 2015).

The Oligocene/Miocene transition gave rise to the cervids, while during the mid-Miocene, species expanded within the antilocaprids, bovids, and giraffes. In turn, the evolution of the

ruminant stomach went hand in hand with the diversification of the Artiodactyla and coincided with the extinction of several genera of perissodactyls (Janis 1976). Several adaptations allowed ruminants to exploit vegetation, grasses in particular, in seasonal environments, including evolutionary trends toward larger body sizes in multiple lineages (Janis 2008). Two adaptive radiations brought about a transition of artiodactyls from browsing to grazing via mixed feeding, made possible by the innovation of the ruminant stomach (Cantalapiedra et al. 2014, Janis 2008). A critical advantage conferred by the ruminant stomach is its ability to efficiently convert cellulose (the structural material that gives plants their rigidity) into carbohydrates; this is achieved via microbial fermentation in the rumen before gastric digestion (Dukes 1955, Estes 1991). In contrast to ruminants, perissodactyls and elephants exhibit hindgut fermentation, in which fiber digestion is comparatively less efficient because fermentation occurs in the large intestine or cecum, after gastric digestion (Estes 1991). In sum, because the site of nutrient absorption within the gastrointestinal tract (the small intestine) occurs posteriorly to fermentation (in the stomach), ruminants more efficiently extract energy from their forage and conserve (or recycle) water compared to hindgut fermenters.

Both ruminant and hindgut fermenters exhibit migratory behavior, but to what extent are different digestive strategies linked to variation in movement strategies? Relative to ruminants, hindgut fermenters can better tolerate low-quality forage. In combination with fermentation in the large intestine (posterior to the small intestine) and an inefficient urea cycle, tolerance for low-quality forage by hindgut fermenters results in long-distance movements being driven more strongly by water availability (Esmaili et al. 2021, Redfern et al. 2003). Reliance on surface water across equid populations is likely rooted in their evolutionary history (Janis 1976). During the Oligocene, climatic conditions in the grasslands of North America—the center of equid evolution—supported relatively larger-bodied genera capable of exploiting high-fiber plants (MacFadden 2005, Muhlbachler et al. 2011). Additionally, the spread of open, dry, and seasonal grasslands during the Miocene favored the dental adaptations that facilitate feeding on more fibrous grasses (MacFadden 2005).

2.3. Effects of Body Size on Migration

In addition to the influence of digestive strategy, body size further shapes migration strategies. The smallest ungulates known to migrate (approximately 22 kg body mass) include Tibetan and Mongolian gazelle (*Procapra*), Thomson's gazelle, dorcas gazelle (*Gazella dorcas*), and roe deer (*Capreolus capreolus*); African elephants are the largest ungulate that migrates (Wilson & Mittermeier 2011). Collectively, two relationships—the isometric relationship between rumen volume and body size and the allometric relationship between metabolic rate and body size—predict higher intake of lower quality food (i.e., more fibrous forage) as body size increases (Demment & Van Soest 1985, Jarman 1974). Consequently, smaller-bodied ruminants track high-quality forage more closely than large ruminants (Merkle et al. 2016, Wilmschurst et al. 2000). Small-bodied ungulates require more energy per unit weight, have lower digestive efficiency, and exhibit more selective diets relative to their larger counterparts (Illius & Gordon 1987, Jarman 1974). Due to the higher metabolic costs of locomotion relative to the benefits, the smallest ungulates (<10 kg) do not benefit from migration and instead forage selectively on high-quality forage (Demment & Van Soest 1985). Larger-bodied ungulates are capable of moving long distances and storing energy as body fat. Although body size is likely correlated positively with probability and distance of natal dispersal (Debeffe et al. 2012), medium-bodied ungulates often migrate the longest distances (Joly et al. 2020, Teitelbaum et al. 2015). Such relative independence from body size suggests that migration

distance in some species could be related to the scale of spatial and temporal variability of forage quality (Aikens et al. 2020b).

2.4. Differences and Commonalities among Tropical, Temperate, and Polar Systems

The global distribution of ungulate migrations is driven largely by productivity, such that populations in low-productivity environments tend to travel longer cumulative distances (Joly et al. 2020). Among ungulates, body size and productivity tend to be related (albeit weakly), such that small-bodied resident species tend to inhabit more productive forests, woodlands, or other closed-canopy systems (Jarman 1974). In combination with the aforementioned influence of body size, this means that most migratory ungulates are intermediate size (>50 kg) or larger and occur in low-productivity environments with strong seasonal or spatial variation in temperature and/or precipitation (Harris et al. 2009).

3. WHY MIGRATE?

It is widely assumed that migration evolved in ungulates because individuals benefit through greater access to resources, escape from harsh seasonal conditions, and lower exposure to predators, pathogens, and parasites (Fryxell et al. 1988). These benefits are thought to enhance individual fitness relative to a resident strategy, which has led to hyperabundant populations of migrants (Fryxell et al. 1988). The strongest evidence currently relates to enhanced foraging, while the evidence that migration reduces predation and disease remains equivocal. An important caveat is that the costs of predation and disease are difficult to quantify, potentially biasing our understanding (Hebblewhite et al. 2008).

3.1. Foraging Benefits of Migration

By moving seasonally between areas, migratory ungulates enhance their access to forage that is relatively high in digestible energy and concentrations of essential nutrients (Albon & Langvatn 1992, Hebblewhite et al. 2008). These foraging benefits are particularly evident during the early growing season when vegetation is at an intermediate stage of growth (hereafter green-up), making plants easy to digest and sufficiently abundant to bolster intake (Hebblewhite et al. 2008). Plant green-up often moves like a wave across the landscape, and migratory ungulates choreograph their movements with this changing phenology (Albon & Langvatn 1992, Holdo et al. 2009), a phenomenon termed green-wave surfing (Aikens et al. 2017, Bischof et al. 2012, Merkle et al. 2016). Indeed, a recent cross-taxa analysis showed that green-wave surfing during springtime is a common feature of migratory ungulates (**Figure 4**) (Aikens et al. 2020b) and appears to increase energetic gain (Albon & Langvatn 1992), body condition (Middleton et al. 2018), and reproductive output (Hebblewhite et al. 2008). In sum, empirical studies support a clear nutritional benefit of migration, which is increasingly being linked to the ability of ungulates to move in step with gradients in plant phenology (i.e., surfing; Aikens et al. 2017, 2020b; Merkle et al. 2016).

3.2. Escape from Harsh Seasonal Conditions

Migration can also provide an escape from inclement weather or forage scarcity throughout the year. In polar and temperate latitudes, winter ranges are often characterized by milder temperatures and greater forage availability compared to summer ranges (Monteith et al. 2011). Deep snow increases energetic costs of locomotion, and accumulated snow can reduce or eliminate

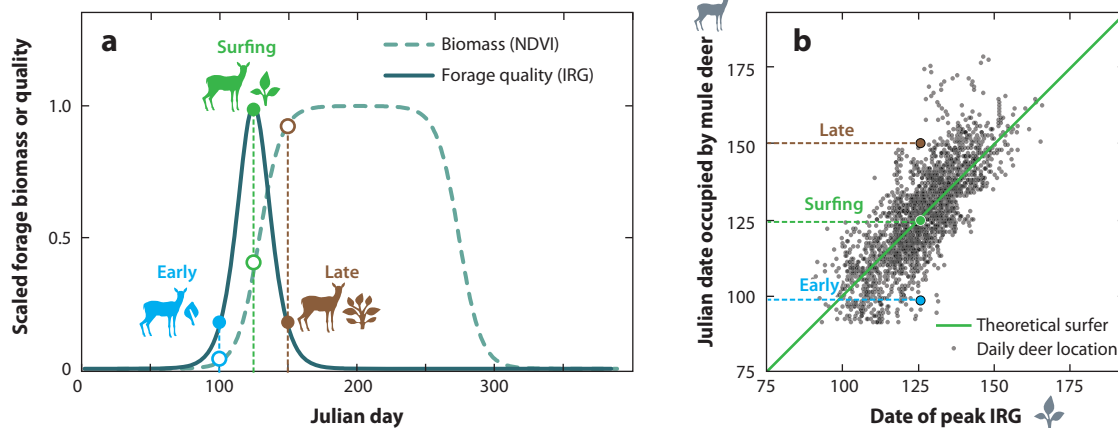


Figure 4

A growing number of studies have documented the importance of what is known as green-wave surfing for migratory ungulates, where migratory animals match their movements with changes in plant phenology that move across the landscape. (a) Bischof et al. (2012) provided a breakthrough technique that estimated the IRG (solid line) as the derivative of a double-logistic curve fit to annual time series of the NDVI (dashed line). The IRG peaks when growth in NDVI is most rapid, which is when forage quality is highest and migrating ungulates should benefit most from occupying a given foraging location. (b) Aikens et al. (2017) provided a rigorous test of the green-wave hypothesis for migratory mule deer in western Wyoming. Mule deer closely tracked peaks in IRG, providing strong evidence for green-wave surfing. Across a 2-month-long migration, daily deer locations were strongly associated in time and space with forage patches at peak IRG. The 1:1 green line of a theoretically perfect surfer is shown for reference. The closed circles in panels a and b illustrate three hypothetical scenarios of a deer using a given habitat patch during migration: early, using a patch before the date of peak green-up (blue); surfing, using a patch at the date of peak green-up (green); and late, using a patch after the date of peak green-up (brown). Abbreviations: IRG, instantaneous rate of green-up; NDVI, normalized difference vegetation index. Figure adapted with permission from Aikens et al. (2017).

access to forage (Parker et al. 1984). Indeed, the arrival of snow often triggers the autumn migration in temperate regions (Monteith et al. 2011). Living year-round on high-elevation summer ranges can have disastrous consequences (Berger 1986), although some sheep and goats do so by exploiting wind-blown ridges where snow cannot accumulate and energy expended for movement is reduced (Courtemanch et al. 2017).

In arid environments, access to water constrains ungulate distributions (Veldhuis et al. 2019), which animals mitigate through migratory or nomadic movements (Nandintsetseg et al. 2016). In African savannas and Central Asian deserts, water-dependent species can only gain access to forage when surface water is within commuting distance (Veldhuis et al. 2019). In the Serengeti, wildebeest, plains zebra, Thomson's gazelle, and common eland (*Taurotragus oryx*) graze on nutrient-rich grasses during the wet season but must migrate to the only permanent source of water—the Mara River—during the dry season (Talbot & Talbot 1963).

3.3. Escape from Predation, Parasitism, and Disease

Avoidance of enemies—namely predators, parasites, and pathogens—may shape the costs and benefits of migration. The potential for migration to buffer against or provide demographic escape from predation has been an influential hypothesis, albeit one with equivocal support (Hebblewhite & Merrill 2007). Two lines of reasoning have been proposed through which migration might dampen top-down control by predators. First, the synchronized births of migrants may constitute a resource pulse, resulting in predator swamping and enhanced survival of young. Estes (1966)

first proposed this idea, which is supported by the observations that migratory wildebeest calve in open areas (where neonates are conspicuous) and exhibit remarkable synchrony in birth timing and that young born outside the birth pulse are at greater risk of predation.

Secondly, migration might provide a spatial refuge from these effects. For example, many mammalian predators are territorial or can only commute locally because of long periods of dependence by young (Fryxell et al. 1988). Because migratory ungulates are only available for part of the year, some predator populations cannot respond numerically (Fryxell et al. 1988). Interestingly, examples exist that demonstrate the opposite pattern, in which migration exposes ungulates to increased predation (Middleton et al. 2013, Monteith et al. 2014), which perhaps recapitulates the importance of forage as a driver of migratory behavior.

Parasites and pathogens have increasingly been linked to animal migration (Altizer et al. 2011). In ungulates, migrants typically have lower parasite burdens than residents. For instance, migratory red deer in Norway had lower tick (*Ixodes ricinus*) loads than residents, and migration distance in reindeer was inversely related to infestation by warble fly (*Hypoderma tarandi*) larvae (Folstad et al. 1991). Interestingly, migratory ungulates appear to carry a higher diversity of parasites than resident species (Teitelbaum et al. 2018). Future studies would benefit from experimental approaches (e.g., anthelmintic treatments) to establish whether parasitism results in fitness costs for migratory ungulates.

4. MECHANISMS OF ORIENTATION AND MOVEMENT

How animals make decisions about where and when to migrate has fascinated scientists for centuries (Alerstam 2006). While movement mechanisms can broadly be classified as search- or memory-based (Mueller & Fagan 2008), migration likely emerges from the integration of multiple mechanisms that operate at different spatial and temporal scales.

4.1. Search Mechanisms in Migratory Movement

Because migration arises through the exploitation of resources that vary across space and time, the maintenance of migratory movements may rely on search behavior. Search-based movements can be either non-oriented (i.e., random search) or oriented (i.e., taxis along a resource gradient; Mueller & Fagan 2008). Non-oriented search relies only on information from an animal's immediate location, whereas oriented search integrates information from within an animal's perceptual range (Mueller & Fagan 2008).

Despite theoretical work demonstrating the importance of perceptual ability in shaping foraging efficiency (Fagan et al. 2017), we know little about the variation in perceptual range across ungulate taxa or how landscape characteristics modify perception (Olden et al. 2004). Theoretical work suggests that the perceptual range of individuals can be expanded by sharing information among individuals (Martínez-García et al. 2013), which may be particularly relevant for species living in fission-fusion societies. For example, by simulating resource and wildebeest movement dynamics, Holdo et al. (2009) showed that only models assuming a large (>80 km) perceptual range reconstructed the Serengeti wildebeest migration. However, it appears likely that social information or memory also plays a role (Holdo et al. 2009).

There are many empirical examples of gradient tracking by migrating ungulates. For example, a diversity of migratory species surf the green wave, often with incredible precision (e.g., Aikens et al. 2020b, Merkle et al. 2016). Some ungulates track receding snowpack to minimize the costs of moving through deep snow and ice (Laforge et al. 2021). Sawyer & Kauffman (2011) described autumn stopover behavior in mule deer, which they attributed to the need to balance access to residual forage (at high elevations) with the risk of getting caught in an early snowstorm. The

frost-wave hypothesis, which was first conceptualized and tested in waterfowl (Xu & Si 2019), could be extended to examine how migrating ungulates track the leading edge of encroaching harsh weather during autumn migration.

4.2. Memory-Based Movement

Memory mechanisms require the acquisition, storage, and retrieval of information derived from past movements (Fagan et al. 2013). Memory can be acquired through genetic programming, individual or social learning (including cultural inheritance), or a combination of genetically encoded and learned behaviors (Liedvogel et al. 2011). Recent work uncovering the critical role of memory in animal movement represents an exciting new paradigm for migration ecology (Merkle et al. 2019). For example, memory can enhance search-based movements by encoding information on the location (i.e., spatial memory) and quality (i.e., attribute memory) of previously visited sites (Fagan et al. 2013). In fact, memory is a prerequisite for systematic search of large areas (Mueller et al. 2011a). For migrating mule deer, memory and high fidelity to migration routes enhanced green-wave surfing and the foraging benefit of migration (Merkle et al. 2019). Models of movement that only included phenology tracking but excluded memory failed to reconstruct the migration routes of mule deer (Merkle et al. 2019) and zebra (Bracis & Mueller 2017). Thus, memory shapes where to go while surfing influences the timing of movements (Aikens et al. 2017), highlighting how different mechanisms of movement interact to create seasonal migrations.

4.2.1. Genetic underpinning of migration. Across the animal kingdom, memory-based movements fall along a continuum from genetically programmed to learned (Alerstam 2006). The role of genetic programming in ungulate migration has been little studied, in part due to the difficulty of controlled experiments (Bolger et al. 2008). Overall, evidence of genetic factors in ungulate migration is sparse. In birds, examples of genetically encoded memory are common in species that are short lived or migrate alone. The fact that ungulates are often long lived and migrate in groups suggest that even if genetic coding plays a role for some migrations, it is unlikely to be the sole driver.

4.2.2. Individual learning. It is often assumed that movement in ungulates falls closer to the learned end of the cognitive spectrum (Bolger et al. 2008), with knowledge acquired through individual or social learning. For example, mule deer exhibit high fidelity, suggesting a strong role of spatial memory and reliance on previous experience (Sawyer et al. 2019). For multiple ungulate taxa, studies clearly show that individuals remember both the location and quality of previously visited foraging patches (Merkle et al. 2019, Ranc et al. 2020). Because lifetime tracking of ungulates remains rare, the age at which learning occurs, and whether it results in fixed preferences for the remainder of life, is not yet known.

4.2.3. Social learning. Social interactions likely also shape how ungulates learn to migrate. Many ungulates are philopatric, suggesting that information on where to establish home ranges or migratory routes could be transferred across generations (i.e., vertical transmission) (Nelson 1998). The rose petal hypothesis formalizes this idea, suggesting that closely related females establish home ranges in close proximity to each other (Porter et al. 1991). For example, the removal of groups of related female white-tailed deer (*Odocoileus virginianus*) resulted in vacant localities for several years (McNulty et al. 1997). The extent to which migration routes are passed down from mother to offspring remains to be rigorously tested. However, bighorn sheep that were translocated into existing herds were able to learn to migrate more quickly than individuals translocated into vacant habitats, providing some evidence of social learning (Jesmer et al. 2018).

4.3. Insights from Translocations and Landscape Alterations

Translocations and rapid alterations of landscapes can often provide new insights into how ungulates acquire the knowledge of how and where to migrate. For example, the construction of veterinary fences starting in the late 1950s bisected traditional migration corridors of ungulates in Botswana. Wildebeest and plains zebra were prevented from accessing water and experienced mass die-offs (Williamson et al. 1988). Shortly after portions of the fence were removed in 2004, however, zebra started to migrate >250 km to reach the previously unavailable habitat (Bartlam-Brooks et al. 2011). Because memory appears to be the key mechanism for this zebra migration (Bracis & Mueller 2017), and because zebra live for approximately 14 years, such movement following a 36-year barrier removal suggests that either rapid exploration by zebra or genetic programming facilitated the reestablishment of migration (Bartlam-Brooks et al. 2011). In contrast, as mentioned in Section 4.2, it took multiple generations of learning and cultural transmission before translocated bighorn sheep began to establish migrations (Jesmer et al. 2018). Animal culture, in this case the culture of migration, occurs when cumulative knowledge is built up over generations of social learning resulting in iterative refinements in behavior (Jesmer et al. 2018). It seems likely that the maintenance of many ungulate migrations relies on cultural transmission.

Understanding the mechanisms that underlie migratory behavior is critical for conservation. For example, if animals must learn to migrate via cultural transmission, then the extirpation of a migratory herd represents the loss of centuries of accumulated knowledge (Jesmer et al. 2018). Efforts to restore extirpated migratory herds are likely to suffer a long-term lag in population growth, as animals must relearn how to best exploit their new environment. Thus, protecting the animals that use traditional migration routes, thereby retaining the benefits of cultural evolution, is critical to sustaining migrations.

Studying the role of memory, learning, and culture in the development and adaptive capacity of ungulate migrations is an exciting avenue for future research. Future research may benefit from building on the foundation provided by the avian literature, which predicts that culture and social learning should play important roles in the development of migration in longer-lived species that migrate in groups (Mueller et al. 2013). Although studying the movement mechanisms of ungulates is challenging, creative use of translocations and experimental manipulations are likely to continue to provide important new insights (Bolger et al. 2008) (**Figure 5**).

5. EFFECTS OF MIGRATION ON COMMUNITIES AND ECOSYSTEMS

5.1. Effects on Primary Producers and Nutrient Transfer

Migration likely facilitates the sheer abundance of ungulates on many landscapes (Fryxell et al. 1988), which has broad consequences for ecosystems. Grazing by large aggregations of migratory wildebeest can enhance light availability and increase nutrients for plants through their feces and urine, thereby maintaining grasses in a state of rapid growth (McNaughton 1979). In fact, grazing can cause a near doubling of vegetative biomass production over the course of the growing season compared to ungrazed sites (McNaughton 1976, McNaughton 1979). This effect can even facilitate grazing conditions for other migratory species; at the end of the growing season, Thomson's gazelle have been observed to graze on resprouting vegetation in areas previously visited by wildebeest (Bell 1971, McNaughton 1976). Today the widespread use of short-term, intensive rotational grazing by domestic livestock, a practice widely regarded as simulating grazing by migratory herds, is employed to bolster net primary production and restore degraded rangelands (Augustine et al. 2011).

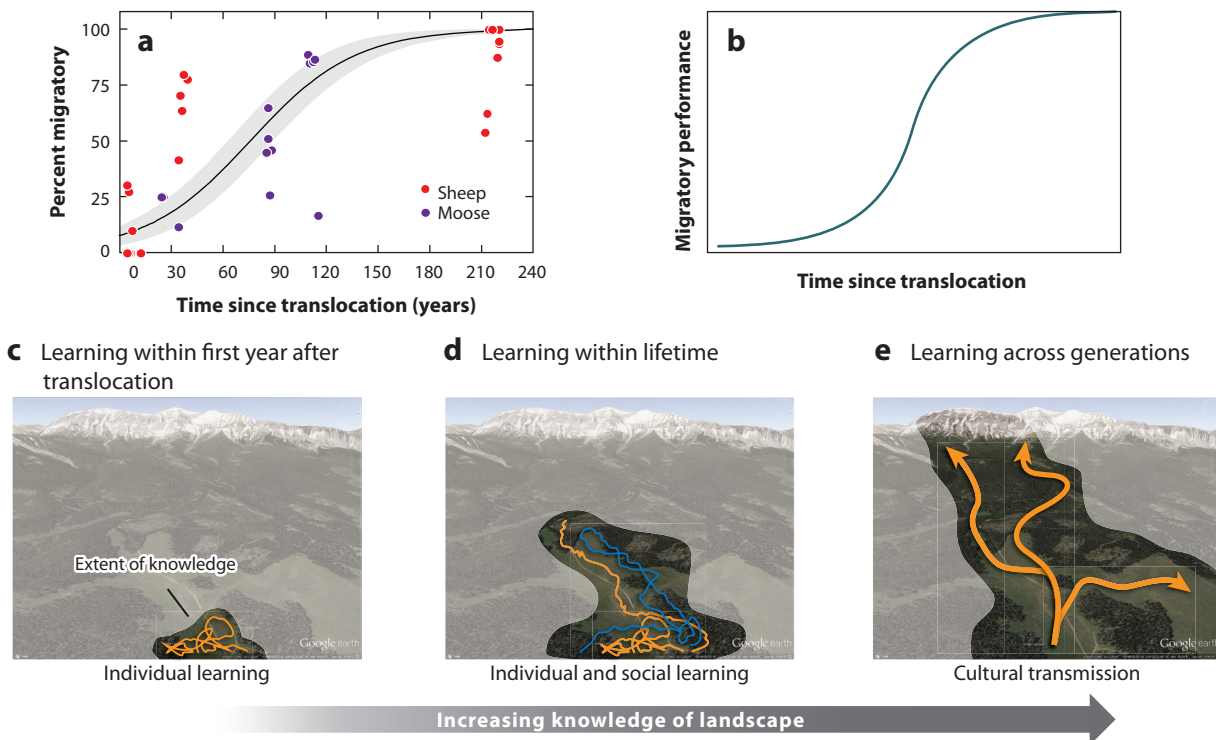


Figure 5

Using translocation and reintroductions can provide new insights into the mechanisms of migration. (*a*) For example, the first evidence that migratory knowledge may be culturally transmitted emerged from translocated bighorn sheep (red points) and moose (purple points) in the western USA, where migration propensity increased on the time scale of generations. The black line shows the fitted values of a generalized linear model, and the grey polygon shows the 95% confidence intervals. Panel *a* adapted from Jesmer et al. (2018). (*b*) Future studies may use translocations to examine whether migratory performance (including spatial memory and gradient-tracking abilities) increases over time [previously shown for reintroduced cranes (Mueller et al. 2013)]. In the absence of genetic mechanisms, spatial knowledge of the landscape is expected to (*c*) increase within the first year following initial translocation, (*d*) with individuals obtaining more knowledge of their landscape within their lifetime via individual and social learning. (*e*) Across generational times, migration corridors can develop within a population through cultural inheritance of knowledge. Population-level corridors, which describe the migratory movements of many individuals learned over time, are represented by orange arrows. Background images in panels *c–e* from Google Earth (<https://earth.google.com/>).

The grazing impacts of American bison support and extend observations from African savannas. Migrations have been lost from most of the species' range, but studies of managed herds provide a picture of their ecological impact. Bison preferentially feed on dominant grasses, which can increase the diversity of other grasses and forbs (Knapp et al. 1999). Effects of bison grazing may be amplified by urine deposition, which increases aboveground biomass and nitrogen concentration (Knapp et al. 1999). Most of these studies have been conducted on captive herds. But a recent study of bison in Yellowstone, one of the only remaining wild migratory populations, illustrates how bison—migrating and grazing in aggregate—can actively engineer a prolonged green wave at the landscape scale (Geremia et al. 2019). This work suggests that the phenology and productivity of North American grasslands may have been radically different when 30 million or more bison moved seasonally across them.

The gradual, annual progression of migratory herds across their year-round range can provide an influx of nutrients and biomass within ecosystems (Bauer & Hoye 2014, Subaluský et al.

2017). For example, in one prominent case, the annual death of an estimated 6,250 wildebeest at river crossings in the Kenyan portion of the Serengeti-Mara ecosystem contributed more than 1,000 tons of biomass to rivers, including an estimated 107 tons of carbon, 25 tons of nitrogen, and 13 tons of phosphorus by dry mass (Subalusky et al. 2017). An important research question is whether and to what extent other migrations—for example, those by barren-ground caribou across Arctic tundra, saiga and Mongolian gazelle across the central Asian steppes, and guanaco across Patagonian mountains and grasslands—have analogous ecosystem-level effects.

5.2. Food Base for Large Carnivores and Scavengers

Migratory ungulates are the primary food for many large carnivores and scavengers around the world. The African savanna typifies the role of migratory ungulates in sustaining food webs from the bottom up. Here, migratory ungulates traverse a vast landscape and diverse habitats, converting the plants they eat to animal biomass, which in turn sustains an extraordinary productivity and abundance of carnivores and scavengers (Dobson 2009). For example, carcasses of drowned animals are consumed by three species of vultures, a stork, the Nile crocodile, and three fish species (Subalusky et al. 2017). In the Greater Yellowstone ecosystem, many of the large and small carnivores and scavengers feed on elk, deer, and other ungulates when these prey are on their mountainous summer ranges; ungulates are largely inaccessible in winter, when they occupy lower elevations along the ecosystem's frontiers (Middleton et al. 2020).

5.3. Human Dimensions of Ungulate Migration

Migratory ungulates provide benefits to people through both subsistence or recreational harvest and ecotourism (e.g., Larsen et al. 2020, Middleton et al. 2020, Parlee et al. 2018). For example, caribou have been a mainstay of numerous indigenous economies and cultures for hundreds, if not thousands, of years (Parlee et al. 2018). In Serengeti National Park, there is evidence that tourism demand is driven more strongly by proximity to the wildebeest migration than price of lodging (Larsen et al. 2020). In Yellowstone National Park, the ability of tourists to see wolves and bears generally relies on their prey base of migratory ungulates, the economic benefit of which has not been quantified but is likely substantial (Middleton et al. 2020).

At the same time, the presence of migratory ungulates can bring significant costs and challenges for agricultural producers. These include crop and forest damage and competition with livestock for forage, as well as disease risk to livestock (Natl. Acad. Sci. Eng. Med. 2017). In the Greater Yellowstone ecosystem, for example, transmission of brucellosis from elk to livestock triggers mandatory quarantine and testing estimated to cost \$150,000 per 400-head of cattle (Boroff et al. 2016); smaller producers may slaughter their entire herd to avoid quarantine altogether. To our knowledge, no studies have comprehensively accounted for the costs of living with migratory ungulates to agricultural producers, much less integrated these with the broader ecosystem and societal benefits. However, recent work accounting holistically for the costs and benefits of large carnivores' presence in ecosystems may provide a useful framework (GREGG et al. 2020).

5.4. Ecosystem Services

Our understanding of how migratory ungulates affect ecological communities and whole ecosystems is still limited, mainly because of the challenges inherent in studying and manipulating such systems at vast scales. Still, drawing together available information suggests that losing migrations can result in a long-term reduction in the productivity of ecosystems as well as the diversity and abundance of species within them. For example, the loss of major migrations could reduce

plant diversity and productivity and alter patterns of plant phenology at large spatial scales (e.g., Geremia et al. 2019, Knapp et al. 1999), change fire regimes and soil nutrient cycling (Veldhuis et al. 2019), alter resources available to other organisms (e.g., Hess et al. 2014, McNaughton 1979), and eliminate the prey base on which carnivores and scavengers rely (e.g., Dobson 2009, Middleton et al. 2020). These effects can span terrestrial and linked aquatic systems and decadal time scales (Subalusky et al. 2017). From an economic perspective, the diminished abundance of migratory ungulates could result in near-term benefits for some stakeholders, particularly in agricultural landscapes, but ultimately result in a loss of biodiversity and ecosystem services with significant value for a broader array of stakeholders. For all these reasons, ecologists have repeatedly warned about the consequences of migration loss for ecosystem function and services (e.g., Berger 2004, Dobson 2009, Middleton et al. 2020).

6. DECLINE OF UNGULATE MIGRATIONS

6.1. Patterns of Decline

The loss of migratory ungulates has occurred across taxa, through time, and across geographic areas (Bolger et al. 2008, Harris et al. 2009). These losses are most apparent for ungulates migrating in aggregations over long distances but have also occurred in short-distance migrations and nomadic herds. Historical accounts of some now-extinct ungulate migrations hint at the magnitude of loss. In Southern Africa, “millions” of springbok (*Antidorcas marsupialis*) once trekked across the Karoo and Western Cape in the eighteenth and nineteenth centuries, with herds “not less than 500,000... in sight at one moment” (Cronwright-Schreiner 1899, p. 217). In North America, up to 30 million bison once roamed in vast herds across the Great Plains before being nearly exterminated in the nineteenth century (Geremia et al. 2019, Kauffman et al. 2018). In Central Asia, large herds of thousands of Asiatic wild asses or khulan (*Equus hemionus*) migrated between the vast steppe and desert regions of Kazakhstan but were extirpated by the 1930s (Bannikov 1981).

Ungulate migrations have been affected by factors that commonly diminish biodiversity: overhunting, disease, habitat loss and fragmentation, and climate change. In some parts of the world, multiple factors are rapidly changing the landscapes that migratory populations require.

6.2. Overharvesting, Hunting, and War

Contemporary examples of rapid population declines due to hunting are widespread. After the collapse of the Soviet Union, for example, uncontrolled hunting for meat and horns caused a 95% decline in the saiga (*Saiga tatarica*) population (from 1,000,000 to 50,000 individuals) in less than 10 years across Kalmykia, Russia, and Kazakhstan (Bekenov et al. 1998). While most saiga populations have been recovering since the early 2000s, the Betpak-dala population has stagnated due to a widespread outbreak of the bacterium *Pasteurella* in 2015 (Kock et al. 2018) (Figure 6a). Armed conflict has caused declines of migratory ungulates through bushmeat hunting by soldiers, destabilization of institutions that manage wildlife, and direct mortality from ordinance (Daskin & Pringle 2018). However, sometimes conflict zones can act as refuges, as was thought to be the case for large mammals that occupied habitats between warring American Indian nations when the western frontier was being explored (Martin & Szuter 1999). In South Sudan’s Boma-Badingilo ecosystem, populations of migratory white-eared kob, tiang (*Damaliscus lunatus tiang*), and Mongalla gazelle (*Eudorcas albonotata*) persisted despite a multi-decadal armed conflict in the region, with the total number of migratory animals numbering over a million (Morjan et al. 2018).

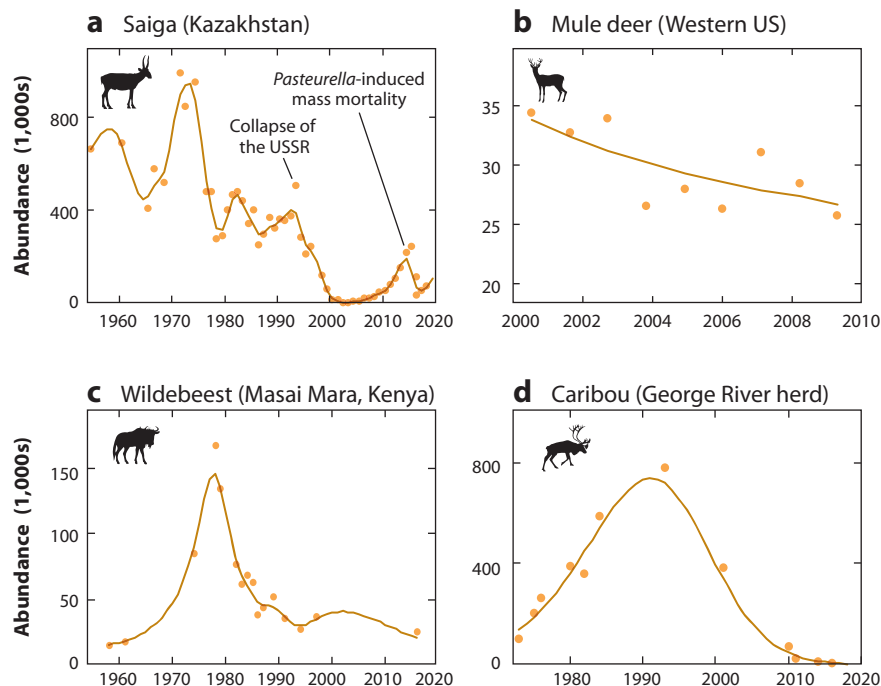


Figure 6

Numerous populations of migratory ungulates worldwide have experienced long-term declines. (a) The Betpak-dala population of saiga in Kazakhstan suffered population collapse following the fall of the Soviet Union due to unregulated harvest. (b) In the American West, the Sublette mule deer herd in Wyoming has declined by 21%, due in part to intensive oil and gas extraction in their concentrated winter range. (c) In the Masai Mara, Kenya, wildebeest have declined by 87% since the late 1970s due to habitat loss and fragmentation caused by agricultural activities. (d) Typical of many caribou across the Arctic, the George River herd has fluctuated over time but declined by 99% from its high in the early 1990s due to a combination of forestry activities and climatic changes. Trends in abundance data were modeled with General Additive Models, and best fit curves are depicted with solid orange lines. See the **Supplemental Appendix** for details.

6.3. Barriers and Habitat Fragmentation

The expansive movements of migratory ungulates make them particularly vulnerable to land-use change, such as agriculture (Msoffe et al. 2019), human settlements (Johnson et al. 2017), energy extraction (Sawyer et al. 2013), and linear-infrastructure construction (Jakes et al. 2018b). Impermeable barriers can have particularly dramatic effects. In the central Kalahari, for instance, fences erected along migratory routes of wildebeest to control disease transmission to livestock blocked access to food and water, contributing to the loss of approximately 50,000 animals during a single drought year (Williamson et al. 1988).

More commonly, habitat loss and fragmentation cause more gradual declines in demographic performance and population growth. For instance, in the Loita Plains of Kenya, agricultural intensification over the past 40 years has reduced rangeland habitat for migratory wildebeest, resulting in the loss of approximately 100,000 animals (Msoffe et al. 2019) (**Figure 6c**). Similarly, long-term monitoring of migratory mule deer in Wyoming demonstrated clear associations between the expansion of oil and gas drilling and population declines (Sawyer et al. 2009) (**Figure 6b**). It is notably difficult to identify the mechanisms underlying declines caused by such disruptions. Changes in

behavior (Sawyer et al. 2013), body condition (Johnson et al. 2017), and stress (Stabach et al. 2015) are often experienced by affected individuals. The demographic consequences of land-use change and development are thus difficult to connect to specific habitat changes, particularly for migratory populations that encounter multiple disturbances within the course of their annual movements. Threshold levels of development are particularly challenging to quantify (but see Sawyer et al. 2020). A clear research priority going forward is to establish long-term, individual-based studies of migratory ungulates in a variety of global ecosystems that can better illuminate how landscape change alters animal space use, behavior, physiology, and ultimately demographic performance.

6.4. Climate Change

The movements of migratory ungulates are fine tuned to environmental gradients that are being altered by climate change. Climatic effects are particularly evident at high latitudes and elevations (Vors & Boyce 2009). Caribou have experienced widespread, synchronous declines because of complex effects related to changing climate and anthropogenic activities (Vors & Boyce 2009) (**Figure 6d**). Earlier and more rapid ice breakup makes traveling more treacherous, as formerly frozen rivers or lakes cannot be crossed safely, leading to mass mortality events (Leblond et al. 2016). Energy expenditure may be particularly affected by ground icing from rain-on-snow events (Hansen et al. 2014) or periods of heavy snowfalls and extremely cold temperatures called dzuds (Bekenov et al. 1998). Dzuds are believed to have led to the extinction of several khulan populations throughout Central Asia (Bannikov 1981) and recently nearly wiped out a small reintroduced population of Przewalski's horse (*Equus ferus przewalskii*) in the Mongolian Gobi (Kaczensky et al. 2011). Warmer temperatures and increased precipitation in the Arctic have favored an earlier onset and increased number of biting insects. Increasingly, caribou are losing access to thermal refugia such as snow patches, which provide relief from biting insects during summer (Vors & Boyce 2009). In temperate areas, rapid spring green-up has been associated with lower pregnancy rates in migratory elk (Middleton et al. 2013) and lower calf recruitment in moose (Monteith et al. 2015). A potential mechanism for these growing-season effects was provided by Aikens et al. (2020a), who showed that drought reshuffles spatial patterns of plant green-up, making it more difficult for migrating mule deer to surf green waves of high-quality forage.

Comparatively fewer empirical studies have found population-level effects of climate change in tropical or subtropical ungulate migrations (but see Payne & Bro-Jørgensen 2016). Arid and semiarid landscapes, such as many savannas in sub-Saharan Africa, support migratory populations that are constrained by the availability of surface water and forage during the dry season (Redfern et al. 2003). Increased frequency and intensity of droughts are predicted to alter when, and for how long, migrants access different portions of their range (Duncan et al. 2012).

Although rigorous comparisons are yet to be conducted, it seems likely that migratory ungulates will be less affected by changes in weather and forage than their resident counterparts (Duncan et al. 2012). Populations with more diverse movement portfolios are likely to be more resilient to climate change (Lowrey et al. 2020). Maintaining intact migrations may be reasonably viewed as a type of climate-change mitigation that will allow animals free movement and the ability to cope with changing conditions.

7. CONSERVING UNGULATE MIGRATIONS

7.1. The Role of Protected Areas and Landscape Connectivity

Protected areas (PAs) have historically played a key role in promoting biodiversity (Gaston et al. 2008), maintaining connectivity (Santini et al. 2016), and conserving migratory species (Thirgood et al. 2004). Yet, as predicted by island biogeography theory, the size and configuration of PAs

limit their capacity for species conservation, especially for migratory species (Bauer & Hoye 2014, Brashares et al. 2001). Although some PAs like Serengeti National Park encompass areas large enough to protect intact ungulate migrations (Thirgood et al. 2004), most do not (Harris et al. 2009). For example, thousands of elk found in Yellowstone (the largest US National Park) during the summer spend their winters on unprotected private lands outside of the park (Middleton et al. 2020). Most individual Mongolian gazelles move annually across areas that are an order of magnitude larger than the region's PAs (Nandintsetseg et al. 2019). In fact, in most parts of the world, the majority of ungulates live outside of PAs in shared multi-use landscapes (Linnell et al. 2020). The recent and widespread use of movement data collected from Global Positioning System (GPS) collars has made clear that setting aside land for protection (land sparing) and maintaining habitat and landscape connectivity in the larger matrix outside of PAs (land sharing) are both critical for conservation of migratory ungulates (Middleton et al. 2020).

7.2. Mapping and Prioritizing Corridors and Other Key Areas

Recognizing that PAs alone cannot conserve migratory ungulates, contemporary conservation efforts have begun working instead at enhancing landscape connectivity across broad regions. This requires consideration of social and economic factors that influence land use and conservation value outside of PAs (Brashares et al. 2001). Conserving transboundary migrations is inherently complex because of the various, and often competing, land uses associated with multi-jurisdictional ownership (Mason et al. 2020). Nonetheless, the first step toward conservation planning for migration is to identify and map migratory corridors and other key habitats (e.g., seasonal ranges, stopovers, water sources, parturition areas) using empirical tracking data. GPS tracking technology and associated analyses now allow migration corridors and stopover habitat to be mapped and prioritized (**Figure 7**) (Kauffman et al. 2018, Sawyer et al. 2009).

7.3. Using Migration Maps to Guide Conservation on the Ground

Detailed maps can help guide conservation efforts across multi-use landscapes by identifying stakeholders, prioritizing key habitats or corridors, and providing a clear way to consider migration in land-use planning (Middleton et al. 2020). By simply overlaying migration maps with relevant spatial data (e.g., fences, roads, vegetation, land-use, etc.), many of the potential threats to migration can be identified (Kauffman et al. 2018). For example, migration maps have been widely used in the western US to target private lands for conservation easement (Tack et al. 2019)—a voluntary, contractual agreement in which private landowners forego development on their land. Migration maps have also been used to identify problematic fences to remove or modify, which is highly beneficial for migrating mule deer and pronghorn (Jones et al. 2020). Mapping migratory routes has also informed planning decisions to avoid potential effects on ungulates from forest uses (Berger 2004), road building (Dobson et al. 2010), and energy development (Sawyer et al. 2009). Growing interest in and awareness of road ecology has led to increased use of migration maps for siting wildlife crossing structures, which are often highly effective. When GPS tracking data are available, simply mapping migratory routes with empirical tracking data is among the most effective science-based strategies to inform land-use planning and conserve migratory ungulates (Kauffman et al. 2021) (**Figure 7**).

7.4. Getting Migration Corridors into Policy and Conservation Planning

Key to the conservation of transboundary ungulate populations is maintaining landscape connectivity, which requires both top-down efforts by national or state governments that can provide

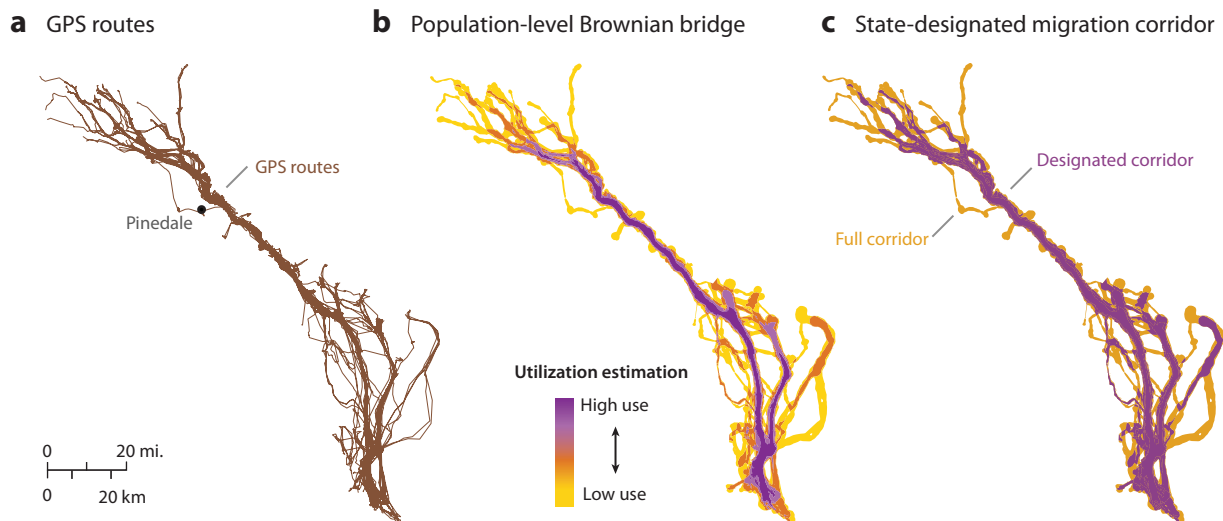


Figure 7

Migration maps built from empirical tracking data have emerged as a powerful tool for science-based conservation. (a) Consecutive GPS locations can be connected to create migration lines, which are useful for visualization of migration routes. (b) Further, researchers can use Brownian bridge movement models to estimate a utilization distribution for each individual path and combine them as a population-level corridor. (c) Such mapping can delineate low- and high-use segments of the corridor in addition to stopovers. In 2016, the Wyoming Game and Fish Department designated this corridor (*shown in purple*) as vital habitat to be managed for no net loss of functionality. Figure adapted with permission from Kauffman et al. (2018). Abbreviation: GPS, Global Positioning System.

coordination and funding and bottom-up efforts by local stakeholders that have intimate knowledge of and concern for a given migration. Importantly, migration maps are easily understood and incorporated into local, regional, and national land-use planning. In the US, for example, migration maps are used by local municipalities to develop planning guidelines to minimize impacts on migrating animals. State legislatures have drafted bills [Wildlife Corridors Act, S.B. 228, 54th Leg., 1st Sess. §1 (N.M. 2019)] and governors have written executive orders [Conserving Colorado's Big Game Winter Range and Migration Corridors, Exec. Order D 2019 011 (Colo. Aug. 21, 2019)] aimed at incentivizing the conservation of ungulate migrations. Similarly, the federal government has established programs and policies, such as Secretarial Order 3362, which directs some federal agencies to work with western US states to enhance migration corridors of mule deer, elk, and pronghorn [Improving Habitat Quality in Western Big-Game Winter Range and Migration Corridors, Secr. Order No. 3362 (Dep. Inter. Feb. 9, 2018)]. Similar policy and conservation efforts are unfolding internationally (Trouwborst 2012). For example, winter movement of khulan during the dzud of 2009–2010 (Kaczensky et al. 2011) was one of the key arguments for doubling the size of the Great Gobi B Strictly Protected Area.

The success of conservation efforts relies on decision makers having easy access to the migration data themselves. Unfortunately, it remains remarkably common for researchers, industry, or government agencies to withhold movement data for proprietary or political reasons, and we note that such approaches are a pervasive hindrance to worldwide efforts to conserve migrations. Data-sharing platforms (e.g., <https://datadryad.org>, <https://www.movebank.org>, <https://eurodeer.org>), global initiatives (<https://cms.int/gium>; Kauffman et al. 2021), and regional consortia (Kauffman et al. 2020) are promising developments that will hopefully become more commonplace.

7.5. Migratory Plasticity and Corridor Conservation

A common assumption is that animals tend to use the same routes year after year, such that protecting a route today ensures its use in perpetuity. However, recent studies have revealed that migratory plasticity in ungulates is more prevalent than previously thought (Morrison et al. 2021). For populations that exhibit highly plastic migratory behaviors, such as Arctic caribou or pronghorn, identifying where conservation efforts should be focused to ensure continued seasonal movements remains a challenge. Future research on this topic will have important conservation implications by revealing how conservation measures might account for species-specific plasticity and how behavioral plasticity affects the ability of species to adapt in a rapidly changing world (Xu et al. 2021a).

7.6. Challenges with Nomadic Species

Nowhere is the challenge of conserving ungulate movements more evident than with nomadic ungulates, like Mongolian gazelle (*Procapra gutturosa*) in Asia (Mueller et al. 2011b, Nandintsetseg et al. 2019), Thomson's gazelles in Africa (Fryxell et al. 2004), and most pronghorn in North America (Berger 2004). GPS tracking data have helped visualize the enormous range and unpredictability of nomadic movements (Joly et al. 2020, Nandintsetseg et al. 2019). Recent studies suggest wide-ranging nomadic movements are related to habitat predictability and heterogeneity (Mueller et al. 2011b) and can be triggered by extreme weather events (Kaczensky et al. 2011). Together, these data highlight the need for dynamic conservation strategies, such as mobile ranger units during critical life stages (Bull et al. 2013) or temporary road closures during mass movements (Whittington et al. 2019).

Because nomadic movements do not follow distinct migration corridors, maintaining large connected landscapes has emerged as a conservation goal, as outlined by the Convention on the Conservation of Migratory Species of Wild Animals (<https://www.cms.int/en/convention-text>) and promoted by the International Union for Conservation of Nature Connectivity Conservation Specialist Group (Hilty et al. 2020). Linear infrastructure and fences are particularly concerning for nomads (Jakes et al. 2018b), but mitigations such as roadway crossings and fence modifications can improve landscape connectivity (Sawyer et al. 2016). Fortunately, new methodologies are emerging to help identify linear features most disruptive to ungulate movement (Xu et al. 2021b). Successful conservation of nomadic ungulates depends on identifying critical habitats and linkages amid the large swaths of habitat these populations require (Nandintsetseg et al. 2019).

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Errata

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