Conserving transboundary wildlife migrations: recent insights from the Greater Yellowstone Ecosystem

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Animal migrations are ecologically, culturally, and economically important. Ungulate populations in many parts of Africa, Asia, Europe, and the Americas migrate long distances to access seasonally available resources, traversing vast landscapes in large numbers. Yet some migrations are declining, raising concerns among scientists and natural resource managers. We synthesize recent advances in ungulate migration ecology with relevance to management and policy. Using case studies from the Greater Yellowstone Ecosystem (GYE), we show how new tools can be applied to map ungulate migrations and assess threats across multiple seasonal habitats, serving as a conservation roadmap. To help conserve ungulate migrations, we also propose a transboundary science, policy, and management framework that could be adapted beyond the GYE and that encompasses the needs of multiple species. The key elements of this framework consist of more widespread mapping and assessment of migrations, improved federal and state coordination across jurisdictional lines, increased investment in private land conservation, and strong engagement of local stakeholders positioned to sustain conservation activities over the long term.

Front Ecol Environ 2019; doi:10.1002/fee.2145

Animal migrations are important to ecosystems and to society (Dobson *et al*. 2010; Bauer and Hoye 2014). Recent scientific interest in ungulate migrations has led to major advances in our understanding of their ecology, but such progress conflicts with the reality that terrestrial migrations are inherently difficult to protect because of their vast scale and transboundary nature. Indeed, many ungulate migrations worldwide are now at risk (Berger 2004; Harris *et al*. 2009).

In a nutshell:

- Long-distance migratory behavior contributes to the productivity of many ungulate populations and appears to be critically important in a number of terrestrial ecosystems
- Ungulates derive major benefits from multiple, distinct seasonal ranges, suggesting that conservation efforts must span year-round ranges
- Mapping and risk assessment provide a fundamental, if incomplete, guide for conserving ungulate migrations, and can catalyze the engagement of key stakeholders
- Leadership by and coordination between federal and state agencies are essential because these entities have the broadest geographic reach, but conservation incentives on private lands are also urgently needed

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Migratory ungulate populations depend on large landscapes to obtain resources, but humans are steadily fragmenting those landscapes and introducing competing land uses. Even the world's largest protected areas cannot fully safeguard migratory herds. For example, the 77,000-km^2 Arctic National Wildlife Refuge in Alaska encompasses only about half the range of the Porcupine caribou (*Rangifer tarandus*) herd, which is consequently exposed to industrial activity and associated risks (Griffith *et al*. 2002). Similarly, the protected areas of the Greater Serengeti–Mara Ecosystem in East Africa, which total about 16,000 km^2, cannot protect wildebeest (*Connochaetes* spp) year-round (Thirgood *et al*. 2004; Rentsch and Packer 2015), and consequently populations experience impacts stemming from bushmeat harvest, livestock grazing, and fencing (Rentsch and Packer 2015; Ogutu *et al*. 2016; Løvschal *et al*. 2017). As compared to these "high-profile" herds, many other migratory ungulates receive even less protection. In the western US, ungulates rely on land that is owned by a vast array of entities and that is managed for a multitude of uses, including mining, residential development, agriculture, and recreation. For instance, in Wyoming, thousands of migratory mule deer (*Odocoileus hemionus*) in a single population traverse public lands administered by four agencies and private lands held by 41 owners (Sawyer *et al*. 2014).

The conservation of ungulate migrations is now a rapidly growing priority for US government agencies and conservation organizations. For example, in 2018, the Secretary of the Interior directed the Bureau of Land Management (BLM), the National Park Service (NPS), and the US Fish and

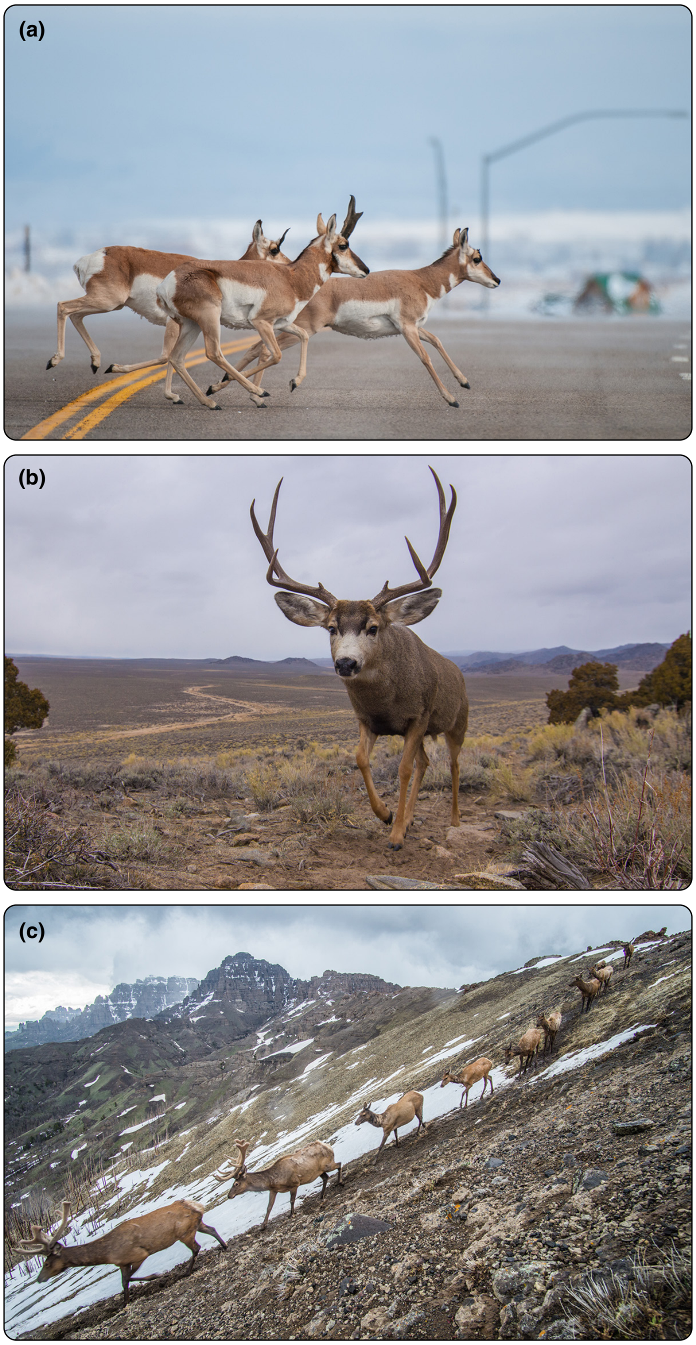

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Figure 1. (a) Pronghorn (*Antilocapra americana*), (b) mule deer (*Odocoileus hemionus*), and (c) elk (*Cervus canadensis*) on their seasonal migrations in the Greater Yellowstone Ecosystem (GYE).

Wildlife Service to work with states and private landowners to increase the protection of migratory elk (*Cervus canadensis*), mule deer, and pronghorn (*Antilocapra americana*) (DOI 2018). In addition, individual federal agencies, such as the NPS, have identified the conservation of migrations as a long-term priority (eg NPS 2012). At the state level, the Wyoming Game and Fish Commission recently adopted a strategy to designate and minimize impacts on ungulate migration corridors (WGFD 2016). Although federal administrative actions can have limited durability and many states still lack specific policies on migrations, these actions indicate a growing concern for migratory ungulate populations in the western US, and may serve as models for future efforts. Given the scale and complexity of ungulate migrations, the success of management and policy – both now and in the future – will likely depend on a strong scientific foundation.

Here, we synthesize insights from recent studies of ungulate migration that are highly relevant to policy and management. We show how detailed tracking can be used to map migrations, identify important habitats, assess conservation needs and opportunities, and engage stakeholders. Drawing on case studies in the Greater Yellowstone Ecosystem (GYE; Figures 1–3), we identify emerging research needs and suggest key elements of a framework for conserving ungulate migrations. Although rooted primarily in the GYE, our insights may be pertinent to many other regions of the world where ungulates traverse large landscapes and complex administrative boundaries.

Advances in the study of ungulate migration

In the past decade alone, global positioning system (GPS) tracking technology has led to the discovery of the longest-known ungulate migrations in both Africa (Naidoo *et al.* 2016) and western North America (Sawyer *et al.* 2016). Coupled with advances in remote sensing and computational analysis, this revolution in tracking technology has led to breakthroughs in several areas of ungulate migration ecology. Key among them are (1) the identification of linkages among migration, population performance, and ecosystem function; (2) recognition of the functional value of each seasonal habitat; (3) the mapping of migration corridors for conservation; and (4) improved understanding and assessment of human impacts on migrations.

Linkages among migration, population performance, and ecosystem function

Society has long valued mass migrations of animals for many reasons, but new research is bringing their ecological importance to the forefront. In ungulates, these advances are rooted in early, seminal studies in the African savanna, which proposed that migratory behavior evolved mainly as a means to access high-quality forage and temporarily escape from predators (Fryxell and Sinclair 1988). Since then, tests of the "forage maturation" and "green wave" hypotheses in elk and mule deer have confirmed that prolonged access to high-quality forage is a key benefit of seasonal migration (Hebblewhite *et al.* 2008; Aikens *et al.* 2017). Importantly, this foraging advantage may help migrants attain greater nutritional condition (eg body fat levels; Middleton *et al.* 2018) and reproductive success (Hebblewhite *et al.* 2008; Rolandsen *et al.* 2017) than their resident (ie non-migratory) counterparts. These observations support the contention of Fryxell *et al.* (1988) that ungulate migration underpins population productivity and abundance. In turn, this abundance has broader effects within food webs, such as sustaining large carnivores (Dobson *et al.* 2010) and fueling cross-ecosystem nutrient subsidies; an example of such a subsidy is when carcasses of drowned terrestrial ungulates (wildebeest) provide nutrients for aquatic scavengers or decompose in rivers, thereby releasing carbon, nitrogen, and phosphorus into the environment over time (eg Subalusky *et al.* 2017). For these reasons, reductions in or the complete loss of ungulate migrations is now seen as potentially catastrophic for some ecosystems (Dobson *et al.* 2010; Løvschal *et al.* 2017). Furthermore, studies highlighting ungulate migrations across the steppes, grasslands, and forests of Asia, Europe, and the Americas (Berger 2004; Harris *et al.* 2009; Kauffman *et al.* 2018) demonstrate how this ecological phenomenon – and consequently its broader impacts for populations and ecosystems – may be far more widespread and fundamental than previously recognized.

The functional value of each seasonal habitat

In North America, it was traditionally believed that the ungulate winter range is a singularly important, limiting habitat and that the migration corridor is simply a path for movement between seasonal ranges; in contrast, the ungulate summer range has received relatively little attention. However, studies have indicated that some areas within migration corridors are very heavily used as stopover sites for feeding or resting by ungulates (Sawyer and Kauffman 2011). Moreover, in spring, ungulates may intentionally pace their movements through the corridor to track greening vegetation, a behavior known as "green-wave surfing" (Bischof *et al.* 2012). Species as diverse as wildebeest (Holdo *et al.* 2009), mule deer (Aikens *et al.* 2017), and red deer (*Cervus elaphus*) (Rivrud *et al.* 2016) all appear to track annual patterns of vegetation green-up, at least to some degree, during migration; some mule deer spend as much as one-third of the year feeding in the migratory corridor (Sawyer *et al.* 2016). As a consequence, investigations have demonstrated not only that migration corridors, like other seasonal ranges, contain habitats that contribute to the annual nutritional cycle but also that the summer range is critical to the nutrition, reproduction, and overwinter survival of ungulates (eg Middleton *et al.* 2013, 2018). This new appreciation of the summer range compounds the importance of corridors because the loss of a migratory corridor translates into the loss of access to critical resources on the summer range. For these reasons, there is now consensus that conserving ungulate migrations requires conserving year-round ranges.

The mapping of migration corridors for conservation

Historically, researchers attempting to map migrations were limited to "connecting the dots" between a handful of successive animal locations obtained by tracking ear-tagged or VHF-collared individuals (eg Craighead *et al.* 1972). In contrast, fine-scale GPS data and other observations can now be combined with various analytic methods to generate probabilistic measures of corridors (Flemming *et al.* 2016; Bond *et al.* 2017). These capabilities represent a breakthrough for management and policy because they provide a spatially explicit footprint of a corridor, a product that is easily incorporated into planning processes. Added benefits for planning include distinguishing corridors that receive high versus low use (eg Sawyer *et al.* 2009), determining fidelity to corridors over multiple years (Wyckoff *et al.* 2018), and discerning corridor breadth.

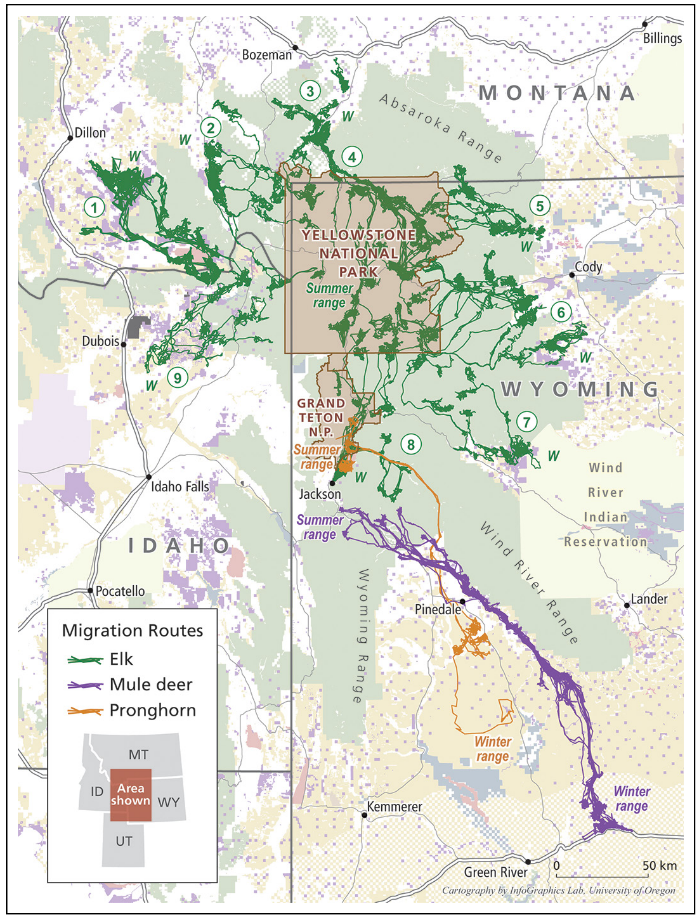

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Figure 2. The long-distance migrations of representative individuals within focal pronghorn (orange), mule deer (purple), and elk (green) populations in the GYE. The base layer in this map shows land ownership; the jurisdictional profiles for each population are detailed in Figure 3. Note that the migrations depicted here are only those highlighted in the main text, and that many other migrations that have been documented in the same geographic region are not shown.

Understanding and assessing human impacts on migrations

New GPS tracking and analytic capabilities have also greatly improved researchers' ability to evaluate human influences on ungulate migration. For example, migratory mule deer actively avoid natural-gas well pads and roads on their winter

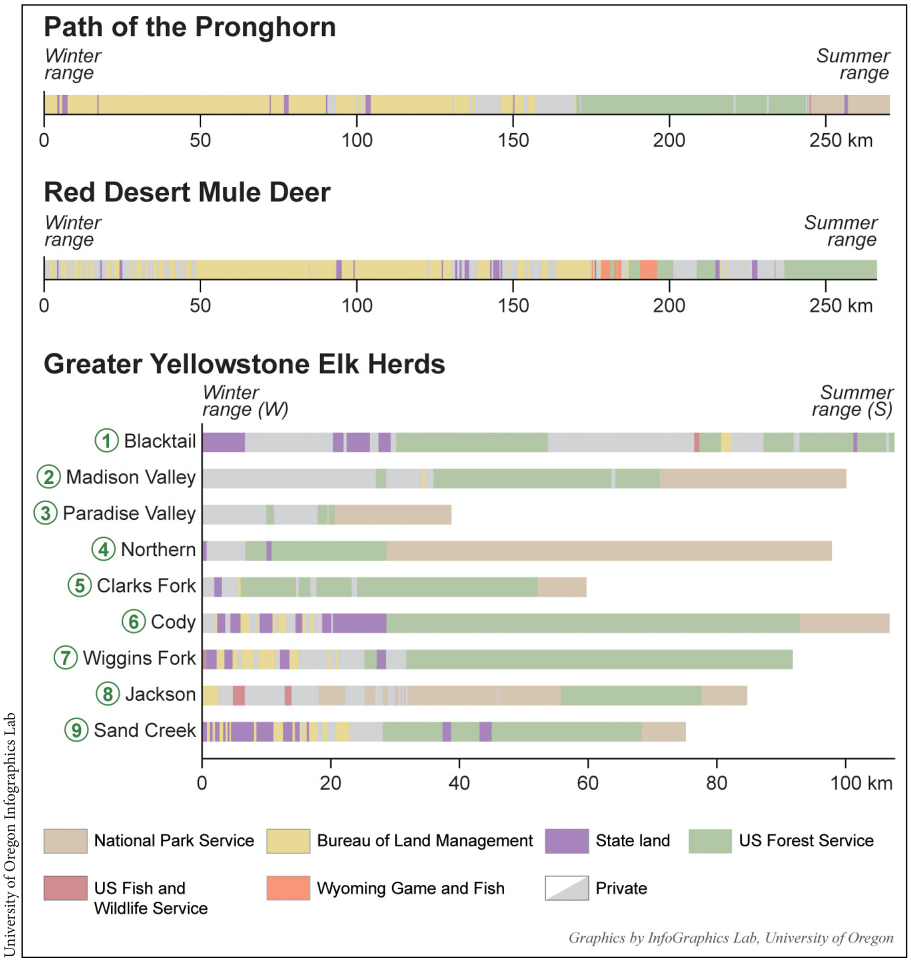

Figure 3. Land ownership within key pronghorn, mule deer, and elk migratory routes in the GYE, illustrating that broad migrations depend on policy, management, and stewardship of the same group of actors but that the importance of each can vary markedly.

range, and these individual risk-avoidance behaviors have been associated with population declines in certain areas (Sawyer *et al.* 2017). Likewise, studies tracking mule deer through mapped corridors have shown increased movement rates (Lendrum *et al.* 2012; Wyckoff *et al.* 2018) and reduced stopover use (Wyckoff *et al.* 2018) over multiple years of expanding energy development. Such behavioral adjustments likely incur energetic and/or foraging costs (Sawyer *et al.* 2013). The high fidelity of mule deer to seasonal ranges and corridors may explain the strength of their responses and associated costs (Sawyer *et al.* 2019). In contrast, other ungulates exhibit greater behavioral flexibility (Eggeman *et al.* 2016), which may lessen their vulnerability to some disturbances. At the same time, the importance of learning and cultural transmission to the persistence of ungulate migration has become clearer (Bracis and Mueller 2017), suggesting that corridors are maintained through cumulative herd knowledge that may not be readily re-learned once lost (Jesmer *et al.* 2018). If so, caution may be warranted when contemplating development activity in the habitats of migratory ungulates. The need to visually compare migrations with current and future development activity and to balance competing land uses highlights the value of "migration assessments" to guide planning (Panel 1).

Ungulate migration as the pulse of an ecosystem

The GYE provides a good example of this scientific progress and its conservation implications. In this vast landscape encompassing ~80,000 km^2, six species of large ungulates – pronghorn, mule deer, elk, bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), and bison (*Bison bison*) – migrate seasonally over distances of up to 240 km (Kauffman *et al.* 2018). Research in the GYE has led to unexpected discoveries of previously unknown migrations, discussed the ecological and cultural roles of migration, and piloted new approaches to migration assessment. We present case studies of three of these species – pronghorn, mule deer, and elk – to illustrate the progress that has been made to date (Figures 1–3). These cases represent only a few of the migrations that occur in the GYE but are instructive because they are particularly well understood.

Pronghorn

One of the first migrations in the GYE to be mapped in detail was that of 300–400 pronghorn that move 150 km between winter range in the Green River Basin and summer range in Grand Teton National Park (GTNP) (Figures 2 and 3). During this migration, the population exhibits high fidelity to a narrow corridor across mixed land ownership (Figures 2 and 3), including three bottlenecks less than 1-km wide (Berger and Cain 2014). In the decade after the mapping of this corridor, which is now known as the "Path of the Pronghorn" (POP), researchers went beyond peer-reviewed publications (eg Berger 2004) to communicate with media organizations and stakeholder groups spanning governmental agencies, non-governmental organizations (NGOs), and industry (Berger and Cain 2014; Kauffman *et al.* 2018). This combination of science and outreach led to numerous conservation actions over many years. For instance, the US Forest Service (USFS) established new protections for a 60-km segment of the migration corridor that passes through USFS lands (Berger and Cain 2014). The Wyoming Department of Transportation built a series of wildlife overpasses and underpasses at sites where the corridor crosses a major highway (Berger and Cain 2014). Land trusts and NGOs retrofitted fencing to allow safer wildlife passage and secured conservation easements to protect private lands from development (Kauffman *et al.* 2018). The POP case has increased public support for

Panel 1. Migration assessments

The purpose of a migration assessment is to package useful information about a specific migration route in a form that is accessible to diverse stakeholders. To assemble a migration assessment, empirical movement data are used to identify migratory routes of a particular herd or population, which are then compared visually with relevant landscape information collected via remote sensing and/or field surveys. These landscape data will typically include, at a minimum, land ownership, land use, roads, and fencing, but may vary with context. For instance, rapid energy development or invasive grasses may pose an acute threat to a population's migration, necessitating special map layers. The assessment process clearly inventories risks to the migration, such as proposed developments, changes in land use, or problematic fences. Land ownership and land-use information also reveal potential management and policy options. For example, the available options for increasing protection of a corridor will depend on whether the land is private or public, and what sorts of land uses the area supports. Finally, and importantly, an assessment holds the potential to catalyze new stakeholder engagement and partnerships by illustrating how the migration intersects their property or land-use interest. An assessment can be distinguished from a peer-reviewed report by its focus on a specific corridor or landscape; adoption of a writing style and graphic format that is understandable by non-specialist audiences (Figure 4a); a comprehensive discussion of potential threats (Figure 4b); and attention to a stakeholder audience that lives, works, and manages land along the corridor.

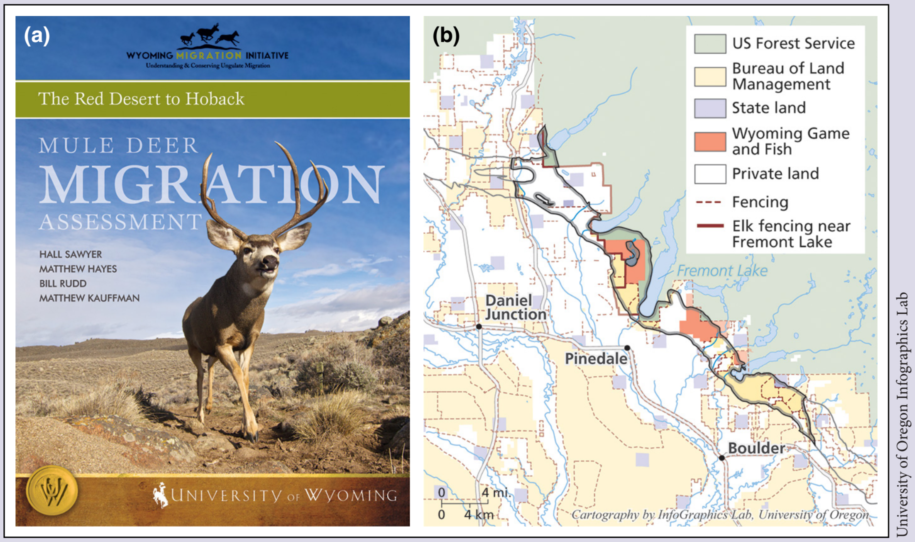

Figure 4. This migration assessment (a) was specifically written and illustrated for a non-specialist audience, (b) to map migrations and evaluate land-use trade-offs and potential threats. For example, in (b), a small segment of the Red Desert to Hoback mule deer migration corridor is shown with land ownership and fence data. At center, following publication of the assessment and subsequent stakeholder processes, a bottleneck crossing a small triangle of private land between a man-made reservoir (Fremont Lake) and the town of Pinedale, Wyoming, was identified and protected by state government. In addition, nearby fencing to keep wintering elk off private lands was identified as hindering mule deer movement, and so gates in the fencing now remain open during migratory periods.

corridor conservation and, in particular, public understanding of how land uses – such as energy development (Berger and Cain 2014) – in distant locations could impact what visitors experience inside protected areas 100 km away. As such, this migration has been the subject of substantial conservation activity over the past 20 years, although many pressures remain, including those from energy (https://bit.ly/36PklQm) and residential (https://bit.ly/2rkvF6K) development.

Mule deer

Researchers have documented numerous mule deer migrations in the GYE. Particularly notable was the discovery that several thousand mule deer, which had been thought to reside year-round in southern Wyoming, actually summered as far as 240-km north in the mountains of the GYE (Figure 2; Sawyer *et al.* 2014). This migration, known as the "Red Desert to Hoback" (RDH) migration, traverses a mix of federal, state, and private lands, and is now recognized as one of the longest terrestrial migrations in the contiguous US (Figures 2 and 3). In the years following this discovery, scientists consolidated RDH research and outreach into a single, magazine-style "migration assessment" to inventory threats and land-use patterns (Panel 1 and Figure 4; Sawyer *et al.* 2014). The assessment divided the migratory corridor into five segments, and investigated current conditions and constraints on connectivity in the corridor. It concluded with a "top-ten list" of threats, which included bottlenecks at risk from residential development, risky highway crossings, and problematic fencing. Mapping coupled with an aerial survey of fences revealed that long-distance RDH migrants crossed, on average, five highways and 171 fences per year (Sawyer *et al.* 2016). The RDH assessment has since been used by governmental agencies and NGOs to coordinate conservation activities, including the state's acquisition of a 1.5-km^2 parcel of land – previously slated for development of lakeside cottages – over which 5000 mule deer migrate through a 400-m bottleneck. The assessment also helped to motivate inclusion of migration corridors in Wyoming's list of "vital" wildlife habitats, elevating their importance in federal land-use planning (WGFD

2016). The completion of risk assessments is now a primary component of Wyoming's migration policy.

Elk

Elk populations in the GYE have received substantial research and management attention over many decades, with the migrations of several major herds having been first mapped almost half a century ago (Craighead *et al.* 1972). However, technological limitations and imposing terrain constrained more detailed research until recently (eg White *et al.* 2010; Middleton *et al.* 2013; Cole *et al.* 2015). Aggregated GPS data show how numerous major herds move annually between high-elevation summer ranges in core areas and low-elevation winter ranges near GYE frontiers (Figure 2; Rickbeil *et al.* 2019). These year-round ranges encompass an area approximately five times the size of Yellowstone National Park (YNP; Figure 2). Elk are particularly important in and immediately around YNP and GTNP because they are highly visible; highly valued by wildlife-watchers, recreational hunters, and commercial hunting guides; and are critical resources for carnivores and scavengers, including grizzly bears (*Ursus arctos horribilis*) and wolves (*Canis lupus*). In the autumn, these elk herds generally leave protected areas and wilderness areas for multiple-use lands held by the USFS, BLM, state agencies, and private landowners. Once settled on their winter ranges, some herds spend as much as 80% of their time on private land. These multiple-use lands are used variously for conservation, livestock grazing, energy development, timber harvest, and recreation; although some of the private lands are protected by conservation easements, most are not. In addition, the proportion of long-distance migrants in some partially migratory herds in the GYE appears to be declining (White *et al.* 2010; Middleton *et al.* 2013; Cole *et al.* 2015), although it is not clear to what extent natural causes (eg predation, periodic drought) versus anthropogenic changes are driving these declines. Near the GYE frontier, irrigated hayfields may provide resident elk populations with a competitive advantage, or incentivize migrants to become resident (Middleton *et al.* 2013; Barker *et al.* 2019). Lower carnivore numbers caused by hunting and lethal control to protect livestock, combined with limited elk hunting access on some private lands, may compound the benefits of a resident lifestyle (Haggerty and Travis 2006; Middleton *et al.* 2013).

Lessons learned

Collectively, these three cases demonstrate that even in one of the world's most iconic, best-protected, and well-studied landscapes, the importance of ungulate migrations was largely overlooked until relatively recently. The pronghorn case reveals the long-term commitment and diverse conservation approaches that are required to conserve migratory ungulates. The mule deer case suggests major migrations may yet remain unknown but that once these are documented, stakeholders can make quick use of accessible, applied research. Finally, the elk case illustrates the critical importance of private lands to migrations, and even to the ecological integrity of large national parks and wilderness areas.

What now? Accelerating transboundary science, policy, and management

Recent studies highlight the importance of migratory behavior to ungulate populations and ecosystems, the roles of multiple seasonal habitats in sustaining migrations, the vulnerability of migrations to disturbance, and the potential of migration assessments to catalyze stakeholder engagement. Research demonstrates that ungulate migrations in the GYE may be truly critical to ecosystem integrity at large scales, particularly in the western US. Although some emerging policies include components geared toward their conservation (eg WGFD 2016; DOI 2018), ungulate migrations in the US still do not generally benefit from explicit, coordinated policy and management encompassing their year-round habitats. We suggest that current and future efforts to conserve ungulate migrations will benefit from innovation in four key areas.

One of the most important areas for innovation is the mapping and assessment of migrations, an approach that has met with some success in the GYE (Panel 1). For instance, during a recent increase in federal mineral leasing, the visual, map-based comparison of a known migration corridor with mineral leases led to sportsmen's groups requesting lease deferrals (https://bit.ly/2PPjdWR). Put simply, map-based assessments that are easily understandable by stakeholders facilitate their informed participation in management and conservation. However, research is needed to improve and contextualize maps and assessments. For example, data limitations may preclude insights into the behavioral flexibility within any given population, thereby constraining information about sustainable levels of disturbance. Research and synthesis are therefore essential to better understand species- and landscape-specific variation in the plasticity of migratory behavior (eg Eggeman *et al.* 2016) and in fidelity to seasonal habitats (eg Sawyer *et al.* 2019). Research is also necessary to predict how climate change will affect the space-use of migratory ungulates, especially given the limited resources available in conservation to develop and implement habitat protections. Furthermore, because ungulate migrations extend across complex social landscapes, future assessments should also engage social and policy scientists to integrate stakeholder knowledge and interests (Cherney and Clark 2009; Morse and Clark 2019). Indeed, the simple act of mapping migrations concerns some landowners, industry representatives, and local governments (https://bit.ly/32pj670), presumably due to a perception that local knowledge and interests may be excluded. Finally, future assessments could integrate the corridor needs of multiple species and even larger taxonomic groups. As an example in the GYE, ungulate migration data could be coupled with spatially explicit assessments of habitat needs for grizzly bear dispersal north of YNP (Peck *et al*. 2017) to identify multispecies priorities.

Second, our experience in the GYE highlights the coordination and leadership roles of federal and state agencies. These agencies have broader authority and geographic reach than other stakeholders, and are therefore the obvious entities to lead large-scale coordination of corridor conservation. Each agency also plays a specific and complementary management role. The federal government owns immense acreages used by migratory ungulates, so that federal land-use decisions on these lands can have major impacts on migratory populations (Figure 5). However, across much of this same area, states have the authority to manage ungulate populations themselves, including such activities as harvest allocation, disease management, and, importantly, the designation of vital habitats such as corridors. Because of these complementary roles, effective federal–state partnership is critical to the conservation of migratory ungulates. In the past, as one example, research and management partnerships related to elk summer and fall ranges resulted in the establishment of habitat quality standards for elk in most national forests across the northwestern US. At the same time, one tool available to state wildlife agencies is the explicit designation of migration corridors and seasonal ranges as important habitats, which may promote more detailed consideration of migrations in federal resource management plans, forest management plans, mineral leasing, and National Environmental Policy Act processes. In this context, Wyoming's new migration policy (WGFD 2016) is an important test case.

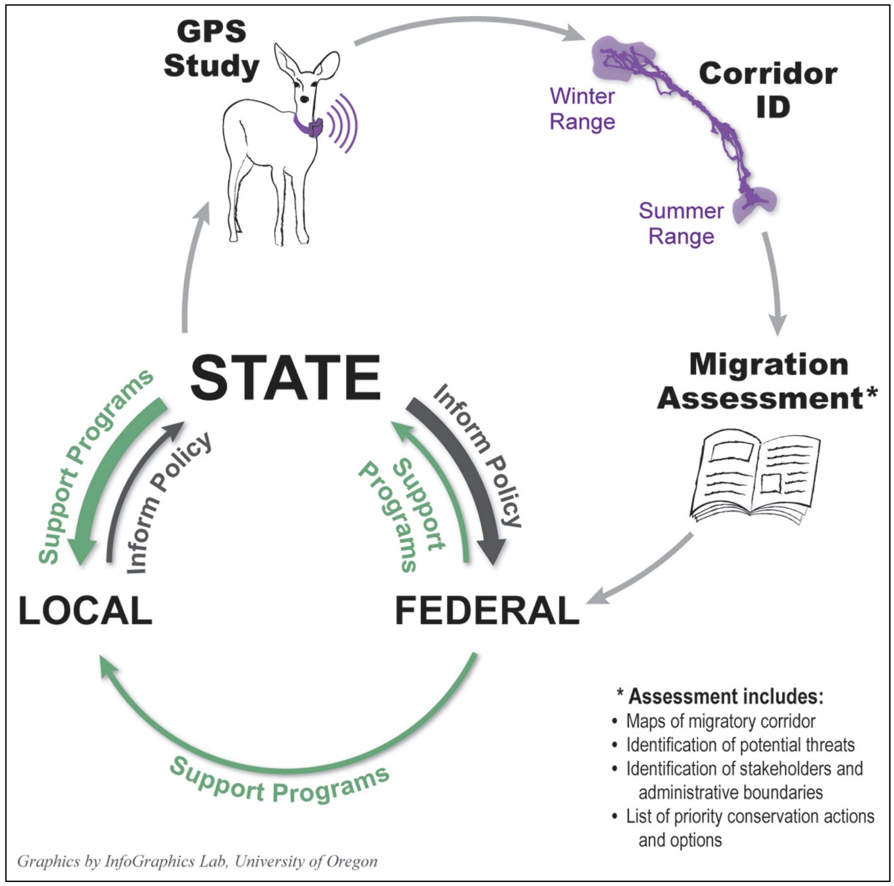

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Figure 5. Many ungulate migrations are now being studied through the use of GPS-collared animals, and collected data can be applied to assessments of conservation needs and opportunities across the year-round ranges of the population. These migration assessments can then inform and stimulate conservation activity in which federal, state, and local entities all play critical roles.

Third, improving conservation of ungulate migrations requires increased habitat protections and stewardship efforts on private lands. Conservation easements are a particularly important tool, and several states already have very active easement programs. For example, Montana is one of the largest easement holders in the nation, with many of these holdings focused on ungulate habitats (https://bit.ly/33uMTww). However, easements can be prohibitively expensive. In the GYE alone, acquiring easements on key private lands is estimated to cost at least $687 million (Heart of the Rockies Initiative 2003). Notably, to our knowledge, recent policy initiatives (eg DOI 2018) do not provide adequate funding to support habitat protections. The Land and Water Conservation Fund (LWCF), one of the most important traditional sources of funding for habitat conservation in the US, could provide critical support for migratory ungulate conservation but was permanently reauthorized and not funded by Congress in early 2019. Still, valuable as they may be, conservation easements are not a panacea; some landowners prefer not to enter into these agreements, and some migratory ungulates face challenges in addition to development. These include other causes of habitat loss and degradation, such as invasions by weeds (eg cheatgrass [*Bromus tectorum*]), and reductions in landowner tolerance when ungulates compete with livestock for forage, transmit diseases (eg brucellosis) to livestock, damage fences or crops, and attract predators. The US Department of Agriculture and Department of the Interior, as well as many state wildlife agencies, have developed programs to provide landowners with financial incentives and technical support to protect habitat and reduce conflicts. The dependence on private lands of all the herds included in our review (Figures 2 and 3) suggests that this is a critical area for migratory ungulate conservation.

A fourth key element to conserving ungulate migrations is fostering greater local participation in conservation efforts (Cherney and Clark 2009). Local knowledge is important to understand migrations and the threats migratory ungulates face, and local and regional voices can influence land-use and wildlife-management decisions. Moreover, local stakeholders may be better positioned to understand conservation opportunities and initiate conservation actions (eg habitat acquisitions, easements, fence retrofitting). The importance of agency coordination and local participation will likely vary with the jurisdictional profile of a migration. In some cases, an agency or NGO coalition may provide primary coordination or leadership, whereas in other cases a watershed organization or a landowner collaborative may prove more effective. Migration assessments (Panel 1) can act as catalysts in this regard, because any conservation effort will depend partly on developing, within stakeholder networks, a collective understanding of ungulate movement patterns, the values they represent, the threats to their persistence, and potential options for their conservation.

Ultimately, future protection of extant ungulate migrations will require a dynamic and context-dependent combination of "top-down" and "bottom-up" policy and management approaches (Figure 5; Cherney and Clark 2009). In this sense, those seeking to conserve ungulate migrations will benefit from ongoing experiments in network governance (Scarlett and McKinney 2016), such as Montana's Blackfoot Challenge, in which agencies, NGOs, and landowners have collaborated to reduce human–wildlife conflicts over many years (eg Wilson *et al*. 2017). Science-based federal and state coordination and leadership may be required to set the stage, but much of the conservation action will occur locally. The most effective solutions will likely come from organizational levels best equipped to understand the interests of regional and local stakeholders, and coordination among them. Unlike legislative protections that are completed (and sometimes reversed) with the stroke of a pen, the conservation of ungulate migrations will require long-term, adaptive efforts that are responsive to environmental change and that remain robust amid continually evolving local, state, and federal interests.

Acknowledgements

ADM received research support from the National Geographic Society (grant WW-100C-17), the Knobloch Family Foundation, the George B Storer Foundation, and the William and Flora Hewlett Foundation (grant 2018-8193). Numerous cooperators shared data to produce the figures, including the Wyoming Game and Fish Department; Montana Fish, Wildlife, and Parks; Idaho Department of Fish and Game; US National Park Service (Yellowstone National Park and Grand Teton National Park); US Fish and Wildlife Service (National Elk Refuge); and the Wildlife Conservation Society. Figures 2–5 were produced by J Merson and A Steingisser (University of Oregon Infographics Lab). Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

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