

WHERE THE DEER AND THE ANTELOPE PLAY: CONSERVING BIG GAME MIGRATIONS AS AN ENDANGERED PHENOMENA

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In the American West, high-profile big game species including mule deer, antelope, elk, moose, bison and bighorn sheep use large landscapes to migrate between winter and summer habitats to obtain the resources they need to survive. The big game species are a vital part of the West's ecology, economy, and culture and are valued by local, national, and international stakeholders. Thanks to large parcels of private and public land and a low human population, many parts of the American West still provide some of the best big game habitats in the world. But these vast, intact landscapes are under threat by ongoing habitat loss and disturbances to seasonal and migratory habitats that result in declines in big game population and the disappearance of migrations.

Addressing the challenge of conserving big game populations and the endangered phenomena of seasonal migration across large landscapes in the American West will require dynamic, innovative, and flexible legal approaches. Those legal approaches should recognize the biological needs of the species themselves and reflect economic policy analysis of conservation in landscapes with multiple land managers. Considering both integrated biological and economic decision frameworks and incentive-based tools to define and implement legal and

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policy structures can produce migratory species conservation more efficiently than less integrated approaches.

Conservation of big game migrations is now a growing priority and initial conservation efforts are beginning to emerge, including the Department of Interior Secretarial Order 3362 “Improving Habitat Quality in Western Big-Game Winter Range and Migration Corridors” and state policies including the Wyoming Game and Fish Department Ungulate Migration Corridor Strategy. This interdisciplinary paper evaluates those emerging policies and finds that the policies miss opportunities to provide higher levels of conservation of migratory species by failing to address key ecological characteristics of migratory species and to incorporate economically efficient hierarchies of management and policy. We conclude by offering thoughts on how future conservation policies might be designed to incorporate both ecology and economics to better conserve migrations.

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INTRODUCTION

“At 4 a.m. on an early May morning, a female mule deer left her winter range headed north. Her destination waited more than 100 miles ahead, in a dramatically different landscape. She wore a GPS collar, and we can trace her waypoints, recorded every hour along her long-distance migration. She is one of many animals carrying similar collars through our western landscapes, giving us a never-before-seen glimpse into the mechanics of long-distance migration and teaching us about the intricate relationships between wild animals and wild landscapes.” – Emilene Ostlind¹

In the American West, big game ungulates (hereinafter “ungulates”) like mule deer, pronghorn, elk, moose, bison, and bighorn sheep often migrate long distances to avoid harsh seasonal climates.² Mountain ranges with lush grasses, wildflowers, and shrubs are ideal ungulate habitat in the summer and early fall.³ But winter in the mountains means deep snowpack of ten feet or more, making the mountains unsuitable year-round habitat.⁴ The solution for winter survival is for animals to migrate down to winter ranges in the basins below.⁵ These basins offer milder winter conditions and are fairly snow-free, making forage available.⁶ However, basins are not ideal summer habitats; they are dry and unproductive in the summer months.⁷ As a result, in the spring, the migrating animals follow the spring forage green-up, moving back to their lush, mountainous summer ranges.⁸ These migrations occur seasonally, year after year to the same habitats, and are critical to ungulate survival and abundance in the American West.⁹ Ecologist Joel Berger, who has studied the “Path of the Pronghorn” – a 193 kilometer migration route used by

1. MATTHEW J. KAUFFMAN ET AL., WILD MIGRATIONS ATLAS OF WYOMING’S UNGULATES 3 (2018).

2. *Id.* at 8. In the lower 48 there are eight ungulate species that migrate: mule deer, elk, pronghorn, moose, bison, bighorn sheep, white-tailed deer, and mountain goats. *Id.* Joel Berger provides the following examples of what is and is not considered migration: “a mouse that moves from my house in winter to the outdoor woodpile during summer and back again would be migratory. . . . By contrast, a mouse that moves 15 kilometers but not back again is not migratory. Similarly, a wolverine (*Gulo gulo*) covering a 1000-kilometer² region between mountain ranges throughout the year would not be migratory because it fails to show seasonal use of discrete ranges.” Joel Berger, *The Last Mile: How to Sustain Long-Distance Migration in Mammals*, 18 CONSERVATION BIOLOGY 320, 321 (2004) (citation omitted).

3. See KAUFFMAN ET AL., *supra* note 1, at 8 (discussing mule deer migration between mountains and Wyoming’s Red Desert).

4. *Id.*

5. *Id.*

6. *Id.*

7. *Id.*

8. See Jerod A. Merkle et al., *Large Herbivores Surf Waves of Green-up During Spring*, 283 PROC. ROYAL SOC’Y B 1, 1 (2016) (reporting on a study tracking ungulate migration and forage quality).

9. See KAUFMANN ET AL., *supra* note 1, at 3 (“These long, regular journeys fuel their abundance and the ecosystems they inhabit.”).

pronghorn migrating between summer ranges in Grand Teton National Park and winter ranges in the Upper Green River Basin – has defined migration as the “seasonal round-trip movement between discrete areas not used at other times of the year.”¹⁰ The Path of the Pronghorn is one among dozens of corridors recently documented, covering distances of up to 240 kilometers.¹¹

While Western migratory ungulates are not in immediate danger of extinction,¹² their migratory behavior is increasingly rare.¹³ For example, in the Greater Yellowstone region, an area prized for its large intact landscapes and low human density, Berger has conservatively estimated a loss or truncation of 58% of historic elk migrations, 78% of pronghorn migrations, and 100% of bison migrations since the 19th century.¹⁴

While the primary function of a migration route is to provide a connection between summer and winter ranges, the “migratory routes themselves have functional attributes that yield important benefits

10. Berger, *supra* note 2, at 321. As Vicky Meretsky, Johnathan Atwell and Jeffery Hyman note in their article *Migration and Conservation: Frameworks, Gaps, and Synergies in Science, Law, and Management*, “if law, policy, and management strategies are to be developed to address the conservation of migrations, a working answer to the question ‘What is migration?’ needs to be formulated.” 41 ENVTL. L. 447, 456 (2011). Mertesky et al. make a distinction between migration, localized station-keeping movements, and ranging behaviors; “localized “station-keeping” movements. . . include foraging. . . commuting. . . and territorial defense.” *Id.* at 457. Ranging movements include “exploratory movements in search of suitable habitat or exploitable resources.” *Id.* For example, American bison that once circuited the great American plains “in search of fresh prairie grasses” exhibited ranging movements. *Id.*

11. In 2008 the Bridger Teton National Forest designated The Path of the Pronghorn Wildlife Corridor, the nation’s first federally protected wildlife corridor. CAROLE ‘KNIFFY’ HAMILTON, U.S.D.A. FOREST SERVICE, PRONGHORN MIGRATION CORRIDOR FOREST PLAN AMENDMENT (May 31, 2008)

https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsbdev3_063055.pdf; Arthur Middleton et al., *Conserving Transboundary Wildlife Migrations: Recent Insights from the Greater Yellowstone Ecosystem*, 18 FRONTIERS ECOLOGY & ENV’T 83, 86 (2019). [hereinafter *Conserving Transboundary Migrations*]

12. The Yellowstone National Park population of bison have been petitioned for listing under the ESA, however, the Fish and Wildlife Service found the petitions “do not present substantial scientific or commercial information indicating the petition may be warranted.” *Endangered and Threatened Wildlife and Plants; 90-Day Findings for Three Species*, 84 Fed. Reg. 46,927, 46,930 (Sept. 6, 2019) (to be codified at 50 C.F.R. pt. 17).

13. Berger, *supra* note 2, at 324.

14. *Id.* Berger notes the causes of the loss of migration in the GYE to be:

(1) little tolerance for bison outside protected areas, (2) concentrations of elk on 23 winter feeding grounds in Wyoming, (3) a 20% increase in the human population in the last decade to (current) more than 370,000, and (4) associated loss of habitat, especially areas crucial to approximately 100,000 wintering ungulates in the southern part of the ecosystem. *Id.*

beyond simple connectivity.”¹⁵ New research brings to light the ecological value of migrations suggesting that they underpin robust ungulate populations which, in turn, provides “broader effects within food webs, such as sustaining large carnivores.”¹⁶ For this reason, reductions or loss of ungulate migrations may have potentially catastrophic implications for some ecosystems.¹⁷ Thus, migrations have a far more widespread and fundamental impact on ungulate populations themselves and the related ecosystems than have been previously recognized by ecologists, wildlife managers, and the general public.¹⁸

In the past decade, GPS tracking data, coupled with advances in remote sensing and computational analysis, have led to major breakthroughs in ungulate migration ecology.¹⁹ Those breakthroughs include: an understanding of how migration affects populations and ecosystem functioning, an understanding of the value of each seasonal habitat (including the recognition of the migration corridor as its own habitat), more advanced mapping of migration habitats for conservation, and an understanding of the human impact on migration.²⁰

Because of GPS tracking data, we know that ungulate populations depend on large, mainly intact, landscapes to obtain the seasonal resources they need.²¹ Thanks to large chunks of private and public land, seasonal climates, and a low human population, many parts of the American West still provide the best year-round ungulate habitats in the world.²² But in some areas, intact landscapes are under threat by

15. Kevin L. Monteith et al., *Functional Attributes of Ungulate Migration: Landscape Features Facilitate Movement and Access to Forage*, 28 *ECOLOGICAL APPLICATIONS* 2153, 2154 (2018).

16. *Conserving Transboundary Migrations*, *supra* note 11, at 85.

17. *Id.*

18. *Id.*

19. *Id.* at 84. Delineating long-distance migration routes was not possible prior to the advancement of GPS technology that enabled fine spatiotemporal scales to be used to estimate utilization distributions combined across animals to determine migration route segments. Holly E. Copeland et al., *Conserving Migratory Mule Deer Through the Umbrella of Sage-Grouse*, 5 *ECOSPHERE* 1, Sept. 2014, at 4. This has enabled scientists to distinguish between migration routes and stopover habitat. *Id.*

20. *Conserving Transboundary Migrations*, *supra* note 11, at 84.

21. *Id.* at 83; *see also* Daniel Glick, *End of the Road?*, *SMITHSONIAN MAG.* (Jan. 2007), <https://www.smithsonianmag.com/science-nature/end-of-the-road-1-142780847/> (noting that the pronghorn’s “extraordinary migration is getting more difficult with each passing year, due to land development. . . obstacles in the animals’ way and a natural gas boom that is carving up their critical winter range.”).

22. KAUFFMAN ET AL., *supra* note 1, at 8.

ongoing habitat fragmentation attributed to energy development (traditional and renewable) and residential development.²³ As a result of declining Western ungulate populations - and particularly of mule deer - scientists, wildlife managers, and conservation groups alike are paying attention to ungulate migrations and advocating for their conservation.²⁴

Conserving ungulate migrations requires that people protect abundant populations, which marks a shift away from the traditional norm of conservation laws preoccupied with conserving rare or endangered species.²⁵ Scholars have addressed the dilemma of conserving the increasingly rare act of migration among abundant populations by classifying migration as an “endangered phenomenon”²⁶—a parallel concept similar to endangered species. Lincoln Brower and Stephen Malcolm have defined an “endangered phenomenon” as “a spectacular aspect of the life history of an animal or plant species involving large numbers of individuals that are threatened with impoverishment or demise, the species per se need not be in peril; rather, the phenomenon it exhibits is at stake.”²⁷ Brower and Malcolm have suggested that “endangered phenomena” serve as an additional conservation theme for the conceptual basis of

23. Copeland, *supra* note 19, at 2. Western ungulates face a gauntlet of challenges during their seasonal migrations. For example, long distance migrants from the Red Desert mule deer herd cross an average of five highways and 171 fences just to complete a round-trip seasonal migration. Hall Sawyer et al., *The Extra Mile: Ungulate Migration Distance Alters the Use of Seasonal Range and Exposure to Anthropogenic Risk*, 7 ECOSPHERE 1, Oct. 2016, at 8. [hereinafter *The Extra Mile*]

24. *Id.*; see also WYOMING GAME & FISH DEP'T, UNGULATE MIGRATION CORRIDOR STRATEGY (January 28, 2019), https://wgfd.wyo.gov/WGFD/media/content/PDF/Habitat/Habitat%20Information/Ungulate-Migration-Corridor-Strategy_Final_012819.pdf (indicating that the Wyoming Mule Deer Initiative has recorded a mule deer decline of 40% in the past twenty years as a result of reduction in habitat and habitat quality).

25. Robert L. Fischman & Jeffrey B. Hyman, *The Legal Challenge of Protecting Animal Migrations as Phenomena of Abundance*, 28 VA. ENV'T'L L.J. 173, 177–78 (2010). Robert Fischman has stated that while “[a]nimal migrations are widely appreciated as among the most awe-inspiring spectacles of nature. . .they are hardly recognized in the law of biodiversity protection.” Robert Fischman, *Migration Conservation: A View From Above*, 41 ENV'T'L L 277, 278 (2011) [hereinafter *View From Above*]. Instead, he notes, we employ an “‘emergency room’ response” under which “species on the brink of extinction consume almost all attention (and resources).” Fischman & Hyman, *supra* note 25, at 175.

26. Lincoln P. Brower & Stephen B. Malcolm, *Animal Migrations: Endangered Phenomena*, 31 AM. ZOOLOGIST, 265, 265 (1991).

27. *Id.* Brower and Malcolm are concerned about a “near future with increasing numbers of species reduced in range and so constrained in numbers that they can no longer exhibit their spectacular life history phenomena.” *Id.*

biodiversity conservation alongside the conservation of rare species.²⁸ This paradigm shift accords with the current view that wildlife law can be used to promote healthy functioning ecosystems (i.e. biodiversity) rather than to just increase populations of individual species of importance.²⁹

The mass migration of western ungulates is a stunning sight and one that has been valued historically by native indigenous communities, undervalued by market hunters in the 1800s, and then restored and highly valued in modern society. Migrating species provide ecosystem services that are of substantial net benefit to humankind.³⁰ Those ecosystem services include: supporting (grazing), provisioning (food base for humans and carnivores), regulating (seed dispersal), and cultural (recreation and heritage).³¹ Big game migrations are a vital part of the West's ecology, economy, culture and natural heritage and are valued by national and international stakeholders, as evidenced by the willingness of people to travel and expend significant amounts of resources to hunt and view ungulates.³² The loss of migrations means losing ecosystem functions that are valued by society.³³

As in all kinds of wildlife conservation, there is a strong human-centric aspect to the conservation of ungulate migrations. In the migration context, this people-centric aspect includes anthropogenic threats to migration, multiple land ownership and management, and diverse values associated with ungulate migrations at the local and national levels.³⁴ In light of the human-centric paradigm of migration, conservation policies should incorporate both new scientific understandings and new economic and institutional understandings. We must “adjust our perspectives and better integrate knowledge about human actions and reactions to species risk into the mix of influences.”³⁵ Addressing the challenge of conserving Western

28. *Id.*

29. ERIC T. FREYFOGLE ET AL., WILDLIFE LAW: A PRIMER 11 (2019).

30. Heather L. Reynolds & Keith Clay, *Migratory Species and Ecological Processes*, 41 ENV'T'L L. 371, 390 (2011).

31. *Id.* at 374.

32. *See id.* at 379 (discussing the ecosystem services of migratory species).

33. *View From Above*, *supra* note 25, at 278.

34. *See Conserving Transboundary Migrations*, *supra* note 11, at 83 (“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.”).

35. Jason Shogren et al., *Why Economics Matters for Endangered Species Protection*, 13 CONSERVATION BIOLOGY 1257, 1260 (1999).

ungulate migrations will require an interdisciplinary approach, one that starts with science as its foundation and includes cultural values but incorporates economic policy analysis of conservation in landscapes with multiple land managers.

Economics is the study of people's decisions, behavior, and interactions within their ecological, economic, and institutional settings.³⁶ Economics creates a foundational ecological, economic, and institutional framework to define and explore policy to promote cost-effective conservation of migratory species. Although economics can inform migratory species conservation by quantifying costs and benefits and examining impact on prices, profits, and development, economics has a larger role to play. Economics can inform appropriate land use and conservation policy in two ways. First, economics can help determine both socially optimal patterns of land use to balance human values for migratory species with other human values for land—including market and non-market values.³⁷ Similarly, economics can determine cost-effective patterns of land use to achieve a goal, even when that goal is purely ecological.³⁸ Second, economics recognizes that human activities can alter a landscape's provision of ecological services.³⁹ Third, economics recognizes that people's reactions to landscape policy determines the impact of that policy on both people and ecology, and when integrated in a policy analysis framework, those reactions and interactions between people and ecosystems can predict whether and how particular policies will alter the behavior of people and species.⁴⁰ Finally, economic analysis identifies ways to use incentives, such as payments (fees) and easements; regulations, such as zoning of land use practices; and public/private land direct conservation action to induce private and public land users to achieve land patterns that protect the migrations of ungulates.⁴¹

36. NICK HANLEY ET AL., INTRODUCTION TO ENVIRONMENTAL ECONOMICS 1 (2019).

37. Charlene Kermagoret & Jerome Dupras, *Coupling Spatial Analysis and Economic Valuation of Ecosystem Services to Inform the Management of an UNESCO World Biosphere Reserve*, 13 PLOS ONE 1, 15 (2018).

38. See Amy Ando et al., *Species Distributions, Land Values, and Efficient Conservation*, 279 SCI. 2126, 2126 (1998) (“[A] better definition of efficiency takes account of differences in land prices. . . [Purchasing in high priced counties] could quickly exhaust limited resources”).

39. Stephen Polasky et al., *Where to Put Things? Spatial Land Management to Sustain Biodiversity and Economic Returns*, 141 BIOLOGICAL CONSERVATION 1505, 1520 (2008).

40. H.J. Albers et al., *Optimal Siting, Sizing, and Enforcement of Marine Protected Areas*, 77 ENV'T'L. RES. ECON. 229, 230 (2020).

41. Polasky et al., *supra* note 39, at 1520; Parkhurst et al., *Agglomeration Bonus: An Incentive Mechanism to Reunite Fragmented Habitat for Biodiversity Conservation*, 41 ECOLOGICAL ECON. 305–21 (2002).

Policy efforts to conserve ungulate seasonal migrations are beginning to emerge. These policies include both federal efforts, namely the Department of Interior Secretarial Order No. 3362 “Improving Habitat Quality in Western Big-Game Winter Range and Migration Corridors,”⁴² as well as individual federal agency actions and state polices such as the Wyoming’s Mule Deer and Antelope Migration Corridor Protection Executive Order⁴³ and New Mexico’s Wildlife Corridors Act.⁴⁴ Despite these initial efforts, the vast majority of ungulate migration corridors remain unprotected, and ungulate populations continue to decline.⁴⁵ While these early policies provide a good starting point, they address only a subset of the migratory ungulate species and miss the opportunity to address key ecological characteristics of migratory species, to incorporate economically efficient hierarchies of management and policy tools, and to provide higher levels of conservation of migratory species for the benefit of all U.S. citizens.

The major issues that remain unresolved in ungulate migration conservation call for: (1) comprehensive inclusion of the full suite of migratory ungulate species and their year-round habitats; (2) both spatial and temporal coordinated management of migrations and seasonal habitat protection across large landscapes; (3) coordinated management of migrations that cross state and international boundaries; (4) incorporation of all values/perspectives—including local, national and tribal values; (5) funding to implement conservation protection; and (6) increased utilization of economic incentive options.

We propose that future ungulate conservation policy address these issues by using a nested hierarchy. Specifically, we propose a cooperative federalism approach that places overall coordination and funding for migration conservation at the federal level. Yet, our approach provides states with an opportunity to remain at the helm of local decisions and implementation, given their experience and information about local tradeoffs decisions. This approach has a

42. Dep’t of Interior, Secretarial Order 3362, Improving Habitat Quality in Western Big-Game Winter Range Migration Corridors (Feb. 2018).

43. OFF. WYO. GOVERNOR MARK GORDON, GOVERNOR GORDON SIGNS WYOMING MULE DEER AND ANTELOPE MIGRATION CORRIDOR PROTECTION EXECUTIVE ORDER (Feb. 14, 2020),

<https://content.govdelivery.com/accounts/WYGOV/bulletins/27bd117>.

44. Wildlife Corridors Act, S.B. 228, 2019 Leg., Reg. Sess. (N.M. 2019).

45. Cf. *Conserving Transboundary Migrations*, *supra* note 11, at 83 (“[M]any ungulate migrations worldwide are now at risk. . . Even the world’s largest protected areas cannot fully safeguard migratory herds.”).

number of benefits. Providing federal coordination across large western landscapes, with multiple managers/owners and across state and international boundaries, offers the best opportunity for conserving the entire ungulate migrations as opposed to just sections of migration corridors. Additionally, due to the amount of migratory habitat on federal land, a federal-centric approach is needed to incorporate tribal and national stakeholder's values alongside those of local and state stakeholders. Finally, this approach provides a federal funding source needed to increase opportunities to incorporate incentive options for private land conservation through both federal and local programs.

Herein we argue for the integration of economics and law with ecology to address corridor connectivity across private, state, tribal, and federal land. This integrated framework can be used to develop more effective and durable policies to reverse the trend of ungulate population declines as a result of migration corridor and seasonal connectivity loss. Part II of this article provides an overview of the ecological needs of migrating ungulates including the recent breakthroughs in ungulate migration ecology. Part III provides an economic policy analysis of conservation in landscapes with multiple managers and discusses economically efficient hierarchies of management and policy tools including incentive-based tools. Part IV evaluates emerging migration conservation policies to determine if they effectively address the needs of the species and incorporate economic policy efficiencies and identifies a number of outstanding issues that remain to be solved. We conclude this section by offering a suggestion that future conservation policy might be best designed under a nested hierarchy or cooperative federalism approach to address the outstanding issues we have identified. Part V concludes by offering some final thoughts about the future of ungulate migratory conservation, including the need for future conservation policies to remain flexible in the face of climate change, which affects landscape conditions and in turn the timing and locale of seasonal ungulate migrations.

MIGRATION ECOLOGY

Ungulate migration has received significant research attention ever since seminal early studies on Serengeti wildebeest, zebra, and

gazelle migrations in the 1980s.⁴⁶ More recently, the view of migration as a phenomenon unique to a handful of iconic landscapes has given way to a growing appreciation that migrations of tens or even hundreds of miles are widespread in ungulates across the grasslands, forests, and tundra of not only Africa but Europe, Asia, and the Americas.⁴⁷ This includes the American West, where migratory behavior has been documented in at least six ungulate species: bison, elk, mule deer, pronghorn antelope, bighorn sheep, and moose.⁴⁸ Interest in the migrations of the American West was stoked by documentation in the 1990s and early 2000s of a 120-mile migration by pronghorn between Upper Green River Basin and Grand Teton National Park in Jackson, WY.⁴⁹

Then, in 2013, after collecting GPS data from 40 mule deer he had collared to study the impact of energy development on the deer's use of winter range in Wyoming's Red Desert, wildlife biologist Dr. Hall Sawyer made an impressive discovery.⁵⁰ Dr. Sawyer and his team inadvertently discovered the longest ungulate migration ever recorded in the lower 48 states.⁵¹ When spring came, some of the collared mule deer migrated from their sagebrush-covered winter ranges to high mountain meadows over 150 miles away.⁵²

As impressive as this migration distance was, it did not stand for long. In 2016, a female mule deer known as Doe #255 trekked over 242 miles during her spring migration and again on her return in the fall.⁵³ Doe #255 migrated from her winter range in the Red Desert of Wyoming all the way past Jackson, Wyoming and over the Teton Range to her summer range location in Island Park, Idaho and retraced her steps on her return in the fall.⁵⁴ Scientists have continued to track

46. See John M. Fryxell & Anthony R.E. Sinclair, *Causes and Consequences of Migration by Large Herbivores*, 3 TRENDS ECOLOGY & EVOLUTION 237 (1988) for an example of scholarship on such a study.

47. See KAUFFMAN ET AL., *supra* note 1, at 6–7 (providing an overview of ungulate habitats); *Conserving Transboundary Migrations*, *supra* note 11, at 83 (providing a similar overview).

48. *Conserving Transboundary Migrations*, *supra* note 11, at 86.

49. Berger, *supra* note 2, at 320.

50. Gregory Nickerson, *America's Longest Mule Deer Migration Discovered in Wyoming*, WYOFIELD (Apr. 22, 2014), <https://www.wyofile.com/americas-longest-mule-deer-migration-discovered-in-wyoming/>.

51. *Id.*

52. *Id.*

53. Christine Peterson, *Wyoming Researchers Discovered a Mule Deer Migration Almost 100 Miles Longer Than the Previous Record*, CASPER STAR TRIB., April 9, 2018.

54. *Id.*

Doe #255 and have learned that she makes this same trek year after year.⁵⁵ The discovery of this extraordinary migration, occurring in a well-studied area, compounded a sense that the phenomenon of migration is much more widespread than initially thought, with much yet to discover than previously appreciated.

In the past 10 years, scientists have made major advances in understanding ungulate migration ecology.⁵⁶ The most relevant of those scientific advancements are summarized below to provide insight into the biological needs of migrating ungulates to inform the discussion of conservation policy options discussed in the remainder of the paper.

I. Habitat Needs of Migratory Ungulates

Ungulates use migration as a strategy to cope with highly seasonal environments. In the mountains and plains of the American West, ungulates generally migrate to higher elevations in the spring and summer to forage on the new vegetation growth behind the melting snowline. They then migrate back down to lower elevations in fall and winter to avoid deep snow.⁵⁷ Migration is the key to survival and reproduction in many populations, because different habitats used throughout the year provide distinct values. Conserving migratory ungulates requires conserving entire year-round ranges.⁵⁸ Unsurprisingly, reviews of the ecology and conservation of ungulate migration have repeatedly identified habitat loss on one or more seasonal ranges as one of the leading causes of declines of migratory ungulates around the world, including in the Greater Yellowstone

55. *Id.*

56. *Conserving Transboundary Migrations*, *supra* note 11, at 84. Breakthroughs in ungulate ecology in the past decade include: “(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.” *Id.*

57. See Rickbeil et al., *Plasticity in Elk Migration Timing is a Response to Changing Environmental Conditions*, 25 GLOB. CHANGE BIOLOGY 2368, 2369 (examining the relationship between the timing of elk migration, snow accumulation, and spring growth). Offering more specifics on the behavior of migration, ecologists Blake Lowery and his co-authors specifically note that “[s]easonal migration has evolved as a complex behavior to enhance fitness and results from interactions between individuals (e.g., learned behavior), their genes, and the environment, notably spatiotemporal variation in resources and interspecific threats (e.g., predation. . .).” Blake Lowery et al., *Characterizing Population and Individual Migration Patterns Among Native and Restored Bighorn Sheep (Ovis Canadensis)*, 9 ECOLOGY & EVOLUTION 8829, 8830 (2019).

58. *Conserving Transboundary Migrations*, *supra* note 11, at 85.

Ecosystem and other parts of the American West.⁵⁹ The conservation of ungulate migrations and seasonal habitats is a growing priority of wildlife managers and conservation organizations.

A. Winter Range

The winter is a period of limited food resources, nutritional deficit, and declining body condition for many wildlife species in northern temperate landscapes.⁶⁰ For migratory ungulates, the winter range has long been viewed as the most limiting seasonal range.⁶¹ During winter, the grasses, forbs, and shrubs that ungulates prefer to eat are generally senescent—holding relatively low nutritional value—and often covered by snow.⁶² Many ungulates reduce their forage intake over the winter, effectively fasting, and reduce activity levels, presumably to conserve energy and minimize risks of mortality.⁶³ Many northern ungulates can lose anywhere from 15–30% of their body mass over winter.⁶⁴

In temperate regions like the Western U.S., ungulates “experience a nutritional bottleneck during winter when forage is lower in digestibility and protein content, and animals are often concentrated at their highest year-round densities.”⁶⁵ Areas where animals concentrate in winter are termed “winter ranges.”⁶⁶ One western state’s wildlife agency, the Wyoming Game and Fish Department, defines winter ranges as areas where “a population or portion of a population of

59. See Grant Harris et al., *Global Decline in Aggregated Migrations of Large Terrestrial Mammals*, 7 ENDANGERED SPECIES RES. 55, 55 (2009) (“Key principles for conserving migrants, exemplified by the SME and Greater Yellowstone Ecosystem (GYE), include securing seasonal ranges.”); Berger, *supra* note 2, at 321 (“[M]ost terrestrial surfaces on Earth remain unprotected. Consequently, extraordinary events that once occurred across vast landscapes. . . have been truncated.”); Douglas T. Bolger et al., *The Need for Integrative Approaches to Understand and Conserve Migratory Ungulates*, 11 ECOLOGY LETTERS 63, 68 (2008) (“[I]f habitat loss occurs in a population near carrying capacity, the density-dependent response in population growth rate could be rapid and severe.”).

60. See Katherine L. Parker et al., *Nutrition Integrates Environmental Responses of Ungulates*, 23 FUNCTIONAL ECOLOGY 57, 58 (2009) (discussing seasonal changes in energy use and the effects of weather and food availability).

61. See *id.* at 59 (“Metabolic and nutritional requirements may preclude animals from feeding in areas with low forage abundance or low nutritive value.”).

62. *Cf. id.* (“Dietary breadth was constrained for white-tailed deer by low forage quality as well as by mobility in snow. For black-tailed deer, the processing of lower quality food in coastal environments in winter resulted in more time spent ruminating and fewer foraging bouts.”) (citation omitted).

63. *Id.*

64. *Id.* at 61.

65. Sawyer et al., *supra* note 23, at 7.

66. See *id.* for use of the term “winter range.”

animals use the documented suitable habitat within this range annually, in substantial numbers, only during the winter.”⁶⁷ Winter range habitats are often located in areas where elevation, slope, aspect, and vegetation combine to provide animals with both food and protection from harsh weather conditions.⁶⁸ As a result, winter range is limited and confined to relatively restricted geographic areas.⁶⁹

Winter ranges often occur at lower elevations on U.S. Bureau of Land Management federal public land or privately-owned lands that have the potential to be impacted by direct and indirect habitat losses resulting from increased levels of human disturbance.⁷⁰ Winter ranges have been long recognized as an important and limiting habitat which has prompted many western states to designate “critical winter range,” the primary ungulate habitat protected in most states.⁷¹

B. Summer Range

After winter subsides, ungulates migrate back to higher elevations to feed on newly emerging grasses, forbs, and shrubs and take cover in forested areas.⁷² Migratory ungulates benefit from consuming high-quality forage found in high-elevation summer ranges attributed to cool weather and prolonged snowmelt.⁷³ This allows some migratory

67. WYO. GAME & FISH DEP’T, STANDARDIZED DEFINITIONS FOR SEASONAL WILDLIFE RANGES (1990),

<https://wgfd.wyo.gov/WGFD/media/content/PDF/Get%20Involved/ShirleyRange-Definitions.pdf>. The winter range definition was adopted in 2004. *Id.* Colorado Parks and Wildlife define winter ranges as “[t]hat part of the overall range where 90% of the individuals are located during the average five winters out of ten from the first heavy snowfall to spring green-up, or during a site specific period of winter as defined for each DAU [data analysis unit].” COLO. PARKS & WILDLIFE, 2020 STATUS REPORT: BIG GAME WINTER RANGE MIGRATION CORRIDORS 18 (May 2020),

<https://cpw.state.co.us/Documents/Hunting/BigGame/2020BigGameWinterRangeandMigrationCorridorsReport.pdf>.

68. MONT. FISH, WILDLIFE & PARKS, BIG GAME WINTER RANGE RECOMMENDATIONS FOR SUBDIVISION DEVELOPMENT IN MONTANA: JUSTIFICATION AND RATIONALE 3 (Jan. 2012).

69. *Id.*

70. Hall Sawyer et al., *Mule Deer and Pronghorn Migration in Western Wyoming*, 33 WILDLIFE SOC’Y BULL. 1266, 1271 (2005) [hereinafter *Wyoming Migration*].

71. See, e.g., *Western Big-Game Migration Program*, NAT’L FISH & WILDLIFE FOUND., https://www.nfwf.org/sites/default/files/2020-04/NFWFbiggame20200414_FS.pdf (discussing efforts to conserve critical winter range by “working with conservation partners across 11 western states: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington and Wyoming.”).

72. KAUFMANN ET AL., *supra* note 1, at 8.

73. Middleton et al., *Animal Migrations Amid Shifting Patterns of Phenology and Predation: Lessons from a Yellowstone Elk Herd*, 94 ECOLOGY 1245, 1246 (2013) [hereinafter *Shifting Patterns*].

ungulates to attain higher body mass and pregnancy rates compared to their non-migratory counterparts.⁷⁴

Kevin Monteith, et al., note “[i]n contrast to winter, summer is viewed as a period of nutritional abundance . . . and is considered a critical period for replenishment of reserves lost during winter.”⁷⁵ One of the most important functions of summer range is to support adult females as they nurse rapidly growing calves or fawns while also building the fat required to support autumn conception and survival over the coming winter.⁷⁶

As a result of their large size and often-protected status at higher elevations within U.S. National Forests and National Park Service lands, summer ranges appear to, at least currently, be the most secure of the seasonal ungulate habitats.⁷⁷

The importance of summer ranges was long underappreciated by wildlife ecologists and managers, perhaps because of a sense that they contain inexhaustible food resources and face little development threat compared to low-elevation winter ranges. But summer range has been increasingly recognized for its critical role in ungulate health.⁷⁸ This new appreciation of summer ranges compounds the importance of migrations corridors, because “the loss of a migratory corridor translates into the loss of access to critical resources on the summer range” and the need to conserve year-round ranges.⁷⁹

C. The Migration Route as a Critical Spring and Fall Habitat

Scientists have long understood the need for ungulates to migrate between winter and summer ranges but tended to view the migration routes themselves only as travel paths between ranges. Recently, this view has given way to a new understanding of the migration route as a critical habitat unto itself.⁸⁰ A series of breakthroughs in this area have

74. *Id.* at 1246.

75. Kevin L. Monteith et al., *Risk-sensitive Allocation in Seasonal Dynamics of Fat and Protein Reserves in a Long-Lived Animal*, 82 J. ANIMAL ECOLOGY 377, 378 (2013).

76. See Parker, *supra* note 60, at 58 (noting that because of lactation, “the highest energy costs for females occur from late winter to mid summer.”); *Shifting Patterns*, *supra* note 74, at 1246 (noting that high-quality summer forage allows for “higher body mass and pregnancy rates.”).

77. *Wyoming Migration*, *supra* note 70, at 1270.

78. *Conserving Transboundary Migrations*, *supra* note 11, at 85.

79. *Id.*

80. Kevin L. Monteith et al., *Functional Attributes of Ungulate Migration: Landscape Features Facilitate Movement and Access to Forage*, 28 ECOLOGICAL APPLICATIONS 2153, 2160 (2018).

been greatly facilitated by technological advances—namely high-resolution remote sensing imagery and fine-scale GPS tracking abilities.

The coupling of remotely sensed vegetation data with GPS point locations from collared animals has demonstrated that many ungulates “surf the green wave,” following the progressive spring green-up along their migration route.⁸¹ Closely surfing the green wave has significant benefits for ungulates. Surfing allows ungulates to consume newly emergent, high-quality forage—grasses, forbs, and shrubs that are high in protein and low in fiber—and pace their movements to maintain optimal intake of this high-quality forage.⁸² Ungulates are able to digest this high-quality forage quickly and maximize their energy intake.⁸³ As plants age, they develop more fiber and are difficult to digest, making older plants a less beneficial food source.⁸⁴

In elk, tracking individual animal movements along with their body-fat levels has shown that better green wave surfers gain more fat.⁸⁵ The body-fat level achieved by the end of the growing season is a critical factor in conception and overwinter survival in elk and other ungulates.⁸⁶ The link between successful green-wave surfing and overall animal health likely explains why migratory ungulates are declining in some areas where barriers and habitat loss limit migratory movements.⁸⁷

The duration of ungulate migrations as well as the associated benefits of surfing the green wave have led scientists and wildlife managers to now think of, and categorize, migration routes (and stopover areas in particular) as a separate critical seasonal habitat that are especially important for forage⁸⁸ and possibly other functions including resting and birthing.⁸⁹ Importantly, this ability to “surf the

81. Merkle, *supra* note 8, at 6 (the green wave hypothesis can be summarized as follows: migratory animals track or ‘surf’ high-quality forage at the leading edge of spring green-up).

82. *Id.* at 2.

83. Hall Sawyer & Matt Kauffman, *Stopover Ecology of a Migratory Ungulate*, 80 J. ANIMAL ECOLOGY 1078, 1079 (2011).

84. Merkle, *supra* note 8, at 1.

85. Arthur Middleton et al., *Green-Wave Surfing Increases Fat Gain in a Migratory Ungulate*, 127 OIKOS 1060, 1064 (2018).

86. *Id.* at 1061.

87. *Id.* at 1066.

88. Wyckoff et al., *Evaluating the Influence of Energy and Residential Development on the Migratory Behavior of Mule Deer*, ECOSPHERE, Feb. 2018, at 1, 2.

89. Compare Parker, *supra* note 60, at 58, for discussion on the differing seasonal energy requirements associated with birthing.

green wave” appears to be a learned behavior, accumulated over generations.⁹⁰

Though there has been less research on the ecology of fall migration down from summer ranges, movement into lower-elevation corridors and basins provides ungulates with an escape from the deep winter snow. Pronghorn, with their small bodies and hooves, leave their summer ranges when the snow first starts to accumulate in mid-October.⁹¹ Mule deer are the next to leave, followed by the larger bodied elk and moose, whose long legs enable them to cope with more snow than the other species.⁹²

D. Stopovers Areas and Bottlenecks

Within migration routes, stopover areas and bottle necks are critical habitats. Thanks to GPS data, scientists have discovered that migrating ungulates do not just make one immediate or continuous movement to winter or summer ranges during their migration,⁹³ spending as much as 95% of their time in what are known as “stopover sites.”⁹⁴ Stopover sites are “habitat patches along the migration route where animals rest and forage to renew energy reserves.”⁹⁵ Because migrating ungulates can spend as much as 95% of their time in stopover areas, conservation of stopover areas has emerged as a conservation priority.⁹⁶ Ecologists have compared stopovers to the restaurants, gas stations, or rest stops that serve weary travelers along interstates.⁹⁷

Bottlenecks are defined as areas where many animals must funnel through one confined or narrow landscape feature (natural or man-made) because there are few or no alternative paths on their migration

90. Brett R. Jesmer, *Is Ungulate Migration Culturally Transmitted? Evidence of Social Learning from Translocated Animals*, 361 SCI. 1023, 1023 (2018).

91. Matt Kauffman, Leader of the Wyoming Cooperative Fish and Wildlife Unit, University of Wyoming, *Ungulate Migrations – A Synthesis of the Science, Wyoming Game and Fish Migration Corridor Public Meeting*, Casper, WY (Feb. 12, 2019).

92. *Id.*

93. Sawyer & Kauffman, *supra* note 83, at 1079.

94. *Id.* at 1083.

95. *Id.* at 1078. The Wyoming Game and Fish Department has defined “ungulate stopover areas” as “localized areas consistently used by ungulates to rest and feed during spring and fall migration. STANDARDIZED DEFINITIONS FOR SEASONAL WILDLIFE RANGES, *supra* note 70, at 2.

96. Sawyer & Kauffman, *supra* note 83, at 1081.

97. Hall Sawyer, Research Biologists and Project Manager, Western Ecosystem Technology, Inc., Integrating Migration Data into Management, *Sustaining Big Game Migrations in the West: Science, Policy, and People Emerging Issues Forum* (Nov. 9, 2015).

route.⁹⁸ These bottlenecks slow the movement of herds, creating stressors on migratory animals and on habitats near the bottleneck. For example, west of Pinedale, Wyoming there is an area called “Trapper’s Point” that is bounded by rivers where several thousand mule deer and pronghorn pass every year during their spring and fall migrations.⁹⁹ This bottleneck has existed for 5,800–6,800 years.¹⁰⁰ Recent rural subdivision development, however, has narrowed the Trapper’s Point bottleneck from one mile to one-half mile in width.¹⁰¹

Because of their importance to successful migration, many migration route conservation efforts to date have focused on preserving bottlenecks and stopover areas.

E. Migratory Diversity Among Populations

As GPS technology continues to enhance ecologists’ ability to track and map animal migrations, they are discovering an increasingly large number of ungulate populations’ movements do not fit within the traditional definitions.¹⁰² Many populations of ungulates include animals that don’t migrate (termed residents), and the migrants themselves may express a number of different movement tactics.¹⁰³ As a result, ecologist Blake Lowery and co-authors argue that instead of adopting “a dichotomous classification (e.g. resident or migrant), seasonal migrations are being increasingly interrupted along a behavioral continuum.”¹⁰⁴ Lowery also observed that “evaluating migratory strategies along a continuum may provide additional insights when describing migratory metrics (e.g., timing) or difference in demographic performance among individuals in a population.”¹⁰⁵

Seasonal migration distances vary widely. Within a given migratory herd, there are often short-distance, medium-distance, and

98. *Wyoming Migration*, *supra* note 70, at 1271. The Wyoming Game and Fish Department has defined an “ungulate migration bottleneck” as “[a]ny portion of an ungulate migration corridor in which migrating ungulates are physically or behaviorally constrained. Examples may include habitat leading to a highway underpass or overpass, a gap between fences or residential subdivisions or other developments, or a route that circumnavigates a lake or reservoir.” STANDARDIZED DEFINITIONS FOR SEASONAL WILDLIFE RANGES, *supra* note 67, at 2.

99. Dennis Feeney et al., *Big Game Migration Corridors in Wyoming*, B-1155 WYO. OPEN SPACES 1, 1 (2004), <http://www.wyomingextension.org/agpubs/pubs/B1155.pdf>.

100. Berger, *supra* note 2, at 324.

101. Feeney et al., *supra* note 99, at 2.

102. Jodi E. Berg et al., *Prevalence and Mechanisms of Partial Migration in Ungulates*, 7 FRONTIERS ECOLOGY & EVOLUTION 1, 2 (2019).

103. *Id.*

104. Lowery et al., *supra* note 57, at 8837.

105. *Id.*

long-distance migrants.¹⁰⁶ Variable migration distances within a single herd benefit the herd.¹⁰⁷ Animals are typically most concentrated in their winter range, where and when forage is lower in digestibility and protein content.¹⁰⁸ Scientists have found that the animals that migrate long distances leave their winter ranges earlier than short and medium-distance migrants in the spring, thus alleviating the competition for limited forage on the winter ranges and most likely increasing the landscape's carrying capacity.¹⁰⁹ The more animals within a herd that migrate longer distances, the more animals a particular winter range may be able to support.¹¹⁰ The inverse is also true: if ungulates no longer migrate, the carrying capacity of the landscape may be diminished and animal populations may decline.¹¹¹

Ecologists increasingly believe that migratory diversity is important for ungulates because it promotes resilience, stability, and productivity within a population.¹¹² Variable migration distances expose animals to different threats that can affect population segments disproportionately.¹¹³ For example, hypothetically migration route diversity could allow a herd to persist even if some of the herd's population perish as a result of increased snow or predation along a particular route segment in a given year.¹¹⁴ Maintaining and promoting migratory diversity can also preserve a variety of seasonal ranges for ungulates, making them less reliant on the environmental conditions of any one particular seasonal range.¹¹⁵ This is similar to salmon's "portfolio effect," where populations with variable migration timings are known to be more resilient to perturbation.¹¹⁶

F. Migration is a Learned Behavior in Ungulates

Many of the seminal studies of animal migration come from ornithology, where it has long been clear that migratory behavior can

106. *The Extra Mile*, *supra* note 23, at 4.

107. *Id.* at 1.

108. *Id.*

109. *Id.* at 7.

110. *Id.*

111. *Id.*

112. Lowery, *supra* note 57, at 8835.

113. *The Extra Mile*, *supra* note 23, at 6.

114. See Lowery, *supra* note 57, at 8836 (migratory diversity "may minimize the effects of disease through reducing transmission rates and densities of any single seasonal range.").

115. *Id.*

116. See Daniel E. Schindler et al., *Population Diversity and the Portfolio Effect in an Exploited Species*, 465 NATURE 609, 609 (2010) (analyzing the variance dampening effect of variability in the annual Bristol Bay salmon returns).

have a strong genetic basis.¹¹⁷ In contrast, scientists have recently found evidence that ungulate migration is a learned behavior, one that is culturally transmitted from mother to young, as opposed to a genetically inherited trait.¹¹⁸ To develop this evidence, scientists studied the behavior of individual migratory bighorn sheep that were translocated into vacant landscapes where extirpated populations of bighorn sheep once existed, or into existing populations of bighorn sheep that had been reestablished three decades before.¹¹⁹ Scientists discovered that the bighorn sheep that were translocated into vacant landscapes failed to migrate, while those that were translocated into existing herds did gradually adopt migratory behavior.¹²⁰

The experiment was replicated in translocated migratory moose, with similar results.¹²¹ Evidence from both experiments suggests that social learning is the primary agent underlying ungulate migratory tendencies.¹²² Social learning occurs when more experienced individuals, who have gained knowledge of local phenological patterns over time, share or demonstrate that knowledge with inexperienced individuals.¹²³ When a socially learned behavior persists and is transmitted from generation to generation, it is known as cultural transmission.¹²⁴ Scientists now have empirical evidence that “learning and cultural transmission underlie the establishment and maintenance of ungulate migration.”¹²⁵

G. Species Plasticity and Migratory Route Fidelity

While social learning can inform ungulates of when and where to migrate, species of migratory ungulates vary widely in their fidelity to

117. Peter Berthold, *Genetic Control of Migratory Behavior in Birds*, 8 TRENDS ECOLOGY & EVOLUTION 254, 254 (1991).

118. Jesmer, *supra* note 90, at 1023.

119. *Id.*

120. *Id.*

121. *Id.*

122. *Id.*

123. *See id.* (requiring extensive periods of time for social learning and cultural transmission to occur).

124. *Id.*

125. *Id.* at 1025. “[S]ocial learning can be highly faithful if it is naturally selected to be so, that is, if there is a natural selection pressure on cognitive mechanisms for them to precisely achieve a faithful reproduction of the input they receive.” Nicolas Claidiere & Dan Sperber, *The Natural Selection of Fidelity in Social Learning*, 3 COMMUNICATIVE & INTEGRATIVE BIOLOGY 350, 351 (2010).

particular migration routes or winter and summer ranges.¹²⁶ The hypothesized advantage of high site fidelity is that habitats which provided food and safety in past years are likely to furnish these resources again in the future, whereas exploratory movements into novel habitats can be risky. As a result, it is also true that animals with high site fidelity may not always forage or migrate in the best locations available. In some cases, an ungulate's use of habitats and migration routes is "dependent on population dynamics and strength of site fidelity."¹²⁷ For example, free-ranging American bison have been shown to opt for site fidelity over forage quality, a behavior that likely explains why management efforts to reduce bison population sizes and to reduce range distribution are often ineffective.¹²⁸ Mule deer also have a "strong fidelity to their migratory routes across seasons and years."¹²⁹ Scientists have speculated that the relative inflexibility of mule deer may be one of the reasons why their populations have generally declined in recent decades. Meanwhile, elk are comparatively flexible in their migratory behaviors, which may, conversely, help explain why their populations have flourished even in many of the same landscapes with declining deer populations.¹³⁰

Pronghorn exhibit the greatest behavioral flexibility of western U.S. ungulates; their migration patterns are unpredictable and vary among individuals and populations.¹³¹ A study of pronghorn migratory patterns in the Red Desert of Wyoming found that 25 percent of the study animals were migratory, 33 percent were nomadic, and 40

126. Hall Sawyer et al., *Migratory Plasticity Is Not Ubiquitous Among Large Herbivores*, 88 J. ANIMAL ECOLOGY 450, 454 (2019) [hereinafter *Migratory Plasticity*]. Behavioral ecologist Dr. Walter Piper noted that "animals learn about both the inherent quality and physical and biotic features of inhabited space. . . and hence, they gain 'site familiarity.'" Walter H. Piper, *Making Habitat Selection More "Familiar": A Review*, 65 BEHAV. ECOLOGICAL SOCIOBIOLOGY 1329, 1329 (2011). Site familiarity has not been well studied and as a result is disregarded by many models of habitat selection. *Id.*

127. Jerod A. Merkle et al., *Bison Distribution Under Conflicting Foraging Strategies: Site Fidelity vs. Energy Maximization*, 96 ECOLOGY 1793, 1800 (2015). High fidelity to specific migration routes may lock animals into patterns that are no longer beneficial. *Id.* Migration routes are resources that have historically been reliable to migrants and fidelity to those routes may constrain an animal's ability to discover new resources and embark on a new route. Wyckoff et al., *supra* note 88, at 3.

128. Merkle et al., *supra* note 127, at 1800.

129. *Migratory Plasticity*, *supra* note 126, at 454. While mule deer exhibit strong fidelity to their migration routes, the timing of their migration varies from year to year and is determined by changes in local weather and vegetative conditions. Kevin L. Monteith et al., *Time of Seasonal Migration in Mule Deer: Effects of Climate, Plant Phenology, and Life-History Characteristics*, 2 ECOSPHERE, Apr. 2011 at 1, 26.

130. *Migratory Plasticity*, *supra* note 126, at 456–57.

131. KAUFFMAN ET AL., *supra* note 1, at 19.

percent were nonmigratory.¹³² An exception to pronghorn migratory unpredictability is the Path of the Pronghorn, a famous 120-mile corridor between summer range in Grand Teton National Park and winter range in the Green River Basin of Wyoming, where local terrain features force pronghorn to utilize the same narrow bottlenecks year after year.¹³³ While the behavioral flexibility exhibited by pronghorn may enable them to adjust to landscape disturbances, their unpredictable movements can also make it difficult for managers to identify and conserve their habitat.¹³⁴

Scientists are still learning and debating the degree of plasticity in migratory ungulates, but the debate itself highlights how important it can be for policymakers to have a basic understanding of ungulate habitat fidelity to “shape conservation planning for large herbivores by identifying populations most at risk and developing conservation actions that accommodate various levels of plasticity.”¹³⁵

H. Ecosystem Consequences of Migration and Its Loss

Migratory behavior appears important to ungulate population productivity; migratory ungulates’ seasonal presence and abundance can have “broader effects within food webs, such as sustaining large carnivores and fueling cross-ecosystem nutrient subsidies.”¹³⁶ Thus, the loss of ungulate migrations can have a significant ecological impact that can extend from “alternation of plant composition and ecosystem processes such as grassland production and nitrogen mineralization to declines in other species including apex predators, to loss of wildlife-tourism-based dollars.”¹³⁷ In African savanna systems, the “carcasses of drowned terrestrial ungulates (wildebeest) provide nutrients for aquatic scavengers or decompose into rivers, thereby releasing carbon,

132. *Id.* Nomadic species are classified as “moving between distinct locations in a seemingly unpredictable manner.” Claire S. Teitelbaum & Thomas Mueller, *Beyond Migration: Causes and Consequences of Nomadic Animal Movements*, 34 *TRENDS ECOLOGY & EVOLUTION* 569, 569 (2019).

133. KAUFFMAN ET AL., *supra* note 1, at 19. While the pronghorn that utilize the Path of the Pronghorn stay faithful to the Path when they migrate, they do not migrate every year. *Id.* Some pronghorn stay on their winter range year round or move to different summer ranges. *Id.*

134. *Id.*

135. *Migratory Plasticity*, *supra* note 126, at 451.

136. *Conserving Transboundary Migrations*, *supra* note 11, at 2–3. Migrations are increasingly being recognized “as fundamental to maintain populations and communities through effects on population productivity and the lateral transport of nutrients within and across ecosystems.” Lowery, *supra* note 57, at 8830.

137. Berg et al., *supra* note 102, at 2.

nitrogen, and phosphorus into the environment over time.”¹³⁸ The loss of ungulate migrations in the American West could be catastrophic in some ecosystems.¹³⁹

Migratory ungulates increase the diversity and productivity of grasslands at large scales. Much insight on this subject has come from classic studies of wildebeest in the Serengeti-Mara Ecosystem, later extended by observations from American bison.¹⁴⁰ With sufficient inputs of rainfall, grazing by large groups of migratory wildebeest can maintain grasses in a state of rapid growth, causing a near doubling of grass biomass over the course of the growing season when compared with ungrazed sites.¹⁴¹ This effect facilitates another migratory species, the Thompson’s gazelle, which uses the areas grazed by wildebeest later in the year.¹⁴² Bison migrations have been lost in most of the species’ range, but studies of conservation herds can give us a picture of their ecological impact. Bison feed on dominant grasses, releasing other grasses and forbs from competition.¹⁴³ Bison urine amplifies their effects by increasing plant biomass and nitrogen concentration.¹⁴⁴ Bison also facilitate other species; for example, some butterflies prefer the vegetation that grows around bison wallows.¹⁴⁵ Ecologist Chris Geremia and co-authors found that bison in Yellowstone National Park – the only truly migratory bison herd remaining – have an engineering effect on the ecosystem, prolonging the “green wave” through grazing, which stimulates plant growth and delays plant maturation.¹⁴⁶ Together these findings suggest the loss of bison, and their migrations, from North American grasslands has profoundly changed ecosystems.¹⁴⁷

138. *Id.*

139. *Conserving Transboundary Migrations*, *supra* note 11, at 3.

140. S.J. McNaughton, *Serengeti Migratory Wildebeest: Facilitation of Energy Flows by Grazing*, 191 *SCI.*, 92–94 (1976) [hereinafter *Wildebeest*]; Chris Geremia et al., *Migrating Bison Engineer the Green Wave*, 116 *PROCS. NAT’L ACAD. SCI.* 25707, 25707 (2019).

141. *Wildebeest*, *supra* note 140, at 92–94; S.J. McNaughton, *Serengeti Ungulates: Feeding Selectivity Influences and Effectiveness of Plant Defense Guilds*, 199 *SCI.* 806, 806 (1978); S.J. McNaughton, *Laboratory-Simulated Grazing, Interactive Effects of Defoliation and Canopy Closure on Serengeti Grasses*, 73 *ECOLOGY* 170, 173 (1992).

142. *Wildebeest*, *supra* note 140, at 93–94.

143. Alan K. Knapp et al., *The Keystone Role of Bison in North American Tallgrass Prairie*, 49 *BIOSCIENCE* 39, 41 (1999).

144. *Id.* at 43; T.A. Day and J.K. Detling, *Changes in Grass Leaf Water Relations Following Bison Urine Deposition*, 123 *AM. MIDLAND NATURALIST* 171, 173 (1990).

145. Anna N. Hess et al., *American Bison Influences on Lepidopteran and Wild Blue Lupine Distribution in an Oak Savanna Landscape*, 18 *J. INSECT CONSERVATION* 327, 336 (2014).

146. Geremia et al., *supra* note 140, at 25707.

147. *Id.*

Ungulate migrations can also redistribute biomass and nutrients widely across landscapes, such as in the case of mass mortality events and subsequent carcass decomposition.¹⁴⁸ For example, the annual death of an estimated 6,250 wildebeest at river crossings in the Kenyan portion of the Serengeti-Mara ecosystem contribute more than 1,000 tons of biomass to rivers; this includes an estimated 107 tons of carbon, 25 tons of nitrogen, and 13 tons of phosphorus by dry mass.¹⁴⁹ Historical accounts of bison mass drownings suggest similar dynamics were at play on the Great Plains.¹⁵⁰

Migratory ungulates are the primary food of many large carnivores and scavengers around the world. The African savanna typifies the role of migratory ungulates in sustaining a food web: here, migratory ungulates traverse a vast landscape and diverse habitats converting the plants they eat to animal biomass, which in turn sustains extraordinary productivity and abundance of carnivores and scavengers.¹⁵¹ These relationships also exhibit an important spatial dimension, whereby the seasonal presence of migratory prey at a specific location provisions local consumers. For example, in the central Arctic, after hunting caribou on winter ranges, some wolves move nearer to caribou calving areas to den – and then take advantage of caribou as they pass through on spring migration.¹⁵² Meanwhile, caribou presence and abundance on summer ranges positively influences reproduction and abundance of wolves in those areas.¹⁵³ In the Sierra Nevada of western North America, some mountain lions appear to fully migrate with populations of mule deer;¹⁵⁴ in the Greater Yellowstone Ecosystem, many of the large carnivores and scavengers in core areas feed in summer on elk, deer, and other ungulates that

148. Amanda L. Subalusky et al., *Annual Mass Drownings of the Serengeti Wildebeest Migration Influence Nutrient Cycling and Storage in the Mara River*, 114 PROCS. NAT'L ACAD. SCI. 7647, 7651 (2017); Robert M. Pringle, *How Large Herbivores Subsidize Aquatic Food Webs in African Savannas*, 114 PROCS. NAT'L ACAD. SCI. 7489, 7489 (2017).

149. Subalusky, *supra* note 148, at 7648.

150. Knapp et al., *supra* note 143, at 45.

151. Andy Dobson, *Food-Web Structure and Ecosystem Services: Insights from the Serengeti*, 364 PHIL. TRANSACTIONS ROYAL SOC'Y B. 1665, 1667 (2009).

152. Lyle R. Walton et al., *Movement Patterns of Barren-Group Wolves in the Central Canadian Arctic*, 82 J. MAMMALOGY 867, 867 (2001).

153. Michael R. Klaczek et al., *Wolf-Caribou Dynamics Within the Central Canadian Arctic*, J. WILDLIFE MGMT. 837, 845–46 (2016).

154. Becky M. Pierce et al., *Migratory Patterns of Mountain Lions: Implications for Social Regulation and Conservation*, 80 J. MAMMALOGY 986, 986 (1999).

generally occupy lower elevations along the ecosystem's frontiers in winter.¹⁵⁵

David Wilcove and Martin Wikelski have asked, "given the panoply of environmental problems we now face, is the fading glory of migration really a significant issue?"¹⁵⁶ They answer their own question with a resounding "yes," because as migrations decline, so do the important ecological properties and services associated with them.¹⁵⁷ They specifically note that "[p]rotecting the abundance of migrations is the key to protecting the ecological importance of migration. As the number of migrants declines, so too do many of the most important ecological properties and the services associated with them."¹⁵⁸ Thus, it is important to maintain abundant populations of migrating ungulates to preserve the ecosystem benefits of migration.

II. *Irreversibility of Migration Loss*

If ungulate seasonal migrations are not sufficiently protected and populations continue to decline, there is a danger that cultural knowledge of migration will not be passed down to offspring and migrations will cease, which illustrates the compounding challenges to sustaining migrations as population declines.¹⁵⁹ Once lost, migration has proven difficult to restore, thus highlighting the importance of proactively protecting native systems and their migratory portfolios.¹⁶⁰

The degree of irreversibility of migration loss is an evolving research area, and the results to date have been based on the unsuccessful efforts to restore bighorn sheep migrations in translocated populations, which has resulted in stagnated herd growth and limited range expansion over time.¹⁶¹

A. The Cautionary Example of Bighorn Sheep

While there are a few positive examples of migration restoration, attempted restorations have come at "high economic costs and represent a diminished resemblance of historic migratory patterns."¹⁶²

155. *Conserving Transboundary Migrations*, *supra* note 11, at 85.

156. David S. Wilcove & Martin Wikelski, *Going, Going Gone: Is Animal Migration Disappearing?* 6 PLOS BIOLOGY 1361, 1361 (2008).

157. *Id.*

158. *Id.*

159. Jesmer, *supra* note 90, at 1025.

160. Lowery, *supra* note 57, at 8837.

161. *Id.*

162. *Id.* at 8830.

Take for example the efforts to restore bighorn sheep, an iconic mountain migratory ungulate that was extirpated across much of its former range in western North America due to overharvest and introduction of non-native respiratory pathogens from domestic livestock.¹⁶³ Despite significant and costly restoration efforts that relied on translocation into historic ranges and augmentation of existing populations, bighorn sheep occupy only a small fraction of their former range and occur in restored populations of fewer than 100 individuals.¹⁶⁴ The lack of restoration success has been partially attributed to the failure of bighorn sheep to restore their migrations once translocated.¹⁶⁵

Historically, bighorn sheep seasonally migrated over relatively long geographic distances to take advantage of forage on summer and winter ranges.¹⁶⁶ Within native bighorn sheep populations, there is significant migratory diversity which leads to overall population resilience.¹⁶⁷ Once translocated, bighorn sheep eventually restored some migratory behavior but migrated shorter distances with notably less variation.¹⁶⁸ The loss of migratory diversity, inclusive of long-distance migrations, is considered a major reason bighorn sheep populations have remained small with limited range expansion over time.¹⁶⁹

The limited recovery of bighorn sheep populations to date represents a cautionary tale about the importance of maintaining native migrations and, specifically, maintaining migratory diversity within populations.¹⁷⁰

163. *Id.*

164. *Id.*

165. *Id.* at 8836.

166. *Id.* As discussed above, the knowledge of migration (i.e. how to exploit landscape resources) is likely socially learned and culturally transmitted. *See also* Jesmer, *supra* note 90, at 1.

167. Lowery, *supra* note 57, at 8836 (noting that “[m]igrations in native populations occurred over relatively long geographic distances and were characterized by appreciable variation among individuals along both distance continuums and a range of variation that was up to four times greater than restored or augmented populations”).

168. *Id.*

169. *Id.*

170. *Id.* As noted by Lowery and his co-authors “[w]hen population knowledge is eliminated or greatly reduced, as in restored or augmented populations, the result is not only a reduction in migratory propensity, but a loss of migratory diversity, inclusive of long distance migrations.” *Id.*

III. Threats to Migration

Western ungulates face a gauntlet of challenges during their seasonal migrations. Advances in GPS tracking and analytics have provided insight into human influences on ungulate migration.¹⁷¹ For example, long-distance migrants of the Red Desert mule deer herd cross an average of five highways and 171 fences to complete a round-trip migration.¹⁷² Because anthropogenic disturbances to migration corridors like roads, well pads, and other infrastructure may not elicit a negative behavioral response until a certain threshold is exceeded, research is being pursued to determine what the thresholds may be for individual ungulate species.¹⁷³

Princeton ecologist Dr. David Wilcove has classified four common threats to all types of migration: habitat destruction, human-created obstacles, overexploitation, and climate change.¹⁷⁴ We discuss the following categories tailored to the specific threats to Western U.S. ungulates.

A. Habitat Loss and Disturbance and Loss

Habitat loss can take two forms for migratory ungulates. The first is direct habitat loss: the conversion of habitat to infrastructure, such as buildings and roads. The second is indirect habitat loss, whereby human disturbance (e.g. noise, movement, traffic) associated with human infrastructure or other activities (e.g. oil and gas drilling, tree thinning, recreational use) acts as a form of perceived risk that prompts behavioral responses analogous to those of predation.¹⁷⁵ Direct habitat loss removes food and shelter from the landscape, while indirect habitat loss reduces animals' use of available forage, affecting their energy intake. Both can result in population-level declines.¹⁷⁶ Ecologists have long understood the importance of direct habitat loss as a driver of declines in migratory wildlife, including ungulates, but only recently have the effects of indirect habitat loss come to light.

171. *Id.* at 8836–37.

172. *The Extra Mile*, *supra* note 23, at 9.

173. Copeland, *supra* note 19, at 7 (current analysis suggests that mule deer make changes in their migratory behavior at or above 1.99–2.82 wells pads/kilometer²).

174. Wilcove & Wikelski, *supra* note 156, at 1361.

175. Samantha P. H. Dwinnell et al., *Where to Forge When Afraid: Does Perceived Risk Impair Use of the Foodscape?*, 29 *ECOLOGICAL APPLICATIONS* 1, 2 (2019).

176. *Id.* at 1–2.

Some of the clearest examples are for ungulates affected by energy development on public lands in the Western U.S.¹⁷⁷

Indirect habitat loss is now known to affect migratory ungulates on both seasonal ranges and migration corridors. In one of the most rigorous, long-term studies of indirect habitat loss on wildlife, Hall Sawyer and colleagues showed that migratory mule deer avoided gas well pads and roads on their winter ranges—staying about 1 kilometer away from them all winter, on average—and this avoidance behavior was the most likely explanation for a 36 percent decline in population numbers and 45 percent decline in hunter harvest over about 15 years.¹⁷⁸ Researchers have also recently begun to better understand how energy development impacts ungulates on their migrations.¹⁷⁹

A recent study by Wyckoff *et al.* looked at mule deer migrations before and during the development of a coal bed methane field in Wyoming's Atlantic Rim Project Area. Researchers found that while mule deer maintained their fidelity to migration routes, they coped with intense development by moving quickly through the area and reducing their use of stopover areas.¹⁸⁰ This is significant because as discussed earlier, during migration, mule deer spend 95 percent of their migration time in stopover areas¹⁸¹ and rely upon the forage found here to replenish lost fat stores after leaving winter ranges.¹⁸² As a result of this study, we are able to make the conclusion that rapid expansion of energy infrastructure into previously intact habitats that support remaining migratory populations is likely to have negative effects on mule deer health.¹⁸³ An important contemporary research direction is to understand what levels or thresholds of development trigger such responses. Evidence from multiple mule deer populations in Wyoming suggests that use of corridors by migratory deer declines sharply when more than 3 percent of the habitat is disturbed as a result of energy development¹⁸⁴

177. Wyckoff *et al.*, *supra* note 88, at 3–4.

178. Hall Sawyer *et al.*, *Mule Deer and Energy Development – Long-Term Trends of Habituation and Abundance*, 23 *GLOB. CHANGE BIOLOGY* 4521, 4527 (2017).

179. KAUFFMAN *ET AL.*, *supra* note 1, at 100.

180. Wyckoff *et al.*, *supra* note 88, at 7–8. In contrast, Wyckoff *et al.* found that impact from residential development on migrating mule deer less pronounced than energy development because the pace of residential development occurs more slowly near existing residential development. *Id.* at 9.

181. *Id.* at 2.

182. *Id.*

183. *Id.* at 10.

184. Hall Sawyer *et al.*, *Migratory Disturbance Thresholds with Mule Deer and Energy Development*, 84 *J. WILDLIFE MGMT.* 930, 934 (2020).

B. Human-Created Obstacles

Impermeable barriers, such as game-proof fencing, have obvious and detrimental effects to migrations, but researchers have also found that the influence of semi-permeable barriers, such as fences and infrastructure (roads, pipelines, etc.) associated with housing development and energy development, also have detrimental effects.¹⁸⁵ For example, it has been shown that ungulates avoid linear structures such as roads, seismic lines, and pipelines, while migrating between seasonal ranges.¹⁸⁶ While avoiding these linear structures, the animals move quickly through developed areas, potentially reducing their use of and benefits from the resources in those areas.¹⁸⁷

Fencing is a particularly pervasive influence for migratory ungulates in the western U.S. A recent review by McInturff *et al.* conservatively estimates that the western U.S. contains about one million miles of fencing.¹⁸⁸ Fences impact ungulates in three ways: (1) ungulates choose not to cross the fence, which impedes movement; (2) ungulates spend time and energy looking for a place to cross a fence; and (3) when attempting to cross a fence, an ungulate may snare its legs in the fence wire, become entrapped, and die.¹⁸⁹ One study found that juvenile ungulates are particularly vulnerable to fence entrapment, and they are perhaps as much as eight times more likely to be caught in a fence than an adult due to their smaller size and inexperience.¹⁹⁰ Most ungulate fence mortalities, particularly in juveniles, are associated with woven fences as opposed barbwire fences.¹⁹¹ Because mule deer typically cross more fences than other types of ungulates, they have a higher probability of getting caught in fences.¹⁹² However, in one study of pronghorn and mule deer responses to fences in a Wyoming county with 6,000 kilometers of fencing, pronghorn were most acutely

185. Wyckoff *et al.*, *supra* note 88, at 10.

186. *Id.*

187. *Id.*

188. Alex McInturff *et al.*, *Fence Ecology: Frameworks for Understanding the Ecological Effects of Fences*, 70 *BIOSCIENCE* (forthcoming 2020), <https://academic.oup.com/bioscience/advance-article/doi/10.1093/biosci/biaa103/5908036>.

189. Justin L. Harrington & Michael R. Conover, *Characteristics of Ungulate Behavior and Mortality Associated with Wire Fences*, 34 *WILDLIFE SOCIETY BULL.* 1295, 1295–96 (2006).

190. *Id.* at 1303.

191. *Id.* at 1301. The authors note that woven fences with a single strand of barb wire on the top pose the greatest mortality risk because of the rigidity of the woven wire and the snagging ability of the barbed wire. *Id.*

192. *Id.* at 1302–03.

affected.¹⁹³ In the study, pronghorn encountered fences about 250 times per year, and failed to cross in about 40 percent of these cases.¹⁹⁴ Behavioral responses included bouncing away from fences, tracing back and forth along them, and becoming trapped within closed pasture.¹⁹⁵

Roads pose another major human-created obstacle for migratory ungulates. When major roads bisect migration corridors, the effects can be dangerous for both animals and humans. In 2019, the Colorado Department of Transportation reported 5,595 animals were killed on Colorado roads, with ungulates, particularly deer, accounting for well over half of that total.¹⁹⁶ In Wyoming, collisions with wildlife are estimated to cost \$24–29 million annually in injuries to people and other damages, and another \$20–23 million in the loss of harvestable wildlife.¹⁹⁷

As a result of the threat to both humans and ungulates, efforts are underway in many locations to create roadway overpasses and underpasses that allow for safe animal road crossings.

C. Climate Change

The fact that migrating ungulates require a range of habitats, from summer to winter, may make them particularly vulnerable to the detrimental impacts of climate change.¹⁹⁸ Scientists have begun to look more closely at migrating ungulates and behavioral plasticity in response to changing environmental conditions to better understand how adaptable they may be to the impacts of climate change.¹⁹⁹ Ungulate migratory mobility suggests they might be able to track changes in the location of suitable environments as conditions shift.²⁰⁰ However, migratory ungulates need to find suitable habitat throughout the entirety of their migration route, and seasonal habitats may be

193. Wenjing Xu et al., *Barrier Behavior Analysis (BaBA) Reveals Extensive Effects of Fencing on Wide-Ranging Animals*, J. APPLIED ECOLOGY (forthcoming 2020).

194. *Id.*

195. *Id.*

196. COLO. DEP'T OF TRANS., 2019 ROADKILL DATA REPORT (2019), <https://www.codot.gov/programs/environmental/wildlife/data/annual-roadkill-reports/raodkill-data-2019.pdf>.

197. CORINIA RIGINOS ET AL., PLANNING-SUPPORT FOR MITIGATION OF WILDLIFE-VEHICLE COLLISIONS AND HIGHWAY IMPACTS ON MIGRATION ROUTES IN WYOMING 3 (2016), <https://rosap.nrl.bts.gov/view/dot/34185>.

198. Robert A. Robinson et al., *Traveling Through A Warming World: Climate Change and Migratory Species*, 7 ENDANGERED SPECIES RSCH. 87, 88 (2009).

199. *Migratory Plasticity*, *supra* note 126, at 451.

200. Robinson et al., *supra* note 198, at 88.

affected by climate change in different ways, particularly high-altitude summer ranges.²⁰¹

Studies in the Greater Yellowstone Ecosystem have recently considered the influence of climate change on migratory elk.²⁰² One study explored the effects of a severe drought and hot summer temperatures – shifts that are consistent with predictions for climate change in the region – on the reproduction of elk in the partially migratory Clarks Fork herd.²⁰³ Whereas 90 percent of female elk usually become pregnant each year in a typical herd, the study documented a 68 percent pregnancy rate in the migratory portion of the Clarks Fork herd.²⁰⁴ The authors found evidence that this low pregnancy rate may have resulted from a shorter “green up” in the high-elevation summer ranges of migratory elk.²⁰⁵ Another study by ecologist Dr. Gregory Rickbeil *et al.* explored the timing of elk migrations in response to changing climatic conditions in the Greater Yellowstone Ecosystem from 2001 to 2017.²⁰⁶ Rickbeil’s analysis revealed that elk adjusted their migration timing to match changing environmental conditions, including earlier snow melt, earlier spring green-up, and changes in snow accumulation.²⁰⁷ The researchers concluded that migrating elk demonstrate significant behavioral plasticity and may be able to maintain their access to high-quality forage even under climate change.²⁰⁸ These two studies together suggest that if climate change reduces the duration of the green-up, migratory ungulates like elk may suffer, but if climate change only alters the timing of the green-up without changing its duration, they may be able to adjust.

Mule deer may be less adaptable to the impacts of climate change because they demonstrate less behavioral plasticity and greater migration route fidelity compared to other migratory ungulates.²⁰⁹ Dr. Ellen Aikens *et al.* found that ongoing drought induced by climate change is predicted to speed up the progression of the spring green-up,

201. *Id.*

202. *Shifting Patterns*, *supra* note 73, at 1245; Rickbeil, *supra* note 57, at 2369.

203. *Shifting Patterns*, *supra* note 73, at 1246.

204. *Id.* at 1249.

205. *Id.* at 1251–52.

206. Rickbeil, *supra* note 57, at 2369.

207. *Id.* at 2376.

208. *Id.*

209. *Migratory Plasticity*, *supra* note 126, at 457.

decreasing the benefits of green-wave surfing for mule deer.²¹⁰ As climate change continues to alter Western landscapes, it can be expected that mule deer may suffer more than elk.²¹¹ This implies conservation efforts that minimize barriers to movement, and reduce habitat fragmentation, are likely needed to ensure that mule deer in particular can successfully adapt to a changing climate.²¹²

Changes in ungulate migration timing and/or routes because of climate change may also pose other environmental, economic, or social consequences. As the climate in the West warms, resulting in less snowfall in some areas, ungulates will likely spend prolonged periods of time on their summer ranges.²¹³ The resulting impacts from this shift in timing may include: predator-prey dynamics, carnivore-livestock conflicts,²¹⁴ disease ecology,²¹⁵ and harvest management.²¹⁶ Adjustments in human adaptation to changing climatic conditions, such as adjusting land use, resource management, or exploitation patterns, may also have future significant effects on migrating species and their habitats.²¹⁷

While traditional migratory species conservation measures have focused on the management of specific protected areas, as species respond and adapt to climate change by altering their routes and range, those initially protected areas may no longer be relevant.²¹⁸ It will be important to continue to (1) study migration route usage; (2) identify shifts away from currently used routes; (3) adaptively manage and

210. Ellen O. Aikens et al., *Drought Reshuffles Plant Phenology and Reduces Foraging Benefits of Green-Wave Surfing for a Migratory Ungulate*, 26 *GLOB. CHANGE BIOLOGY* 4215, 4222 (2020).

211. *Migratory Plasticity*, *supra* note 126, at 457.

212. Aikens et al., *supra* note 210, at 4222–23.

213. *Id.*

214. Rickbeil, *supra* note 57, at 2378. Wolf depredation on cattle has a correlation to elk migration timing as wolves tend to turn to cattle as a prey source after elk migrate off winter ranges. *Id.* Scientists suspect that migration timing alterations as a result of climate change may result in an increase in wolf depredation on cattle. *Id.*

215. *Id.* The spread of brucellosis is of particular concern. Brucellosis is a zoonotic disease that is transmitted from elk to cattle. *Id.* The transmission rate of the disease depends upon the amount of time cattle come into contact with elk in the late winter and early spring and changing elk migration timing will have an impact on this dynamic, perhaps for the better. *Id.*

216. *Id.* Hunting seasons are often timed to promote the harvest of resident elk and to avoid the harvest of migratory elk (or at least to maintain a target ratio of migrant: non-migrant). *Id.* Changes in migration timings could certainly affect this management objective. *Id.*

217. Robinson, *supra* note 198, at 95.

218. *Id.* at 94.

conserve future key forage areas; and (4) remove the restrictions on sites that are no longer being used.²¹⁹

ECONOMIC PRINCIPLES THAT APPLY TO CONSERVING MIGRATIONS

In thinking about the conservation of Western ungulate migrations, it is important to understand human actions and drivers of migratory species value and conservation action. Far broader than just adding up the financial costs and benefits, economic analysis brings people and institutions alongside ecological considerations to inform choices about cost-effective conservation policy. Economic analysis of species conservation, spatial configuration of habitat conservation, and spatial bio-economic conditions, together with environmental federalism provide a comprehensive framework to best establish conservation policy for migratory species.

I. How Does Economics Inform Species Conservation?

Conservation of species creates value to society through both people's use of species—such as hunting—and people's non-use of species—such as knowing that a species or biodiversity exist. Species conservation has a public good characteristic because it is both non-rival—one person's recreational viewing of the species does not diminish someone else's viewing value—and non-excludable—it is prohibitively expensive to exclude people from capturing value from species conservation. As with all public goods, the market by itself provides too little species conservation compared to overall societal value, which implies that government institutions have a role to play in conserving species for societal wellbeing. Government actions include direct land ownership, direct management of species, regulations that define species conservation actions for private, state, and federal land, and policies to provide incentives for species conservation on private lands. Economics can define cost-effective policies to generate socially preferred levels of public goods. In terms of conserving migratory species, economics can also help define the nature of the coordination that landowners and policymakers confront when thinking about creating cost-effective migration routes across space and time.

Species conservation policy must reflect the interactions of people and species. Forming policies that focus only on natural science can lead to costly inefficiencies. Similarly, forming human-centered policies can lead to unexpected and undesired conservation losses.

219. *Id.*

Economics matters for species conservation in at least three ways.²²⁰ First, economics identifies how peoples' actions, strategic and otherwise, contribute to determining the risks and threats faced by species.²²¹ Second, economics measures the opportunity cost of protecting species.²²² Third, people respond to economic incentives, and their response can contribute to species conservation.²²³ Overall, economics provides a framework that integrates human and species behavior, which provides a platform for developing conservation policy that reflects species, people, and their strategic interactions.

Economic analysis informs species conservation policy in many ways, including measuring non-market values of species and habitats, analyzing private incentives for species conservation, leveraging private-public interactions, considering negative and positive externalities, and defining coordination strategies. Economic analysis of species conservation over time considers the role of forthcoming information and uncertainty in making conservation policy that reflects the possibility of irreversible losses from species extinctions or habitat destruction.²²⁴ Within economics, the reserve site selection (RSS) literature places an emphasis on identifying locations for establishing protected areas by considering the maximum number of species that can be conserved for a given budget, or the least cost way of conserving a target number of species; finding that more species are conserved per dollar when land costs are considered in the site selection process.²²⁵ Within RSS, the concept of "complementarity" considers that the species conservation value of a particular unit of land being considered for conservation depends on the species conservation value/characteristics of all of the other conserved sites.²²⁶ This complementarity implies that decisions regarding species conservation must occur at a landscape scale rather than at a per-parcel scale.²²⁷ Ecologists also emphasize the role of the spatial configuration of

220. Shogren et al., *supra* note 35, at 1257.

221. *Id.*

222. *Id.*

223. *Id.*

224. See generally Heidi J. Albers, *Modeling Ecological Constraints on Tropical Forest Management: Spatial Interdependence, Irreversibility and Uncertainty*, 30 J. ENV'T ECON. & MGMT. 73, 73 (1996) [hereinafter *Modeling Constraints*]; Heidi J. Albers et al., *Valuation of Tropical Forests: Implications of Uncertainty and Irreversibility*, 8 ENV'T & RES. ECON. 39, 39 (1996); Heidi J. Albers & Michael J. Goldbach, *Irreversible Ecosystem Change, Species Competition, and Shifting Cultivation*, 22 RES. & ENERGY ECON. 261, 261 (2000).

225. Amy Ando et al., *supra* note 38, at 2126–28.

226. *Id.*

227. *Id.*

conserved land in protecting species. Integrating these two disciplines into economic-ecologic analyses has resulted in examinations of the compactness and fragmentation of conserved habitat and land networks; positive externalities and minimum habitat size; and spatial tradeoffs between development and matrix and core habitats.²²⁸ Additionally, economic policies such as agglomeration bonuses and habitat leases provide incentives for private conservation that generate public goods across the world.

II. *Economic Goals of Migratory Species Conservation*

Relevant to migratory species conservation, economic analysis can be used to define the socially preferred level of species and habitat conservation based on coordinated efforts, which can be based on a goal to maximize net social benefits or achieve a population size for least cost.

To achieve a conservation goal based on maximizing the net social benefits, economic analysis considers all values from the proposed conservation action, including ecosystem services as well as “existence values” (value of knowing a species exists or even value in knowing long-distance migrations continue to occur) that have no market exchange value and therefore require the development of economic valuation be considered in the analysis.²²⁹ In addition to considering all market and non-market benefits, such analysis recognizes the values wherever they occur. That implies that someone living far from a species who never views that species still derives an existence value that must be included in the calculation of the maximum net social benefits.

In other situations, a policy’s goal may not center on maximizing net social benefits, instead it may center on other goals including specific population size for a species or a level of species persistence. In that case, economic tools can identify the least cost manner of achieving that goal, while still considering all market and non-market costs.²³⁰ This cost effectiveness analysis increases the efficiency of achieving a conservation goal, even when that goal is not set to reflect the point of maximum net social benefits.

For goals of maximizing net social benefits or of cost-effectively achieving conservation, budget constraints can pose complications.

228. *Modeling Constraints*, *supra* note 224, at 73; Hayri Önal et al., *Optimal Design of Compact and Functionally Contiguous Conservation Management Areas*, 251 EUR. J. OPERATIONAL RSCH. 957, 957–68 (2016).

229. *Id.*

230. *Id.*

Although all market and non-market values should be considered in conservation policy analysis, values accrue in a dispersed fashion and are not captured in financial resources that can be used by a land manager.²³¹ For example, although a fee to enter an open space produces income for managers, not all values from that open space are captured, including recreation values above the fee and ecosystem services produced by the open space.²³² Many costs of managing that open space, however, must be covered with cash itself.²³³ The cash budget of a manager forms an additional constraint toward the pursuit of a conservation goal.²³⁴ In addition, the need to capture value as cash can influence the policies managers pursue to achieve a conservation goal, such as implementing entry fees or hunting license fees.²³⁵ Due to the inability to capture all values as income, governments impose taxes to generate funding to cover the costs of achieving the desired level of non-market conservation values created by protected migratory habitat.²³⁶ Governments can provide agencies and managers with some of that tax revenue to provide a budget for conservation activities on the targeted migratory routes or habitats. For example, revenue generated from state taxes is provided to wildlife management agencies to conserve the non-game species such as prairie dogs and non-game birds that do not receive much public attention but play key roles in ecosystem health needed for effective migration.²³⁷

Economic analysis identifies and evaluates tradeoffs that policymakers can use to make decisions rather than imposing mandates for a particular outcome. For example, as previously discussed, some migratory species may irreversibly lose the knowledge required to migrate successfully under some circumstances. In the presence of such

231. *Id.*

232. See Amy W. Ando & Payal Shah, *Demand-Side Factors in Optimal Land Conservation*, RES. & ENERGY ECON. 203, 203 (2010) (discussing balancing conservation needs with a decline in people's willingness to pay for conservation the further the conservation area is from them); Sara Kaffashi et al., *Exploring Visitors' Willingness to Pay to Generate Revenues for Managing National Elephant Conservation Center in Malaysia*, 56 FOREST POL'Y ECON. 9, 9 (2015) (discussing how visitor's willingness to pay entry fees is related to the experience provided to them by the conservation area, among other factors); Pallab Mozumder et al., *Lease and Fee Hunting on Private Lands in the U.S.: A Review of The Economic and Legal Issues*, 12 HUM. DIMENSIONS WILDLIFE 1 (2007).

233. *Id.*

234. *Id.*

235. *Id.*

236. *Id.*

237. Bruce A. Stein et al., *Reversing America's Wildlife Crisis: Securing The Future of Our Fish and Wildlife*, NAT'L WILDLIFE FED'N 1, 9 (2018).

irreversibility, economic policy analysis can determine the amount of precaution—rather than mandating a particular level of precaution or mandating the banning of an action that could produce an irreversible outcome—when facing such irreversibility.²³⁸ Economics frames migratory risk management as a balance of the costs and benefits of alternative risk reduction strategies.

III. *Economics of Spatial Coordination*

Although maximizing net social benefits from conservation is a societal goal, achieving it means that some groups or locations bear costs while others enjoy the benefits. In a migratory species example, conservation activities on private lands to conserve elk migrations may impose costs on those landowners while the benefits of conservation accrue to visitors to the region who view the elk.²³⁹ In economics, a conservation policy is “Pareto-improving” if all individuals who incur net costs can be compensated to make them neutral while other individuals capture net benefits.²⁴⁰

In ungulate migrations, a spatial mismatch of costs and benefits may arise. Migratory species might damage resources in one area but provide important ecosystem services in others.²⁴¹ Addressing this spatial mismatch requires “spatial subsidies,” which are payments to people or locations that incur damage costs from public agencies or people located in areas that receive benefits.²⁴² Spatial subsidies are used in the monarch butterfly migration to ensure sufficient incentives across the landscape by calculating costs associated with overwintering in Mexico and summering/breeding in the U.S. and Canada.²⁴³

238. See generally Kenneth J. Arrow & Anthony C. Fisher, *Environmental Preservation, Uncertainty, and Irreversibility*, 88 Q. J. ECON. 312 (1974) (exploring the implications of uncertainty surrounding environmental costs of economic activities); *Modeling Constraints*, *supra* note 227, at 74.

239. HANLEY ET AL., *supra* note 36.

240. *Id.*

241. Kenneth J. Bagstad et al., *Ecosystem Service Flows From a Migratory Species: Spatial Subsidies of the Northern Pintail*, 48 AMBIO 61, 61–62 (2019); Darius J. Semmens et al., *Accounting for the Ecosystem Services of Migration Support and Spatial Subsidies*, 70 ECOLOGICAL ECON. 2236, 2236 (2011).

242. Parkhurst, *supra* note 41, at 305–21.

243. See Matthias Schroter et al., *Assessing Nature’s Contribution to People*, 359 SCI. 270, 270–71 (2018) (discussing various beneficial contributions from nature); Michelle A. Haefele et al., *Willingness to Pay for Conservation of Transborder Migratory Species: A Case Study of the Mexican Free-Tailed Bat in the United States and Mexico*, 66 ENV’T MGMT. 229, 230 (2018); Darius Semmens et al., *Quantifying Ecosystem Service Flows at Multiple Scales Across the Range of Long-Distance Migratory Species*, 31 ECOSYSTEM MGMT. 255, 259 (2018); Michelle A. Haefele et

IV. *Hierarchies of Management*

The provision of most public goods occurs through the actions of many actors and organizations, ranging from federal government agencies to state and local agencies to individual landowners.²⁴⁴ The total level of conservation of public goods provided results from an aggregation across all of these conservation actors.²⁴⁵ With species conservation and some ecosystem services, the value generated by an agency in one location is a function of the values created elsewhere.²⁴⁶ For example, if one state provides enough conservation to effectively protect a particular species, the value of further conservation actions in another state may not be high because the first state's actions reduce the need for conservation elsewhere. If each state considers only protections within their jurisdictions, the states inefficiently duplicate each other's efforts, which may produce lower overall levels of conservation than if the states had coordinated their actions. In the case of migratory ungulates, the need for coordination of conservation activities is even higher.²⁴⁷ Uncoordinated conservation of two states can produce local seasonal habitat conservation benefits, but coordinated conservation produces broader, annual habitat conservation benefits.²⁴⁸ For example, if states do not coordinate conservation, migratory species may face barriers between the two states' conservation areas that limit benefits of conservation because the species can't access the conserved area. Coordinated conservation considers the entire migratory route in making state-based decisions. In practice, different conservation organizations or actors consider and

al., *Multi-Country Willingness to Pay for Transborder Migratory Species Conservation: A Case Study of Northern Pintails*, 157 *ECOLOGICAL ECON.* 321, 322 (2019).

244. Heidi J. Albers & Amy W. Ando, *Could State-Level Variation in the Number of Land Trusts Make Economic Sense?*, 79 *LAND ECON.* 311, 311 (2003).

245. *Id.*

246. *Id.* at 313–14.

247. *Id.* at 322.

248. *Id.* at 313–14 (considering the efficient “industry structure” of private land conservation trusts that reflects that “the production of some level of conservation benefits . . . is not a simple function of the quantity of land measured in total acres. Rather, it is a function of which particular pieces of land have been conserved” and that “because conserved parcels create ‘spillover’ benefits when appropriately paired, the production of conservation benefits is a function of bundles of land parcels rather than of the sum of benefits from individual parcels.” They find that states that have ecosystem services that require spatial patterns of conservation produce those services with a smaller number of land trusts who coordinate across localities.).

operate over different scales, sometimes internalizing the coordination costs and sometimes reacting to other actors' decisions.²⁴⁹

From this perspective, a conservation agency with the level of jurisdiction that considers the full migration route could be an appropriate level of management because of an ability to coordinate across all relevant actors and locations.²⁵⁰ In contrast, local authorities may have more on-the-ground knowledge about both ecological and socioeconomic factors of specific geographies that influence the effective implementation of conservation policy. In practice, conservation decision-making occurs in a nested hierarchy with each level having different types of information, budget constraints, policy tools, and potentially different conservation goals.²⁵¹

The economics of environmental federalism literature addresses questions of the efficient level of governmental management for ecosystem services, with particular emphasis on air pollution.²⁵² In the U.S., regulatory authority has oscillated between periods of relatively greater centralized and decentralized control.²⁵³ In general, local

249. See Heidi J. Albers et al., *Patterns of Multi-Agent Land Conservation: Crowding In/Out, Agglomeration and Policy*, 30 RES. & ENERGY ECON. 492, 492 (2008) [hereinafter *Crowding In/Out*] (exploring the “impact of public conservation and public policy on the quantity and configuration of private land conservation . . . [and] showing how land conservation agents might interact strategically in space depending on preferences.”); Heidi J. Albers et al., *A Spatial-Econometric Analysis of Attraction and Repulsion of Private Conservation by Public Reserves*, 56 J. ENV'T ECON. & MGMT. 33, 33–45 (2008) [hereinafter *Spatial-Econometric*] (performing data analysis to determine how conservation organizations' decisions interact in three states with different spatial ecosystem service benefit functions and requirements for coordination across space).

250. See Albers & Ando, *supra* note 244, at 312 (emphasizing the need for conservation groups to coordinate and determine relative need).

251. See *Working Group: Hierarchies in Conservation*, NAT'L INST. FOR MATHEMATICAL & BIOLOGICAL SYNTHESIS, http://www.nimbios.org/workinggroups/WG_conservation (last visited Sept. 21, 2020) (identifying hierarchies and challenges to decision-making in conservation).

251. Taking advantage of the short period of time in which migratory birds use particular areas as stopovers, The Nature Conservancy's BirdReturns program uses annual rental payments to northern California rice farmers to flood their fields for longer periods to create “pop up” wetland habitat for migratory waterbirds. Statistical models of associations between waterbird abundances and habitat conditions are combined with predictions of the spatial distribution of naturally flooded areas to identify rice fields where additional water applications would yield the highest biological return in each season. An auction mechanism is used to enroll farmers with high value fields into the program each year to improve cost-effectiveness. Gregory H. Golet et al., *Using Ricelands to Provide Temporary Shorebird Habitat During Migration*, 28 ECOLOGICAL APPLICATIONS 409, 409–26 (2018).

252. Wallace E. Oates, *A Reconsideration of Environmental Federalism*, (Resources for the Future, Working Paper 01–54).

253. See E. Donald Elliott et al., *Toward a Theory of Statutory Evolution: The Federalization of Environmental Law*, 1 J.L. ECON. & ORG. 313, 326–35 (1985) (tracking the evolution of environmental lawmaking between federal and state entities).

regulatory authority for providing local public goods is thought to be more efficient due to interjurisdictional competition and better information about the cost of public good provision and local preferences.²⁵⁴ However, in the case of air quality as a public good and air pollution as a negative externality, it raises two reasons as to why it may be socially undesirable to leave the authority for pollution control exclusively to state and local governments. First, local governments have no incentives to consider the impact of pollution created in their jurisdiction that causes damage in other jurisdictions, which leads to less pollution control than is socially preferred at a larger scale.²⁵⁵ Federal governments, in contrast, have a mandate to consider environmental damage (and benefits) that accrue to any citizen, regardless of their location.²⁵⁶ Second, states may lower environmental standards to secure a competitive advantage for polluting firms located in their state, creating a pollution control level desirable at a regional or federal scale.²⁵⁷

Oates and Schwab find that decentralized environmental authority can lead to efficient outcomes, provided individuals and capital are mobile across jurisdictions, there is a large number of jurisdictions, there are no interjurisdictional externalities, and governments maximize the social welfare in their jurisdiction.²⁵⁸ Violation of these conditions—such as pollution crossing jurisdictional boundaries—can lead to decentralized environmental policies that are too lax or too stringent.²⁵⁹ The efficiency of decentralized environmental regulation also hinges on strategic interactions between local governments and asymmetric information.²⁶⁰ Oates succinctly summarizes the tradeoffs highlighted

254. Bouwe R. Dijkstra & Per G. Fredricksson, *Regulatory Environmental Federalism*, 2 ANN. REVIEW RES. ECON. 319, 327 (2010).

255. Per G. Fredricksson & Daniel L. Milliment, *Strategic Interaction and the Determination of Environmental Policy Across the U.S. States*, 51 J. URB. ECON. 101, 119 (2002).

256. Dijkstra & Fredricksson, *supra* note 260, at 327.

257. Mitch Kunce & Jason Shogren, *On Interjurisdictional Competition and Environmental Federalism*, 50 J. ENV'T ECON. & MGMT. 212, 212–13 (2005) [hereinafter *Interjurisdictional Competition*]; Dietmar Wellisch, *Location Choices of Firms and Decentralized Environmental Policy with Various Instruments*, 37 J. URB. ECON. 290, 292 (1995).

258. Wallace Oates & Robert M. Schwab, *Economic Competition Among Jurisdictions: Efficiency Enhancing or Distortion Inducing?*, 35 J. PUB. ECON. 333, 335 (1988).

259. *Interjurisdictional Competition*, *supra* note 257, at 292.

260. See Mitch Kunce & Jason Shogren, *On Environmental Federalism and Direct Emission Control*, 51 J. URB. ECON. 238, 242–43 (2002) (identifying different considerations local governments might have for altering conservation standards); John A. List & Charles F. Mason, *Optimal Institutional Arrangements for Transboundary Pollutants in a Second-Best World*:

in the environmental federalism literature: “[w]e are left with a choice between two alternatives: suboptimal local decisions on environmental quality or inefficient uniform national standards. And which of these two alternatives leads to a higher level of social welfare is, in principle, unclear.”²⁶¹

The recent renewable resource federalism literature also finds tradeoffs in determining the appropriate level of jurisdiction that reflects heterogeneity across landscapes in terms of preferences and technologies.²⁶² That literature focuses on renewable resources, such as fisheries, in which different jurisdictions extract the resources from a common pool resource, often a metapopulation. In that case, one jurisdiction’s extraction reduces the resource available to another jurisdiction, and the resource disperses across jurisdictional boundaries.²⁶³

A. Hierarchies of Management Specific to Ungulate Migration Conservation

Conservation of migratory ungulates differs from pollution and renewable resource federalism literature in at least two ways. First, the pollution example relies on negative externalities across jurisdictions while many migratory ungulates fit more closely within a positive externality or public good context. At the federal level, public land and wildlife managers must consider the benefits of migratory conservation that accrue to people who do not live in the jurisdictions where the conservation actions, and costs, occur. Second, although migratory ungulates are harvested game species, they provide many non-extractive and non-consumptive benefits within and beyond jurisdictions, while the renewable resource economics federalism literature focuses on extraction value and competition for extraction across jurisdictions. In contrast, the public good nature of the non-consumptive benefits of migratory ungulates implies gains from

Evidence from a Differential Game with Asymmetric Players, 42 J. ENV’T ECON. & MGMT. 277, 279 (2001).

261. Oates, *supra* note 258, at 9.

262. See James N. Sanchirico & James E. Wilen, *Optional Spatial Management of Renewable Resources: Matching Policy Scope*, 50 J. ENV’T ECON. & MGMT. 23, 44 (2005) (identifying marginal tradeoffs in conservation policy as to fisheries); Christopher Costello & Daniel Kaffine, *Private Conservation in Turf-Managed Fisheries*, 30 NAT. RES. MODELING 30, 32–33 (2017); James N. Sanchirico, *Characterizing Uncertainty and Learning in the Economics of Resource and Environmental Management* (forthcoming 2020).

263. Sanchirico & Wilen, *supra* note 262, at 44; Costello & Kaffine, *supra* note 262, at 32–33; Sanchirico, *supra* note 262.

cooperation across jurisdictions, albeit with coordination costs.²⁶⁴ In addition, much of the renewable resource federalism literature assumes that a federal policy is uniform across all locations, which is not a relevant assumption in the migratory ungulate context and drives outcomes away from federal jurisdiction. For migrations, federal or centralized management provides landscape-wide policy scope that internalizes migrations across jurisdictional boundaries, obviating coordination costs. In addition, federal tax dollars reflect non-local values from conservation of migratory species. However, local management provides an ability to tailor decisions to local habitat conditions, preferences for consumptive and non-consumptive uses of the species, and management technologies. Management of migrating species also generates spatial distribution considerations, with winners and losers within a managing state or local jurisdictions and beyond.

Economic analysis of how conservation institutions can interact in the presence of uncertainty and information gaps, a range of potentially conflicting land management goals, and various regulatory and policy tools to promote conservation of migratory species could prove useful in defining the appropriate management hierarchy and provide insights into policies at each level of management that will create the desired level and pattern of conservation.

V. *Economic Analysis and Tools for Migratory Species Conservation*

Despite the policy and academic explorations of integrated economic-ecologic systems to improve species conservation, science-based policy analysis for seasonal ungulate migrations remains limited. Conserving migratory ungulates poses two issues beyond those of species conservation in general. First, ungulate migration corridor conservation requires a high degree of habitat connectivity.²⁶⁵ Second, ungulates migrate over large distances, which means that large amounts of land across many landowners or jurisdictions need conservation activities.²⁶⁶ Yet, with ungulates using each portion of their migration corridor for limited periods of time, seasonal or temporary conservation actions within working landscapes can provide species conservation benefits that may obviate the need for protected

264. See e.g., Albers & Ando, *supra* note 244, at 312 (identifying costs and benefits of group coordination); *Crowding In/Out*, *supra* note 249, at 492; *Spatial-Econometric*, *supra* note 249, at 33–45.

265. *Conserving Transboundary Migrations*, *supra* note 11, at 85.

266. *Id.*

areas covering the entire migration route for the whole year. A range of economic tools can inform these and other issues surrounding migration conservation including: portfolio analysis for choosing collections of pathways for conservation; spatial bioeconomic and RSS approaches to defining patterns of conservation; and incentive-based approaches to achieve those patterns of conservation in multi-owner landscapes.

A. Portfolio Theory

One goal of managing an asset that has uncertainty or variability in its value is to maximize the average or expected value of that asset.²⁶⁷ Typically, a manager wants to reduce the variability across time of the asset's value.²⁶⁸ In that case, asset managers consider a portfolio of assets instead of focusing on one particular asset.²⁶⁹ Combining assets into a portfolio leads to the diversification of risk.²⁷⁰ The risk-mitigating tool of portfolio management can be applied to species conservation as well.²⁷¹ Risks associated with climate change interact with and affect the spatial distribution of species in uncertain ways. This complicates conservation planning but can be mitigated by spatial applications of portfolio theory. For example, Ando and Mallory applied the modern portfolio theory to the Prairie Pothole Region and found that by allocating conservation among wetlands subregions, they could reduce uncertainty and maximize conservation returns.²⁷²

267. Harry Markowitz, *Portfolio Selection*, 7 J. FIN. 77, 77 (1952).

268. *Id.*

269. *Id.*

270. See Frank Figge, *Bio-folio: Applying Portfolio Theory to Biodiversity*, 13 BIODIVERSITY & CONSERVATION 827, 827 (2004) (“[g]enes, species and ecosystems are often considered to be assets. The need to ensure a sufficient diversity of this asset is being increasingly recognized today. Asset managers in banks and insurance companies face a similar challenge”); G. Cornelius Van Kooten & Erwin H. Bulte, *The Economics of Nature: Managing Biological Assets*, 23 ENV'T & RES. ECON. 472, 472–74 (2002); Amy Ando & Payal Shah, *The Economics of Conservation and Finance: A Review of the Literature*, 8 INT'L REV. ENV'T & RES. ECON. 321, 321 (2016) (“portfolio theory has been harnessed to help guide conservation planning under uncertainty.”).

271. Ando & Shah, *supra* note 270, at 321.

272. Amy W. Ando & Mindy L. Mallory, *Optimal Portfolio Design to Reduce Climate-Related Conservation Uncertainty in the Prairie Pothole Region*, 109 PROCS. NAT'L ACAD. SCI. 6484, 6484 (2012):

“we adapt Modern Portfolio Theory (MPT) to optimal spatial targeting of conservation activity, using wetland habitat conservation in the Prairie Pothole Region (PPR) as an example. This approach finds the allocations of conservation activity among subregions of the planning area that maximize the expected conservation returns for a given level of uncertainty or minimize uncertainty for a given expected level of returns. We find that using MPT instead of simple diversification in the PPR can achieve a value of the conservation objective per dollar spent that is 15% higher for the same level of risk. MPT-based portfolios can

In the context of Western ungulate migrations, a single herd of mule deer may travel through many separate migration pathways before rejoining in the winter range. Animals on different individual pathways face different risks including disease, predation/hunting, storms, and migration disrupting barriers.²⁷³ Choosing only one migration route for conservation implies “rolling the dice” because the individuals that use that route all face the same level of risk—one bad event and that segment of the herd, and the conservation benefit of conserving that route, is lost. Rather than establishing conservation priorities across multiple migration routes based on ecological parameters alone, such as shortest distance or highest use, that prioritization could employ a portfolio theory approach at the landscape level to reduce risk uncertainty and maximize conservation returns (i.e., economic efficiency). Selecting a portfolio of pathways based on the degree of correlation in the risks faced on migration paths can mitigate risk to the herd as a whole.

B. Reserve Site Selection and Bioeconomic Analysis

Economic analysis informing the location of protected areas (areas with restrictions on land/resource use to provide habitat for species) includes systematic conservation planning including RSS and spatial bioeconomic analysis. Both RSS and spatial bioeconomic analysis incorporate varying degrees of the spatial considerations critical for migratory species, and they provide platforms to further incorporate the spatial and dynamic management needs posed by seasonal migrations.

The economic RSS literature solves a maximum coverage problem (maximizing the expected number of species conserved for a given budget) or a set coverage problem (minimizing the expected cost of protecting a given number of species). Because species persistence may be higher for agglomerated or connected conservation parcels, several analyses aim directly at establishing particular patterns of reserve networks by forcing the selection of reserve sites to be close together or compact.²⁷⁴ For conservation of terrestrial migratory species, the

also have 21% less uncertainty over benefits or 6% greater expected benefits than the current portfolio of PPR conservation.”

273. See Lowery, *supra* note 57, at 8836.

274. E.g. Constantine Toregas & Charles ReVelle, *Binary Logic Solutions to a Class of Location Problem*, 5 GRAPHICAL ANALYSIS 145, 153 (1973); Richard Church & Charles ReVelle, *The Maximal Covering Location Problem*, 32 PAPERS REGIONAL SCI. ASS'N 101, 101-02 (1974); Amy W. Ando et al., *Species Distributions, Land Values, and Efficient Conservation*, 279 SCI. 2126, 2126 (1998); Naidoo et al., *Integrating Economic Costs Into*

conservation RSS differs from classic RSS because it does not aim at conserving a number of species and instead focuses on conserving sets of sites that produce physical connectivity between two seasonal species locations, such as the winter and summer ranges.²⁷⁵ Many computational approaches to defining reserve sites to create physical connectivity do not incorporate how the migratory species uses the habitat within the connecting corridors and moves through the corridor, as in “functional connectivity.”²⁷⁶

In contrast, bioeconomic models incorporate biological characteristics and functions of species or ecosystems with economic decision frameworks to determine optimal management that considers

Conservation Planning, 21 TRENDS ECOLOGY & EVOLUTION 681, 683 (2006); Nelson et al., *Identifying the Impacts of Critical Habitat Designation on Land Cover Change*, 47 RES. & ENERGY ECON. 89, 100–06 (2017); Christopher Costello & Stephen Polasky, *Dynamic Reserve Site Selection*, 26 RES. & ENERGY ECON. 157, 157 (2004); Armsworth et al., *Land Market Feedbacks Can Undermine Biodiversity Conservation*, 103 PROCS. NAT'L ACAD. SCIS. 5403, 5404–05 (2006); Snyder et al., *One-and Two-Objective Approaches to an Area-Constrained Habitat Reserve Site Selection Problem*, 119 BIOLOGICAL CONSERVATION 565, 565 (2004); Sahan T.M. Dissanayake & Hayri Önal, *Amenity Driven Price Effects and Conservation Reserve Site Selection: A Dynamic Linear Integer Programming Approach*, 70 ECOLOGICAL ECON. 2225, 2225 (2011); Hayri Önal et al., *supra* note 228, at 957; Amy W. Ando et al., *supra* note 38, at 2126; Stephen C. Newbold & Juha Siikamaki, *Prioritizing Conservation Activities Using Reserve Site Selection Methods and Population Viability Analysis*, 19 ECOLOGICAL APPLICATIONS 1774, 1774 (2009). In addition, some RSS problems include probabilistic models of species persistence from specific reserve configurations.

275. Richard Schuster et al., *Optimizing the Conservation of Migratory Species Over Their Full Annual Cycle*, NATURE COMM., Apr. 15, 2019, at 2 (incorporating predictive models of a species over the full annual cycle into spatial optimization approaches to select reserve sites); Tara G. Martin et al., *Optimal Conservation of Migratory Species*, 8 PLOS ONE, Aug. 2007, at 1 (accounting for the need for “migratory connectivity” across the annual cycle, raising questions about conservation site selection that considers only portions of the migratory species’ habitat needs); Bistra Dilkina & Carla P. Gomes, *Solving Connected Subgraph Problems in Wildlife Conservation*, INT’L. CONF. INTEGRATION ARTIFICIAL INTELLIGENCE (AI) & OPERATIONS RSCH. (OR) TECHN. IN CONSTRAINT PROGRAMMING, 102, 102–16 (2010) (formulating several computational approaches to solving a subgraph problem with a connectivity requirement. Using that work and addressing large computational issues); John M. Conrad et al., *Wildlife Corridors as a Connected Subgraph Problem*, 63 J. ENV’T ECON. & MGMT. 1, 7–15 (2012) (solving a site selection problem to link two core habitat areas while facing a budget constraint and applying that corridor design solution method to grizzly bears. Incorporating information about least-cost distances for species moving across the “resistance surface” between two core areas); Bistra Dilkina et al., *Trade-Offs and Efficiencies in Optimal Budget-Constrained Multispecies Corridor Networks*, 31 CONSERVATION BIOLOGY 192, 194–98 (2016) (defining the optimal corridor design for a single species’ movements based only on ecology and describing the costs of such an approach and the suboptimality of that corridor in a multi-species setting. They then apply that model in a Montana case of two species with different characteristics, values, and habitat needs and define the cost savings of an approach that identifies conservation sites using both species and economic values in decisions).

276. Heidi J. Albers et al., *Economics of Habitat Fragmentation: A Review and Critique of the Literature*, 11 INT’L REV. ENV’T & RES. ECON. 97, 108–19 (2017) [hereinafter *Fragmentation*].

economics and ecology together.²⁷⁷ Many bioeconomic models include a metapopulation structure for the species, with subpopulations located in “patches” across the sea/landscape, and define a dispersal matrix that depicts the species movements between subpopulations, although dispersal and what happens to species during that dispersal is largely left unexplored.²⁷⁸ Other bioeconomic models characterize species movements directly through explicit equations of motions across space or through simulations of the (stochastic) spatial process of species movement within economic decision/optimization frameworks for defining temporary or permanent conservation areas, development patterns, policies to reduce wildlife disease spread, and timber harvest.²⁷⁹ In addition, many studies conduct spatial bioeconomic analysis of landscape management approaches to address an invasive species, with a wide range of characterizations of how the species moves across space.²⁸⁰ However, relatively few of those analyses depict the process of seasonal migration itself and are described below.²⁸¹

277. *Id.* at 111.

278. Economists have typically focused on dispersal between patches in metapopulation models rather than the location and process of dispersal itself. Heidi J. Albers et al., *The Role of Restoration and Key Ecological Invasion Mechanisms in Optimal Spatial-Dynamic Management of Invasive Species*, 151 *ECOLOGICAL ECON.* 44, 44 (2018);

James N. Sanchirico & James E. Wilen, *Bioeconomics of Spatial Exploitation in a Patchy Environment*, 37 *J. ENV'T ECON. & MGMT.* 129, 129 (1999); James N. Sanchirico & James E. Wilen, *Optimal Spatial Management of Renewable Resources: Matching Policy Scope to Ecosystem Scale*, 50 *J. ENV'T ECON. & MGMT.* 23, 23 (2005); Martin D. Smith et al., *The Economics of Spatial-Dynamic Processes: Applications to Renewable Resources*, 57 *J. ENV'T ECON. & MGMT.* 104, 104 (2007).

279. *Fragmentation*, *supra* note 276, at 109–19; Stephen K. Swallow & David N. Wear, *Spatial Interactions in Multiple-Use Forestry and Substitution and Wealth Effects for the Single Stand*, 25 *J. ENV'T ECON. & MGMT.* 103, 103 (1993); Richard Horan et al., *Spatial Management of Wildlife Disease*, 27 *APPLIED ECON. PERSP. & POL'Y* 483, 484 (2005).

280. *See Fragmentation*, *supra* note 276, at 111 (recognizing spatial models incorporating species behavior); Rebecca S. Epanchin-Niell & Alan Hastings, *Controlling Established Invaders: Integrating Economics and Spread Dynamics to Determine Optimal Management*, 13 *ECOLOGY LETTERS* 528, 528 (2010).

281. *See* Atte Moilanen & Mar Cabeza, *Single-Species Dynamic Site Selection*, 13 *ECOLOGICAL APPLICATIONS* 913, 913–15 (2002) (combining a classic reserve site selection model with an “incidence function” based meta-population model to aid in selecting a subset of sites to conserve with a goal of species persistence); Heidi J. Albers et al., *Abstract: Protecting Salmonid Species with Riparian Buffer Zones: An Economic Optimization Approach*, in *RIPARIAN MGMT. HEADWATER CATCHMENTS: TRANSLATING SCI. INTO MGMT., CONF. PROGRAM, U. B.C.* 1, 15 (2007) (examining the optimal location of riparian buffer zones accounting for the influence of riparian buffers on the mortality of fish as a function of the water temperature throughout their migration route to the ocean); M. Punt & B. Kaiser, *Seismic Shifts from Regulations: Spatial Trade-Offs in Marine Mammals and the Value of Information from Hydrocarbon Seismic Surveying* (2019), (unpublished manuscript) (on file with author) (using a spatially explicit bio-

Only a few bioeconomic models have considered terrestrial migratory species. In one study, Skonhoft and co-authors used a bioeconomic model to analyze the seasonal migration of moose between two regions, including analysis of the moose providing positive hunting benefits in one location and resource damage in the other location.²⁸² In another, Maloney and co-authors parameterize a simulation model of elk migration toward their winter range with collar data and then explore the elk's spatial reaction to supplementation winter feeding locations that truncate the migration and the resulting spread of brucellosis within herds.²⁸³ Cisneros-Pineda and Albers have used a stylized spatial model of annual ungulate migrations between winter and summer ranges and a population model to define the optimal locations of energy development to minimize the impact of development on the ungulate population and undertook a sensitivity analysis around the ungulate energy losses associated with fidelity to the migration route, off-route forage opportunities, and energy development stress.²⁸⁴ Finally, using more detailed and dynamic ecological modeling of the plant species that ungulates use as food, Cisneros-Pineda et al. examined the tradeoffs between energy development and hunting values for ungulates.²⁸⁵ These spatial bioeconomic analyses demonstrate that efficient conservation must be based on the spatial response of the migratory species across the landscape or the conservation will not effectively nor efficiently protect species.

Although relatively few, the existing economic RSS and spatial bioeconomic analyses addressing terrestrial migrations begin with a landscape perspective that reflects species behavior.²⁸⁶ In the context

economic model and a value of information model to assess the tradeoffs between the cost savings in oil exploration from seismic testing and the decline in habitat quality from seismic testing for marine mammals, using evidence that whales appear to react to seismic testing by altering their migration routes).

282. Anders Skonhoft & Jon Olaf Olaussen, *Managing a Migratory Species That is Both a Value and a Pest*, 81 *LAND ECON.* 34, 47 (2005).

283. Matthew Maloney et al., *Chronic Wasting Disease Undermines Efforts to Control the Spread of Brucellosis in the Greater Yellowstone Ecosystem*, 30 *ECOLOGICAL APPLICATIONS* 1, 10–12 (2020).

284. Alfredo Cisneros-Pineda & Heidi J. Albers, *Optimal Locations of Development to Minimize Impact on Seasonally Migrating Ungulates (2020)* (unpublished draft) (on file with author).

285. Alfredo Cisneros-Pineda et al., *Impacts of Cattle, Hunting and Natural Gas Development in a Rangeland Ecosystem*, 431 *ECOLOGICAL MODELING* 1, 1–2 (2020).

286. *Fragmentation*, *supra* note 276, at 111.

of conserving ungulate migrations and seasonal habitats, conservation policies cannot focus only on subsets of the species' habitat but instead must consider how the species use and move across the entire landscape. With terrestrial migrations, the migration process—depicted in spatial bioeconomic analysis as a specific dispersal process—generates the need to assess conservation activities in particular locations to generate functional connectivity across the landscape. Using the concept of complementarity from RSS, conservation of a portion of an ungulate's migration corridor has far less conservation value if that portion does not connect to other conserved portions of the corridor and ultimately the full year-long habitat range. Connectivity, therefore, increases the importance of defining conservation policy at the landscape level rather than management of individual parcels and sites, which has implications for the relevant policies and for the development of management institutions that have coordinating authority across private and various types of public land.

C. Economics of Conservation Patterns Across Multiple Landowners and Jurisdictions

To protect migratory ungulates, economic policies and legal/management institutions must be developed to maintain the functional connectivity of conservation required to support migrations. Conservation-targeted public land management policies and private land acquisitions (fee total or conservation easements) can create and maintain connectivity in key locations, which could reflect the RSS issues discussed above. However, the sheer magnitude of the area involved limits the ability of any one public or private conservation actor to include fully connected migration corridors into a protected area system, nor would it be politically popular. The large areas involved, and the fact that Western ungulate migrations cross land that is a mix of private, state, tribal, and federal land and across state and international boundaries,²⁸⁷ raises questions both about policies that create incentives for appropriate patterns of conservation on private land and about the right level of management to coordinate for landscape level conservation outcomes.

Economic frameworks of individual land owner conservation decisions on a landscape scale incorporate interactions across landowners in situations with negative impacts—such as invasive

287. *Conserving Transboundary Migrations*, *supra* note 11, at 85.

species spread—and positive impacts—such as creating minimum habitat sizes—on neighbors.²⁸⁸ Investigations of economic policies including subsidies, taxes, and payments, explore how to create patterns of conservation on private land.²⁸⁹ The USDA Conservation Reserve Program’s payments for conserving agricultural land has been modified to also address conservation of particularly ecologically valuable locations of private land and has been analyzed by economists to define payments to generate particular spatial patterns of conservation.²⁹⁰ Of particular interest for creating patterns of private land conservation, such as connected locations for migratory species, are “agglomeration bonus” payments that encourage neighbors to conserve land across a shared border to create connectivity²⁹¹ and

288. The spatial bioeconomic literature considers policies to induce landowners to internalize the externality caused by moving/spreading public “bads,” such as invasive species, through individual incentives and cooperation. See e.g., Rebecca S. Epanchin-Niell & James E. Wilen, *Optimal Spatial Control of Biological Invasions*, 63 J. ENV’T ECON. & MGMT. 260, 262–63 (2012); Rebecca S. Epanchin-Niell & James E. Wilen, *Individual and Cooperative Management of Invasive Species in Human-Mediated Landscapes*, 97 AM. J. AGRIC. ECON. 180, 180–82 (2014). Using information about the spatial production functions for ecosystem services but without a bioeconomic framework, Albers, Ando, and Batz use both positive and negative values from contiguity to examine how private and public actors with conservation goals can use conservation location choices to induce agglomerated or dispersed patterns of conservation. *Crowding In/Out*, *supra* note 249, at 492. They test empirically for such spatial crowding in/out in several states and in California’s reserve network. *Id.*

289. For a review, see Heidi J. Albers et al., *Economics of Habitat Fragmentation: A Review and Critique of the Literature*, 11 INT’L REV. ENV’T & RES. ECON. 97 (2017).

290. See David J. Lewis & Andrew J. Plantinga, *Policies for Habitat Fragmentation: Combining Econometrics with Based Landscape Simulations*, 83 LAND ECON. 109, 119–21 (2007) (examining uniform and spatially heterogenous subsidies to achieve less fragmented forests); David J. Lewis et al., *Targeting Incentives to Reduce Habitat Fragmentation*, 91 AM. J. AGRIC. ECON. 1080, 1088–89 (2009) (same); David J. Lewis et al., *The Efficiency of Voluntary Incentive Policies for Preventing Biodiversity Loss*, 33 RES. & ENERGY ECON. 192, 205–08 (2011) (measuring the impact of payments with a spatially explicit model of ecological benefits); Erik Nelson et al., *Efficiency of Incentives to Jointly Increase Carbon Sequestration and Species Conservation on a Landscape*, 105 PROCS. NAT’L ACAD. SCIS. 9471, 9471–72 (2007) (integrating econometric, policy, carbon, and species models to simulate the response of landowners to incentive-based policies and the landscape patterns they create).

291. Rodney B. W. Smith & Jason F. Shogren, *Voluntary Incentive Design for Endangered Species Protection*, 43 J. ENV’T ECON. & MGMT. 169, 169–80 (2001) (using spatial experiments with such payments and with coordination/communication to further explore the ability to create socially-desirable patterns of conservation). See also Parkhurst, *supra* note 41, at 305–21 (2002) (exploring the efficacy of another voluntary incentive system: the agglomeration principle); Gregory M. Parkhurst & Jason F. Shogren, *Spatial Incentives to Coordinate Contiguous Habitat*, 64 ECOLOGICAL ECON. 344, 344 (2007); Gregory M. Parkhurst & Jason F. Shogren, *Smart Subsidies for Conservation*, 90 AM. J. AGRIC. ECON. 1192, 1192–95 (2008); Travis Warziniack et al., *Creating Contiguous Forest Habitat: An Experimental Examination on Incentives and Communication*, 13 J. FOREST ECON. 191, 191–204 (2007). Banerjee and co-authors examine how information matters in such settings. Simanti Banerjee et al., *Agglomeration Bonus in Small and Large Local Networks: A Laboratory Examination of Spatial Coordination*, 84 ECOLOGICAL

similar incentive mechanisms that can be combined with other policies to achieve a pattern of connected conservation.²⁹² Determining the appropriate incentive structure to induce desirable spatial patterns of conservation is complicated by heterogeneity among landowners²⁹³ and the lack of public information about the payment required to induce each private actor to conserve.²⁹⁴ Various economists have developed and explored bidding and auction mechanisms to improve conservation outcomes in settings where the conservation benefits accrue as a function of the spatial configuration of conservation.²⁹⁵ Still, these incentive-based policies have not been used to create migratory pathway conservation for ungulate species despite offering some great promise.

ECON. 142, 148 (2012); Simanti Banerjee et al., *The Impact of Information Provision on Agglomeration Bonus Performance: An Experimental Study on Local Networks*, 96 AM. J. AGRIC. ECON. 1009, 1025–26 (2014). See also Martin Drechsler et al., *An Agglomeration Payment for Cost-Effective Biodiversity Conservation in Spatially Structured Landscapes*, 32 RES. & ENERGY ECON. 261, 273–74 (2010) (finding that agglomeration bonuses are more cost effective and produce more conservation than homogenous payments in a German program for butterfly conservation); Frank Wätzold & Martin Drechsler, *Agglomeration Payment, Agglomeration Bonus or Homogeneous Payment?*, 37 RES. & ENERGY ECON. 85, 97–98 (2014) (finding that spatially heterogeneous payments improve cost-effectiveness of conservation).

292. Carson Reeling et al., *Policy Instruments and Incentives for Coordinated Habitat Conservation*, 73 ENV'T & RES. ECON. 791, 791–808 (2018) (discussing voluntary conservation agreements with assurances (VCAAs) that allow landowners to implement conservation practices with the assurance that no land use restrictions are imposed if the practices continue. Dreschler compares different types of conservation payments in a spatially structured landscape: input-based, where conservation measures are rewarded, and output-based, where conservation outcomes are rewarded); Gregory M. Parkhurst et al., *Tradable Set-Aside Requirements (TSARs): Conserving Spatially Dependent Environmental Amenities*, 63 ENV'T & RES. ECON. 719, 741–42 (2014) (proposing combining tradeable set-aside requirements (TSARs) with agglomeration bonuses).

293. Simanti Banerjee et al., *The Impact of Information Provision on Agglomeration Bonus Performance: An Experimental Study on Local Networks*, 96 AM. J. AGRIC. ECON. 1009, 1015 (2014).

294. Martin Drechsler, *Performance of Input- and Output-based Payments for the Conservation of Mobile Species*, 134 ECOLOGICAL ECON. 49, 49 (2017); Martin Drechsler et al., *An Agglomeration Payment for Cost-Effective Biodiversity Conservation in Spatially Structured Landscapes*, 32 RES. & ENERGY ECON. 261, 262 (2010).

295. E.g., Md Sayed Iftekhhar & Uwe Latacz-Lohmann, *How Well do Conservation Auctions Perform in Achieving Landscape-Level Outcomes? A Comparison of Auction Formats and Bid Selection Criteria*, 61 AUSTL. J. AGRIC. & RES. ECON. 557, 557 (2017); Stephen Polasky et al., *Implementing the Optimal Provision of Ecosystem Services*, 111 PROCS. NAT'L ACAD. SCIS. 6248, 6248 (2014); Drechsler, *supra* note 294, at 49; Laure Bamière et al., *Agri-Environmental Policies for Biodiversity when the Spatial Pattern of the Reserve Matters*, 85 ECOLOGICAL ECON. 97, 97 (2013); M. Agee & T. Crocker, *Three-stage TSARs, Interdependent Values, and Biodiversity Production on Private Lands* (2018) (unpublished manuscript) (on file with author) (further developing the TSAR concept in combination with auctions to achieve patterns of conservation from private landowners).

Spatial conservation policies such as agglomeration bonuses can incentivize private land conservation in configurations that promote connectivity.²⁹⁶ Combining public land conservation locations with agglomeration bonuses can even further encourage appropriate patterns of habitat conservation for migratory species.²⁹⁷ Yet, inducing private and public landowners to create socially preferred patterns of conservation on a landscape to support migrations requires focal points (or common themes) to help in the coordination across policies and among numerous actors.

VI. *Spatial-Temporal Opportunities for Increasing Conservation Bang for the Buck*

Although the large areas and long distances of ungulate migrations complicate conservation decisions and conservation policy, the fact that migrating ungulates use particular portions of a seasonal habitat or migration route for only a portion of the year provides opportunities for innovative conservation programs.²⁹⁸ Instead of creating large protected areas or funding easements that create and protect ungulate migratory habitat all year, seasonal or short-term policies that reflect the spatial-temporal needs of the migratory species could limit costs while still providing species protection. Such policies could include time-specific easements on private property, such as moving cattle and lowering fences during high-migration periods or seasonal regulatory land use restrictions. Economists have recently begun to focus research on such space-time focused actions across landscapes.²⁹⁹ Conservation organizations have implemented some “dynamic conservation” practices such as temporarily flooding agricultural land and temporary lighting reductions for migratory birds, and dynamic conservation practices hold promise for application in the ungulate migration conservation context.³⁰⁰

296. Parkhurst, *supra* note 41, at 305–21.

297. *Id.*; *Crowding In/Out*, *supra* note 249, at 492; *Spatial-Econometric*, *supra* note 249, at 33–45.

298. See Golet, *supra* note 251, at 409 (discussing the use of rice field flooding in California to create temporary wetlands for migrating birds).

299. Heidi J. Albers et al., *Introduction to Spatial Natural Resource and Environmental Economics*, 32 RES. & ENERGY ECON. 93, 93 (2010).

300. Kyle G. Horton et al., *Bright Lights in the Big Cities: Migratory Birds' Exposure to Artificial Light*, 17 FRONTIERS ECOLOGY & ENV'T 209, 213 (2019); Mark D. Reynolds et al., *Dynamic Conservation for Migratory Species*, 3 SCI. ADVANCES 1, 1 (2017).

CRAFTING LEGAL AND POLICY SOLUTIONS TO CONSERVE
UNGULATE MIGRATIONS THAT INCORPORATE ECOLOGY AND
ECONOMICS

Despite the grandness and increasing rarity of the phenomenon, migration generally, and western ungulate migration specifically, was a neglected topic in the field of conservation and biodiversity law.³⁰¹ This is likely the case because, until recently, scientists and managers lacked a clear understanding of the importance of migration to populations and overall ecosystem function, and also because traditional wildlife conservation strategies most often take population rarity as the rationale and the triggering mechanism to protect species and are ill-designed to address conservation of abundant migratory animals.³⁰²

Despite the slow start, conservation policies addressing ungulate migrations are beginning to emerge at both the state and federal level. However, emerging policies, particularly at the federal level, appear to be mostly symbolic, and the implementation of some state policies appear to be bottlenecked by differing views on how to define the problem of ungulate migration and the best methods for determining what strategies should be employed to achieve successful protection.³⁰³ As a result, ungulate migrations in the Western U.S. still do not benefit from an explicit, coordinated policy approach encompassing their year-round habitats.

In this section, we provide an overview of current and emerging Western ungulate migration policies at the state and federal level, review and analyze those policies, and find the need to better address the ecological needs of the species and integrate human actions and reactions (i.e. economics) to improve the efficiency of conservation policy.

301. *View From Above*, *supra* note 25, at 278.

302. Heather L. Reynolds & Keith Clay, *Migratory Species and Ecological Processes*, 41 ENV'T L. 371, 390 (2011). In fact, conservation itself has broadly been defined as the “biology of scarcity” and the seminal issue of conservation has been to understand the threshold for minimum viable populations. Brower & Malcolm, *supra* note 26, at 265.

303. David N. Cherney, *Securing the Free Movement of Wildlife: Lessons from the American West's Longest Land Mammal Migration*, 41 ENV'T L. 599, 605 (2011). Cherney, citing his previous work with Susan Clark, observed three major political problem definitions asserted by stakeholders: the ecological-scientific definition (who advocate for federal protection), the local rights definition (who advocate for a bottom-up approach that entails private conservation of private lands), and the cultural value definition (who advocates for a combination of the two, calling for the maximization of conservation while concurrently imposing the least infringement on other values). *Id.* (citing David N. Cherney & Susan G. Clark, *The American West's Longest Large Mammal Migration: Clarifying the Common Interest*, 42 POL'Y SCIS., 95, 98–101 (2009)).

I. Current Policies That Address Ungulate Migration

Migration conservation policies are primarily emerging at the state level, although there have been relevant developments at the federal level as well. This section provides an overview of some of those emerging policies.

A. State Level Policies

As a result of their primary responsibility to manage wildlife within their jurisdictions in trust for the residents of their states, states have taken the lead in ungulate migration conservation to date. There are a number of conservation efforts underway in many states, with much of it moving too quickly to capture in this article. However, below we have provided an overview of four of the more developed state ungulate migration conservation policies from Wyoming, Colorado, New Mexico, and California.

1. Wyoming

Recognizing that ungulate migration corridors and stopover areas are “vital to maintaining big game populations,” the Wyoming Game and Fish Commission adopted its Ungulate Migration Corridor Strategy in February of 2016 and has since updated it in January of 2019.³⁰⁴ The Strategy calls for the Wyoming Game and Fish Department to designate ungulate migration corridors based on available scientific data and then to conduct a risk assessment for each designated corridor to determine the threats and opportunities for conservation.³⁰⁵ The Strategy also directs the Department to work on a case-by-case basis with federal land managers by recommending measures to conserve ungulate migration corridors when the federal government is revising land use plans and/or reviewing federal surface-disturbing projects (such as oil and gas leasing on federal land).³⁰⁶

304. *Ungulate Migration Corridor Strategy*, *supra* note 24.

305. *Id.*

306. *Id.*

The Strategy further calls for the Department to designate “ungulate migration bottlenecks”³⁰⁷ and “ungulate stopover areas”³⁰⁸ within migration corridors as “vital” habitats, and as a result of that designation, “[t]he Department is directed by the Commission to recommend no significant declines in species distribution or abundance or loss of habitat function.”³⁰⁹ To date, the Wyoming Game and Fish Department has officially designated three mule deer migration corridors in Wyoming as vital habitats, and has proposed designation of two additional mule deer migration corridors and one pronghorn migration corridor.³¹⁰

Wyoming’s designation effort was placed on hold, however, during the fall of 2019 after pushback from the agricultural industry, the oil and gas industry, and local governments.³¹¹ Concerned about insufficient local stakeholder participation and potential takings claims associated with deferred oil and gas leases in migration corridors, the Wyoming legislature had proposed to take the authority to designate additional ungulate migration corridors away from the Wyoming Game and Fish Department and instead place it in the hands of county commissioners who would receive recommendations from a working group of local stakeholders.³¹² To counter this legislative effort, Wyoming Governor Gordon issued an Executive Order delegating to his office the authority to designate mule deer and pronghorn migration corridors after they have been proposed by the Wyoming Game and Fish Department.³¹³ To propose a migration corridor to the

307. Defined as “[a]ny portion of an ungulate migration corridor in which migrating ungulates are physically or behaviorally constrained. Examples may include habitat leading to a highway underpass or overpass, a gap between fences or residential subdivisions or other developments, or a route that circumnavigates a lake or reservoir.” WYO. GAME & FISH DEP’T, STANDARDIZED DEFINITIONS FOR SEASONAL WILDLIFE RANGES (1986, revised 2015), <https://wgfd.wyo.gov/WGFD/media/content/PDF/Habitat/Habitat%20Information/Seasonal-Range-Definitions.pdf>.

308. Defined as “[l]ocalized areas consistently used by ungulates to rest and feed during spring and fall migration.” *Id.*

309. *Id.*

310. WYO. GAME & FISH DEP’T, MIGRATION CORRIDOR MAPS & DATA, <https://wgfd.wyo.gov/wildlife-in-wyoming/migration/corridor-maps-and-data> (last visited Sept. 21, 2020).

311. Angus M. Thuermer Jr., *Governor Wants Lawmakers to Back off From Wildlife Migration Bill*, WYOFILE (Oct. 22, 2019), <https://www.wyofile.com/gov-wants-lawmakers-to-back-off-from-wildlife-migration-bill/>.

312. H.R. B. 0029, 65th Leg. Sess. (Wyo. 2020). The working groups of local stakeholders must represent the following interests: agriculture, mining, oil and gas, conservation groups, outdoor recreation and sportsmen’s groups, wind energy and other impacted industries, and municipal government. *Id.*

313. OFF. WYO. GOVERNOR MARK GORDON, *supra* note 43.

Governor, the Wyoming Game and Fish Department must have three or more years of animal location and fine-scale movement data from a sampled population of animals.³¹⁴ Prior to designating a migration corridor, the Governor must seek recommendations from local area working groups.³¹⁵ The Executive Order only addresses mule deer and pronghorn migrations, and only applies to conservation of migration corridors and the stopovers and bottlenecks within them, and does not address conservation of the species' entire seasonal ranges.³¹⁶

2. *Colorado*

In August of 2019, Colorado Governor Jared Polis signed Executive Order D 2019-011 which recognizes that “wildlife are essential to Colorado’s outdoor recreation economy and landscape heritage” and notes that “Colorado’s population continues to grow, placing pressure on the natural habitats that wildlife depend upon for survival.”³¹⁷ The Executive Order directs the Colorado Department of Natural Resources to compile a report on the location of migration corridors in the state, identify policy, regulatory, and legislative opportunities to conserve big game migrations, incorporate big game migration corridors into public education and outreach efforts, and meet with stakeholders.³¹⁸ The Executive Order further directs the Colorado Department of Transportation to incorporate big game migration into all levels of its planning, and to identify priority areas for big game crossings over and under roadways.³¹⁹

3. *New Mexico*

New Mexico was a leader in the protection of migrating animals with early legislation. In 2003, the New Mexico Legislature passed a memorial directing the New Mexico Department of Transportation and the New Mexico Department of Game and Fish to share information about wildlife crossing.³²⁰ The New Mexico Legislature passed two subsequent memorials in 2011 and 2013 directing the Transportation and Game and Fish Departments to develop a pilot

314. *Id.*

315. *Id.*

316. *Id.*

317. Colo. Exec. Order D-2019-011, CONSERVING COLORADO’S BIG GAME WINTER RANGE AND MIGRATION CORRIDORS (Aug. 21, 2019).

318. *Id.*

319. *Id.*

320. Eliza Murphy, *New Mexicans Move to Make Roads More Wildlife-Friendly*, HIGH COUNTRY NEWS (Aug. 2, 2004) <https://www.hcn.org/issues/279/14901>.

traffic safety project and to identify high collision areas and educate the public on how to avoid them.³²¹

Then, in March of 2019, the New Mexico Legislature passed a first of its kind statute, the Wildlife Corridors Act.³²² The Act directs the Department of Transportation and the Department of Game and Fish to work together to develop a Wildlife Corridors Action Plan to identify “highway crossing that pose a risk to successful wildlife migration or that pose a risk to the traveling public because large mammals use the crossing.”³²³ The Act requires the Departments to publish a prioritized “wildlife corridors project list” based on a set list of criteria, to be implemented as funding becomes available.³²⁴ Further, it requires the identification of other human-caused barriers affecting wildlife habitat and movement,³²⁵ the habitat and movement needs of species of concern, projections of anticipated effects of drought and other stressors on wildlife habitat and wildlife movement, an analysis of the economic benefits anticipated from preserving wildlife movement patterns including the potential impact of reduced wildlife/vehicle road collisions and a requirement to collaborate with tribal entities, among other requirements.³²⁶ New Mexico’s Wildlife Corridors Act is the most advanced piece of migration corridor conservation to date and New Mexico has been celebrated as “the first state to adopt a comprehensive program to identify wildlife corridors and begin to address barriers to wildlife movement.”³²⁷

4. *California*

In 2010, the California Department of Fish and Wildlife and the California Department of Transportation Commission jointly released the California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California, recognizing “a functional network of connected wildlands is essential to the continued support of

321. Michael Dax, *New Mexico’s Wildlife Corridor’s Act: A Path Toward Success*, Rewilding Earth Blog, <https://rewilding.org/new-mexicos-wildlife-corridors-act-a-path-toward-success/>.

322. Wildlife Corridors Act, S.B. 228, 2019 Leg. Reg. Sess. (N.M. 2019).

323. *Id.* § 3 (B)(1).

324. *Id.* § 4.

325. Human caused barriers are defined in the Act as “a road, culvert, commercial or residential development or other human-made structure that has the potential to affect the natural movement of wildlife across the landscape.” *Id.* § 2(A).

326. *Id.* § 3.

327. Katy Schaffer, *New Mexico Governor Signs First-of-Its-Kind Wildlife Corridor Act into Law*, WILDLANDS NETWORK BLOG (Apr. 1, 2019), <https://wildlandsnetwork.org/blog/new-mexico-governor-signs-first-of-its-kind-wildlife-corridor-act-into-law/>.

California's diverse natural communities in the face of human development and climate change."³²⁸ In addition to providing a statewide essential habitat connectivity map, the report also includes "guidance for mitigating the fragmenting effects of roads and for developing and implementing local and regional connectivity plans."³²⁹

In September of 2018, California Governor Jerry Brown signed the California Executive Order B-54-18 Biodiversity Initiative, upon the recommendation of an assembled group of California biodiversity experts who came together in 2017 to draft the Charter to Secure the Future of California's Native Biodiversity.³³⁰ The Executive Order directs the Secretaries of Food & Agriculture and Natural Resources to implement the Biodiversity Initiative to "promote deeper understanding of current and future threats to California's biodiversity; protect native vegetation; manage and restore natural and working lands and waterways; and explore appropriate financing options to achieve these goals."³³¹ As a result of the Executive Order, the California Department of Transportation (Caltrans) and the California Department of Fish and Wildlife (CDFW) must provide an updated assessment of essential habitat connectivity statewide to enable the integration of biodiversity conservation with transportation and infrastructure planning.³³² Staff from Caltrans and CDFW are also piloting a regional symposium to "gather information and expert input to identify wildlife passages and barriers to the State Highway System and potential funding opportunities to remediate those barriers."³³³

328. Spencer et al., *California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California*, Prepared for CAL. DEP'T TRANS., CAL. DEP'T FISH & GAME, & FED. HIGHWAYS ADMIN. (Feb. 2010).

329. *Id.*

330. Cal. Exec. Order No. B-54-18 1 (Sept. 7, 2018), <https://californiabiodiversityinitiative.org/pdf/executive-order-b-54-18.pdf>. "In California, long distance migrations are rare, and mule deer are one of the few that migrate." *Mule Deer (Odocoileus hemionus)*, CAL. DEP'T FISH & WILDLIFE, <https://wildlife.ca.gov/Regions/6/Deer/Natural-History> (Last visited Sept. 12, 2020).

331. *Id.*

332. NAT'L FISH & WILDLIFE FUND., 2019 CALIFORNIA ACTION PLAN FOR IMPLEMENTATION OF DEPARTMENT OF THE INTERIOR SECRETARIAL ORDER 3362: "IMPROVING HABITAT QUALITY IN WESTERN BIG-GAME WINTER RANGE AND MIGRATION CORRIDORS" 2 (2019), <https://www.nfwf.org/sites/default/files/rockymountains/Documents/California2020ActionPlan.pdf>.

333. *Id.*

B. Existing Federal Migration Efforts

As discussed in the ecology section of this article, much of the year-long Western U.S. ungulate habitat is located on land owned and controlled by the federal government. Large amounts of ungulate summer range occur in mountainous habitats controlled by the United States Forest Service (USFS) and much of the winter ranges in lower elevation sage-brush basins is controlled and managed by the Bureau of Land Management (BLM).³³⁴ Discussed below are the existing efforts to address ungulate migrations at the federal level.

1. Bureau of Land Management

Recognizing that “[r]obust and sustainable elk, deer, and pronghorn populations contribute greatly to the economy and well-being of communities across the West” and that “the habitat quality and value of . . . western big-game populations are often degraded or declining” the Secretary of the Department of Interior (DOI), Ryan Zinke, signed Secretarial Order 3362 Improving Habitat Quality in Western Big-Game Winter Range and Migration Corridors on February 9, 2018.³³⁵ Consistent with the Trump administration approach of deferring to states,³³⁶ the Order directs the BLM and other bureaus to work in close partnership with the western states to “enhance and improve the quality of big-game winter range and migration corridors habitat on Federal lands under the management jurisdiction of this Department in a way that recognizes states authority to conserve and manage big-game species and respects private property rights.”³³⁷ Notably, the Order fails to mention tribes and focuses instead only on federal/state effort to conserve winter range and migration corridors.

Specifically, the Order directs the BLM, Fish and Wildlife Service, and the National Park Service to evaluate how each bureau can contribute to state and other efforts to improve the quality and condition of priority big-game winter and migration corridor habitat and instructs all bureaus to “update all existing regulations, orders, guidance documents, policies, instructions, manuals, directives,

334. *Id.*

335. Secretarial Order No. 3362, *supra* note 42, at 1–2.

336. See Memorandum from Ryan Zinke, Secretary of the Interior, to Heads of Bureaus and Offices, (Sept. 10, 2018), at 1 (reaffirming a DOI policy from 1983 that found “authority of the States to exercise their broad trustee and police powers as stewards of the Nation’s fish and wildlife species on public lands and waters under the jurisdiction of the Department.”).

337. Secretarial Order No. 3362, *supra* note 42, at 1.

notices, implementing actions, and any other similar actions to be consistent with this Order.”³³⁸ To achieve the objectives of the Order, western states were asked “to identify 3-5 priority migration corridor or winter range habitats for big game species within their states” through State Action Plans.³³⁹ The DOI has provided grant funding to states to implement some of their identified priorities, and other grant funding has also been made available through the Department of Transportation to address highway related threats.³⁴⁰

It should also be noted that Secretarial Order 3362 only applies to elk, mule deer, and pronghorn migration conservation and thus misses the opportunity to conserve additional migrating ungulates including moose and bighorn sheep. Additionally, the Order only addresses conservation of the winter range and migration corridors of elk, mule deer, and pronghorns and does not address conservation on summer ranges therefore failing to provide full coverage of these animals’ year-long habitats.

Despite the intent of Secretarial Order 3362, some have expressed concern that the DOI bureaus, particularly the BLM, have failed to successfully implement its call to action.³⁴¹ Because Secretarial Orders are merely policy statements of the Secretary, representing the Secretary’s marching orders to the bureaus, and are not subject to the rulemaking requirements of the Administrative Procedures Act,³⁴² they do not carry the force of law and are therefore not binding or

338. *Id.* at 5.

339. NAT’L FISH & WILDLIFE FUND., *supra* note 332, at 4. All State Action Plans submitted to date are available at <https://www.nfwf.org/programs/rocky-mountain-rangelands/state-action-plans>.

340. Dep’t of Interior, *Secretary Bernhardt Announces \$10.7 Million in Public-Private Support for Big Game Migration Corridors* (May 3, 2019), <https://www.doi.gov/pressreleases/secretary-bernhardt-announces-107-million-public-private-support-big-game-migration>; Off. of Wyo. Governor Mark Gordon, WYDOT Receives \$14.5 Million Federal Grant for Wildlife Crossing Project (Nov. 14, 2019) [hereinafter Wyo. Press Release], <https://governor.wyo.gov/media/news-releases/2019-news-releases/wydot-receives-14-5-million-federal-grant-for-wildlife-crossing-project>.

341. Letter from Wyo. Outdoor Council, to Mary Jo Rugwell, Wyo. State Dir. of Bureau of Land Mgmt. (December 3, 2018), <https://wyomingoutdoorcouncil.org/wp-content/uploads/2018/12/BLM-Migration-Letter.pdf>; *See How the Interior Department Turned its Back on Big Game Migration Corridors*, ROCKY MOUNTAIN WILD, <https://rockymountainwild.org/protectbiggame/> (last visited Sept. 12, 2020) (noting that “[s]ince the release of the State Action Plans in October of 2018, DOI has continued pushing oil and gas development on nearly 1.2 million acres of priority big game landscapes identified by states”).

342. Administrative Procedure Act, 5 U.S.C. §§ 551–59 (2018); 5 U.S.C. §§ 701–06, 1305, 3105, 3344, 4301, 5335, 5372, 7521 (2018).

enforceable.³⁴³ As this Secretarial Order appears to do little more than encourage conversations between federal and state wildlife managers and provide an opportunity for limited funding to states for ongoing migration research and threat mitigation, it appears to have had limited effects.

Beyond the Secretarial Order, the BLM is also required by the Federal Land Policy and Management Act (FLPMA) to implement a multiple-use and sustained yield approach to management of lands within its jurisdiction.³⁴⁴ Wildlife and fish are among the multiple-uses that the BLM is to manage on public lands in a “combination that will best meet the present and future needs of the American people.”³⁴⁵ In 2016, the BLM proposed to amend its land use planning regulations, known as BLM Planning Rule 2.0.³⁴⁶ That proposed planning rule included a provision that would have required the BLM, when revising its land use plans, to consider and document “areas of key fish and wildlife habitat such as big game winter and summer areas, bird nesting and feeding areas, habitat connectivity or wildlife migration corridors, and areas of large and intact habitat[.]”³⁴⁷ However, the BLM Planning Rule 2.0 was never implemented because the United States Senate passed a legislative repeal of the rule under the Congressional Review Act in 2017.³⁴⁸ Had it not been repealed, the BLM planning rule would have required to the BLM to address ungulate migrations and seasonal range in its land use planning efforts, which may have likely resulted in more active work by the BLM to conserve ungulate migration.

343. *Christensen v. Harris Cnty.*, 529 U.S. 576, 587 (2000); Charles Wilkinson, *The Role of Bilateralism in Fulfilling the Federal-Tribal Relationship: The Tribal Rights-Endangered Species Secretarial Order*, 72 WASH. L. REV. 1063, 1076 n.43 (1997).

344. *Federal Land Policy and Management Act of 1976*, 43 U.S.C. §§ 1701–85 (2018). The principle of multiple-use and sustained yield is defined as “the management of the public lands and their various resources so that they are utilized in the combination that will best meet the present and future needs of the American people. . . including but not limited to, recreation, range, timber, minerals, watershed, wildlife and fish, and natural scenic, scientific, and historical values; and harmonious and coordinated management of the various resources without permanent impairment of the productivity of the land and the quality of the environment with consideration being given to the relative values of the resources and not necessarily to the combination of uses that will give the greatest economic return or the greatest unit output.” 43 U.S.C. § 1702(c) (2018).

345. *Id.* § 1702(c).

346. Resource Management Planning, 81 Fed. Reg. 89,580, 89,580 (Dec. 12, 2016) (to be codified at 43 C.F.R. pt. 1600).

347. *Id.* at 89, 666–67.

348. H.R.J. Res. 44, 115th Cong. (2017); Pub. L. No. 115–12, 131 Stat. 76 (2017).

2. *The United States Forest Service*

In 2008, the Bridger Teton National Forest designated the first federal migration corridor, the Path of the Pronghorn in Northwestern Wyoming.³⁴⁹ The pronghorn that utilize this migration route make a round-trip annual migration of up to 340 miles from their summer habitat in Grand Teton National Park to their winter range in the Green River Basin outside of Pinedale, Wyoming.³⁵⁰ Conservation of this particular corridor was of critical importance because its disruption would have likely caused the extinction of pronghorn in Grand Teton National Park.³⁵¹ The Bridger-Teton's designation, however, only ensures the corridor's protection on National Forest System lands, not the entirety of the migration route that continues on across BLM and private land; thus, leaving it susceptible to threats on lands under other jurisdictions.³⁵² David Cherney has noted this as "particularly troubling since the majority of perceived threats to the migration—rural housing and natural gas development—did not occur within the Bridger-Teton National Forest."³⁵³ In reality, Cherney notes, the Path of the Pronghorn was a largely "symbolic endeavor signifying that the pronghorn migration is important to the region."³⁵⁴ The Path of the Pronghorn remains the only federally designated migration route.

Actions undertaken by the USFS are governed by both the Multiple Sustained Yield Act (MUSYA) which requires that National Forests be managed for multiple uses,³⁵⁵ and the National Forest Management Act (NFMA) which requires individual forest's planning efforts "provide for diversity of plant and animal communities based on the suitability and capability of the species land area to meet overall multiple-use objectives."³⁵⁶ When the USFS revised its planning regulations in 2012, it included a provision requiring that revised forest plans "provide for social, economic and ecological sustainability within the Forest Service authority and within the inherent capability of the

349. HAMILTON, *supra* note 11, at 1.

350. *Id.*

351. Joel Berger, *Is it Acceptable to Let a Species Go Extinct in a National Park?*, 17 CONSERVATION BIOLOGY 1451, 1452 (2003).

352. HAMILTON, *supra* note 11, at 1. The amended Bridger Teton Forest Plan requires that "all projects, and infrastructure authorized in the designated Pronghorn Migration Corridor will be designed, timed and/or located to allow continued successful migration of the pronghorn that summer in Jackson Hole and winter in the Green River basin." *Id.*

353. Cherney, *supra* note 303, at 610.

354. *Id.* at 611.

355. Multiple-Use Sustained-Yield Act of 1960, 16 U.S.C. §§ 528–31 (2018).

356. National Forest Management Act of 1976, 16 U.S.C. §§ 1600–87 (2018).

plan area.”³⁵⁷ With regards to ecological sustainability, the rule requires that forest plans must include components to “maintain or restore the ecological integrity of terrestrial and aquatic ecosystems and watersheds in the plan areas including plan components to maintain or restore structure, function, composition and connectivity . . .”³⁵⁸ In a paper discussing a proposed method the USFS could use to model species connectivity, Matthew Williams and his co-authors note that the USFS’s “explicit incorporation of connectivity as a management objective could substantially improve connectivity conservation in the United States.”³⁵⁹ How the USFS will utilize the connectivity in the 2012 planning rule remains to be seen, as few forest plans have yet to be completed under the new rule.

II. *Analysis of Current Institutional Approaches*

We reviewed and assessed the current state and federal policies addressing ungulate migration against two factors: (1) the ecological needs of the migratory ungulates, and (2) the economic efficiency of the policies. Overall, we found that while the existing policies present a good starting point, there remains a need to better integrate the ecological needs of migratory ungulates and an opportunity to utilize emerging economic principles to address species migration in future policy.

The major issues that remain unresolved in ungulate migration conservation include: (1) the need to include the full suite of migratory ungulate species and their year-round habitats; (2) the need for coordinated management of migrations and seasonal habitat protection across large landscapes with many land owners/managers; (3) the need to address conservation of migrations that cross state and international boundaries; (4) the lack of solicitation and incorporation of local, tribal and national values/perspectives; (5) the need for significant funding to implement conservation protection; and (6) missed opportunities to utilize economic incentive options, particularly on private land. These issues are discussed in detail below.

357. National Forest System Land Management Planning, 77 Fed. Reg. 21,162, 21,264 (Apr. 9, 2012) (to be codified at 36 C.F.R. pt. 219).

358. *Id.*

359. Matthew A. Williamson et al., *Incorporating Wildlife Connectivity into Forest Plan Revision Under the United States Forest Service’s 2012 Planning Rule*, CONSERVATION SCI. & PRAC. (Dec. 2019), <https://largelandscapes.org/wp-content/uploads/2020/01/Incorporating-wildlife-connectivity-into-forest-plan-revision-under-the-United-States-Forest-Services-2012-planning-rule.pdf>.

A. The Need for Comprehensive Inclusion of the Full Suite of Migratory Ungulate Species and Their Year-Round Habitats

Migration is an important and endangered phenomenon across numerous ungulate species in the West including elk, mule deer, pronghorn, bison, moose, and bighorn sheep. With the possible exception of mule deer, there is little evidence that any of these species warrant more or less protection than another. Yet, policies such as SO 3362 and Wyoming EO focus on only a few at a time for conservation. This selective targeting of species for conservation could prove particularly confusing for stakeholders in areas where multiple species share the same corridors. Future policies should apply to any ungulate species that exhibits migratory behavior.

There is now consensus among ecologists that conserving ungulate migrations will require conserving year-round ranges.³⁶⁰ Our analysis of existing state and federal migratory ungulate conservation policies reveals a focus on conservation of the migration corridor itself and sometimes includes the conservation of winter ranges; these policies fail to incorporate conservation of ungulate summer range. This approach fails to account for what ecologists have repeatedly highlighted: the importance of each seasonal habitat, or the year-round ranges, of these migratory species. Because ungulate winter ranges often occur on low elevation BLM or privately-owned land, and summer ranges often occur in high-elevation mountainous areas managed by the USFS or the National Park Service, public lands are of critical importance to migrating ungulates and some of the major threats to migrating ungulates are occurring on federal lands. Summer ranges provide migratory ungulates with an opportunity to replenish reserves lost during the winter³⁶¹ that are critical particularly to adult female ungulates as they nurse growing calves, fawns, or lambs.³⁶² Loss of summer habitat can have negative consequences for migrating ungulates and underpin conservation efforts that are focused on migrator corridors and winter ranges.³⁶³

Instead of picking and choosing which species and habitats to protect, future conservation policies need to take a holistic approach and conserve the entire year-round range of migratory ungulates.

360. *Conserving Transboundary Migrations*, *supra* note 11, at 85.

361. Monteith, *supra* note 75, at 378.

362. Parker, *supra* note 60, at 58; *Shifting Patterns*, *supra* note 77, at 124.

363. *Conserving Transboundary Migrations*, *supra* note 11, at 83.

B. The Need for Coordinated Management of Ungulate Migration and Seasonal Habitat Protection Across Large Landscapes

The large landscape scale of ungulate migrations and seasonal habitats, crossing lands owned privately and publicly across multiple states and even international boundaries, makes their conservation a particularly complicated problem. While migration distances vary among species and within individual populations, to migrate ungulates require a large landscape with functional, intact habitats. Thanks to large parcels of private and public land, the American West continues to provide some of the best ungulate habitats in the world. But these landscapes are owned and managed by a variety of private and public entities and are used for a number of different uses including energy development, residential development, agriculture, and recreation, which leads to habitat fragmentation and habitat loss.³⁶⁴ The various agencies managing the land crossed by migrating ungulates are also managed under different mandates and have different constituencies making coordination of policies a challenge.³⁶⁵

Emerging ungulate conservation policies have primarily occurred at the state level, which reflects the state's role as the primary manager of wildlife within their political boundaries. Given their local knowledge and relationships with local stakeholders, states are well-situated to implement incentive and regulatory policies to promote conservation on private lands in locations that generate important habitat for migratory species.³⁶⁶ States are, however, limited in their ability, legally or politically, to manage wildlife and wildlife habitats on federal land.³⁶⁷ This has proven true in the migration corridor conservation context—as evidenced by the fact that despite the state prioritization of ungulate migration routes and winter ranges by western states via the State Action Plans submitted to the Department of Interior under the umbrella of Secretarial Order 3362, the

364. *Id.*

365. Fischman & Hyman, *supra* note 25, at 205.

366. *See id.* (highlighting the importance of local knowledge and that many states already have active easement programs).

367. *See* Martin Nie et al., *Fish and Wildlife Management on Federal Lands: Debunking State Supremacy*, 47 ENV'T L. 797, 803–04 (2017) (noting that the federal government has constitutional authority and obligations related to land management and that states' land ownership is limited); Middleton et al., *Harnessing Visitors' Enthusiasm for National Parks to Fund Cooperative Large-Landscape Conservation* (December 2020), <https://doi.org/10.1111/csp2.335>.

Department, through the BLM, continues to issue oil and gas leases within these state prioritized areas.³⁶⁸

There remains an outstanding need for additional coordinated policy and management strategies to encompass the full breadth of ungulate migrations across large landscapes and encompassing land that is owned by multiple entities (private, state and federal). As discussed in the economic section of this paper, federal or centralized management likely provides the best opportunity for a landscape-wide policy scope that internalizes migrations across jurisdictional boundaries and also obviates coordination costs among state and federal actors.

When considering policies to address the landscape scale challenge posed by migrations, it is important to remember that ungulates use each portion of their migration corridor and seasonal habitats for limited periods of time.³⁶⁹ Utilizing seasonal/temporary conservation actions within working landscapes can provide species conservation benefits that obviate the need for protected areas covering the entire migration route for the whole year.³⁷⁰ A range of economic tools can inform these and other issues surrounding migrations including portfolio analysis for choosing collections of pathways for conservation, spatial bioeconomic and RSS approaches to defining patterns of conservation, and incentive-based approaches to achieve those patterns of conservation in multi-owner landscapes.

C. The Need for Coordinated Management of Migrations that Cross State and International Boundaries

In addition to crossing multiple land ownership boundaries, migration movements also cross state and international boundaries. We analyzed the State Action Plans to determine how many of the state-identified priority migration corridors and winter ranges cross state and international boundaries. Our research indicated that out of forty-eight total identified migration routes and winter ranges, sixteen migration corridors cross state boundaries, five migration corridors likely cross state boundaries, and three migration corridors cross

368. ROCKY MOUNTAIN WILD, *supra* note 341, at 14 (noting that since the release of the State Action Plans in October of 2018, DOI has continued to issue oil and gas leases within the state to prioritize migration routes and winter range habitats).

369. Reynolds et al, *supra* 302, at 1 (noting that migratory species conservation efforts may require additional temporal solutions).

370. *Id.* (noting that the temporal solutions allows for less intrusive short-term agreement).

international boundaries.³⁷¹ Although this analysis examines a small sample of migration routes, it does indicate the frequency at which migration routes cross state and international borders.

As mentioned above, states manage wildlife populations within the boundaries of their jurisdiction for the benefit of the residents of the state, but their jurisdiction ends at state boundaries. Fischman and Hyman have noted that when regulation of migration corridors in one state provides uncompensated benefits in an adjacent state (a likely outcome with long-distance ungulate migrations), the state lacks full incentives to regulate.³⁷² Thus, individual state conservation of migrations will be “politically difficult unless either the federal government provides mandates or incentives for collective actions for the states to voluntarily cooperate in the form of a compact or agreement.”³⁷³ The same is true for migrations that cross international boundaries.³⁷⁴

Economically efficient hierarches of management should be considered to reduce cost, speed up development of conservation, and address conservation across the entire landscape. As discussed in the economics section, the most efficient hierarchy of management in this situation is at the federal level.³⁷⁵ Federal coordination of efforts to conserve migrations and habitats that cross state and international boundaries can improve the cost-effective provision of migration conservation. Current state approaches to ungulate migration and seasonal habitat are inconsistent and lack uniformity, which can further exacerbate conservation efforts, particularly in the face of population declines. Sufficient state policies may not emerge in time to prevent dramatic declines in population or range to the point at which they are difficult or impossible to reverse.³⁷⁶ Without a formal mechanism to promote and institutionalize intergovernmental and international cooperation, organic cooperative processes will be slow to evolve and likely not efficient from an economics perspective.³⁷⁷ However, placing

371. *State Action Plans for the Implementation of the Department of Interior Secretarial Order 3362: “Improving Habitat Quality in Western Big Game Winter Range and Migration Corridors,”* NAT’L FISH & WILDLIFE FOUND., <https://www.nfwf.org/programs/rocky-mountain-rangelands/state-action-plans>. Spreadsheet analysis is on file with the authors.

372. Fischman & Hyman, *supra* note 25, at 206.

373. *Id.*

374. *Id.* at 203.

375. *Id.* at 206–07.

376. Hyman et al., *Statutory Reform to Protect Migrations as Phenomena of Abundance*, 41 ENV’T L. 407, 437 (2011).

377. Martin Nie et al., *supra* note 367, at 930.

ungulate migration and seasonal range conservation solely at the federal level has a number of downsides as well, as discussed in the final section of this paper.

D. The Lack of Incorporation of Local, Tribal, and National Values/Management Perspectives

In addition to extending across complex natural landscapes, ungulate migrations also extend across complex and dynamic social landscapes as well.³⁷⁸ Because ungulate migrations cross iconic Western landscapes, some of it tribal and much of it public land managed for all American people, and because western ungulates embody aspects of our cultural heritage, national values are attached to their management and preservation as well as local values. Jeffery Hyman and co-authors have suggested the following list of national values associated with species migrations: ecological, cultural, psychological, aesthetic, inspirational, recreational, historic, and economic.³⁷⁹ Additionally, Secretarial Order 3362 notes that “hunters and tourists travel to Western States from across our Nation and beyond to pursue and enjoy this wildlife.”³⁸⁰ The loss of migrations will include the loss not only of ecosystem functions but also of social values and cultural heritage.³⁸¹ With people all across the country holding these values dear, socially efficient policies to promote conservation of migratory ungulates should incorporate local, tribal, and national stakeholder perspectives.

Although states can and do capture revenue from hunters and tourists who visit these locations, states are less able to capture revenues from the existence and cultural values felt by people who do not visit or have “use values” for migratory species.³⁸² In addition, states may prioritize the values and opinions of particular in-state stakeholders over others, for political or economic reasons, rather than focusing on the net benefits of conservation that accrue to all citizens and stakeholders.³⁸³

378. Joshua Morse & Susan Clark, *Corridor of Conflict*, in *Human-Wildlife Interactions: Turning Conflict into Coexistence* 150, 150 (Beatrice Frank et al. eds., Cambridge University Press 2019).

379. Hyman et al., *supra* note 376, at 410.

380. Secretarial Order No. 3362, *supra* note 42, at 2.

381. Fischman, *supra* note 25, at 278.

382. See Nie et al., *supra* note 367, at 810–11 (noting that attempts to fund non-game species conservation efforts have been ineffective at raising funds).

383. Stephanie Kurose et al., *Unready and Ill-Equipped: How State Laws and State Funding are Inadequate to Recover America's Endangered Species*, CTR. FOR BIOLOGICAL DIVERSITY

Our analysis of current state and federal policies reveals a need to provide opportunities for national values and perspectives to be incorporated into ungulate migration conservation policies along with local stakeholder perspectives and values. Some of the recent policy developments in Wyoming are particularly troubling because they seem designed to exclude national values and perspectives by placing responsibility for conservation of migration corridors at the politically charged gubernatorial level rather than at the expert agency level and seek input from a narrowly defined group of stakeholders. These developments are in spite of the fact that those migrations stretch across large landscapes, cross land owned by private, state, tribal, and federal entities, and cross state boundaries.³⁸⁴

Additionally, recognition and incorporation of the tribal role and tribal values associated with western ungulate conservation is a significant need that must be addressed in future policy. Of the existing migration conservation policies, New Mexico's Wildlife Corridors Act does the best job recognizing and incorporating tribal authority and values. The New Mexico Wildlife Corridors Act requires the New Mexico Game and Fish Department to create a wildlife corridors action plan that shall contain opportunities to consult with "New Mexico Indian Nationals, tribes or pueblos" both in-state and in neighboring states to protect migration corridors that cross state and tribal lines,³⁸⁵ and then it requires that consultation actually occur.³⁸⁶

Secretarial Order 3362, on the other side of the spectrum, failed to include tribal governments in its approach to create partnerships with states to conserve elk, mule deer, and pronghorn winter range and migration corridors.³⁸⁷ To date, tribes have not been included in the distribution of funding stemming from Secretarial Order 3362 for wildlife winter range and migration conservation.³⁸⁸ Perhaps in an

ACTION FUND 1, at 2 (Feb. 2019), <https://centeractionfund.org/wp-content/uploads/CBD-AF-Unready-and-ill-equipped-State-ESA-Laws.pdf>

(noting that funding mechanisms have resulted in bias in favor of game species conservation over conservation of nongame species and plants).

384. Wyo. Exec. Order No. 2020 1, 1 (Feb. 14, 2020) (on file with author) (providing limits on the authority of state agencies to establish regulations for the protection of mule deer and antelope migration).

385. Wildlife Corridors Act, *supra* note 322, at 3(B)(10).

386. *Id.* at 3(C).

387. Secretarial Order 3362, *supra* note 42, at Sec. 1.

388. See U.S. DEPT. OF INTERIOR, *Interior Partners with Private Land Owners to Fund Conservation Initiatives* (Mar. 1, 2019), <https://www.doi.gov/pressreleases/interior-partners-private-land-owners-fund-conservation-initiatives>; NAT'L FISH & WILDLIFE FOUND., *Western Big Game Migration 2019 Grant Slate* (2020),

attempt to correct this federal error, Senator Tom Udall (D-N.M.) and Representative Rubin Gallego (D-Ariz.), after consultation with tribes, introduced the Tribal Wildlife Corridors Act of 2019, which allows tribes to nominate a corridor within Indian Land, and if it meets the required criteria, requires the Secretary of the Interior to work with the tribes to provide technical assistance and resources for conservation efforts.³⁸⁹ Passage of this bill would help fill the hole left by Secretarial Order 3362, which failed to incorporate tribal values and to include a tribal consultation in the conservation of western big game winter ranges and migration corridors.

The Department of Interior's Secretarial Order 3362 has also failed to meaningfully provide an opportunity for the incorporation of national values and perspectives into policy and management by heavily deferring migration corridor and winter range management to the states. This is concerning because the Secretarial Order addresses public land management, which the federal government has a responsibility to carry out for the public's benefit.³⁹⁰

Incorporating national and local values into migration conservation is a difficult task because national and local values, and their attendant management preferences and perspectives, are often at odds with one another. For example, in the context of the Path of the Pronghorn conservation effort, David Cherney and Susan Clark observed that migration corridors conservation is often supported by individuals from the ecological-scientific perspective but often opposed by stakeholders with the local rights perspective.³⁹¹

In their book chapter entitled "Corridors of Conflict," Joshua Morse and Susan Clark explore the social context surrounding the effort to designate the Red Desert to Hoback mule deer migration route in Wyoming.³⁹² In their analysis, Morse and Clark note that a common concern expressed by the migration stakeholders they interviewed was a perceived lack of desire on the part of state and federal agencies to collaborate with the public.³⁹³ Morse and Clark additionally note that competing interests represented by the "Old West" interests (stereotypically utilitarian) and "New West" interests

<https://www.nfwf.org/sites/default/files/rockymountains/Documents/western-big-game-2019-grant-slate.pdf>.

389. S. 2891, 116th Cong. § (a)(1); (5); (6) (2019).

390. Nie et al., *supra* note 367, at 804.

391. Cherney & Clark, *supra* note 303, at 96; *see also* Glick, *supra* note 21, at 53, 56–58.

392. Morse & Clark, *supra* note 378, at 150.

393. *Id.* at 167.

(stereotypically conservation oriented) are rarely addressed in the management policy process surrounding migration conservation.³⁹⁴ Moving forward, Morse and Clark suggest that the migration conservation problem be grounded in social concerns (recognizing the social process and governance definitions) as well as biophysical concern.³⁹⁵

We agree and suggest that federal tax dollars provided in support of migration conservation could provide inducements for states to incorporate all values—whether local, tribal, or national—in developing migratory conservation plans.

E. The Lack of Funding to Implement Conservation Protection

In our analysis of the State Action Plans, big game vehicle collisions on state and federal highways stood out as the top listed threat with forty out of forty-eight total priority areas identifying this threat.³⁹⁶ Addressing this threat, particularly at a comprehensive scale, will require a significant funding investment. For example, in 2019, the Wyoming Department of Transportation received a \$14.5 million federal grant from the U.S. Department of Transportation to help fund wildlife crossing along a 19-mile stretch of federal highway in Wyoming, a project that is estimated to cost between \$12 and \$36.5 million.³⁹⁷ Using that \$12–\$36.5 million dollar range as a back-of-the-envelope estimate of the costs associated with remediating road-crossing threats per corridor, and multiplying that threat by the forty (out of forty-eight total) state migration and winter range priorities identified in the State Actions, indicates \$480 million–\$1.46 trillion will be needed to remediate the road-crossing threat in these identified projects.³⁹⁸ However, the identified priorities in the State Action Plans represent a small percentage of the total migration corridors and winter range habitats that are likely in need of vehicle collision threat remediation, so the total amount of funding needed is likely significantly higher.

Funding is also currently lacking to implement habitat protection and stewardship efforts on private land via economic incentives.³⁹⁹

394. *Id.* at 154.

395. *Id.* at 172. Morse and Clark caution about putting ecology and wildlife biology solely in the drivers search because it forces “social and cultural considerations into the rear.” *Id.* at 171.

396. *State Action Plan Analysis*, *supra* note 371.

397. Wyo. Press Release, *supra* note 340.

398. *State Action Plan Analysis*, *supra* note 371.

399. *Conserving Transboundary Migrations*, *supra* note 11, at 7.

Conservation easements, one important tool in this mix, have been successfully employed to conserve ungulate migration habitat on private lands but they are expensive.⁴⁰⁰ Many states have active easement programs, but funding for conservation easements primarily comes from federal sources or from a few limited states programs. In the Greater Yellowstone Ecosystem alone, it is estimated that acquiring easements on key private lands would cost at least \$687 million; however, this number is 15–20 years old and is likely a significant under-estimation of the cost today.⁴⁰¹ At the global scale, it is estimated that there is a need for conservation funding that is twenty to thirty times greater than exists today, reaching a total of \$200–300 billion per year.⁴⁰²

Most states are currently not in a position to supply the additional funding for ungulate migration and seasonal habitat conservation.⁴⁰³ State wildlife agencies remain largely dependent on hunting and fishing license fees to operate.⁴⁰⁴ With the decline of hunters and fishers, and the increasing need to address non-game species conservation, state wildlife budgets are stretched thin.⁴⁰⁵ One could assume that under the “user-pay, user-benefit” model, states would readily direct big game hunting and license fees to ungulate conservation, but given the declining revenues and increasing demands to conserve non-game species to preclude ESA listings, significant state funding for migration corridors is unlikely. Again, the use of federal tax dollars that capture the value of migratory species conservation to non-state citizens could enable states to undertake more socially valuable migratory ungulate conservation actions by increasing budgets. Recovering America’s

400. *Id.*

401. *Id.*

402. Credit Suisse et al., *Moving Beyond the Donor Funding Toward an Investor-Driven Approach*, 1, at 6 (Jan. 2014), <https://earthmind.org/sites/default/files/2014-ConservationFinanceMovingBeyondDonorFundingInvestorDrivenApproach.pdf>.

403. David Willms & Anne Alexander, *The North American Model of Wildlife Conservation in Wyoming: Understanding It, Preserving It, and Funding Its Future*, 14 WYO. L. REV. 659, 665 (2014); Robert L. Fischman et al., *State Imperiled Species Legislation*, 48 ENV'T L. 81, 81–82 (2018); Stephanie Kurose et al., *supra* note 386, at 1; Alejandro E. Camacho et al., *Assessing State Laws and Resources for Endangered Species Protection*, 47 ENV'T L. REP. 10837, 10838 (2017).

404. Nathan Rott, *Decline in Hunters Threatens How U.S. Pays For Conservation*, NAT'L PUB. RADIO (2018), <https://www.npr.org/2018/03/20/593001800/decline-in-hunters-threatens-how-u-s-pays-for-conservation>; J.F. Organ et al., *The North American Model Of Wildlife Conservation*, WILDLIFE SOC'Y TECHNICAL REV. 1, at 24 (Dec. 2012), <https://wildlife.org/wp-content/uploads/2014/05/North-American-model-of-Wildlife-Conservation.pdf>.

405. Bruce A. Stein et al., *Reversing America's Wildlife Crisis: Securing the Future of our Fish and Wildlife*, NAT'L WILDLIFE FED'N, Mar. 2018, at 9.

Wildlife Act (RAWA),⁴⁰⁶ a proposed federal bill that would provide significant federal funding to state and tribal governments to fund proactive species conservation, could be a possible source of dedicated funding for migration conservation.

F. Missed Opportunities to Utilize Economic Incentive Options

Western migratory ungulates rely upon habitat and resources located not only on public land, but also on private land, sometimes to a significant extent. For example, the western Wyoming Sublette herd of mule deer in Wyoming crosses public lands managed by four federal agencies and private lands held by forty-one owners during its seasonal migrations.⁴⁰⁷ In the Sublette mule deer herd example, the forty-one landowners over whose land the migrating mule deer cross are providing habitat and forage that is essential to maintain the mule deer's migratory behavior and therefore their rates of survival and reproduction.⁴⁰⁸ Although many migratory ungulates traverse private land, emerging state ungulate migration conservation policies are limited in their ability to create conservation on those lands because of a lack of funding to implement economic incentive programs.

As discussed in the economics section of this paper, this situation creates an imbalance in the achievement of the conservation goal to maximize net social benefits associated with ungulate migration conservation because private landowners are asked to bear a net cost associated with conserving wildlife on their land while others enjoy the net benefit of that conservation effort in the form of an abundance of animals. To have a "Pareto-improving" migration conservation policy, all individuals who incur net costs need to be compensated to make them neutral while other individuals capture net benefits.⁴⁰⁹

Many western landowners are in the agricultural business, known to be a tenuous business as a particularly harsh winter, a drought, or a drop in beef prices can make it hard to make ends meet. Providing economic incentives to landowners who voluntarily agree to implement conservation practices on some of their land in migration corridors, or other important seasonal habitat, can provide landowners

406. *Id.*

407. *Conserving Transboundary Migrations*, *supra* note 11, at 83.

408. *See id.* at 85 (noting the importance of the certain areas in the migration corridors as resting stops and source of food for ungulates).

409. Yang Liu et al. *Pareto-Improving and Revenue-Neutral Congestion Pricing Schemes in Two-Modes Traffic Networks*, 10 *NETNOMICS* 123, 123 (2009).

with compensation for their efforts, perhaps helping to make ends meet, while also enhancing habitat and safe passage for ungulates.

Conservation of ungulate migrations on private lands is happening to some degree at the state level⁴¹⁰ and should be encouraged through supportive federal programs. Support at the federal level could come through the expansion and/or targeting of the U.S. Department of Agriculture (USDA) Conservation Reserve Program,⁴¹¹ Fish and Wildlife Service Partners for Fish and Wildlife Program,⁴¹² or through the creation of a new initiative targeting ungulate migration and seasonal habitat conservation using existing Farm Bill conservation programs administered by the Natural Resource Conservation Service, similar to its 2010 Sage Grouse Initiative.⁴¹³ For example, the Conservation Reserve Program, which is administered by USDA's Farm Service Agency, uses a combination of rental payment contracts, cost-share payments for grassland restoration or reforestation, and other incentive payments to retire cropland from production and create habitat for high-priority wildlife species, but it has not been used extensively for conserving migratory ungulate habitat.⁴¹⁴ Beyond the Conservation Reserve Program, USDA conservation programs, overseen by the Natural Resource Conservation Service, can provide cost-share incentives for land management practices such as grassland restoration, improved fencing, or other actions that can benefit ungulate migration and for permanent protection of habitat through conservation easements.⁴¹⁵ In the past case of the Sage Grouse Initiative, the Natural Resource Conservation Service set aside specific funding through the Environmental Quality

410. For example, the Colorado Habitat Partnership receives 5 percent of deer, elk, pronghorn and moose license revenue which generates around \$2–2.5 million each year for projects. Colo. Parks & Wildlife, *Habitat Partnership Program (HPP)* (Aug 2018), <https://cpw.state.co.us/Documents/LandWater/PrivateLandPrograms/About-HPP-Program.pdf>. This revenue is used to develop partnerships to reduce conflicts caused by deer, elk, pronghorn and moose to agriculture. *Id.* The Wildlife and Natural Resource Trust, a trust created and funded by the Wyoming Legislature, “provides funding to enhance and conserve wildlife habitat and natural resource values throughout the state.” WYO. WILDLIFE & NAT. RES. TR. (Aug. 19, 2020), <https://wwnrt.wyo.gov/home>.

411. 16 U.S.C § 3831 (2018).

412. Partners for Fish and Wildlife Program, U.S. FISH & WILDLIFE SERV. (Jan 28, 2020), <https://www.fws.gov/partners>.

413. *Sage Grouse Initiative*, NAT. RES. CONSERVATION SERV., <https://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/national/programs/initiatives/?cid=steldevb1027671> (last visited Sept. 13, 2020).

414. MEGAN STUBBS, CONG. RESEARCH SERV., R40763, AGRICULTURAL CONSERVATION: A GUIDE TO PROGRAMS 8 (2020).

415. *Id.* at 5, 16.

Incentives Program, Conservation Stewardship Program, and Agricultural Conservation Easement Program to target Farm Bill dollars to areas important to the bird's recovery.⁴¹⁶ More recently, the Regional Conservation Partnership Program offers a mechanism for local and state organizations and agencies to develop projects that target Natural Resource Conservation Service program dollars towards specific resource needs, including wildlife conservation.⁴¹⁷ In Wyoming, the program has already been used to target resources to migration corridor conservation.⁴¹⁸

Although funding through such programs isn't guaranteed, as they are operated on a competitive basis, recent successes with incentives for short term, intra-year conservation activities could prove cost-effective for promoting "pop-up" conservation—or dynamic conservation—on some types of private land, such as removal of cattle and domestic animal feed and removal of migration-barrier fences on ranchland during migration seasons.⁴¹⁹ Such incentive-based programs to encourage conservation can fail to produce the socially-desirable pattern of conservation on their own, but pairing rental payments/easements with additional payments—such as agglomeration bonuses—can help achieve such patterns and would be necessary to create the functional connectivity across migration corridors necessary to support migratory populations.⁴²⁰ In some respects, the Sage Grouse Initiative and Regional Conservation Partnership Program have accomplished this by tailoring incentives to particular regions and providing easier access to, and in some cases, enhanced incentives for landowner/producer participation.⁴²¹

416. *Working Lands for Wildlife: Sage Grouse Initiative in Colorado*, NAT'L RES. CONSERVATION SERV. COLO., https://www.nrcs.usda.gov/wps/portal/nrcs/detail/co/programs/financial/eqip/?cid=nrcs144p2_062766 (last visited Sept. 22, 2020).

417. *Regional Conservation Partnership*, NAT'L RES. CONSERVATION SERV., <https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/programs/financial/rcpp> (last visited Sept. 23, 2020).

418. *Id.*

419. Reynolds et al., *supra* note 302, at 1 (exploring dynamic conservation strategies that tailor the delivery of habitat to when and where it is most needed for the conservation of migratory species in general with an application to migratory water birds).

420. See Parkhurst & Shogren, *Spatial Incentives*, *supra* note 291, at 344 (discussing the use of agglomerated bonuses as a mechanism to prevent diverging incentives); Parkhurst & Shogren, *Smart Subsidies*, *supra* note 291, at 1193, 1195 (noting that smart subsidies, which provide additional payoff for neighboring lots retired, minimized fragmentation in comparison to compulsory measures).

421. NAT'L RES. CONSERVATION SERV. COLO., *supra* note 416.

With proper foresight and planning, economic incentives can bring private landowners into the solutions to spatially complex coordination of conservation across large landscapes with many private and public landholdings.

COOPERATIVE FEDERALISM APPROACH TO WESTERN MIGRATORY UNGULATE CONSERVATION

The development of future conservation policies will require a coordinated approach among researchers, policy makers, private land owners, and natural resource managers.⁴²² That coordinated approach will need to take full advantage of emerging migratory connectivity science and use dynamic, innovative, and flexible legal and policy approaches supported by federal and state institutional commitments to integrate nimble and effective developments of migratory connectivity science into conservation measures at the appropriate level. In addition to integrating the ecology into ungulate migration conservation policies, considering principles of economics when devising future policies enables more, and more efficient, migratory species conservation. Thus, an integrated approach that starts with ecology as its foundation, but also incorporates key principles of economics when devising and crafting conservation policy, is more likely to result in durable policies that respond and adapt to the ecological needs of the species and optimize social benefits. The realities of climate change also require that any policy that is prescribed to conserve ungulate migration be sufficiently adaptable so as to allow animals to adapt their migrations to new circumstances.

At a foundational level, ecological science is telling us we need to better conserve the endangered phenomena of ungulate migrations to preclude future population declines of some of the West's most iconic species. While emerging migration conservation policies offer an optimistic start to the establishment of conservation protection for migrating ungulates, these policies remain incomplete for the reasons identified above. However, developing a more explicit, coordinated policy to address these challenges and improve protection of migratory ungulates is a complex undertaking, compounded by the landscape scale and transboundary nature of migration, and the different views and values stakeholders place on migration conservation both at a local and national level.

422. Meretsky et al., *supra* note 10, at 451.

To address the remaining challenges of western ungulate migratory conservation we have identified in this paper, we echo other scholars⁴²³ in suggesting a cooperative federalism approach that provides an opportunity to integrate federal and state institutions and includes a mix of regulatory prescriptions and incentive-based inducements to create a best-case scenario for migration conservation. This proposed voluntary bottom-up approach is preferred to the status quo of cobbled-together, uncoordinated state and federal policies because it not only provides consistency and funding, but also includes a cooperative federal approach that allows states to effectively implement this strategy at the state level.⁴²⁴ Further, it could signal that the conservation of migrating ungulate populations has a high national priority relative to competing demands, authorizing lead federal agencies to design and implement a diversity of approaches to the problem by tailoring of conservation solutions at the state level. Accordingly, the proposed plan would speed the implementation of solutions and species protection.⁴²⁵

I. Cooperative Federalism Policy Components

David Cherney has stated that there is no silver bullet to conserve ungulate migration corridors, instead there needs to be a “portfolio of contextual solutions” within each stakeholder’s jurisdiction.⁴²⁶ Cherney has further noted that the “technically elegant—and often inspiring—form of migratory conservation is to permanently protect corridors through comprehensive legislation.”⁴²⁷ However, this approach is often not politically viable in complex political landscapes, nor is it likely to be sufficiently comprehensive because it fails to capture state, tribal and local knowledge about wildlife. Yet there are also pitfalls at the other end of the spectrum with a state focused approach as identified in the challenges to existing policy’s in the prior section.

The designation of a national wildlife corridors across private, state, tribal, and federal public land with attendant restrictive regulations is not a politically viable solution,⁴²⁸ and the designation of

423. See Hyman et al., *supra* note 376, at 441 (explaining how legislation may incorporate cooperative federalism); Fishman & Hyman, *supra* note 25, at 206 (explaining the ways commentators envision the federal government coordinating state actors).

424. See Hyman et al., *supra* note 376, at 431 (noting that a comprehensive law may still allow for multiple approaches to be taken).

425. *Id.*

426. Cherney, *supra* note 303, at 615.

427. *Id.* at 616.

428. *Id.*

national corridors strictly on federal public land may not be an ecologically sufficient solution as it fails to capture the full seasonal range of the migrating species as evidenced by Cherney's analysis of the only national designated migration corridor to date, the Path of the Pronghorn.⁴²⁹ We suggest states and tribes are in the best position to identify and designate critical migratory corridors and seasonal habitat in need of protection as well as to work with private landowners to implement conservation on private land. However, it is also clear from our analysis that there is a need for stronger federal policy in this space to more effectively implement conservation action on public land, address conservation across state and international borders, incorporate national and local values into policy development, and, importantly, to provide a stable and dedicated funding source for conservation efforts (particularly for incentive based conservation and to address highway reconstruction costs).

The conservation of ungulate migrations requires the need for balance between national coordination and local implementation.⁴³⁰ A new federal law should include incentives for states to adopt ungulate migration and seasonal habitat protections into state conservation plans that are consistent with federal policies and define permissible land uses within designated corridors and key seasonal habitats, and once complete, it should include funding to implement identified projects. Specific incentive options to accomplish this include providing direct grants to states or the more complicated incentive of offering relief from federal regulation.⁴³¹ As Fischman and Hyman note, "funding is an essential lubricant to interstate cooperation with national objectives."⁴³² As regulatory polices to address private land conservation of ungulate migration and seasonal habitats are not likely be well received or efficiently implemented, future policies should include a bolstering of incentive options to address private land conservation.

Jeffery Hayman and his colleagues have noted that within that cooperative federalism concept, underneath the umbrella of a federal ungulate migration policy there should be a range of legal approaches

429. *Id.* at 609–12.

430. Fischman & Hyman, *supra* note 25, at 219 (suggesting the Coastal Zone Management Act is a helpful federal model to replicate as it encourages coastal states to develop management plans governing coastal zone land uses in exchange for federal aid and cooperation in implementing the state programs).

431. Hyman et al., *supra* note 376, at 431.

432. Fischman & Hyman, *supra* note 25, at 219.

proactively available to benefit ungulate migrations to improve the ability to adaptively tailor a response to conservation threats and political sensitivities.⁴³³ And a federal conservation law “need not stand in contrast to a bottom-up collaboration...[r]ather a law that authorizes a variety of legal approaches . . . can support bottom-up actions as part of a multi-pronged strategy.”⁴³⁴

Hayman and his co-authors envisioned that such a voluntary, bottom-up approach would “fund and leverage[] private conservation actions, authorize[] land acquisitions of corridors areas and winter ranges, direct[] the land management agencies to protection migrations, and provide[] incentives for state and local implementation of standards and practices for fencing, roads, and development—and that coordinates their approaches.”⁴³⁵ They suggest that such an approach is likely to result in ungulate migration conservation that is quicker and more efficient than a strictly state-led bottom-up approach.⁴³⁶

A cooperative federalism approach to ungulate migration conservation is further supported by the fact that the states, tribes, and the federal government have obligations to manage wildlife in trust for the public.⁴³⁷ While states manage wildlife within their political boundaries, under the state ownership of wildlife doctrine in “trust” for the residents of a state,⁴³⁸ there also exists a trust obligation on the part of the federal government to manage federal lands and federal resources for the entire public’s benefit⁴³⁹, and that trust responsibility extends to the conservation of wildlife.⁴⁴⁰ In some instances, like the Endangered Species Act context for example, the federal interest in

433. *Id.* at 418.

434. *Id.* at 431.

435. *Id.*

436. *Id.*

437. Nie et al., *supra* note 367, at 911.

438. FREYFOGLE ET AL., *supra* note 29, at 23 (providing the historical context for the state ownership of its wildlife doctrine and explaining that “states owned wild animals, lawmakers announced, but in a special way: they owned them in trust for the people generally and with a duty to manage them for the benefit of the many rather than the few.”).

439. See Charles F. Wilkinson, *The Public Trust Doctrine in Public Land Law*, 14 U.C. DAVIS L. REV. 269, 316 (1980) (noting that the public trust doctrine has “a measured, carefully delineated role to play in public land law. The doctrine does not prohibit the transfer of public lands, but the limitation on transfers is only one branch of the doctrine. The trust concept can be useful as a backdrop for judicial decision-making, as an aid in determining legislative intent and as a yardstick in assessing administrative action or inaction.”).

440. Nie et al., *supra* note 367, at 911.

wildlife may preempt that of the states.⁴⁴¹ But as Martin Nie and co-authors have noted, in cases where there are no competing objectives between the state and federal public trust, a “cooperative form of co-trusteeship is possible.”⁴⁴² Mary Christiania Wood has used the term co-trusteeship to describe the multiple trust obligations at the federal, state and tribal levels, as they apply to the interjurisdictional nature of salmon conservation,⁴⁴³ also a large landscape migration conservation challenge with multiple state and federal actors. The co-trustee approach provides a way to reframe an often-adversarial relationship between the federal, tribal, and state governments and creates a framework for establishing “mutual rights to transboundary assets along with collective responsibilities for conserving the resource.”⁴⁴⁴

This framework is particularly helpful to apply to the case of ungulate migration and seasonal habitat conservation across large landscapes that include a mix of private, state and federal public land. A cooperative federalism approach strikes this co-trusteeship balance by placing coordination and funding at the federal level but still allowing states to continue to exercise their responsibilities to implement migration conservation at the state and tribal levels.

CONCLUSION

Ungulate migrations represent one of the toughest wildlife conservation scenarios because of extent of their migrations, over lands owned by a variety of entities and across multiple political jurisdictions, different landscapes, and landowners. The successful conservation of migratory ungulates requires an integrated policy strategy that incorporates the fundamentals of migratory ungulate ecology including conservation of migration corridors, particularly bottlenecks and stopovers sites, as well as the need to preserve the entirety of seasonal habitats including summer and winter ranges.

Yet, successful conservation also requires the incorporation of economic considerations into policy decision-making as it leads to more conservation of migratory ungulates for any budget level. Economic perspectives around coordination of decisions across locations, using incentives to induce private conservation actions,

441. *Id.* at 848.

442. *Id.* at 911.

443. Mary Christiania Wood, *Advancing the Sovereign Trust of Government to Safeguard the Environment for Present and Future Generations (Part I): Ecological Realism and the Need for a Paradigm Shift*, 39 ENV'T L. 43, 84–86 (2009).

444. Nie et al., *supra* note 367, at 911.

recognizing spatial-temporal opportunities for cost savings, and acknowledging the local and non-local costs and benefits of ungulate conservation can all help to produce policies that provide the socially desirable levels of migratory ungulate conservation for least cost.

A cooperative federalism approach offers an opportunity to integrate not only ecology and economics into future policy, but also to integrate federal, tribal, and state institutions to create a best-case scenario to migration conservation. However, that cooperative federalism approach needs to be set based on a framework that recognizes mutual-management authority and responsibility at the state, tribal and federal level to address the conservation of migratory species across large landscapes that cross jurisdictions of state, federal, tribal, and private lands.

The alternative is to continue to cobble together uncoordinated state and federal policies and continue to scramble for funding sources. A proactive solution is preferred because it offers a higher degree of efficiency—more conservation per budget—than can arise from piecemeal strategies. With more efficiency from using both ecological and economic insights, policies can reverse population declines and conserve for future generations the ability to witness long distance ungulate migrations, described by Joel Berger as “[a]mong the Earth’s most stunning, yet imperiled, biological phenomena.”⁴⁴⁵ Without new conservation policies that address the remaining challenges we have identified in this paper, the biological phenomena of western ungulate migrations may be lost in some instances, resulting in significant changes to plant community composition and ecosystem processes to the loss of wildlife tourism-based dollars.

445. Berger, *supra* note 2, at 320.