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Hindered Hooves and the Wires that Bind Them

By

Wenjing Xu

A dissertation submitted in partial satisfaction of the

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in

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of the

University of California, Berkeley

Committee in charge:

Professor Lynn Huntsinger, Co-chair
Professor Arthur D. Middleton, Co-chair
Professor Justin S. Brashares

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Abstract

Hindered hoofs and the wires that bind them

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Wenjing Xu

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor Lynn Huntsinger, Chair

Long-distance animal movements have long fascinated humans. However, such movements necessarily translate to a requirement for extensive habitat, rendering the animals susceptible to natural and anthropogenic environmental changes, especially landscape fragmentation induced by linear infrastructure. In particular, fencing might be the most pervasive yet the least understood linear infrastructure that can extensively alter animal movement behavior, space use, and population dynamics. Importantly, fencing is often situated in social-ecological systems where humans and wide-ranging animals co-exist, hence altered wildlife spatial ecology subsequently affects human communities at the same time. In this dissertation, I examined wildlife responses to environmental changes, in particular fencing-induced fragmentation, and the complex social-ecological contexts of fenced landscapes. Working with collaborators, I first developed a guiding framework that synthesizes the pathways through which migratory ungulates respond to natural and anthropogenic environmental changes on a global scale. We then zoomed into two wide ranging sympatric ungulates, pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) in southeast Wyoming, and examined their behavioral and spatial responses to fences. Specifically, we developed a spatial- and temporal-explicit approach, Barrier Behavior Analysis (BaBA), with which we quantified the within- and among-individual variations in barrier behaviors along a fence density gradient. Finally, we situated fences in social-ecological systems to understand why and how fences became wide-spread around the world, as well as their coupled social and ecological impacts. Combing theories and methods in movement ecology, behavior ecology, rangeland ecology, and landscape ecology, this work provides new insights into ungulate movement in a changing world. By elucidating the impacts of fences across social and ecological boundaries, this research also marks a step in developing effective strategies to make the landscape connected for both humans and wildlife.

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As I am typing these words, many people from my homeland, including some family members, are living with the terror of ongoing or impending isolation and starvation due to institutional failure. I will always remind myself of my own privilege.

Chapter 1. Introduction

LONG-DISTANCE UNGULATE MOVEMEMNT IN A FRAGMENTED WORLD

The long-distance migrations of ungulates, or hooved mammals, have long fascinated and inspired humans (Milner-Gulland *et al.* 2011). From the Central Asia highlands and North America prairies to African Savannahs and South America steppes, migration allows ungulates to optimize energy intake, escape harsh seasonal conditions, and avoid predators, parasites, and diseases (Altizer *et al.* 2011; Merkle *et al.* 2016; Kauffman *et al.* 2021a). In addition to the benefits for the ungulates themselves, migration influences critical ecological processes and couples biodiversity and ecosystem functioning (Bauer & Hoye 2014; Subalusky *et al.* 2017). Importantly, these movements have played a significant role in sustaining humanity for thousands of years by providing a seasonal influx of nutrients and, in the process, become central to cultural symbolism and practices across the planet.

Despite their ecological, economic and cultural importance, ungulate migrations are shrinking and disappearing at an alarming rate in the era of rapid global change (Bolger *et al.* 2008; Harris *et al.* 2009). Because long-distance migrations often span large landscapes and steep environmental gradients, migratory ungulates can be particularly susceptible to environmental change (Tucker *et al.* 2018). In the Greater Mara region in East Africa, for example, migrations of wildebeest, zebra, and Thomson's gazelle have collapsed because of massive land conversion and competition with livestock (Said *et al.* 2016; Løvschal *et al.* 2017). The slaughter of tens of millions of bison in North America led to the remaining population being unable to maintain mass migration in the 19th century and modern-day land use mosaic has set barriers to the recovery of the species and their free-ranging movements (Pejchar *et al.* 2021). As scientists and practitioners continue to design conservation and restoration efforts targeting migratory ungulates, we must first understand how these ungulates respond to various forms of environmental changes (Barker *et al.* 2021).

Landscape fragmentation, the process of breaking apart and reducing intact habitat, is a primary threat to long-distance animal migration (Fahrig 2007; Haddad *et al.* 2015), and is often induced by linear infrastructures such as roads, railroads, pipelines, and fences (Ibisch *et al.* 2016; McInturff *et al.* 2020). However, the ecological consequences of fragmentation *per se* are not always clear (Fahrig 2017). This is partly because different species, different populations of the same species, or even different individuals within a population can respond differently to a given barrier (Sih 2013; McInturff *et al.* 2020). Long-term, individual-based research can be key to illuminating the differential impacts of linear barriers on individuals, and how these responses scale up to influence animal space use and population dynamics (Clutton-Brock & Sheldon 2010; Kauffman *et al.* 2021a). The advancement of movement ecology and telemetry technologies in the past two decades have respectively provided theories and tools to conceptualize and quantify individual movement and space use in response to barriers (Nathan *et al.* 2008; Cagnacci *et al.* 2010; Kays *et al.* 2015).

In the body of work included in this dissertation, I draw on concepts from behavioral ecology, rangeland ecology, landscape ecology, and social-ecological systems to explore ungulate movement behavior in response to environmental changes, with a focus on fragmentation caused by fences. Working with collaborators, I present a novel framework that delineates the plasticity of ungulate migration and used this framework to guide a literature review. We then focus on fences, which have caused not only landscape fragmentation but also social transformations in many rangelands around the world. We consider the multi-scale effects of fences on individual-based animal movement behavior, space use, demography using pronghorn *Antilocapra americana* and mule deer *Odocoileus hemionus* in southwestern Wyoming as an example. Collectively, this dissertation seeks to elucidate the ecological and social complexities in our increasingly fragmented world through the lens of animal movement. This work also provides guidance on how to utilize behavior information to inform conservation actions that improve landscape connectivity and restore ecological processes.

STUDY SITE

The study site for the field research herein is located in western Wyoming (110.03 W, 42.907 N, elevation 1,949–3,997 m), an area that encompasses the southern extent of the Greater Yellowstone Ecosystem. The area is a mosaic of public and private land, primarily administered by the Bureau of Land Management, private landowners, and the U.S. Forest Service. The northern part of the study area belongs to Sublette County, and the southern part belongs to Sweetwater County. This semi-arid region has old, snowy winters with an average temperature of 29° F (-2 °C) and warm summers with an average temperature of 83° F (28 °C).

The southern part of the area is the lower elevation Green River Basin, characterized by sagebrush *Artemisia sp.* and sagebrush grasslands interspersed with riparian tributaries of the Green River. The landscape shifts into mountainous terrain as elevation increases towards the northern end, characterized by mid-elevation aspen *Populus tremuloides* and lodgepole pine *Pinus contorta*, and higher elevation Engelmann spruce *Picea engelmannii* and alpine fir *Abies lasiocarpa*. The area provides habitat for thousands of migratory pronghorn and mule deer with various movement patterns ranging from residents to long-movement migrants.

The dominant human activities in the area are livestock production and energy development. Energy development partly overlaps with pronghorn and mule deer wintering areas and comprises mostly federal lands (Sawyer *et al.* 2017, 2019a). Residential areas are concentrated around the town of Pinedale and the rest of the study area is sparsely populated.

Fences in the study area are associated with livestock pastures, private property, and right-of-way along roads. Importantly, fences are not distributed evenly. Fence density is higher in the rangelands of the Green River Basin compared to the forested areas to the north. Most fences in the region are four- or five-strand barbed wire, sometimes with woven wire attached at the bottom. In recent years, some barbed-wire fences has been modified by replacing the bottom strand of barbed wire with smooth wire and lifting it higher from the group. Such modification is intended to convert conventional fences into “wildlife-friendly” fences that facilitate wildlife crossings (Paige & Stevensville 2008; Paige 2012).

OVERVIEW OF DISSERTATION

My dissertation research is comprised of six chapters. Chapter 2 of the dissertation, “The plasticity of ungulate migration in a changing world”, provides a broad theoretical framework for Chapter 3 and 4 and presents an overview of how migratory ungulates respond to natural and human-induced environmental changes. By integrating concepts from behavioral ecology and movement ecology, my collaborators and I argue for a comprehensive framing of migratory plasticity, which encompasses not only migratory propensity (*whether* to migrate) but also spatiotemporal changes (*when* and *where* to migrate). We first develop a novel typological framework delineating the full spectrum of migration changes, then use this framework to guide a comprehensive review. Finally, we discuss implications for future research and conservation efforts. With the accumulating interest in better understanding the effects of changing environment on wildlife ecology, the concept of plasticity provides a behavioral lens with which animals are not merely passively affected by environmental changes but actively adapting to them.

In Chapter 3, I take a closer look at how fences, a common cause of fragmentation in rangelands, affect the movement behavior of migratory ungulates. Specifically, my collaborators and I develop a spatial- and temporal-explicit approach, Barrier Behavior Analysis (BaBA), to examine individual-level movement behaviors when animals encounter fences. We then apply BaBA to wide-ranging sympatric pronghorn *Antilocapra americana* and mule deer *Odocoileus hemionus* in southeast Wyoming. Additionally, we aggregate the behavioral responses of pronghorn and mule deer to examine species-specific responses to fencing and to identify problematic fence segments. We showcase how this information can guide fence modification or removal as a conservation strategy to improve landscape connectivity for target species. With more than 1 million miles of fences estimated in the western US (McInturff *et al.* 2020), this work contributes substantially to our understanding of the impacts and of how we might strategize to tackle this problem.

The previous two chapters indicate that behavioral plasticity, or within-individual variations in behaviors, might be a key mechanism by which animals adapt to fragmented landscapes. In Chapter 4, we test this hypothesis by examining behavioral variations at individual levels. Specifically, we examine the presence of within-individual variations (or plasticity) and among-individual variations (or behavioral types) in barrier behaviors of pronghorn and mule deer along a fence density gradient in southwest Wyoming. Furthermore, we investigate the behavioral correlation between barrier behaviors and animal space use in order to examine how localized fence effects on animal movement behavior can scale up to broader space-use patterns. Finally, we examine whether barrier behaviors affect individual survival. Collectively, this chapter integrates concepts and methods from behavioral ecology into movement ecology and provides detailed evidence on the complexity of fence effects on animal behavior, space use, and demography.

In Chapter 5, I adopt a broader, interdisciplinary perspective to understand why and how fences became widespread around the world. Fences are embedded within complex social-ecological systems and affect not only ecological processes like animal movement but also social dynamics such as human-nature relationships and land practices. In order to fully understand fences' ecological impacts, it is essential to take the social-ecological nature of fences into consideration. Drawing from three key case studies from the US, China, and South Africa, my collaborator and I delineate five social pathways through which fencing shapes social-ecological dynamics in a landscape. These pathways are human mobilities, land practices and land use, economic relationships, and human-nature relationships. Within each pathway, we discuss how changes in the social dimension of a fenced system can be translated into ecological shifts. Overall, we showed that the social-ecological context renders fencing a more impactful feature than observed only for its ecological impacts.

In my final chapter, Chapter 6, I review the main themes and results that emerge from this dissertation work. In these concluding remarks, I reflect on the importance of behavioral plasticity of wild-ranging animals to actively respond to the ever-changing world, especially when facing direct barriers that hinder their movement. I hope that my dissertation research has further promoted the formalization of the subdiscipline “fence ecology”, and provided examples of how to better understand the multi-scale, interdisciplinary effects of linear barriers of fence-alike.

Chapter 2. The plasticity of ungulate migration in a changing world

This chapter provides a broad theoretical framework for Chapter 3 and 4 and presents an overview of how migratory ungulates respond to natural and human-induced environmental changes. The chapter has been previously published and is reproduced here with kind permission of the co-authors and Wiley.

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ABSTRACT

Migratory ungulates are thought to be declining globally because their dependence on large landscapes renders them highly vulnerable to environmental change. Yet recent studies reveal that many ungulate species can adjust their migration propensity in response to changing environmental conditions to potentially improve population persistence. In addition to the question of *whether* to migrate, decisions of *where* and *when* to migrate appear equally fundamental to individual migration tactics, but these three dimensions of plasticity have rarely been explored together. Here, we expand the concept of migratory plasticity beyond individual switches in migration propensity to also include spatial and temporal adjustments to migration patterns. We develop a novel typological framework that delineates every potential change type within the three dimensions, then use this framework to guide a literature review. We discuss broad patterns in migratory plasticity, potential drivers of migration change, and research gaps in the current understanding of this trait. Our result reveals 127 migration change events in direct response to natural and human-induced environmental changes across 27 ungulate species. Species that appeared in multiple studies showed multiple types of change, with some exhibiting the full spectrum of migratory plasticity. This result highlights that multi-dimensional migratory plasticity is pervasive in ungulates, even as the manifestation of plasticity varies case by case. However, studies as far have rarely been able to determine the fitness outcomes of different types of migration change, likely due to the scarcity of long-term individual-based demographic monitoring as well as measurements encompassing a full behavioral continuum and environmental gradient for any given species. Recognizing and documenting the full spectrum of migratory plasticity marks the first step for the field of migration ecology to employ quantitative methods, such as reaction norms, to predict migration change along environmental gradients. Closer monitoring for changes in migratory propensity, routes, and timing may improve the efficacy of conservation strategies and management actions in a rapidly changing world.

INTRODUCTION

Ungulate migrations spanning global grasslands and forests have long fascinated humans and are increasingly recognized for their impacts on ecosystem structure and function (Bauer & Hoye 2014; Middleton *et al.* 2020). Because these migrations span large landscapes and steep environmental gradients, they are often considered particularly vulnerable to global environmental change (Bolger *et al.* 2008; Harris *et al.* 2009; Teitelbaum *et al.* 2015). Compounding this perceived vulnerability is the common assumption that migration patterns are static traits in large mammals (Gaillard 2013; Eggeman *et al.* 2016). As a result, altered ungulate migration patterns are considered an alarming harbinger of declining population viability (Berger 2004; Wilcove & Wikelski 2008).

At the same time, a number of recent studies have suggested that changes in migratory behavior within an individual's lifetime might be relatively common in ungulates. Importantly, for example, accumulating observations of individuals switching between resident and migrant status marked the first applications of the term "plasticity" to ungulate migration behavior (Eggeman *et al.* 2016; Berg *et al.* 2019; Peters *et al.* 2019). Besides their propensity to migrate, ungulates can also alter their migratory behavior in space and time. For example, ungulates can adopt new ranges and migration corridors (Skarin *et al.* 2015; Xu *et al.* 2019) or modify the timing and duration of migratory movements (Le Corre *et al.* 2016; Rickbeil *et al.* 2019). Despite the widespread acknowledgment that *where* and *when* to migrate are as fundamental as *whether* to migrate in describing migration tactics (Gurarie *et al.* 2017), these spatial and temporal migration changes appear as idiosyncratic observations and have not yet been fully integrated into our conception of behavioral plasticity. The emerging recognition of migratory plasticity in ungulates carries important implications for ecology and conservation, yet we still lack an understanding of its extent and mechanisms.

Animals alter behavior in response to environmental change via two pathways: **contemporary evolution** and **phenotypic plasticity** (Box 1.; (Van Buskirk 2012; Winkler *et al.* 2014). Avian studies of migration change have supported both mechanisms (Hairston *et al.* 2005; Knudsen *et al.* 2011). For migratory ungulates, however, phenotypic plasticity is likely the dominant mechanism for three reasons. First, theory suggests migration evolved in ungulates to cope with variable environments (Avgar *et al.* 2013) and is maintained by learning and cultural transmission – one dominant mechanism of behavioral plasticity (Brown 2012; Jesmer *et al.* 2018). Phenotypic plasticity in individual migration behavior (sometimes deemed migratory flexibility, (Eggeman *et al.* 2016) appears fundamental to an ungulate's ability to respond to rapid environmental change. Second, unlike in many birds, migration in ungulates is not a direct mapping of genotype or phenotype, making it flexible by nature (Bolger *et al.* 2008; Hebblewhite & Merrill 2011; Berg *et al.* 2019). Finally, long generation time among ungulates reduces the likelihood that contemporary evolution occurs quickly enough to respond to rapid environmental change (Chevin *et al.* 2010; Winkler *et al.* 2014).

A comprehensive understanding of the scope and degree of **migration change** will bring predictive and mechanistic insights to migration ecology. Clearly described phenotypic dynamics over an environmental gradient link external selection pressures to phenotypic outcomes (i.e., the maintenance of migratory variations in evolutionary processes) (Dingemanse *et al.* 2010; Fusco & Minelli 2010). Understanding the interface between environment and behavior will also help to predict behavioral change in modified environments and conditions (Palkovacs *et al.* 2012). Furthermore, understanding migration change can be crucial for conservation. Evidence across taxa has shown that behavioral plasticity can maintain or improve population persistence under environmental change (Møller *et al.* 2008; Beever *et al.* 2017). In this sense, changes in ungulate migration may not always indicate decline, but rather resilience. Knowledge of the prevalence, extent, mechanisms, and ultimately, the outcomes of migration change can significantly inform effective conservation efforts. A prerequisite to achieve these advances in migration ecology and conservation is to establish a common framework to unify idiosyncratic observations of changes in migration behaviors and to clearly classify types of changes (Berg *et al.* 2019).

Here we argue that the concept of **migratory plasticity** should be expanded beyond migratory propensity (*whether* to migrate) to include the spatial and temporal patterns of migration (*when* and *where* to migrate). We introduce a novel framework to conceptualize and identify the full spectrum of migratory plasticity (Fig. 1). To demonstrate the utility of our framework and assess current evidence of migratory plasticity, we conducted a literature review to classify documented migration change events, and their inferred causes, within the framework. This classification of migration change offers novel insights into the fine-scale behavioral variations of migratory ungulate populations in context with a spectrum of environmental changes. We discuss current knowledge gaps, including the almost complete absence of studies that link migration changes to demographic consequences. Finally, we suggest future research avenues to understand the mechanisms of migratory plasticity, and we emphasize the importance of considering plasticity within the management and conservation of migratory ungulates.

EVALUATING MIGRATORY PLASTICITY WITH A TYPOLOGICAL FRAMEWORK

Our framework classifies migration change into three interconnected dimensions to describe the extent and diversity of migration change (Fig. 1). These dimensions include migration propensity (*whether to migrate*), spatial change (*where to migrate* and *along which route*), and temporal change (*when to migrate* and *for how long*). **Migration propensity** describes whether an individual migrates. **Spatial change** can manifest in four ways: (I) animals move from the original start range along a historic migration route but stop before or after the original end range, (II) animals move from the original start range but along a new migration route to reach to the original end range, (III) animals move from the original start range along a new migration route to reach a new end range, or (IV) animals move from a new start range along a new migration route to reach a new end range. Finally, **temporal change** can occur in both migration timing (departure and/or arrival date) and duration (time spent on a migration route).

To examine the prevalence of these three dimensions of migration change in ungulates and their potential relationships with different types of environmental change, we conducted a comprehensive literature review based on a combination of a snowball search, whereby we reviewed papers cited by pre-identified key studies, and a systematic search of Web of Science using the query "TS = (Ungulate AND (migration OR "migrat* behavior") AND (change OR shift OR decrease OR loss))". We classified each migration change event reported in relevant studies based on our framework (detailed review method in Appendix S1).

We found that migratory plasticity is widespread and can include simultaneous behavioral changes in multiple dimensions. We recorded 127 migration change events documented in 116 studies for 27 ungulate species worldwide, covering all types of migration change proposed by our framework (Fig. 2, Data S1). Of the 127 change events, 33.9% involved a change in migration propensity, 86.8% involved spatial change, and 35.4% involved temporal change. Species that appeared in multiple studies often exhibited multiple changes, with some species exhibiting every type of migration change (e.g., elk [*Cervus canadensis*], Box 2).

We also found that changes in migration were associated with 12 different types of environmental change, including biotic interactions (density dependence, intraspecific interaction, and predation), anthropogenic interferences (human disturbance, harvest, habitat fragmentation, habitat loss, translocation management, and supplementary feeding), and climate and weather (climate change, extreme weather, and inter-annual climatic variations). Habitat loss (29 events, 28.7%), inter-annual climatic variations (27 events, 26.7%), and habitat fragmentation (27 events, 26.7%) were the most frequent correlates of migration change.

To investigate potential relationships between types of environmental changes and migration changes, we evaluated migration change events derived from primary studies (101 out of the 127 migration change events). We found no consistent relationship between types of environmental change and specific migration changes (Fig. 3). This lack of relationship may indicate that ungulates can respond to multiple environmental changes simultaneously, in multiple dimensions. This complexity of response may have complicated researchers' abilities to disentangle the external causes of migration change and link these causes to fitness consequences. In addition, interdependence in the three dimensions of migratory plasticity can obfuscate causal relationships between the environment and migratory patterns. For example, a change in migratory duration could be the result of an animal adjusting its migration route rather than a direct response to environmental dynamics. In other cases, an individual's migratory propensity change from resident to migratory could be followed by high variability in timing or routes. Furthermore, internal factors, such as genetics, personality, learning, and physiological condition, can play a significant role in the type and degree of migratory plasticity manifested by individuals (Berg *et al.* 2019). However, much of the work on how internal factors contribute to migration patterns and behavioral plasticity remains theoretical rather than empirical, limiting our ability to explore this in the review.

Below, we synthesize the 101 migration change events by change type and discuss potential environmental and non-environmental causes driving each of the three dimensions of migration change. This synthetic evaluation for each dimension of behavioral change provides a foundation on which to build future knowledge of the demographic and conservation-related consequences of migration changes. It is worth noting that our results reflect the existing scope of current literature, which is influenced by research methodology, data availability, and funding, and thus may not yet reflect the full suite of ecological processes in play.

Migration Propensity

Partial migration describes the variation among individual migration propensity (i.e., migrant vs. resident) within a population and is recognized as the rule rather than the exception in ungulates (Dingle & Drake 2007; Cagnacci *et al.* 2016); hence, *whether* an individual migrates is a fundamental starting point for studies of migration ecology and evolution. Recent evidence that migratory propensity can switch within an individual's lifetime adds another layer of complexity to "*whether* to migrate" (Eggeman *et al.* 2016). Consequently, it is important to consider both the migration tactic individuals employ and whether that tactic changes over time. Among the 101 empirical migration change events, 34 events (33.7%) of migration propensity change were documented in 22 of the 27 (81.5%) species studied.

Altered migration propensity has been speculated to improve fitness by decreasing risk (e.g., predation risk avoidance hypothesis) or by increasing nutrition (e.g., forage maturation hypothesis) (Middleton *et al.* 2013; White *et al.* 2014; Eggeman *et al.* 2016). Changes to the distribution of high quality forage can also affect migration propensity (Barker *et al.* 2019a). Among the 34 propensity change events documented in the literature we reviewed, five were influenced by predation (14.7%, e.g., (Hebblewhite & Merrill 2011; White *et al.* 2014) and eleven by inter-annual climate conditions (32.4%, e.g., (Fieberg *et al.* 2008; Cagnacci *et al.* 2011).

Still, not all changes in migration propensity are voluntary decisions. Habitat fragmentation and loss (11, or 32.4% and 10, or 29.4%, of the 34 propensity change events) often led to forced residence of migrants, possibly increasing intraspecific competition and reducing population fitness (Said *et al.* 2016). Forced-resident populations can sometimes persist at a low population density if individuals develop alternative foraging strategies during residence, as observed in formerly migratory bighorn sheep in northwest Wyoming (Courtemanch *et al.* 2017).

Although propensity changes have been documented in 22 ungulate species, this dimension of migratory plasticity is not ubiquitous, even within populations that exhibit partial migration. For example, over seven years of monitoring thirty-six individuals from a partially migratory moose population (*Alces alces*), Sweanor and Sandegren(Sweanor & Sandegren 1988) found that no individuals altered migration propensity. Similarly, mule deer (*Odocoileus hemionus*) exhibit some spatial and temporal changes in migration pattern (Fig. 2) while displaying high fidelity to their migrant-resident status (Sawyer *et al.* 2019c). The reason for interspecies variation in migration propensity plasticity remains unknown, but spatial memory (Merkle *et al.* 2019), mating strategies (Peters *et al.* 2019), and the range species experience across environmental gradients (Mueller *et al.* 2011) may be important factors.

Spatial Changes

Conservation planning for migratory species often relies on identifying critical spatial components of animal ranges, such as stopover sites, high-use corridors, and bottlenecks (Sawyer *et al.* 2009; Sawyer &

Kauffman 2011). Understanding spatial change in migratory plasticity will therefore prove particularly relevant to current conservation measures (Allen & Singh 2016). In our review, spatial change was observed in 81 of the 101 (80.2%) migration change events in 22 ungulate species. Type I change, in which the migration route was shortened or lengthened, was the most frequently observed type of spatial change (44, or 43.6% of the 81 change events), followed by Type III (19 events, 18.8%) in which an altered migration route led to a new end range.

The most common environmental changes reported to correlate with migratory spatial change were habitat fragmentation and habitat loss (both 19, or 54.3%, of the 81 spatial change events), and harvest by humans (14 events, 17.3%). Accordingly, these categories of environmental change often have strong spatial characteristics (e.g., clumped or distributed along linear infrastructure) and directly alter the accessibility or quality of migratory routes and seasonal ranges, thereby altering spatial preference of migratory ungulates. Density-dependent factors (8 events, 9.9%) also influenced space use by ungulates. Dramatic population growth, for example, in a barren-ground caribou (*Rangifer tarandus granti*) population in southwest Alaska led to an erratic migratory pattern in some individuals, shifting traditional seasonal ranges into novel areas to create new subpopulations (Hinkes *et al.* 2005).

Generally, the four types of spatial change in migration can be explained by three factors: 1) **locomotion capacity**, 2) **site fidelity**, and 3) **navigation mechanism**. The importance of locomotion capacity can be illuminated by ungulate response to fencing; fences can affect species differently based on the animals' inclination or capacity to jump. For example, mule deer are more likely to jump fences than pronghorn (Scott 1992). Thus, mule deer may more readily cross fences without significant spatial change, whereas pronghorn may alter behavior significantly to circumvent barriers (Type II or Type III), if they are able to do so at all (Sheldon & Lindzey 2006; Kauffman *et al.* 2018).

Site fidelity can also influence spatial change. For example, Tibetan antelope (*Pantholops hodgsonii*) have high site fidelity to summer ranges, which serve as shared calving sites and locations for gene exchange across sub-populations (Schaller 1998; Xu *et al.* 2019). When a railway bisected a key migration route, animals still attempted to reach the same summer site by modifying migration routes to cross the railway (Type II; (Xu *et al.* 2019). In contrast, barren-ground caribou display low site fidelity and more readily migrated to different summer calving site locations (Type III; (Hinkes *et al.* 2005). Species with particularly low site fidelity are often considered nomadic and are believed more capable of maintaining population viability when faced with various external changes than species with high site fidelity (Mueller *et al.* 2011; Teitelbaum & Mueller 2019).

Lastly, navigation can influence the types of spatial changes exhibited. Migratory ungulates appear to be guided by both sensory perception and memory (Bracis & Mueller 2017). Animals relying predominantly on perception can more quickly adjust behaviors in response to immediate conditions. For example, zebras (*Equus burchelli*) perceive and respond to precipitation rapidly and can reorient and even reverse migration to avoid adverse conditions (Type III; (Bartlam-Brooks *et al.* 2013). This ability may partially explain the rapid recovery of zebra migration in Botswana after fence removal (Type I; (Bartlam-Brooks *et al.* 2011). Alternatively, memory-dominated navigation may result in more rigid migratory behavior (Bracis & Mueller 2017; Merkle *et al.* 2017; Sawyer *et al.* 2019c). As demonstrated by translocated moose and bighorn sheep, restoring lost knowledge of optimal migration paths can take decades (Jesmer *et al.* 2018). In such cases, protecting existing migration habitats and social structure to maintain spatial memory and cultural transmission of the population appears paramount for conservation (Brakes *et al.* 2019).

However, perception and memory are not mutually exclusive and may both contribute to a decision to migrate. Roe deer (*Capreolus capreolus*) and mule deer can use "scouting behavior" to explore immediate environmental conditions, leading to high interannual variability in migration propensity (Gurarie *et al.* 2017; Jakopak *et al.* 2019). After beginning migration, however, roe deer show a high degree of site fidelity, suggesting that the "*whether to migrate"* decision is based on perception of the immediate environment, whereas "*where to migrate"* is more likely influenced by their previous experience (Gurarie *et al.* 2017).

Temporal Changes

Temporal change was documented in 54 of the 101 (53.5%) empirical migration change events (Fig. 2). Migration timing was more frequently examined than migration duration (15 events, or 34.7% of the 101 events vs. 19 events, or 18.8%). Migrants often adjust migration phenology to accommodate interannual variations in weather, forage availability, and predation risk (e.g., (Bischof *et al.* 2012; Middleton *et al.* 2018). However, migratory timing may shift outside the interannual range if triggered by one of two pathways: (1) the local environmental gradient exceeds its interannual normal range, or (2) environmental changes obstruct ungulates' ability to track the natural gradient.

Abnormal environmental gradients often result from climate change or extreme weather events (29.6% of the 54 temporal change events). Across all migratory taxa, the most common responses to climate change involve changes to the timing or duration of migration (Beever *et al.* 2017). However, temporal behavioral change may not always keep pace with climate change. When climate change affects an area where migration is cued by emerging vegetation, vegetation may respond to climate faster than ungulates. This could lead to a phenological (or trophic) mismatch, in which migrants arrive at a site before or after peak vegetation nutrition, reducing nutrient intake and influencing fitness (Post & Forchhammer 2008; Gustine *et al.* 2017).

In addition to climate change, land use practices can create an abnormal environmental gradient by altering the nutritional landscape. For example, elk in Wyoming that were provided supplementary feed during winter spent less time migrating during spring, arrived on summer range later, and departed for winter range earlier than unfed elk (Jones *et al.* 2014). Although fed elk gained an immediate benefit of obtaining easy food, such temporal change may ultimately be maladaptive if it causes elk to miss peak green-up, resulting in decreased access to quality forage throughout the year (Jones *et al.* 2014). Additionally, unintentional supplementary feeding areas such as irrigated agricultural land can alter traditional nutritional benefits of migration and may lead to year-long residency, increasing the potential for human-wildlife conflict (Krausman *et al.* 2014; Barker *et al.* 2019b).

The second pathway causing temporal change in migration occurs when ungulates' abilities to track an existing natural environmental gradient are obstructed, for example, by habitat fragmentation and loss (35.6% of temporal change events, (Middleton *et al.* 2018). Certainly ungulates may lose access to migration routes or seasonal ranges when movement is obstructed by impermeable physical barriers, but even semi-permeable features can alter migration phenology without causing conspicuous spatial change (Sawyer *et al.* 2013). For instance, mule deer in Wyoming sped up when crossing energy development areas without changing their direction or route, creating short-term phenological mismatches between vegetation green-up and migration (Sawyer *et al.* 2013). Notably, animals attempted to correct for these mismatches by slowing down after moving through the development areas. Although the demographic consequences of changes in migration speed or reduced stopover use are unknown, these mule deer clearly modify their migratory behavior in response to energy development through relatively flexible *en route* scheduling.

Exceptions to migratory plasticity

Despite the prevalence of migratory plasticity, we observed important exceptions whereby ungulate populations were unable to adapt their migratory strategy to environmental changes. We found substantial differences in the capacity for plasticity among well-studied species, between populations of a single species, and even among individuals in the same population. For example, some elk frequently alter their migration propensity, whereas mule deer have not been observed to alter their migration propensity (Sawyer *et al.* 2019c). Even among elk, some individuals appear more likely to alter migration propensity than others (Eggeman *et al.* 2016). Similarly, a recent review revealed a wide range of plasticity in the migration propensity of white-tailed deer, with the range of switch rates fluctuating between 7% and 39% across six studies (Berg *et al.* 2019). Understanding variation within the degree of plasticity is critical for accurately predicting population trajectories and estimating the capacity of species or populations to withstand disturbance (Chevin *et al.* 2010).

Additionally, some highly plastic species experience strong limitations imposed by the physical landscape. For instance, although pronghorn have been observed to employ six types of migration change across all three dimensions (Fig. 2), one well-known population in the Greater Yellowstone Ecosystem can only access winter range through a narrow bottleneck, restricting the population's ability to adjust its migratory path (Berger *et al.* 2006). Unfortunately, empirical evidence on migrations that *do not* change is extremely limited in current literature (but see (Sawyer *et al.* 2019b). To better recognize the extent and limits of migratory plasticity, reporting non-plastic migration (including due to physical environmental barriers) is at least as important as, if not more important than, reporting migration change.

Importantly, our results reveal strong species and geographic biases within existing migration ecology literature, and we caution against generalizing our findings to understudied species and areas. More than half (52.0%) of all migration change events were observed in the top four most-studied species, and only a few studies were conducted in North Africa, Central Asia, and Latin America despite their known ungulate diversity. Given that the development of migration plasticity is likely highly dependent on local historical dynamics (David *et al.* 2004; Fusco & Minelli 2010), and that modern global environmental change exhibits high spatial heterogeneity (Walther *et al.* 2002), it is necessary to expand research of ungulate migratory plasticity beyond current "model" species and geographic locations. Due to the high variability of migratory plasticity across individuals, populations, and species, applying any overly general prediction of how migrations change may be a detriment to species that are less understood.

TOWARDS MECHANISTIC UNDERSTANDING OF MIGRATORY PLASTICITY

Migratory plasticity appears much more prevalent among ungulates than previously appreciated, indicating that multidimensional migratory plasticity likely comprises a fundamental component of ungulate behavioral ecology. At least 27 ungulate species in habitats ranging across tropical, temperate, and arctic regions have been observed to exhibit some (and often more than one) forms of migratory plasticity (Fig. 2) in response to various types of environmental change (Fig. 3). Collectively, the studies we reviewed indicate that responses of migratory ungulates to environmental change vary across species, space, and time. Notably, different types and dimensions of migration change often occur simultaneously. Hence, properly capturing behavioral dynamics requires measuring full aspects of migration change. For example, it is unknown whether animals with less-plastic migration propensities compensate for environmental change via higher plasticity in migration timing or route setting. Expanding the concept of migratory plasticity to also include spatial and temporal dimensions will achieve a more holistic understanding of the extent of plasticity across species and populations.

Gaining predictive insights of migration change

A clearer delineation of migration change types sets the stage for applying ecological theories and techniques to better predict migration behavior in altered environments. For instance, the **reaction norm** concept in behavioral ecology (David *et al.* 2004; Charmantier *et al.* 2008; Spiegel *et al.* 2017) offers a valuable and intuitive measure of phenotypic plasticity of migration. Reaction norms are quantified by estimating individual variability in relation to environmental change to examine causes and selective consequences of phenotypic plasticity and diversification across species and taxa (Charmantier *et al.* 2008; Dingemanse *et al.* 2010; Pfennig *et al.* 2010). When the behavior-environment relationship is nonlinear, specified behavioral reaction norms can illustrate the thresholds at which migration change may be expected or exacerbated. The potential of reaction norms to predict thresholds has been supported by recent work showing that migrating mule deer exhibit much stronger avoidance of energy development above a threshold level of surface disturbance (Sawyer *et al.* 2020).

Currently, applications of reaction norms remain rare in ungulate migration work, largely limited by study designs (Chapman *et al.* 2011). With the assumption that migration characteristics are fixed, most studies were not designed to examine the dynamics of the migration pattern. Rather, migrations are mostly characterized by a snapshot of propensity, temporal attributes, or spatial characteristics averaged over time, potentially neglecting the change process among variations. Even when migration changes are acknowledged, characterization of the states between which changes occur are often oversimplified. For example, in early studies of partial migration, migratory propensity was often treated as a dichotomy of resident vs. migratory (Berg *et al.* 2019). More recent work in which partial migration was observed along a behavioral continuum marked a step towards applying reaction norms to understand variation in migration propensity (Cagnacci *et al.* 2011; Gurarie *et al.* 2017; Barker *et al.* 2019a). Given the interdependence of multiple dimensions of migratory plasticity, the concept of behavioral continuum could also be applied to the temporal and spatial dimensions. The types of migration change defined in our framework can serve as baselines along which behavioral continua can be measured. For example, Spatial Type II can be measured as the largest distance between the old and new routes, and Spatial Type III can be quantified as the percentage overlap between the old and new ranges.

It is critical, yet difficult, to determine proper metrics for environmental gradients and the spatiotemporal scale at which these metrics are measured to match the behavioral continuum (Martin *et al.* 2011; Murren *et al.* 2014). Most of the papers we reviewed documented environmental change categories, but not the severity of such changes. Partially due to the difficulty of teasing apart confounding environmental variables, causal relationships between environment and migration changes are sometimes inferred but not empirically examined. The lack of a consistent correlation between types of migration change and environmental change (Fig. 3) demonstrates that more nuanced environmental measures are required for predicting migration changes. For example, instead of using a binary measurement of presence and absence, habitat loss can be measured as percentage land use change (Sawyer *et al.* 2020), and predation risk can be calculated as relative probability of predator-prey encounters (e.g., (Prugh *et al.* 2019). Advances in technologies such as remote sensing and on-animal environmental sensors will play an increasingly important role in accurate quantification of environmental changes (Pettorelli *et al.* 2014; Kays *et al.* 2015).

Consequences of migratory plasticity

Currently, ungulates with more plastic migration behavior are considered more resilient to environmental change (Sawyer *et al.* 2019c; Teitelbaum & Mueller 2019). However, phenotypic plasticity can still be associated with costs at the individual and the population level (Ghalambor *et al.* 2007). The uncertainty of whether migratory plasticity is beneficial is further complicated by varying levels of plasticity across different populations and individuals. Species with more flexible migratory behavior may indeed react to the changing environment more readily, but whether the behavioral response is strong or fast enough to compensate for the impacts of environmental change remains unknown (Hendry *et al.* 2008; Van Buskirk 2012; Sawyer *et al.* 2019b). For example, the same behavioral adaptation may have disparate demographic impacts on ungulates with different navigation mechanisms. A change of migration route may allow perception-driven animals to continue tracking high-quality forage but cause reduced foraging efficiency if they rely on spatial memory to learn migration behaviors. For animals in the latter case, corridors maintained through cumulative herd knowledge may not be readily re-learned once lost (Bracis & Mueller 2017; Jesmer *et al.* 2018). Moreover, adaptive behavioral change itself can lead to a population decline (Kokko 2011).

Furthermore, the population consequences of migration change may not remain consistent over time. Even a migration change that relieves the immediate negative impacts of environmental change may ultimately prove maladaptive (Fahrig 2007; Wong & Candolin 2015). For example, animals attracted to agriculture fields or supplementary feeding sites might be engaged in maladaptive behavioral responses due to growing mortality associated with increasing contact with humans or predators (Sigaud *et al.* 2017; Simon & Fortin 2020). Increasingly swift and severe environmental change may leave little time for migratory plasticity to manifest and may irreversibly impact population viability. Indeed, rapid environmental change is already a reality for many ungulate populations (e.g., (Said *et al.* 2016; Pei *et al.* 2019).

To better understand the consequences of migratory plasticity, future studies should prioritize long-term, individual-based migration monitoring paired with demographic or fitness information and environmental gradients. Such studies are of paramount importance to record and classify types of migratory plasticity, differentiate decreases in population viability from baseline population dynamics, examine causes and consequences of migration change, reveal interspecific differences in plasticity, and bridge the gap between migration ecology and evolution (Gaillard 2013; Eggeman *et al.* 2016). Improved tracking technology has brought long-term migration monitoring at a finer spatiotemporal scale within reach for ungulates of all sizes (Kays *et al.* 2015). On the other hand, very few studies couple ungulate migration change with demographic information or proxies of fitness over the period of behavioral change, and almost all of existing studies come from resource-rich model ecosystems (e.g., (Mahoney & Schaefer 2002; Middleton *et al.* 2013).

Without direct fitness measurements corresponding to migration change, consequences of migration changes might be inferred by comparing the fitness of individuals with different migration patterns in the same species or population (e.g., (Hebblewhite & Merrill 2011; White *et al.* 2014). Still, most studies consider a migrant-resident dichotomy, potentially overlooking a multitude of other important differences, such as that of individuals migrating long versus short distances within a population (Sawyer *et al.* 2016). Emerging advances in long-term wildlife tracking technologies and methods to measure physiological traits in free-living animals may provide necessary data that can inform physiological mechanisms and evolutionary theory of migratory plasticity (Hegemann *et al.* 2019).

IMPLICATIONS OF MIGRATORY PLASTICITY FOR CONSERVATION

A better understanding of the causes and consequences of migratory plasticity could significantly inform contemporary conservation and management efforts of ungulate populations. Common conservation strategies involve identifying and protecting key migration habitats, such as wintering areas, parturition ranges, migration corridors, and bottlenecks (Berger *et al.* 2008; Sawyer *et al.* 2009). These strategies rely on assumptions that migratory animals move regularly in the identified areas and that changes to movement pattern warrant prevention (Harris *et al.* 2009; Mueller *et al.* 2011). Indeed, it has been occasionally documented and widely argued that alterations in migration patterns are often accompanied by dramatic decreases in population size, overall fitness, or even collapse of the associated ecosystem (Said *et al.* 2016; Løvschal *et al.* 2017).

However, as we refine our understanding of migratory plasticity as a default attribute for many migratory ungulates, these assumptions face two challenges. First, not all migration changes reduce population viability. Conversely, migratory plasticity can sometimes facilitate population resilience to external changes. As discussed in the previous section, some migration changes represent tactical strategies to mitigate immediate negative impacts (e.g., (Sawyer *et al.* 2013). Second, the efficiency of conservation approaches hinges on the drivers of migratory plasticity and the type of plasticity manifested. Some environmental factors, such as climate or predator density, fluctuate despite the boundaries of areas protected by conservation or management actions. In response, ungulates might alter migration patterns to cope with these environmental variations outside of the protected habitat. If migration drastically varies in space, a fixed conservation area will become a barrier, limiting migratory plasticity. Given that today's protected areas are often accompanied with fenced boundaries or intense human pressure along their borders, attempted conservation actions might actually fail to support or even constrain a population's resilience to environmental changes (Jones *et al.* 2018a; Veldhuis *et al.* 2019).

Despite the challenges faced by migratory ungulates, migratory plasticity indicates potential positive outcomes for migration conservation. We suggest that managers identify conservation concerns beyond merely whether migration is changing, but how and why. For anthropogenic disturbances, it could be beneficial for government agencies to conduct before-during-after migration monitoring, which has, to date, yielded some of the only research showing clear causal relationships between environmental and migration changes (e.g., (Sawyer *et al.* 2013, 2017). Management actions aimed at facilitating adaptive behavioral adjustment may prove most beneficial for the conservation of migratory ungulates (Buchholz *et al.* 2012). For example, a management plan that focuses on maintaining social structure that allows for cultural transmission of optimal migratory strategies would be more effective than a plan aiming only to prevent migration change. In addition, understanding the degree to which migration is flexible makes it possible to project dynamic migration patterns and resultant population vulnerability, and to identify and protect corridors for species that are less responsive to environmental change (Blumstein 2015; Spiegel *et al.* 2017). With demographic information, researchers and managers can evaluate whether an observed migration change is optimal, beneficial, or maladaptive and identify change thresholds that would result in fitness impacts (Angilletta *et al.* 2003; Chevin *et al.* 2010). These predictions can assist prioritization and allocation of resources by determining circumstances where intervention by managers is needed (e.g., (Lewison *et al.* 2015; Allen & Singh 2016). Recognizing the extent of migratory plasticity in ungulates may even unveil new lines of inquiry and conservation, such as the restoration of migrations previously thought to be lost.

CONCLUSION

Studies of migration changes have proliferated in recent years and comprise an important component of the field of movement ecology, yet our understanding of the implications of migratory plasticity, especially in ungulates, remains in its infancy. Our synthesis of current knowledge reveals that migratory plasticity is common in ungulates worldwide. Distilling dynamic migration patterns into *whether*, *where*, and *when* under the proposed migratory plasticity framework allows us to recast the widely-accepted binary narrative that migration is either declining or thriving. Using a common typological framework to describe and compare behavioral change offers a key opportunity to identify environmental disturbance thresholds beyond which populations start to decline. Currently, the lack of concurrent demographic information has restricted us to ask new questions about when plasticity indicates adaptation as opposed to population decline or collapse.

To inform theoretical understanding and contemporary conservation, mechanistic insights regarding causes and consequences of migratory plasticity can be developed via deliberate study designs and data collection emphases. Specifically, where possible, insights would be gained by 1) collecting long-term individual-based tracking data; 2) conducting concurrent long-term physiological or demographic monitoring; 3) quantifying behavior to measure behavioral continua of *whether, where,* and *when* animals migrate; 4) measuring the type and magnitude of environmental change; 5) linking migratory plasticity to fitness consequences; and 6) expanding studies beyond current model species and geographic ranges.

Importantly, recognizing behavioral plasticity in migratory ungulates does not conflict with efforts to conserve migratory routes or behaviors, nor does it imply that predictable, high-quality resources are unimportant for migratory herds. Indeed, retaining knowledge of multiple, viable migration routes can be important for many ungulate species to take advantage of long-term spatiotemporal variability in resources. The precautionary principle should be employed when wildlife and land managers and developers are uncertain about the plasticity of a species or a population. Fundamentally, conserving populations requires understanding the full breadth of behavioral adaptations they may employ, and perhaps more importantly, recognizing animals as agents responding dynamically to their world.

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BOX 1: GLOSSARY

Contemporary evolution: Heritable trait evolution observed in contemporary time (i.e., less than a few hundred generations).

Phenotypic plasticity: Includes the ability of a single genotype to create multiple phenotypes through developmental responses to environmental cue, or the ability of an individual organism to alter its phenotype (behavior) in response to changes in environmental conditions. In **migratory plasticity**, the second ability is more commonly studied in ungulates. Note that changed behavior can be adaptive or maladaptive. The latter includes disruptive changes leading to a decline or cessation of migration.

Migration change vs. migration variation: Migration variation refers to co-existence of different migration patterns in one population (i.e., mixed migrants and residents in one population). Migration change refers to dynamic transitions among the variations (i.e., individual switch from migratory to resident).

Reaction norm: The set of phenotypes (i.e., behaviors) that can be produced by an individual genotype over an environmental gradient.

Migration propensity: Whether an individual adopts a migratory or residency tactic.

Nomadism: A movement type in which individuals or populations of animals move frequently between locations with irregular timing and/or direction, producing both within-year and between-year variability in location and movement patterns.

Partial migration: Populations of animals that are composed of a mixture of resident and migratory individuals.

Locomotion capacity: The set of traits (e.g., biomechanical or morphological machineries) that enables the focal individual to execute or facilitate movement.

Site fidelity: The tendency to return to the same sites and ranges each year.

Navigation mechanism: The set of traits (e.g., cognitive or sensory machineries that obtain and use information) that enables the focal individual to orient its movement in space and/or time.

BOX 2: ELK: A CASE STUDY IN MIGRATORY PLASTICITY

Elk (*Cervus canadensis*) exhibit particularly plastic migratory behavior. Most populations of elk are partially migratory, with some individuals migrating seasonally and others residing on a shared range year-round (Barker *et al.* 2019a). Despite past belief that migratory behavior is fixed at the individual level, recent long-term studies reveal that some elk switch between migratory and resident behaviors (Eggeman *et al.* 2016). Elk that do migrate display a range of behavioral adaptations including migrating to or from a different seasonal range, migrating along a different route, and beginning or ending migration earlier or later.

Migratory elk are remarkably flexible in their spatial use of the landscape. For example, elk in Colorado forged a new migration route to avoid pressure from human hunters (Type II; (Conner *et al.* 2001), and elk in Yellowstone found a new migration route to a new seasonal range in response to high risk of mortality from both human hunters and natural predators (Type III; (White & Garrott 2005). Elk also change the distance migrated along traditional routes in response to changes in land use and forage availability (Type I; (Craighead *et al.* 1972; Jones *et al.* 2014). Transplanted elk in Canada and the northern United States have established entirely new migrations (Type IV; (Allred 1950; Fryxell *et al.* 2008), albeit sometimes over historical migration routes, indicating a strong propensity for learning and flexibility.

Alternatively, or in addition, to changing where they migrate, elk also change when they migrate. Elk have been noted to alter both the timing (Jones *et al.* 2014; Rickbeil *et al.* 2019) and the duration of migration (Middleton *et al.* 2018), often to align movements with forage phenology. Elk also alter the timing of migration in response to other factors including changing precipitation regimes (Rickbeil *et al.* 2019), human hunting activities (Conner *et al.* 2001), and risk of predation (White & Garrott 2005). However, a highly plastic migration strategy does not promise an optimal fitness outcome. In some cases, elk have retained historic migratory patterns despite decreased survival (White & Garrott 2005), reproduction (Middleton *et al.* 2013), or recruitment (Cole *et al.* 2015). Thus, behavioral plasticity may, but does not always, allow migrants to compensate for unfavorable environmental conditions.

FIGURE 1: TYPOLOGICAL FRAMEWORK FOR MIGRATORY PLASTICITY

Migratory plasticity can manifest as changes in three dimensions: migration propensity, spatial migration patterns, and temporal migration patterns. Migration propensity focuses on whether an individual migrates. Spatial change focuses on where animals migrate and can be classified as one of four types based on alterations to the starting range, ending range, and/or migration route. Temporal change is measured via migration timing and duration. These three dimensions are interdependent, and changes in one dimension can lead to alterations in other dimension(s). Hence, multiple types of migration change within and across dimensions can, and often do, co-occur.

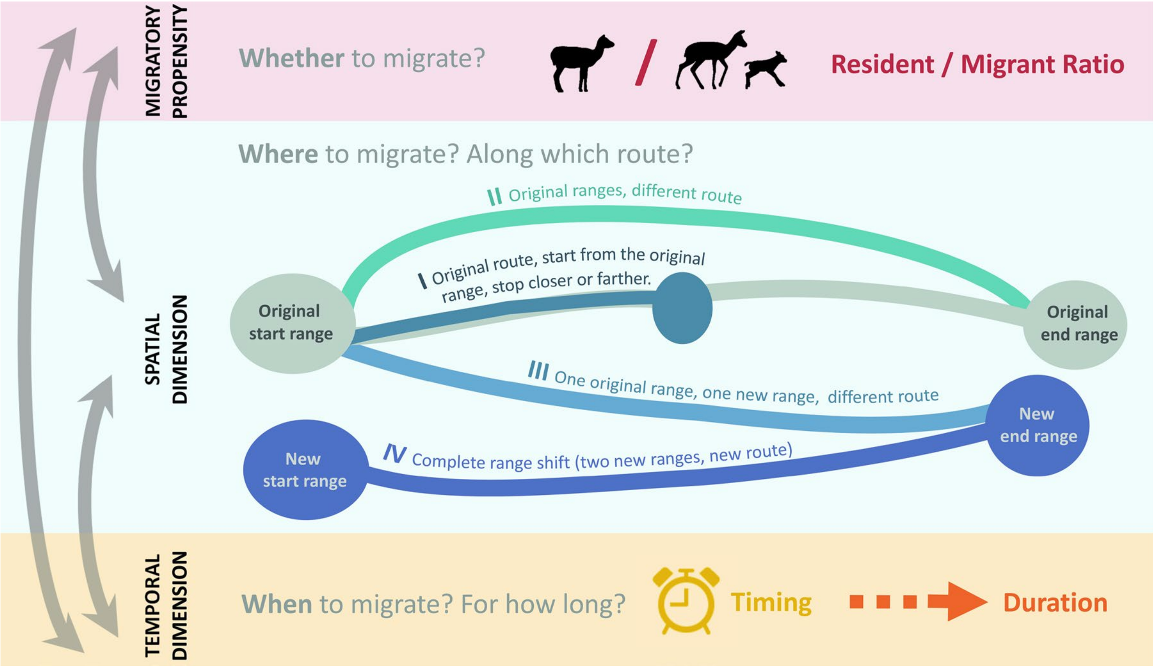


FIGURE 2: FREQUENCY AND TYPE OF MIFRATION CHANGE EVENTS REVIEWED

Black number labels are the number of studies for each species, and the map shows the geographic distribution of these studies. Most individual studies only focus on a narrow aspect of migration when examining changes. Considering multiple studies together, however, reveals that most species can modify multiple aspects of their migration patterns in response to environmental changes.

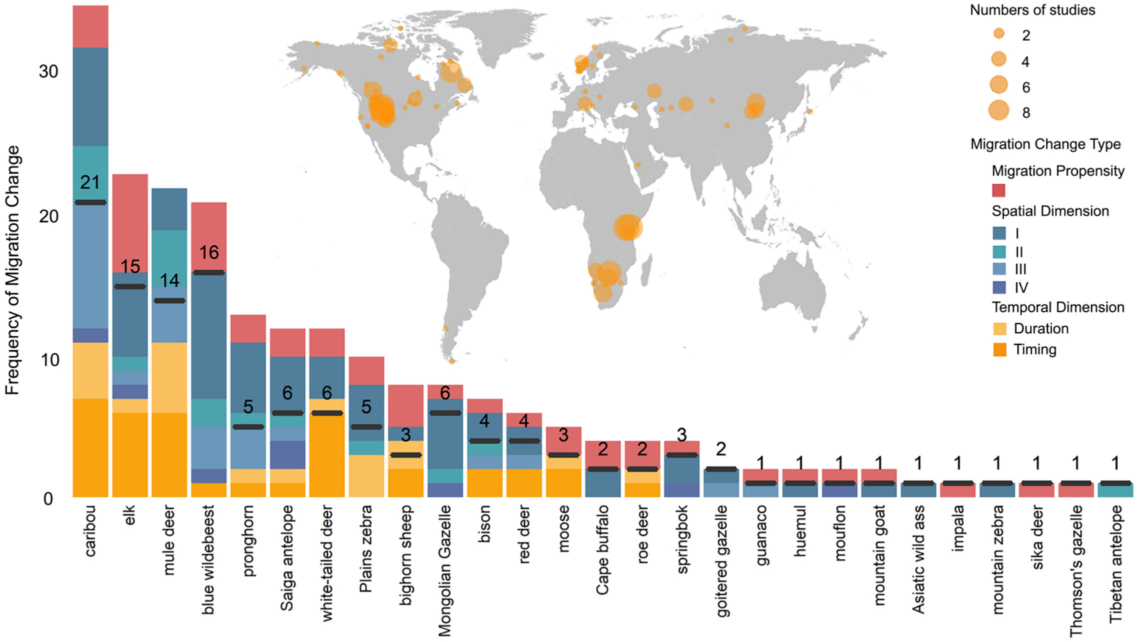
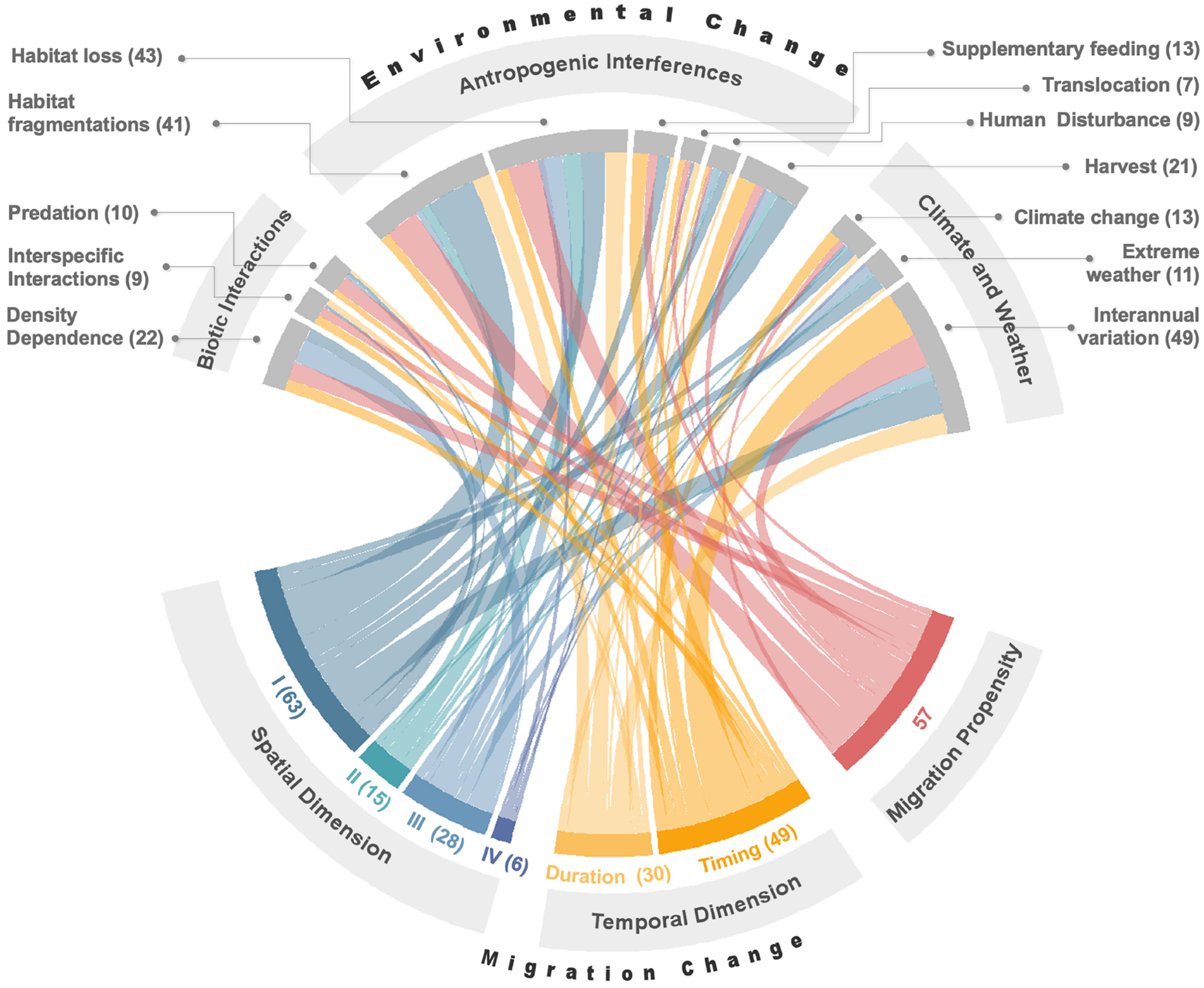


FIGURE 3: THE INTERRELATIONS BETWEEN TYPES OF ENVIRONMENTAL CHANGE AND MIGRATION CHANGE BASED ON LITERATURE WITH PRIMARY DATA

Labels represent the number of migration change events that are associated with the corresponding type of migration or environmental change. Width of the links is proportional to the number of events that show connections between the two types of change. One migration change can be correlated with multiple types of environmental change, and one environmental change can cause changes in multiple aspects of ungulate migration. Types of environmental change is not the sole determinant of types of migration change.



SUPPLEMENTARY TEXT S1: LITERATURE REVIEW METHOD

For this review we concentrated on finding literature documenting changes in migration for terrestrial ungulates in the orders Perissodactyla (odd-toed ungulates) and Artiodactyla (even-toed ungulates), hereafter as “ungulates”. We conducted a snowball search (Lecy & Beatty 2012), reviewing all literature cited in pre-identified key literature (Berger 2004; Harris *et al.* 2009; Lindström *et al.* 2014; Hardesty-Moore *et al.* 2018; Tucker *et al.* 2018). We summarized commonly used terms in this key literature in order to guide a systematic search on Web of Science, generating the following search query: “TS = (Ungulate AND (migration OR "migrat* behavior") AND (change OR shift OR decrease OR loss))”, where “TS” = Topic. We refined the search to exclude medical, pharmaceutical, or chemistry research areas and set the time span to be all years (1864-2018) and included all the Web of Science databases. We ran the search in May 2019, which yielded 1,405 results.

We then conducted a 2-stage literature review. At the first stage, the abstract of each key reference and Web of Science result was scanned and then added to a literature review database if ungulate migration change was mentioned and if it was not an already listed paper. We broadly considered ungulate species conducting various kinds of movement between distinct locations (two or more), including nomadism and seasonal migration over both long (hundreds of kilometers) or short distances (tens of kilometers). A total of 340 papers were added to a database for detailed reading, most of which were published after 2000 (Figure S1).

At the second stage, the 340 papers were divided up among the authors to record species, location, method, types of migration change, and type of environmental change that caused migrations to change. Migration changes were classified based on the proposed migratory plasticity framework (main text, Fig. 1). We prioritized directly using data presented in the paper. For example, GPS tracks of an individual over years can clearly show specific types of propensity, spatial, and temporal variations. However, old literature may lack such detailed data. In that case, we relied on key words authors mentioned to describe the migration change. For example, many papers used migrant/resident ratio, a population-level measurement, to proximate change in migration propensity. Although sometimes migrant/resident ratio change can be caused by reasons other than behavioral change (such as differential mortality rates), we considered the ratio change to be a propensity change if the authors described the migration change indicating a propensity change was involved, and the observed changes happened within a species’ lifetime. Another example is that without movement data it was hard to accurately measure whether animals have changed routes or ranges. In this case, the classification strictly followed authors’ descriptions.

Environmental changes were recorded as was presented in the paper. Because most environmental changes were described qualitatively, we grouped them into 12 types within 3 general categories in order to examine potential relationships between types of environmental change and migration change. Note that these categories are not mutually exclusive. For example, climate change could be related to anthropogenic interferences. I) Biotic interactions, including: 1) predation - natural predation pressure, 2) intraspecific interaction - social learning and/or cultural transmission from mother or conspecifics, 3) density dependence - changes in population numbers and density. II) Anthropogenic interference, including: 1) harvest - direct mortality from humans, 2) human disturbance - human activity from human development and/or other presence, 3) habitat fragmentation - barriers or land use change that break up habitat needed for migration, 4) habitat loss - barriers or land use change that eliminates viable habitat needed for migration, 5) supplementary feeding - forage intentionally or unintentionally (such as provided by agricultural land) provided by humans that influences the need for migration, and 6) translocation - the relocation of population by humans for reintroduction. III) Climate and weather, including 1) climate change - large scale changes in timing of seasons, and thus, forage availability and increased frequency and intensity of weather events, 2) extreme weather - extreme wet and droughts cycles, and 3) inter-annual variation - natural changes in seasonal conditions such as temperature, rainfall and snow depth.

During the second stage of detailed reviewing, we excluded papers that lacked information that clearly define migration change. We only included studies in which the environmental changes were based on primary data collection, literature references, or expert knowledge, rather than merely inferences. Lastly, we excluded papers using identical datasets for identical ungulate populations. The 2-stage reviewing process left 116 papers to include in the analysis and are listed in Data S1.

Chapter 3. Barrier Behavior Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates

Chapter 2 shows that migratory ungulates can flexibly adjust their movement patterns in response to environmental changes. In this chapter, I take a closer look at how fences, a common cause of fragmentation in rangelands, affect the movement behavior of migratory ungulates. This chapter has been previously published and is reproduced here with kind permission of the co-authors and Wiley.

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ABSTRACT

As human activities expand globally, there is a growing need to identify and mitigate barriers to animal movements. Fencing is a pervasive human modification of the landscape that can impede the movements of wide-ranging animals. Previous research has largely focused on whether fences block movements altogether, but a more nuanced understanding of animals' behavioral responses to fences may be critical for examining the ecological consequences and prioritizing conservation interventions. We developed a spatial- and temporal-explicit approach, Barrier Behavior Analysis (BaBA, available as an R package), to examine individual-level behaviors in response to linear barriers. BaBA classifies animal-barrier encounters into six behavior categories: *quick cross*, *average movement, bounce, back-and-forth*, *trace*, and *trapped*. We applied BaBA to wide-ranging female pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) in an area of western Wyoming, USA with > 6,000 km of fencing. We found both species were extensively affected by fences, with nearly 40% of fence encounters altering their normal movements, though pronghorn were more strongly affected than mule deer. On average, an individual pronghorn encountered fences 250 times a year – twice the encounter rate of mule deer. Pronghorn were more likely to bounce away from fences, whereas deer engaged in more *back-and-forth, trace*, and *average movement* near fences. We aggregated these behavioral responses to demonstrate how BaBA can be used to examine species-specific fencing permeability and to identify problematic fence segments in order to guide fence modification or removal. Our work provides empirical evidence on how fences affect wildlife movement. Importantly, Barrier Behavior Analysis (BaBA) can be applied to evaluate other linear features (such as roads, railways, and pipelines) and habitat edges, enhancing our ability to understand and mitigate widespread barrier effects to animal movement.

INTRODUCTION

Animal movements connect disparate habitats in space and time, and sustain critical ecosystem functions and services (Lundberg & Moberg 2003; Bauer & Hoye 2014). Yet the movements of wide-ranging animals also render them vulnerable to landscape fragmentation caused by anthropogenic barriers (e.g., roads, pipelines). Fencing, which has been implemented since the beginning of human civilization, is among the most pervasive of these barriers (Kotchemidova 2008; Jakes *et al.* 2018). The total length of fencing around the world may now exceed that of roads by an order of magnitude (Jakes *et al.* 2018), and continues to grow due to a global trend toward land partition and privatization (Linnell *et al.* 2016; Yu *et al.* 2016; Weldemichel & Lein 2019b).

Terrestrial wide-ranging mammals, such as migratory ungulates, are particularly susceptible to fence effects because fences directly block movement paths. Some of these effects are intentional and carry conservation benefits. For instance, fences are used to reduce roadway mortality (Clevenger *et al.* 2001), control disease transmission (Mysterud & Rolandsen 2019), and facilitate endangered species recovery (e.g. woodland caribou, (Cornwall 2016). Fences also carry indirect conservation benefits in some systems, such as the US West, where maintaining livestock grazing as a viable land use may protect some wildlife habitat from exurban development (Cornwall 2016; Jakes *et al.* 2018). However, fences also carry conservation costs. Impermeable fences, such as border and veterinary fences, completely block animal movement and often induce drastic population declines subsequently (Woodroffe *et al.* 2014; Said *et al.* 2016). Semi-permeable fences allow a degree of connectivity, but may still reduce movement efficiency and compromise animals' ability to access valuable resources (Cozzi *et al.* 2013; Jakes *et al.* 2018). In some cases, animals avoid areas near fences altogether, such that high fence density significantly diminishes habitat effectiveness (Zhang *et al.* 2014). The nature and strength of fence effects varies by species, according to such factors as movement capacity, diet preference, and adaptability to disturbance (Cozzi *et al.* 2013; Burkholder *et al.* 2018).

To date, most studies on fence effects have focused on measuring animal crossing rates (Bauman *et al.* 1999; Jones *et al.* 2020b), mortality risk (Harrington & Conover 2016), or population distribution (Zhang *et al.* 2014; Said *et al.* 2016; Stabach *et al.* 2016). While this information is valuable for basic management and land-use planning, animals' behavioral responses to fencing appear substantially more complex. For example, upon encountering a fence line, animals may "patrol" along boundaries, seeking breaks for crossing opportunities (Gates *et al.* 2011; Nandintsetseg *et al.* 2019), or immediately deflect away (Vanak *et al.* 2010). Animals may also move more quickly in the immediate vicinity of fences (Mark Peaden *et al.* 2017). For animals less sensitive to fencing, there might be no visible changes in movement patterns at all (Cozzi *et al.* 2013). Identifying the full suite of behavioral responses, and how these vary by species, is a key step toward understanding the consequences for individual physiology, population demography, and species interactions.

A better understanding of wildlife responses to fencing is also critical to conservation. Increasingly, land and wildlife managers seek to facilitate ungulate movement through fence removal (Alexander & Ferguson 2010) or fence modification to meet "wildlife-friendly" standards (Paige & Stevensville 2008; Paige 2015). Studies have shown that proper modification locations are critical for mitigation effectiveness (Burkholder *et al.* 2018; Jones *et al.* 2018b, 2020b). Given the sheer amount of fencing in some areas (Poor *et al.* 2014; Løvschal *et al.* 2017; Sun *et al.* 2020) and the costs of removal and modification (Huijser *et al.* 2009)Gray and Hemenway, pers. Comm.), the ability to identify problematic fences is a major challenge for land and wildlife managers. Recent advances in animal tracking technology have created new opportunities to identify movement behaviors near fences, and to link behaviors to spatially explicit fence maps.

In this study, we examined near-fence behaviors of two migratory ungulate species which are of growing conservation concern across the western US, pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*). Pronghorn ecology remains relatively poorly understood among North American ungulates, but the species is subject to intensive conservation and restoration efforts in some parts of the range (Jones 2014; Sawyer *et al.* 2019a), including habitat improvement and fence removal and modification (Jones *et al.* 2020b). Meanwhile, mule deer is a species of conservation concern in a number of western US states, sometimes due to habitat loss and potentially barriers (Sawyer *et al.* 2017). We adopted a comparative approach because these species often co-occur, but exhibit different general responses to fences. Specifically, mule deer are known to jump over fences readily, whereas pronghorn prefer to crawl under fences (Jones 2014; Jones *et al.* 2018b). The reluctance to jump means that pronghorn movements can be completely blocked by woven-wire sheep or barbed-wire fences with low bottom wires (<40 cm) – the two most common types of fences across their home range in North America (Gates *et al.* 2011). To investigate these two species' behavioral responses to fences, we developed and applied a repeatable method that categorizes individual movement behaviors in response to linear barriers such as fences (Barrier Behavior Analysis, BaBA). We conducted this work in western Wyoming, USA – a region known for some of the longest remaining ungulate migrations in North America and where fencing is a ubiquitous landscape feature (Sayre 2015; Middleton *et al.* 2020). We identify extensive, complex behavioral responses of these wildlife to fences, examine spatial and temporal characteristics of these responses, and demonstrate how BaBA might be used in to inform conservation efforts.

MATERIALS AND METHODS

Study area

Our study area (17,420 km^2) is located in western Wyoming (110.03 W, 42.907 N, elevation 1949 – 3997 m, Figure 1). This semi-arid region provides habitat for thousands of migratory pronghorn and mule deer that migrate 30 – 160 km between seasonal ranges (Sawyer *et al.* 2005). The southern part of the area is the lower elevation Green River Basin, characterized by sagebrush (*Artemisia sp.*) and sagebrush grasslands interspersed with riparian tributaries of the Green River. The landscape shifts into mountainous terrain as elevation increases towards the northern end, characterized by mid-elevation aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*), and higher-elevation Engelmann spruce (*Picea engelmannii*) and alpine fir (*Abies lasiocarpa*). Most fencing in the study area is associated with livestock pastures, private property, and right-of-ways along roads. Fence density is higher in the rangelands of Green River Basin compared to the forested areas to the north. Most fences in the region are four- or five-strand barbed wire, sometimes with woven-wire attached at the bottom (Figure 1). We refer readers to (Sawyer *et al.* 2019a) for a more detailed description of this area.

Animal tracking data and fence data

For each species, we used GPS (Telonics, Mesa, Arizona) locations collected from 12 adult females in 2014 and 12 different adult females in 2016 (Xu *et al.* 2020). We focused on tracking females because they represent the reproductive segment of the population. We selected individuals that followed a variety of migration routes, which allows us to examine larger numbers of fences across the area (Figure S1). Data for each individual spanned Jan 1 to Dec 31. GPS positions were collected every two hours and each animal-year had fix rate success of ≥ 99% (Sawyer *et al.* 2017, 2019a)for detailed animal capture and data collection protocols). The 24 mule deer were all migratory and traveled from a shared winter range in the basin to three general summer ranges in higher elevation forest areas (Figure 1). In contrast, the 24 pronghorn varied across a migration behavioral continuum (Cagnacci *et al.* 2011) from long-distance migrants to residents. The two species shared a general winter range, but tended to spatially segregate in summer when mule deer migrated to higher elevation areas (Sawyer *et al.* 2005). For each species, we defined their home range using 95% kernel density estimation on all GPS points. We also calculated cumulative movement distances by summing all step lengths for each individual in the corresponding year.

We combined existing digital fence layers from the Bureau of Land Management, U.S. Forest Service, and Wyoming Game of Fish Department. We validated our fence layer by manually checking fence lines against the sub-meter resolution (0.3-0.5m) remote sensing imagery base maps in ArcGIS 10.5. To label each fence line, we dissolved all fence features before applying the "multipart to single part" tool in ArcGIS (Xu *et al.* 2020). Our fence compilation process identified the location of fences but did not distinguish between fence types (e.g., woven wire vs. barbed wire).

Fence Behaviors Analysis

BaBA is a spatial- and temporal-explicit method to identify and classify barrier behaviors based on GPS tracking data relative to linear spatial features. We categorized each animal's response to a fence encounter into three general categories (Figure 2). The first was ***normal movement***, wherein the encounter location is permeable enough for the animal to quickly cross the barrier (*quick cross*), or the animal does not change its movement pattern notably (*average movement*). Although ***normal movement*** may still cause extra energy expenditure, the barrier does not conspicuously influence animals' mobility. The second was ***altered movement***, wherein the animal either quickly moves away from the barrier (*bounce)*, stays close by going back and forth (*back-and-forth)*, or moves along the barrier (*trace*). Note that *back-and-forth* and *trace* may sometimes lead to successful crossings, but the behavioral response caused a prolonged delay in the movement pattern, so we consider the event as an *altered movement*. The third was ***trapped***, wherein animal locations are constantly near barriers, indicating the animal might be constrained, or choose to stay, in one enclosed area (*trapped*). *Trapped* also includes cases where the animal is able to cross one barrier line but only to enter in the proximity of another one.

With GPS data and fence location as input, BaBA identifies continuous GPS locations that fall within fence buffer area as encounter events. These events are subsequently classified into one of the six barrier behavior types based on the encounter duration, straightness of the encounter movement segment, and numbers of trajectory-fence intersections. The output of BaBA is a spatial data frame with each row representing an encounter event annotated with animal ID, time of occurring, duration of the event, numbers of intersections between fences and this movement segment, and classified event type. A step-by-step BaBA guide can be found in Appendix S1.

For pronghorn and mule deer, we used BaBA with fence buffer distances every 10 meters from 50m – 150m and used *quick cross* events as indicators to identify the optimal fence buffer distance that best captured animal crossing attempts (Appendix S1). To compare pronghorn and mule deer fence behaviors, we calculated the mean and the standard deviation of numbers of each type of fence behavior across individuals, by species. We conducted a sensitivity analysis of BaBA results by adjusting parameter settings and GPS temporal intervals (Appendix S2).

Identifying and prioritizing problematic fences

We spatially joined the BaBA result generated from the optimal fence buffer distance with the fence layer to create a fencing evaluation map. We characterized each fence line by the total number of animal encounters that occurred along it, the total number of unique individuals that interacted with it, and the total number of each barrier behavior along it. For each fence line, we calculated a permeability index to evaluate how often it alters animal movement, defined by the ratio of non-***normal movement*** events (*bounce* + *trace* + *back-and-forth* + *trapped*) to total encounter events, weighted by numbers of unique individuals encountered and scaled to 0-1. Because not all mapped fences were encountered by animals equally, we only included ones with at least 10 encounters to ensure sufficient information exist for calculating the permeability index. All analysis were programed in R (R Core Team 2016), and the script are available in R package "BaBA" at github.com/wx-ecology/BaBA.

RESULTS

Fence and home range

Fencing digitization and correction generated 6244.33 km of fence in the study area, with a density of 0.36 km/km^2 (Figure 1). Results of home range and movement distance calculations confirmed a widely dispersed movement pattern of pronghorn (Figure S1). The total range size of the 24 pronghorn was 5726.7 km^2, with an accumulated movement distance of 1551.4 ± 201.0 km per year, 68% longer than that of a mule deer (991.8 ± 91.0 km). On the other hand, deer were more migratory and the range of the 24 individuals (3793.9 km^2) delineated their seasonal habitats and migration corridor. The average fence density in pronghorn range was 0.91 km/km^2, compared to 0.59 km/km^2 for mule deer.

Fence Behaviors Analysis

For pronghorn, a 110-meter fence buffer best captured the *quick cross* events, while for mule deer, this optimal distance was 90 m (Figure 3, Appendix S1). Pronghorn encountered fences on an average of 248.5 ± 94.8 (mean ± standard deviation, same below) times per year, twice the rate of mule deer (119.3 ± 86.2). Both species had similar *quick crossing* rates, with 51.0 ± 6.1% for pronghorn and 51.6 ± 10.5 % for mule deer. Among non-crossing behaviors, pronghorn *bounced* away from fences (76.4 ± 7.6%) more frequently than mule deer (64.7 ± 12.5%) (Mann-Whitney $p < 0.05$). When animals did spend time near fences and were not trapped (i.e. they were engaged in *average movement*, *back-and-forth*, or *trace* behaviors), mule deer were more likely to maintain *average movement* patterns than pronghorn (63.8 ± 14.2% vs. 57.0 ± 13.1%, Mann-Whitney $p < 0.05$). For both species, the *back-and-forth* to *trace* ratio was about 3:2.

Pronghorn were impacted by fences more in summer than in winter (Figure 4), as fence encounters increased May through September (summer encounters increased by 52.1 ± 46.5% compared to the winter encounters, Mann-Whitney $P < 0.05$). Specifically, pronghorn performed more *bounce* and *quick cross* behaviors, but other longer-lasting behaviors did not increase as much. In contrast, some mule deer individuals even encountered fences less in the summer, and the changes were not significant across individuals between winter and summer (Mann-Whitney $P = 0.26$).

Identifying and prioritizing problematic fences

Fence segments elicited different behavioral responses from pronghorn and mule deer, indicating some were more permeable than others. Cumulative levels of behavioral responses weighted by the number individuals detected at each fence segment provided a spatially-explicit map, revealing a species-specific permeability landscape for pronghorn and deer. The highest concentration of problematic fences appeared to coincide with the central part of the study area that both pronghorn and deer utilize as winter range (Figure 5A and B). Notably, fences in the southeast corner of the study area with higher impermeability for mule deer also appeared to be problematic for pronghorn. Figure 5C and D showcased one fence that was problematic for both species and this zoom-in view further demonstrated species difference at a finer scale. Pronghorn often bounced at the southern section of this fence, yet mule deer encounters tended to happen at the west with high occurrences of *back-and-forth*.

DISCUSSION

Scientists and conservationists increasingly recognize of the ubiquity and potential impacts of fencing on global biodiversity, and have called for empirical studies of fence ecology to guide conservation and management (Durant *et al.* 2015; Jakes *et al.* 2018). Our work answers this call, revealing extensive effects of fencing on the movement behavior of two wide-ranging ungulate species in western North America, effects which are expressed via a suite of specific behavioral responses. Specifically, the pronghorn and mule deer we studied crossed fences about half the time they encountered fences, but in the other half of these encounters mainly adopted *bounce*, *trace*, and *back-and-forth* behaviors to avoid fences or find potential crossings. We show how fence effects vary in space and time and affected these two highly mobile ungulate species differently. Importantly, we demonstrate that when summed and mapped, these behaviors can aid in identifying problematic fence segments, potentially aiding in mitigation programs. Our method, BaBA, is applicable to any linear barrier and habitat edges, illustrating how future work can harness tracking data to understand and ameliorate constraints on animal movements.

Importantly, our study shows that behavioral responses to fences are more complex than simply crossing or not crossing them. For both pronghorn and deer, nearly 40% of fence encounters altered their normal movement. Among the non-normal fence behaviors, *bounce* was the most common for both species, indicating that animals often move away from fences if they cannot quickly cross. Such avoidance of fences can drive animals away from high-quality resources and reduce habitat use effectiveness (Jones *et al.* 2019) – a barrier effect reported for a wide range of species including wildebeest (Stabach *et al.* 2016), African elephant (Vanak *et al.* 2010), and Przewalski's gazelle (Zhang *et al.* 2014). The other two altered fence behaviors, *back-and-forth* and *trace*, could be particularly costly, especially when resources are not available along fences. For example, Mongolian gazelle (*Procapra gutturosa*) were observed to trace border fences for as long as 59 days (Nandintsetseg *et al.* 2019). Lastly, although not frequently detected in our study, *trapped* events often occurred in areas with high fence density – for example, near exurban properties or livestock pastures. Constraining animal movements for prolonged periods within limited areas may trigger human-wildlife conflicts (Zhang *et al.* 2014).

Our results are likely a conservative estimation of actual fencing impacts in our study area. For highly mobile animals like pronghorn and mule deer, our moderate 2-hour GPS interval might not capture nuanced movement changes caused by fencing in a shorter time period (Appendix S2, Appendix S3). On the other hand, fine scale GPS tracking data manifests high spatiotemporal autocorrelation. While we focused on barrier behaviors of females in this study, males might be more constrained by fences because their large horns could prevent them from crossing underneath. Altogether, though the wildlife can still move across the study area, it is conceivable that connectivity and habitat function are substantially compromised across large portions of the landscape due to the cumulative effects of fence behaviors. Our future research will focus on evaluating potential ecological and demographic consequences of the different types of fence behaviors.

Our results also illuminate the species-specific nature of fence impacts on wildlife. Compared to mule deer, pronghorn encountered fences twice as often, which might be associated with their longer cumulative movement distance and dispersed movement patterns (Figure S1). It is possible that fences contribute to the relatively long movement distances of pronghorn by constantly redirecting them and making directed point-to-point movements difficult. Similarly, Ockenfels et al. (Ockenfels *et al.* 1997) found that fenced roads significantly constrain the shapes of pronghorn home range. At a broader scale, fence construction across the American West (Sayre 2015) could shape the geographic distribution of pronghorn, confining them to a portion of their historical range. Pronghorn also exhibited larger seasonal variations in fence behaviors than mule deer, encountering fences 1.5 times more in summer than in winter. This pattern is likely a result of pronghorn simply moving more than deer during the summer and the spatial distribution of fences in our study area. Most pronghorn are an obligate to open plains and basins, whereas mule deer migrate into mountainous areas where fences are sparse, resulting in a much higher fence density in pronghorn year-round home range. It is generally recognized that winter is a critical season for pronghorn fitness and survival (Keating 2002). However, our study underlines an unexpected conservation challenge that summer as well is a costly season for pronghorn considering energy spent interacting with fences. Given one recent estimate of over 1 million km of road-side fences and pasture fences in the American West (McInturff *et al.* 2020), fence modifications for conservation might be more urgent than currently recognized.

The spatial-explicit BaBA results, when viewed cumulatively, can be used to prioritize fence modification efforts (Figure 5). The distinctive distributions of problematic fences for the two species highlights the importance of the species-specific perspective when evaluating conservation needs in fenced landscapes. Pronghorn and deer shared several of the most problematic, or least permeable, fences, which highlight obvious areas to prioritize fence mitigation. The prioritization maps also highlight conservation challenges for conserving wide-ranging animals. Our map resulted from only 24 sampled animals. Additional animal tracking data might further expand the numbers and the distribution of problematic fences, especially for pronghorn because of their expansive movement pattern. Further, problematic fences were dispersed widely across the study area, overlapping with a complex mosaic of public and private land ownerships (Middleton *et al.* 2020). Collaborative efforts and integrated land use management are likely necessary to ensure success of fence modifications for these wildlife.

Though we focus on fences here, BaBA can be widely applied to other types of linear barriers (e.g. roads, pipelines) and habitat edges (e.g. woody-cultivated ecotones). These applications can potentially aid in a wide range of conservation projects – such as constructing wildlife passages at optimal locations along highways and railroads (Xu *et al.* 2019). Yet, we caution that types of barrier behaviors classified by BaBA are solely based on physical characteristics of movement trajectories, and its application and interpretation should be informed by species movement characteristics, spatial precision of barrier locations, and temporal resolution of GPS data (Appendix S1). For example, the *trace* behavior can be extremely costly (Gates *et al.* 2011; Nandintsetseg *et al.* 2019) or can be a navigation tactic that boosts animal foraging and movement efficiency (Rostro-García *et al.* 2015; Dickie *et al.* 2017). Second, for demonstration purposes, we chose individuals that range over relatively large areas. Yet, when applied to management of populations, we recommend a more representative sampling design, ideally with multiple years of data to obtain sufficient encounter rates across fences.

To date, most fences on earth are still undocumented or unmapped (Jakes *et al.* 2018). Our study area alone contained 6244 km fences, more than double the length of the US-Mexico border (3145 km). Yet this only represents a small fraction of the total amount of fence in north America and beyond (McInturff *et al.* 2020). With the increasing availability of high-resolution remote sensing images and the rapid development of the field of computer vision, methods like deep learning can be applied in detecting fences systematically at a landscape scale (Christin *et al.* 2019). With the benefit of such technological advancement, we hope BaBA can be strengthened and play a significant role in generating synoptic knowledge across species and systems, underpinning the burgeoning subdiscipline of fence ecology and conservation.

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FIGURE1: STUDY AREA AND TYPICAL FENCE STRUCTURE IN THE AREA.

Upper right: 4-strand barbed wire fence. Lower-right: woven wire sheep fence.

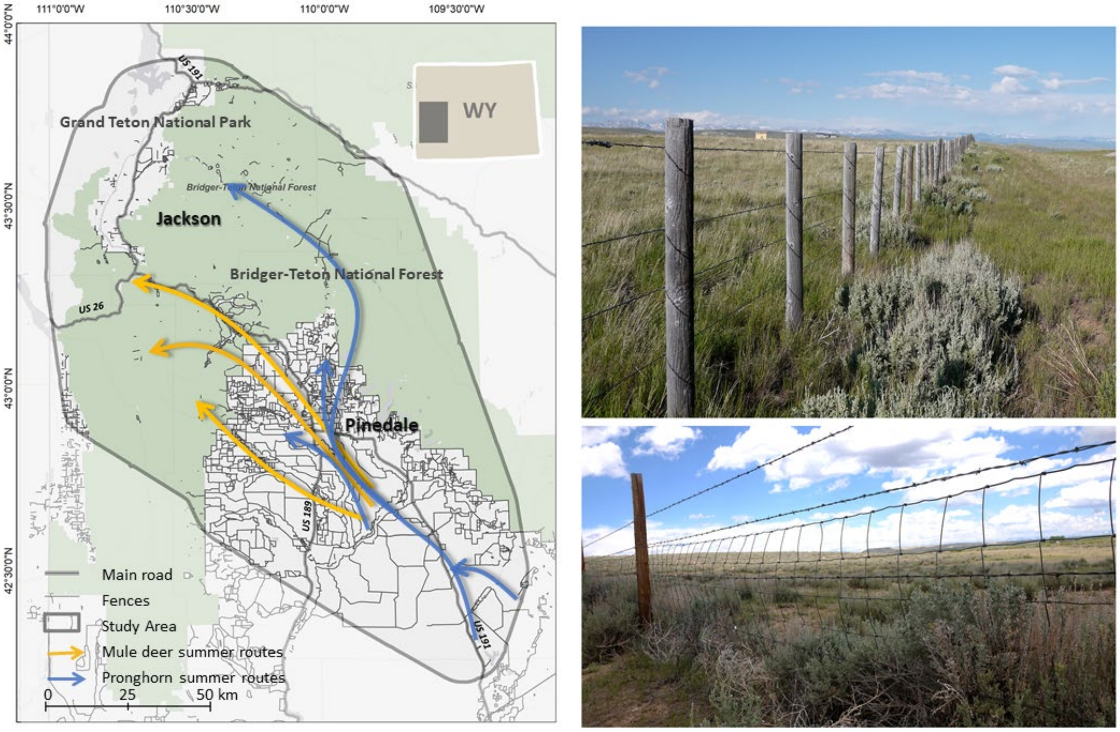


FIGURE2: THE SIX BEHAVIORAL TYPES IDENTIFIED IN BARRIER BEHAVIOR ANALYSIS.

When a fence does not represent a significant barrier to movement, an animal can conduct **normal movement**, including (1) quick cross and (2) average movement. Otherwise, animals may (3) bounce away from fences, or (4) move back-and-forth and (5) trace along the fence to seek a potential crossing. In some cases, an animal may become (6) trapped in a fenced area and forced to remain in close proximity to fences for a prolonged period.

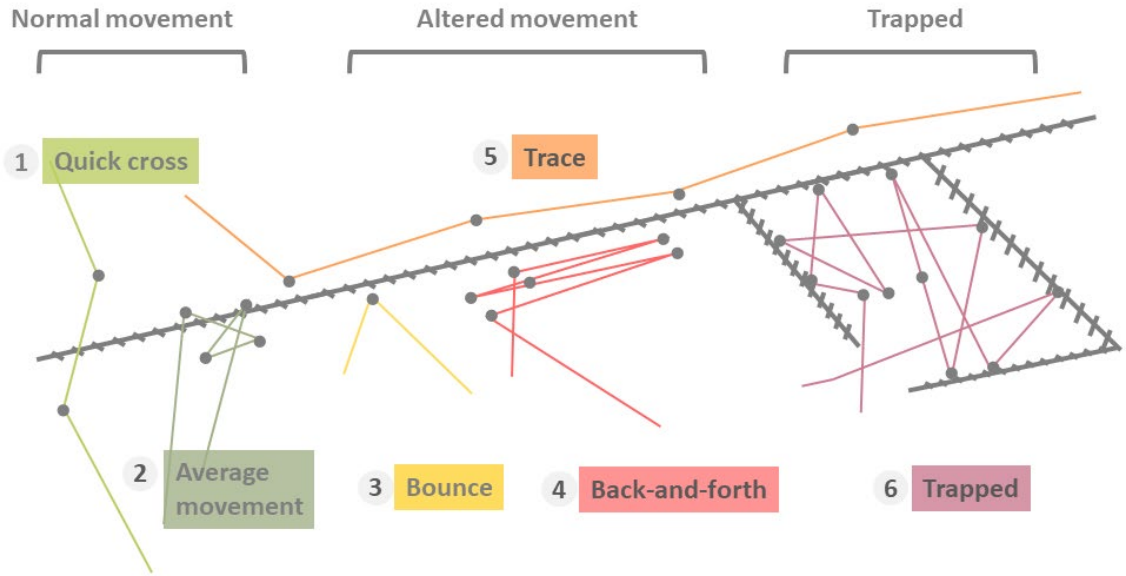


FIGURE3: ANNUAL INDIVIDUAL FREQUENCY OF BARRIER BEHAVIORS. Grey bars show the standard deviation of total fence encounters across the 24 individuals. The optimal distance for capturing fence crossing behaviors is 110 meters for pronghorn, and 90 meters for mule deer (highlighted bars).

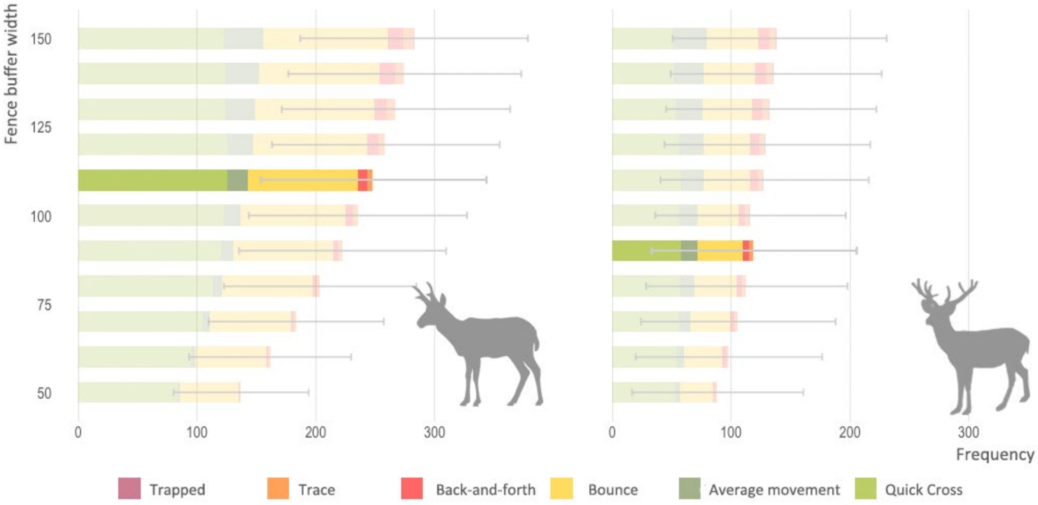


FIGURE 4: SEASONAL VARIABILITY OF BARRIER BEHAVIOR.
Pronghorn (n=24) had a large, single peak seasonal variation in fence encounters with more bounce and quick cross behaviors during the summer (May - September, pink shade) compared to the winter (November - March, blue shade). Mule deer (n=24) showed variable barrier behaviors throughout the year, with a slight, but not significant, increase in frequency during the summer.

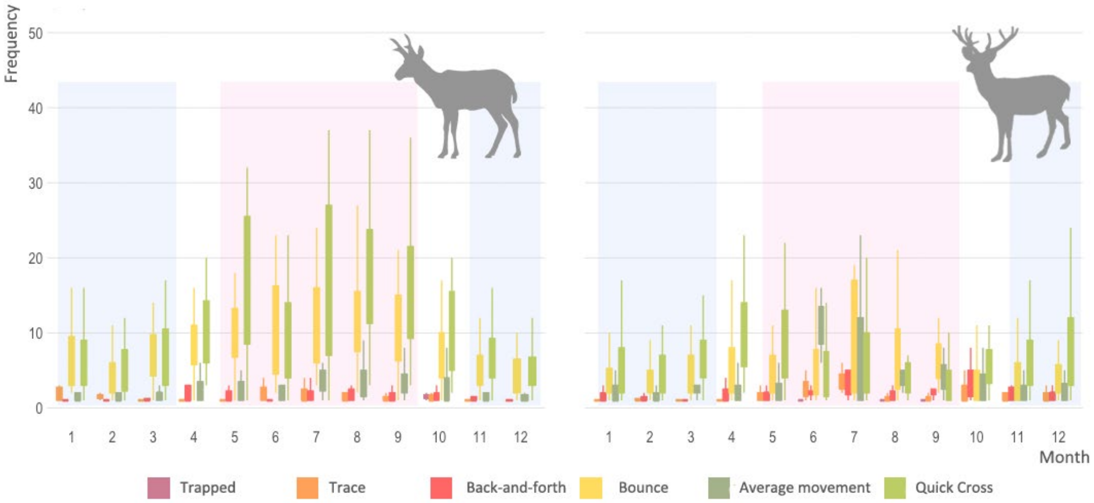
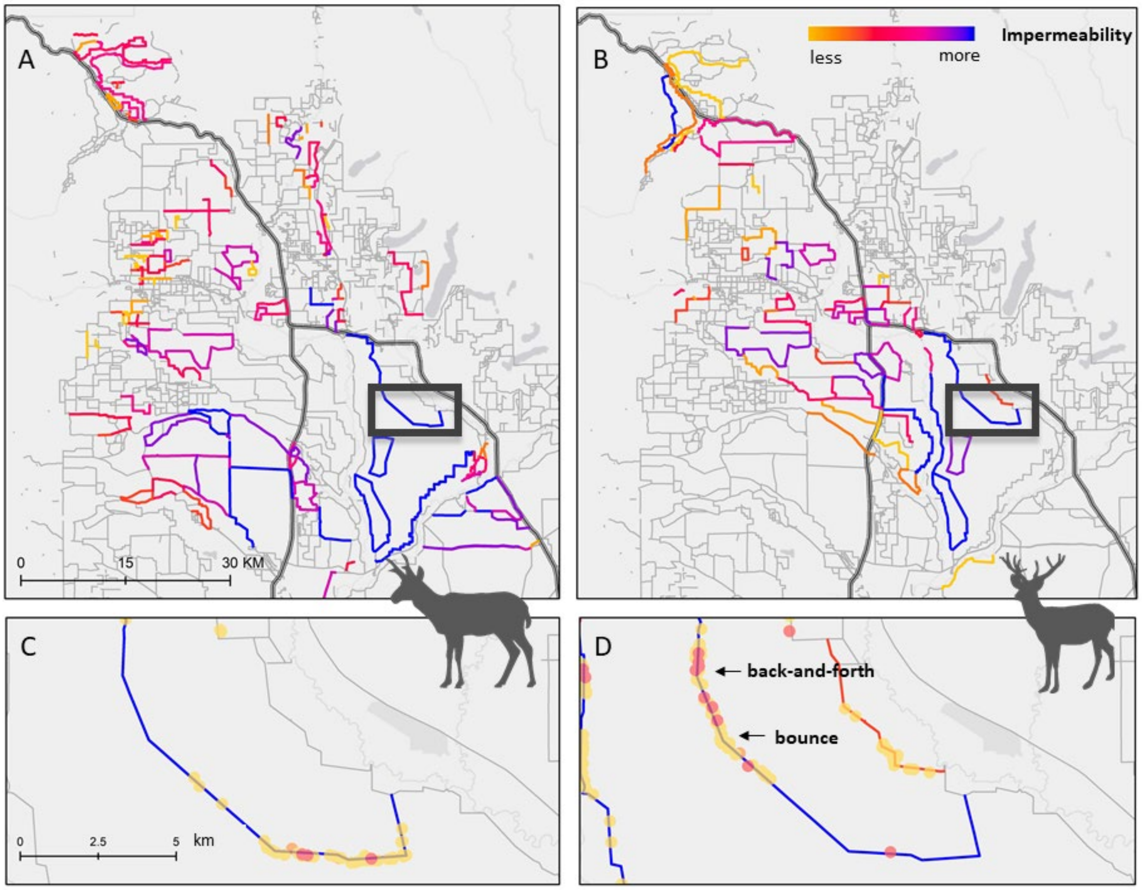


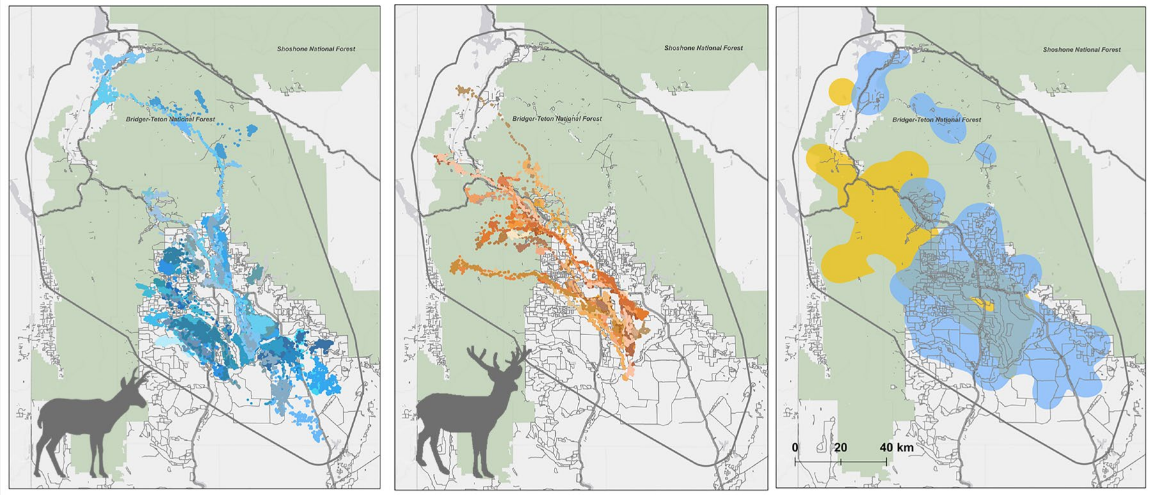
FIGURE 5: FENCING MITIGATION PRIORITIZATION FOR (A) PRONGHORN AND (B) MULE DEER MOVEMENT.

Only fence lines that had more than 10 total encounters are highlighted in colors. C and D show the zoom-in view of the boxed area in the top panels overlaid with classified fence encounter events.



SUPPLEMENARY FIGURE S1: MOVEMENT TRACKS AND HOME RANGE OF PRONGHORN AND MULE DEER.

GPS data for the 24 pronghorn-years (left) and 24 mule deer-years (middle), and 95% kernel density home range (right) generated from the pronghorn (blue shade) and mule deer (yellow shade) GPS data.



APPENDIX S1: BaBA STEP-BY-STEP PROCEDURES AND INTRODUCTION TO R PACKAGE “BaBA”.

BaBA (Barrier Behavior Analysis) is a function of the R package “BaBA” (available at github.com/wx-ecology/BaBA) that classifies barrier encounter events into six categories: *quick cross*, *average movement*, *bounce*, *trace*, *back-and-forth*, and *trapped*. These categories describe spatial and temporal characteristics of movement segments near barriers and interpretations of their ecological consequences need to be situated in species and environmental contexts. Below, we first introduce the six parameters used in BaBA and describe how these parameters are applied to classify behaviors. Then, we use our pronghorn and mule deer case study to discuss how to assign values to the BaBA parameters. The workflow of the BaBA process is demonstrated in Figure S1.1 and an overview of major criteria for each behavior type is listed in Table S1.1. To install the latest development version of BaBA, in an R session, type:

```
devtools::install_github("wx-ecology/BaBA”)
```

BaBA parameters and process

- **d:** barrier buffer distance, in meters, if the barrier is in projected coordination system. Otherwise, in units of the barrier layer. The width of the barrier buffer will determine which GPS positions are considered in close proximity to barriers.
- $\mathbf{t_b}$**:** The maximum duration of an encounter event to be considered as a short barrier interaction (i.e. *quick cross* or *bounce*), in hours.
- $\mathbf{t_p}$**:** The minimum duration of an encounter event to be considered as a prolonged barrier interaction (i.e. *trapped*), in hours.
- **w:** window extent, in days. Defines the length of a time period where a moving window method will be applied to calculate average movement straightness.
- **tolerance:** Maximum duration to allow some occasional GPS locations to be outside of barrier buffer in one continuous encounter event (see caveats section below), in hours.
- **max_cross**: Maximum number of crosses (trajectory-barrier intersections) allowed in *trace* and *back-and-forth* behavior (see caveats section below).

BaBA identifies and groups any continuous GPS positions that are within **d** of barriers as encounter events. Based on its duration $\mathbf{t_i}$, an encounter event is identified as short ($\mathbf{t_i < t_b}$), median ($\mathbf{t_b < t_i < t_p}$), and prolonged ($\mathbf{t_i > t_p}$). Any prolonged event with $\mathbf{t_i}$ longer than $\mathbf{t_p}$ is classified as *trapped*.

For short events, BaBA extends the event trajectory by including one movement location before and one after the encounter event. If the extended trajectory intersects a fence line, the event is classified as *quick cross*. If the extended trajectory has no intersection with any fence line, it means the animal stayed for a short amount of time within the fence buffer area and quickly moved away: the event is labeled as *bounce*. When the location before and/or after the event trajectory is missing (such as when the encounter event is at the beginning or the end of the GPS record) and no crossing of a barrier is identified with the locations available, the event is labeled as *unknown*.

For median events, BaBA calculates movement segment straightness ($\mathbf{str_i}$) of each event to evaluate whether the focal event is different from average movement straightness. Straightness is a telling indicator of barrier effects because linear barriers like fencing and roads often alter movement path orientation and animals cannot keep heading straight along their original movement direction unless they are parallel to the barrier. Path straightness is the ratio between the displacement distance and the accumulated step length of a trajectory, ranging from 0 (sinuous) to 1 (straight) (Benhamou 2004). Because baseline movement straightness can vary greatly across individuals and time, especially for migratory animals, we calculate local average straightness ($\overline{\mathbf{str}_{iw}}$) and standard deviation ($\boldsymbol{\sigma}_{iw}$) by applying a moving window method on all $\mathbf{t}_i$-hour movement segment (same duration as the focal event) from **w/2** days before till **w/2** days after the focal event. The window moves along the movement trajectory within the defined time period one location at a time. Given certain GPS interval **int**, the total number of sampled movement segments is **w*24/int+1**. For example, to calculate a 7-day baseline straightness for an encounter event that lasts 10 hours and with a 2-hour GPS interval, BaBA calculates the average ($\overline{\mathbf{str}_{iw}}$) and standard deviation ($\boldsymbol{\sigma}_{iw}$) straightness of all 10-hour movement segments starting at or after 3.5 days before the encounter event and ending at or before 3.5 days after it (85 segments in total). The user may choose to exclude any location that falls within a barrier buffer using "**exclude_buffer**" argument in the function and the straightness will only be calculated on $\mathbf{t}_i$-hour-long segments that are constituted of continuous locations outside of barrier buffers. When the barrier deployment is dense, however, choosing to do so can greatly reduce the number of straightness measurements that are averaged over. Therefore, in our pronghorn and mule deer case study, we included all GPS locations to calculate the average straightness ($\overline{\mathbf{str}_{iw}}$).

With $\overline{\mathbf{str}_{iw}}$ and $\boldsymbol{\sigma}_{iw}$ calculated, BaBA uses one-standard-deviation criteria to determine whether the target encounter event is different from the average movement at the time. Encounter events are classified as an *average movement* if $\mathbf{str}_i$ is within $\overline{\mathbf{str}_{iw}} \pm \boldsymbol{\sigma}_{iw}$, *back-and-forth* if $\mathbf{str}_i < \overline{\mathbf{str}_{iw}} - \boldsymbol{\sigma}_{iw}$ (the movement of the encounter event is more sinuous than the normal), and *trace* if $\mathbf{str}_i > \overline{\mathbf{str}} + \boldsymbol{\sigma}$ (the movement of the encounter event is less sinuous than the normal). When there is less than half of **w*24/int+1** movement segments included in the calculation of $\overline{\mathbf{str}_{iw}}$ and $\boldsymbol{\sigma}_{iw}$, the encounter event will be classified as *unknown*.

Caveats of BaBA

Misclassifications can occur in BaBA and here we listed some of the common causes and potential solutions.

1. Curvy, zig-zagged, or discontinuous barriers with the inadequacy of GPS trajectory in representing actual movement routes (often related to coarse GPS temporal resolution). When barriers are curvy or discontinuous, GPS trajectories between two locations can result in some intersections with the barriers even though the animal did not cross the barrier. This is especially problematic for *back-and-forth* and *trace* events because these behaviors are assumed to happen along one relatively straight fence line. To counter this problem, BaBA has an adjustment parameter max_cross to allow some trajectory-barrier intersections in *back-and-forth* and *trace*. When intersections are greater than max_cross, the event will is reclassified as *unknown*.
2. High GPS temporal resolutions. This is an opposite problem as listed in (1). Theoretically, high-frequency GPS data can capture nuanced animal movement near barriers (e.g. (Bischof *et al.* 2019), and applying BaBA on such data may achieve higher classification accuracy. However, when more details of movement are captured, a clear-cut setting of barrier buffer distance across the whole landscape may exclude many median-long encounter events when animals just shortly go farther away from barriers but quickly come back. Even though it is not a specific problem we encounter in our case study, users can specify a tolerance in the BaBA function of our R package to tolerate some occasional GPS locations outside of barrier buffer in one continuous encounter event.

3. High barrier density and messy barrier deployment. Using our case study as an example, fences are denser around towns, causing some identified barrier encounter events actually composed of several continuous encounter events spread across multiple fence buffers, and many of these events are classified as *trapped*. If using data with higher GPS temporal intervals, such events might be broken down into a couple of *normal* and *altered* events. Such cases are not necessarily false classification, but nuanced behavioral responses might be overwhelmed by the prolonged length of the encounter event. One solution is to have very well IDed barrier layers so one can count for the number of different barrier buffers one encounter event crosses (not currently implemented in BaBA).

Parameterizing BaBA: pronghorn and mule deer case study as an example

Determining fence buffer distance **d** is critical. When **d** is too small, crossing events may be missed. When **d** is too large, extra locations will be included and events might be misclassified. Because we lack empirical knowledge of the distance at which pronghorn and mule deer react to fences, we used *quick cross* events to identify the optimal fence buffer distance for each species of interest. As **d** increases and more movement points get included in the buffer area, *quick cross* events will first increase then fluctuate or decrease (Figure S1.2). Alternatively, users may use resource selection function to quantify animals' response to fences (e.g. (Stabach *et al.* 2016) and use the response curve as guidance for determining **d**. By applying fence buffer distances every 10 meters from 50m - 150m, we define the optimal buffer as the distance at which the number of *quick cross* events begins to level off (< 1 % increase). We defined $\mathbf{t_b}$ and $\mathbf{t_p}$ as 4 hours and 36 hours, respectively, based on local biologist recommendations. We used 7 (168 hours) for **w**. We recommend users balance target species ecology (e.g. movement rate and scale), barrier density, research or management objectives, and data quality (e.g. temporal intervals and spatial accuracy) when determining $\mathbf{t_b}$, $\mathbf{t_p}$, and **w**. To most accurately classify *back-and-forth* and *trace* behaviors near discontinuous or irregular fences, we visualized 10% of randomly selected median encounter events and decided to set **max_cross** as 4. We reclassified such behaviors with >4 intersections with fences as *unknown***.**

Chapter 4. Fencing amplifies individual differences in movement and survival for two migratory ungulates

The previous two chapters indicate that behavioral plasticity, or within-individual variations in behaviors, might be a key mechanism that animals use to adapt to fragmented landscapes. In this chapter, we test this hypothesis by examining behavioral variations at individual levels.

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ABSTRACT

Fences have recently been recognized as one of the most prominent linear infrastructures on our planet. Fences have far-reaching effects on wildlife, including triggering complex movement responses in wide-ranging herbivores. As animals travel across a fenced landscape with varying fence density levels, they adjust movement behaviors to balance the trade-offs between the benefits of accessing resources and the energy costs of coping with fences. In this study, we investigate the multi-scale effects of fencing on animal movement behavior, space use, and survival by quantifying variation in individual responses to fence barriers in pronghorn and mule deer along a fence density gradient in southwest Wyoming, USA. Our results highlight a high level of plasticity in animal movement behavioral responses to fences. Particularly, individuals can differ in degree and even direction in their responses to a fence density gradient. Although individuals did not show unique behavioral types in their responses to fences at low to moderate fence densities, individual differences became apparent at high fence densities. Overall, response to fences and total space use was positively correlated for mule deer, but not pronghorn. Relatedly, fence density negatively affected mule deer monthly survival, but not that of pronghorn, with a caveat that we had a larger number of repeated measurements for mule deer than pronghorn. By creatively integrating the disciplines of movement ecology, behavioral ecology, and fence ecology, this study provides new evidence that fencing may disproportionately affect some species and, under certain conditions, individuals within the same species. Accordingly, managing landscapes for lower fence densities may help prevent irreversible behavioral shifts, and their associated fitness costs, in wide-ranging animals.

INTRODUCTION

Migration, a captivating natural phenomenon, enhances animal resource acquisition with important implications for the fitness of individuals and the dynamics of populations (Avgar *et al.* 2013; Middleton *et al.* 2018; Kauffman *et al.* 2021a). However, terrestrial animal migrations are increasingly impeded by linear infrastructures worldwide (Barker *et al.* 2021; Kauffman *et al.* 2021b), among which fences are one of the most prevalent and impactful (Jakes *et al.* 2018; McInturff *et al.* 2020). As migratory animals move across fenced landscapes, individuals encounter fences repeatedly, sometimes hundreds of times in a year, and each encounter requires a movement response - whether to cross, detour, or avoid the barrier (Xu *et al.* 2021b). Each fence encounter and its subsequent movement response (hereafter "barrier behavior") is associated with varying energetic costs and altered space use in proximity to the barrier (Beyer *et al.* 2016). However, whether and how these localized effects associated with animal movement responses to fences scale up to influence larger-scale space use and population dynamics remain unknown.

Fences, like other forms of anthropogenic disturbances, do not affect all species or individuals equally (Wong & Candolin 2015; McInturff *et al.* 2020). In the western US, for example, mule deer (*Odocoileus hemionus*) are considered better at negotiating fences than pronghorn (*Antilocapra americana*) because of their greater ability to jump over fences (Jones 2014; Jones *et al.* 2018b). Within pronghorn, migratory and resident animals may show different levels of avoidance of fences (Jones *et al.* 2019). However, most research on fence effects has focused on animal movement responses at the species and population level and uses population mean to represent individual responses (McInturff *et al.* 2020). Despite accumulating evidence shown that individual differences can be prevalent in animal spatial behaviors (Spiegel *et al.* 2017; Hertel *et al.* 2020; Stuber *et al.* 2022), little is known about how different individuals may respond to fences differently.

Individual variations in barrier behavior can be driven by external environmental conditions. Specifically, fence density is likely a key factor shaping animals' movement responses to fences (McInturff *et al.* 2020). Fences are often not distributed evenly across the landscape. As animals move across a fence density gradient, they may adjust their barrier behavior to balance trade-offs between the benefits of accessing resources beyond fences and the energetic and risk costs of going through or around a fence. For example, pronghorn have been observed to reduce crossing rates in densely fenced areas (Jones *et al.* 2019). In behavior ecology, adjustments of a behavior (e.g. movement) in response to a changing environmental condition (e.g. fence density) is referred to as "behavioral plasticity" (Wong & Candolin 2015). Importantly, individuals can vary in the degree or even direction of their behavioral responsiveness to a given environmental gradient, a phenomenon termed "individual plasticity" (Dingemanse & Wolf 2013; Hertel *et al.* 2020).

In addition to behavioral plasticity, individual variations in barrier behavior can also be driven by intrinsic differences in certain behavioral expressions among individuals (i.e., "behavioral type", sometimes referred to as "personality"). Because different individuals may occupy distinct spaces of a landscape due to varying movement characteristics and habitat preferences (Chapman *et al.* 2011; Barker *et al.* 2021; Xu *et al.* 2021a), fence conditions experienced by a particular individual can be markedly different from others. As such, individuals may develop distinct types of barrier behavior. For example, some individuals tend to cross fences predominantly while others prefer to move around the barrier. These behavior types can be correlated with larger-scale space use patterns, resulting in "behavioral syndromes" (Sih *et al.* 2004; Hertel *et al.* 2020). For example, animals that tend to detour when encountering fences might exhibit longer total movement distances and larger range sizes. Because large-scale animal space use is closely related to population fitness (Hebblewhite *et al.* 2008; Middleton *et al.* 2018; Kauffman *et al.* 2021a), understanding the potential presence of behavior types in individual responses to fences can provide needed information to link fence effects on movement behavior to population dynamics.

The Behavioral Reaction Norm (BRN) is a useful framework in behavior ecology for jointly quantifying both individual plasticity and behavior type (Dingemanse *et al.* 2010; Spiegel *et al.* 2017). BRN describes the behavioral expression of one individual along an environmental gradient, with the intercept of BRN representing the individual's behavioral type and the slope representing behavioral plasticity. Individual plasticity exists when the slope differs among the BRN of different individuals. Finally, BRNs can be used to quantify the correlations of two or more distinct behavioral traits measured along the same environmental gradients thus examining the presence of behavioral syndromes (Hertel *et al.* 2020). Although the BRN has been widely adopted by behavioral ecologists in experimental or simulation settings, the integration of BRN with field-based movement ecology studies remains rare until recently (Hertel *et al.* 2019, 2020; Webber *et al.* 2020).

In this study, we aim to shed light on the multi-scale effects of fences on animal movement and population dynamics by examining individual variations in barrier behaviors of two sympatric migratory ungulates, pronghorn and mule deer, in southwest Wyoming, USA. To do so, we drew from the disciplines of movement ecology, behavioral ecology, and fence ecology. By applying BRNs on long-term GPS tracking data from 61 pronghorn and 96 mule deer, we first examined the presence of behavior type and individual plasticity in animal movement responses to fences as a function of fence density. GPS tracking data is advantageous, though surprisingly rarely used, in analyzing individual movement variation because it allows individual-level monitoring across an environmental gradient for an extended period (Spiegel *et al.* 2017; Hertel *et al.* 2019). Second, we tested whether individual barrier behaviors are linked to their larger-scale space use, hence forming behavioral syndromes. Third, we conducted a known-fate survival analysis to examine whether barrier behaviors of pronghorn and mule deer influence individual survival. Our results revealed context-based barrier behavioral types, individual plasticity, and behavioral syndrome, representing one of the first studies to link the effects of linear barriers on individual behavior, movement ecology, and population dynamics. Our study provided new evidence on ecological effects across ecological levels and pointed to the possibility that some animals might be more susceptible to fences than others under certain circumstances.

METHODS

Study area

Our study area is located in the Green River Basin of western Wyoming, USA (Fig. 1, 110.09 W, 42.84 N). It is a semi-arid region south of Grand Teton National Park with elevations ranging from 1,940 m to 3,997 m. The lower-elevation areas are characterized by sagebrush steppe (*Artemesia spp.*) interspersed with riparian zones along tributaries of the Green River. The landscape shifts into mountainous terrain as elevation increases in the north and west, characterized by mid-elevation aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*), and higher elevation Engelmann spruce (*Picea engelmannii*) and alpine fir (*Abies lasiocarpa*). The dominant fence types in the study area include livestock pasture fencing, property fencing, and roadside fencing. The most common fence structure is barbed wire fencing with three to five strands. Other structures include woven-wire fencing and 'wildlife-friendly' fencing (Paige 2012), typically characterized by a smooth and elevated bottom wire. Fences are not distributed evenly in the area, with the highest fence density occurring near the town of Pinedale (Fig. 1B).

Fence data

A spatial fence layer was compiled based on the digital fence archive from the Bureau of Land Management, U.S. Forest Service, and the Wyoming Game and Fish Department. We merged fence layers from the three agencies, removed duplicated records, and visually validated each fence feature against a submeter-resolution satellite imagery basemap in ArcGIS Pro v.2.8.3. We drew additional line features if a fence was clearly visible on the basemap but was not mapped in the existing fence layer. We visited 335 fence locations in summer 2018 and summer 2021 to conduct ground-truthing to improve the fence layer accuracy. Information on fence structure was not available for the majority of the fences mapped. Hence, we did not differentiate by fence structure in our analyses. Our final fence layer contained 9100 km of linear fencing in the study area.

Movement data and space use metrics

We used GPS-collar data from 61 female pronghorn monitored between 2014 and 2017 for 3 to 24 months, and 96 female mule deer monitored between 2002 and 2018 monitored for 12 to 75 months. The GPS fixes were collected every 2 hours and transmitters emitted a mortality signal if collars remained stationary for > 8 hours. Further details of animal capture and data collection protocols can be found in (Sawyer *et al.* 2017) and (Sawyer *et al.* 2019a). The two species in our study area shared a general winter range but were segregated in summer when the majority of mule deer migrated to higher elevation mountains (Fig. 1). Mule deer in this region are mostly migratory, whereas pronghorn use a mix of resident and migrant movement strategies. Migration routes and distance varied among individuals, which allowed us to examine the barrier behavior and space use of animals with varying experiences of different levels of fence density throughout their range. After removing the months with less than 28 monitoring days, our analysis was based on a total of 818 pronghorn-months and 1397 deer-months.

Based on the movement trajectory of each individual-month, we calculated the total monthly movement distance and range size. Range size was calculated based on the Brownian bridge movement model with a 99% utilization distribution (Horne *et al.* 2007). We overlapped monthly ranges with the fence layer to calculate the average fence density (km/km^2) each individual experienced in a given month. Finally, we used net squared displacement plots to visually label every individual-month with a migration status (Bunnefeld *et al.* 2011). If migration occurred in a month for more than 7 days, the month was labeled with 1, otherwise, it was labeled as 0.

Barrier behavior analysis

To quantify animal movement responses to fences, we conducted Barrier Behavior Analysis (BaBA) using the R package "BaBA" (Xu *et al.* 2021b). BaBA identifies individual-level barrier encounter events by extracting continuous GPS locations that fall within barrier buffer areas and classifies the events into six behavior categories: *quick cross*, *average movement, bounce, back-and-forth*, *trace*, and *trapped*. For this study, we grouped the latter four behaviors into *altered movement* because they would not occur if the target barriers are permeable for animal movement (Appendix S1). *Quick cross* means an individual can quickly move from one side of the barrier to the other side. Although *average movement* and *altered movement* both represented a situation where an individual did not cross the encountered fence, the individual's movement characteristics near the fence did not differ from when it was away from the barrier in *average movement,* while *altered movement* represented the opposite (Appendix S1). For each species, we ran BaBA with fence buffer distances every 10 m from 50 m to 150 m, and used *quick cross* events to identify the buffer distance that best captured animal crossing attempts. We kept all other parameters as the default setting of the package. Similar to Xu et al (2021b), we found 110 m and 90 m to be the optimal buffer distance for pronghorn and mule deer, respectively, and the BaBA output resulting from the optimal buffer distance was used in the following analyses.

Next, we summarized individual barrier behaviors on a monthly basis in order to examine individual-level behavioral variations. Specifically, we summed the frequency of the three barrier behavior groups each individual conducted in a month. We then conducted a multivariate Poisson Log-Normal Principle Component Analysis (PLN-PCA) using the R package "PLNmodels" followed by varimax rotation (Aitchison & Ho 1989; Chiquet *et al.* 2018). The intention of PCA is two-fold: 1) to summarize the barrier behavior measures into a reduced number of uncorrelated components; 2) to transform count measurements that follow a multinomial distribution into Gaussian latent variables to facilitate the following statistical analyses. Based on Bayesian information criteria, the best PLN-PCA model contained two axes explaining > 63.19 % of the variation (Appendix S2). We hence kept the first two behavioral axes and used the resulting PCA scores per individual-month in the following statical analyses. The first axis (PC1) predominantly described the relative frequency of *average movement* an animal conducted in a given month. In order words, and a lower PCA score represents lower frequency of *average movement* relative to other barrier behaviors for the individual in a given month. The second axis (PC2) represented a contrast between *quick cross* and *altered movement*, and the lower the score is, the more *altered movement* the individual exhibit in comparison to *quick cross* in a given month. Hence, we further referred to PC1 as "unaltered behavior propensity" and PC2 as "quick cross tendency".

Statistical analyses

Individual plasticity and behavioral types

In order to examine behavioral types and individual plasticity in animal movement responses to fences, we first quantified behavioral reaction norms (BRNs) for individual pronghorn and mule deer. We quantified BRNs by fitting univariate Bayesian mixed models with the PCA scores of each barrier behavioral axis as a response variable using R package "MCMCglmm" (Hadfield 2010; Dingemanse & Dochtermann 2013). To assess how individuals differ in their barrier behavior plasticity to a fence density gradient, namely whether there is individual plasticity in barrier behaviors, we parameterized two sets of models with the following random effect structures: 1) random intercept model with individual ID as the random effect (Individual effects, I), and 2) random regression models with ID as random intercept and fence density as the random slope (Individual x Environmental effects, IxE). In both sets of models, we controlled for month, fence density, and migration status as fixed effects. To take the circular nature of "month" into consideration, we transformed month into sin(month) and cos(month). We then compared the two sets of models using the deviance information criterion (DIC) to confirm the presence of I x E effects. We used the top models (models with lower DIC) as the BRN models of each barrier behavior axis of each species, with which we estimated the population-average change in barrier behavior axes with covariates (fixed effects).

We quantified behavioral types in each barrier behavior axis of each species based on the BRN models (Dingemanse & Dochtermann 2013; Houslay & Wilson 2017). Commonly, the extent of behavioral types can be measured as "repeatability (R)", which standardizes the among-individual variance at the intercept by the total phenotypic variance, ranging from 0 to 1 (Nakagawa & Schielzeth 2010; Hertel *et al.* 2020). However, when individuals differ in their behavioral plasticity (i.e. when IxE is present), the amount of among-individual variation becomes dependent on the environmental values centered at the intercept (in our case, fence density), and the R estimate becomes "conditional R" ((Nakagawa & Schielzeth 2010). In order to examine how barrier behaviors R may change as fence density increases, we calculated conditional R along a fence density gradient between 0 and 2 km/km^2 following (Schielzeth & Nakagawa 2021). This fence density range covers over 95% of the plausible fence density levels experienced by any studied animal in a given month (Appendix S3). We fit additional models for each barrier behavior axis by recentering fence density at different levels and calculated individual variance and residual variance in each model in order to confirm that we did not mistake environmental trends in residual variance (i.e., heteroscedasticity) for I x E (Ramakers *et* *al.* 2020), Appendix S4). All univariate models were fit with uninformative, parameter-expanded priors for the random effects and Gaussian error structures. We ran models with 420,000 iterations with a burn-in of 20,000 and a thinning rate of 100. Estimated model coefficients and credible intervals were based on 8,000 posterior samples. We inspected trace plots to ensure mixing of chains and absence of autocorrelation between posterior samples.

Correlation between barrier behavior and space use pattern

To examine whether barrier behaviors and space use patterns form behavioral syndromes, we fitted multivariate Bayesian mixed models with two barrier behavior axes and two space use metrics (total movement distance, km; range size km^2) as response variables for each species. We again used fence density in animals' monthly range, sin(month), cos(month), and migration status as fixed effects, individual ID as random intercept, and fence density as random slope. Because of the presence of IxE hence the context-dependent among-individual variance (Mitchell & Houslay 2021), we fit four models with fence density centered at four values to calculate behavioral covariance at each low, medium, high, and very high fence densities, representing 25%, 50%, 75%, and 90% percentile of plausible fence density in an animal's monthly range (corresponding to fence densities of 0.39 km/km^2, 0.68 km/km^2, 1.00 km/km^2, and 1.49 km/km^2, respectively, Appendix S3). We calculated the correlation between the two barrier behaviors and the two space use metrics by dividing the covariance between two behaviors by the product of the square roots of their variances (Houslay & Wilson 2017). The multivariate models were fit with uninformative, parameter-expanded priors, and the models were run with 840,000 iterations, 40,000 burn-in, and 100 thinning. All trace plots were visually inspected to ensure the mixing of chains and the absence of autocorrelation between posterior samples. To assist the interpretation of the behavioral correlation, we also fit univariate models with each of the four response variables to calculate their conditional repeatability centered at the four fence density levels. These multivariate models were parameterized the same as previous univariate models.

All mixed-effect models are listed in Appendix S5. For all models, we calculated summary indices of the model posterior distribution using R package "bayestestR" (Makowski *et al.* 2019a). For all models, we report the posterior mean of the parameters of interest along with their 95% confidence intervals. We judged the plausibility of these effects based on their probability of direction (pd%) which indicates the probability that a given estimate is of the same sign as the posterior mean. Parameters with pd > 95 % were considered as having a significant effect.

Survival analysis

To assess the potential influences of barrier behavior on pronghorn and mule deer survival, we used known-fate survival models implemented in the "rmark" R package (Laake 2013). We created monthly encounter histories for all monitored animals and censored animals if collar failure occurred or animals died from capture-related causes. The censored dataset included 93 mule deer and 61 pronghorn. We used monthly metrics of individual barrier behaviors and movement to create four a priori models based on hypothesized effects of fences on survival: 1) the total number of monthly fence encounters regardless of specific barrier behaviors, 2) total number of monthly altered movement encounters, 3) monthly fence density within the home range, 4) no effects of fences on survival (null model). We ran models for pronghorn and mule deer separately and ranked models for each species based on Akaike's information criterion corrected for sample size (AICc; (Burnham & Anderson 2002). We considered models within 2

ΔAICc of the top model to be competitive and evaluated whether covariates were informative by calculating 95% confidence intervals. All statistical analyses were conducted in R v.4.0.2.

RESULTS

Among the 818 pronghorn-month and 1397 mule deer-month of GPS data, BaBA identified a total of 18,901 and 21,454 fence encounters respectively (Appendix S1), translating to 23.1 ± 16.1 monthly fence encounters per individual pronghorn and 15.4 ± 12.1 per individual mule deer. The distribution of the two behavioral axes resulting from the PLN-PCA largely overlapped, suggesting the observed barrier behavior variations of the two species were similar (Appendix S2).

Both pronghorn and mule deer were highly plastic in their behavioral response to fence density. Importantly, we found strong evidence for an IxE effect in both species as evidenced by the DIC model comparison (Fig. 2). Specifically, the random regression models outperformed random intercept models and all Δ DIC between random intercept models and random regression models were > 45 (Appendix S6). Based on the fixed effect results, higher fence density was associated with higher unaltered behavior propensity and higher quick cross tendency at the population level (Table 1). Migration status significantly influenced mule deer barrier behaviors but not those of pronghorn (Table 1). Specifically, mule deer had a lower unaltered movement propensity and lower quick cross tendency during migration.

We did not find strong evidence for behavioral types in the barrier behaviors of both species, instead the among-individual variations were highly dependent on fence density. Conditional R was nearly negligible in both species at low fence density (Fig. 3, Appendix S8). Yet, conditional R increased as fence density increased, suggesting a divergence in barrier behaviors among individuals. Still, even at a very high level of fence density (1.49 km/km^2), the conditional R value of barrier behaviors was < 0.3 for both species. In general, mule deer demonstrated relatively higher R in both barrier behavior axes across the fence density gradient (Appendix S8). As for space use characteristics, mule deer demonstrated moderate repeatability in range size at low fence density (R = 0.38, CI = [0.28, 0.49]), and relatively high repeatability in total movement distance when fence density is high (R = 0.44, [0.33, 0.56]) and very high (R =0.67, CI = [0.56, 0.78], Appendix S8).

We found behavioral correlations between barrier behaviors and range size in mule deer, although the sign and magnitude of the correlations were dependent on fence density (Fig.4 C, D). Specifically, mule deer individuals with higher unaltered behavior propensity tended to have smaller monthly range sizes when fence density was < 1 km/km^2 (r ~ -0.50, pd > 99%). Individuals with a higher quick cross tendency, on the other hand, had a larger range size when fence density was ⩾ 1 km/km^2 (r ~ -0.50, pd > 97%). While pronghorns showed similar patterns of correlations between range size and quick cross tendency, we were much more cautious in our interpretation given that all posterior correlations had higher uncertainty (i.e. all included 0 within the 95 % credible intervals, Fig.4 A, B).

We found evidence for the effects of fences on survival in mule deer. The top model included an effect of fence density on survival (Appendix S9). Based on this model, mule deer survival decreased with increasing fence density within an animal's home range (Figure 5). For pronghorn, on the other hand, all models were competitive (within 2 AIC units, Appendix S9), hence we could not a distinguish better performing model over the null model. In addition, the confidence intervals for fence density (β = -0.47; 95% CI = -0.96 to 0.03), altered movement count (β = -0.05; 95% CI = -0.12 to 0.02), and total fence encounters (β = -0.02; 95% CI = -0.05 to 0.02) all overlapped zero indicating that they were non-informative.

DISCUSSION

Since the invention of barbed-wire fencing in the late 19th century in the western U.S., fencing has rapidly spread across the world and become one of its most prominent linear infrastructures (McInturff *et al.* 2020; Xu & Huntsinger 2022). Today, fencing is one of the major obstacles to the movement of wide-ranging ungulates (Jakes *et al.* 2018; Xu *et al.* 2021b). Our results suggest that plasticity is the dominant mechanism of variation in animals' movement responses to fences, or barrier behaviors, as animals move across a fence density gradient. Notably, the direction and magnitude of such plasticity varied among individuals. As a result of the individual plasticity, the presence of barrier behavior type and behavior syndromes were context-dependent; high fence density amplified the among-individual differences in barrier behaviors in both species. Additionally, fence density may have negatively affected animal monthly survivability. Taken together, our study provides new evidence that fences trigger complex movement responses from pronghorn and mule deer, and these responses may scale up to alter animal space use with potential implications for population dynamics. By integrating movement ecology, behavioral ecology, and fence ecology, our findings provide empirical evidence that fencing, like many other human-induced rapid environmental changes, unequally shapes the behavioral responses of different individuals (Sih 2013; Xu *et al.* 2021a; Gunn *et al.* 2022).

Our results showed that barrier behaviors of both pronghorn and mule deer were highly plastic against fence density gradients (Table 1, Figure 2). By adjusting the relative frequency of different types of barrier behavior, animals might be able to adjust for different energy costs for coping with fences as they move across a fence density gradient (Xu *et al.* 2021b). An important caveat is that animals' plastic responses to fence density could be confounded by fence structure (e.g. 4-strand barbed wire, woven wire), which is known for playing an important role in how ungulates respond to fences. For example, due to the lack of ability to jump, pronghorn might only take detours when encountering woven wire fencing. Unfortunately, we did not have fence structure information in our study area and could not take this factor into consideration. Additionally, the outputs of the barrier behavior analysis (i.e. the raw counts of different types of barrier behaviors) are dependent on the temporal resolution of the GPS data (Xu *et al.* 2021b). While the fix rate of our dataset is 2 hours, a higher fix rate would be able to capture more fence encountering events and depict variations in barrier behaviors at a finer scale.

Both pronghorn and mule deer exhibited strong individual plasticity, suggesting that individuals could deviate greatly from each other in the direction and magnitude of their responsiveness to fence density (Figure 2). This suggests that individuals were not bonded to a specific response to a fence density gradient. Individual plasticity could be associated with various factors such as genetic make-up, sex, life-history stage, and social interactions (Dingemanse & Wolf 2013; Hertel *et al.* 2020). In our case, individuals' experience with the environment might also play a role. Because greater environmental variation should cause a greater phenotypic response (Hendry *et al.* 2008), future research can examine the hypothesis that individuals that traverse larger geographic areas thus experiencing a steeper fence density gradient might show higher sensitivity in behavioral responses (steeper slopes in BRNs).

We found that among-individual variations in barrier behavior were dependent on fence density. Although individuals exhibited similar types of barrier behavior when fence density was low to moderate, higher fence density led to greater among-individual differences (Figure 3, Appendix S8). Still, at a very high fence density (1.5km/km^2), less than 30% of total barrier behavior variations were explained by individual behavior types. Such repeatability estimates were lower than the average repeatability of behavioral traits (R = 0.37, Bell *et al.* 2009), and even lower than the repeatability of spatial behavior recently estimated in a meta-analysis (R =

0.67 – 0.82, Stuber *et al.* 2022). The low repeatability might be partly due to our monthly-basis of our analyses. For migratory animals like mule deer and pronghorn that conduct seasonal movements, higher repeatability (hence a stronger presence of behavior types) can be expected from longer-term barrier behaviors (Hertel *et al.* 2021). However, if the trend of increasing repeatability of barrier behaviors as fence density increases continues, we can expect divergence in barrier behaviors in densely fenced systems, potentially putting individuals of different behavior types under different selection pressures. This can be concerning because the "very high" fence density (1.5 km/km^2) in our study area is not uncommon in other ecosystems home to wide-ranging ungulates. For example, 1.5 km/km^2 is roughly the average fence density at the Kenya-Tanzania borderland (Tyrrell *et al.* 2022), and is lower than the average fence density in Northern Montana (estimated to be 2.4 km/km^2, (Poor *et al.* 2014). We speculate that at least some segments of the wide-ranging species in densely fenced landscapes have already been disproportionally influenced.

Our behavior syndrome analysis revealed that individual barrier behaviors were correlated with broader-scale space use under certain contexts. For mule deer, individuals with higher unaltered behavior propensity generally also exhibited smaller range size, and individuals with higher quick cross tendency were associated with larger range size when fence density is high (Figure 4). In other words, individuals who predominantly display *quick cross* might be able to access larger areas while individuals exhibiting *altered movement* or *average movement* might tend to stay in a confined area. While barrier behavior-space use correlations in pronghorn were not significant, the direction of these correlations was consistent with that of mule deer. This might be partly due to the fact that mule deer individuals on average were tracked for a longer time period, hence generating more repeated measurements of individual behaviors. With the continuing advancement in animal tracking technologies (Nathan *et al.* 2022), future research should take advance of the increasingly available long-term or even lifetime dataset that is required for a better understanding of individual behavior variations.

Whereas we could not make a direct connection between barrier behaviors to demographic outcomes, we found evidence that high fence density reduces mule deer monthly survival (Figure 5). Individuals in densely fenced areas are exposed to higher risks to be entangled in wires, which often leads to mortality (Rey *et al.* 2012; Harrington & Conover 2016). Our survival analysis was intended to serve as a complement to our behavior-focused study. A comprehensive survival analysis should take into consideration of other factors that may also influence individual survival, such as migration strategy (Schuyler *et al.* 2019), location of migration corridor (Sawyer *et al.* 2019b), and winter severity (Jones *et al.* 2020a), and energy development in the area (Sawyer *et al.* 2017). In addition, there might be lag effects between the occurrence of barrier behaviors and mortality that we could not account for. Nonetheless, our study provides new evidence that directly connects fence density with ungulate survival. Further understanding of the demographic consequences of fences requires long-term individual-based monitoring paired with a suite of demographic (i.e. fat gain, recruitment) and environmental measurements (Festa-Bianchet *et al.* 2017).

Our study highlights three lessons for conservation and management in fenced landscapes. First, because individual-level barrier behaviors may have cumulative effects on broader-scale space use, an accurate evaluation of the impacts of linear infrastructure needs to take an integrated monitoring approach that considers animal behaviors near and away from the barrier as well as large-scale space use patterns (Beyer *et al.* 2016; Xu *et al.* 2019; Robb *et al.* 2022). Second, because of the high behavioral plasticity animals exhibit along a fence density gradient, fence removal should be an effective strategy to mediate the modification of fences on animal movement. In cases where boundaries might be essential for land management, such as cross-fences for rotational grazing, technologies such as virtual fencing can be an ecologically beneficial alternative to physical fences (Umstatter 2011). Third, one of the biggest challenges in large-scale fence conservation and management is the lack of systematic fence location and structure data. Currently, most fences around the world have never been mapped. Among the few areas where fence locations are documented, fence structure was generally unknown (as was the case in this study). Further development of the field of fence ecology and management hence does not only require synergies among behavioral ecologists, movement ecologists, and conservation biologists to obtain a context-based view of the multi-scale impacts of linear barriers, but also collaborations between computer scientists and ecologists to automate fence identification over space and time.

ACKNOWLEDGEMENTS

We are grateful to T. Langford, Q. Huang, G. Ferguson, E. Hausser, and J. Zhu for their technical and financial contributions to improving the fence layer. We thank G. Zuckerman for creating a movement visualization tool. We thank the members of the movement ecology group at the Senckenberg Biodiversity and Climate Research Centre (SBiK-F) and the members of the Middleton lab at UC Berkeley, particularly T. Müller and K. Barker, for providing comments during the development of this project. WX is supported by the Philomathia Graduate Fellowship in Environmental Science and the short-term research grant from the German Academic Exchange Service. ADM and WX are supported by National Geographic WW-100C-17 and Knobloch Family Foundation.

FIGURE 1: STUDY AREA IN SOUTHWEST WYOMING.

Study area overlaid with (A) movement tracks of pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) and (B) fences.

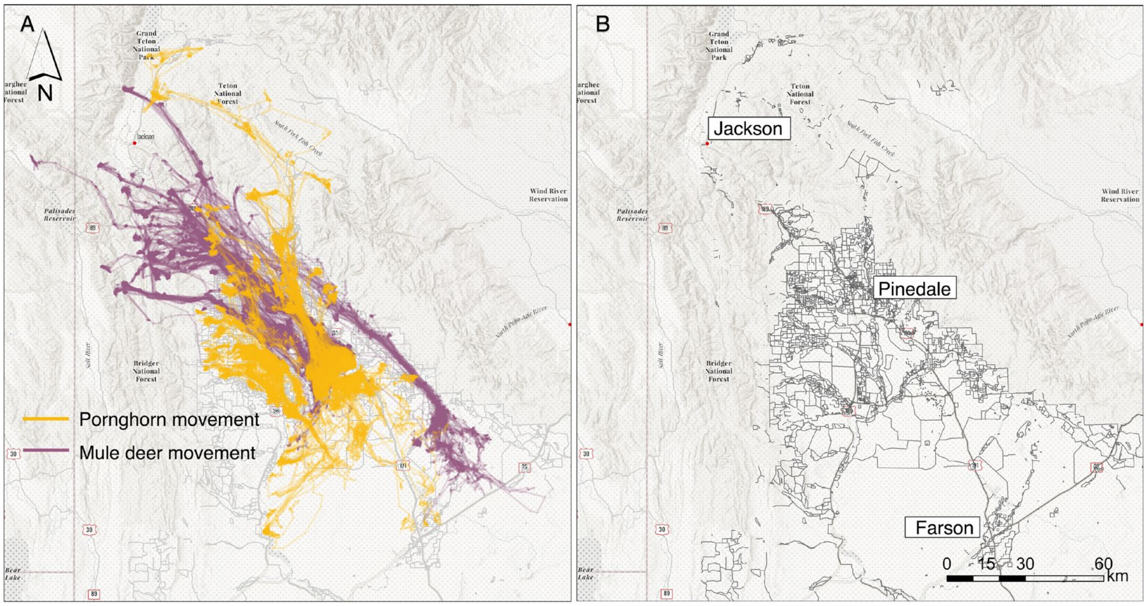


FIGURE 2: BEHAVIOR REACTION NORMS (BRNs).

BRNs of barrier behaviors for pronghorn (A and B) and mule deer (C and D) as a function of fence density. Each line represents an individual.

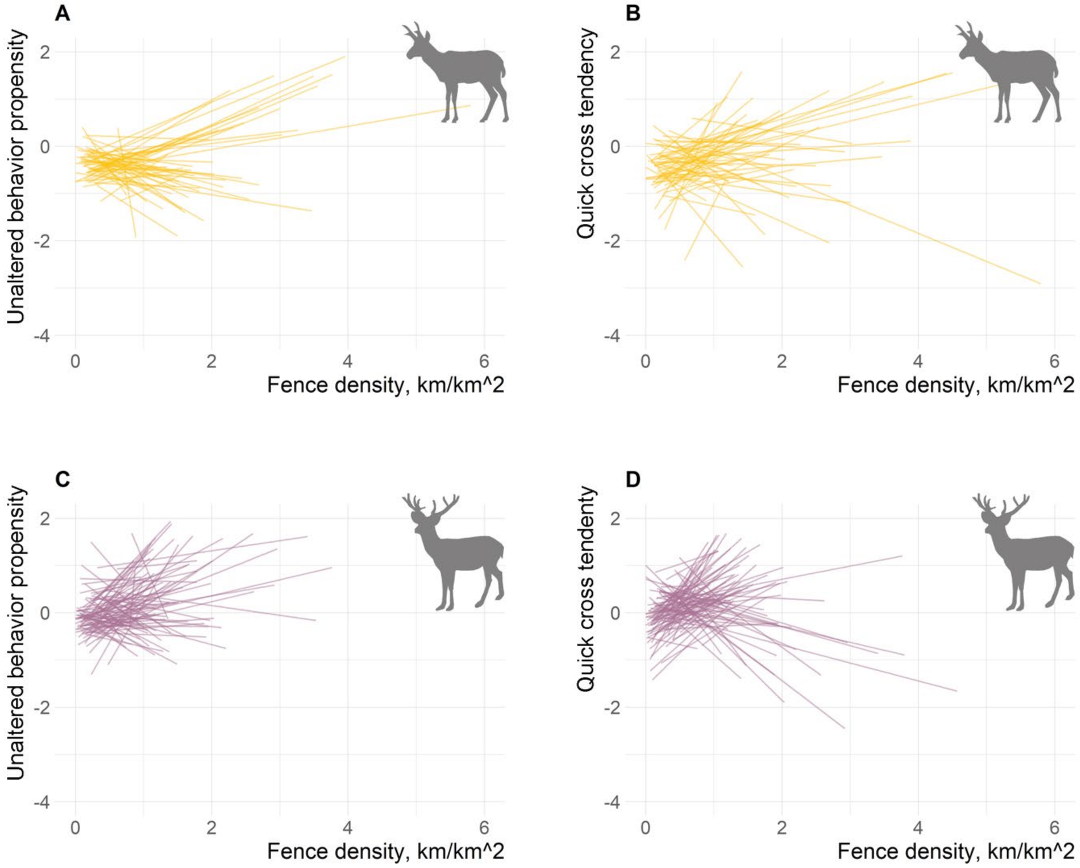


FIGURE 3: CONDITIONAL REPEATABILITY ALONG A FENCE DENSTIY GRADIENT.

Conditional repeatability of unaltered behavior score (A, C) and quick cross score (B, D) for pronghorn and mule deer. Lines represent 500 draws from the posterior distribution of the top BRN models. The four dashed lines represent 25%, 50%, 75%, and 90% percentile of fence density in an animal's monthly range (i.e. 0.39 km/km2, 0.68 km/km2, 1.00 km/km2, and 1.49 km/km2, respectively).

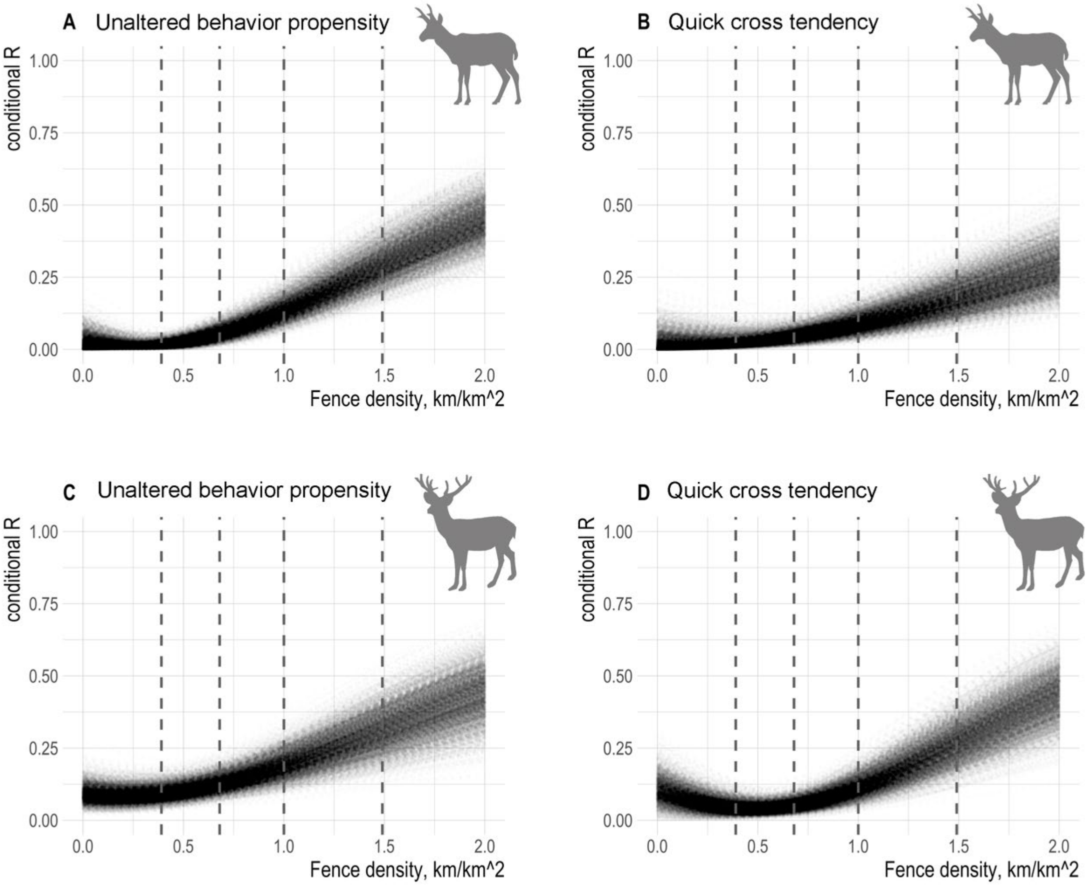


FIGURE 4: CORRELATION BETWEEN BARRIER BEHAVIORS AND SPACE USE.

Correlations between two barrier behavior components (unaltered behavior propensity, A and C; quick cross tendency, B and D) and the two space use metrics (range size and total distance) for pronghorn and mule deer at four fence density scenarios. Points represent the posterior means. Low, medium, high, and very high fence density correspond to 0.39 km/km2, 0.68 km/km2, 1.00 km/km2, and 1.49 km/km2 of fences within animals monthly home range. The significant correlations based on pd > 95% are marked with an asterisk.

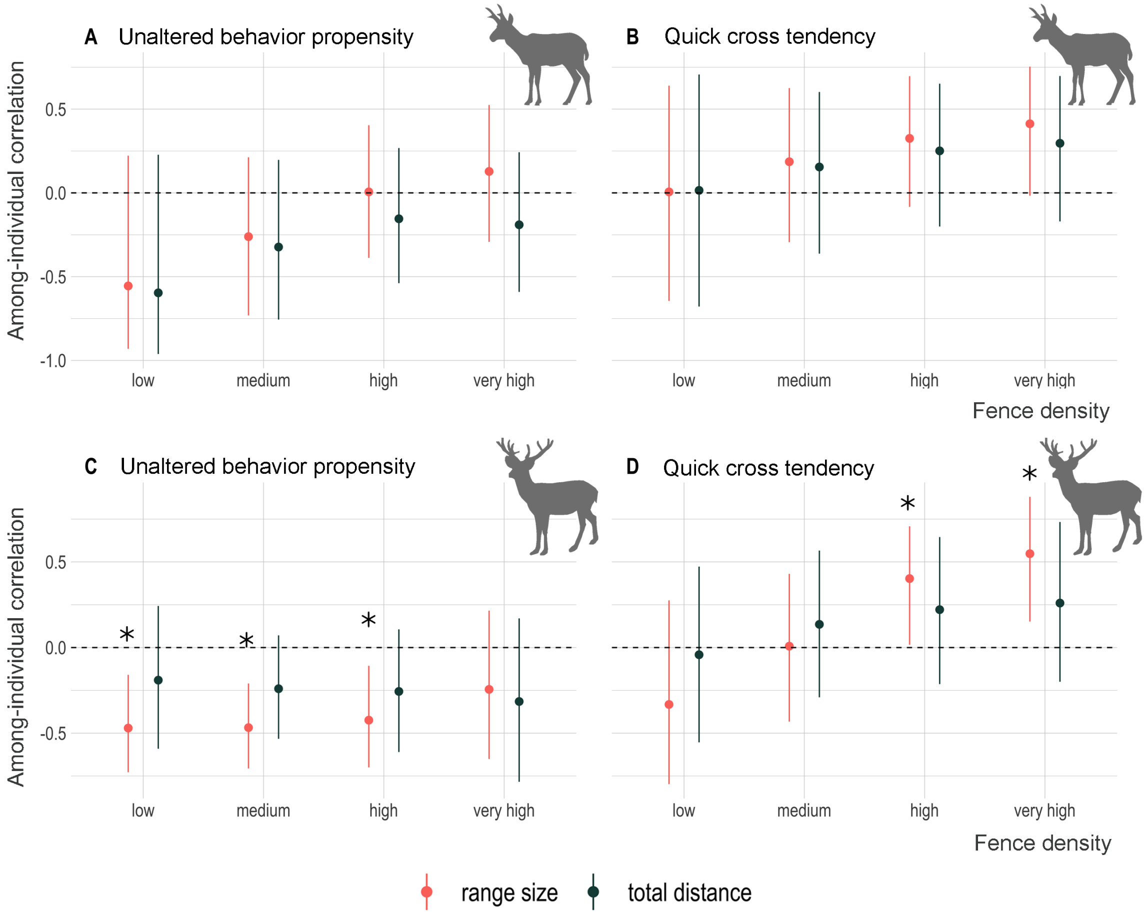


FIGURE 5: predicted mule deer monthly survival as a function of fence density an individual experienced in its monthly range (km/km^2).

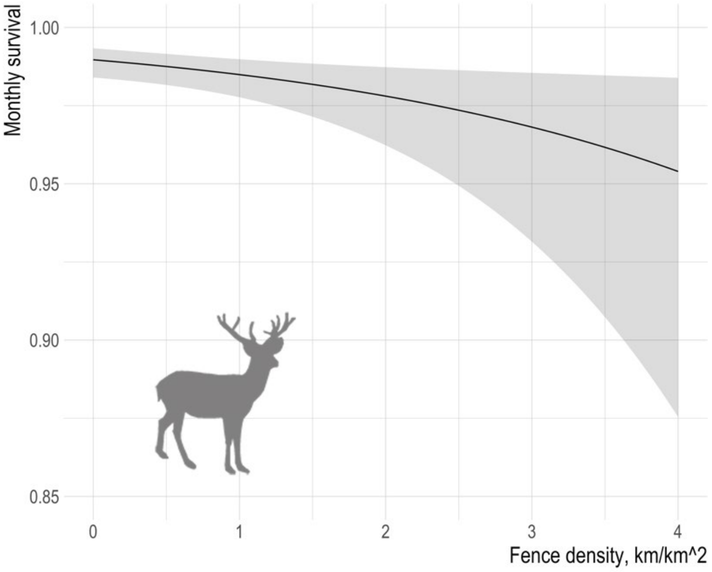


TABLE 1. FIXED EFFECTS OF UNIVARIATE BAYESIAN MIXED MODELS. Posterior mean and probability of direction (pd %, in grey) of fixed effects from the univariate Bayesian mixed effects of pronghorn and mule deer. The random effects of all models were individual ID as random intercepts and fence density as random slopes, representing the effects of individual-environment interaction. Plausible effects (pd% > 95) are indicated in bold. More Bayesian model summary indices are detailed in Appendix S7.

Spp.	Trait	fence_density	sin(month)	cos(month)	mig_status1
pronghorn	Unaltered behavior propensity	**0.242**	0.047	**0.224**	0.130
		99.62	87.20	100	95.00
	Quick cross tendency	0.122	**-0.105**	-0.015	0.038
		93.67	97.75	59.82	65.92
mule deer	Unaltered behavior propensity	**0.523**	**0.131**	**0.107**	**-0.176**
		100	99.67	99.60	99.88
	Quick cross tendency	**0.227**	-0.035	0.046	**0.460**
		99.42	77.05	86.80	100

APPENDIX S1: BARRIER BEHAVIOR ANALYSIS (BaBA)

Barrier behavior analysis (BaBA) utilizes animals tracking data and fence spatial location to identifies animals encounter with fences within a user-determined buffer (Fig. S1.1). In this study, we applied 110 meter for pronghorn and 90 meter for mule deer. All these encounter events were than classified into six barrier behavior types, as illustrated in Fig. S1.2. Detailed description of BaBA can be found in (Xu *et al.* 2021b). In this study, we focused on three major barrier behavior groups (quick cross, average movement, altered movement, Fig. S1.3, Fig. S1.4) because many behavior types within altered movement were rare events when summarizing on a monthly basis. Additionally, the consequence of altered movement types should be distinct from quick cross and average movement.

FIGURE S1.1: Total number of fence encounters for an individual in a month identified by BaBA before classifying them into different barrier behaviors based on 818 pronghorn-month and 1397 deer-month. Pronghorn encountered more fences in the summer compared to other seasons. In contrast, mule deer encountered less fences in the summer. This is partly due to that mule deer summer ranges were located at higher elevation mountainous areas where fences were sparsely distributed. In contrast, pronghorn yearly range was mostly in the plain areas where fences were common.

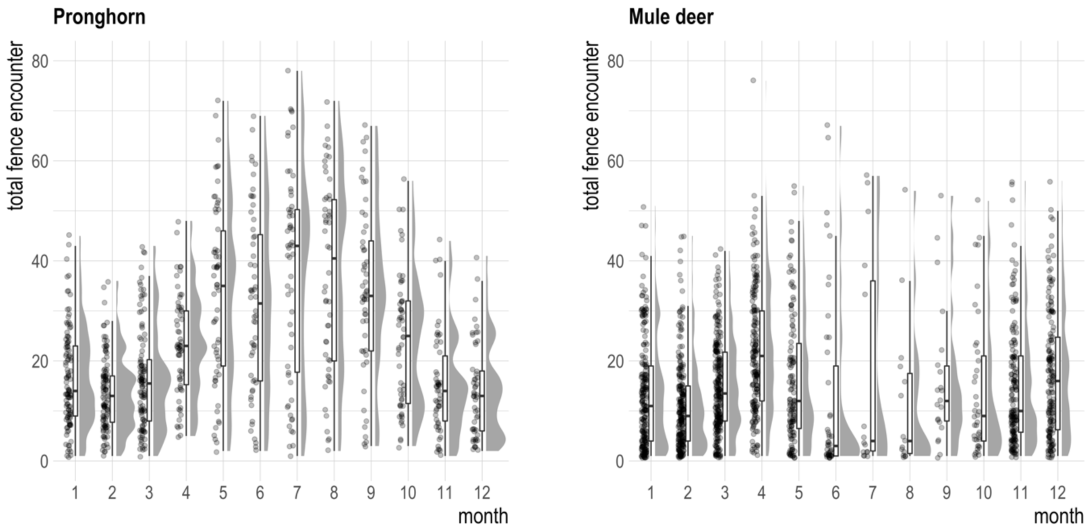


FIGURE S1.2: The three barrier behavior groups (six barrier behavior types) identified in Barrier Behavior Analysis. Figure adapted from (Xu *et al.* 2021b).

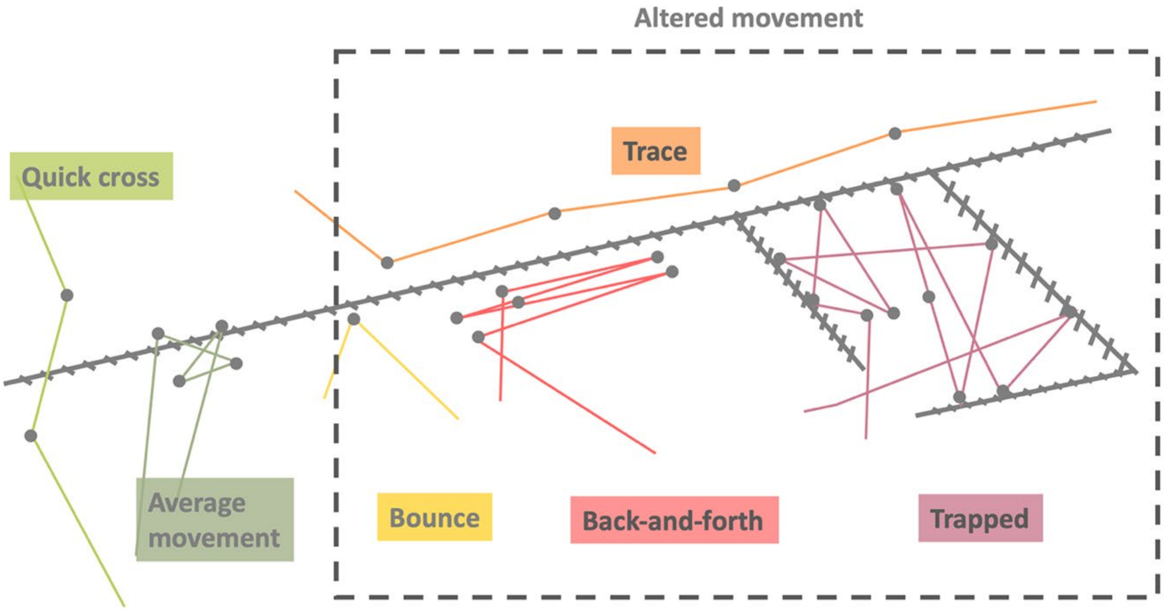


FIGURE S1.3: Distribution of the three groups of barrier behaviors.

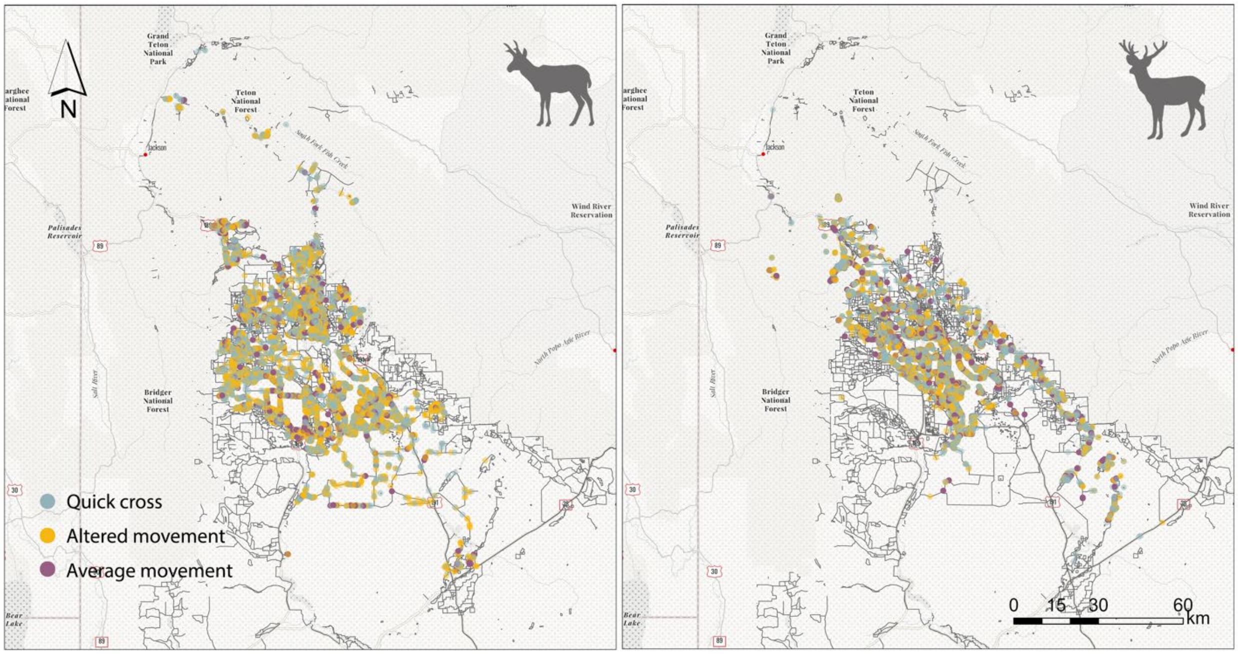
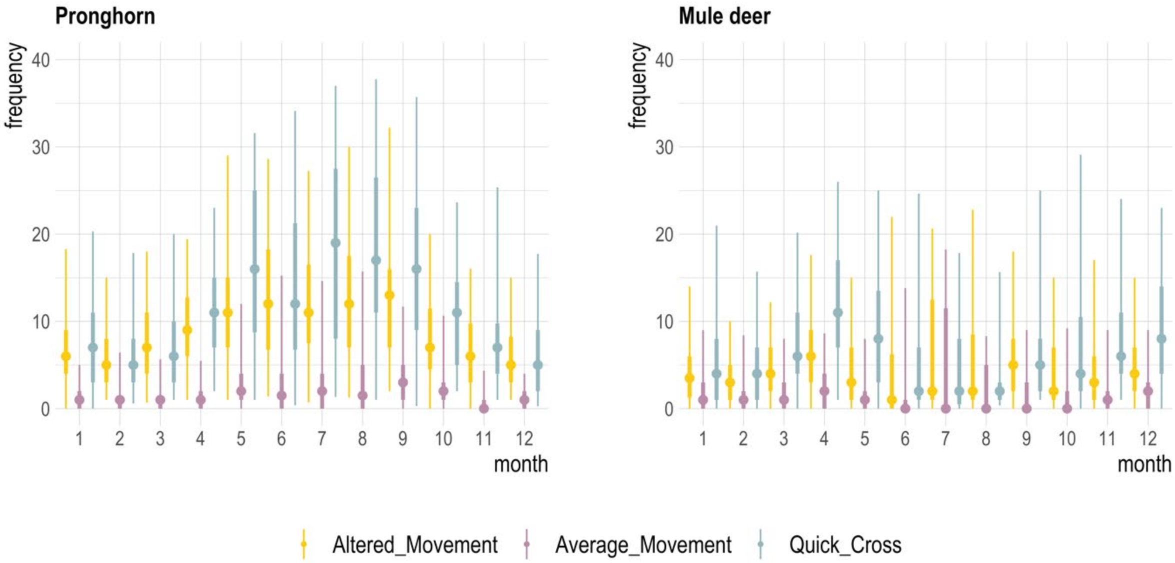


FIGURE S1.4: Monthly counts of the three groups of barrier behavior performed by an individual based on 818 pronghorn-month and 1397 deer-month.



APPENDIX S2 Barrier behavior analysis (BaBA) Poisson lognormal principle component analysis (PLN-PCA) results

FIGURE S2.1 PCA plot showing PC scores of all samples (dots) and loadings of variables (arrows). Ellipses represent the 95% probability contour for cluster classification.

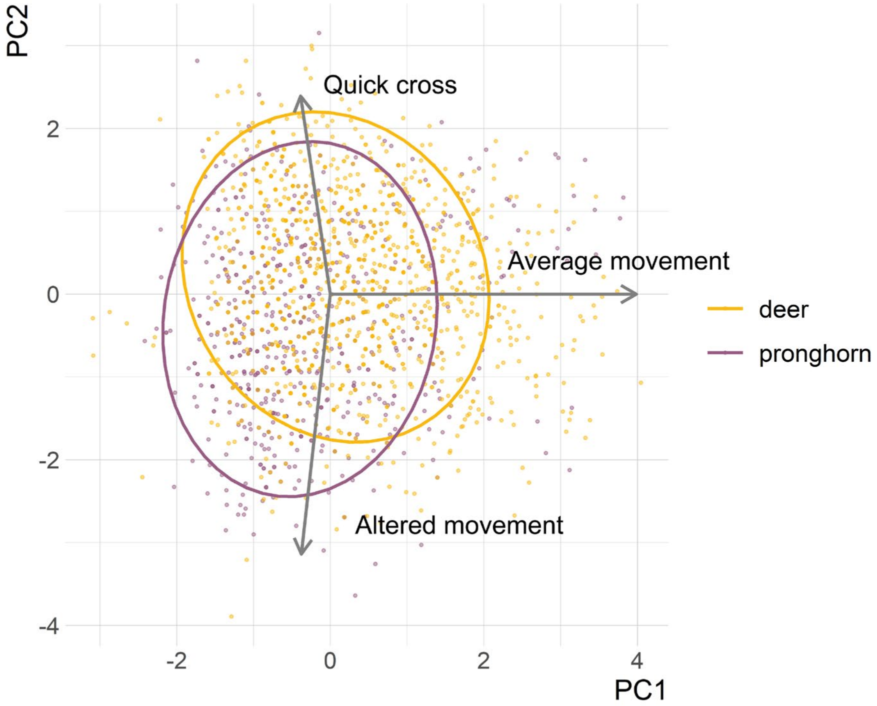
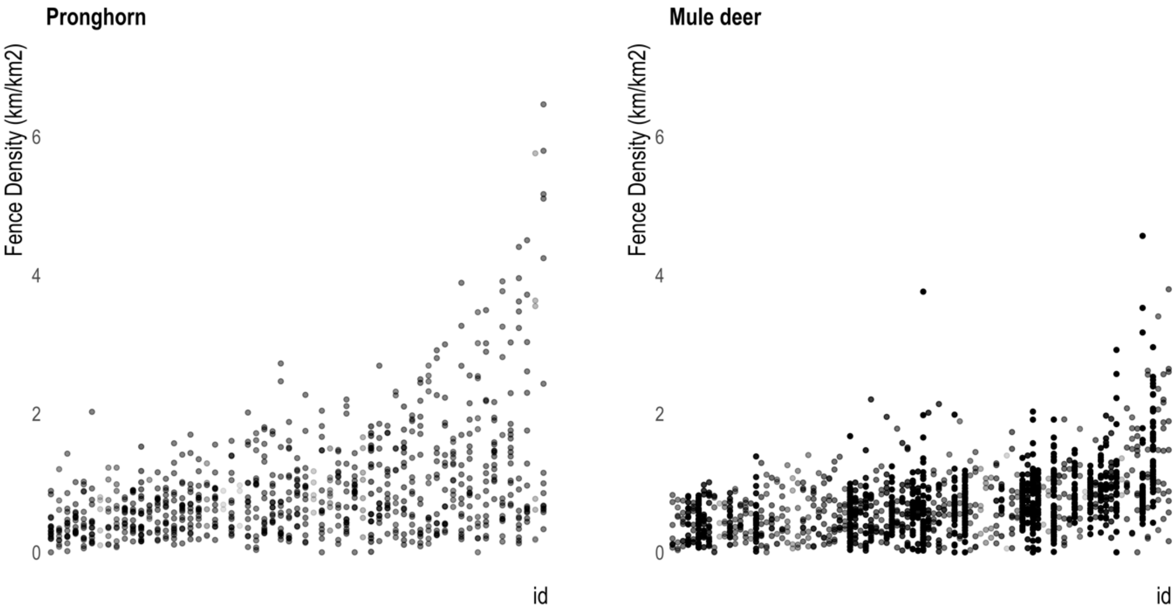


TABLE S2. Factor loadings, eigenvalues, and proportion of the total variance explained by the first two axes extracted by PLN-PCA. The first axe (PC1) predominantly described the relative frequency of *average movement* an animal conducted upon encountering a fence in a given month, and the second axe (PC2) represented a contrast between *quick cross* and *altered movement*. Although *average movement* and *altered movement* both represented an animal that did not cross the encountered fence, the former represented the situation when the animal's movement characteristic near the fence did not differ from when it was away from the barrier and the latter represented the opposite Hence, we further referred PC1 as "unaltered behavior propensity" and PC2 as "quick cross tendency".

	PC1	**PC2**
Eigenvalue	369.9	180.3
% variance explained	42.49%	20.70%
Quick cross	-0.125	**0.591**
Average movement	**0.985**	
Altered movement	-0.122	**- 0.806**

APPENDIX S3: FENC EDENSITY IN AN ANIMAL'S MONTHLY RANGE

FIGURE. S3. Fence density in an animal's monthly range arranged by individuals. For both species, different individuals may be exposed to different levels of fence density. For example, some pronghorn individuals may only move through areas with fence density < 2 km/km^2, while others might experience fence density as high as 6 km/km^2 in some months. Because of such different experience with the environment, individuals might develop different strategies to deal with barriers.



APPENDIX S4: UNIVARIATE MODELS RESULTS

TABLE S4. Individual and residual variance of univariate models with fence density centered at low, medium, high, and very high fence densities, representing 25%, 50%, 75%, and 90% percentile of plausible fence density in an animal's monthly range (corresponding to fence densities of 0.39 km/km^2, 0.68 km/km^2, 1.00 km/km^2, and 1.49 km/km^2, respectively). The consistent estimate of residual variance confirmed that our models with homogenous residuals were appropriate.

	Trait	**Centering**	**Individual Variance**			**Residual Variance**		
			Mean	**Lower CI**	**Upper CI**	**Mean**	**Lower CI**	**Upper CI**
pronghorn	Unaltered Behavior Propensity	Low	0.00	0.00	0.01	0.62	0.56	0.68
		Median	0.02	0.00	0.05	0.62	0.56	0.68
		High	0.08	0.04	0.13	0.62	0.56	0.68
		Very high	0.25	0.14	0.40	0.62	0.56	0.68
	Quick cross tendency	Low	0.02	0.00	0.06	0.91	0.81	1.00
		Median	0.04	0.00	0.08	0.91	0.81	1.00
		High	0.07	0.02	0.13	0.90	0.82	1.00
		Very high	0.17	0.06	0.29	0.90	0.81	0.99
Mule deer	Unaltered Behavior Propensity	Low	0.08	0.04	0.13	0.78	0.72	0.85
		Median	0.11	0.06	0.17	0.78	0.72	0.85
		High	0.17	0.09	0.27	0.78	0.72	0.84
		Very high	0.32	0.13	0.51	0.78	0.72	0.84
	Quick cross tendency	Low	0.03	0.00	0.07	0.79	0.73	0.86
		Median	0.04	0.01	0.07	0.79	0.73	0.86
		High	0.09	0.04	0.15	0.79	0.73	0.86
		Very high	0.27	0.12	0.44	0.79	0.73	0.85

APPENDIX S5: LIST OF MODELS BUILT IN THIS STUDY

TABLE S5. List of models fitted in this study for each species. A total of 48 models were fit (24 for each species). All models share the same set of fixed effects: fence density (km/km^2), sin(month), cos(month), and migration status (binary variable, 0 – not migrating; 1 - migrating). Fence density was centered differently in each model in order to calculate the corresponding conditional repeatability of the response variable at the specific fence density level. Fence density centering levels included low - 0.39 km/km2, median - 0.68 km/km2, high - 1.00 km/km2, very high - 1.49 km/km2, representing 25%, 50%, 75%, and 90% percentile of the fence density in an animal's monthly range. Random effects I represents that individual ID was used as random intercept. Random effects IxE represents that individual ID was used as random intercept and fence density was used as random slope. All modeled were fitted using R package "MCMCglmm" and we would like to acknowledge the detailed tutorial provided by (Hadfield 2010; Houslay & Wilson 2017; Hertel *et al.* 2020; Mitchell & Houslay 2021)

Model Type	Response variable	Fence density centering	Random effects	Model ID
Univariate	Unaltered movement propensity	none	I	01
		none	I x E	02
		low	I x E	03
		median	I x E	04
		high	I x E	05
		very high	I x E	06
	Quick cross tendency	none	I	07
		none	I x E	08
		low	I x E	09
		median	I x E	10
		high	I x E	11
		very high	I x E	12
	Total movement distance	low	I x E	13
		median	I x E	14
		high	I x E	15
		very high	I x E	16
	Monthly range size	low	I x E	17
		median	I x E	18
		high	I x E	19
		very high	I x E	20
Multivariate	All four variables above	low	I x E	21
		median	I x E	22
		high	I x E	23
		very high	I x E	24

APPENDIX S6: UNIVARIABLE MODEL COMPARISON

TABLE S6. DIC comparison between univariable model 1 and 2, 7 and 8 (Appendix S4) for pronghorn and mule deer respectively.

	Pronghorn		**Mule deer**	
	PC1	**PC2**	**PC1**	**PC2**
DIC (M1, I)	2096.2	2352.3	3762.7	3796.3
DIC (M2, I x E)	1986.0	2294.7	3717.4	3727
∆ DIC	110.2	57.6	45.3	69.3

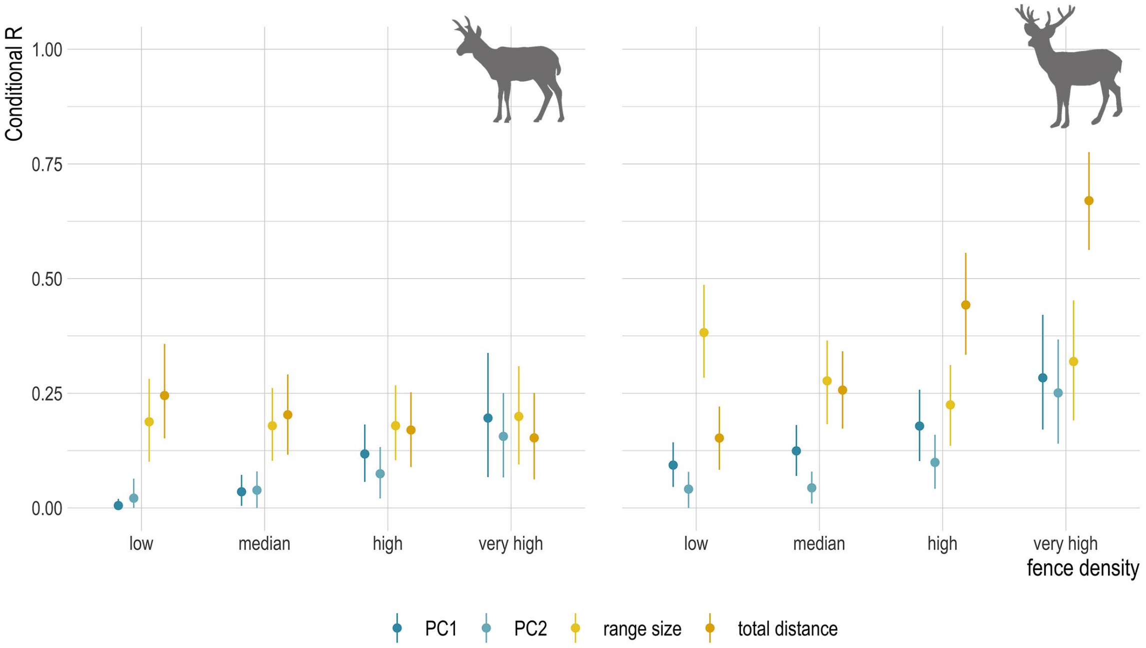
APPENDIX S7: FIXED EFFECTS OF UNIVARIATE BAYESIAN MIXED EFFECT MODELS

TABLE S7. Summary of the posterior distribution of the fixed effects of the univariate Bayesian mixed effect models examining the effects of fence density, seasonality, and migration status on the two barrier behavior components (Unaltered movement propensity, PC1; Quick cross tendency, PC2) of pronghorn and mule deer. The random effects of all models are individual ID as random intercepts and fence density as random slopes, representing the effects if individual-environment interaction. CI represents confidence interval. PD represents probability of direction, also known as the Maximum probability of effect. PD illustrates the effect existence and can be interpreted as the probability that a parameter is strictly positive or negative. It is a Bayesian equivalent of the frequentist *p*-value. ROPE % is an index of significance, informing whether a parameter is related or not to a non-negligible change in the outcome. It was calculated at the 89% highest density interval (the default). All indices were calculated using R package 'bayestestR' (Makowski *et al.* 2019b, a).

Trait	Covariates	Posterior mean	95% CI	PD %	ROPE %
Pronghorn, PC1	Fence density	0.242	[0.07, 0.40]	99.72	2.21
	sin(month)	0.047	[-0.03, 0.13]	87.20	92.58
	cos(month)	0.224	[0.14, 0.31]	100	0.00
	Migration status 1	0.130	[-0.02, 0.29]	95.00	34.96
Pronghorn, PC2	Fence density	0.122	[-0.04, 0.28]	93.67	38.94
	sin(month)	-0.105	[-0.20, 0.00]	97.75	44.49
	cos(month)	-0.015	[-0.12, 0.09]	59.82	97.11
	Migration status 1	0.038	[-0.14, 0.23]	65.92	71.69
Mule deer, PC1	Fence density	0.523	[0.37, 0.68]	100	0.00
	sin(month)	0.131	[0.04, 0.22]	99.67	24.15
	cos(month)	0.107	[0.02, 0.19]	99.60	43.04
	Migration status 1	-0.176	[-0.29, -0.06]	99.88	6.45
Mule deer, PC2	Fence density	0.227	[0.05, 0.41]	99.42	5.02
	sin(month)	-0.035	[-0.13, 0.06]	77.05	94.69
	cos(month)	0.046	[-0.04, 0.13]	86.80	92.74
	Migration status 1	0.460	[0.35, 0.57]	100	0

APPENDIX S8: CONDITIONAL REPEATABILITY OF BARRIER BEHAVIORS AND SPACE USE

FIGURE S8. Conditional repeatability of the two barrier behavior components (PC1 - unaltered movement tendency and PC2 - quick cross tendency) and the two space use metrics (monthly range size and total movement distance) for pronghorn and mule deer. Each conditional repeatability was calculated by centering fence density at corresponding levels: low - 0.39 km/km2, median - 0.68 km/km2, high - 1.00 km/km2, and very high - 1.49 km/km2, representing 25%, 50%, 75%, and 90% percentile of plausible fence density in an animal's monthly range.



APPENDIX S9: SURVIVAL MODEL COMPARISON.

TABLE S9. Rankings of known-fate monthly survival models for pronghorn and mule deer.

Spp.	Model covariates	k	AICc	ΔAICc	Weight	Deviance
Pronghorn	Fence density	2	92.14	0	0.36	88.13
	Null	1	92.60	0.46	0.28	24.44
	Altered movement count	2	93.10	0.95	0.22	89.08
	Total fence encounters	2	94.03	1.89	0.14	90.02
Mule deer	Fence density	2	278.08	0	0.56	274.07
	Null	1	280.27	2.19	0.19	82.94
	Total fence encounters	2	281.08	3.00	0.13	277.07
	Altered movement count	2	281.52	3.44	0.10	277.51

Chapter 5. Minding the boundary: social-ecological contexts for fence ecology and management

This chapter takes an interdisciplinary perspective to understanding why and how fences became widespread around the world. The chapter has been previously published and is reproduced here with kind permission of the co-authors and Wiley.

Xu, W., Huntsinger, L. Minding the boundary: social-ecological contexts for fence ecology and management. *Frontiers in Ecology and the Environment.(2022).*

ABSTRACT

Fencing is a globally ubiquitous yet largely underestimated human infrastructure. To date, most research and management of fencing has focused on its biophysical outcomes. However, fencing is often part of coupled human and natural systems and inevitably impacts social and ecological dynamics and the links between them. Drawing from three key case studies from the US, China, and South Africa, we delineate five social pathways through which fencing shapes social-ecological dynamics in a landscape. We show that the social functions and physical appearance of fencing conjointly form a positive feedback loop that stimulates the proliferation of fences across entire landscapes, rendering fencing a more impactful feature than expected from its ecological impacts alone. The emerging field of fence ecology and management must embrace the social-ecological complexities of fenced landscapes to minimize unanticipated social consequences.

INTRODUCTION

> *The first man who, having fenced in a piece of land, said "This is mine," and found people naive enough to believe him, that man was the true founder of civil society.*
>
> *- Jean-Jacques Rousseau, 1754*

Fencing is a globally ubiquitous linear infrastructure (Hayward & Kerley 2009; Jakes *et al.* 2018). Encroaching on nearly all cultural and natural landscapes globally, fences are likely more impactful than roads (Figure 1, (Løvschal *et al.* 2017; McInturff *et al.* 2020; Sun *et al.* 2020). Recent recognition that fencing can reorganize an entire ecosystem has prompted an effort to formalize fence ecology, a discipline examining "*the interactions between fences, organisms, ecosystems, and societal needs*" (McInturff *et al.* 2020). Yet current syntheses of fence research have largely focused on the biophysical aspects. A comprehensive framework that situates fencing in coupled human and natural systems, or social-ecological systems (SESs), is needed to solidify the interdisciplinary foundation of this burgeoning field.

In SESs, humans, animals, and land interact with each other in profound ways. Dividing one from another with fences alters social and ecological dynamics and the connections between them (Hayward & Kerley 2009; Hoole & Berkes 2010). However, fences are often proposed to solve a purportedly "straightforward biological problem," such as forage competition with livestock and human-wildlife conflict, without considering that these problems are complex issues driven by mixed ecological, social, economic, and political forces (Li & Huntsinger 2011; Evans & Adams 2016). The rhetoric of the "technological fix" obscures potentially critical social impacts and their ecological feedbacks, leading to unanticipated negative outcomes for society and ecosystem (Ferguson 1990). Clearly, examination and management of fencing requires researchers and managers to embrace the social-ecological contexts of fenced landscapes.

Here, we review the impacts and characteristics of large-scale fencing as part of SESs. Drawing from three key case studies from western US, western China, and South Africa (WebPanel 1), we delineate five interdependent pathways through which fencing's social impacts can be imprinted on ecosystems (Table 1, Figure 2a, b). We further demonstrate that the combination of fencing's physical characteristics and social impacts can create a positive feedback loop that stimulates the proliferation of large-scale fencing across the landscape (Figure 2c), rendering it a powerful landscape intervention that can drive major transformations in SESs.

SOCIAL PATHWAYS THROUGH WHICH FENCING SHAPES ECOSYSTREMS

> *Our human landscape is our unwitting autobiography, reflecting our tastes, our values, our aspirations, and even our fears, in tangible, visible form.*
>
> *– Pierce Lewis, 1979*

Building fences is a practice of demarcating space, rendering resources into objects of ownership and governance (Netz 2004). As early as the Neolithic Age, people used fencing to claim territory or protect property (Kotchemidova 2008). Since then, fencing's utility has grown and now includes diverse purposes across social and cultural geographies, such as ameliorating large wildlife-vehicle collisions along roads, deterring invasive species, reducing livestock depredations by predators, managing livestock breeding, and preventing disease transmission (McInturff *et al.* 2020). Importantly, the diverse functions of fencing are rarely blatantly beneficial or harmful and instead vary widely by context (McInturff *et al.* 2020).

Drawing from three key case studies from three continents (WebPanel 1) and supplemented by other literature identified by using a snowball approach, we examine the nuanced effects of fencing in SESs. Our discussions largely focus on pasture and conservation fencing because it is the predominant research foci of fence ecology literature. We extend the (McInturff *et al.* 2020) fence ecology framework to include the impacts of fencing on five social factors: human mobility, land practices and land use, economic relationships, social relationships, and human-nature relationships (Figure 2). We identified these themes by extracting, examining, and categorizing the relevant contents from the literature. Below, we describe each of these factors and how they imprint an ecosystem (summarized in Table 1).

Human Mobility

Perhaps the most conspicuous fencing social impact is on human movement. The advent of barbed-wire fencing in the late 19th century in the western US ended long cattle drives from the Great Plains to markets in the North (Webb 1959). More recently, fencing obstructs the daily commute of farmworkers in South Africa (Snijders 2012) and western China's pastoralists have had to reduce or change their large-scale annual migrations when extensive fencing became part of the landscape as a result of land allocation policy (Næss 2013). While herders in Qinghai, China once used several grazing areas seasonally each year, government fencing has created separate household land allotments, reducing most herd movements to only once a year. Some families stopped moving herds entirely and became sedentary (Cao *et al.* 2011).

In contrast, fencing can enforce human movement. In South Africa, going hand in hand with land privatization and protected area establishment, fencing has enforced sometimes violent displacement of Black residents (Spierenburg & Wels 2006; Brandt & Spierenburg 2014). Remarkably, mobility has been used as a direct protest against the existence of fencing, as residents have continued crossing fences for generations despite increasing attempts to restrict them (Brandt & Spierenburg 2014).

The movement of humans, like the movement of animals, can shape ecosystems at multiple levels. At the local scale, restricting previously mobile humans can cause intensified resource use, leading to soil loss, species decline, and composition shifts. At the landscape scale, altered large-scale pastoralist movements essentially redistribute the human footprint, which can have cascading effects on primary productivity, fire dynamics, and system resilience (McNaughton 1985; Western *et al.* 2009). Such impacts are especially prominent when human movement and distribution is shaped by strictly defined impermeable fences where sharp habitat edges can be rapidly created.

Land Practices and Land Use

Fencing has reshaped livestock-based land practices across the world. In the early 20th century, shortly after barbed-wire fencing was first invented, fences quickly spread across US rangelands, organizing livestock production into bounded areas (WebPanel 1). A cowhand's duties largely changed from tending cattle to mending fences (Liu 2009). Today, grazing management in the West continues to evolve under the influence of fencing. For example, the US Department of Agriculture Natural Resources Conservation Service (NRCS) subsidizes dividing large pastures into smaller ones as ranchers shift from continuous grazing or long rotations to higher frequency rotational grazing as can be required by the agency to meet planning requirements (Knight *et al.* 2011).

Changes in land practices in pastoral societies induced by fencing are equally, if not more, profound. In China, previously collaborative tasks, such as communal herding and pasture care, become infeasible with fragmentation into fenced pastures (Cao *et al.* 2011; Li & Huntsinger 2011). Pastoralists must often herd on and beside major roads to get around the fences that enclose formerly common pastures, which often means longer travel distance and more dangers for animals and herders (Li & Huntsinger 2011). Reduced access to seasonal forage means herders more often have to purchase supplementary feeds (Miao *et al.* 2018). As fencing increases costs and reduces the benefits of pastoral practice in Asia and Africa, some herders switch to production modes such as commercial ranching, cultivation, and tourism (Lamprey & Reid 2004; Wu & Du 2008; Weldemichel & Lein 2019a), while others lease or sell their land and become wage laborers (Williams 2002; Li & Huntsinger 2011).

Diversification of production modes can result in rapid land-use change. In parts of east and southern Africa, external investors rapidly bought up most of the newly divided pastoral lands and converted them to commercial agriculture or private game reserves (Brandt & Spierenburg 2014). Overall, the previous mixed-use of land shared by people, livestock, and wildlife gradually shifted to specialized and intensified uses.

The effects of land use change on biodiversity and ecosystem functions are well studied. Sedentarized pastoralism or intensified commercial livestock husbandry leads to regional concentrations of herbivory, likely to heighten disease transmission risk and reinforce habitat fragmentation (Næss 2013). Evidence shows even moderate increases in land-use intensity in many grassland ecosystems can cause biotic homogenization, biodiversity loss, and ecosystem function shift (Allan *et al.* 2015). In southern Kenya, for example, wildlife populations and grass productivity decreased sharply on privatized ranches following land subdivision and fencing, while the wildlife population increased steadily on adjacent land under mobile pastoralism (Western *et al.* 2009).

Economic Relationships

Fences can effectively reduce financial loss by excluding, for example, crop-raiding animals, livestock predators, and wildlife poachers, but are expensive to build and to maintain (Table 2). Fencing can deteriorate rapidly so frequent maintenance is needed. Not uncommonly, agencies and individuals have had to stop maintaining fences due unanticipated long-term financial costs (e.g. (Weldemichel & Lein 2019a). However, few studies have tracked large fencing projects long term to accurately examine the economic outcomes.

The high costs of fencing imply that only some people can afford and benefit from the investment, which can entrench economic stratification. With notable exceptions (Lesorogol 2005), the division and distribution of lands is often not random or just (Williams 2002; Weldemichel & Lein 2019a). In South Africa, only those who can afford it, often outsiders, are able to acquire land from the division of a community commons, creating a landless, impoverished class (Snijders 2012; Brandt & Spierenburg 2014). In China, although in accordance with policy all households are assigned a piece of land from the community's grazing lands, richer households are the first able to build fences. The unfenced land is used as open access grasslands open to everyone, including the holders of the fenced parcels, as community management institutions are dismantled with land allocation. The enclosure of parcels by richer households pushes poorer community members to marginalized land that becomes overused and can barely sustain their livelihoods (Li *et al.* 2007). Globally, women, who often cannot own land, may be left landless following land division (Weldemichel & Lein 2019a). Such stratifications gradually marginalize traditional livelihoods that rely on mobility or access to large areas, fueling change in land practices and ecological conditions. At times the economically disadvantaged are then pushed to employ illegal means to achieve a measure of food and income, such as poaching and night grazing in forbidden areas (Mbaiwa *et al.* 2008).

The economic burdens of fencing can translate to ecological burdens. First, lack of maintenance due to financial difficulties can compromise or even nullify the benefits of having fencing in the first place (McInturff *et al.* 2020). Unmaintained fences can lose tension and become more dangerous to wildlife because animals are more easily entangled. Some landholders in Australia cannot afford maintain their sections of the dingo fence, contributing to the fact that in 200 years this longest fence in the world has done little to resolve human-dingo conflicts (Smith & Appleby 2018). Second, the economic inequalities induced by fencing can exacerbate landscape fragmentation. In Inner Mongolia, some herders who fenced early intentionally keep their livestock outside their own land as much as possible, picking clean the resources of those too poor to fence (Williams 1996a). Fencing becomes a means of co-opting common resources both inside and outside the enclosure. In northern Tibet, overgrazing increased from 27.41% to 83.02% of the total grazing land area with the introduction of grazing exclusion fencing, resulting in overall ecological loss (Sun *et al.* 2020).

Social Relationships

The famous adage "good fences make good neighbors" implies that physical boundaries can promote peaceful coexistence. For the Merak and Sakteng pastoralists in Bhutan, fencing has become a part of cultural identity and serves to maintain social harmony (Wangdi & Norbu 2018). However, fencing sometimes alienates community members from each other. In western China, social gatherings, including singing, dancing, and horseracing, declined following land division and fencing (Williams 1996a; Cao *et al.* 2011), along with other reciprocal bonds of friendship, solidarity, trust, and shared memory (Li & Huntsinger 2011). Moreover, sudden increases in fencing can cause violent territorial conflicts (Wu & Du 2008; Cao *et al.* 2011). In the "fence-cutting war" in Texas, landless cattlemen formed armed bands to destroy fences that prevented them from accessing grass and water, causing over $20 million worth of damage in 1883 alone (Netz 2004). Over time, direct conflicts may die off but altered social relationships can last for generations.

Fencing may also cause or enforce social stratification. In southern Africa, social relationships became depersonalized in fenced landscapes as the community is increasingly defined by "owners versus non-owners" and "us versus them" (Brandt & Spierenburg 2014). The presence of fencing can legitimize accusation and punishment of the "others"; any local community member who dared to enter a fenced game reserve was labeled a "poacher" (Spierenburg & Wels 2006). Social stratification tied to resources often goes hand-in-hand with economic stratification and altered land practices (Figure 2b).

On the other hand, strong social relationships can condition the physical permeability of fencing. Similar to what (Ostrom 1990) describes as the peer relations that enable community management of common pool resources, fences can be treated as social agreements. In Montana, a ranching community reinforced a highly held value for individual property rights and controlled livestock movement through fencing. At the same time, fences were generally held to be porous for local hunters that followed community protocols (Yung & Belsky 2007). Importantly, where ownership, property, and territories are based on long term development of social relations, such as in many indigenous societies, fences are used sparingly if at all. The lack of fences as a physical signal of ownership, a common western notion, has been argued to have made it easier for European colonists to justify taking land since the native inhabitants were just "living off nature," and fenceless land was obviously unowned and "free for the taking" (Cronon 1983).

Divisions in social relationships can become ecologically meaningful. In the 1950s Namaqualand, South Africa, fenced "white" and "colored" farms under apartheid policies became landscapes with quite different vegetation communities visible even today (Rohde & Hoffman 2008). Such vegetation divergence can also be found at the Norway-Finland, US-Mexico, and China-Mongolia borders, to name a few (Beck *et al.* 1990; Williams 2002; Normand *et al.* 2017). Additionally, weakened reciprocal social relationships can compromise optimal resource management and overall SES resilience (Conte & Tilt 2014). Traditional unfenced pastoral boundaries tend to be "fuzzy" and flexible (Fernandez-Gimenez 2002). Herders frequently exchange information and share resources, allowing for variation in herding locations in response to weather, disease, and other forces. However, with flexible boundaries hardened by fences and social relationships dissipated, capacity to tolerate disturbances weakens, resulting in rangeland deterioration and system resilience decline (Li & Huntsinger 2011). This feeds into the ecological consequences of altered mobility, land practices, and economic status (Figure 2b).

Human-Nature Relationships

The previously discussed social impacts redefine human-nature relationships. In southern and eastern Africa, fencing disassociates local communities from nature physically by limiting human mobility, and symbolically by altering cultural practices and core values (Hoole & Berkes 2010; Løvschal *et al.* 2017). In addition, fencing can alienate people from land by facilitating government agency administration (WebPanel 1), and by enabling neoliberal notions that commodify nature, promoting markets and transactions (Sayre 2008). For example, in South Africa, parts of Europe, and Texas, among others, fencing can make wildlife a legally defined commodity and wildlife ownership has become a profitable business (Snijders 2012; Huntsinger *et al.* 2014), a phenomenon that Hayward and Kerley (Hayward & Kerley 2009) described as “a start on domesticating wildlife”.

Fences can distort human perceptions of land and result in inappropriate science and management. When land is divided people have assumed that differences between adjacent divided parcels are a solely a result of ecological or physical drivers without always considering social and economic histories that may be responsible for the observed ecological phenomenon (Benjaminsen *et al.* 2006; Hongslo 2015). In southern Africa, for example, such notions have led to a narrative about rangeland degradation on communal land, which feeds into land use policies that urge fragmentation and private land ownership (Rohde & Hoffman 2008; Hongslo 2015). Western range science for most of the 20th century took for granted the desirability of dividing rangelands into bounded areas, each with a determinable number of livestock belonging to a single owner (Sayre 2017). Arguably, the imposition of such notion on pastoral areas in the past century has led to nearly universal failures of development projects around the world (Ferguson 1990; Sayre 2017).

THE LOOMING SOCIAL-ECOLOGICAL TRAGEDY

> *We shape our dwelling and afterwards our dwellings shape us.*
>
> *– Winston Churchill, 1943*

The physical form of fencing means it can easily self-generate. When fencing encloses a plot, it provides a physical boundary for the neighboring plot. To erect fencing around the neighboring plot then requires less material and intellectual input, encouraging (or even forcing) neighbors to adopt fences too (Wu & Du 2008). This partially contributes to the fact that major road and protected area fences often draw an accumulation of subsidiary fences around them (Said *et al.* 2016; Weldemichel & Lein 2019a). As established boundaries reduce remaining open space and drive increases in land parcel values, more people are incentivized to claim resources and properties with fencing (Said *et al.* 2016). As such, fencing creates a positive feedback loop leading to its proliferation and rapid spread over extensive areas (Figure 2c, (Løvschal 2020).

Furthermore, the perpetuation of fencing is often a one-directional process: a fenced landscape rarely returns to being fenceless (Løvschal 2020). Divided private land has been re-consolidated in a few cases, such as by the Malpai Borderlands Group in the US and in Dalrymple Shire, Australia (Reid *et al.* 2014). More often, however, the repeated financial and labor investments in fence construction and maintenance as well as the ecological changes induced by fencing mean that the cost to return to an unfenced landscape and to restore ecological processes accumulates over time. Although fencing may initially trigger discontent, people become accustomed to this organization of land and labor and increasingly accept, or even support, more fencing (Williams 1996b; Bauer 2005), eventually losing social relationships that enabled unfenced land use and stewardship. With an altered perception of tenure and community, taking down one fence in a fully fenced landscape does little to incentivize others to do the same. In addition, in many US cases, fencing is underwritten by government agencies which require landowners to contain their livestock and make them liable for damage caused by loose stock (Centner 2000). Moreover, traditional knowledge and collective memory associated with open landscapes become superfluous in the new fenced landscape organization (Williams 1996b;

Hoole & Berkes 2010). Lost knowledge and memory seldom recover, rendering the fencing process nearly irreversible.

Altogether, as more fences are constructed, opportunities to pursue fundamentally different land management strategies become increasingly rare (Lamprey & Reid 2004; Snijders 2012). The proliferation of fencing may eventually reach a tipping point after which the process of land enclosure becomes unstoppable (Løvschal *et al.* 2017). Considering fencing's multi-scale social and ecological impacts as synthesized here and by (McInturff *et al.* 2020)), complete SES transformation or even collapse can occur without deliberate policy and management interventions. For example, researchers predict that the unprecedented expansion of fencing in southwest Kenya may eventually lead to the end of pastoralism as well as a complete cease of megafauna migration (Said *et al.* 2016; Løvschal *et al.* 2017). By then, social-ecological processes, functions, and relationships in the system would be redefined.

ADVANCING FENCE ECOLOGY RESEARCH AND MANAGEMENT

> *There where it is we do not need the wall:*
> *He is all pine and I am apple orchard.*
> *My apple trees will never get across*
> *And eat the cones under his pines, I tell him.*
> *He only says, 'Good fences make good neighbors.'*
>
> *- Robert Frost, 1914*

Historically, many societies, through reciprocal social relationships, usufructuary property rights, community management of common pool resources and other social infrastructure, have not required fencing to achieve long-term sustainability. But now fencing has become a ubiquitous and essential part of various SESs. Many might be approaching a tipping point leading to SES transformation. In order to predict whether and when a tipping point might occur, and to anticipate social changes that may have undesirable consequences, future research should focus on how to measure factors influencing the long-term costs and benefits of fencing from the perspectives of stakeholders. We also encourage researchers to study fences other than those for conservation or livestock, which may reveal novel insights about the functions of fencing beyond those in this article.

The complex social-ecological connections in fenced landscapes render interdisciplinary dialogues essential in fence research. Our comprehensive view situating fencing in SESs provides a guiding framework for social and natural scientists to find common ground for collaboration (Figure 2). For example, combining human movement and animal movement research in fenced landscapes can assist in quantitatively examining interactions between social and ecological responses to fencing. Additionally, the framework allows scholars to analyze aspects of fenced systems while contributing to systematic understandings of social-ecological systems and the emerging field of fence ecology.

Despite continued increases worldwide, large-scale fence construction, maintenance, impact mediation, and removal still lack management guidelines (McInturff *et al.* 2020). In 2015, 45 scientists authored a policy directive calling for the development of multilateral fencing policies (Durant *et al.* 2015), yet such policies have not appeared as of today. In continuously pushing for policy establishment at local, regional, national, and international levels, we caution that no one solution fits all and decisions must be based on research with a social-ecological foundation. The interconnection between social and ecological systems and fencing's tendency to proliferate determines that the impacts of fencing, even if they appear to be solely ecological, are likely to include social and political impacts that cannot be mitigated just by physically restricting or removing fences. Because social connectivity can be as important as physical connectivity, restoring fenced landscapes likely requires adaptive co-management and resilience building that recouples social and ecological dynamics (Hoole & Berkes 2010). In some cases, understanding and promoting customary social rules may improve transboundary connectivity even with the physical fencing still in place (Yung & Belsky 2007). A prominent example is the "right to roam" in Europe, which codifies the general public's right to access certain privately owned land. Overall, the future of fence ecology and management must embrace a macro view through space, time, and disciplinary boundaries.

CONCLUSION

By enumerating some of the social-ecological impacts of fencing, we complement the emerging field of fence ecology with critical interdisciplinary insights. We show that many ecological consequences of fencing are socially rooted, and that the social-ecological impacts of fencing are not dichotomously beneficial or harmful but highly context-dependent. Importantly, by situating fencing in SESs, we revealed an otherwise hidden feedback loop in fenced landscapes that can amplify fencing's social and ecological impacts, which in turn can lead to SES transformations. As connectivity becomes increasingly important in global conservation schemes, insights gained from the emerging field of fence ecology may illuminate broader discussions in how to reconnect fragmented landscapes for both humans and wildlife. Essentially, when putting "*good fences make good neighbors*" back to its context, we may realize that "*there where it is we do not need the wall.*"

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PANEL 1: WHAT IS A FENCE?

Many linear structures can function like a fence to enclose resources and to bar unwanted entrance from other humans or organisms, such as walls, sonic “fences,” hedgerows, or even trenches (Figure 1d). Yet, a classic fence can be described as a physical linear feature (i.e. a pole) with vertical load-bearing components with connecting noncontinuous structures (i.e. boards, wires, rails, and nettings) spanning these components. Such structure bears a unique history and social-ecological functions from other fence-like structures. More detailed discussion about “what is a fence” can be found in McInturff et al 2020. In this article, we focus on large-scale fencing – fences with a certain morphological uniformity across a sizable geographic region. Such fences are often associated with regional or national land management needs and are the most relevant to ecological research.

FIGURE 1: FENCES IN VARIOUS SOCIAL-ECOLOGICAL SYSTEMS.
(a) Fencing demarcating private and public lands in western U.S.; (b) livestock fences on the Tibetan plateau, decorated with prayer flags; (c) electrified fences around a wildlife conservancy in South Africa (credit: Laura Gigliotti); (d) trenches that serve the purpose of fences on the Qinghai-Tibetan plateau where fence materials are in short supply.

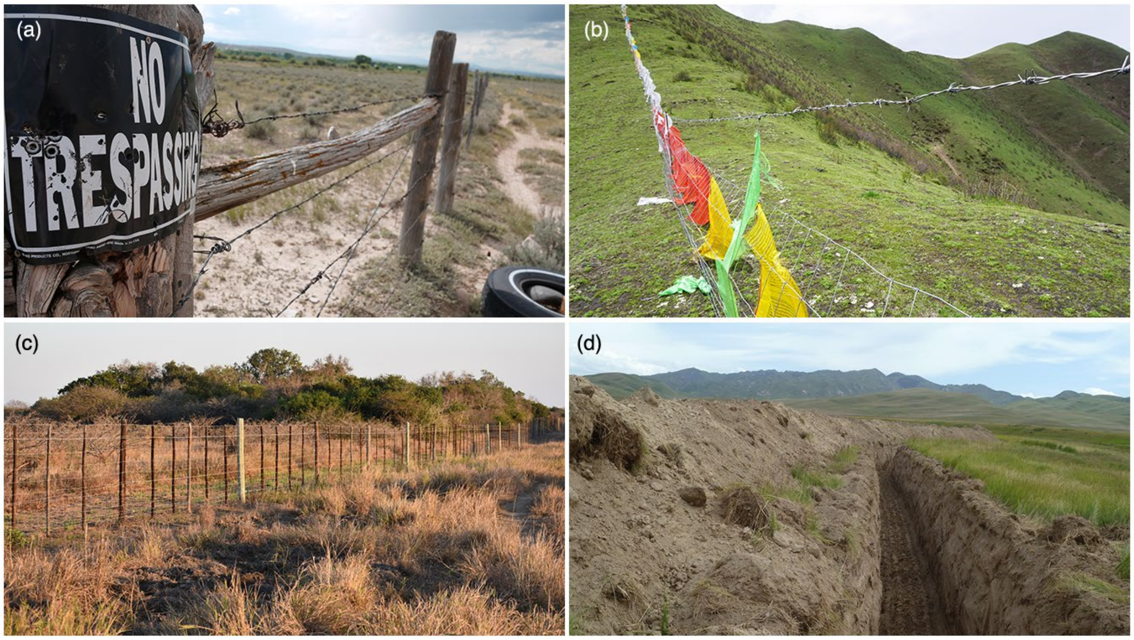

FIGURE 2: SOCIAL ECOLOGICAL DYNAMICS OF A FENCED LANDSCAPE. In a social-ecological system (SES), fencing can influence social and ecological subsystems at multiple levels. Specifically, fencing's effects on the social system can be passed on to the ecosystem along five social-ecological pathways (a). Social impacts of fencing interact with each other (b) thus amplifying fencing's influences on both the social and ecological subsystem. Additionally, the physical and social impacts stimulate self-perpetuation and proliferation of fencing across space and time (c). Altogether, large-scale fencing can drive major transformations of SESs. The grey arrows are beyond the scope of this article and were discussed in McInturff et al. 2020.

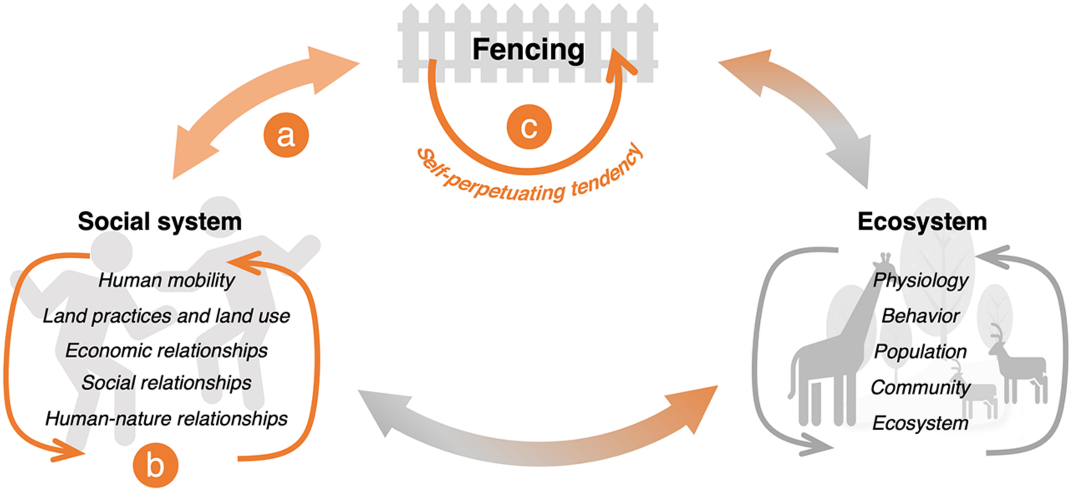

TABLE 1: SOCIAL PATHWAYS THROUGH WHICH FENCING SHAPES ECOSYSTEMS

Social pathways	***Example feedbacks on ecosystem***
Human Mobility	
Affect movement patterns	Soil loss and quality decline; affect primary productivity; shift community composition; alter animal behavior and distribution; affect ecosystem processes and resilience
Sedenterization	
Displacement	
Land practices and land use	
Alter reciprocal land practices	Species partitioning or regional concentration; alter disease dynamics; habitat fragmentation; shift primary productivity; cause biodiversity loss
Production mode diversification	
Land-use change or intensification	
Economic relationships	
Hefty cost	Reduce fence efficiency; affect animal physiology and behaviors; exacerbate landscape fragmentation
Economic stratification	
Social relationships	
Weaken social interaction	Modulate fencing's physical permeability; influence resource management efficacy; exacerbate landscape fragmentation; reduce system resilience
Incentivize conflicts	
Social stratification	
Human-nature relationships	
Dissociation and alienation	Inappropriate science and management provisions; Links back to most of the ecological impacts mentioned above through feedbacks on other social impacts
Alter human perception of nature	

TABLE 2: EXAMPLES OF THE CONSTRUCTION COST OF FENCING

Location	***Year***	***Main Purpose***	***Cost/km****	***Structure***	***Source***
Tibetan Autonomous Region, China	2000s	Keep livestock	$1,000	1.2 m – 1.5 m high	(Richard *et al.* 2006)
Southwest USA	1930s	Keep livestock	$2,245	1.3 m high 4-strain barbed wire	(Sayre 2015)
Montana, USA	2011	Keep livestock	$5,151	4-strand barbed wire	(Knight *et al.* 2011)
Australia	2000s	Exclude invasive species (feral cats, fox, and rabbits)	$6,700	1.15 m high	(Moseby & Read 2006)
Australia	2000s	Exclude invasive species (feral cats, fox, and rabbits)	$9,500	1.8 m high wire netting fence w/ 2 electric wires and a foot apron	(Moseby & Read 2006)
Kruger National Park, South Africa	1960s	Protected area boundary	$31,250	1.8 to 2.4 m high, sections have dropped today	(Hayward & Kerley 2009)
USA-Mexico border	Suspended	Political border security, exclude people	$3.9 million – 16 million	12 m high	(Deeds & Whiteford 2016)

WEBPANEL 1: TALES OF FENCING ACORSS CONTINENTS: THREE KEY CASE STUDIES

Western United States

The western U.S. is the place where barbed-wire fencing for livestock production found its first ubiquitous use. Barbed-wired was invented amidst the Homestead Era in the late 19th century when rangelands in the West were operated under "open range" and newly settled farmers found themselves needing to *fence out* roaming cattle from their cultivated land. With increases in the extent and value of crop production, and the allocation of the public domain to settlers, *fencing in* animals, land, and resources became more common in law and practice (Netz 2004). In the early 20th century, a study by US Department of Agriculture and the US Forest Service showed that fencing improved livestock production and rangeland conditions. In fact it also fit notions of private property enshrined in the US Constitution. Even though the scientific rigor of this research and its conclusion have been disputed today, fencing has been underwritten by an array of federal agencies and has been promoted and subsidized in both public and private land ever since (Sayre 2015). Fences effectively marked the closure of open range in the West and today's "open range" designations no longer signify the complete absence of fences but merely their absence along remote roadways, despite the statutes that may remain on the book in some areas (Webb 1959; Sayre 2017).

Western China

The proliferation of fencing in western China did not start until the 1980s. Responding to the idea that rangeland resources were being squandered, China initiated the Grassland Contract Policy, aiming to convert extensive grazing systems on shared land into more intensive "modern" production regimes based on enclosed pastures and individuated property rights (Williams 2002; Li & Huntsinger 2011). By 2013, the policy covered 71% of China's rangeland area, encompassing nearly 30% of China's total territory (Gongbuzeren *et al.* 2015). On the northern Tibetan Plateau alone, 33, 200 km^2 of land were fenced between 2004 and 2012 (Yu *et al.* 2016). Local government officers are highly motivated to promote fence construction because it provides quantifiable performance indicators such as "the area fenced in a fiscal year." In areas where fence materials are in short supply, huge trenches may be dug in upland meadows to act as "fences" (Figure 1d). Despite some initial doubts, pastoralists see the subsidized fencing as one of the few concrete benefits that they can receive from the government, and fencing has gradually gained popularity (Figure 1b, (Bauer 2005).

Eastern Cape, South Africa

Fences first appeared in Eastern Cape in the late 19th century when the "shepherd-and-kraal" livestock system was transformed into enclosed private production mainly owned by white farmers. The introduction of the Fencing Act in 1883 further promoted a period of expanding enclosure. From 1883 to 1911, the average area of enclosed land by division in Eastern Cape increased from 8.6% to 33% (Van Sittert 2002). The second wave of fencing is associated with stock farm - game farm conversions in the second half of the twentieth century (Brandt & Spierenburg 2014). The enactment of the Game Theft Act of 1991 created a legal framework in which wild animals (i.e. game) that before were common goods can now be private property as long as landowners build an "adequate enclosure" for them (defined as 2.4-m high fences for large animals and 1.4-m high fences for other animals in Eastern Cape), triggering a tenfold increase in wildlife prices over the following decade (Aylward & Lutz 2003), as well as an expansion of highly impermeable fencing (Figure 1c). Today, at least one-sixth of South Africa’s land has been converted based on such wildlife-based production (Snijders 2012).

Chapter 6. Concluding remarks

Being able to cope with changing environmental conditions is key for migratory animals. Both resources and risks vary across space and time, hence wide-ranging animals might have evolved ways to adjust movement behaviors in response to these environmental variations. As human activities and climate change exacerbate the uncertainties in environmental variation, information on whether animals can keep pace with novel environmental conditions is critical for identifying animals that are especially susceptible in a changing world.

A change in behavior is often the first response to environmental changes in many species. For migratory ungulates, behavior changes often include adjustments in migration behaviors, which is exhibited as a shift in migratory patterns at the landscape level. As shown in Chapter 2, migratory plasticity is a prevalent strategy that ungulates adopt in response to natural and human-induced environmental changes. Specifically, migratory ungulates around the world have been documented to adjust whether, when, and where to migrate. However, not all species show the ability to adjust migration behavior across all three dimensions. In fact, some species might be more flexible in response to environmental change, while others show higher fidelity in their migration behavior.

Not all behavioral responses, however, are adaptive. The first step toward examining the consequences of behavioral change is to quantify behavioral changes. In Chapter 3, we develop a novel approach, Barrier Behavior Analysis (BaBA), that categorizes animal movement behavior upon encountering a linear barrier, which allows further quantitative analysis of barrier-induced behavioral changes. Our results show that animal movement behavior in response to fencing appears more complex than solely preventing animals from crossing. By applying BaBA to pronghorn and mule deer, we show that the two sympatric ungulates are both extensively affected by fences. Importantly, we show some species differences in barrier behaviors. On average, pronghorn encounter fences at twice the encounter rate of mule deer. Additionally, pronghorn are more likely to bounce away from fences.

Individual-based behavior information allows us to investigate individual differences in barrier behaviors. The variations in barrier behavior described in Chapter 3 indicate that individuals within the same species likely present different barrier behavior types hence their average behavioral expression differs (i.e. among-individual differences). In addition, individuals likely demonstrate behavioral plasticity with which they adjust the relative frequency of different types of barrier behavior in response to environmental conditions (i.e. within-individual differences).

Chapter 4 confirms these predictions by examining individual barrier behaviors along a fence density gradient. Yet, the among-individual variations are dominantly individual plasticity (i.e. individuals respond to increasing fence density differently), rather than differences in behavior types, at least when fence density is low. This result again highlights the importance of plasticity in animal response to various environmental conditions. Furthermore, we show that different individuals exhibit different levels and even directions of plasticity.

Localized behavior responses can scale up to changes in larger-scale space use. By examining the correlation between barrier behavior and space use metrics, Chapter 4 concludes that animals that can quickly cross fences also exhibit larger range sizes. Such correlation is more prominent when fence density is high. This result indicates that if fences or other linear barriers continue to grow in the area, there is a potential separation between individuals that cross fences more often and range widely, and individuals that exhibit small range sizes and interact with fences less frequently. Considering the trade-off between the risk and energy expenses associated with fence crossing itself, and the better resource access associated with larger range size, further studies are needed to quantitatively examine the relative demographic benefits of both strategies.

As a physical feature that triggers tremendous ecological impacts as discussed in previous chapters, there are historical, economic, and political reasons why fences are ubiquitous around the world. Chapter 5 synthesizes the potential social effects of fencing, which form feedback loops with fencing's ecological impacts that stimulate the proliferation of fences. The experiences from cases around the world point to an important lesson that the ecological impacts of fences, especially in areas where human and wildlife co-exist, cannot be mediated solely by technological and physical solutions.

IMPLICATIONS AND OUTLOOK

Taken together, my dissertation supports three conservation lessons. First, the conservation of migratory ungulates should take into consideration animal movement plasticity and allow for changes in migration patterns. In many cases, altering movement is the animals' strategy to cope with environmental changes and strict place-based conservation is not always beneficial for animals under novel environmental conditions. Second, considering the species-specific and sometimes individual-specific responses to linear barriers, no one solution for improving landscape connectivity will fit all. The ecology of target species as well as environmental conditions both contribute to how animals respond to the changing environment. We provided examples of how behavioral information can be utilized to guide species-specific conservation prioritization in Chapter 3. Third, fencing, as well as many other linear infrastructures, should not be only viewed as a physical, technological intervention in a landscape. Rather, social connectivity can be as important as physical connectivity, and restoring fenced landscapes likely requires adaptive co-management and resilience building that recouples social and ecological dynamics.

Linear infrastructures are expected to continue to expand in the following decades (Laurance *et al.* 2014; Palen *et al.* 2014), yet studies of the multi-scale effects of these infrastructures, especially of fences, on wide-ranging animals are still in their infancy. Most wildlife ecology studies have focused on population-level responses and utilized the mean-field approach which takes the population mean to represent individual responses (McInturff *et al.* 2020). However, recent studies have shown that personality is prevalent in wildlife spatial behaviors (Hertel *et al.* 2020; Stuber *et al.* 2022). Individual-based studies such as that in Chapter 4 might assist revealing the detailed mechanisms of whether and how animals respond to linear barriers. Behavior ecology has developed sophisticated analytical methodologies that can be integrated into movement ecology for such individual-based analyses (Spiegel *et al.* 2017; Payne *et al.* 2021).

Further development of the subdiscipline of fence ecology also relies on the development of a large-scale fence database. Knowing the location of fencing is a fundamental step toward a systematic and transferable understanding of fencing's impacts across ecosystems and promoting conservation planning (Tyrrell *et al.* 2022). Unlike roads and railways, however, fencing has not been mapped globally, partly contributing to its omission in global conservation assessments (Ibisch *et al.* 2016; McInturff *et al.* 2020). The rapid development of deep learning provides an intriguing opportunity with which fence locations, and even structures, can be automatically identified through high-resolution remote sensing images (Christin *et al.* 2019), although obtaining high-resolution images across large geographic regions might be financially difficult. Multilateral collaborations between government agencies, research institutes, and private sectors might be needed to support such efforts.

Although the discussion of social-ecological systems remains theoretical in this dissertation, empirical research that examines wildlife movement in coupled human-natural systems will likely complete the missing elements in understanding animal movement in a changing world. This will be particularly important in systems where humans also employ a mobile lifestyle to optimize resource utilization, such as many pastoral systems around the world. Overall, I hope the body of work in this dissertation can contribute to a broader scientific conversation about better understanding and promoting landscapes that sustain both biodiversity and people.

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