



Perspective

A fence runs through it: A call for greater attention to the influence of fences on wildlife and ecosystems



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ABSTRACT

Fencing is a nearly ubiquitous infrastructure that influences landscapes across space and time, and the impact of fences on wildlife and ecosystems is of global concern. Yet the prevalence and commonness of fences has contributed to their “invisibility” and a lack of attention in research and conservation, resulting in a scarcity of empirical data regarding their effects. Stakeholders, including scientists, conservationists, resource managers, and private landholders, have limited understanding of how fences affect individual animals, populations, or ecosystem processes. Because fences are largely unmapped and undocumented, we do not know their full spatial extent, nor do we fully comprehend the interactions of fences with wild species, whether positive or negative. To better understand and manage fence effects on wildlife and ecosystems, we advocate for an expanded effort to examine all aspects of *fence ecology*: the empirical investigation of the interactions between fences, wildlife, ecosystems, and societal needs. We first illustrate the global prevalence of fencing, and outline fence function and common designs. Second, we review the pros and cons of fencing relative to wildlife conservation. Lastly, we identify knowledge gaps and suggest research needs in fence ecology. We hope to inspire fellow scientists and conservationists to “see” and study fences as a broad-scale infrastructure that has widespread influence. Once we better understand the influences and cumulative effects of fences, we can develop and implement practical solutions for sustaining wildlife and ecosystems in balance with social needs.

1. Introduction

Globally, wildlife contend with shrinking natural habitats in landscapes dominated by an expanding human footprint and the accumulating influence of infrastructure (Sanderson et al., 2002; Johnson et al., 2005; Leu et al., 2008). Linear transport and energy infrastructures (e.g., roads, pipelines, power lines, canals) often have negative impacts on native wildlife and ecological processes through direct mortality, creating barriers and hazards, or altering behavior (Bevanger, 1998; Lemly et al., 2000; Trombulak and Frissell, 2000; Taylor and Knight, 2003; Benítez-López et al., 2010). The resulting habitat fragmentation, population declines, and disrupted ecosystem processes (e.g., seasonal migrations (Berger, 2004)), have broad-scale effects on wildlife and natural ecosystems and have prompted substantial investment in

research and mitigation.

Fencing is nearly ubiquitous yet has received far less research attention than roads, powerlines, and other types of linear infrastructure. Worldwide, lands are laced with countless kilometers of fences erected by diverse stakeholders at different scales for widely varying purposes. Collectively, fences form extensive and irregular networks stretching across landscapes, and their influence on wildlife and ecosystems is likely far-reaching. Yet fencing is largely overlooked and is essentially “invisible” in terms of systematic research and evaluation.

We see parallels with road ecology in the widespread influence of fences. In recent decades, substantial investment into the study of road ecology has driven its advancement as a science, leading to improved public safety and wildlife conservation. Yet in many landscapes fences are more prevalent than roadways. Unlike roads, fences have vertical

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Fig. 1. Fence densities vary widely in different landscapes. (a) Roadside boundary/livestock fence in rural landscape; (b) pasture fence in exurban landscape; (c) yard fence in suburban landscape.

structure that imposes unique hazards and barriers for wildlife, are typically unregulated, are constructed and maintained largely by private landholders, but we may be able to mitigate some of their ecological effects in a cost-effective manner.

To date, most empirical research on wildlife-fence interactions and fence systems has been limited in scope, often focused on single species at local spatial scales. Existing studies have largely addressed fence impacts on ungulates or at-risk species, often motivated by mortalities and barriers to known movements (e.g., [Mbaiwa and Mbaiwa, 2006](#); [Harrington and Conover, 2006](#)). Large gaps exist in the empirical science on wildlife-fence interactions and we need more information to support wildlife conservation and resource management. We lack knowledge on the broad-scale and cumulative effects of fence infrastructure on a multitude of species, population demographics, and ecosystem processes. We do not know the longer-term or ecosystem-level consequences of fences, even of those fences erected for specific conservation objectives.

There is a fledgling but growing movement in North America and elsewhere to install wildlife friendlier fence designs ([Paige, 2012](#),

[2015](#)), now advocated by many conservation groups and government agencies. Yet most of the practical experience with fences—their design, utility, installation, and modifications—resides among private landholders and government resource managers, whose knowledge is built on field trials and circulated via peers. Private landholders, including livestock growers, construct and maintain most fences, are familiar with their location and structure, and need them to be functional. Working with these stakeholders represents an excellent opportunity to develop effective fence solutions that maintain local economies, reduce impacts to wildlife, and sustain dynamic ecosystems. Without a systematic understanding of fences—their purpose, design, extent, and ecological effects—we cannot communicate or collaborate effectively for conservation goals, nor create more sustainable landscapes where people and wildlife can co-exist.

Therefore, we advocate for a greater focus on *fence ecology*: the empirical investigation of the interactions between fences, wildlife, ecosystems, and societal needs. In nearly every fenced landscape, there are opportunities to study and better understand the influence of fences on wildlife populations and ecological processes at multiple scales. In

addition, there is an urgent need to examine alternative fence designs and systems that are more sustainable for people and wildlife and to provide a clearer understanding of the use of fencing in the context of wildlife conservation and management.

In this essay, we first illustrate the prevalence of fencing and offer a brief overview of contemporary fence functions and typical designs. Second, we review the positive and negative effects of fencing as it relates to wildlife conservation. Lastly, we identify knowledge gaps and suggest research opportunities in fence ecology. We examine our current level of knowledge, which is largely limited to wildlife-fence interactions at small spatial scales. We advocate for interdisciplinary research that examines issues at larger spatial scales and with a larger suite of stakeholders—shifting focus from studying effects on individual animals or small groups of wildlife to entire populations and ecosystem processes. Because the influence of fences on nature applies globally, we invite specialists worldwide to pursue a better understanding of fence ecology within their own ecological and social setting. A better understanding of the full ramifications of fence infrastructure will inform conservation decision-making and encourage creative alternatives.

2. Fence functions and types

Fences serve to protect and manage resources, delineate land ownership, and define political boundaries (Kotchemidova, 2008). The first fences were constructed of readily available natural materials at relatively small scales, and required considerable investment in labor (Baudry et al., 2000; Woods et al., 2017). The invention of barbed wire in 1874 made it possible to fence vast areas with little cost and effort (Liu, 2009). Barbed wire and other mass-manufactured materials bolstered a rapid proliferation of fencing, which has fundamentally altered landscapes and cultures worldwide.

Today, fences continue to proliferate as land uses shift, natural and rural areas are developed or exploited, and transportation networks multiply (Linnell et al., 2016; Li et al., 2017; Løvschal et al., 2017). The design, density, and extent of fencing are highly variable between urban, rural, and open or natural landscapes. For example, Fig. 1 illustrates the dissimilarity in fence type and density in three landscapes of western North America—each area presents different challenges and consequences for wildlife and conservation.

Fences are spatially extensive, creating vertical obstacles for wildlife to cross, and are constructed with varying degrees of permeability. In many rural areas, fencing far exceeds roads in linear extent. We compared fencing spatial data from Seward et al. (2012) to available road spatial data for southern Alberta, Canada (Alberta Base Features Data - Spatial Data Warehouse© 2017). We found that the linear extent of fences was twice that of all roads per township, 16 times the extent of paved roads, 7 times the extent of two-track roads, and 4 times the extent of gravel roads (Fig. 2).

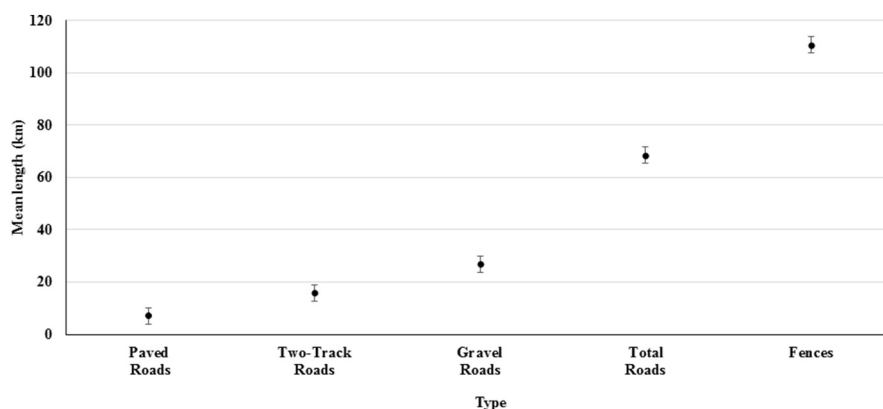


Fig. 2. The extent of fences on a landscape may far exceed that of roads. Comparison of the mean kilometers of fences per township to the mean kilometers of three types of roads per township in southern Alberta, Canada. Each error bar was constructed using the 95% confidence interval of the mean. Fence data obtained from Seward et al. (2012); road data obtained from the Alberta complete road layer of the Alberta Base Features Data (©Spatial Data Warehouse Ltd., 2017). (Disclaimer: *The Minister and the Crown provides this information without warranty or representation as to any matter including but not limited to whether the data/information is correct, accurate, or free from error, defect, danger, or hazard and whether it is otherwise useful or suitable for any use the user may make of it.*)

As land use change transformed once contiguous landscapes, the proliferation of fences has accelerated the fragmentation of ecosystems. For example, in the eastern Qinghai-Tibetan Plateau region of China, the rapid spread of fences created ecosystem-level impacts due to a shift from traditional pastoralism to land privatization (Li et al., 2017). The erection of fences altered the grazing behavior of yaks (*Bos grunniens*), which increased grazing intensity, degraded pastures, and changed the vegetation community and ecological regime (Li et al., 2017). In the Greater Mara ecosystem of East Africa, rapid proliferation of fencing threatens the region's great animal migrations and traditional Maasai pastoralism (Løvschal et al., 2017). In Asia, Europe, and North America, shifts in global politics have resulted in an increase in impermeable boundary fences erected along international borders, fragmenting landscapes and presenting barriers to animal movements (Lasky et al., 2011; Linnell et al., 2016).

Contemporary purposes of fencing fall into four categories, which often overlap: (1) livestock (i.e., pasture or range) fence to control domestic livestock; (2) exclusion fence to protect public safety and private or public resources; (3) boundary fence to delineate land-holdings or political boundaries; and (4) conservation fencing to protect at-risk species. Worldwide, these fence categories employ a wide variety of construction designs, materials, and spatial distribution across the landscape (Table 1). The impact that fence designs have on wildlife varies from positive (e.g., protection from poaching), in the case of conservation fences, to primarily negative (e.g., barriers to movement) in the case of the other three types of fences (Table 1). However, even fences designed to have positive benefits for focal species may have negative consequences for other species.

3. The dichotomy of fences: conservation tool or ecological threat?

Within the world of conservation, debate about fences stems from the equivocal nature of an infrastructure that can be a valuable instrument for management and protection or cause wildlife mortality and ecological tragedy—or both (Pfeifer et al., 2014; Woodroffe et al., 2014). Fences are often erected to safeguard threatened species, sensitive habitats, or to manage vegetation objectives using livestock grazing as a tool. Conversely, many managers and conservationists promote removal or modification of existing fences to increase ecological connectivity and reduce harmful impacts to wildlife. In light of this dichotomy, we provide a schematic interpretation (Fig. 3) to illustrate the far-reaching interactions that fences have on wildlife. This schematic is not exhaustive, but provides a framework for discussion.

Wildlife interactions with fences can be direct (physical) or indirect (behavioral), and lead to positive or negative consequences (Fig. 3). On the positive side, fencing designed specifically for conservation can reduce mortality of target species, help restore ecosystem connectivity across transportation corridors by guiding wildlife to safe crossing

Table 1
Design, distribution, and general impact to wildlife of the various fence types found around the world.

Type	Purpose	Ownership	Spatial extent	Primary design	Impact to wildlife
Livestock (pasture or range) fence	Control domestic livestock distribution	Private	Extensive	Barbed wire usually 3–5 strands (contain large domestic animals) Woven wire (contain small to medium domestic animals) Woven wire topped with barbed wire	Semi-permeable to all wildlife Impermeable for medium and large mammals
Exclusion fence	Protect social or natural resources.	Local government	Restricted (e.g., right-of-way fences along highways)		Impermeable for medium and large mammals Semi-permeable to small mammals, birds, and reptiles
Boundary fence	Control movement of people or wildlife across political or landholder boundaries	Federal government	Restricted (e.g., USA/Mexico border fence)	Variable based on location (e.g. country) and purpose	Impermeable to all wildlife except species that can fly over
Conservation fence	Protect imperiled species and wildlife communities	Environmental non-government organizations	Limited (e.g. Scotia Sanctuary, Australia)	Woven wire fencing averaging 2 m in height and usually with electrified wires	Positive for the species trying to protect Potential barrier or impediment to other wildlife in the area

opportunities, and reduce wildlife-human conflict, thus increasing social acceptance of wildlife. When employed as a tool in wildlife management, fences may deliver positive results for target species and habitats (Hayward and Kerley, 2009). Fencing can contain and protect sensitive natural areas, particularly within areas heavily modified by habitat loss and degradation (Homyack and Giuliano, 2002; Miller et al., 2010), deter poaching (Dupuis-Désormeaux et al., 2016), and protect sensitive species by reducing predation (Young et al., 2013; Cornwall, 2016; Ringma et al., 2017). Fencing can also limit disease transmission by separating wildlife and livestock (VerCauteren et al., 2007; Lavelle et al., 2010), stem encroachment of invasive and non-native species into protected areas (see Hayward and Kerley, 2009, for review), and minimize crop and livestock depredation conflicts, fostering greater social tolerance of wildlife (Huygens and Hayashi, 1999; King et al., 2017). Fences are increasingly used to keep wild and domestic animals off transportation corridors and guide them towards safe crossings (Leblond et al., 2007; Huijser et al., 2016), which increases human safety, reduces wildlife mortality, and maintains connectivity for wildlife (Beckmann et al., 2010). Fences will continue to be an important and effective management tool—the challenge is to recognize their full ecological context and potential adverse effects.

Negative consequences of wildlife-fence interactions can be classified as direct or indirect. Direct effects involve physical contact between the individual and the fence. These include direct mortality, injuries, and hair loss, which can result in reduced individual- or population-level fitness. The most observable impact is direct mortality, which can happen immediately when an animal collides with fencing or slowly when animals are caught in fences and die from exposure, starvation, or predation. Direct mortality of a wide range of birds and mammals from fence collisions and entanglements has been documented worldwide (Allen and Ramirez, 1990; Baines and Andrew, 2003; Harrington and Conover, 2006; Booth, 2007; Rey et al., 2012). More difficult to measure are injuries and hair loss that occur from encounters with fences while crossing. Jones (2014) documented hair loss in pronghorn (*Antilocapra americana*) as a result of crossing barbed wire fences and postulated the implications. The rate of wildlife mortality and injury as a result of direct contact with fences is largely unknown because most cases go unreported or unnoticed, or the carcasses are scavenged.

Indirect effects of fences on wildlife manifest themselves as changes in behavior and biology. These include heightened stress of negotiating fences, separation of neonates from mothers (Harrington and Conover, 2006), obstructed movements, habitat loss, and fragmentation. Stress occurs when animals are temporarily entangled, search frantically for a place to cross by pacing up and down the fence (Seidler et al., 2018), or must negotiate multiple fences in a landscape. These impacts can accumulate over time and contribute to increased energy expenditure, higher mortality rates, and decreased overall fitness of individuals. Young that cannot negotiate a fence and are separated from adults can die of dehydration, exposure, or predation (Harrington and Conover, 2006), and the loss of neonates reduces recruitment and potentially population size. Many of these indirect effects are difficult to observe, quantify, and fully evaluate.

Fences often delineate and separate areas of modified terrain (e.g., tilled agriculture, grazed pasture, urbanization, etc.) and some, such as veterinary cordon or wildlife-proof fences, stretch for kilometers across large regions. Such fences act as barriers, isolate remnant habitats, and fragment landscapes (Hobbs et al., 2008). As barriers and obstacles, these fences limit or block wildlife movements and influence wildlife behavior, with potential individual- and population-level consequences that ultimately alter the ecological integrity of natural systems (Berger, 2004; Sawyer et al., 2013; Jakes et al., 2018). Impermeable fences or large-scale fence networks can jeopardize the fecundity and survival of individuals and populations, reduce genetic connectivity, and alter ecological processes such as herbivory and nutrient flow (Hilty et al., 2006; Taylor et al., 2006). When fences severely fragment an ecosystem, wildlife populations become isolated, reducing genetic

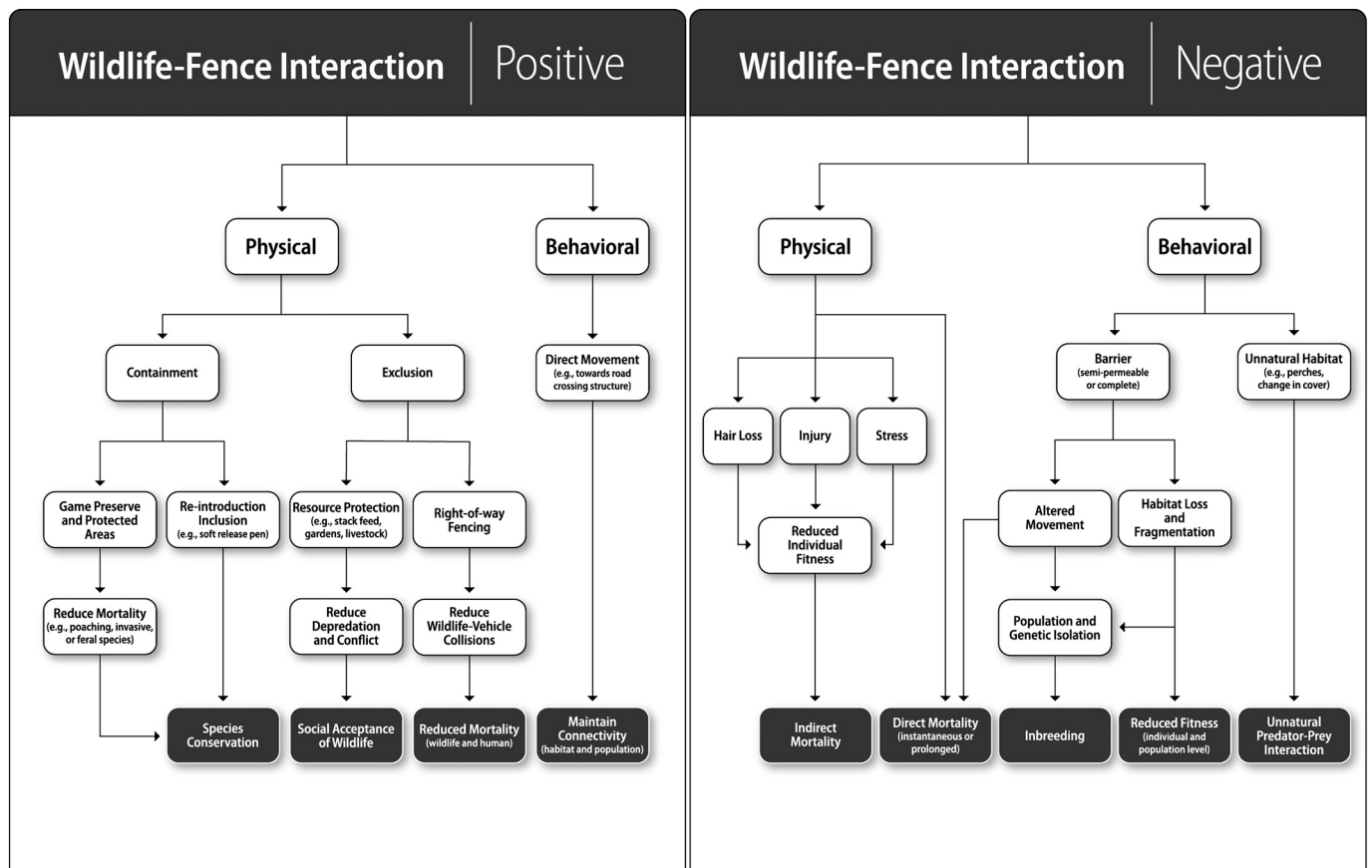


Fig. 3. Depiction of the positive and negative interactions between wildlife and fences. The shaded boxes represent outcomes of the various interactions.

exchange, diversity, and individual and population fitness (Jaeger and Fahrig, 2004; Ito et al., 2013).

In North America in recent decades, greater attention has been given to the effects of fences on wildlife, especially ungulates and grouse, with studies focused on the obstacles that fences pose for long distance migration and dispersal, and their effect on connectivity for wildlife across landscapes (Berger, 2004; Hilty et al., 2006; Taylor et al., 2006; Seidler et al., 2015). As a result, various fence modifications and crossings have been promoted to reduce animal injury, mortality, and ease animal passage (e.g., Paige, 2012, 2015). For example, in the United States, resource agencies have widely adopted fence markers to increase visibility for lesser prairie-chicken and greater sage-grouse, and smooth bottom wire to aid pronghorn passage. Many designs have been based on trial and error in the field, yet progressively more attention is being given to testing the effects of specific fence modifications on particular species (Stevens et al., 2013; Van Lanen et al., 2017; Burkholder et al., 2018; Jones et al., 2018). Although promoted by agencies and conservation organizations, the implementation of wildlife-friendlier fence designs across landscapes is patchy and by no means universal.

Even fences constructed for particular conservation purposes can produce unintended consequences. For example, veterinary cordon fences erected across Botswana to control disease transmission between livestock and wild ungulates led to dramatic and devastating declines in migratory ungulates (Williamson and Williamson, 1984; Mbaiwa and Mbaiwa, 2006). The extensive dingo (*Canis lupus dingo*) and rabbit-proof fences of Australia were erected to protect livestock and grazing lands, but altered predator-prey dynamics of endemic and introduced species with negative consequences for vegetation and ecosystems (Newsome et al., 2001; Johnson et al., 2007). Protected area and agricultural fences in east Africa fragment landscapes, alter ecological

functions and wildlife movements, and can aggravate tensions between wildlife conservation and the livelihoods of local communities or nomadic pastoralists (Reid et al., 2004; Fynn et al., 2016). Depending on design, maintenance, and the social and ecological context, fences erected with the best of intentions may actually exacerbate conservation conflicts.

4. Knowledge gaps and research opportunities

The current empirical research on the interactions between fences, wildlife, and ecosystems, especially at broad scales, is slim. Opportunities for study range from fence design and efficacy, to biological and ecological influences, to understanding the social aspects of fence systems and adoption of change—topics that are often interwoven. Advancing our understanding of the influence of fence infrastructure begins with identifying knowledge gaps so that questions can be posed and tested. Fence-related empirical research can inform and shape solutions for conservation, on-the-ground mitigation actions, systematic monitoring, and adaptive management (Table 2).

4.1. Fence extent and design

Most linear anthropogenic features that cross landscapes are readily mapped and incorporated into spatial analyses. Fences are largely unmapped and undocumented: we do not know the full extent of where they are, and we do not have efficient methods or tools to catalogue their design, purpose, and condition. Assessment of fence influences at landscape and ecosystem scales is hampered by a lack of elementary data on the magnitude, type, condition, and density of existing fence infrastructure. Efforts to generate geospatial fence data have so far used modeling to approximate the density of fences at regional scales,

Table 2
Suggested knowledge gaps and general research opportunities in fence ecology.

	Knowledge gaps	Research opportunities	Actions	Outcomes
Design & extent	Fence extent & condition	<ul style="list-style-type: none"> • Methods for geospatial analysis of fence distribution and condition. 	<ul style="list-style-type: none"> • Test mapping methods using drone technology, or high-resolution aerial imagery with automated GIS processes. • Model fence types using land tenure records. 	<ul style="list-style-type: none"> • Ability to map, quantify, and evaluate fence infrastructures for research and conservation.
	Efficacy of designs	<ul style="list-style-type: none"> • New designs for specific wildlife mitigations. • Efficacy of wildlife fence designs. • Biological & ecological costs/benefits of conservation fences. 	<ul style="list-style-type: none"> • Use trail cameras to assess wildlife and livestock fence interactions and response to modifications. • Conduct cost/benefit analyses of various designs incorporating ecological and biological factors. 	<ul style="list-style-type: none"> • Improved designs to sustain wildlife and ecosystems while maintaining fence purpose. • Adapt fence systems to reduce unintended consequences. • Reduce the number of fences erected to control livestock.
Wildlife	Behavior & biology	<ul style="list-style-type: none"> • Alternative methods to manage livestock distribution. • Species' perception, reaction to, and physical negotiation of various fence types. • Influence of fences on species' distribution. • Biological response to stress or energy loss due to fences. 	<ul style="list-style-type: none"> • Use trail cameras to assess wildlife-fence interactions. • Use spatial fence layer data as a covariate in habitat and distribution modeling. • Compare stress and energy levels (e.g., corticosteroid levels, fat reserves) between individuals occupying areas with different fence densities or types. 	<ul style="list-style-type: none"> • Designs and mitigations to ease animal crossing, movements, and reduce biological impacts.
	Population	<ul style="list-style-type: none"> • Rates of injury and mortality due to fences. • Physical and biological factors that contribute to injury, mortality, stress, population-level effects. 	<ul style="list-style-type: none"> • Conduct transects to assess mortality rates. • Assess fence density and its relationship to range-wide population demographics, size, connectivity (genetic relatedness and movement rates). 	<ul style="list-style-type: none"> • Designs and mitigations that reduce impacts on populations.
Ecosystems	Landscape-level effects	<ul style="list-style-type: none"> • Influence of fencing and distribution at landscape scales on species and ecosystems. • Fence hotspots that impede wildlife movements. • Influence of conservation fences on ecological communities or processes. 	<ul style="list-style-type: none"> • Use spatial fence layer data as a covariate in habitat and movement modeling and assess influence of fences on migration pathways. • Utilize data from trail cameras to assess effects on multiple species or ecological processes. 	<ul style="list-style-type: none"> • Alter fence systems to mitigate problem designs and locations. • Adapt fence systems and infrastructure to sustain the ecological community and functions.
	Soils	<ul style="list-style-type: none"> • Changes in soil chemistry, moisture regimes, soil microbiomes, compaction or erosion due to fences. 	<ul style="list-style-type: none"> • Assess soil characteristics along and away from fence lines to determine similarities and differences 	<ul style="list-style-type: none"> • Mitigate soil impacts; sustain healthy soils.
	Vegetation	<ul style="list-style-type: none"> • Fence effects on vegetation composition, condition, and succession. 	<ul style="list-style-type: none"> • Assess vegetation community types along and away from fence lines. 	<ul style="list-style-type: none"> • Sustain ecosystem functions, native species, and healthy vegetation communities. • Mitigations to sustain or restore ecosystem processes.
	Ecological processes	<ul style="list-style-type: none"> • Fence effects on herbivory patterns (wild and domestic), seed dispersal, nutrient flow, or other ecosystem processes. 	<ul style="list-style-type: none"> • Assess impacts of domestic and wild animals along fence lines towards changes in soil composition, seed dispersal, or nutrient flow. 	<ul style="list-style-type: none"> • Incorporate local knowledge and perceptions and develop appropriate projects to balance conservation with local values and economies.
Social dimensions	Local culture	<ul style="list-style-type: none"> • Influence of land tenure systems on fence use and design. • Influence of values, traditions, and perceptions of wildlife on the adoption of conservation projects. • Social/cultural factors that contribute to wildlife conflict. 	<ul style="list-style-type: none"> • Use surveys, public and private meetings with local stakeholders and community leaders to understand local concerns and collaborative opportunities. 	<ul style="list-style-type: none"> • Increase adoption of fence alternatives to benefit wildlife and ecosystems.
	Economic costs and incentives	<ul style="list-style-type: none"> • Social and economic incentives, risks, and rewards of adopting conservation fence systems. • Modes of collaboration and dissemination that promote conservation fence projects. • Value of socializing project costs (partnerships, cost-share, volunteer labor). 	<ul style="list-style-type: none"> • Assess stakeholder perspectives on wildlife-fence interactions and conservation fence projects. • Evaluate efficacy of outreach and cost-share systems. • Assess cost-benefit of roadway fencing in terms of insurance savings. 	<ul style="list-style-type: none"> • Increase adoption of fence alternatives to benefit wildlife and ecosystems.

combining field surveys with a synthesis of existing spatial data sets (Poor et al., 2014). An effort to map fence lines across southern Alberta with remote imagery was found to be 94% accurate, but the process was tedious and time consuming (Seward et al., 2012). In some landscapes, fence type and condition can be modeled based on land tenure records combined with ground-truthing (Poor et al., 2014). However, fence condition, permeability, and extent changes over time with maintenance and land use, so the shelf life of mapping data must be considered when weighing methods, effort, and accuracy. Any examination of fences across landscapes will greatly benefit from the development of more efficient methods and use of new technologies, such as drones or high resolution imagery (Table 2), to quantify and evaluate fence infrastructure at large scales for geospatial analysis.

Empirical studies of specific fence designs and their effects on wildlife are relatively sparse (Karhu and Anderson, 2006; Stull et al., 2011; Van Lanen et al., 2017; Burkholder et al., 2018; Jones et al., 2018). The basic specifications for wildlife-friendlier fence designs were conceived for adult ungulates in North America (Karsky, 1988) but do not account for the reduced abilities of juvenile, pregnant, stressed, or injured individuals, other species (e.g., large carnivores), or the effects of seasonal changes (e.g., snow, flooding) or topography (e.g., terrain, slope). Fence modifications to benefit multiple species must be tailored to the fence purpose, context, species present, and ecosystem (Paige, 2012, 2015). Practical testing of various types of fences, gates, wildlife crossings, funneling techniques, and other modifications intended for conservation objectives will provide insight into their efficacy and how wildlife respond. The use of non-invasive methods such as trail cameras can facilitate evaluation of various fence modifications and their efficacy in creating passage for wildlife (Table 2).

4.2. Biological and ecological effects of fences

Fence impacts on wildlife are usually observed at the individual or local group level, such as individual mortalities or barriers to herd movements. Some of these impacts may be dismissed as inconsequential, especially since rates (i.e., mortality) are usually unknown. These impacts are often dismissed because scientists, managers, and policymakers are most concerned with populations, meta-populations, and ecosystems for wildlife management and conservation. Unless cumulative effects of fences can be measured and understood, they are not addressed. Only a few studies have examined the influence of fences at large enough scales to generate meaningful knowledge at population levels. For example, both Rey et al. (2012), and Harrington and Conover (2006) measured mortality due to wire fences at landscape scales, finding dramatically higher annual mortality rates for juveniles versus adults. Fences are a major source of mortality for grouse species in Europe and North America and may be a factor driving population declines (Baines and Andrew, 2003; Wolfe et al., 2007; Stevens et al., 2013). In contrast, a survey of lions (*Panthera leo*) in 11 African countries showed populations were significantly closer to carrying capacities within fenced reserves than in unfenced regions (Packer et al., 2013).

However, these studies only scratch the surface. There are ample opportunities to examine fence influences on wildlife populations and ecosystems, including individual-level effects that may accumulate to influence population size, alter movements across landscapes, and affect vegetation communities or ecosystem processes such as nutrient flow. Many fence effects on individuals (e.g., injury, energy cost, or loss of fitness from navigating fences) are difficult to measure, which makes it difficult to determine if they scale up to influence population demographics. Research that examines cumulative effects of these impacts on populations across landscapes is sparse to nonexistent. Improved methods are needed to detect and quantify potential population consequences (Table 2).

Fences often induce a behavioral response in wildlife and we lack significant information on these responses—that is, how animals perceive, physically negotiate, and habituate to fences. A handful of studies

have documented particular species' reaction to fences or fence modifications (e.g., Asian elephants (*Elephas maximus*, Chelliah et al., 2010), greater sage-grouse (Stevens et al., 2013), mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*, Burkholder et al., 2018), and pronghorn (Jones et al., 2018; Seidler et al., 2018)). However, the cumulative stress and behavioral outcomes from crossing multiple fences on a landscape is poorly understood. Most of our understanding of animal perception and interaction with fences is built on anecdote rather than empirical study. Advances in technology such as camera traps or fine temporal-scale GPS collars with accelerometers can be used to assess behavioral interactions of wildlife with fences (Table 2).

Fences for mitigation efforts may benefit some species at the expense of others or the larger ecosystem. For example, wildlife crossing structures and associated barrier fencing significantly reduces wildlife-vehicle collisions but animals must learn the location of crossing opportunities and that it is safe to use them (Huijser et al., 2016). It may also cause stress on animals as they learn to negotiate novel structures (Seidler et al., 2018). Investigating species' sensitivity to barriers and stress and whether such stress compromises fitness or has population-level effects will provide insight to improve conservation fence systems (Table 2).

Biodiversity and ecological processes (e.g., herbivory, seed dispersal, nutrient flow) can be affected by the shift, loss of, or increase of animal (both domestic and wildlife) movements that are shaped by fence infrastructures (Todd and Hoffman, 1999; Wu et al., 2009; Augustine et al., 2013). However, there is an immense lack of understanding relative to fence effects on community or ecological systems. Research can identify and target movement bottlenecks, barriers, and critical habitats at meaningful scales for functional and resilient ecosystems, which will inform biodiversity conservation. More studies using vegetation transects and soil assessments at and away from fences will provide information on the role fencing plays in shaping vegetation communities, moisture regimes, and nutrient cycling (Table 2).

4.3. Human dimensions of fence ecology

Often the easiest aspect of a conservation problem is the technical solution and the most difficult is the human factor. Conservation is a social issue, and empirical study of the social aspects of fence ecology can help improve outreach, innovation, adoption, and conservation. In any given cultural context, a better understanding of local norms, values, perceptions, and social influencers can provide insight into how best to implement conservation projects (Mulder and Coppolillo, 2005; St John et al., 2010).

Cultural, economic, and political factors influence the use of a particular fence system and the adoption of innovations for conservation. Land tenure systems, cultural traditions, experiences with wildlife conflict, and personal and community values regarding various species all feed into the acceptance of change for conservation. Cultural perceptions, values, and status of early adopters influence how conservation practices are understood and accepted (Mulder and Coppolillo, 2005). Conceptual application of social science research, such as diffusion of innovation theory, can provide a framework for examining the technical, cultural, and political characteristics that shape the adoption of conservation practices (Mascia and Mills, 2018).

Understanding the costs and benefits to stakeholders, individual or community autonomy and control, and the influence of peers and authority figures can provide insights into how fence innovations are perceived and adopted (St John et al., 2010; Knight et al., 2011). Socializing costs through partnerships and incentives can accelerate the acceptance of conservation projects in a community (Mascia and Mills, 2018). Some government agencies and conservation organizations offer incentives to cover the cost of fence materials or labor for conservation projects, yet there is rarely follow-up monitoring of such programs to determine if they achieve their objectives. Moreover, government

incentive programs can at times work at cross-purposes. For example, a federal agricultural program in the United States heavily subsidizes pasture cross-fencing for livestock distribution, resulting in a proliferation of fencing in rangelands inconsistent with incentives from the same agency that promote conservation fence and habitat projects for wildlife (Toombs and Roberts, 2009; Knight et al., 2011). Ultimately, a deeper understanding of how to navigate the human dimensions of wildlife-fence issues is essential to implementing effective and successful conservation practices. Insights can be gained through stakeholder surveys and interviews that assess perspectives on wildlife-fence interactions and adoption of, or resistance to, conservation fence projects (Table 2).

5. Conclusions

Whether a fence is a tool or a problem for wildlife and ecosystem conservation is in the eye of the beholder. A landholder, producer, wildlife/habitat manager, or researcher will each have a different perspective on the utility and risk of fences for conservation. Fence ecology must be based on ecological concepts and science-driven results from empirical data. It must seek solutions to help balance the social needs for fencing with conserving wildlife and natural ecosystems. As a result, fence ecology can provide a clearer understanding of fence functions and impacts so that stakeholders can communicate effectively.

The impact of fences on wildlife and ecosystem processes is of global concern, but the study of fence influences on wildlife and ecological systems is in its infancy. Fences are largely taken for granted, which has led to their “invisibility” and lack of attention in conservation biology, leaving us with little empirical data regarding their effects on wildlife. Moreover, we have been left without a common understanding among stakeholders regarding the pros and cons of fencing. A more holistic understanding of fence ecology will open extensive opportunities to shape conservation at broad scales. Innovative research will provide better understanding of the cumulative and broad-scale influences of fences on populations and ecosystem processes, and help develop designs and mitigations that reduce fence impacts. Empirical study of fence ecology will advance conservation and management, with the ultimate goal of restoring functioning, intact, and resilient landscapes. We hope to inspire fellow scientists and conservationists around the world to “see” and study fences as a pervasive infrastructure that has profound influence on wildlife and ecosystems.

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References

Allen, G.T., Ramirez, P., 1990. A review of bird deaths on barb-wire fences. *Wilson Bull.* 102 (3), 553–558.

Augustine, D.J., Milchunas, D.G., Derner, J.D., 2013. Spatial redistribution of nitrogen by cattle in semiarid rangeland. *Rangel. Ecol. Manag.* 66 (1), 56–62.

Baines, D., Andrew, M., 2003. Marking of deer fences to reduce frequency of collisions by woodland grouse. *Biol. Conserv.* 110 (2003), 169–176.

Baudry, J., Bunce, R.G.H., Burel, F., 2000. Hedgerows: an international perspective on the origin, function and management. *J. Environ. Manag.* 60 (1), 7–22.

Beckmann, J.P., Clevenger, A.P., Huijser, M.P., Hilty, J.A. (Eds.), 2010. *Safe Passages: Highways, Wildlife, and Habitat Connectivity*. Island Press.

Benítez-López, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other

infrastructure on mammal and bird populations: a meta-analysis. *Biol. Conserv.* 143 (6), 1307–1316.

Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals. *Conserv. Biol.* 18 (2), 320–331.

Bevanger, K., 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. *Biol. Conserv.* 86, 67–76.

Booth, C., 2007. Barbed wire action plan. https://www.wildlifefriendlyfencing.com/WFF/This_action_plan_files/action_plan.pdf/, Accessed date: 15 May 2018.

Burkholder, E., Jakes, A.F., Jones, P.F., Hebblewhite, M., Bishop, C.J., 2018. To jump or not to jump: mule deer and white-tailed deer fence crossing decisions. *Wildl. Soc. Bull.* 42 (3), 420–429.

Chelliah, K., Kannan, G., Kundu, S., Abilash, N., Madhusudan, A., Baskaran, N., Sukumar, R., 2010. Testing the efficacy of a chili-tobacco rope fence deterrent against crop-raiding elephants. *Curr. Sci.* 99 (9), 1239–1243.

Cornwall, W., 2016. To save caribou, Alberta wants to fence them in. *Science* 353 (6297), 333.

Dupuis-Désormeaux, M., Davidson, Z., Mwololo, M., Kisio, E., MacDonald, S.E., 2016. Usage of specialized fence-gaps in a black rhinoceros conservancy in Kenya. *Afr. J. Wildl. Res.* 46 (1), 22–32.

Fynn, R.W.S., Augustine, D.J., Peel, M.J.S., de Garine-Wichatitsky, M., 2016. Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife-livestock coexistence. *J. Appl. Ecol.* 53, 388–397.

Harrington, J.L., Conover, M.R., 2006. Characteristics of ungulate behavior and mortality associated with wire fences. *Wildl. Soc. Bull.* 34 (5), 1295–1305.

Hayward, M.W., Kerley, G.I.H., 2009. Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? *Biol. Conserv.* 142 (1), 1–13.

Hilty, J.A., Lidicker Jr., W.Z., Merenlender, A.M., 2006. *Corridor Ecology: The Science and Practice of Linking Landscape for Biodiversity Conservation*. Island Press.

Hobbs, R.J., Galvin, K.A., Stokes, C.J., Lockett, J.M., Ash, A.J., Boone, R.B., Reid, R.S., Thorton, P.K., 2008. Fragmentation of rangelands: implications for humans, animals and landscapes. *Glob. Environ. Chang.* 18 (4), 776–785.

Homyack, J.D., Giuliano, W.M., 2002. Effect of streambank fencing on herpetofauna in pasture stream zones. *Wildl. Soc. Bull.* 30 (2), 361–369.

Huijser, M.P., Fairbank, E.R., Camel-Means, W., Graham, J., Watson, V., Basting, P., Becker, D., 2016. Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife-vehicle collisions and providing safe crossing opportunities for large mammals. *Biol. Conserv.* 197, 61–68.

Huygens, O.C., Hayashi, H., 1999. Using electric fences to reduce Asiatic black bear predation in Nagano prefecture, central Japan. *Wildl. Soc. Bull.* 27 (4), 959–964.

Ito, T.Y., Lhagvasuren, B., Tsunekawa, A., Shinoda, M., Takatsuki, S., Buuveibaatar, B., Chimeddorj, B., 2013. Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia. *PLoS ONE* 8 (2) (p.e0056995).

Jaeger, J.A.G., Fahrig, L., 2004. Effects of road fencing on population persistence. *Conserv. Biol.* 18 (6), 1651–1657.

Jakes, A.F., Gates, C.C., DeCesare, N.J., Jones, P.F., Goldberg, J.F., Kunkel, K., Hebblewhite, M., 2018. Classifying the migration behaviors of pronghorn on their northern range. *J. Wildl. Manag.* 82 (6), 1229–1242.

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A., Mulders, R., 2005. Cumulative effects of human developments on arctic wildlife. *Wildl. Monogr.* 60 (36 pp.).

Johnson, C.N., Isaac, J.L., Fisher, D.O., 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proc. R. Soc. Lond. Ser. B* 247 (1608), 341–346.

Jones, P.F., 2014. Scarred for life: the other side of the fence debate. *Hum. Wildl. Interact.* 8 (1), 150–154.

Jones, P.F., Jakes, A.F., Eacker, D.R., Seward, B.C., Hebblewhite, M., Martin, B.H., 2018. Evaluating responses by pronghorn to fence modifications across the northern Great Plains. *Wildl. Soc. Bull.* 42 (2), 225–236.

Karhu, R., Anderson, S., 2006. The effect of high-tensile electric fence designs on big-game and livestock movements. *Wildl. Soc. Bull.* 34 (2), 293–299.

Karsky, R., 1988. *Fences*. Publication #8824 2803. U.S. Department of Agriculture, Forest Service, Missoula Technology and Development Center, Missoula, MT (210 pp.).

King, L.E., Lala, F., Nzumu, H., Mwambungu, E., Douglas-Hamilton, I., 2017. Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. *Conserv. Biol.* 31 (4), 743–752.

Knight, K.B., Toombs, T.P., Derner, J.D., 2011. Cross-fencing on private US rangelands: financial costs and producer risks. *Rangelands* 33 (2), 41–44.

Kotchemidova, C., 2008. The culture of the fence: artifacts and meanings. *Counterblast J. Cult. Commun.* 2, 1–4.

Lasky, J.R., Jetz, W., Keitt, T.H., 2011. Conservation biogeography of the US-Mexico border: a transcontinental risk assessment of barriers to animal dispersal. *Divers. Distrib.* 17 (4), 673–687.

Lavelle, M.J., Fischer, J.W., Hygnstrom, S.E., White, J.J., Hildreth, A.M., Phillips, G.E., Vercauteren, K.C., 2010. Response of deer to containment by a poly-mesh fence for mitigating disease outbreaks. *J. Wildl. Manag.* 74 (7), 1620–1625.

Leblond, M., Ouellet, J., Poulin, M., Courtois, R., Fortin, J., 2007. Electric fencing as a measure to reduce moose-vehicle collisions. *J. Wildl. Manag.* 71 (5), 1695–1703.

Lemly, A.D., Kingsford, R.T., Thompson, J.R., 2000. Irrigated agriculture and wildlife conservation: conflict on a global scale. *Environ. Manag.* 25 (5), 485–512.

Leu, M., Hanser, S.E., Knick, S.T., 2008. The human footprint in the West: a large-scale analysis of anthropogenic impacts. *Ecol. Appl.* 18 (5), 1119–1139.

Li, L., Fassnacht, F.E., Storch, I., Bürgi, M., 2017. Land-use regime shift triggered the recent degradation of alpine pastures in Nyanpo Yutse of the eastern Qinghai-Tibetan Plateau. *Landsch. Ecol.* 32 (11), 2187–2203.

Linnell, J.D.C., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., Kusak, J., Majic, A., Skrbinsek, T., Potocnik, H., Hayward, M.W., Milner-Gulland, E.J.,

- Buuveibaatar, B., Olson, K.A., Badamjav, L., Bischof, R., Zuther, S., Breitenmoser, U., 2016. Border security fencing and wildlife: the end of the transboundary paradigm in Eurasia. *PLoS Biol.* 14 (6), e1002483.
- Liu, J.S., 2009. *Barbed Wire: The Fence That Changed the West*. Mountain Press Publishing Company.
- Løvschal, M., Bøcher, P.K., Pilgaard, J., Amoke, I., Odingo, A., Thuo, A., Svenning, J.C., 2017. Fencing bodes a rapid collapse of the unique Greater Mara ecosystem. *Sci. Rep.* 7 (41450). <https://doi.org/10.1038/srep41450>.
- Mascia, M.B., Mills, M., 2018. When conservation goes viral: the diffusion of innovative biodiversity conservation policies and practices. *Conserv. Lett.* 11, e12442. <https://doi.org/10.1111/conl.12442>.
- Mbaiwa, J.E., Mbaiwa, O.I., 2006. The effects of veterinary fences on wildlife populations in Okavango Delta, Botswana. *Int. J. Wilderness* 12 (3), 7–23 (41).
- Miller, J.J., Chanasyk, D.S., Curtis, T., Willms, W.D., 2010. Influence of streambank fencing on the environmental quality of cattle-excluded pastures. *J. Environ. Qual.* 39 (3), 991–1000.
- Mulder, M.B., Coppolillo, P., 2005. *Conservation: Linking Ecology, Economic, and Culture*. Princeton Univ. Press.
- Newsome, A.E., Catling, P.C., Cooke, B.D., Smyth, R., 2001. Two ecological universes separated by the dingo barrier fence in semi-arid Australia: interactions between landscapes, herbivory and carnivory, with and without dingoes. *Rangel. J.* 23 (1), 71–98.
- Packer, C., Loveridge, A., Canney, S., Caro, T., Garnett, S.T., Pfeifer, M., Zander, K.K., Swanson, A., MacNulty, D., Balme, G., Bauer, H., Begg, C.M., Begg, K.S., Bhalla, S., Bissett, C., Bodasing, T., Brink, H., Burger, A., Burton, A.C., Clegg, B., Dell, S., Delsink, A., Dickerson, T., Dloniak, S.M., Druce, D., Frank, L., Funston, P., Gichohi, N., Groom, R., Hanekom, C., Heath, B., Hunter, L., Delongh, H.H., Joubert, C.J., Kasiki, S.M., Kissui, B., Knocker, W., Leathem, B., Lindsey, P.A., MacLennan, S.D., McNutt, J.W., Miller, S.M., Naylor, S., Nel, P., Ng'weno, C., Nicholls, K., Ogutu, J.O., Okot-Omoya, E., Patterson, B.D., Plumpton, A., Salerno, J., Skinner, K., Slotow, R., Sogbohossou, E.A., Stratford, K.J., Winterbach, C., Winterbach, H., Polasky, S., 2013. Conserving large carnivores: dollars and fence. *Ecol. Lett.* 16 (5), 635–641.
- Paige, C., 2012. *A Landowner's Guide to Wildlife Friendly Fences: How to Build Fence With Wildlife in Mind*, Second edition. Private Land Technical Assistance Program, Montana Fish, Wildlife and Parks, Helena, Montana.
- Paige, C., 2015. *A Wyoming Landowner's Handbook to Fences and Wildlife: Practical Tips for Fencing With Wildlife in Mind*, Second edition. Wyoming Wildlife Foundation, Laramie, Wyoming.
- Pfeifer, M., Packer, C., Burton, A.C., Garnett, S.T., Loveridge, A.J., MacNulty, D., Platts, P.J., 2014. In defense of fences. *Science* 345 (6195), 389.
- Poor, E.E., Jakes, A., Loucks, C., Sutor, M., 2014. Modeling fence location and density at a regional scale for use in wildlife management. *PLoS ONE* 9 (1), e83912.
- Reid, R.S., Thornton, P.K., Kruska, R.L., 2004. Loss and fragmentation of habitat for pastoral people and wildlife in east Africa: concepts and issues. *Afr. J. Range Forage Sci.* 21 (3), 171–181.
- Rey, A., Novaro, A.J., Guichón, M.L., 2012. Guanaco (*Lama guanicoe*) mortality by entanglement in wire fences. *J. Nat. Conserv.* 20 (5), 280–283.
- Ringma, J.L., Wintle, B., Fuller, R.A., Fisher, D., Bode, M., 2017. Minimizing species extinctions through strategic planning for conservation fencing. *Conserv. Biol.* 31 (5), 1029–1038.
- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild. *BioScience* 52 (10), 891–904.
- Sawyer, H., Kauffman, M.J., Middleton, A.D., Morrison, T.A., Nielson, R.A., Wyckoff, T.B., 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. *J. Appl. Ecol.* 50 (1), 68–78.
- Seidler, R.G., Long, R.A., Berger, J., Bergen, S., Beckmann, J.P., 2015. Identifying impediments to long-distance mammal migrations. *Conserv. Biol.* 29 (1), 99–109.
- Seidler, R.G., Green, D.S., Beckmann, J.P., 2018. Highways, crossing structures and risk: behaviors of greater Yellowstone pronghorn elucidate efficacy of road mitigation. *Glob. Ecol. Conserv.* 15, e00416. <https://doi.org/10.1016/j.gecco.2018>.
- Seward, B., Jones, P.F., Hurley, T.A., 2012. Where are all the fences: mapping fences from satellite imagery. In: *Proceeding of the Pronghorn Workshop 25*, pp. 92–98.
- St John, F.A.V., Edwards-Jones, G., Jones, J.P.G., 2010. Conservation and human behaviour: lessons from social psychology. *Wildl. Res.* 37, 658–667.
- Stevens, B.S., Naugle, D.E., Dennis, B., Connelly, J.W., Griffiths, T., Reese, K.P., 2013. Mapping sage-grouse fence-collision risk: spatially explicit models for targeting conservation implementation. *Wildl. Soc. Bull.* 37 (2), 409–415.
- Stull, D.W., Gulsby, W.D., Martin, J.A., D'Angelo, G.J., Gallagher, G.R., Osborn, D.A., Warren, R.J., Miller, K.V., 2011. Comparison of fencing designs for excluding deer from roadways. *Hum. Wildl. Interact.* 5 (1), 47–57.
- Taylor, A.R., Knight, R.L., 2003. Wildlife responses to recreation and associated visitor perceptions. *Ecol. Appl.* 13 (4), 951–963.
- Taylor, P.D., Fahrig, L., With, K.A., 2006. Landscape connectivity: a return to the basics. In: *Crooks, K.R., Sanjayan, M. (Eds.), Connectivity Conservation*. Cambridge University Press, pp. 29–43.
- Todd, S.W., Hoffman, M.T., 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecol.* 142 (1–2), 169–178.
- Toombs, T.P., Roberts, M.G., 2009. Are Natural Resources Conservation Service range management investments working at cross-purposes with wildlife habitat goals on western United States rangelands? *Rangel. Ecol. Manag.* 62 (4), 351–355.
- Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv. Biol.* 14 (1), 18–30.
- Van Lanen, N.J., Green, A.W., Gorman, T.R., Quattrini, L.A., Pavlacky Jr., D.C., 2017. Evaluating efficacy of fence markers in reducing greater sage-grouse collisions with fencing. *Biol. Conserv.* 213, 70–83.
- VerCauteren, K.C., Lavelle, M.J., Seward, N.W., Fischer, J.W., Phillips, G.E., 2007. Fence-line contact between wild and farmed cervids in Colorado: potential for disease transmission. *J. Wildl. Manag.* 71 (5), 1594–1602.
- Williamson, D., Williamson, J., 1984. Botswana's fences and the depletion of the Kalahari's wildlife. *Oryx* 18 (4), 218–222.
- Wolfe, D.H., Patten, M.A., Shochat, E., Pruett, C.L., Sherrod, S.K., 2007. Causes and pattern of mortality in lesser prairie-chickens *Tympanuchus pallidicinctus* and implications for management. *Wildl. Biol.* 13 (sp1), 95–104.
- Woodroffe, R., Hedges, S., Durant, S.M., 2014. To fence or not to fence. *Science* 344 (6179), 46–48.
- Woods, C.L., Cardelús, C.L., Scull, P., Wassie, A., Baez, M., Klepeis, P., 2017. Stone walls and sacred forest conservation in Ethiopia. *Biodivers. Conserv.* 26 (1), 209–221.
- Wu, G.-L., Du, G.-Z., Liu, Z.-H., Thirgood, S., 2009. Effect of fencing and grazing on a Kobresia-dominated meadow in the Qinghai-Tibetan plateau. *Plant Soil* 319 (1–2), 115–126.
- Young, L.C., VanderWerf, E.A., Lohr, M.T., Miller, C.J., Titmus, A.J., Peters, D., Wilson, L., 2013. Multi-species predator eradication within a predator-proof fence at Ka'ena Point, Hawai'i. *Biol. Invasions* 15 (12), 2627–2638.