

RESEARCH ARTICLE

Barrier Behaviour Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates

Wenjing Xu¹  | Nandintsetseg Dejid²  | Valentine Herrmann³  | Hall Sawyer⁴  | Arthur D. Middleton¹

¹Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, USA

²Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt, Germany

³Smithsonian Conservation Biology Institute, Smithsonian Institution, Front Royal, VA, USA

⁴Western Ecosystems Technology, Inc., Laramie, WY, USA

Correspondence

Wenjing Xu
Email: wenjing.xu@berkeley.edu

Funding information

German Federal Ministry of Education and Research, Grant/Award Number: BMBF 01LC1820A; Knobloch Family Foundation; Smithsonian Conservation Biology Institute; National Geographic Society, Grant/Award Number: WW-100C-17; Buffalo Bill Center of the West; William and Flora Hewlett Foundation; Greater Yellowstone Coalition

Handling Editor: Matt Hayward

Abstract

1. 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' behavioural responses to fences may be critical for examining the ecological consequences and prioritizing conservation interventions.
2. We developed a spatial- and temporal-explicit approach, Barrier Behaviour Analysis (BaBA, available as an R package), to examine individual-level behaviours in response to linear barriers. BaBA classifies animal-barrier encounters into six behaviour 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.
3. 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.
4. We aggregated these behavioural 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.
5. *Synthesis and applications.* Our work provides empirical evidence on how fences affect wildlife movement. Importantly, Barrier Behaviour 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.

KEYWORDS

animal movement, BaBA package, barrier mitigation, conservation prioritization, fence, linear barriers, ungulate, wildlife migration

1 | INTRODUCTION

Animal movements connect disparate habitats in space and time, and sustain critical ecosystem functions and services (Bauer & Hoyer, 2014; Lundberg & Moberg, 2003). 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 (Jakes et al., 2018; Kotchemidova, 2008). 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 towards land partition and privatization (Linnell et al., 2016; Weldemichel & Lein, 2019; Yu et al., 2016).

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 (Said et al., 2016; Woodroffe et al., 2014). Semipermeable 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 vary by species, according to such factors as movement capacity, diet preference and adaptability to disturbance (Burkholder et al., 2018; Cozzi et al., 2013).

To date, most studies on fence effects have focused on measuring animal crossing rates (Bauman et al., 1999; Jones et al., 2020), mortality risk (Harrington & Conover, 2016) or population distribution (Said et al., 2016; Stabach et al., 2016; Zhang et al., 2014). While this information is valuable for basic management and land-use planning, animals' behavioural 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 Peadar 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 behavioural responses, and how these vary by species, is a key step towards 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 (e.g. Alexander & Ferguson, 2010) or fence modification to meet 'wildlife-friendly' standards (Paige, 2015; Paige & Stevensville, 2008). Studies have shown that proper modification locations are critical for mitigation effectiveness (Burkholder et al., 2018; Jones et al., 2018, 2020). Given the sheer amount of fencing in some areas (e.g. Løvschal et al., 2017; Poor et al., 2014; Sun et al., 2020) and the costs of removal and modification (Huijser et al., 2009, B. Gray and A. 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 behaviours near fences, and to link behaviours to spatially explicit fence maps.

In this study, we examined near-fence behaviours 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., 2019), including habitat improvement and fence removal and modification (Jones et al., 2020). 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., 2018). 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' behavioural responses to fences, we developed and applied a repeatable method that categorizes individual movement behaviours in response to linear barriers such as fences (Barrier Behaviour 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 (Middleton et al., 2020; Sayre, 2015). We identify extensive, complex behavioural responses of these wildlife to fences, examine spatial and temporal characteristics of these responses and demonstrate how BaBA might be used to inform conservation efforts.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area (17,420 km²) is located in western Wyoming (110.03 W, 42.907 N, elevation 1,949–3,997 m, Figure 1). This semi-arid region provides habitat for thousands of migratory pronghorn

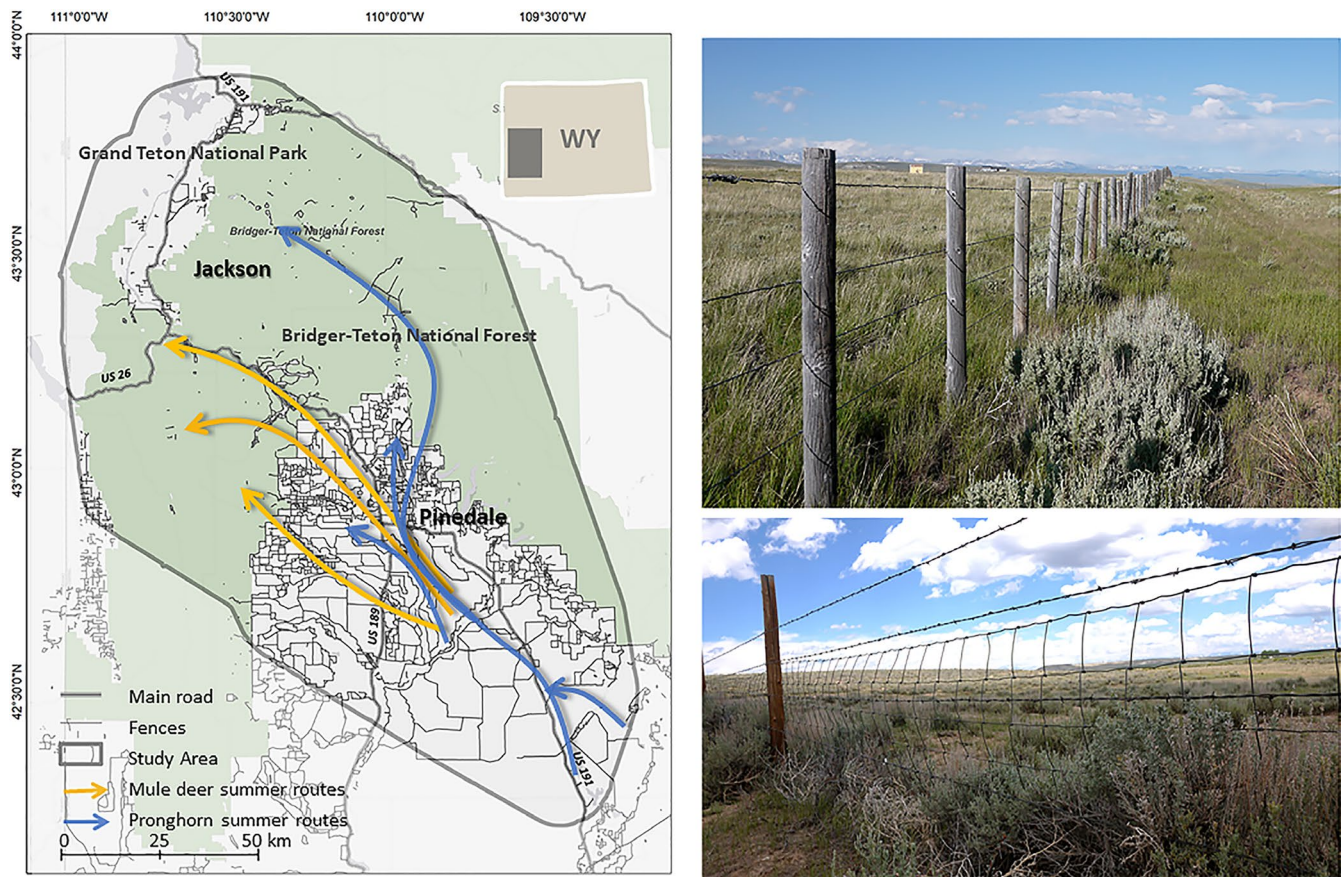


FIGURE 1 Study area and typical fence structure in the area. Upper right: four-strand barbed wire fence. Lower right: woven wire sheep fence

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. (2019) for a more detailed description of this area.

2.2 | Animal tracking data and fence data

For each species, we used GPS (Telonics) 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 January 1 to December 31. GPS positions were collected every 2 hr and each animal-year had fix rate success of $\geq 99\%$ (refer to Sawyer et al., 2017, 2019 for detailed animal capture and data collection protocols). The 24 mule deer were all migratory and travelled 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 behavioural 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 submetre resolution (0.3–0.5 m) 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).

2.3 | Fence Behaviours Analysis

Barrier Behaviour Analysis is a spatial- and temporal-explicit method to identify and classify barrier behaviours 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 behavioural 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 behaviour 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 m from 50 m to 150 m 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 behaviours, we calculated the

mean and the standard deviation of numbers of each type of fence behaviour across individuals, by species. We conducted a sensitivity analysis of BaBA results by adjusting parameter settings and GPS temporal intervals (Appendix S2).

2.4 | 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 behaviour 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 analyses were programmed in R (R Core Team, 2020), and the script is available in R package BaBA at <https://github.com/wx-ecology/BaBA>.

3 | RESULTS

3.1 | Fence and home range

Fencing digitization and correction generated 6,244.33 km of fence in the study area, with a density of 0.36 km/km² (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 5,726.7 km², 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). Deer were more migratory and the range of the 24 individuals (3,793.9 km²) delineated their seasonal habitats and migration corridor. The average

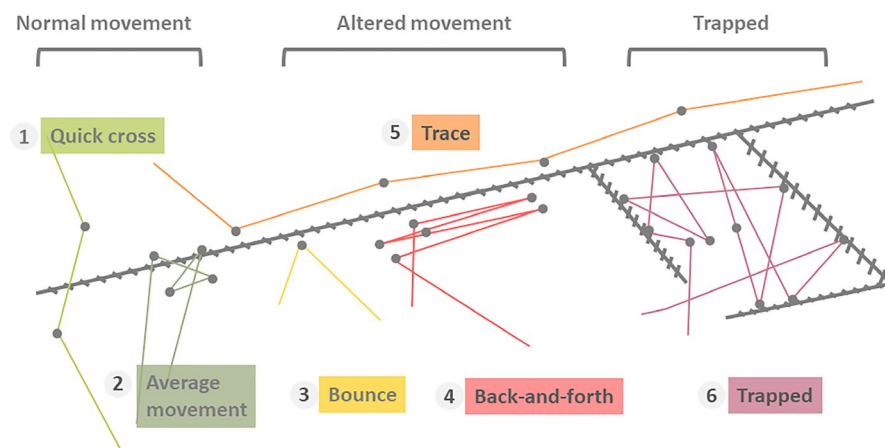


FIGURE 2 The six behavioural types identified in Barrier Behaviour Analysis. When a fence does not represent a significant barrier to movement, an animal can conduct *normal movement*, including (1) quick cross and (2) average movement. Otherwise, animals may (3) bounce away from fences or (4) move back-and-forth 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 proximity to fences for a prolonged period

fence density in pronghorn range was 0.91 km/km^2 , compared to 0.59 km/km^2 for mule deer.

3.2 | Fence Behaviours 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 \pm SD, same below) times per year, twice the rate of mule deer (119.3 ± 86.2). Both species had similar *quick crossing* rates, with $51.0 \pm 6.1\%$ for pronghorn and $51.6 \pm 10.5\%$ for mule deer. Among non-crossing behaviours, pronghorn *bounced* away from fences ($76.4 \pm 7.6\%$) more frequently than mule deer ($64.7 \pm 12.5\%$; 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* behaviours), mule deer were more likely to maintain *average movement* patterns than pronghorn

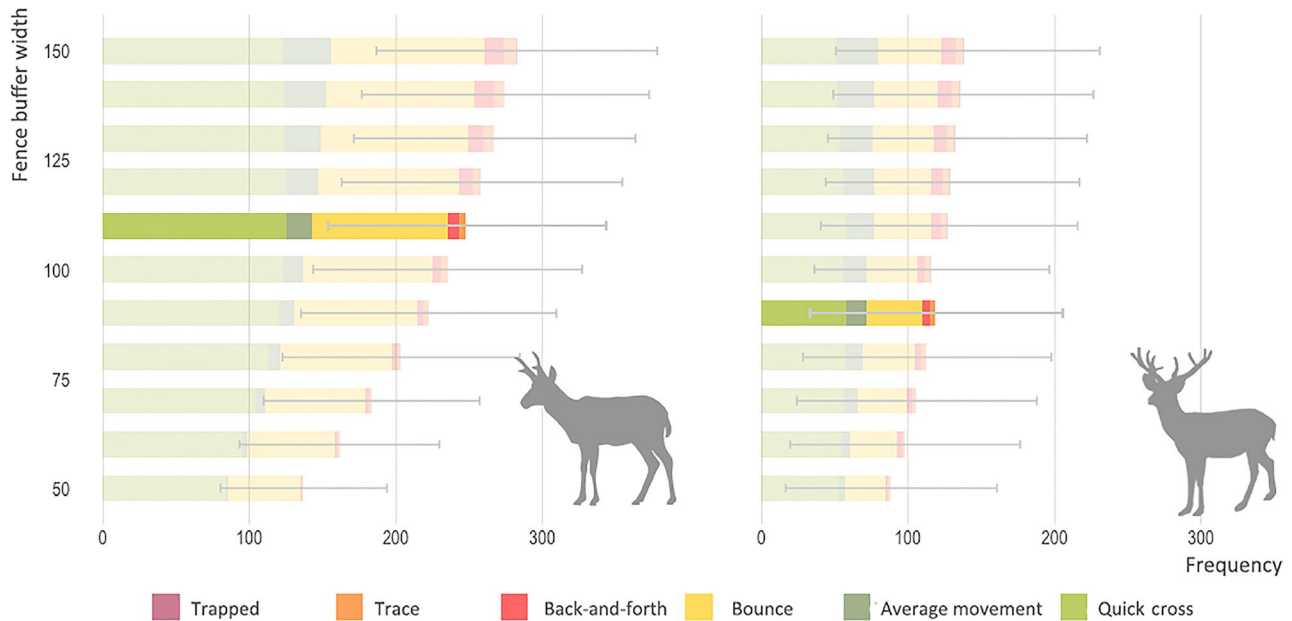


FIGURE 3 Annual individual frequency of barrier behaviours. Grey bars show the standard deviation of total fence encounters across the 24 individuals. The optimal distance for capturing fence crossing behaviours is 110 m for pronghorn, and 90 m for mule deer (highlighted bars)

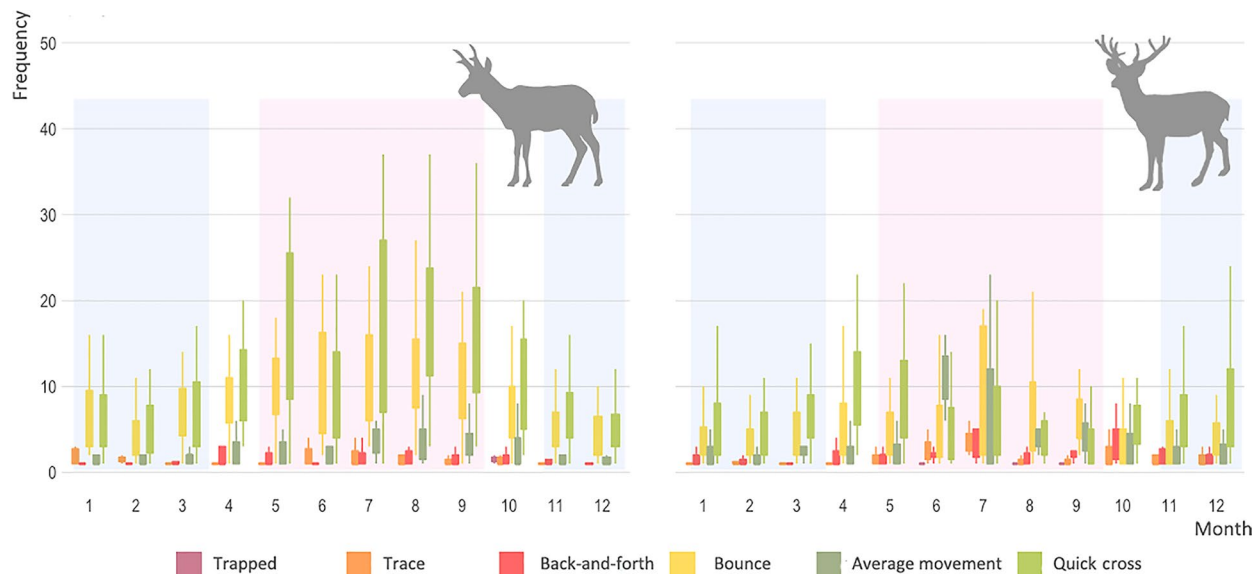


FIGURE 4 Seasonal variability of barrier behaviour. Pronghorn ($n = 24$) had a large, single peak seasonal variation in fence encounters with more bounce and quick cross behaviours during the summer (May–September, pink shade) compared to the winter (November–March, blue shade). Mule deer ($n = 24$) showed variable barrier behaviours throughout the year, with a slight, but not significant, increase in frequency during the summer

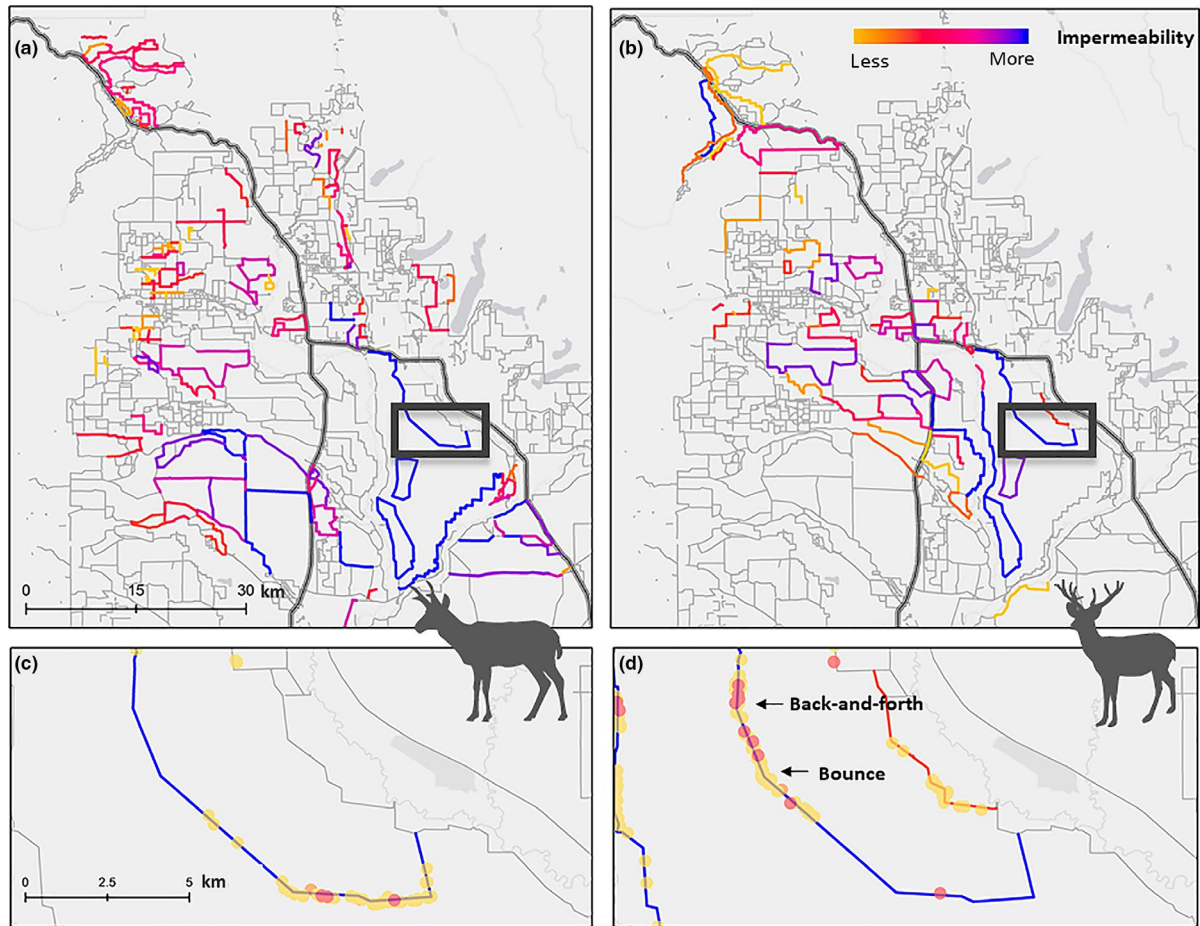


FIGURE 5 Fencing mitigation prioritization for (a) pronghorn and (b) mule deer movement. Only fence lines that had more than 10 total encounters are highlighted in colours. (c and d) show the zoom-in view of the boxed area in the top panels overlaid with classified fence encounter events

($63.8 \pm 14.2\%$ vs. $57.0 \pm 13.1\%$, 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 $52.1 \pm 46.5\%$ compared to the winter encounters, Mann-Whitney $p < 0.05$). Specifically, pronghorn performed more *bounce* and *quick cross* behaviours, but other longer lasting behaviours 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 $p = 0.26$).

3.3 | Identifying and prioritizing problematic fences

Fence segments elicited different behavioural responses from pronghorn and mule deer, indicating some were more permeable than others. Cumulative levels of behavioural 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,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,d showcase 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*.

4 | DISCUSSION

Scientists and conservationists increasingly recognize 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 behaviour of two wide-ranging ungulate species in western North America, effects which are expressed via a suite of specific behavioural 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*

behaviours 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 behaviours can aid in identifying problematic fence segments, potentially aiding in mitigation programmes. 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 behavioural 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 behaviours, *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 *Connochaetes taurinus* (Stabach et al., 2016), African elephant *Loxodonta africana* (Vanak et al., 2010) and Przewalski's gazelle *Procapra przewalskii* (Zhang et al., 2014). The other two altered fence behaviours, *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-hr GPS interval might not capture nuanced movement changes caused by fencing in a shorter time period (Appendices S2 and S3). Fine-scale GPS tracking data manifest high spatiotemporal autocorrelation. While we focused on barrier behaviours 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 behaviours. Our future research will focus on evaluating potential ecological and demographic consequences of the different types of fence behaviours.

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. (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 behaviours 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 roadside 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 highlight 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. Furthermore, 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.

Although 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 behaviours 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* behaviour 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 (e.g. Dickie et al., 2017; Rostro-García et al., 2015). 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 6,244 km fences, more than double the length of the US–Mexico border (3,145 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.

ACKNOWLEDGEMENTS

We thank M. Thonhoff, D. Woolwine, L. Keith, A. Hemenway and B. Gray for assistance with field site visits and insights on fencing in the West. T. Langford contributed substantially to the fence mapping and calibration. J. Stabach, B. Robb, A. Van Scoyoc, the Middleton lab at UC Berkeley, and the Conservation GIS lab at the Smithsonian Conservation Biology Institute, and two anonymous reviewers provided constructive comments. W.X. was supported by the Smithsonian Predoctoral Fellowship and the Tu family. A.M. and W.X. received support from the National Geographic Society grant WW-100C-17, the Buffalo Bill Center of the West, the Knobloch Family Foundation, the William and Flora Hewlett Foundation and the Greater Yellowstone Coalition. N.D. was supported by the German Federal Ministry of Education and Research (BMBF 01LC1820A).

AUTHORS' CONTRIBUTIONS

W.X., N.D., H.S. and A.M. conceived the ideas; W.X. and V.H. designed the methodology; H.S. collected the data; W.X. analysed the data; W.X. led the writing of the manuscript. All authors contributed critically to the writing and editing, and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.6078/D1FBOR> (Xu et al., 2020).

ORCID

Wenjing Xu  <https://orcid.org/0000-0001-5657-2364>

Nandintsetseg Dejid  <https://orcid.org/0000-0002-5376-3808>

Valentine Herrmann  <https://orcid.org/0000-0002-4519-481X>

Hall Sawyer  <https://orcid.org/0000-0002-3789-7558>

REFERENCES

- Alexander, A., & Ferguson, K. (2010). Delineating and decommissioning of park and veterinary fences. In K. Ferguson & J. Hanks (Eds.), *Fencing impacts: A review of the environmental, social, and economic impacts of game and veterinary fencing in Africa with particular reference to the Great Limpopo and Kavango Zambezi Transfrontier Conservation Areas* (pp. 223–227). University of Pretoria: Mammal Research Institute.
- Bauer, S., & Hoyer, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, 344(6179), 1242552. <https://doi.org/10.1126/science.1242552>
- Bauman, P. J., Jenks, J. A., & Roddy, D. E. (1999). Evaluating techniques to monitor elk movement across fence lines. *Wildlife Society Bulletin*, 27(2), 344–352.
- Burkholder, E. N., 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. *Wildlife Society Bulletin*, 42(3), 420–429. <https://doi.org/10.1002/wsb.898>
- Cagnacci, F., Focardi, S., Heurich, M., Stache, A., Hewison, A. J. M., Morellet, N., Kjellander, P., Linnell, J. D. C., Mysterud, A., Neteler, M., Delucchi, L., Ossi, F., & Urbano, F. (2011). Partial migration in roe deer: Migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos*, 120(12), 1790–1802. <https://doi.org/10.1111/j.1600-0706.2011.19441.x>
- Christin, S., Hervet, É., & Lecomte, N. (2019, October 1). Applications for deep learning in ecology. In H. Ye (Ed.), *Methods in ecology and evolution*. British Ecological Society. <https://doi.org/10.1111/2041-210X.13256>
- Clevenger, A. P., Chruszka, B., & Gunson, K. E. (2001). Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin*, 29(2), 646–653.
- Cornwall, W. (2016). To save caribou, Alberta wants to fence them in: Controversial proposal envisions the construction of a massive, predator-free pen. *Science*, 353(6297), 333. <https://doi.org/10.1126/science.353.6297.333>
- Cozzi, G., Broekhuis, F., McNutt, J. W., & Schmid, B. (2013). Comparison of the effects of artificial and natural barriers on large African carnivores: Implications for interspecific relationships and connectivity. *Journal of Animal Ecology*, 82, 707–715. <https://doi.org/10.1111/1365-2656.12039>
- Dickie, M., Serrouya, R., McNay, R. S., & Boutin, S. (2017). Faster and farther: Wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*, 54(1), 253–263. <https://doi.org/10.1111/1365-2664.12732>
- Durant, S. M., Becker, M. S., Creel, S., Bashir, S., Dickman, A. J., Beudels-Jamar, R. C., Lichtenfeld, L., Hilborn, R., Wall, J., Wittemyer, G., Badamjav, L., Blake, S., Boitani, L., Breitenmoser, C., Broekhuis, F., Christianson, D., Cozzi, G., Davenport, T. R. B., Deutsch, J., ... Pettorelli, N. (2015). Developing fencing policies for dryland ecosystems. *Journal of Applied Ecology*, 52(3), 544–551. <https://doi.org/10.1111/1365-2664.12415>
- Gates, C. C., Jones, P., Sutor, M., Jakes, A., Boyce, M. S., Kunkel, K., & Wilson, K. (2011). The influence of land use and fences on habitat effectiveness, movements and distribution of pronghorn in the grasslands of North America. In *Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes?* (pp. 277–294). Springer New York. <https://doi.org/10.1007/978-1-4614-0902-1>
- Harrington, J. L., & Conover, M. R. (2016). Characteristics of ungulate behavior and mortality associated with wire fences. *Wildlife Society Bulletin*, 34(5), 1295–1305.
- Huijser, M. P., Duffield, J. W., Clevenger, A. P., Ament, R. J., & McGowen, P. T. (2009). Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: A decision support tool. *Ecology and Society*, 14(2). <https://doi.org/10.5751/es-03000-140215>
- Jakes, A. F., Jones, P. F., Paige, L. C., Seidler, R. G., & Huijser, M. P. (2018). A fence runs through it: A call for greater attention to the influence of fences on wildlife and ecosystems. *Biological Conservation*, 227, 310–318. <https://doi.org/10.1016/j.biocon.2018.09.026>
- Jones, P. F. (2014). Scarred for life: The other side of the fence debate. *Human-Wildlife Interactions*, 8(1), 150–154. <https://doi.org/10.26077/mppv-tt76>
- 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. *Wildlife Society Bulletin*, 42(2), 225–236. <https://doi.org/10.1002/wsb.869>
- Jones, P. F., Jakes, A. F., MacDonald, A. M., Hanlon, J. A., Eacker, D. R., Martin, B. H., & Hebblewhite, M. (2020). Evaluating responses by sympatric ungulates to fence modifications across the Northern Great Plains. *Wildlife Society Bulletin*, 44(1), 130–141. <https://doi.org/10.1002/wsb.1067>

- Jones, P. F., Jakes, A. F., Telander, A. C., Sawyer, H., Martin, B. H., & Hebblewhite, M. (2019). Fences reduce habitat for a partially migratory ungulate in the Northern Sagebrush Steppe. *Ecosphere*, 10(7), <https://doi.org/10.1002/ecs2.2782>
- Keating, K. A. (2002). *History of pronghorn population monitoring, research, and management in Yellowstone National Park* (pp. 1–70). U.S. Geological Survey. <https://doi.org/10.3133/70159756>
- Kotchimidova, C. (2008). The culture of the fence: Artifacts and meanings. *Counterblast-The Journal of Culture and Communication*, 2, 1–4.
- Linnell, J. D. C., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D., Reljic, S., Kusak, J., Majic, A., Skrbinek, 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 Biology*, 14(6), 1–13. <https://doi.org/10.1371/journal.pbio.1002483>
- 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. *Scientific Reports*, 7. <https://doi.org/10.1038/srep41450>
- Lundberg, J., & Moberg, F. (2003). Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems*, 6(1), 87–98. <https://doi.org/10.1007/s10021-002-0150-4>
- Mark Peaden, J., Justin Nowakowski, A., Tuberville, T. D., Buhlmann, K. A., & Todd, B. D. (2017). Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. *Biological Conservation*, 214, 13–22. <https://doi.org/10.1016/j.biocon.2017.07.022>
- McInturff, A., Xu, W., Wilkinson, C. E., Dejid, N., & Brashares, J. S. (2020). Fence ecology: Frameworks for understanding the ecological effects of fences. *BioScience*, biaa103. <https://doi.org/10.1093/biosci/biaa103>
- Middleton, A. D., Sawyer, H., Merkle, J. A., Kauffman, M. J., Cole, E. K., Dewey, S. R., Gude, J. A., Gustine, D. D., McWhirter, D. E., Proffitt, K. M., & White, P. J. (2020). Conserving transboundary wildlife migrations: Recent insights from the Greater Yellowstone Ecosystem. *Frontiers in Ecology and the Environment*, 18(2), 83–91. <https://doi.org/10.1002/fee.2145>
- Mysterud, A., & Rolandsen, C. M. (2019). Fencing for wildlife disease control. *Journal of Applied Ecology*, 56(3), 519–525. <https://doi.org/10.1111/1365-2664.13301>
- Nandintsetseg, D., Bracis, C., Olson, K. A., Böhning-Gaese, K., Calabrese, J. M., Chimeddorj, B., Fagan, W. F., Fleming, C. H., Heiner, M., Kaczensky, P., Leimgruber, P., Munkhnast, D., Stratmann, T., & Mueller, T. (2019). Challenges in the conservation of wide-ranging nomadic species. *Journal of Applied Ecology*, 56(8), 1916–1926. <https://doi.org/10.1111/1365-2664.13380>
- Ockenfels, R. A., Carrel, W. K., & van Riper, C. (1997). Home ranges and movements of pronghorn in Northern Arizona. *Arizona Game and Fish Department Wildlife Bulletin*, 3, 45–61.
- Paige, C. (2015). *A Wyoming landowner's handbook to fences and wildlife: Practical tips for fencing with wildlife in mind* (pp. 1–56). Wyoming Community Foundation. <https://westernlandowners.org/publication/a-wyoming-landowners-handbook-to-fences-and-wildlife/>
- Paige, C., & Stevensville, M. T. (2008). *A landowner's guide to wildlife friendly fences* (pp. 1–56). Montana Fish, Wildlife and Parks. https://www.nrcs.usda.gov/wps/PA_NRCSCConsumption/download/?cid=nrcseprd1080608&ext=pdf
- Poor, E. E., Jakes, A., Loucks, C., & Suito, M. (2014). Modeling fence location and density at a regional scale for use in wildlife management. *PLoS ONE*, 9(1), e83912. <https://doi.org/10.1371/journal.pone.0083912>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rostro-García, S., Kamler, J. F., & Hunter, L. T. B. (2015). To kill, stay or flee: The effects of lions and landscape factors on habitat and kill site selection of cheetahs in South Africa. *PLoS ONE*, 10(2), <https://doi.org/10.1371/journal.pone.0117743>
- Said, M. Y., Ogutu, J. O., Kifugo, S. C., Makui, O., Reid, R. S., & de Leeuw, J. (2016). Effects of extreme land fragmentation on wildlife and livestock population abundance and distribution. *Journal for Nature Conservation*, 34, 151–164. <https://doi.org/10.1016/j.jnc.2016.10.005>
- Sawyer, H., Beckmann, J. P., Seidler, R. G., & Berger, J. (2019). Long-term effects of energy development on winter distribution and residency of pronghorn in the Greater Yellowstone Ecosystem. *Conservation Science and Practice*, 1(9). <https://doi.org/10.1111/csp2.83>
- Sawyer, H., Korfanta, N. M., Nielson, R. M., Monteith, K. L., & Strickland, D. (2017). Mule deer and energy development—Long-term trends of habituation and abundance. *Global Change Biology*, 23(11), 4521–4529. <https://doi.org/10.1111/gcb.13711>
- Sawyer, H., Lindzey, F., & McWhirter, D. (2005). Mule deer and pronghorn migration in Western Wyoming. *Wildlife Society Bulletin*, 33(4), 1266–1273. <https://doi.org/10.1098/rspb.2001.1703>
- Sayre, N. F. (2015). The coyote-proof pasture experiment. *Progress in Physical Geography: Earth and Environment*, 39(5), 576–593. <https://doi.org/10.1177/0309133314567582>
- Stabach, J. A., Wittemyer, G., Boone, R. B., Reid, R. S., & Worden, J. S. (2016). Variation in habitat selection by white-bearded wildebeest across different degrees of human disturbance. *Ecosphere*, 7(8), 1–17. <https://doi.org/10.1002/ecs2.1428>
- Sun, J., Liu, M., Fu, B., Kemp, D., Zhao, W., Liu, G., Han, G., Wilkes, A., Lu, X., Chen, Y., Cheng, G., Zhou, T., Hou, G. E., Zhan, T., Peng, F., Shang, H., Xu, M., Shi, P., He, Y., ... Liu, S. (2020). Reconsidering the efficiency of grazing exclusion using fences on the Tibetan Plateau. *Science Bulletin*, 65(16), 1405–1414. <https://doi.org/10.1016/j.scib.2020.04.035>
- Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation*, 143(11), 2631–2637. <https://doi.org/10.1016/j.biocon.2010.07.005>
- Weldemichel, T. G., & Lein, H. (2019). Fencing is our last stronghold before we lose it all. A political ecology of fencing around the Maasai Mara national reserve, Kenya: Authors. *Land Use Policy*, 87, 104075. <https://doi.org/10.1016/j.landusepol.2019.104075>
- Woodroffe, R., Hedges, S., & Durant, S. M. (2014). To fence or not to fence. *Science*, 344(6179), 46–48. <https://doi.org/10.1126/science.1246251>
- Xu, W., Dejid, N., Herrmann, V., Sawyer, H., & Middleton, A. (2020). Data from: Barrier Behavior Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates. *Dryad Digital Repository*, <https://doi.org/10.6078/D1FB0R>
- Xu, W., Huang, Q., Stabach, J., Buho, H., & Leimgruber, P. (2019). Railway underpass location affects migration distance in Tibetan antelope (*Pantholops hodgsonii*). *PLoS ONE*, 14(2), e0211798. <https://doi.org/10.1371/journal.pone.0211798>
- Yu, C., Zhang, X., Zhang, J., Li, S., Song, C., Fang, Y., Wurst, S., & Wu, J. (2016). Grazing exclusion to recover degraded alpine pastures needs scientific assessments across the Northern Tibetan Plateau. *Sustainability (Switzerland)*, 8(11), 1–6. <https://doi.org/10.3390/su8111162>
- Zhang, L., Liu, J., McShea, W. J., Wu, Y., Wang, D., & Lü, Z. (2014). The impact of fencing on the distribution of Przewalski's gazelle. *Journal of Wildlife Management*, 78(2), 255–263. <https://doi.org/10.1002/jwmg.653>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Xu W, Dejid N, Herrmann V, Sawyer H, Middleton AD. Barrier Behaviour Analysis (BaBA) reveals extensive effects of fencing on wide-ranging ungulates. *J Appl Ecol*. 2021;58:690–698. <https://doi.org/10.1111/1365-2664.13806>