

A framework for understanding semi-permeable barrier effects on migratory ungulates

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Summary

1. Impermeable barriers to migration can greatly constrain the set of possible routes and ranges used by migrating animals. For ungulates, however, many forms of development are semi-permeable, and making informed management decisions about their potential impacts to the persistence of migration routes is difficult because our knowledge of how semi-permeable barriers affect migratory behaviour and function is limited.

2. Here, we propose a general framework to advance the understanding of barrier effects on ungulate migration by emphasizing the need to (i) quantify potential barriers in terms that allow behavioural thresholds to be considered, (ii) identify and measure behavioural responses to semi-permeable barriers and (iii) consider the functional attributes of the migratory landscape (e.g. stopovers) and how the benefits of migration might be reduced by behavioural changes.

3. We used global position system (GPS) data collected from two subpopulations of mule deer *Odocoileus hemionus* to evaluate how different levels of gas development influenced migratory behaviour, including movement rates and stopover use at the individual level, and intensity of use and width of migration route at the population level. We then characterized the functional landscape of migration routes as either stopover habitat or movement corridors and examined how the observed behavioural changes affected the functionality of the migration route in terms of stopover use.

4. We found migratory behaviour to vary with development intensity. Our results suggest that mule deer can migrate through moderate levels of development without any noticeable effects on migratory behaviour. However, in areas with more intensive development, animals often detoured from established routes, increased their rate of movement and reduced stopover use, while the overall use and width of migration routes decreased.

5. *Synthesis and applications.* In contrast to impermeable barriers that impede animal movement, semi-permeable barriers allow animals to maintain connectivity between their seasonal ranges. Our results identify the mechanisms (e.g. detouring, increased movement rates, reduced stopover use) by which semi-permeable barriers affect the functionality of ungulate migration routes and emphasize that the management of semi-permeable barriers may play a key role in the conservation of migratory ungulate populations.

Key-words: Brownian bridge movement model, connectivity, migration routes, mule deer, stopovers

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Introduction

Migration is unique among animal movement strategies because of the impressive distances that animals travel, the predictability of their return and, for many species, the sheer number of individuals involved (Dingle 1996; Milner-Gulland, Fryxell & Sinclair 2011). Migratory ungulates have received much attention because of their role as drivers of ecosystem processes (McNaughton 1985; Hobbs 1996), their value to humans as harvestable resources (Vors & Boyce 2009) and their potential as flagship species for landscape-level conservation (Thirgood *et al.* 2004). Recent global declines in the abundance and distribution of migratory ungulates (Berger 2004; Bolger *et al.* 2008; Harris *et al.* 2009) underscore the need to better understand the consequences of disruptions to migratory behaviour. Declines in migratory ungulates have been clearly linked to excessive harvest and land-use changes (e.g. agricultural development) on seasonal ranges (Bolger *et al.* 2008), but neither overharvest nor fragmentation of seasonal ranges actually affect the migration route itself. In contrast, anthropogenic features, such as roads, fences, power lines and pipelines, often overlap or bisect migration routes and are commonly cited as sources of habitat fragmentation or barriers with the potential to impede animal movement (Bolger *et al.* 2008; Harris *et al.* 2009; Dobson *et al.* 2010). Despite this recognition, our knowledge of how such barriers affect migration when they overlap with a migration route is limited.

It is clear that impermeable barriers, such as game-proof fences, inhibit the connectivity of migration routes, such that entire seasonal ranges become inaccessible. A total loss of connectivity presumably eliminates the ecological benefits of migration, which can include tracking gradients in high-quality forage (McNaughton 1985; Wilmshurst *et al.* 1999), accessing water holes (Williamson

& Williamson 1984; Bolger *et al.* 2008) and reducing predation (Fryxell & Sinclair 1988; Hebblewhite & Merrill 2007). In some cases, impermeable barriers have caused population declines that resulted in the loss of thousands of migratory ungulates (Williamson & Williamson 1984; Whyte & Joubert 1988; Spinage 1992; Ben-Shahar 1993).

Most anthropogenic features, however, are at least semi-permeable to ungulates, and the assumption that semi-permeable barriers elicit similar effects (i.e., loss of migration function, population declines) is not yet supported by empirical evidence, nor have the potential mechanisms for such effects been explored. While the emergence of corridor ecology research (e.g. Hilty, Lidicker & Merenlender 2006) has improved the awareness of barrier effects, most conservation attention has focused on impermeable barriers (e.g. Dobson *et al.* 2010; Holdo *et al.* 2011). This is due in part to the difficulties associated with studying subtle and potentially long-term behavioural changes in migratory animals. However, recent improvements in GPS technology have advanced the study of migratory animals, and rapid increases in energy and urban development have prompted new interest in understanding how migratory ungulates might be influenced when semi-permeable barriers are constructed within their routes.

To facilitate a mechanistic understanding of semi-permeable barrier effects, we distinguish here between ‘connectivity’ and the ‘functional attributes’ of a migration route. For our purposes, connectivity simply describes whether or not animals are able to move from one seasonal range to another, whereas the functional attributes of a route include access of locally important resources such as stopover sites, movement corridors and escape terrain, which allow animals to track vegetation phenology and balance predation risk (Fig. 1). Thus, when connectivity is lost due to construction of an impermeable

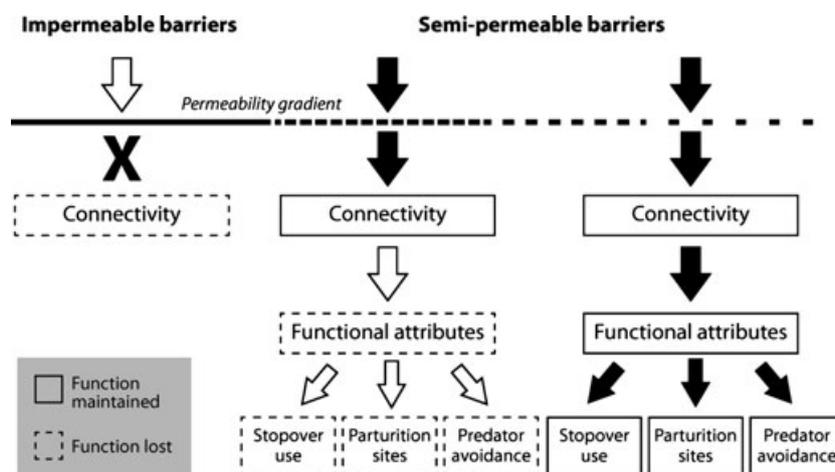


Fig. 1. Conceptual model that distinguishes between ‘connectivity’ and ‘functional attributes’ of a migration route and illustrates how each are affected by barriers (white arrows). Impermeable barriers impede connectivity such that animals can no longer migrate between seasonal ranges. In contrast, semi-permeable barriers often allow connectivity to be maintained, but the functional attributes of the migration route can be compromised, especially as permeability decreases.

barrier, the functional attributes of the migration route are also lost, along with the benefits of the seasonal range. Importantly, however, when connectivity remains intact because barriers are semi-permeable, the functional attributes of the migration routes may or may not be compromised. Thus, distinguishing between connectivity and functional attributes clarifies that impermeable and semi-permeable barriers may affect ungulate migration through different mechanisms.

Here, we propose a general framework to evaluate semi-permeable barrier effects on migratory ungulates, with the goal of expanding the discussion of barrier effects beyond the broad assumption that anthropogenic features will unconditionally impede migration. Our framework consists of three steps. First, the potential barrier is identified and measured in a way that facilitates the detection of development thresholds that alter behaviour. Roads, for example, are commonly viewed as potential barriers to migration (Dobson *et al.* 2010). However, a road or network of roads may not elicit a behavioural response until some threshold (e.g. road density, traffic levels, road width, etc.) is exceeded (Dyer *et al.* 2002; Frair *et al.* 2008). Thus, whether the potential barrier is a road, fence or other development, it should be measured in a way that considers likely thresholds. Second, the behavioural responses to a given anthropogenic feature are measured. We note that simply determining whether animals continue to migrate after construction of a potential barrier (e.g. Carruthers & Jakimchuk 1987; Ito *et al.* 2005) only provides information on connectivity and may overlook important behavioural changes. To examine whether semi-permeable barriers reduce the benefits of migration, specific migration behaviours (e.g. rate of movement, fidelity) must be quantified before and after the construction of the potential barrier (or in areas with and without barriers). These may include traditional metrics such as net-squared displacement and rate of movement, or the more advanced utilization distribution (UD) metrics now possible with movement-based kernel density estimation (MKDE; Benhamou 2011) and Brownian bridge movement models (BBMM; Horne *et al.* 2007; Kranstauber *et al.* 2012). Next, to predict how the observed behavioural changes may influence the functionality of the migration route, it is necessary to characterize functional attributes (e.g. stopover sites, escape terrain, parturition) of the migratory landscape. This third step highlights the importance of linking observed behavioural changes to functional attributes of the migratory landscape, thereby providing a means to evaluate how the benefits of migration may be altered by behavioural changes caused by barriers.

We illustrate our framework using empirical data from migratory mule deer *Odocoileus hemionus* in Wyoming, USA. Like many areas of western North America, ungulate ranges in Wyoming are experiencing unprecedented levels of energy development (Sawyer, Kauffman & Nielson 2009; Sawyer *et al.* 2009). Although the scale and intensity

of development are rapidly increasing (Copeland *et al.* 2009), we know little about whether energy infrastructure alters migratory behaviour, the functionality of migration routes or the ecological benefits of migration. Here, we use GPS movement data to examine the behavioural response of two migratory mule deer populations to varying levels of energy development. Using migration routes identified prior to large-scale natural gas development as the baseline, our goal was to determine how mule deer migration was influenced by increased levels of gas development. We examined several complementary metrics of behavioural change and evaluated how they affected the functional attributes of the migratory landscape, with an emphasis on understanding how semi-permeable barriers alter the benefits of migration. By revealing differential responses of mule deer to varying levels of development, our findings highlight the importance of considering semi-permeable barriers in land-use planning – an urgent goal amid ongoing global declines in ungulate migration.

Materials and methods

STUDY AREA

Our study was conducted in the 1100-km² Atlantic Rim Project Area (ARPA), located in south-central Wyoming. The ARPA is generally characterized by rolling topography, prominent ridges and dry canyons dominated by sagebrush *Artemisia* sp., black greasewood *Sarcobatus vermiculatus* and other mixed shrubs *Purshia tridentata*, *Chrysothamnus* sp., *Cercocarpus* sp. Elevations range from 1920 to 2530 m. The ARPA contains two distinct mule deer winter ranges known as the Dad and Wild Horse winter ranges. The Dad winter range supports 500–1000 mule deer, whereas the Wild Horse range supports 1500–2000. Population-level migration routes for both winter ranges were identified in 2005 and 2006 (Sawyer *et al.* 2009), during a period of exploratory energy development that we refer to as Phase 1 (Figs 2 and 3). Shortly thereafter, the Bureau of Land Management (BLM) approved development of *c.* 2000 wells to extract coal-bed methane from the ARPA (BLM 2007). Although most of the development was planned for areas outside of mule deer migration routes, there were two areas where development overlapped with migration routes, including the 33.6-km² Dry Cow Creek located northeast of the Dad winter range (Fig. 2) and the 15.5-km² Wild Horse Basin located east of the Wild Horse winter range (Fig. 3).

ANIMAL CAPTURE AND DATA COLLECTION

We captured 47 mule deer during Phase 1 and equipped animals with store-on-board GPS collars that collected locations every 2.5 h (Sawyer *et al.* 2009). Between February 2005 and November 2006, we collected 116 494 locations from the 47 deer to document spring and autumn migrations. We refer readers to Sawyer *et al.* (2009) for further details on Phase 1. During Phase 2, we captured 56 mule deer and equipped them with GPS collars programmed to collect locations every 2 hours during migration. Collars collected data for spring and autumn migrations of 2008,

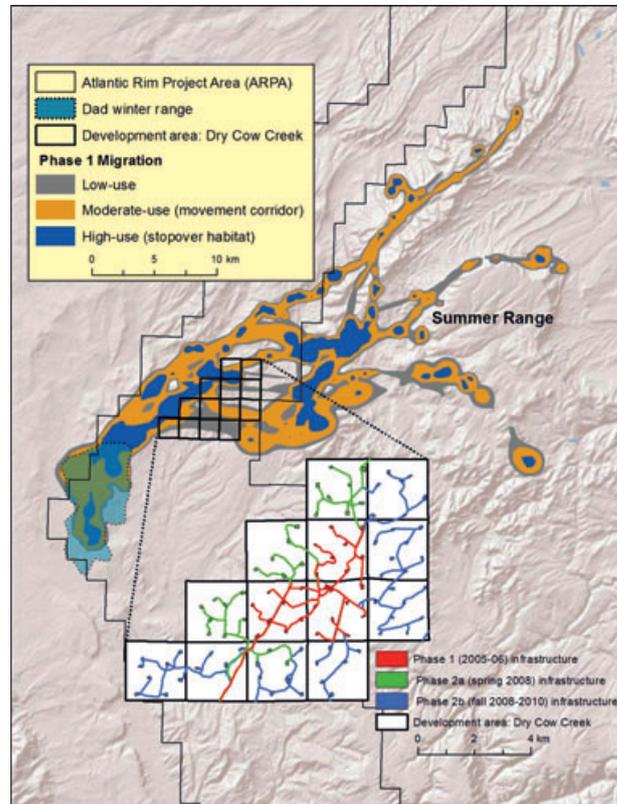


Fig. 2. Location of 33.6-km² Dry Cow Creek development area within the population-level migration route estimated for mule deer from the Dad winter range during Phase 1. Map insert shows the level of gas development in Dry Cow Creek during Phase 1 (2005–06), Phase 2a (spring 2008) and Phase 2b (autumn 2008–2010). Infrastructure includes roads (linear features) and gas pads (small squares).

2009 and 2010. During Phase 2, we recovered 191 302 GPS locations from 50 of the 56 marked animals. Of those 50 animals, 39 (26 in Wild Horse winter range and 13 in Dad winter range) lived long enough to complete at least one migration. Fix success of GPS collars was high (99%), so our analysis was not affected by missing locations.

IDENTIFYING THE POTENTIAL BARRIER

A critical component of studying barrier effects is to quantify potential barriers in terms that allow thresholds to be considered (Dyer *et al.* 2002; Frair *et al.* 2008). The potential barriers in our study included road networks and well pads associated with gas development. We used 10-m resolution satellite imagery acquired from Spot Image Corporation (Chantilly, VA, USA) to quantify road and well pad densities during each phase of development. We recognize that roads and well pads can have varying levels of human disturbance (e.g. traffic), depending on the type of wells (e.g. drilling vs. producing) and associated production facilities (Sawyer, Kauffman & Nielson 2009). However, we did not distinguish between road and well pad types because all roads in our development areas were improved gravel and *c.* 10 m wide, and well pads were similar in size and type.

DETECTING CHANGES IN MIGRATORY BEHAVIOUR

We sought to identify potential individual and population-level behavioural responses during migration. We calculated movement rates of mule deer ($n = 43$) through the development areas and

used a standard two-sample *t*-test ($\alpha = 0.10$) to determine whether movement rates varied between Phases 1 and 2. Movement rates were only calculated for animals that moved through development areas and were based on the movement sequence that included one location either side of the development area. To evaluate movement in the context of the larger migration route, we also calculated movement rates in undeveloped habitat, between the development areas and summer ranges. For a small sample of animals that collected data in both study phases ($n = 4$), we compared migration routes between years to assess whether animals detoured around the development area.

We used the Brownian bridge movement model (BBMM) to estimate population-level migration routes for GPS-collared deer from both the Dad and Wild Horse winter ranges. The BBMM uses time-specific location data to estimate a UD along a movement route, where the probability of being in an area is conditioned on the start and end locations, the elapsed time between locations and the speed of movement (Horne *et al.* 2007). We used the 'bbmm' package in R (R Foundation for Statistical Computing, Vienna, Austria) to estimate UDs for individual migration routes. Population-level migration routes were then estimated by averaging the individual UDs within each winter range and study phase. These population-level UDs provide a probabilistic measure of the migration route, where the height of UD reflects intensity of use and the contours of the UD delineate the surface area, or width of the route. Overall, the Phase 1 period (spring 2005–spring 2006) included 55 migrations (42 spring, 13 autumn) collected from 35 deer, whereas Phase 2 (spring 2008–autumn 2010) included 86 migration routes (56 spring, 30 autumn) from 39 deer. The Phase 1 population-level migration

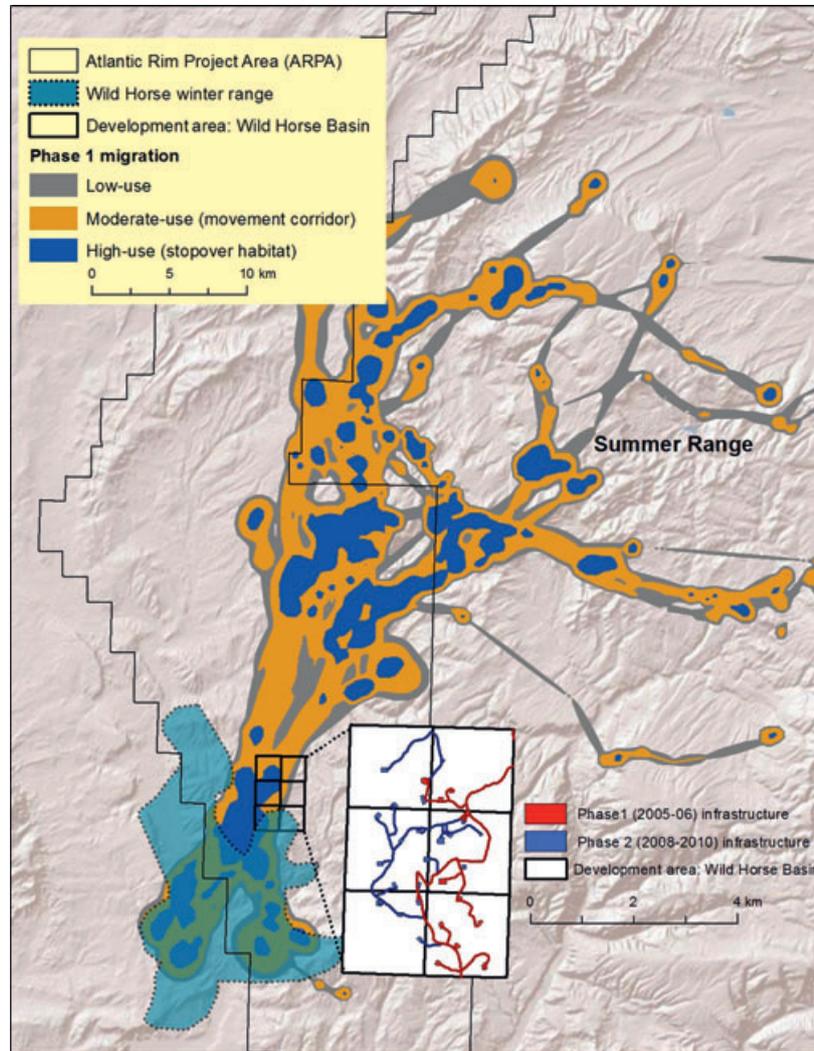


Fig. 3. Location of 15.5-km² Wild Horse Basin development area within the population-level migration route estimated for mule deer from the Dad winter range during Phase 1. Map insert shows the level of gas development in Wild Horse Basin during Phase 1 (2005–06) and Phase 2 (2008–2010). Infrastructure includes roads (linear features) and gas pads (small squares).

route for the Wild Horse winter range included 37 migrations by 23 deer, while the Dad winter range included 18 migrations by 12 deer (Figs 2 and 3). The Phase 2 population-level migration route for the Wild Horse winter range included 61 migrations by 23 deer. Phase 2 development in Dry Cow Creek was split into Phase 2a (spring 2008) and 2b (autumn 2008–autumn 2010), to account for the development activity during the summer of 2008. The population-level route for the Dad winter range included 12 migrations by 12 deer in Phase 2a, and 13 migrations by 9 deer in Phase 2b.

To evaluate whether the intensity of deer use (i.e. height of the UD) within migration routes changed in the development areas, we used the UD of migration routes estimated during Phase 1 as a reference and examined whether observed changes in the Dry Cow Creek and Wild Horse Basin were statistically different than those expected in a larger portion of the migration route. To do this, we designed a randomization procedure that estimated the expected change in deer use for a larger area (3 km buffer) surrounding both Dry Cow Creek and Wild Horse Basin development areas. For Dry Cow Creek, we randomly

selected 13, 2.6-km² units (equal to the size of the development area) from a larger sample of 51 and then calculated the percentage change in UD volume relative to Phase 1. This process was conducted 500 times and provided an estimate of the amount of change expected in any combination of 13, 2.6-km² units sampled from the larger 132-km² area. A similar process was repeated in Wild Horse Basin, except we randomly selected 6, 2.6-km² units from a larger sample of 21. We calculated 90% confidence intervals to test whether the changes observed in the development areas were more or less than expected based on the permutation results. Our randomization analysis used the three-dimensional structure or volume of UDs to detect changes in population-level migration use and is conceptually similar to the volume of intersection method described by Millsaugh *et al.* (2004). We also calculated the change in the amount of migration surface area, as defined by the outer 99% contour of the population-level migration routes in the Dry Cow Creek and Wild Horse Basin during Phases 1 and 2. This simple, two-dimensional metric is useful for detecting change in the width of a migration route.

IDENTIFYING FUNCTIONAL ATTRIBUTES OF THE MIGRATORY LANDSCAPE

For temperate ungulates that migrate along elevation gradients, functional attributes of the migratory landscape can be generally characterized as either stopover habitat where animals spend most of their time, or the intervening movement corridors where animals travel quickly (Sawyer *et al.* 2009; Sawyer & Kauffman 2011). We defined migratory segments as either stopover habitat or movement corridors, although we note that future studies may use or reveal additional functional attributes, such as parturition sites (e.g. Singh *et al.* 2010; Barbknecht *et al.* 2011). Stopover sites were classified as the highest 25% quartile in the UD, whereas the 50–75% quartiles were considered movement corridors (Sawyer *et al.* 2009). At the individual level, we calculated the area of stopover habitat for each deer ($n = 43$) before and after development to assess whether this functional attribute was influenced by increased levels of development.

Results

IDENTIFYING THE POTENTIAL BARRIER

The Dry Cow Creek area was partially developed during Phase 1, with road and well pad densities of 0.56 km km^{-2} and 0.77 km^{-2} , respectively. However, by the spring of 2008 (Phase 2a), road and well pad densities increased to 1.07 km km^{-2} and 1.49 km^{-2} , respectively. Following construction in summer 2008 (Phase 2b), the road and well pad densities increased further to 1.92 km km^{-2} and 2.82 km^{-2} , respectively (Fig. 2). Compared to Dry Cow Creek, gas development in Wild Horse Basin was smaller in size and intensity. Road and well pad densities during Phase 1 were 0.83 km km^{-2} and 0.65 km^{-2} , respectively, and increased to 1.51 km km^{-2} and 1.86 km^{-2} during Phase 2 (Fig. 3).

CHANGES IN MIGRATORY BEHAVIOUR

At the individual level, movement rates of deer in the Dry Cow Creek development steadily increased from $1.06 \pm 0.26 \text{ km h}^{-1}$ (mean \pm SE) in Phase 1 to 1.68 ± 0.21 in Phase 2a, and 1.94 ± 0.18 in Phase 2b (Fig. 4). Movement rates in Phase 2b were higher than those observed in Phase 1 ($t_{11} = -2.68$, $P = 0.021$). Concurrently, movement rates of deer after they had moved through the development area steadily decreased from 1.25 ± 0.12 in Phase 1 to 0.79 ± 0.27 in Phase 2a, and 0.21 ± 0.05 in Phase 2b (Fig. 4). The rate of deer movement in undeveloped areas was lower in Phase 2b compared with Phase 1 ($t_{11} = 7.68$, $P < 0.001$). Of the 4 deer that collected data in both Phase 2a and 2b, three animals appeared to alter their routes in response to development by diverging from the previous year's path near the development boundary and then moving back to the path c. 3–4 km beyond the development (Fig. 5). Overall, the detours used by these animals bypassed approximately 8 km of their original migration route. At the population level, the intensity of deer use, as indicated by the UD volume, declined by 10% and 53% in Phases 2a and 2b, respectively (Fig. 6). The 53% decrease was statistically significant and coincided with road and well pad densities of 1.92 km km^{-2} and 2.82 km km^{-2} , respectively. Similarly, the surface area of migration routes in the Dry Cow Creek steadily decreased from 23.4 km^2 in Phase 1 to 21.5 km^2 in Phase 2a (-8%) and 15.4 km^2 in Phase 2b (-34%).

In contrast to the altered movement rates that followed development in the Dry Cow Creek, we did not detect any individual or population-level responses in the smaller and less concentrated development of Wild Horse Basin. Movement rates through the development area did not differ ($t_{17} = 0.56$, $P = 0.579$) between Phase 1 ($1.24 \pm 0.30 \text{ km}$

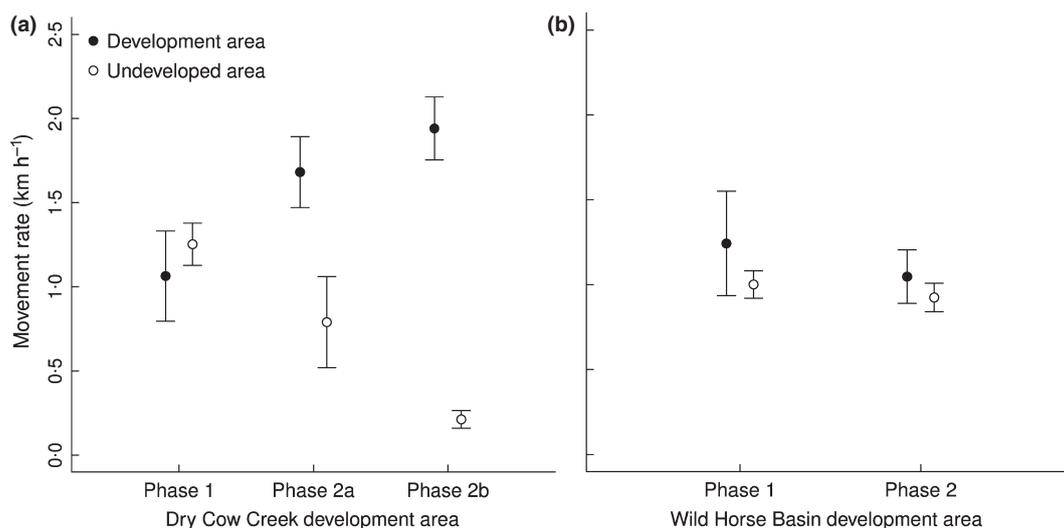


Fig. 4. (a) Movement rates (mean $\text{km h}^{-1} \pm \text{SE}$) of mule deer through the Dry Cow Creek development area during Phases 1, 2a and 2b. Movement rates through the developed area were higher during Phases 2a and 2b compared with Phase 1, whereas movement rates through undeveloped habitat decreased. (b) Movement rates of mule deer through the Wild Horse Basin development area during Phases 1 and 2. Movement rates through developed and undeveloped areas were similar in both phases.

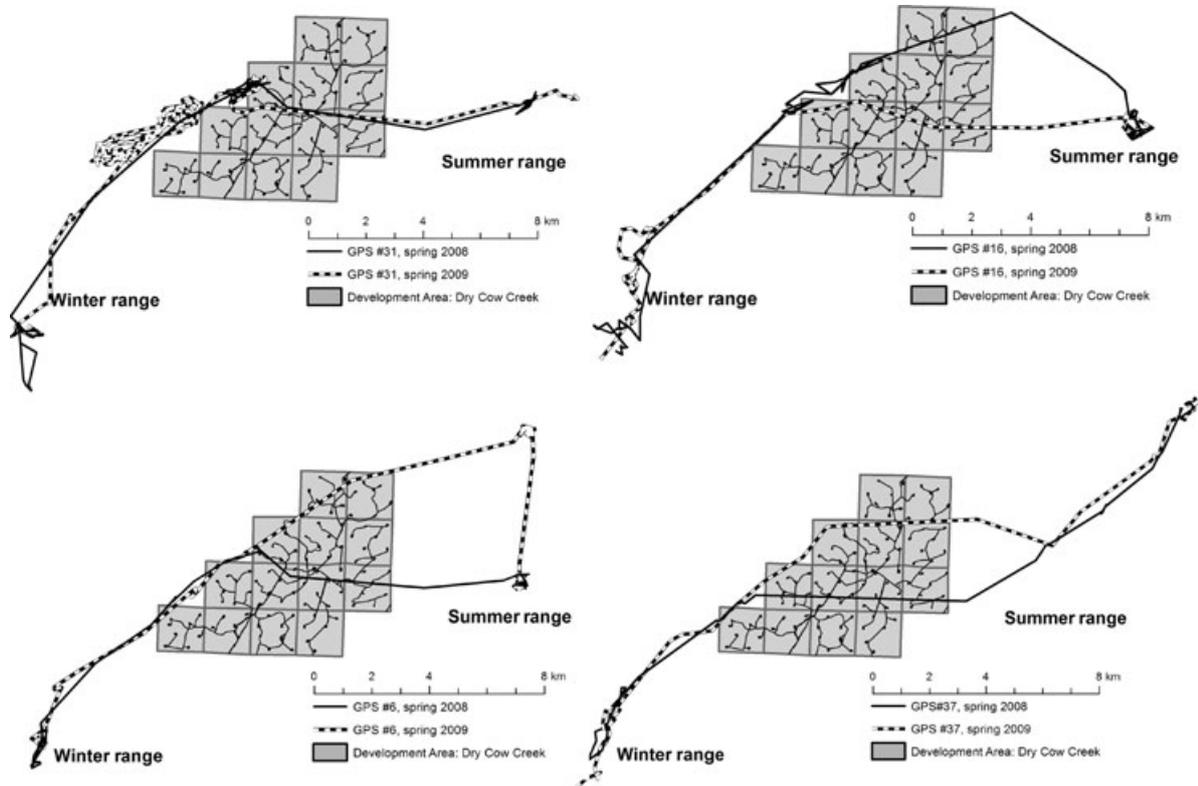


Fig. 5. Migration routes of four mule deer during Phase 2a and Phase 2b through the Dry Cow Creek development area. Deer #31 moved through the central portion of Dry Cow Creek in both Phases 2a and 2b, whereas Deer #16, #6 and #37 all show clear detours around or through different portions of the developed areas before and after development.

hr^{-1} ; mean \pm SE) and Phase 2 (1.05 ± 0.15 ; Fig. 4). Concurrently, movement rates outside of the development area also did not differ ($t_{17} = 0.66$, $P = 0.516$) between Phase 1 ($1.00 \pm 0.08 \text{ km hr}^{-1}$; mean \pm SE) and Phase 2 (0.92 ± 0.08 ; Fig. 4). At the population level, the intensity of deer use decreased by 23% in Phase 2, but was within the confidence intervals of the expected variance in deer use (Fig. 6). The surface area of migration route was similar between Phase 1 (10.9 km^2) and Phase 2 (12.1 km^2).

FUNCTIONAL ATTRIBUTES OF MIGRATORY LANDSCAPE

For individual deer migrating through Dry Cow Creek, the area of stopover habitat decreased as development increased, with an average of $1.63 \pm 0.43 \text{ km}^2$ (mean \pm SE) during Phase 1, $1.16 \pm 0.38 \text{ km}^2$ in Phase 2a and $0.66 \pm 0.19 \text{ km}^2$ in Phase 2b (Fig. 7). The area of stopover habitat used during Phase 2b was marginally lower than Phase 1 ($t_9 = 2.04$, $P = 0.07$). For individual deer migrating through Wild Horse Basin, the area of stopover habitat was similar ($t_{19} = -0.611$, $P = 0.548$) between Phase 1 ($1.30 \pm 0.34 \text{ km}^2$) and Phase 2 ($1.63 \pm 0.41 \text{ km}^2$; Fig. 7).

Discussion

Sustaining migratory ungulate populations in the face of widespread development and land-use change poses diffi-

cult conservation challenges across the globe (Bolger *et al.* 2008; Harris *et al.* 2009). Increased levels of development create a variety of barriers (e.g. roads, pipelines, fences) that are semi-permeable to ungulates; yet, we know little about how these types of barriers influence migratory behaviour or the persistence of migratory populations. We found that changes in migratory behaviour of two mule deer populations in western Wyoming varied with the size and intensity of semi-permeable barriers associated with gas development. In migration routes exposed to a larger, more concentrated development (i.e. Dry Cow Creek), mule deer use declined by 53% and movement rates nearly doubled ($1.06\text{--}1.94 \text{ km h}^{-1}$). The decline in deer use and accelerated movement rates reduced both the surface area of the migration route and area of stopover use. In contrast, we did not detect any changes in migratory behaviour through Wild Horse Basin, where the development area was smaller and infrastructure less concentrated. The intensity of deer use, surface area of the routes, movement rates of animals, and stopover use were similar before and after gas development. Presumably, the absence of any detectable response by migrating deer in this area was a function of permeability thresholds, due to either the lower level or smaller size of the development. Additionally, timing stipulations restricted development activities (i.e. drilling) in Wild Horse Basin between 1 November and 30 April – a time period that includes

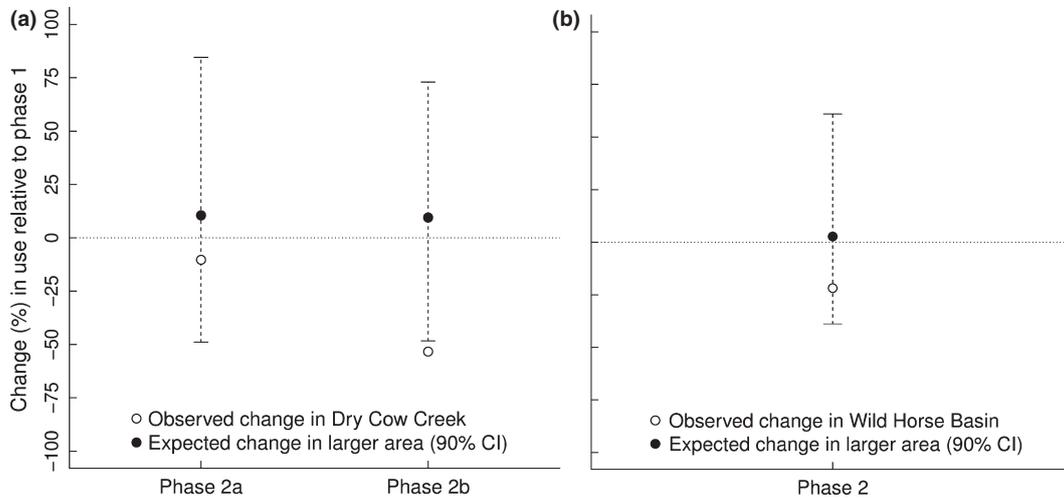


Fig. 6. (a) Change in population-level deer use in Dry Cow Creek development area during Phases 2a and 2b, relative to a larger 132-km² area and using Phase 1 as a reference level. (b) Change in population-level deer use in Wild Horse Basin development area during Phase 2, relative to a larger 54-km² area and using Phase 1 as a reference level.

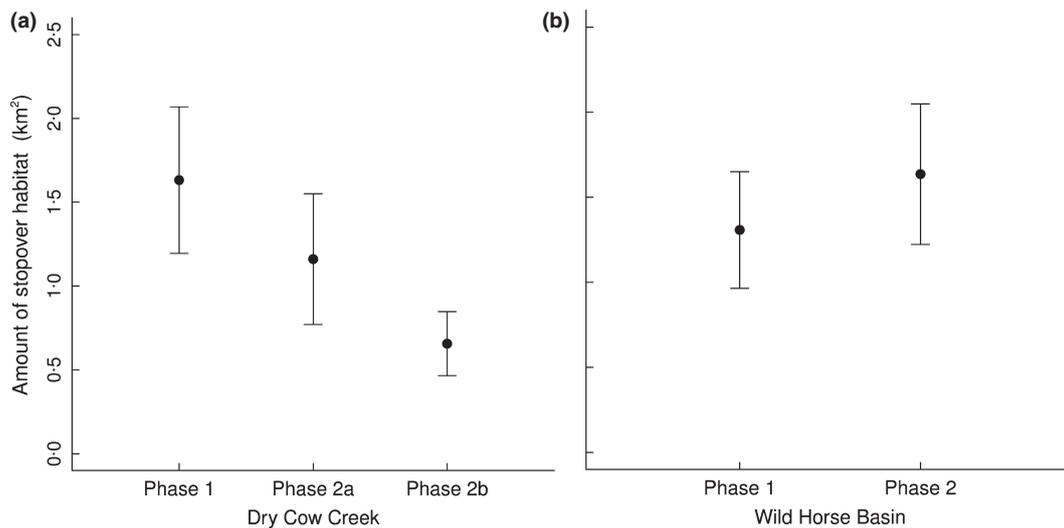


Fig. 7. (a) Area of stopover habitat (mean km² ± SE) used by mule deer in the Dry Cow Creek development area during Phases 1, 2a and 2b, and (b) Wild Horse Basin development area during Phases 1 and 2.

much of the spring and autumn migrations. Reducing traffic levels can reduce disturbance to mule deer (Sawyer, Kauffman & Nielson 2009), so these restrictions may have mitigated the potential barrier effects by minimizing disturbance to mule deer.

Our finding of individual and population-level responses to semi-permeable barriers makes clear that anthropogenic features can affect migration, even when connectivity between seasonal ranges is maintained. However, it is of interest whether these behavioural changes reduce the functionality of migration routes and ultimately, whether the functional loss could affect demography and persistence of migrants that use impacted routes. For example, stakeholders involved with this study have posed the question, 'Why does it matter if deer migrate more quickly through the development area?' Without a reasonable

answer to this question, agencies and industry are less motivated to modify, or attempt to mitigate, development plans that overlap with ungulate migration routes. Recent work suggests mule deer spend 95% of the migration period in stopovers, essentially using them to slow down their migration to exploit forage quality gradients created by phenological delays associated with elevation (Sawyer & Kauffman 2011). Our analyses suggest that development within a route can increase movement rates and alter migration route function by reducing stopover use. Although only 15% of the migration route in Dry Cow Creek was classified as stopover habitat, a 60% (1.63–0.66 km²) reduction in the size of these areas is concerning. Any behavioural change that impedes access to or discourages use of stopover habitat is likely to reduce the ability of animals to optimally forage and track vegetation

phenology. Whether such a functional loss has measurable demographic consequences is unknown, but given the importance of summer nutrition for body condition and reproduction (Cook *et al.* 2004; Parker, Barboza & Gillingham 2009; Tollefson *et al.* 2010), lost foraging opportunities during migration certainly have the potential to incur energetic and demographic costs. Further study, as has been done with avian taxa (e.g. Hoyer *et al.* 2012), is needed to link altered migratory behaviour by ungulates to fitness metrics (e.g. body condition, reproduction, survival).

Sawyer *et al.* (2009) suggest that semi-permeable barriers situated in movement corridors are less likely to impact migration route function than barriers in stopover areas, because animals do not rely on movement corridors as primary sources of forage. We caution, however, that changes in migratory behaviour within movement corridors have the potential to influence other, more subtle migration route functions. For example, it is possible that ungulates collect information on forage phenology while travelling through movement corridors to optimize the rate at which they access peak digestibility of forage (Sawyer & Kauffman 2011). Interestingly, our results suggest that when animals move more rapidly through developed areas, they tend to offset the quick movement by slowing down once they return to undeveloped habitat. This pattern is consistent with the hypothesis that increased movement rates create short-term phenological mismatches, and that animals attempt to correct for these mismatches by slowing down after moving through developed areas. Given the potential consequences of phenological mismatches (Post & Forchhammer 2008), this movement pattern warrants further research, especially in areas where development projects bisect long segments of migration routes. Of additional concern is that many migratory ungulates show high fidelity to migration routes (Berger, Cain & Berger 2006; Sawyer *et al.* 2009; Bunnefeld *et al.* 2011), and it is unknown how detours made along the route due to disturbance will influence movement rates and the ability of animals to track phenology. Certainly, when deer bypass 8 km of their traditional migration routes, like those in Dry Cow Creek, the functionality of that particular segment is effectively lost. Thus, there are a variety of mechanisms (i.e. increased movement rates and detouring) by which semi-permeable barriers may diminish the ability of migrants to track optimal forage conditions.

Most ungulate populations are partially migratory (Cagnacci *et al.* 2011; Hebblewhite & Merrill 2011), but the proportion of migratory animals is typically larger than the resident segment (Fryxell, Greever & Sinclair 1988; Bunnefeld *et al.* 2011). Our study was no exception, as only four of the 103 GPS-marked animals were resident. Recent studies suggest that the ratio of migratory to resident animals may shift when the benefits of migrating no longer exceed the benefits of a resident strategy (Hebblewhite & Merrill 2011). For example, elk populations have become increasingly resident in areas where

differential levels of predation on neonates and changes in habitat quality favour the resident strategy (Hebblewhite *et al.* 2006; Hebblewhite & Merrill 2011; Middleton *et al.* in press). Our work highlights the possibility that, like changes in predation or habitat quality, the effects of semi-permeable barriers on migration route function have the potential to reduce the benefits of migration and favour resident animals. Given that ungulate migrations generally occur along traditional routes that are learned and passed on from mother to young (McCullough 1985; Sweaner & Sandegren 1988; Nelson & Mech 1999), it may be difficult to restore migratory landscapes by removing barriers once migratory subpopulations have dwindled (but see Bartlam-Brooks, Bonyongo & Harris 2011). In general, ungulates that demonstrate strong fidelity to narrow, linear pathways (Berger, Cain & Berger 2006; Sawyer & Kauffman 2011) may be more vulnerable to barrier effects than those exhibiting more nomadic migratory patterns, such as wildebeest *Connochaetes taurinus* (Holdo, Holt & Fryxell 2009) and Mongolian gazelles *Procapra gutturosa* (Mueller *et al.* 2011). However, in contrast to populations that follow distinct migration routes, mitigating the potential effects of semi-permeable barriers for nomadic populations will be difficult because of their unpredictable movements across the landscape (Mueller *et al.* 2011).

Ideally, our study would have followed the same animals through the entire study period, such that changes in individual movements could be more closely examined. For example, the 4 animals that collected data during two phases revealed that increased levels of development may lead to individual animals detouring and bypassing entire segments of their traditional routes. Other work has found that increased levels of human disturbance may interact with environmental conditions to discourage older individuals from migrating (Singh *et al.* 2012). Thus, we suspect that evaluating individual movements through time would provide more insight into the mechanistic drivers of the behavioural changes we observed and reduce the amount of variation in the metrics of interest. For future studies, we recommend the same animals be marked through the entire study period so that individual and population-level movement patterns can be examined in more detail. Also critical to detecting changes in behaviour is the collection of baseline data before intensive development. In our case, had state and federal agencies not required both pre- and post-development study phases, changes in migratory behaviour would have gone undocumented.

CONCLUSIONS AND RECOMMENDATIONS

Managing migratory ungulates is especially difficult because of the long distances they move, often across a mix of land ownership and land-use practices. As energy development and other human disturbances expand, it is increasingly important to understand how migrating

ungulates respond to the semi-permeable barriers. Our study suggests that increased levels of gas development in migration routes may encourage detouring, increase movement rates, reduce the area of stopover use by individuals and reduce the overall amount of deer use and constrict the size of migration routes at the population level. The existence of such behavioural changes suggests that certain levels of development, while still allowing connectivity between seasonal ranges, may nevertheless reduce route functionality and the benefits of migration. Ultimately, demographic costs associated with barriers are the most desirable currency in which to measure the effects of development on migratory ungulates. In the absence of such data, quantifying behavioural changes and functional attributes of the migratory landscape before and after development provides an intuitive first step for understanding the consequences of semi-permeable barriers for the persistence of migratory ungulates.

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