Beyond protected areas: Private lands and public policy anchor intact pathways for multi-species wildlife migration

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ABSTRACT

Migration is a critical strategy in maintaining populations, and pathways used by individuals lend insight into habitat quality and connectivity. Yet sustaining migration among large-ranging wildlife poses a challenge for conservation, particularly among landscapes that include a diverse matrix of land tenure. Such is the case in the Northern Great Plains (NGP), a sagebrush (*Artemisia* spp.) steppe and grassland ecosystem that is home to the longest-ever recorded migrations by both pronghorn (*Antilocapra americana*) and greater sage-grouse (*Centrocercus urophasianus*). Here, we identify migratory pathways for both species, and measure the ability of current conservation and policy to maintain cross-taxa migration in the face of continued cultivation. Migratory behavior was similar between species in their timing and duration of migration, and in their use of stopovers along the way. Large and intact private and public working lands largely underpinned migratory pathways, whereas protected areas provided another 5% of habitats. Most pathways for sage-grouse were within state- and federally-designated sage-grouse Core Areas, which contain regulatory caps on anthropogenic disturbance on public lands and help guide conservation efforts; these benefits extended to over half of pathways used by pronghorn. Among private lands, both species largely migrated through intact grazing lands, including many that were already perpetually protected from cultivation with conservation easements. Optimization of remaining private parcels provides managers with a spatial tool to prioritize private-lands conservation, and suggests that comprehensive conservation of shared migratory pathways for pronghorn and sage-grouse in the NGP is within reach of completion given the ongoing pace of conservation.

1. Introduction

Migratory species are critical in shaping biodiversity and ecosystem function, and are key indicators of habitat connectivity for themselves and other species (Bauer and Hoye, 2014; Dingle, 2014; Sinclair et al., 2015). Yet sustaining migratory behavior among wide-ranging terrestrial species poses one of the greatest challenges to wildlife conservation globally (Bowlin et al., 2010; Dingle, 2014). The scale of migratory pathways often eclipses the footprint of seasonal home ranges, as populations traverse landscapes that may transcend jurisdictional, and even international boundaries. When these movements transcend ownership boundaries, the ability of conventional protected areas (e.g., national parks) to conserve migratory pathways is wholly inadequate

(Berger, 2004; Bauer and Hoye, 2014; Newmark, 1987). Rather, an all-lands approach that includes publically-protected areas and privately-owned working lands provides the greatest opportunity for migratory populations to persist.

Migrations are particularly vulnerable among grasslands systems, the biome with the greatest disparity between land area conserved versus that lost to development (Hoekstra et al., 2005). The Northern Great Plains of North America is a globally important temperate grassland and shrubland system, providing a migratory stage for multiple taxa including mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse). Pronghorn are endemic and iconic to shrubland and grassland habitats of western North America, whose

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migratory movements have been increasingly recognized as central to large-scale, cross-jurisdictional conservation (Berger et al., 2006). Particularly well known is the 'Path of the Pronghorn', where pronghorn migrate 116–258 km between breeding range in Grand Teton National Park and federally managed and privately-owned winter range in Sublette County Wyoming, USA (Sawyer et al., 2005). To date, this pathway has received > $10M USD investments in conservation across state, federal and NGO entities (Berger and Cain, 2014). Based in part on this work, there is growing awareness of the conservation value of pronghorn migration corridors across their range in North America. Although Wyoming may harbor the most well-known route, new findings show migratory populations in the Northern Great Plains moving up to 2.6 times farther (> 400-km each way) between Canada and Montana to optimize forage intake and to escape deep northern snows (Jakes et al., 2018).

Whether terrestrial mammalian and avian corridors confer protection to one another remains an open question for conservation. The Northern Great Plains provides a model system for investigating multi-species conservation as this landscape also boasts the longest migratory movements of a sagebrush (*Artemisia* spp.) obligate, the sage-grouse. Here, sage-grouse undertake annual obligate migrations farther than any other galliform (> 120 km one way; Fedy et al., 2012; Newton et al., 2017) as they move in stepping-stone fashion (Dingle, 2014) along their migratory pathways (Newton et al., 2017). With delineated migrations of individual species' in hand, this landscape can now help conservationists understand whether migratory behaviors and pathways are shared across taxa, and if conservation of migration for one species confers protections for other migratory species. Resulting science is paramount to formulating a strategy to conserve multi-species pathways for migration and sustain functional connectivity within an ecosystem.

These longest observed migrations by both pronghorn and sage-grouse suggest that the Northern Great Plains still retains functional ecosystem processes. However, the persistence of both species is linked to risk of future land use change within a matrix of native and human-modified habitats. Cropland conversion is the greatest source of habitat loss and fragmentation in the Northern Great Plains (Samson et al., 2004). While pockets have been spared from cultivation, the extent of irrigated and dryland crops continue to expand into more marginally-productive lands (Lark et al., 2015; Wright and Wimberly, 2013). Migratory populations of both sage-grouse (Newton et al., 2017) and pronghorn (Christie et al., 2017; Jakes, 2015) in the Northern Great Plains have demonstrated avoidance of cultivated lands. Furthermore, agricultural expansion remains a leading cause of population declines and local extinctions among migratory ungulates (Bolger et al., 2008), and is implicated as the primary driver of sage-grouse extirpation in the Northern Great Plains (Aldridge et al., 2008). A secondary threat to migration is human infrastructure, particularly that arising from energy development and transportation which includes networks of roads, transmission lines, fences, and oil and gas wells that further impede ungulate migration (Jakes, 2015; Lendrum et al., 2013, 2012).

Using science to first identify migratory pathways for each species and then examine whether multi-species corridor conservation is possible is a critical need among terrestrial species (Runge et al., 2014; Sawyer et al., 2009). The well-known migratory movements of the Serengeti wildebeest (Thirgood et al., 2004) are 95% contained in one of the largest protected area networks in the world, automatically conferring protection on the entire population of migratory individuals. However, similar to the rest of terrestrial landscapes, the Northern Great Plains is a patchwork of mostly private working lands and public lands of multiple-use along with an intermittent network of protected areas. Thus, developing a rationale and framework for maintaining multi-species, cross-guild migrations in perpetuity among these shared tenure landscapes remains a critical conservation challenge. Breakthroughs in quantitative tools used to identify migratory pathways (Horne et al., 2007) and in modeling frameworks to guide policy and management (Runge et al., 2014) can help address these multiple challenges. Identifying which specific lands, a mix of private, public, and even potential improvements to protected area networks provides practitioners with concrete guidance for protecting single-species migration corridors (Berger and Cain, 2014).

Here we characterize multi-species connectivity and conservation between migratory pronghorn and sage-grouse in the Northern Great Plains. Specifically, we measure the extent of current conservation and policy in maintaining cross-taxa migration, and use estimated migratory pathways to prioritize future private-lands conservation measures. First, we identify individual pathways for use as a currency in migratory analyses by fitting Brownian Bridge movement models (BBMM; Horne et al., 2007) to Global Positioning System (GPS) remote tracking data from migratory pronghorn and sage-grouse. Second, we use migratory pathways to characterize spatial and temporal overlap between taxa to identify the extent of multi-species conservation opportunities. Third, we tested for the multi-species benefits of U.S. policy protections for sage-grouse to conserve pronghorn pathways. Lastly, we combine this knowledge in light of the anticipated risk of private lands to cultivation (Smith et al., 2016) within a prioritization framework to develop a tool for practitioners to conserve this large-scale, multi-species migratory landscape, which may become increasingly important at the edges of these species ranges.

2. Materials and methods

2.1. Study area

Our study took place in a portion of the Northern Great Plains ecoregion colloquially termed the "Hi-Line," an ecotone where sagebrush steppe gives way to mixed-grass prairie along the Milk River Basin in Montana and Saskatchewan (Fig. 1). Climate is cool temperate, with mean temperatures of 21.3 °C during summer and −11.8 °C in winter, with ~30-cm of annual precipitation and 86-cm of snowfall (Glasgow, Montana, USA, National Weather Service Station). This region was characterized by largely native mixed-grass prairie and sagebrush-steppe, with dominant cool-season grasses including rhizomatous wheatgrasses (e.g. *Pascopyrum smithii*), needlegrass (*Stipa* spp.), and Sandberg's bluegrass (*Poa secunda*). Breeding and summer ranges for both species within our sample occurred north of the Milk River, which is the northeastern most range for both sage-grouse (Schroeder et al., 2004) and pronghorn (Yoakum, 2004). Summer ranges are defined by a matrix of cultivated lands and temperate grasslands of aforementioned grass species interspersed with sparse stands of silver sagebrush (*Artemisia cana*). Winter ranges for sage-grouse occurred among dominant stands of Wyoming big sagebrush (*A. tridentata wyomingensis*) south of the Milk River, where expansive shrubland flats are interrupted by rugged breaks along the Missouri River. Pronghorn typically remain north of the Milk River but will occasionally winter in areas similar to sage-grouse.

Land tenure was comprised of a mix of privately-owned lands (55%), public lands (40%), and protected areas (5%). Approximately half (52%) of private lands are large, intact ranches that provide native sagebrush grasslands, of which approximately 5% are under a conservation easement. Conservation easements in this landscape are primarily administered by the Nature Conservancy (TNC; 37%), US Fish and Wildlife Service (FWS; 34%), and Montana Fish, Wildlife, and Parks (19%), and perpetually prohibit uses that destroy or degrade habitat, while allowing for compatible economic uses, including livestock grazing. Remaining private lands are utilized for production of annual crops, typically winter or spring wheat. Reducing conversion of sagebrush steppe to cropland is a primary focus for conservation, such that scientists developed a tool to spatially identify cultivation risk within Montana to target future conservation efforts (Smith et al., 2016); no such products are available for Canada. Public lands cannot be cultivated; rather, most are under a multiple-use mandate with cattle
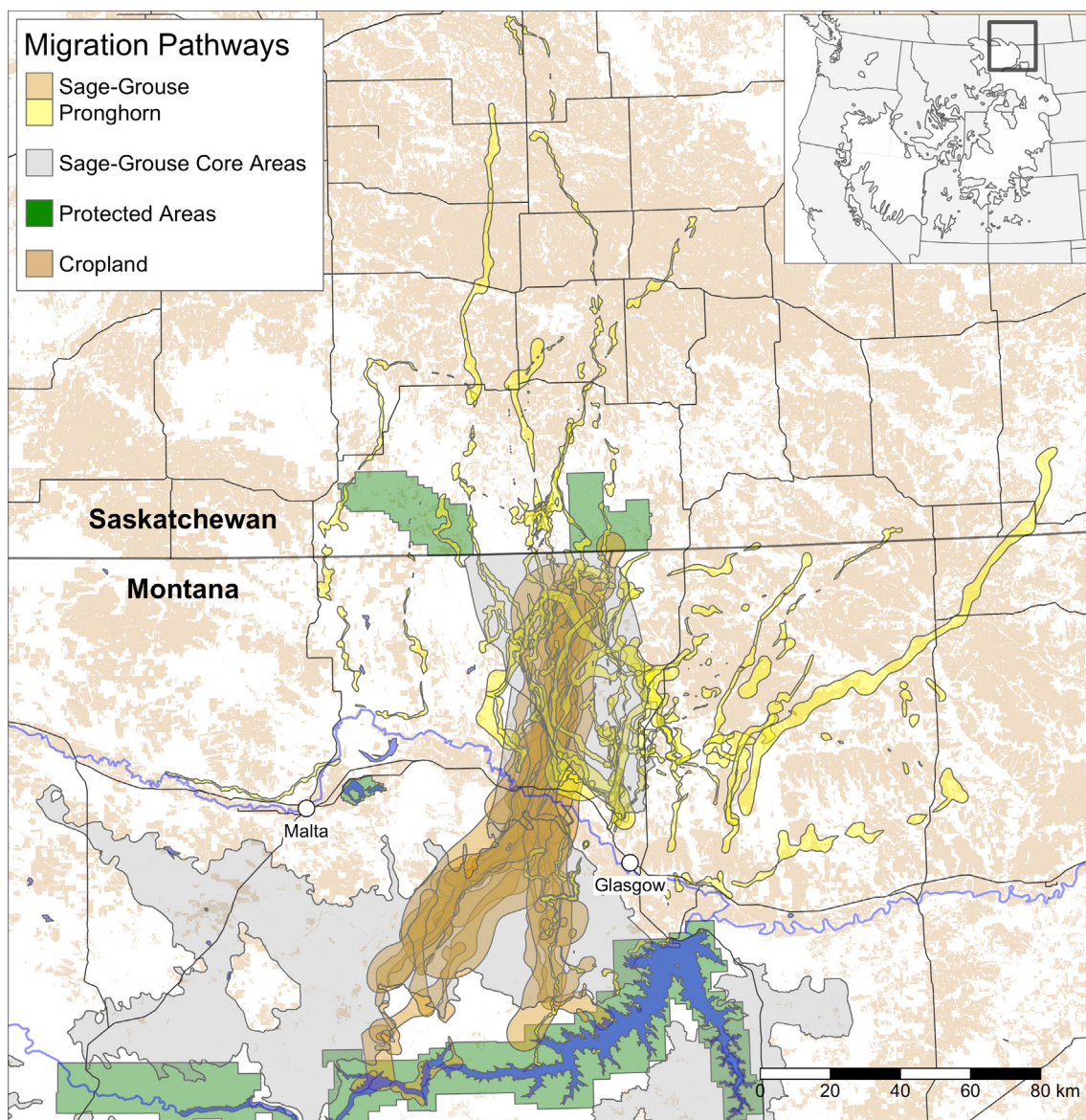
Fig. 1. Individual migratory pathways for both sage-grouse (*Centrocercus urophasianus*) and pronghorn (*Antilocapra americana*) in the Northern Great Plains, Montana, USA, and Saskatchewan, Canada. Migration took place across a network of protected areas, cropland, and sage-grouse Core Areas. Inset displays study area within occupied range of sage-grouse (Schroeder et al., 2004). Migratory pathways were calculated as 95% isopleths from utilization distributions estimated using Brownian bridge movement models, and were fit separately for each spring and autumn migration period, as well as for facultative winter migrations.

grazing as the primary land use. Protected areas with a wildlife emphasis include Grasslands National Park of Canada (GNP), FWS National Wildlife Refuge (Bowdoin and Charles M Russell [CMR]) and Waterfowl Production Areas, the American Prairie Reserve (APR; www.americanprairie.org), and a TNC 'grass bank,' which provided ranchers with discounted grazing leases in exchange for conservation measures on their private lands.

The study area also encompassed three Montana sage-grouse Core Areas (hereafter core areas; Montana Executive Order No. 12-2015), which includes Montana's only Connectivity core area with the intent to maintain sage-grouse migratory movements between Saskatchewan and Montana. This executive order also established a 10M USD stewardship fund to support conservation easements and other projects for sage-grouse, primarily within core areas (https://sagegrouse.mt.gov/). The two non-connectivity core areas in this landscape were subsequently adopted as US Federal Priority Areas for Conservation (PACs) for sage-grouse by the FWS (U.S. Fish and Wildlife Service, 2013). Generally, core areas were identified by both FWS and states as

landscapes necessary for the long-term persistence of sage-grouse. Core areas include regulatory stipulations on public lands, including limited surface disturbance from energy development and also guide practitioners on where to invest in conservation actions such as conservation easements that alleviate threats of development (e.g. cultivation or subdivision) to sage-grouse populations (Copeland et al., 2014).

2.2. Sage-grouse and pronghorn migratory data

Eighteen sage-grouse males and females were captured from 2010 to 2011 on communal breeding grounds (leks) during the March–April breeding season, and again in early autumn (September–October) once juveniles had grown large enough to be affixed with tracking technology. Birds were fitted with backpack-style GPS transmitters (North Star Science and Technology, King George, VA, USA). Solar-powered transmitters collected locations every 6-h (i.e. 4 locations per day). Pronghorn females were captured on their wintering grounds north of the Milk River, near Glasgow, MT, USA from 2009 to 2010. In total, 40

pronghorn females were fitted with necklace-style GPS transmitters, programmed to collect locations every 2 or 4 h (Lotek Wireless, Newmarket, Ontario, Canada). Fix-rates for both species were high (> 95%), obviating the need to accommodate habitat-induced bias (Frair et al., 2010). All trapping and data collection were conducted under approval of the University of Montana Institutional Animal Care and Use Committee (IACUC; 065-09DNWB-010810) for sage-grouse, and by Montana Fish, Wildlife, and Parks and the Saskatchewan Ministry of Environment for pronghorn (IACUC 11-2007).

Because our primary interest was to describe and prioritize conservation for migration among sage-grouse and pronghorn, we subset datasets for both species to include only those individuals that migrated, and locations that occurred during migration. Sage-grouse from this population undertake annual obligate migration between breeding and wintering grounds (Newton et al., 2017; Tack et al., 2012), whereas pronghorn were from a partially migratory population in which 55% exhibited seasonal migrations (Jakes et al., 2018). All marked sage-grouse undertook additional facultative winter migrations, defined as migration from one winter range to another in response to extreme environmental events (Dingle and Drake, 2007; Jakes et al., 2018), from their typical winter ranges further southward toward CMR during a winter with record setting snowfall in 2010–2011 (Newton et al., 2017). Similarly, 34% of migratory pronghorn and 20% of resident pronghorn made facultative winter migrations (Jakes et al., 2018). We used migratory data from seasonal and facultative winter migrations for both species, though omitted migratory data from post-fawning migration exhibited by pronghorn (n = 6; Jakes et al., 2018) as there was no comparable behavior by sage-grouse.

We identified migratory movements of both species using net-squared displacement (NSD), calculated as the distance between the point of capture and all successive locations (Bunnefeld et al., 2011). Nonlinear models were fit to sage-grouse NSD measurements, and parameter estimates associated with the onset and cessation of migration were used to delineate migratory movements (Newton et al., 2017). For pronghorn, comparative thresholds among NSD measurements were used to identify first if and when individuals made migratory movements (Jakes et al., 2018).

2.3. Estimating migratory pathways

Migratory pathways were previously identified for sage-grouse, represented as 95% isopleths from utilization distributions (UD) estimated by BBMM (Horne et al., 2007) fit to data from spring, autumn, and winter migration data among individuals (Newton et al., 2017). We applied the same analytical approach of Newton et al. (2017) to pronghorn, by fitting BBMM to location data from each individual's spring, autumn, and facultative winter migrations, using an estimated location error of 20-m. In cases where there were missed fixes that exceeded 12-h, we split the dataset and fit separate BBMM to meet the assumption of random movement between successive locations (Horne et al., 2007). However, this was rarely an issue because overall fix rate for pronghorn was > 98% (Jakes et al., 2018). We estimated distinct UD and resulting isopleths using data from each individual's seasonal or winter migration, which we define as an "individual-level" pathway. We also report estimates of Brownian motion variance (BMV) for each species and season, which provides a measure of uncertainty in estimating pathways (Horne et al., 2007). For each species, we merged all individual-level pathways into one combined pathway representing the complete footprint of all 95% isopleths estimated for each sage-grouse and pronghorn.

2.4. Assessing efficacy of targeted policy

We calculated the proportion of individual-level pathways from each species that were encompassed by sage-grouse core areas. Because we were also interested in the conservation benefit added from Montana's connectivity core area developed specifically for this population, we calculated overlap separately for this area. Current core area policy has specific caps on surface disturbance (5%), restricts disturbing activities during critical sage-grouse breeding seasons (March 15–July 15), and helps target additional conservation measures for sage-grouse (e.g. conservation easements). Future efforts may seek to limit disturbance during peak migration periods. Therefore, we calculated frequency of dates among locations associated with pronghorn and sage-grouse migration to assess temporal overlap between species.

2.5. Characterizing land tenure among pathways

To characterize land tenure across migratory pathways, we summarized ownership underlying individual and combined pathways as protected areas (GNP, USFWS NWR, TNC, and APR); public lands including US federal lands which mostly included Bureau of Land Management (BLM; 99%), State of Montana and Saskatchewan Provincial lands (i.e. Crown lands); and private lands classified as either intact grasslands, those under perpetual conservation easements, or cultivated. We used data from the US Public Land Survey System (www.cadastral.mt.gov; accessed 21 July 2018), and from the Canada Lands Survey (http://www.nrcan.gc.ca; accessed 21 July 2018) to determine ownership and size of cadastral boundaries (hereafter 'parcels').

2.6. Spatial tool for prioritizing conservation easements

We sought to provide practitioners a spatial tool to prioritize private lands for conservation easements in light of anticipated cropland expansion. Within the purview of conservation triage, which allocates resources to areas with both the greatest biological value and risk (Hobbs and Kristjanson, 2003), the most beneficial land prioritization scheme would rank intact private parcels such that those at the highest risk to conversion to cropland and most important for migration would be prioritized first for conservation. To develop such a tool, we used a systematic conservation planning (SCP; Margules and Pressey, 2000) approach with integer linear programming (ILP) to identify areas for targeted conservation (Beyer et al., 2016). Specifically, we developed a suite of minimum set problems, which within the context of conservation planning, uses an algorithm to identify optimal (or near optimal) coverage for a user-defined amount of spatially-explicit conservation features among a set of planning units, while minimizing the cost associated for conserving planning units implicated in a solution (Ball et al., 2009). While SCP is typically used in reserve design applications, it can be a useful tool for prioritizing areas for targeted conservation (Reinhardt et al., 2017).

We used land ownership parcel boundaries (hereafter "parcels", mean = 107 ha, SD = 84.5 ha) as planning units for analyses (http://svc.mt.gov/msl/mtcadastral/; accessed 9 July 2018). Because our goal was to prioritize for conservation lands at risk to cultivation, we treated parcels that were publicly owned, under protected area status, or privately owned yet already under perpetual conservation easement as "fixed" into any conservation solution across minimum set problems, as we assumed these parcels were not vulnerable to being converted to cropland. Conversely, we excluded already cultivated private lands from being selected among solutions, as our intent was not to implicate costly restoration practices in a landscape where migration across taxa is currently functional. Because we were primarily interested in identifying for conservation landscapes shared by both species, we summarized the sum individual UD values for sage-grouse and pronghorn, and created a new surface as the product of summed UDs for both species. We set proportional optimization targets ranging from 0.5 to 0.9, by increments of 0.05, for each conservation feature, which allowed us to identify a hierarchy of the best available parcels for conserving migration when targeting future easements and other conservation measures. Finally, we calculated the cost associated with conserving each parcel as the inverse mean value of cultivation

probability. Using the inverse mean of cultivation probability treated parcels with the highest probability of cultivation as having the lowest cost, therefore being implicated among solutions. Minimum set conservation problems have typically been solved using a heuristic approach (e.g. simulated annealing) with Marxan (Ball et al., 2009), though we used ILP to solve conservation planning problems as it provided more efficient and higher quality (i.e. near-optimal) solutions (Beyer et al., 2016). We implemented conservation planning problems using the prioritizR package in program R (https://github.com/prioritizr) implemented with the Gurobi optimization solver (Gurobi Optimization, Inc, 2016).

3. Results

We used 30 individual pathways derived from BBMM estimated for 18 individual sage-grouse, previously developed by Newton et al. (2017), which consisted of 5 spring, 18 autumn, and 7 winter migration pathways (Fig. 1). Of the 40 captured pronghorn, 23 made at least one migration between 2009 and 2010, allowing us to fit a total of 47 individual BBMM including for 19 spring, 16 autumn, and 12 facultative winter migrations (Fig. 1). Some seasonal migrations among pronghorn (22%) included at least one stopover, particularly during spring migration (Jakes et al., 2018), whereas all sage-grouse made at least one stopover (range 1–16) across seasonal migrations (Newton et al., 2017). Mean BMV combined across seasons was higher for sage-grouse (41,357) than pronghorn (6787; Supplemental table), which resulted in larger estimated pathways for greater sage-grouse. Wider pathways led to larger areas encompassed by sage-grouse among species-specific mapping exercises, due to greater uncertainty likely arising from longer re-locations intervals (i.e., fewer location) to estimate pathways.

Peak dates of migration across individuals were similar for pronghorn and sage-grouse during spring (7 April for sage-grouse; 6 April for pronghorn), autumn (15 November for sage-grouse; 18 November for pronghorn) and facultative winter migrations (10 January for sage-grouse; 2 January for pronghorn; Fig. 2). Individual sage-grouse took an average of 18, 14, and 12 days to complete spring, autumn, and facultative winter migrations, respectively; which was within at least 3 days of the mean migration durations of 20, 11, and 10 days for spring, autumn, and facultative winter migrations by pronghorn (Jakes et al., 2018). However, variation in timing of migration across individuals was greater for pronghorn than sage-grouse across all migratory seasons (Fig. 2).

Individual migratory pathways of sage-grouse in the USA largely fell within state and federally protected landscapes, with at least half of all but two pathways encompassed by core areas (Fig. 3). Furthermore, Montana's only connectivity core area provided on average an additional 19% coverage (range 0–66%) to individual sage-grouse pathways (Fig. 3). Seven of the nine individual pathways that had at least 10% of their area outside of core areas were from facultative winter migrations (Fig. 3). Pronghorn also benefited from sage-grouse core areas covering portions of two-thirds of pronghorn pathways, including 8 pathways that were completely encompassed by core areas (Fig. 3).

Most of the combined pathways for sage-grouse (89%) and pronghorn (59%) were composed by BLM and private lands, while protected areas encompassed < 5% of pathways for both species (Table 1). Tenure underlying individual-level pathways revealed variation in use by individual and season for both species (Fig. 4). Sage-grouse pathways were largely intact, with cultivation only composing on average 5% of individual pathways (range 0–16%), compared to an average of 18% for pronghorn (range 0–77%). Conservation easements encompassed upwards of 15% of individual sage-grouse seasonal pathways (mean 4%; Fig. 4), whereas protected areas provided upwards of 46% coverage for sage-grouse facultative winter migrations, as birds migrated to lands on CMR. Use of conservation easements was also prevalent in pronghorn pathways across seasons, and protected area use was most evident during facultative winter migrations as pronghorn traversed Bowdoin and CMR National Wildlife Refuges (Figs. 1, 4).

The average cultivation probability among private lands within our study area was 0.52, while private lands that were cultivated had a mean cultivation probability of 0.71, compared to 0.39 among uncultivated lands. Optimizing private lands conservation to encompass migratory overlap between sage-grouse and pronghorn found solutions implicating 70 to 90% of conservation features, demonstrating that at least 65% of overlapping migratory features were already within public lands, private lands under easement, and protected areas. Solutions capturing 70%, 75%, 80%, 85%, and 90% of overlapping areas encompassed 1310, 5368, 6978, 10,625, and 17,506-ha of private lands. Map outputs of results provide practitioners with a guide for future easements, which are largely aggregated around public lands and existing conservation easements near the Milk River (Fig. 5).
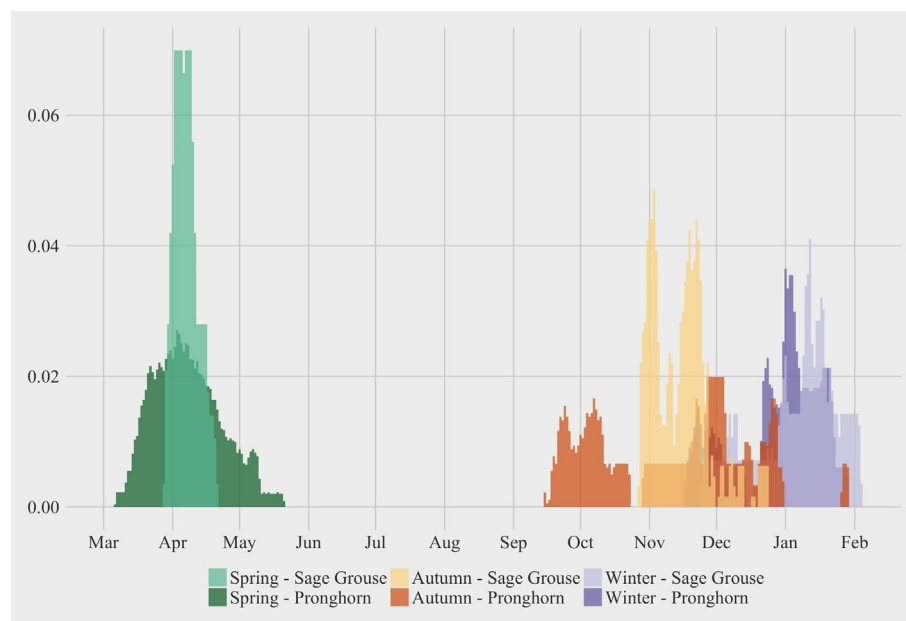

Fig. 2. Density of migration locations for sage-grouse (*Centrocercus urophasianus*) and pronghorn (*Antilocapra americana*) during spring, autumn, and facultative winter migratory events. Peak migration date was similar between species across all seasons, though pronghorn migration across individuals typically lasted longer than that of sage grouse.
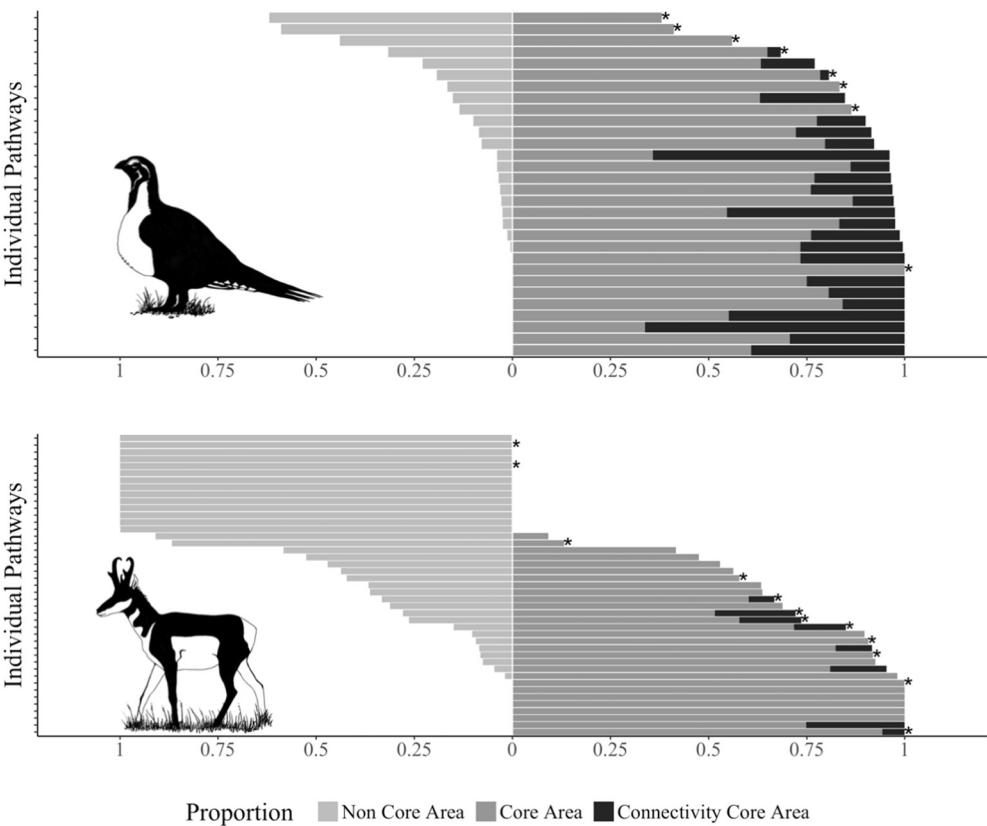
Fig. 3. Proportion of individual pathways for sage-grouse (top; *Centrocercus urophasianus*) and pronghorn (bottom; *Antilocapra americana*) within (right) and outside (left) of Montana's Sage Grouse Core Areas. Core Areas include two areas targeted for breeding populations (dark gray), and a third designated specifically for connectivity (black). Asterisks denote pathways for facultative winter migrations.

Table 1
Proportion land tenure (and area in ha) among combined migratory pathways for sage-grouse (*Centrocercus urophasianus*) and pronghorn (*Antilocapra americana*) identified as US Bureau of Land Management (BLM), private lands (for both USA and CAN), Montana State lands, Saskatchewan Provincial lands, and protected areas including US Fish and Wildlife Service National Wildlife Refuges, Grasslands National Park of Canada, and the American Prairie Reserve. Other federal lands (e.g., US Department of Defense) which made up < 1% of pathways are not listed.

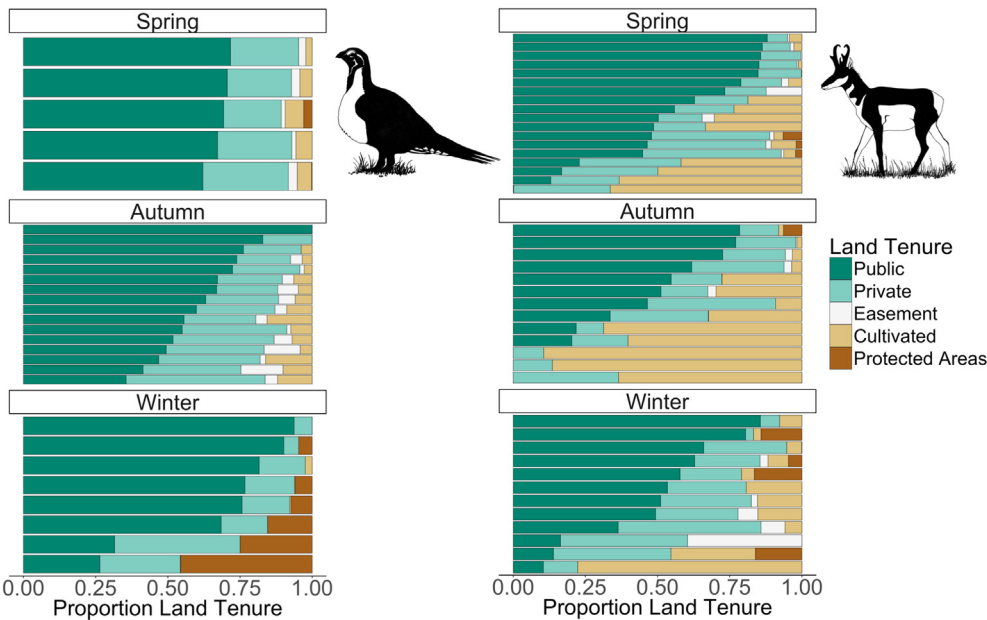| Species	BLM	Private (USA)	Private (CAN)	State (MT)	Provincial (SK)	Tribal	Protected areas
Sage-grouse	0.61 (259,877)	0.28 (119,972)	0.00	0.06 (27,338)	0.00	0.00	0.05 (20,001)
Pronghorn	0.22 (91,327)	0.37 (150,346)	0.14 (56,172)	0.10 (38,921)	0.06 (25,647)	0.09 (36,413)	0.02 (9763)

Fig. 4. Percent land tenure among individual migration pathways for sage-grouse (left; *Centrocercus urophasianus*) and pronghorn (right; *Antilocapra americana*) during autumn, spring, and facultative winter migrations. Publicly tenured lands under US Federal, state and provincial ownership, encompassed the majority of pathways followed by private lands; which were defined as either intact grassland and sagebrush steppe (Private), cultivated, or under perpetual conservation easement (Easement). Protected areas included Grasslands National Park of Canada, Charles M. Russell and Bowdoin National Wildlife Refuges, and lands owned by the American Prairie Reserve and Nature Conservancy.
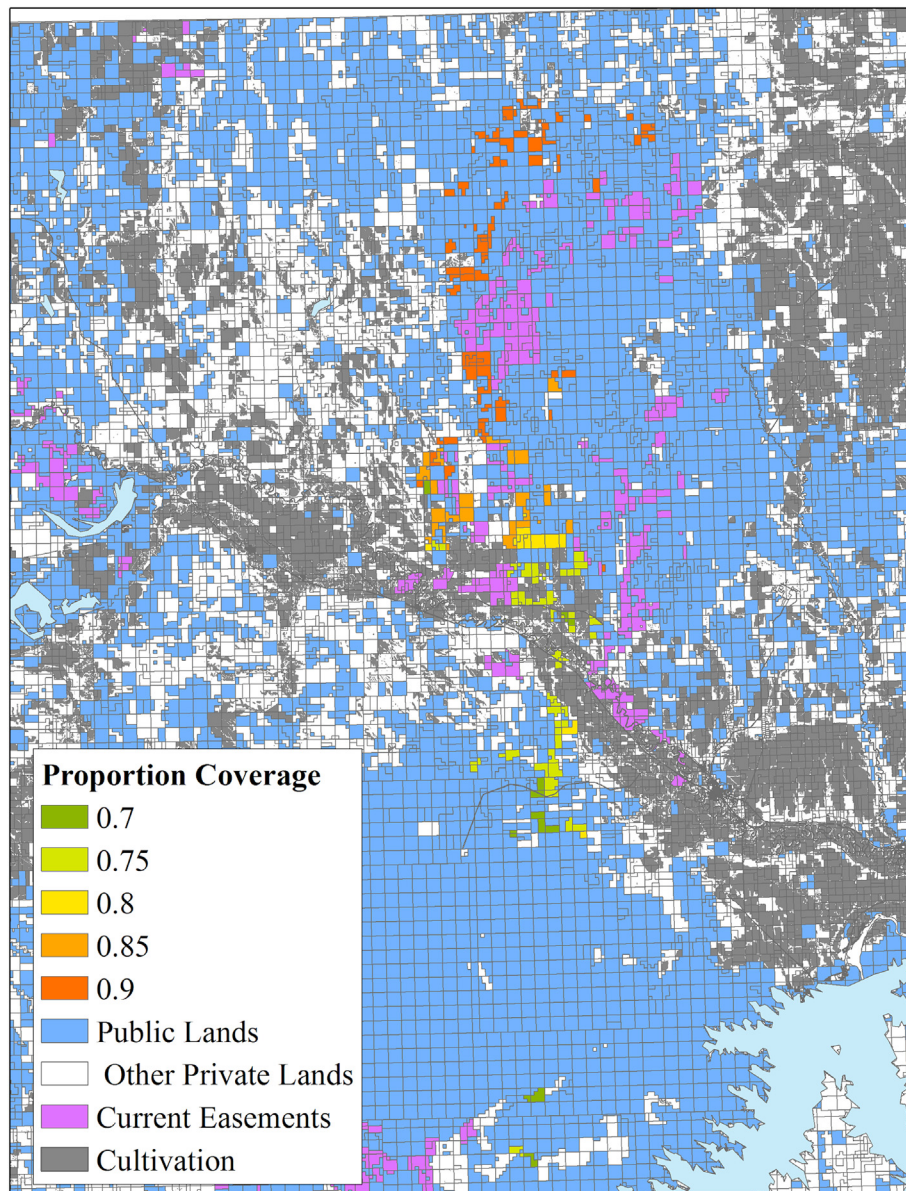
Fig. 5. Map displays optimal solutions to target conservation easements on private lands while conserving 70%–90% of migratory pathways for both sage-grouse and pronghorn in northern Phillips and Valley counties, Montana. Intact parcels were selected based on increasing coverage of migratory pathways while targeting those with the highest probability of cultivation (Smith et al., 2016). The smallest solution (70%) totaled 1417-ha, while 90% coverage of pathways required 17,980-ha of private lands.

4. Discussion

Estimating and mapping migration for sage-grouse and pronghorn revealed spatial overlap in pathways between divergent taxa, as well as similar behavior in speed, duration, and stopover frequency during migration (Jakes et al., 2018; Newton et al., 2017). Sage-grouse pathways coalesced to form an integrated pathway among intact grassland and sagebrush steppe between breeding grounds as far north as GNP, travelling toward CMR during winter. Whereas pronghorn demonstrated a greater diversity in individual migratory pathways than sage-grouse as they used a diffuse network of breeding grounds at the northern portion of their range. Shared space use during migration is likely explained by a propensity for intact grasslands and sagebrush steppe, which underlain largely privately-owned rangelands and multiple-use federal lands with targeted sage-grouse conservation policy. Environmental cues such as the onset and senescence of herbaceous growth may explain concurrent timing of migration, as peak autumn

and spring migration for both species were within three days of each other for both species. Similarly, extreme snowfall likely triggered facultative winter migrations by both species in early January of 2011. Indeed resource quality, temperature, and precipitation converged to explain timing of sage-grouse altitudinal migration in Wyoming (Pratt et al., 2017), while migratory ungulates similarly track weather patterns and plant phenology during migration (Merkle et al., 2016; Monteith et al., 2011).

Policy to limit surface disturbance on public lands comprising at least half of pathways will be critical in maintaining mammalian and avian migration. Public lands underlying pathways remain relatively intact despite their proximity to oil and gas reserves of which ~1500 shallow gas wells have already been developed (http://bogc.dnrc.mt. gov/). While most wells in this region have become uneconomical for continued production, emerging technologies in gas recovery may provide renewed development opportunities (Thatcher et al., 2003). Infrastructure associated with energy development can accumulate into

large habitat loses that act to further degrade and fragment intact landscapes for wildlife (Allred et al., 2015). Negative impacts to sage-grouse behavior and demography from energy development are well documented (Aldridge and Boyce, 2007; Carpenter et al., 2010; Doherty et al., 2008; Holloran et al., 2009). Whereas the influence of energy infrastructure on pronghorn is less-studied and results are more nuanced. Energy development as measured by oil and gas well density was negatively correlated with abundance indices (Christie et al., 2015) and implicated in reducing winter habitat quality for pronghorn (Beckmann et al., 2012); while impacts of energy development on pronghorn resource selection are generally equivocal (Jakes, 2015; Christie et al., 2017; Beckmann et al., 2012). Though many of the same studies find that roads negatively impact pronghorn resource selection and survival (Christie et al., 2017; Taylor et al., 2016; Jakes, 2015).

Sage-grouse core area policy limits anthropogenic surface disturbance (e.g. well pads and roads) to specified caps (5%) and focuses additional sagebrush conservation work such as conservation easements (https://sagegrouse.mt.gov/Grants). Core areas provided well-targeted protections to sage-grouse migration, particularly with the addition of a connectivity area specific to this population. In fact, most sage-grouse pathways that were outside of core area boundaries were from facultative winter migrations, which largely occurred on rugged landscapes within CMR that were not typical of sage-grouse winter habitat (Newton et al., 2017). Core areas implemented for sage-grouse conservation may also extend conservation measures to migratory pronghorn, as over half of pronghorn individual migratory pathways were mostly encompassed by sage-grouse breeding and connectivity core areas. This is not the first example of sage-grouse conservation compatible with that of needs for migratory ungulate populations (Copeland et al., 2014; Gamo and Beck, 2017). Yet there is a key caveat in extending benefits of sage grouse policy to pronghorn migration in this landscape, as areas outside core areas may be developed more intensively. Terrestrial migration relies on connectivity of the entire route, such that impediments beyond core areas that act to severe connectivity would negate benefits afforded within these areas. Ultimately maintaining pronghorn migration will rely on conservation beyond sage-grouse core areas as well.

Fences are perhaps the most ubiquitous anthropogenic feature on this landscape that may impede migration, particularly for pronghorn that must make every step along migratory pathways. Marking fences with flagging has been effective in reducing collisions when used in concert with available spatial planning tools for sage-grouse (Stevens et al., 2012; Van Lanen et al., 2017). Similarly, spatial data on fence locations and effective mitigation techniques are available to aid crossing by pronghorn in this landscape (Poor et al., 2014; Jones et al., 2018). Using pathways identified in this research could help practitioners target cost-efficient fence modifications across land tenures to facilitate ungulate migration.

While an increasing anthropogenic footprint will remain a persistent source of fragmentation, the greatest and most imminent threat to conserving migration in the Northern Great Plains is that of expanding cultivation among intact private grasslands. In 2015 alone, over 1,000,000-ha of grasslands were lost to cultivated croplands in the Great Plains (WWF 2017 Plowprint). Loss of migration is often sudden and consequences to population persistence are severe (Bolger et al., 2008). Sage-grouse in our studied population were completely dependent on migration, with obligate migration documented across five years of observation (Newton et al., 2017; Tack et al., 2012), such that the loss of migratory behavior would likely result in extirpation. In contrast, pronghorn were partially migratory with approximately half the population choosing to undertake migration each year. Switching between migratory and resident behavior has been observed in this pronghorn population and other ungulates (Eggeman et al., 2016; Jakes et al., 2018), though losing migration behavior would likely reduce regional populations. As is the case in so many landscapes, the Northern Great Plains would be left with reduced and sedentary populations that must adapt and are vulnerable to human-dominated landscapes (Tucker et al., 2018).

The risk to sedentary populations who persist at the edge of their range may be heightened. Wildlife population densities are typically lower near range boundaries, as key niche requirements that give rise to abundance are less likely to overlap in space (Brown, 1984; Brown et al., 1995). Spatially disparate habitat needs may explain the behavior of additional facultative winter migrations in this landscape by both sage-grouse and pronghorn, particularly when coupled with extreme weather events. In response to already marginal habitats that experience greater environmental stochasticity, conservation efforts to maintain migration as a proxy to sustain functional connectivity in perpetuity will be critical to the persistence of these populations.

Map output of parcels provides practitioners with a roadmap for prioritizing conservation easements in this landscape, and will be available to those for evaluating future expenditures upon request. Yet maintaining migration across taxa will likely be one of several objectives when funding conservation, in which case map tools can be used additively with existing strategies to conserve grassland and sagebrush steppe habitats in this landscape (Walker et al., 2013). This framework for prioritizing land units (e.g. parcels) for conservation is transferable to any system with spatial data on features of both conservation interest and impending risk. Furthermore, as more spatial data becomes available or improved it can be easily incorporated to inform future decisions.

Two assumptions we made in developing a conservation easement prioritization tool were that public lands were "fixed" among solutions, and that marked individuals were representative of their respective populations. Regarding public lands, transfer to private ownership, such as the sale of provincial crown lands in Canada (e.g. https://realty.alberta.ca/), may ultimately lead to agricultural conversion of these currently protected parcels and remains a conservation challenge. Undertaking conservation easements prior to the sale of lands to private entities among these lands is a tool that could be used to alleviate future threats to cultivation and development. Individually tracked sage-grouse appeared to follow similar pathways with a high degree of overlap across years, and tracking during extreme winter weather revealed further facultative movements that are likely to be rare. Thus, we likely observed the extent of sage-grouse pathways from this particular population. Pronghorn individuals however, used more disparate pathways with less overlap such that future tracking would likely lead to the discovery of novel pathways in this landscape. In which case, developing models predictive of pronghorn connectivity could better inform future efforts for maintaining pronghorn migration.

Our optimization scheme sought to target parcels with the highest cultivation probability though it is important to note that these probabilistic estimates are static with respect to past cultivation and technologies, and may not be representative of future cultivation patterns. Furthermore, estimates of cultivation probability rely only on biotic features such as soil type and aspect, and ignore the key social and economic determinants that ultimately drive the fate of uncultivated sagebrush grasslands. For example, in nearby Petroleum County, Montana, 6000-ha of intact prairie was recently lost to cultivation among lands that had a mean cultivation probability of 0.19, less than half that from across the study area. While spatial planning tools will serve as a helpful guide, local practitioners with on-the-ground knowledge of more imminent risk to conversion (e.g. from non-generational ownership transfer), will require the flexibility necessary to ensure this landscape remains a functional ecosystem for migratory taxa.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.03.017.

Acknowledgements

granted permission to capture, track and recover radio-marked sage-grouse and pronghorn. Field assistance from O. Duvuvuei, D. Hitch, and Quicksilver Air for capture and surveillance of sage-grouse and pronghorn. The U.S. Bureau of Land Management, World Wildlife Fund, Montana Fish, Wildlife and Parks, Saskatchewan Ministry of Environment, and Parks Canada - Grasslands National Park all contributed in-kind and financial support throughout these projects. We appreciate conceptual guidance from T. Griffiths, J. Carlson, M. Sather, and S. Fields. Comments from J. Beck and two anonymous reviewers greatly improved the quality of this manuscript. Findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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