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The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk

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Abstract. Partial migration occurs across a variety of taxa and has important ecological and evolutionary consequences. Among ungulates, studies of partially migratory populations have allowed researchers to compare and contrast performance metrics of migrants versus residents and examine how environmental factors influence the relative abundance of each. Such studies tend to characterize animals discretely as either migratory or resident, but we suggest that variable migration distances within migratory herds are an important and overlooked form of population structure, with potential consequences for animal fitness. We examined whether the variation in individual migration distances (20–264 km) within a single wintering population of mule deer (*Odocoileus hemionus*) was associated with several critical behavioral attributes of migration, including timing of migration, time allocation to seasonal ranges, and exposure to anthropogenic mortality risks. Both the timing of migration and the amount of time animals allocated to seasonal ranges varied with migration distance. Animals migrating long distances (150–250 km) initiated spring migration more than three weeks before than those migrating moderate (50–150 km) or short distances (<50 km). Across an entire year, long-distance migrants spent approximately 100 more days migrating compared to moderate- and short-distance migrants. Relatedly, winter residency of long-distance migrants was 71 d fewer than for animals migrating shorter distances. Exposure to anthropogenic mortality factors, including highways and fences, was high for long-distance migrants, whereas vulnerability to harvest was high for short- and moderate-distance migrants. By reducing the amount of time that animals spend on winter range, long-distance migration may alleviate intraspecific competition for limited forage and effectively increase carrying capacity. Clear differences in winter residency, migration duration, and risk of anthropogenic mortality among short-, moderate-, and long-distance migrants suggest fitness trade-offs may exist among migratory segments of the population. Future studies of partial migration may benefit from expanding comparisons of residents and migrants, to consider how variable migration distances of migrants may influence the costs and benefits of migration.

Key words: carrying capacity; long-distance migration; mule deer; partial migration; seasonal ranges; ungulate migration.

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INTRODUCTION

Partial migration, in which some individuals of a population migrate seasonally while others do not, is a common behavioral strategy across migratory taxa, including invertebrates, fish, birds, and mammals (Lundberg 1988, Chapman et al. 2011). Among ungulates, partial migration is widespread, and yet migratory individuals tend to strongly outnumber residents because of the nutritional benefits associated with migration (Fryxell and Sinclair 1988, Fryxell et al. 1988, but see Middleton et al. 2013). Migrating in concert with emerging vegetation affords animals prolonged access to highly digestible forage (Albon and Langvatn 1992, Hebblewhite et al. 2008, Sawyer and Kauffman 2011), which can increase nutritional condition (White 1983) and bolster survival and reproduction (Fryxell and Sinclair 1988). Migration to a separate summer or wet season range has the additional benefit of alleviating resource depletion on the winter or dry season range (Monteith et al. 2011).

Within partially migratory populations, the dramatic journeys of migratory herds, such as wildebeest (*Connochaetes taurinus*) in Serengeti (Holdo et al. 2011) and pronghorn (*Antilocapra americana*) in North America (Berger 2004), have historically received the most research and conservation attention (Bolger et al. 2008, Harris et al. 2009). Nevertheless, recent observations of migratory herds declining alongside thriving resident herds (Hebblewhite et al. 2006, Middleton et al. 2013) and segments of migratory populations exhibiting disparate demographics (Monteith et al. 2014) have prompted interest in the environmental conditions that regulate the balance of migration and residency. Comparing the performance of migrants versus residents (Hansen et al. 2010, Cagnacci et al. 2011, Gaidet and Lecomte 2013) has allowed researchers to explore how changing climatic conditions, land-use practices, predation regimes, and other factors affect the relative abundance of these alternative strategies (Hebblewhite et al. 2006, Hebblewhite and Merrill 2011, Middleton et al. 2013). Such knowledge can be used to better manage migratory subpopulations and predict how populations might respond to future environmental conditions (Fryxell and Holt 2013).

Amidst the proliferating study of partial migration, animals are often characterized discretely as either migratory or resident. However, our studies of partially migratory populations show that individuals within these populations migrate across a wide range of distances (Sawyer et al. 2005, Monteith et al. 2011, Sawyer and Kauffman 2011, Middleton et al. 2013, Jones et al. 2014). Migration distance could potentially influence when animals migrate, how animals allocate time to seasonal ranges, and the level of anthropogenic disturbance encountered along the route. We hypothesize that variable migration distances within migratory subpopulations may represent an important but unexplored form of population structure, which may affect the costs and benefits of migration (Fig. 1).

Here, we investigate variation in migration distances within a mule deer herd of the western United States. For mule deer and other ungulates, migration is a learned behavior thought to be culturally transmitted from mother to young (McCullough 1985, Sweanor and Sandegren 1988, Bauer et al. 2011). Although some ungulates such as elk (Eggeman et al. 2016) and pronghorn (White et al. 2007, Kolar et al. 2011, Collins 2016) can exhibit plasticity in their migratory behaviors, mule deer typically show strong fidelity to migration routes between seasons and across years (Garrott et al. 1987, Thomas and Irby 1990, Sawyer et al. 2009). Thus, the distances that individual deer migrate are consistent across years (Sawyer and Kauffman 2011). We sought to evaluate whether individuals of different migration distance classes also share key behavioral and environmental attributes of migration, including timing of migration, time allocation to seasonal ranges, and exposure to anthropogenic disturbance. Our study herd included the longest mule deer migration ever recorded (Sawyer et al. 2014) and allowed us to investigate deer behavior across a wide range of migration distances (20–264 km). We show how migration distance can influence timing of migration, duration of residency on seasonal ranges, and exposure to mortality risk, all of which have important demographic and conservation implications.

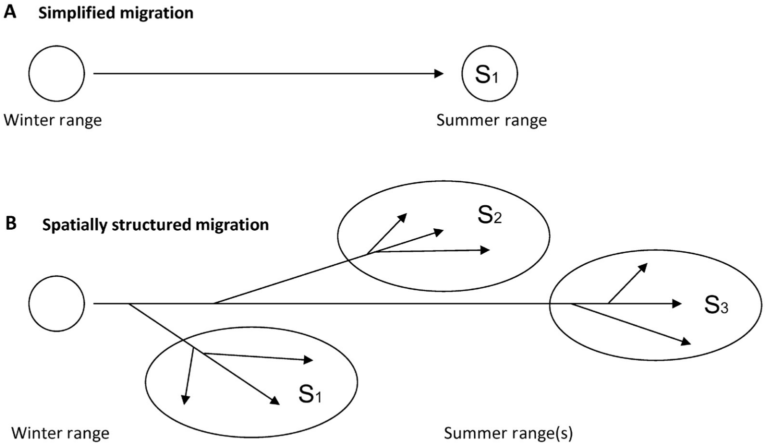

Fig. 1. (a) Migration is often treated as a discrete behavior within a population, where animals migrate from one seasonal range to another. With only one conceptualized summer range equidistant from the winter range, the decision to migrate carries the same fitness trade-offs (S_1) for all migrants. (b) When animals from the same population migrate variable distances to multiple summer ranges, the fitness trade-offs associated with migration (S_1, S_2, S_3) may depend on how far animals migrate, the environmental conditions they encounter along the migration routes, and distinct summer ranges they utilize.

MATERIALS AND METHODS

Study area

We sampled mule deer from a herd that winters in the Red Desert of southwest Wyoming. These animals vary from residents that remain in the desert all year to migrants that travel up to 264 km to summer ranges in the mountains of northwest Wyoming, United States. Their migration routes cross a variety of habitats, including desert basins, rolling foothills, agricultural fields, forests, and high mountain basins. Most of the Red Desert winter range is federal land administered by the Bureau of Land Management (BLM) and managed for multiple uses, including recreation, wilderness, livestock grazing, and energy development (BLM 1997). Mule deer that migrate longer distances cross a mix of jurisdictional boundaries, including private, state, and federal lands (BLM and US Forest Service). Mule deer herds in the region are managed by the Wyoming Game and Fish Department (WGFD) and hunted each autumn. Harvest is currently restricted to males, but female harvest was common in previous decades (e.g., 1990s). Although duration of the hunting season varies by hunt area, the number of Wyoming residents permitted to harvest one male deer is unlimited (WGFD 2014). As a result, hunting pressure is high in areas close to roads and with gentle terrain. We refer readers to Sawyer et al. (2014) for a detailed description of study area.

Animal capture and data collection

We used helicopter net-gunning to capture 50 adult female deer, including 32 in January 2011, 13 in January 2012, and five in December 2012. Deer were captured on winter range immediately north of Interstate 80 and equipped with store-on-board GPS radio collars (TGW-4500; Telonics, Mesa, Arizona, USA) programmed to collect locations every 13 h during summer (June 15–September 15) and every three hours for the remainder of the year. We programmed collars to drop off on 1 April 2013. The winter of 2010–2011 was unusually severe, and deer herds throughout western Wyoming suffered substantial mortality. Of the 32 animals captured during that winter, 14 died before spring migration. Overall, we recovered 28 collars that had at least one year of data and were suitable to evaluate migratory patterns. Of those, 17 collected data for two years. All mule deer were captured with protocols consistent with the University of Wyoming Institutional Animal Care and Use Committee and following recommendations of the American Society of Mammalogists (Sikes et al. 2011).

Analysis

We used net squared displacement (NSD) to calculate the start and end dates of spring and autumn migrations, which in turn determined the amount of time that individuals spent on winter and summer ranges. Application of NSD has proved effective at discerning a variety of migration parameters (e.g., timing) and patterns (e.g., migratory vs. nomadic) for ungulates with fine-scale GPS data (Bunnefeld et al. 2011). We set the starting position to 15 December, when mule deer occupied their winter range. Using the NSD plot of each animal, we determined the following: (1) timing of spring and autumn migrations, (2) time allocated to winter range and summer range each year, and (3) time allocated to migration, including spring and autumn migrations combined. For animals with longitudinal data (n = 17), we averaged their metrics across years, so that the animal was treated as an experimental unit. To determine whether these migration metrics were influenced by migration distance, we first grouped animals into one of three possible migration classes: (1) short-distance migrants that traveled <50 km between seasonal ranges, (2) moderate-distance migrants that moved 50–150 km, and (3) long-distance migrants that traveled >150 km. We then used one-way analysis of variance (ANOVA) with post hoc pairwise Bonferroni tests to evaluate differences in migration metrics (α = 0.05) between the three groups.

We examined whether animals in each distance class were influenced differently by three key sources of anthropogenic mortality risk: harvest vulnerability, roads, and fences. We estimated harvest vulnerability and exposure to road and fence crossings for each migration class to evaluate how these anthropogenic factors vary across migration distance classes. Because harvest vulnerability is largely a function of security cover (Conner et al. 2001, Proffitt et al. 2013), we used the proportion of security cover in each hunt area as a surrogate to harvest vulnerability, where high amounts of security cover reflect low harvest vulnerability and vice versa. We defined security cover as areas with forested cover or slopes >5% that were more than 500 m from open road (Proffitt et al. 2013). We derived forest cover from the National Land Cover Database (30-m resolution; Homer et al. 2015). We used ArcGIS Spatial Analyst (Environmental Systems Research Institute, Redlands, California, USA) to derive slope values from a 30-m digital elevation model (http://www.uwyo.edu/wygisc/geodata/). We quantified the amount of security cover in hunt areas defined by the WGFD (Appendix S1). Because most mule deer were exposed to harvest before autumn migration, we used the hunt area that each individual animal resided in during summer as an indicator to how vulnerable it was to harvest. Although our study animals could not be legally harvested under current regulations, we used the metric of harvest vulnerability to index how mortality risk could change as a function of migration distance. We restricted number of road crossings to state and federal highways where the speed and volume of traffic pose serious risk (Forman et al. 2003). We inventoried and digitized fences from a helicopter flight along the migration routes (Sawyer et al. 2014).

RESULTS

Of 28 marked mule deer, 27 (96%) were migratory. Migration distances ranged from 20 to 264 km, with 26% (n = 7) of animals classified as short-distance, 44% (n = 12) as moderate-distance, and 30% (n = 8) as long-distance migrants (Fig. 2). One-way distance traveled by short-, moderate-, and long-distance migrants was 25 ± 6 (mean ± 95% CI), 96 ± 13, and 227 ± 28 km, respectively. In the spring, timing of migration varied with migration distance (ANOVA, $F_{2,24}$ = 25.16, P < 0.001), with long-distance migrants leaving winter range 24 d before moderate- and 28 d before short-distance migrants (Fig. 3). Average start date (Julian day ± 95% CI) of spring migration was 122 ± 6 d for short-, 118 ± 4 d for moderate-, and 94 ± 9 d for long-distance migrants. In the autumn, animals from all distance classes left summer range within 14 d of one another, but moderate-distance migrants left earlier than short- and long-distance migrants (ANOVA, $F_{2,24}$ = 5.67, P = 0.009). The average start dates of autumn migrations were 300 ± 5 d for short-, 286 ± 5 d for moderate-, and 298 ± 9 d for long-distance migrants.

Migration distance was strongly associated with the amount of time animals allocated to seasonal ranges (Fig. 4). Time allocated to winter range was 167 ± 22 d (mean ± 95% CI) for

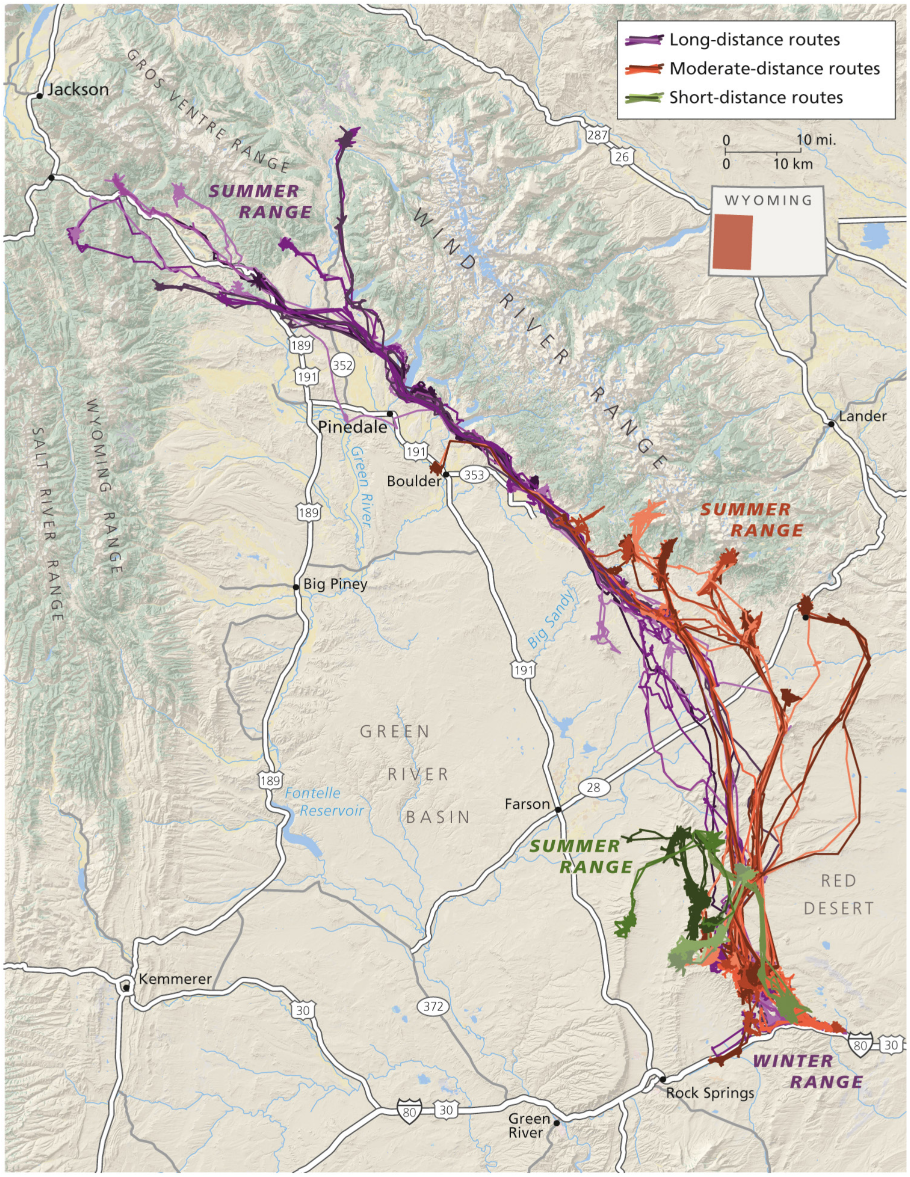

Fig. 2. Short (<50 km)-, moderate (50–150 km)-, and long (>150 km)-distance migration routes for adult female mule deer originating from a common winter range in western Wyoming, United States.

short-, 166 ± 9 d for moderate-, and 95 ± 18 d for long-distance migrants (Fig. 4). Notably, the long-distance migrants spent 71 fewer days on winter range compared to those migrating short and moderate distances ($F_{2,15}$ = 32.21, $P < 0.001$). Time allocated to summer range was 170 ± 6 d (mean ± 95% CI) for short-, 145 ± 5 d for moderate-, and 144 ± 6 d for long-distance migrants (Fig. 4). Animals migrating short distances spent 25 and 26 more days on summer range compared with those migrating moderate and long distances ($F_{2,24}$ = 20.96, $P < 0.001$). Time allocated to migration across both spring and autumn was 9 ± 3 d (mean ± 95% CI) for short-, 28 ± 11 d for moderate-, and 114 ± 32 d for long-distance migrants (Fig. 4). On average, animals migrating long distances spent 86 and 105 more days migrating each year compared with moderate- and short-distance migrants, respectively ($F_{2,24}$ = 31.0, $P < 0.001$); they also spent more

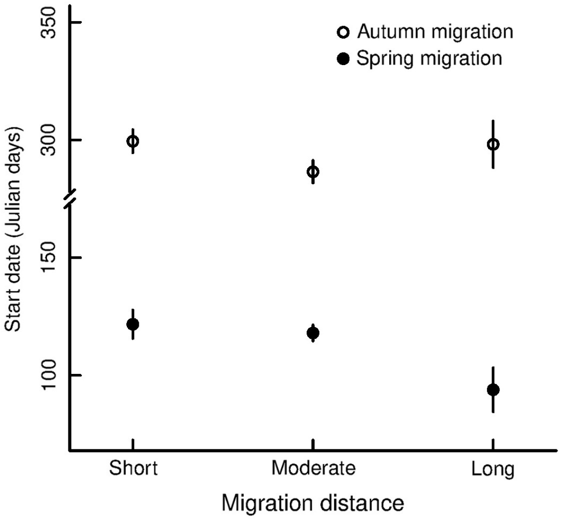

Fig. 3. Average initiation dates (mean ± 95% CI) of spring and autumn migrations of adult female mule deer for short (<50 km)-, moderate (50–150 km)-, and long (>150 km)-distance migrants in western Wyoming, 2011–2013.

time on migrating than on winter range. Spring migration alone lasted 6 ± 1 d (mean ± 95% CI) for short-, 16 ± 5 d for moderate-, and 54 ± 12 d for long-distance migrants. Autumn migration was 3 ± 1 d (mean ± 95% CI) for short-, 12 ± 10 d for moderate-, and 60 ± 23 d for long-distance migrants.

Based on 95% CIs, anthropogenic mortality factors, including harvest vulnerability, highway crossings, and fences, all varied with migration distance. Harvest vulnerability, as indexed by an inverse relationship with security cover, was significantly lower in hunt areas occupied by long-distance migrants compared with those used by moderate- and short-distance migrants. Security cover in hunt areas occupied by short-, moderate-, and long-distance migrants was 10% ± 0%, 38% ± 13%, and 68% ± 8%, respectively. The hunt area occupied by short-distance migrants had the lowest amount of security cover, making them the most vulnerable to harvest. Moderate- and long-distance migrants crossed an average of 1.8 ± 0.65 (mean ± 95% CI) and 5.8 ± 1.18 highways, respectively, to complete a migration cycle, whereas short-distance migrants did not cross any highways. Similarly, moderate- and long-distance migrants crossed (mean ± 95% CI) 17 ± 9 and 171 ± 18 fences, respectively, whereas short-distance migrants did not cross any fences.

Discussion

Ungulates in partially migratory populations are often categorized discretely as migrant or resident, but our findings suggest this distinction obscures important variability in the behavior of migrants and the environmental conditions they encounter. One-way movements between seasonal ranges of mule deer in our study herd varied more than 10-fold, from 20 to 264 km. These highly variable migration distances were associated with dramatic differences in timing of migration, time allocated to seasonal ranges, and exposure to anthropogenic mortality factors. For this herd, discretely categorizing animals as migrant or resident would fail to capture the wide range of behavioral responses to environmental conditions, exposure to anthropogenic risk, and potentially, the costs and fitness benefits associated with migration. Instead, migration distance strongly influenced the year-round behaviors and habitat associations of mule deer, representing an important influence on population structure for this partially migratory herd.

Several comprehensive studies have shown that the timing of migration in mule deer (Monteith et al. 2011, Lendrum et al. 2013) and other large herbivores (Grovenburg et al. 2009, Jones et al. 2014) is determined largely by local weather

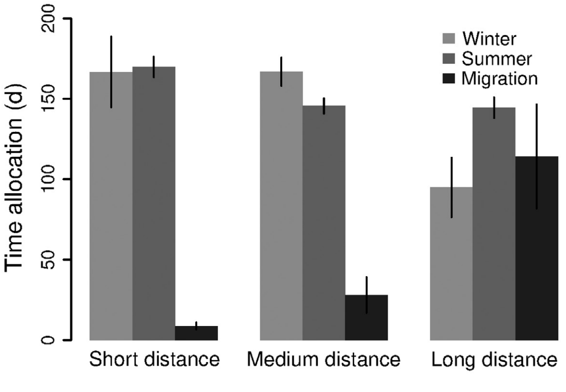

Fig. 4. Time allocation (mean ± 95% CI) of mule deer that migrated short (<50 km), moderate (50–150 km), and long (>150 km) distances to winter, summer, and migration periods in western Wyoming, 2011–2013.

patterns, plant phenology, and in some instances, state-dependent characteristics such as age, sex, or nutritional status (Monteith et al. 2011, Singh et al. 2012). Yet, we found long-distance migrants (>150 km) initiated spring migration more than three weeks earlier than individuals that occupied the very same winter range but migrated shorter distances. The timing of ungulate migration is normally attributed to changes in local weather and vegetative conditions (Garrott et al. 1987, Holdo et al. 2009, Monteith et al. 2011), so it is unclear why long-distance migrants initiated spring migration early. Although it is possible that migration timing influences the distance of migration, we hypothesize that long-distance migrants initiate spring migration early simply to ensure they arrive at a time when emerging vegetation provides high-quality forage. Indeed, female mule deer exhibit strong fidelity to their migration routes (Sawyer et al. 2009) but not to their migration timing, which varies from year to year (Monteith et al. 2011). This favors the idea that migration distance influences timing, not the other way around. Short-, moderate-, and long-distant migrants all began autumn migration within 14 d of one another, despite occupying summer ranges dozens or hundreds of kilometers apart. Although beyond the scope of this study, the consistent timing of autumn migration begs the question of what sort of trigger or cues mule deer respond to across vastly different landscapes and environmental conditions that would synchronize their timing. We suspect that prior studies may have been limited in their ability to detect an effect of migration distance on timing because those populations traveled <75 km (Monteith et al. 2011, Lendrum et al. 2013), and such effects on migration timing may only be evident in landscapes that still support unusually long migrations (>150 km). Regardless of the explanation, the fact that long-distance migrants initiated spring migration 30 d before the moderate- or short-distance migrants reveals a clear behavioral difference associated with migration distance that may carry consequences for individual fitness and population dynamics.

A key finding from our study was that migration distances appeared to influence how animals allocated time to winter and migration periods. Animals that migrated long distances spent approximately 100 additional days migrating compared with those that migrated moderate or short distances. Further, long-distance migrants spent approximately 70 fewer days on winter range compared with moderate- and short-distance migrants. An important implication is that differences in migration timing and residency on winter range effectively decrease time on winter range during a time of year critical to survival and reproduction (Parker et al. 2009). In temperate regions, most ungulates experience a nutritional bottleneck during winter when forage is lower in digestibility and protein content, and animals are often concentrated at their highest year-round densities (Bishop et al. 2009, Monteith et al. 2011), resulting in important feedbacks into density-dependent mortality and population dynamics (Bartmann et al. 1992, Monteith et al. 2014).

By reducing the amount of time spent on winter range, individuals not only alleviate intraspecific competition for a limited forage supply, but also increase access to new forage growth (Monteith et al. 2011). Similarly, by spending 114 d of the year migrating, long-distance migrants displace browsing pressure across a separate and dispersed seasonal range. We hypothesize that long-distance migrants enhanced their own net nutritional gain by occupying a third seasonal range (i.e., the migration route) and, consequently, increased the potential carrying capacity for the overall herd. In our case, 30% of the deer herd (i.e., long-distance migrants) reduced winter residency by more than three months; such a reduction in occupancy of winter range has a clear potential to increase carrying capacity for herds limited by winter range, which has often been reported (Bishop et al. 2009). Notably, reduced residency on winter range only occurred with long-distance migrants. Thus, the potential benefit of increased carrying capacity via reduced time allocated to winter range might conceivably be lost in landscapes that can no longer support long-distance migrations. Although declines of mule deer across western North America have been attributed largely to habitat loss and drought (deVos et al. 2003, Monteith et al. 2014), we suspect that the loss of long-distance migrations may compound these declines by further reducing carrying capacity.

Long-distance migrants spent nearly one-third of the year migrating, which supports the emerging science that migration routes function not only as travel corridors, but also as key foraging habitat in both spring and autumn (Sawyer et al. 2009, Sawyer and Kauffman 2011, Blum et al. 2015). Traditionally, mule deer and other ungulate management in the western United States has focused almost exclusively on winter range, yet a growing body of research is showing that the nutritional contributions of summer range (Cook et al. 2004, Tollefson et al. 2011) and other seasonal habitats to the ungulate fitness are equally important (Monteith et al. 2013). Migration corridors may be uniquely beneficial, because the nutritional benefit of time spent in such habitats can be amplified by accessing forage plants that are near peak digestibility and protein content as animals exploit phenological gradients (Albon and Langvatn 1992, Hebblewhite and Merrill 2007, Sawyer and Kauffman 2011). Altogether, this body of work highlights the need for researchers and managers to recognize migration corridors as a distinct seasonal range, critical to the nutrition, productivity, and abundance of ungulates.

Our focus on long-distance migration informs how the alteration in migration habitat could gradually erode herd productivity, even in large, relatively undisturbed landscapes like western Wyoming. In our study area, animals migrating short distances did not have to contend with any highway crossings or fences, whereas the long-distance migrants crossed an average of five highways and 171 fences just to complete a round-trip seasonal migration. The presence of such anthropogenic factors operating on distinct population segments could alter their relative abundance within the herd, either through direct mortality or indirectly by reducing the benefits of migration (sensu Middleton et al. 2013, Monteith et al. 2014). Our observations also indicate how harvests planned without consideration of migratory structure within a herd could disproportionately affect a particular population segment (e.g., Knight 1970, Rudd et al. 1983, Hebblewhite and Merrill 2011). Long-distance migrants were less vulnerable to harvest because they occupied rugged, mountainous terrain that provided abundant security cover. In contrast, residents and short-distance migrants appeared to be more vulnerable to harvest because of the open and easily accessible desert habitat they occupy, which may help explain the low relative abundance of resident animals in this population. Obviously, the vulnerability of any migratory herd would increase if the hunting seasons overlapped with autumn migration, as deer movements are predictable and constrained to narrow corridors during that period.

The management and conservation of migratory ungulates is a top priority for agencies and conservation organizations around the globe. The growing body of literature has helped understand the fitness benefits underlying ungulate migration by comparing behavioral, nutritional, and demographic metrics of migratory and resident animals (Hebblewhite and Merrill 2009, 2011, Robinson et al. 2010, Cagnacci et al. 2011, Mysterud et al. 2011, Gaidet and Lecomte 2013, Middleton et al. 2013, Monteith et al. 2014). Our study moves past the simple migrant–resident dichotomy to show that variable migration distances within a single herd can influence both the timing of migration and the amount of time animals allocate to seasonal ranges. Our observation of reduced winter residency among long-distance migrants also suggests a mechanism by which long migrations may increase ungulate carrying capacity via the displacement of browsing pressure from common winter ranges to migration routes, thereby increasing the net forage base available to the herd. Additionally, variable migration distances can expose animals to strikingly different levels of anthropogenic disturbance, particularly fences and roads, which could affect population segments disproportionally. We encourage future studies of partial migration to expand comparisons beyond residents and migrants to account for variable migration distances among the migratory segments of the population. We hypothesize that distinct fitness trade-offs may exist in populations where a wide range of migration distances are available to animals.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1534/full