



RESEARCH ARTICLE

All routes are not created equal: An ungulate's choice of migration route can influence its survival

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Abstract

1. Our knowledge of migration ecology has progressed quickly in concert with technological advances that collect fine-scale movement data through time. We now know that migration plays a critical role in the annual nutritional cycle of large herbivores and that sustaining functional migratory routes is key to long-term conservation. Yet, we lack basic information on whether one migratory route may function better than another, or more specifically, if choosing one route over another has fitness consequences – knowledge that could help inform conservation and restoration efforts.
2. Here, we examined how a suite of migratory parameters influenced the survival of mule deer *Odocoileus hemionus* that shared a common winter range in New Mexico, USA, but migrated to various summer ranges in Colorado, USA. We used a Cox proportional hazard model and longitudinal global positioning system data collected over a 7-year period to investigate whether the mortality risk of 66 deer was affected by choice of migratory route, summer range, migration distance, speed or the number of administrative boundaries each route crossed.
3. We found mule deer survival was not influenced by migratory distance, speed or number of administrative boundaries, but was strongly affected by the choice of migratory route and summer range. The magnitude of these effects was surprisingly large, doubling or tripling mortality risk. Cumulative survival rates showed that regardless of summer range, individuals migrating along high-use *exterior* routes had cumulative survival rates approximately 30% lower than individuals migrating along high-use *interior* routes. To our knowledge, this is the first direct evidence that a mammal's choice of migration route can influence its probability of survival.
4. *Synthesis and applications.* Our finding that large herbivores may experience up to three times higher mortality risk by using a different migratory route reveals a novel link between migration and demography. Importantly, our results also suggest that spatially explicit model parameters and predictions could help in the conservation and restoration of migratory populations by identifying specific migratory routes or seasonal ranges that reduce survival.

KEY WORDS

demography, migratory populations, migratory route, mortality risk, mule deer, survival, ungulate conservation, ungulate migration

1 | INTRODUCTION

Recent advances in global positioning system (GPS) technology and remote sensing have greatly increased our understanding of animal movements (Kays, Crofoot, Jetz, & Wikelski, 2015). In particular, studies of large herbivore migration have benefited from the collection of fine-scale movement data to reveal the intricacies of migratory behaviour (Cagnacci et al., 2016; Martin et al., 2018; Peters et al., 2018), the role of plant phenology (Aikens et al., 2017; Bischof et al., 2012; Merkle et al., 2016) and the benefits of migration for individual and population performance (Hebblewhite & Merrill, 2009; Middleton et al., 2018; Rolandsen et al., 2017). Migration behaviour is thought to underpin the abundance of many large herbivore populations (Fryxell, Greever, & Sinclair, 1988; Fryxell & Sinclair, 1988) and this contemporary body of work has begun to unravel the mechanics of how migration is specifically linked to demography.

Concurrently, global declines in migratory ungulates combined with widespread habitat loss and land use change have prompted research and conservation efforts aimed at identifying and protecting migratory routes (Berger, 2004; Bolger, Newmark, Morrison, & Doak, 2008; Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009). For example, provided with a year or more of GPS data, researchers can delineate the migratory routes of individuals and populations (Sawyer, Kauffman, Nielson, & Horne, 2009). Delineating population-level ungulate migration corridors has proven to be an effective conservation tool at local and regional scales in North America and other continents (Bond, Bradley, Kiffner, Morrison, & Lee, 2017; Coe et al., 2015) because it provides a spatially explicit footprint of migratory habitat that can be used to help inform management and conservation actions.

Recent studies have also highlighted the important functional role that migratory routes play in the annual nutritional cycle of large herbivores by providing foraging and resting habitat (Monteith, Hayes, Kauffman, Copeland, & Sawyer, 2018; Sawyer & Kauffman, 2011). The recognition that migratory habitat is functionally important for nutrition as well as movement (Aikens et al., 2017) carries an implicit, but rarely examined assumption that habitat quality, predation risk, human disturbance and other factors should vary within and among migratory routes. Additionally, migratory routes tend to be spatially complex; rather than using just one defined route or corridor between seasonal ranges, migratory ungulate populations often utilize a network of routes, with some routes used more heavily than others (Sawyer et al., 2009). The importance of migratory routes as foraging and resting habitat, coupled with the spatial complexity of multiple routes or networks, suggests that migratory routes and movement behaviour within them may influence fitness and demography – a potentially important link which has not been

fully explored. Understanding whether one migration route may be better than another, or more specifically, if choosing one route over another has fitness consequences, may have important consequences for future research, management and conservation.

The rapid accumulation of fine-scale movement data has created new opportunities to explore how or if spatially explicit migratory parameters (e.g. migratory route) influence the survival of individuals. Past studies have linked the survival of large herbivores to weather patterns, vegetation, predation risk (Bender, Lomas, & Browning, 2007; DeCesare et al., 2014) and other factors known to directly affect or index nutritional condition (Bishop, White, Freddy, Watkins, & Stephenson, 2009; Monteith et al., 2013, 2014). Furthermore, some studies have suggested migratory ungulates have lower rates of survival than their resident counterparts (Nicholson, Bowyer, & Kie, 1997; Schuyler, Dugger, & Jackson, 2019), and within the migratory segment, those that migrate further may encounter more anthropogenic risks (Sawyer, Middleton, Hayes, Kauffman, & Monteith, 2016). Expanding this growing body of work to understand how mortality risk might be influenced by various migratory parameters could further solidify the connection between migration and demography, and importantly, refine our ability to detect, and potentially mitigate, previously unknown risk factors that regulate large herbivore populations.

Here, we used GPS data collected over a 7-year period to investigate how mule deer *Odocoileus hemionus* survival was influenced by migratory route, summer range, migration distance, speed and the number of administrative boundaries each route crossed. Consistent with other mule deer herds (Sawyer et al., 2009), the migratory routes of our study population radiated out to multiple summer ranges from one common winter range. So, while individuals were exposed to the same conditions on winter range, they encountered different environmental and anthropogenic conditions the remainder of the year, depending on which migratory route they followed.

2 | MATERIALS AND METHODS

2.1 | Study area

We captured mule deer on their winter range in a 70-km² portion of the upper San Juan Basin in northwest New Mexico, USA (36° 55'N, 107° 22'W; Figure 1). This area was characterized by rolling topography and canyons ranging in elevation from 1,800 to 2,194 m, and a mix of pinyon (*Pinus edulis*) and juniper (*Juniperus scopulorum*) woodlands interspersed with pockets of sagebrush (*Artemisia* sp.) grasslands. The area was administered by the Bureau of Land Management, but surrounded by a mix of tribal, US Forest Service and private lands, and has a long history of energy development, leading to high

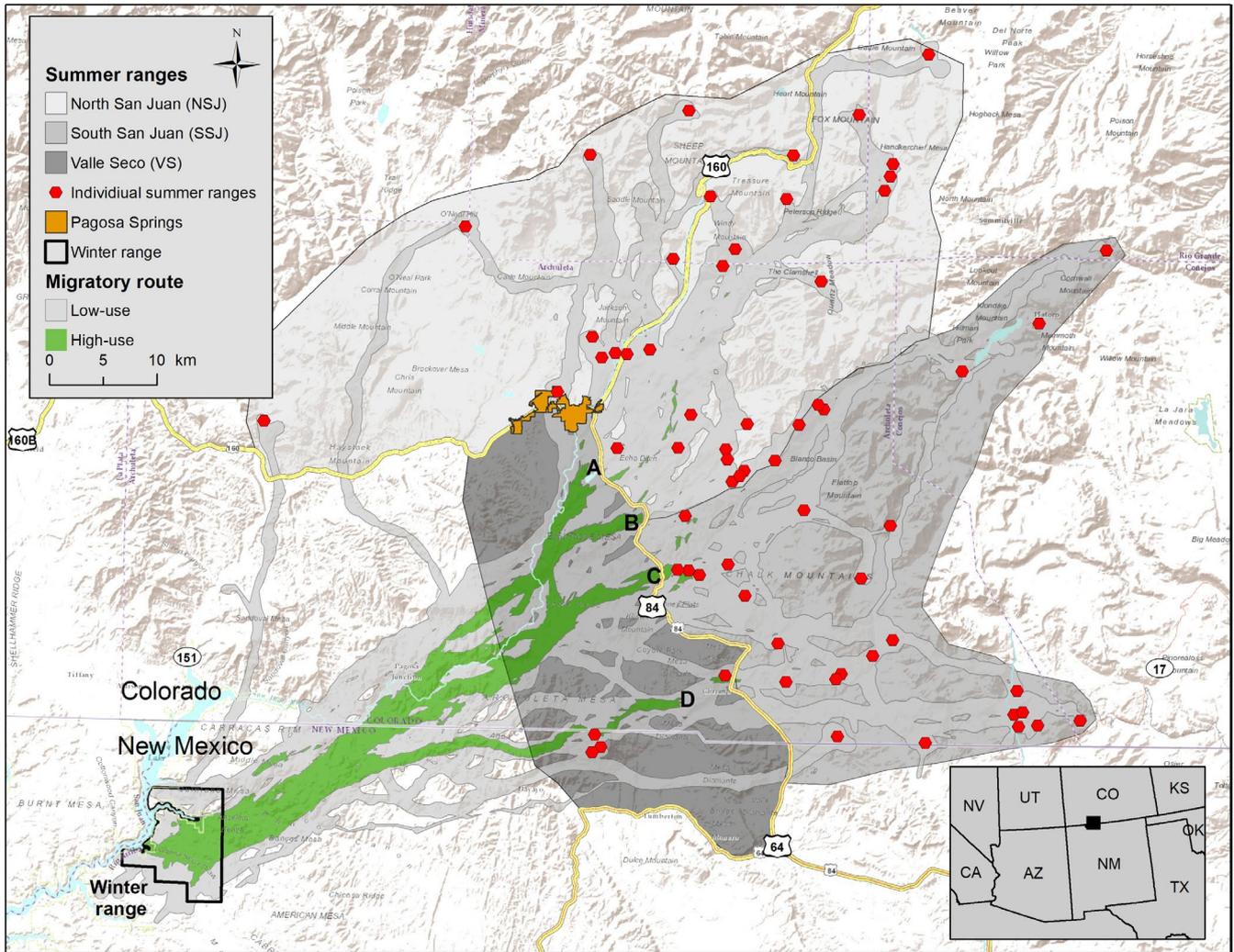


FIGURE 1 Location of common winter range and the North San Juan, South San Juan and Valle Seco summer ranges relative to low-use and high-use migratory routes used by mule deer in northern New Mexico and southern Colorado, USA 2011–2017. High-use migratory routes were grouped as exterior (A and D) and interior (B and C)

densities of roads and well pads for oil and natural gas (Bureau of Land Management, 2003). From their common winter range, deer migrated north-east through mid-elevation ponderosa *Pinus ponderosa* and scrub oak *Quercus gambelii* communities to high-elevation subalpine and alpine summer ranges in three areas of the San Juan Mountains of Colorado, USA: the Valle Seco (VS), the North San Juan (NSJ) Mountains and the South San Juan (SSJ) mountains (Figure 1). US Highways 160 and 84 separated the lower elevation VS from the higher elevation NSJ and SSJ summer ranges. The Rio Blanco River separated the NSJ and SSJ, where migratory routes clearly diverged to respective summer ranges. During migrations, deer traversed a mix of landownership and administrative boundaries, crossed US Highways 160 and 84, and gained 300–1,200 m in elevation.

2.2 | Animal capture and data collection

We used helicopter net-gunning to capture adult female mule deer during winter. All deer were captured with protocols consistent

with those of the University of Wyoming Institutional Animal Care and Use Committee and followed suggestions of the American Society of Mammalogists (Sikes & Gannon, 2011). We collared 42 animals in December 2011, 8 in January 2013, 10 in January 2014, 4 in January 2015 and 6 in March 2016. All 70 animals were equipped with GPS collars (Telonics, Mesa, Arizona, USA) programmed to collect locations every 2 hours for 25 months. Animals that lived through each 25-month period were recaptured and equipped with new collars that operated for another 25 months. This process was repeated until all collars dropped off in April 2018, so that data of the original 42 collared animals spanned up to 6.5 years. Collars had mortality sensors that changed very high frequency pulse rate when animals remained stationary more than 8 hours. When mortalities were detected during periodic telemetry flights, collars were later recovered and GPS data downloaded. We determined the date of mortality by mapping GPS locations and locating the first cluster of stationary points to determine the exact day when the animal quit moving (Anderson & Lindzey,

2003). Cause-specific mortality information was not available for most animals because collars were typically not recovered until several weeks after death. Hunting was not a source of mortality for any deer in our study. Four individuals died prior to completing a full migration and were excluded from analysis because their migration route and summer range could not be determined.

2.3 | Survival analysis

We measured five migratory parameters that we hypothesized could influence survival, including: (a) high-use migratory routes, (b) summer range, (c) migratory distance, (d) speed of migration and (e) a land ownership metric that quantified the number of administrative boundaries each route crossed. We followed the methods of Sawyer et al. (2009) to identify high-use migration routes by first estimating a utilization distribution (UD) using the Brownian bridge movement model (Horne, Garton, Krone, & Lewis, 2009) for each spring and autumn migration completed by each animal. We then averaged the seasonal UD for each animal together so that a single animal-specific UD reflected its migratory route, regardless of the number of years it was alive. To determine the population-level migration route, we stacked polygons representing the 99% contours of all animal-specific UD and counted the number of polygons overlapping each cell in a 50 × 50 m grid spanning the entire study area (Sawyer et al., 2009). The maximum count associated with any cell was the total number of marked animals ($n = 66$) while the minimum count was 1. High-use routes were delineated as those cells used by > 10% (i.e. >7) of collared individuals (Figure 1) – a subjective, but informative cut-off that focuses on routes used by many marked animals rather than those only used by a few. From this method, we identified four distinct high-use migratory routes (A, B, C and D; Figure 1). Migration paths that did not follow any of the high-use routes to summer range were classified as low-use routes. The four high-use routes and remaining low-use routes were used as individual factors in our survival analyses, but we also grouped routes into high-use exterior (A and D), high-use interior (B and C) and low-use categories as potential parameters. We grouped routes this way because exterior routes occurred on the periphery of the broader migratory network, where we hypothesized individuals could encounter different conditions than those on the interior, or that exterior routes somehow limit the spatial extent of the population's migratory footprint. We assigned individuals to one of the five migratory route categories (A, B, C, D or low-use) because deer utilized the same route every year (Sawyer, Merkle, Middleton, Dwinnell, & Monteith, 2019).

We assigned mule deer into one of the following three summer ranges: (a) NSJ, (b) SSJ and (c) VS (Figure 1). Lastly, we used land ownership data to calculate the number of administrative boundaries crossed by each individual route. This metric ranged from 6 to 90 and was intended to reflect the jurisdictional complexity of each route. Migration distance was measured as the distance along the migration route between winter and summer range. Migration distance or summer ranges of individuals did not change annually because mule deer from this population and others tend to use the

same route year after year (Sawyer, Merkle, et al., 2019). We computed migration speed as the rate of movement (km/hr) separately for both the spring and autumn migration periods of each year.

We used a Cox proportional hazard (CPH) model (Andersen & Gill, 1982) to estimate the potential effects of migratory parameters on deer survival. A CPH model can estimate the relationship between multiple parameters and the instantaneous probability of death, referred to as the hazard function (Therneau & Grambsch, 2000). Once the hazard function is estimated, the ratios of hazard can be used to compare the relative effects of particular parameters on the risk of mortality. Like other survival analyses, the key assumptions of the CPH include: (a) marked animals are representative of the broader population, (b) mortality risk is independent among animals, (c) hazard functions of individuals are proportional to a baseline hazard and (d) animals are censored randomly (Murray, 2006). Our attempt to randomly capture animals while congregated on winter range is the standard approach for achieving a representative sample from a migratory ungulate population. Mortality risk was independent among animals because we did not capture more than one deer from the same group and sampled across the study area. Potential bias introduced by censoring individuals of unknown fates or due to transmitter malfunction was not an issue because all animals either died during the study or survived.

We created annual baseline hazard functions by including year as a stratum in our CPH so that the proportional hazards assumption was only required within years. An additional benefit of including year in the model was accounting for potential annual variation in survival within mule deer populations (Monteith et al., 2014) and allows us to isolate the effects of individual parameters. For model selection, we fitted all possible combinations of the five migration factors and their interactions when possible. We ensured parameters in the same model were not pairwise correlated by using the *hetcor* function in the 'polycor' R package (correlation coefficient $|r| \geq 0.60$; see Table S1 in Supporting Information). After estimating all possible models under these restrictions, we ranked models using Akaike's information criterion (ΔAIC_c) corrected for small sample sizes (Burnham & Anderson, 2002; see Table S2). Once the top model was identified by the lowest AIC_c , we used Schoenfeld residuals to assess model fit (Schoenfeld, 1982), where residuals for each covariate were defined for every individual that died (Therneau & Grambsch, 2000). To test the assumption of proportional hazards assumption within years, we ranked the Schoenfeld residuals associated with each covariate in the order of deaths and plotted the ranked residuals over time. A non-zero slope in this plot indicates a lack of proportionality. After the assumption of proportional hazards was confirmed, we then calculated 90% confidence intervals (CI) for various hazard ratios to determine statistical significance and make inferences on the magnitude of the effect each parameter had on mortality risk. We also used hazard ratios and CIs from our top model to visualize the spatial variation in risk by predicting mortality risk for individual migratory routes. We plotted relative risk of mortality by dividing it into three equal-area percentile bins that reflected low, moderate and high risk. Lastly, we plotted the cumulative survival

probabilities over the duration of study to further examine and illustrate effects of model parameters on deer survival.

3 | RESULTS

Of the 66 marked deer that lived through at least one migration, 44 died during our 6.5-year study period. Most deaths ($n = 22$) occurred during the winter (December–March), followed by a smaller number of deaths in spring (April–June; $n = 11$) and autumn (September–November; $n = 7$). Only six animals died during summer (July–August). The number of deer monitored each year ranged from a maximum of 43 in 2012 to a minimum 23 in 2017. All marked deer seasonally migrated 38–114 km to summer ranges in Colorado, with an average distance of 73 km (SE = 2.12). The number of deer that migrated to each of the three summer ranges, and along each of the four high-use migratory routes varied (Table 1). Fifty-six per cent of deer ($n = 18$) that migrated on high-use exterior routes went to the NSJ summer range, 31% to the SSJ summer range ($n = 10$) and 13% to the VS summer range ($n = 4$). Similarly, 46% of deer that migrated on high-use interior routes went to the NSJ summer range ($n = 13$) and 54% to the SSJ summer range ($n = 15$). No deer that followed an interior route went to the VS summer range. Overall, the total number of deer that migrated to the NSJ and SSJ summer ranges were similar, but only four deer migrated to the VS summer range (Table 1).

Our top CPH survival model included summer range and the migratory route parameter categorized as high-use interior, high-use exterior and low-use (Figure 1; Table 2). Migration distance, migratory speed and the number of administrative boundaries were not included in the top model. The next best survival model included only the migratory route parameter categorized as high-use exterior, high-use interior and low-use ($\Delta AIC_c = 0.964$). The proportionality tests for each factor in the model showed minimal disproportionality in any dimension or globally (p ranged from 0.14 to 0.56 across factors, global $p = 0.30$), indicating the proportional hazards assumption was met.

Mule deer survival was influenced by choice of migration route, where mortality risk was nearly three times higher (mean [90% CI];

2.76 [1.54, 4.96]) for deer using exterior routes compared to interior routes (Table 2). We could not distinguish differences in mortality risk between low-use routes and interior or exterior routes (Table 2). Summer range also had a clear influence on mule deer survival and was notably lower in the SSJ summer range compared with the NSJ and VS summer ranges (Table 2; Figure 2). Specifically, the mortality risk (i.e. hazard ratio) of deer using the SSJ summer range was approximately 2 (1.904) times higher than the NSJ summer range and 3 (2.99) times higher than the VS summer range (Table 2). In contrast, the mortality risk of deer migrating to the NSJ compared to the VS summer ranges were not different, as evidenced by the CI containing 1 (Table 2; hazard ratio = 0.636, 90% CI = 0.226–1.790).

Deer that migrated along interior routes to summer ranges NSJ and SSJ had cumulative survival rates 27%–33% higher compared to deer that migrated along exterior routes (Figure 2). Cumulative survival was highest for deer that migrated along interior routes to NSJ summer range (0.54; Figure 2). Individuals with the lowest survival used exterior routes to access the SSJ summer range (0.04; Figure 2). We note that inferences to the VS summer range were limited by small sample size ($n = 4$; Table 1). Overall, the effects of both migration route and summer range were evident in model predictions for individual migratory routes that clearly showed higher risk associated with use of the exterior routes and the SSJ summer range (Figure 3).

4 | DISCUSSION

Recent studies have revealed the critical roles that migration behaviour and migratory habitats play in the nutritional ecology of large herbivores, as a means to track emerging, high-quality vegetation (Aikens et al., 2017; Merkle et al., 2016; Myrsetrud, Vike, Meisingset, & Rivrud, 2017) and improve nutritional condition (Hebblewhite & Merrill, 2009; Middleton et al., 2018; Rolandsen et al., 2017). This growing body of work is adding new urgency to the conservation of migratory corridors – not just the seasonal ranges on either end of them – as a strategy for sustaining large herbivore populations around the globe (Berger, 2004; Harris et al., 2009). However, our study strongly suggests that migratory routes and summer destinations vary in their influence on ungulate survival. Specifically, we found the risk of mortality for individual deer was nearly three times higher when they used some routes (exterior) compared to others (interior) and that mortality risk could double depending on choice of summer range. These findings are important to our basic understanding of migration and further suggest that different migration corridors may have different value to conservation and restoration efforts.

Similar to research that has shown variation in seasonal-range quality can influence individual fitness (Searle, Rice, Anderson, Bishop, & Hobbs, 2015), our work shows some migration routes may confer greater fitness benefits than others (sensu Briedis & Bauer, 2018). Regardless of summer range destination, we found the survival of deer was 27%–33% lower for animals that migrated along

TABLE 1 Number of mule deer that used high-use interior, high-use exterior and low-use migratory routes to access North San Juan, South San Juan and Valle Seco summer ranges in southwest Colorado, USA, 2011–2017

Summer range	Migratory routes				Low-use	Total
	High-use exterior		High-use interior			
	A	D	B	C		
North San Juan	18	0	10	3	2	33
South San Juan	0	10	3	12	4	29
Valle Seco	0	4	0	0	0	4
Total	18	14	13	15	6	66

TABLE 2 Cox proportional hazards coefficients, standard errors, hazard ratios and 90% confidence intervals for best model effect of summer range and migratory route on the mortality risk of adult female mule deer in northern New Mexico and southern Colorado, USA, 2011–2017

Parameter	Levels compared		Relative hazard			90% CI	
	Base	Target	Estimate	SE	Hazard ratio	Lower	Upper
Summer	VS	SSJ	1.097	0.651	2.990	1.027	8.734
Summer	NSJ	SSJ	0.644	0.330	1.904	1.106	3.279
Summer	NSJ	VS	-0.453	0.629	0.636	0.226	1.790
Route	Exterior	Low-use	-0.425	0.561	0.654	0.260	1.646
Route	Interior	Exterior	1.016	0.356	2.762	1.538	4.960
Route	Interior	Low-use	0.591	0.569	1.806	0.708	4.606

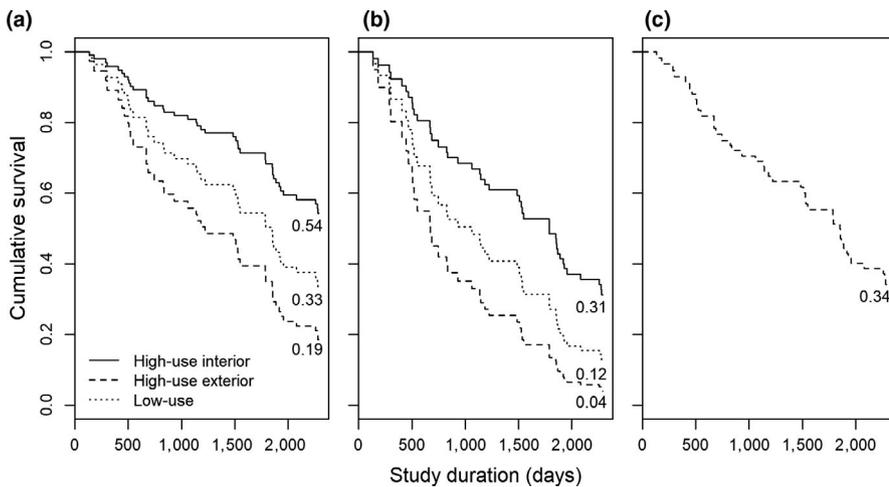


FIGURE 2 Cumulative survival rates for mule deer that migrated along high-use interior, high-use exterior and low-use migratory routes to (a) North San Juan, (b) South San Juan and (c) Valle Seco summer ranges in Colorado, USA, 2011–2017

routes categorized as exterior compared to interior. This is, to our knowledge, the first evidence of varying demographic benefits associated with the choice of migration routes in ungulates. Indeed, perhaps due to the challenges inherent in monitoring the migrations of enough individuals over a significant time period (Furey, Vincent, Hinch, & Welch, 2015; Trierweiler et al., 2014), such evidence is rare in any migratory taxa. In one example, however, a study of an Atlantic puffin *Fratercula arctica* colony, Fayet et al. (2016) found that breeding success varied among migratory routes. In another juvenile salmon (*Oncorhynchus nerka*) and hatchery steelhead smolts (*Oncorhynchus mykiss*), the choice of a route influenced early marine survival (Furey et al., 2015; Healy et al., 2017). With such differential impacts on fitness, the choice of migration routes may even result in selection for certain genetic traits over time (Delmore & Irwin, 2014). Despite limited evidence to date, our work combined with these studies in birds and fish suggest that a link between migratory routes, fitness and demography could exist more widely across taxa. Better understanding this relationship could shed new light on the process by which migratory behaviours and routes regulate populations.

In the context of land use planning and conservation efforts, this spatially explicit connection between migratory route and survival carries important management and conservation application. Specifically, limited financial resources and competing land uses may force managers to prioritize one or two routes from a suite of available routes for conservation action. Provided adequate

data, such prioritizations can be made with numerical-based criteria, where migratory corridors used by a larger proportion of the sampled population are assumed to be more important than those used by fewer animals, that is, high-use routes (Sawyer et al., 2009). Although biologically intuitive, this approach alone does not account for differences in quality among corridors. Our findings show that modelling survival with migratory parameters can reveal spatially explicit differences in mortality risk – knowledge that can help detect risk factors and target conservation activity (e.g. habitat protection or enhancement) at specific migratory routes or seasonal ranges.

Although our study indicates mortality risk can be influenced by choice of migratory route, it does not identify the specific factor(s) responsible for different survival rates. Given that 50% of deer died during the winter, we hypothesize that some of the differential mortality risk observed between migratory routes may be a function of forage quality at stopover sites (Sawyer & Kauffman, 2011), which in turn have nutritional carry-over effects that manifest on winter ranges (Harrison, Blount, Inger, Norris, & Bearhop, 2011). Our CPH modelling suggests that migratory distance and speed (Schuyler et al., 2019) were not driving factors, despite migration being a dangerous activity for birds (Klaassen et al., 2014; Scott & Holmes, 2002) and mammals (Nicholson et al., 1997; Sawyer et al., 2016).

Of course, there are other factors that could influence the quality or fitness benefits of migratory routes, including linear features

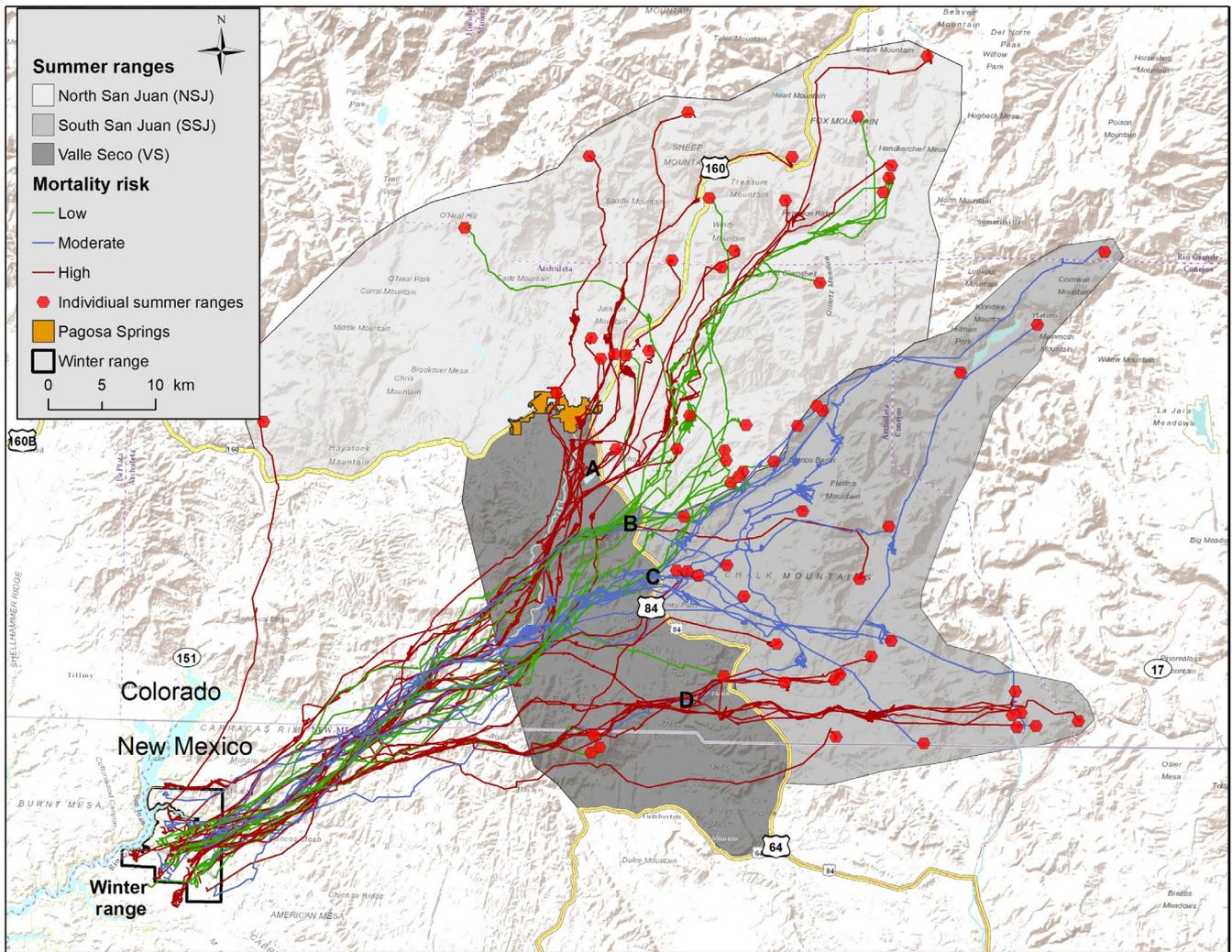


FIGURE 3 Predicted relative risk of mortality for individual mule deer ($n = 66$) in northern New Mexico and Southern Colorado, USA, 2011–2017. Mortality risk of mule deer migrating on high-use exterior routes (A and D) was three times higher than deer migrating on high-use interior routes (B and C)

like roads and fences (Løvschal et al., 2017), or other anthropogenic disturbances such as residential development, energy production and recreation (Sawyer et al., 2013). All high-use routes crossed US Highway 84 – a busy two-lane highway notorious for deer-vehicle collisions – but highway segments with the highest rates of wildlife-vehicle collisions corresponded to exterior route (A) near the town of Pagosa Springs, Colorado, USA (Colorado Department of Transportation, 2019). Relatedly, exterior routes (A) appeared to intersect with most of the expanding residential development associated with Pagosa Springs. Such development has been linked to changes in migratory behaviour, including increased rates of movement and reduction in stopover habitat (Lendrum, Anderson, Monteith, Jenks, & Bowyer, 2013; Sawyer et al., 2013; Wyckoff, Sawyer, Albeke, Garman, & Kauffman, 2018), and more broadly to lower recruitment rates (Johnson et al., 2017). Thus, it may be possible that expanding residential development around the town of Pagosa Springs and other regions in or adjacent to exterior routes increased the mortality risk of deer migrating through those areas

(see Figure S1). Another possible contributing factor may be spatial variation in predation risk (e.g. DeCesare et al., 2014) that could expose animals migrating along exterior routes to higher rates of predation. Cause of death was not determined for most animals in our study, but of the few we documented ($n = 11$), cougar *Puma concolor* predation ($n = 7$) was the most common source.

Our finding that summer range influenced deer survival builds on a growing body of literature that recognizes the importance of summer-autumn range to the annual nutritional cycle of large herbivores (Cook et al., 2004). Unlike winter ranges that have long been viewed as the most critical habitat, or limiting factor, for temperate ungulate populations (Mautz, 1978), the link between summer-autumn nutrition and fitness has only emerged in recent decades (Hurley et al., 2014; Proffitt, Hebblewhite, Peters, Hupp, & Shamhart, 2016). Although individual effects are state dependent (Monteith et al., 2013), summer range nutrition can influence body condition, pregnancy and recruitment of young (Proffitt et al., 2016; Tollefson, Shipley, Myers, Keisler, & Dasgupta, 2010). Relatedly, our results

suggest that some summer ranges are better than others (sensu Searle et al., 2015) and can directly influence the mortality risk of individuals – specifically adult females, which represent the reproductive segment of the population. Our study did not address the question of why the mortality risk of mule deer in one summer range (SSJ) was twice as high as another (NSJ), but like differences observed among migratory routes, we hypothesize that summer range differences arose due to carry-over effects of summer habitat and forage quality (Harrison et al., 2011; Hurley et al., 2014; Monteith et al., 2013). While disentangling the mechanism(s) responsible for variable mortality risk among summer ranges is an important future research need, the basic recognition that some summer ranges perform better than others may, nonetheless, immediately help direct or target management and conservation efforts aimed at improving habitat.

Utilizing a summer range or migratory route that increases mortality risk could be considered maladaptive behaviour on the part of mule deer. Site fidelity has been associated with maladaptive behaviour in other migratory ungulates that continue to use traditional habitats impacted by development, rather than seek out new habitats (Faille et al., 2010). In contrast to ungulates that exhibit flexible migratory behaviours (Peters et al., 2018), mule deer may be further predisposed to continue utilizing non-optimal routes because of their rigid migratory behaviours characterized by high fidelity to routes, irrespective of age, geography or reproductive status (Sawyer, Merkle, et al., 2019). Regardless of whether certain species are more prone to maladaptive migratory behaviours than others, the variable mortality risk we observed among migratory routes represents another form of differential migration – where the demographic consequences of migratory connectivity can be markedly different for distinct groups of individuals within the same population (Briedis & Bauer, 2018).

5 | CONCLUSIONS

Understanding how vital rates or demography may vary within a migratory population can help identify specific places (e.g. migratory routes or seasonal ranges) where certain groups are at most risk (Briedis & Bauer, 2018). Our study provides a novel link between migration and demography by revealing that large herbivores may occupy the same general seasonal ranges, but increase mortality risk by nearly three times simply by using a different migratory route. Combining survival models with spatially explicit migratory parameters offers a new set of tools for the conservation and recovery of migratory populations by targeting management efforts at specific seasonal ranges and migratory routes that reduce survival or other vital rates.

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AUTHORS' CONTRIBUTIONS

H.S. conceived the ideas and collected the data; C.W.L. and T.L.M. analysed the data; W.X. conducted the literature review; H.S. and A.D.M. led the manuscript writing. All authors contributed critically to the editing and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.js6j0pr> (Sawyer, LeBeau, LeBeau, McDonald, Xu, & Middleton, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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