Unintended consequences of species translocations: changes in distribution and habitat selection of mule deer following introduction of elk

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Abstract

Translocation of animals for conservation has a long history of successes and failures since humans began intervening with species distributions in the early part of the 20th century. Effects of translocations on other species occupying the area of introduction are rarely considered in species management plans. We hypothesized that the introduction of a large-bodied ungulate, Rocky Mountain elk (*Cervus canadensis nelsoni*), would cause a shift in the spatial distribution and winter habitat selection of a smaller-bodied ungulate, Rocky Mountain mule deer (*Odocoileus hemionus hemionus*), already occupying the study area in northeastern Nevada. We examined mule deer survey locations during an 8-year time interval from 1993 to 2001 to test hypotheses related to potential competition with or displacement of mule deer following introduction of elk in 1997. We used geospatial statistics to quantify changes in seasonal distributions of mule deer and a resource selection function (RSF) framework to model changes in selection of resources by mule deer before and after elk were translocated into our study area. Our results indicated that mule deer exhibited a shift in their core distribution by approximately 5.72 km after the introduction of elk. Mule deer changed their use of habitat by selecting shallower slopes, more north-facing aspects, and areas farther from the elk release site, where most of the elk congregated. Mule deer selected habitats with more pinyon-juniper tree cover and mixed shrublands prior to the elk translocation, indicating a potential tradeoff in thermal cover and forage quality. This research is one of the few empirical studies to describe competitive interactions between elk and mule deer on a shared winter range in North America. Implications of this research have importance for managers concerned with restoring communities to their native conditions especially where the potential for competition with non-indigenous species or other competing species with similar niche requirements exists.

Key words: competition, elk, mule deer, resource selection functions, translocation

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Introduction

For the past several centuries, humans throughout the world have been translocating species to restore depleted habitats, propagate existing populations, and conserve sensitive species from extinction (Griffith et al. 1989; Seddon et al. 2007). Research related to the effects of translocations on both native and non-native species and the corresponding plant communities that respond to translocated animals has been relatively scant compared to the large number of translocations that have been conducted (Lyons et al. 2016). Reintroductions of native species and introductions of non-native species often have well-intended and specific purposes, but they are rarely set up with controlled experimental designs or hypothesis testing (Macnab 2006). Conservationists often have a single species focus with regards to species recovery and multi-species and competitive interactions among or between species are rarely considered (Flesch et al. 2016). Regardless, scientists and land managers alike are becoming increasingly concerned with unintended consequences of moving species to new ecosystems because of unforeseen outcomes such as disease transmission, damage to native vegetation, and competition with native or extant species for space and forage (Seddon et al. 2007).

Spatial and temporal competition for resources between sympatric species of ungulates has been well described in the ecological literature (Connell 1983; Belovsky 1984; Hobbs et al. 1996; Stewart et al. 2002). In cold and arid ecosystems, such as the Great Basin Desert, intense competition for limited resources, including forage and water, may occur between large mammals such as mule deer, pronghorn (*Antilocapra americana*), elk, feral horses (*Equus ferus*), and domestic livestock (Berger 1985; Oedekoven and Lindzey 1987; Lindzey et al. 1997; Stewart et al. 2003, 2010; Gooch et al. 2017). Competitive interference may occur as aggressive behaviors that include charging, chasing, or physical displacement from water sources and forage sites (Berger 1985; Gooch et al. 2017). Alternatively, exploitive competition (Keddy 2001) may occur when resources (such as forage or water) are depleted by one species to the detriment of another species that does not occupy those sites at the same time (i.e.

temporal avoidance). Influences of niche partitioning may be apparent when two or more species with similar habitat requirements overlap in space and time but strongly separate on another niche axis such as diet (Hobbs et al. 1996; Stewart et al. 2003).

Mule deer populations have declined throughout their range and those declines underscore the importance of understanding the relationships between deer and habitats as well as with competitors (McKee et al. 2015; Heffelfinger 2018). Previous studies examined both spatial and dietary differences and competitive interactions between populations of mule deer and elk that had co-existed for many years (Johnson et al. 2000; Stewart et al. 2002, 2003, 2010) and those species typically exhibit dietary differences, but not spatial separation. Nevertheless, the short-term changes in distribution and differences in space-use between species have not been examined when one of those species is introduced to ranges exclusively occupied by the other.

Mule deer are a species of conservation concern because of their once ubiquitous distribution in the western United States and more recently, range-wide population declines (Bergman et al. 2015; Johnson et al. 2017). Of particular concern are losses to mule deer habitat through fragmentation and impacts to migration corridors (Berger 2004; Sawyer et al. 2009; Bergman et al. 2015; Blum et al. 2015). Additionally, a recent study on sage-grouse (*Centrocercus urophasianus*), an important species of conservation concern, indicated crucial conservation areas for sage grouse overlapped winter ranges of mule deer by 52–91% and migration corridors by 66–77% (Copeland et al. 2014). Those authors emphasized the importance of improving and conserving habitat for both mule deer and sage-grouse where they co-exist (Copeland et al. 2014). Anecdotally, mule deer populations have declined in many landscapes where elk populations have expanded their distributions and elk populations have increased significantly, though a direct causal relationship has not been proven (Oedekoven and Lindzey 1987; Lindzey et al. 1997; Bergman et al. 2015).

According to historical maps of elk distribution in North America, elk were relegated to relatively small, patchy occupied habitat in northeastern Nevada, where water was available on an annual basis (Thomas and Toweill 1982). In northeastern Nevada, Rocky Mountain elk (*C. canadensis nelsoni*) were released in several areas historically occupied only by mule deer to provide additional opportunity for recreational hunters (NDOW 2001). In some cases, water developments were established to provide elk a seasonal source of free-standing water where they did not previously exist. Hence, elk in this study system may act as a competitor to mule deer due to their year-round presence in water-limited areas where historically mule deer occupied on a seasonal basis.

Our objectives were to determine if mule deer were displaced by an introduced competitor, as evidenced by a significant change in winter habitat use after the introduction of elk on winter range. We predicted any potential competitive interactions would be most apparent in areas where these two species are concentrated on mule deer wintering areas, and that elk occupy on an annual basis. We quantified the spatial distribution of mule deer and elk over an 8-year time interval from 1993–2001 to determine the effects on resource selection by mule deer during winter and to test hypotheses related to competition between those recently sympatric ungulates. We hypothesized that mule deer would shift both spatial distribution and selection of resources after the introduction of a larger and highly adaptable competitor. Although we were limited by the inferences we could make with data that was collected without the primary objective of investigating these hypotheses, our retrospective analysis of the data examines spatial differences in movements and selection of habitat by mule deer on from helicopter survey locations over a relatively small temporal scale. If GPS radio collars or other means of tracking fine scale movements of mule deer would have been available our study design would have been much stronger. Nonetheless, our findings contribute towards an overall goal to better understand management implications between sympatric ungulates and potential consequences from species introductions.

Methods

Study Area

The study area is located in northeastern Nevada, encompassing Spruce Mountain (40°51’14” N, 115°10’45” W) and surrounding foothills (**Fig. 1**). Seasonal ranges occupied by mule deer in winter (December–March) varied in elevation from 1,500 m to over 3,400 m. Mule deer in this mountain range were generally migratory, although a small resident population occupies the study area year-round (Gruell and Papez 1963). The majority of mule deer that occupy the Spruce Mountain study area during winter begin migrating in late autumn from the adjacent East Humboldt Mountain range (40°52’14” N, 115°12’48” W) when snow accumulates in excess of about 25 cm at upper elevations (Gruell and Papez 1963). The elk introduction (release site) occurred during winter of 1997 at approximately 40°30’36″N, 114°49’35″W on the southern flank of Spruce Mountain (**Fig. 2**).

Figure 1. Map showing the Spruce Mountain study area in northeastern Nevada, Elko County, USA. Black circles represent mule deer locations from autumn 1993 through spring 2001.

Figure 2. Map of elk telemetry locations (red dots) for cow elk (n = 12) and population level kernel density estimates from telemetered elk locations in relation to locations of mule deer observed during 1998–2001 and the location of the elk release site (1997) in Elko County, NV, USA.

Climate in the region is influenced by northern Pacific storms characterized by heavy winter precipitation (December through March) and relatively xeric summers with occasional precipitation in the form of thunderstorms. Annual summer precipitation ranges from 10 cm to 40 cm (Western Regional Climate Center: Cooperative climatological data summaries). Winter precipitation is highly variable and typically occurs in the form of snow at upper elevations (> 2,500 m). At lower elevations (< 2,500 m) soils are characterized by volcanic ash and dominated by sagebrush (*Artemisia tridentata* and *A. nova*) with annual precipitation from 30.5 cm to 38.1 cm (Bristow et al. 2014).

The study area encompasses a variety of vegetation communities typical of the Great Basin including dominant shrubs such as mountain big sagebrush (*Artemisia tridentata*),bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus viscidiflorus*). Grassland communities such as bluebunch wheatgrass (*Pseudoroegneria spicata*), needle grass (*Stipa spp*), and exotic annual grasses (*Bromus tectorum*) occur at lower and mid-elevations. Sub-alpine zones were dominated by pinyon-juniper woodlands (*Pinus monophylla*, *Juniperus osteosperma*), and a variety of other conifers including limber pine (*Pinus flexilis*) and white fir (*Abies concolor*) (Critchfield and Allenbaugh 1969). Pinyon-juniper woodlands are a mix of early and late-seral successional phases with varying degrees of canopy closure (Tausch and Tueller 1977; Bristow et al. 2014).

Statistical Analyses

We used an existing data set of mule deer helicopter surveys conducted in autumn and early winter to examine the effects of introduced elk on spatial use patterns and habitat selection of mule deer before and after the release of approximately 150 elk during winter of 1997. Data on elk release sites and mule deer helicopter surveys were obtained from the Nevada Department of Wildlife (NDOW). Helicopter surveys consisted of directed-search transect method (Bender et al. 2003; Mason et al. 2006). NDOW typically used a Bell 206 Jet Ranger III to survey mule deer on winter ranges. A primary observer was located in the front seat of the helicopter, while a secondary observer and data recorder were positioned in the rear seat of the helicopter. Helicopter surveys were conducted following hunting seasons (generally ending on the second week of November) each year to minimize bias or changes in animal distribution due to hunting pressure (Bender et al. 2003; Sawyer et al. 2016). Survey dates for autumn ranged from 17 November–18 December (median 13 December); and 8 March to 13 April (median 16 March) for all spring surveys. We collected information on group composition including group size, age and sex class of animals, and location of group observed (Keegan et al. 2011). All data locations were converted to Universal Transverse Mercator (UTM) for spatial analyses. Because those data were obtained after management actions were completed, a before-after-control-impact (BACI) or other manipulative study design was not possible. The following methods outline the post-hoc analysis that was completed to provide inference on the original research questions and predicted outcomes. Additionally, we collected snow depth information to account for potential changes in distribution due to winter snow depths, from the nearest available weather station (approximately 50 km to the southwest) in which snow depth information was available (**Fig. 3**). We acknowledge that some assumptions must be made using the limited data provided in this manuscript and that any inferences made from the statistical methods we describe must be taken with caution. For instance, we only have survey locations from mule deer observed approximately twice annually for the duration of this study. Unfortunately, no radio collar or movement information on mule deer was available for this study due to the post-hoc nature of the analysis.

Figure 3. Mean monthly snow depth for March and December from snow telemetry station located on Green Mountain Bench (location 40°23’00” N, 115°32’00” W) for 1993–2001 in Elko County, NV, USA.

We used multi-response permutation procedures (MRPP; Oehler et al 2003; Stewart et al 2015) to determine if the spatial distribution of mule deer differed from random points and also to examine if selection occurred during the study period using the *mrpp* function in R package “Blossom” version 1.4 (R v 3.6.1, **www.r-project.org**, accessed 20 October 2019). MRPP analyses are nonparametric statistics that rely on random permutations of data based on Euclidian distances (average within-group distances) between identified groups (Talbert and Cade 2005), which in our case were locations of mule deer from helicopter observations. We compared the spatial distribution of mule deer locations prior to the introduction of elk (1993–1996, n= 318) with the locations of mule deer for 4 years following the introduction of elk to the study area (1998–2001, n = 184) and binned the locations by season for autumn (November or December) and spring (March or April) to account for temporal variability in space use by mule deer and due to limitations on data available for the study. Additionally, we quantified spatial distribution of mule deer before and after elk introduction using kernel density estimates based on group locations of mule deer using the ArcGIS extension ArcMET (ArcMet 10.2.2

v3, **http://www.movementecology.net**, accessed 30 Jun 2019). We calculated 50 m resolution utilization distributions for each time period using a bivariate Gaussian kernel with a fixed smoothing parameter (Worton 1989). We further calculated contour intervals of 95%, 90%, and 50% to represent the outer, inner, and core range of mule deer activity respectively (Keating and Cherry 2009). We did not include mule deer data from the year 1997, the first year of the elk introduction, because mule deer were likely to be only partially affected by the initial release of elk and to allow for a settling period for elk to be established on the landscape (Yott et al. 2011). To our knowledge, the elk release site was not occupied by humans or vehicles for more than a few hours on the day that elk were released from livestock trailers, thus it is unlikely that human presence had any long-term effects on mule deer behavior or distribution. Twelve adult cow elk (n = 12) were radio-collared with very high frequency (VHF) radio collars and monitored monthly via fixed-wing aerial telemetry for approximately 3 years post release. We calculated bivariate kernel density estimates for telemetered elk (n = 79 locations) during the months of November, December, and April to map the spatial distribution of elk during the winter after the translocation occurred using ArcMap (ESRI, Redlands, CA).

We estimated resource selection functions (RSFs) with a use-availability design for mule deer locations within a general resource selection framework for telemetry data (Johnson et al. 2006). We generated RSFs by fitting generalized linear mixed-effects models with a binomial error distribution and logit link function using the “lme4” package in program R (Johnson et al. 2006; Blum et al. 2015; McKee et al. 2015). To develop RSFs we chose variables known to be important habitat components for mule deer (Pierce et al. 2004; Blum et al. 2015; McKee et al. 2015) including vegetation class, slope (%), aspect [sine (east-west) and cosine (north-south)], elevation (m), terrain ruggedness (Sappington et al. 2007), distance to water (m), and distance to the elk release site (m). We standardized all continuous variables using the ‘*scale’* function in program R, which allowed for direct comparisons of effect sizes of parameter estimates (Boyce 2006). Additionally, we reclassified vegetation classes to 5 functional cover types based on the distribution of deer locations and available cover in our study area (Kie et al. 2002). Those generalized vegetation classes included: big sagebrush steppe (reference category), mixed shrubland, mixed conifer, pinyon-juniper, and salt desert scrub.

We developed separate RSFs for each time before and after elk introduction to ascertain if selection of resources changed over the course of the entire study period (1993–2001). We fit models for two time intervals corresponding to the period before elk introduction (1993–1996) and after elk were introduced on the Spruce Mountain study (1998–2001). We considered all available covariates for both time periods to directly compare the potential change in parameter estimates and their associated effect sizes on resource selection by mule deer before and after the introduction of elk. Additionally, we used 85% confidence intervals to assess the statistical significance of individual parameter estimates for standardized model coefficients to account for uncertainty in parameter estimation (Arnold 2010; Thalmann et al. 2015; Aho et al. 2017). We used the model results from resource selection functions to create maps of predicted mule deer habitat before and after elk introduction by first calculating a continuous raster surface for each model by solving the logistic equation: $w(x) = \exp(\beta_0 + \beta_1 X_1 + \cdots + \beta_i X_i)$ using the raster calculator in ArcGIS (v.10.3.1). We then rescaled resource selection maps from 0 to 100 to directly compare raster results before and after elk introduction. We converted the rescaled continuous raster maps into categorical values (10 equal interval bins) using the ‘slice’ function in ArcGIS and ranked the predicted habitat categories in order of increasing resource use (1 = lowest to 10 = highest) based on use vs availability (Boyce 2006; Morris et al. 2016). We quantified differences between the resulting maps using the ‘Minus’ function in ArcGIS (Spatial Analyst v.10.3.1) and calculated the standard deviation in pixel values for each cell using the raster calculator. We then quantified the changes in predicted use for each vegetation class by summing the total acreage for all habitats (1 through 10) and dividing by the individual pixel count for each habitat category to calculate the change in total resource use.

Results

The spatial distribution of mule deer varied significantly from random locations (MRPP analysis: $n = 318$ locations before elk and $n = 184$ locations after elk, $P < 0.001$). Mule deer were more widely dispersed during spring (MRPP; $\delta = 8.70$)than autumn (MRPP; $\delta = 5.52$) surveys and average within-group distance varied significantly by season and year ($P < 0.001$; **Fig. 4**). The spatial distributions of mule deer were significantly more clustered before the introduction of elk compared to years after elk were present on the landscape for all seasons with the exception of spring 1995 (MRPP before elk = 1.48, MRPP after elk = 1.77, $P < 0.001$; **Fig. 2**). Kernel density estimates between the two time periods also indicated a shift in use of space by mule deer after elk were introduced to the study area. Examination of the 95% contour (outer range) and 50% contour (core range) of the utilization distributions indicated that mule deer expanded their distribution by approximately 5.72 km to the northeast, and that the two core areas of use before elk (**Fig. 5a**) became one continuous core activity center with a more even distribution of space use across the landscape following the introduction of elk (**Fig. 5b**). The outer range (95% contour level) of mule deer distribution increased by 24.1% from 455.4 km^2 in the period before elk to 600.5 km^2 after elk were introduced (**Fig. 5**). The inner core range (50% contour level) increased by 32.4% from 104.2 km^2 before elk to 154.8 km^2 after elk introduction (**Fig. 5**).

Figure 4. Multi-Response Permutation Procedure (MRPP) within-group delta values by year and season for mule deer locations before (a) and after (b) introduction of elk in eastern Nevada, USA. Delta values represent within-group Euclidean distances between groups in meters.

Figure 5. Percent contour levels from kernel density estimates (KDE) based on mule deer locations before elk introduction (a) from autumn 1993 to spring 1996 and and after elk introduction (b) from autumn 1998 to spring 2001 in eastern Nevada, USA. Contour levels were calculated from utilization distribution (UD) and represent the 95% (outer range), 90% (inner range), and 50% (core activity range) from 50-m resolution GIS raster of the utilization distribution (UD).

We evaluated all covariates used in resource selection functions before elk introduction and after elk release to determine whether those variables changed over time (**Table 1**). Mule deer proportionally used more of the pinyon-juniper habitat type than any other habitat category during the before-elk and after-elk time periods (**Table 2**). The second most preferred habitat category for mule deer was mixed shrubland, and the least used of the five habitat types was mixed conifer (**Table 2**). When comparing relative importance of habitat use between time periods, mule deer showed modest but significant changes in preference for vegetation class (**Fig. 6**). Pairwise comparisons of habitat categories indicated that relative importance of mixed shrubland was significantly lower before elk introduction compared to the time period after elk (13.2% relative importance before, 19.3% after elk, $P < 0.0005$ after Bonferroni correction for multiple comparisons). Relative use of pinyon-juniper habitat by mule deer also decreased from 84.6% before elk were introduced to 76.4% importance during the time period after elk were introduced ($P < 0.0005$, after Bonferroni correction for multiple comparisons, Fig. 6).

Table 1. Descriptive statistics for variables used in resource selection functions. Locations were obtained from groups of mule deer observed on helicopter surveys before the introduction of elk (n = 318) from 1993–1996 and after elk (n = 184) were released from 1998–2001 on Spruce Mountain, NV, USA.

Table 1a.Before elk 1993–1996

	Used Locations				**Available Locations**			
Variable	**Mean**	**SD**	**Min.**	**Max.**	**Mean**	**SD**	**Min.**	**Max.**
Elevation (m)	2,276	212	1,738	2,894	2,147	243	1,723	3,034
Slope (°)	12.2	6.2	1.3	24.9	9.7	6.5	0.2	33.1
Terrain ruggedness	–0.08	0.58	–1.00	1.00	0.003	0.004	0.000	0.035
Cosine aspect	0.08	0.81	–1.00	1.00	–0.02	0.70	–1.00	1.00
Sine aspect	–0.08	0.58	–1.00	1.00	0.01	0.72	–1.00	1.00
Distance to water (m)	2,454	1,652	240	10,950	3,374	2,226	94	11,215
Distance to elk (m)	101	49	17	240	124	63	3	299

Table 1b. After elk 1998–2001

	Used Locations				**Available Locations**			
Variable	**Mean**	**SD**	**Min.**	**Max.**	**Mean**	**SD**	**Min.**	**Max.**
Elevation (m)	2,232	288	1,773	2,895	2,149	246	1,724	3,035
Slope (°)	10.8	6.6	1.3	27.9	9.5	6.5	0.2	33.0
Terrain ruggedness	0.004	0.004	0.000	0.016	0.003	0.004	0.000	0.035
Cosine aspect	0.17	0.75	–1.00	1.00	–0.03	0.70	–1.00	1.00
Sine aspect	0.05	0.64	–1.00	0.97	0.01	0.72	–1.00	1.00
Distance to water (m)	3,091	1,654	426	7,696	3,281	2,230	95	11,215
Distance to elk (m)	126	65	17	298	117	58	3	275

Table 2. Percentage of available and used vegetation classes before the introduction of elk (1993–1996) and after elk were released (1998–2001) on Spruce Mountain, NV, USA, derived from a 30-m resolution habitat layer obtained from www.landfire.gov.

Habitat type	Available habitat (%)	Before elk use (%)	After elk use (%)
Mixed Conifer	2.5	2.5	5.4
Big Sagebrush Steppe	7.9	7.5	9.8
Mixed Shrubland	29.8	18.9	23.4
Pinyon-Juniper	53.4	67.3	51.6
Salt Desert Scrub	6.3	3.8	9.8

Figure 6. Relative importance (use multiplied by availability, rescaled to 100%) for mule deer locations for years before (1993–1996) and after (1998–2001) the introduction of elk to Spruce Mountain, NV, USA. Asterisks indicate significant differences of multiple group (pairwise) comparisons using Bonferroni corrections (significance level of 0.0005).

Mule deer avoided mixed conifer and selected both pinyon-juniper and mixed shrubland relative to the proportional use of big sagebrush steppe (reference category) before the introduction of elk but did not show any selection or avoidance of these habitats after elk introduction (Fig. 7). They also exhibited strong selection for salt desert scrub after elk were introduced (Fig. 7). Mule deer in our study system used lower slopes after elk were introduced compared to their selection for intermediate slopes before elk. They selected for more northern aspects (cosine of aspect) than random during both time periods (Fig. 7). Mule deer selected for eastern aspects before elk and more western aspects after elk introduction, although the confidence intervals for sine aspect in the post elk period overlapped 0. Mule deer did not show selection or avoidance of water sources during either time period, but instead used water in proportion to availability throughout the landscape. Mule deer exhibited strong selection for higher elevations during both time periods. After the introduction of elk, mule deer selected areas farther from the elk release site (Fig. 7) indicating a strong avoidance of elk after their introduction to the study area.

Figure 7. Standardized model coefficients (β ± 85% C.I.) from mule deer resource selection functions estimated using observed groups of mule deer before (a) and after (b) elk introduction to the study area in northeast Nevada, USA from 1993–2001. Habitat classes are in relation to the reference category (sagebrush steppe) for habitat classes used in resource selection functions.

Results from our habitat selection ranking and predictive maps indicated mule deer exhibited strong decreases in use of available habitat compared to years before elk (Table 3, Fig. 8). The largest change in habitat selection occurred near the core range of mule deer activity—after elk were introduced, a decrease of 50–83% of available habitat occurred in the top three values of available habitat prior to elk (Fig. 8; Table 3).

Table 3. Predicted mule deer habitat (ha) ranked from lowest (1) to highest (10) value and change in

selection direction (%) from before elk to after elk introduction on Spruce Mountain, NV, USA. Mule deer habitat value was calculated from resource selection functions.

Habitat Rank	Before elk area (ha)	After elk area (ha)	Change (%)
1	631,026	455,229	–28%
2	272,736	467,613	71%
3	113,814	119,484	5%
4	51,606	37,431	–27%
5	20,691	16,335	–21%
6	9,306	8,217	–12%
7	5,211	3,978	–24%
8	3,231	1,620	–50%
9	2,286	567	–75%
10	684	117	–83%

Figure 8. Predicted probability of mule deer habitat selection on Spruce Mountain, NV, USA before (a) and after elk introduction (b), and the comparison between the two maps using standard deviation (c) and change (%) in predicted value (d) for each pixel in the study area.

Discussion

Our hypotheses that smaller-bodied mule deer would be spatially displaced and change how they selected resources in the presence of larger-bodied, introduced elk were supported. Mule deer were more widely dispersed during both spring and autumn surveys after elk were introduced to the study area, and they shifted their core activity use to the periphery of their former range. We posit these observed changes were likely due to an avoidance of elk and likely resulted in decreased fitness consequences. Similarly, habitat selection changed significantly during the period after elk were introduced, and most notably, mule deer strongly avoided the elk release site (**Fig. 7**). Our results complement previous studies that have described differences in niche partitioning (Stewart et al. 2002, 2003, 2010) and competition for resources (Johnson et al. 2000) between these sympatric species where they have co-occurred on the landscape for long time periods. Our results demonstrate that mule deer may exhibit changes in habitat selection and use of space when confronted with a novel and larger-bodied competitor (elk) especially on shared winter ranges in arid environments like the Great Basin.

Competition for limited resources plays a major role in the distribution of animals across the landscape (Hutchinson 1959; Connell 1983; Schoener 1983; Hobbs et al. 1996) yet is not typically incorporated in species distribution models or management plans. Animals often make tradeoffs in the face of increased interspecific competition by sacrificing preferred habitat characteristics for marginal habitat with less cost including energetic cost of contest competition or loss of resources to exploitive competition (Wilmshurst et al. 2000). The specific mechanism by which competition occurs is poorly understood in many species of ungulates, although the subject has been studied in mule deer and elk for at least several decades (Berbach 1993; Lindzey et al. 1997; Johnson et al. 2000; Stewart et al. 2010). Most studies have described either indirect effects or dietary niche partitioning of these two species where they have co-existed for many years. Our study is the first to examine the short-term impacts to mule deer by Rocky Mountain elk where no overlap in distribution occurred between the two species, prior to the elk translocation. Mule deer in our study system exhibited a shift in spatial distribution and habitat use following introduction of elk over a relatively short timeframe (changes occurred over a four-year time span). This displacement was largely inferred from our analysis of changes in selection of resources and spatial analyses of mule deer location data.

As a caveat to our findings, we did not directly measure a behavioral or demographic response to this mule deer population. Rather, we observed a response in the mule deer locations (and corresponding changes in resource selection) that corresponded to the same time frame when the elk translocation occurred, based on the data available. Unfortunately, a true replicated study design was not possible given the post-hoc nature of the analysis and the data that was collected when the translocation occurred. Nonetheless, we are confident that the observed changes are related to the introduction of the elk, and that we controlled for as many factors as possible in the analysis. Although weather covariates were not available at the spatial locations, where we observed mule deer, we did obtain March and December snow depth data from the nearest available snow telemetry site (approximately 50 km to the southwest) which indicated that snow depth was variable both before and after the elk introduction, the average monthly snow depth did change appreciably over the course of the study duration (**Fig. 3**), although March was more variable than December and had higher overall snow depths, which may have contributed to differences in elevations used by mule deer. As indicated by the spatial distribution of the elk telemetry points (**Fig. 2**), the distribution of elk did not appear to vary significantly during the 4 years post translocation. Additionally, the core of the elk range, as indexed by the kernel density estimates from telemetered elk (n = 12) was very near the elk release for the duration of the study. We feel the strong presence of telemetered elk, coincided with the major core of distribution where mule deer were observed prior to the elk introduction.

We cannot rule out alternative causations of these observed shifts in distribution such as changes in forage quality or availability, temperature, or other environmental explanations. Additionally, we did not control for the possibility of changes in other large mammals such as feral horses or domestic livestock that occurred in low numbers in our study area (BLM 2017). Nevertheless, we believe that these alternative hypotheses are unlikely as explanatory factors because winter conditions remained relatively constant over the course of our study, and field personnel conducting helicopter surveys did not document or note significant changes in domestic livestock or feral equids prior to or immediately following the introduction of elk to the study site.

Our results provide support for this hypothesis as a possible explanation because of changes in habitat selection and the changes in the distribution of mule deer we observed following the introduction of elk to the study area. The first introduction of elk occurred in 1997 in our study area and elk numbers have continued to increase. Population estimates for the elk population on Spruce Mountain indicate that the elk population may have increased by as much as 25% during the course of this study, whereas the mule deer population estimate for the Ruby Mountain deer herd (the deer herd in our study system is a part of a larger metapopulation) declined by more than 17% during the same time period (NDOW 2001). Indeed, harvest rates and opportunity for mule deer hunting also declined during years following elk translocation, where mule deer harvest averaged about 1,900 bucks annually for the management area (Nevada deer hunt units 101–109) during the 3 years prior to the elk introduction and then declined to an average of about 1,000 mule deer bucks harvested in the 5 years post elk introduction, a decrease of nearly 47% (NDOW, unpublished data). Although, the study area we examined was only one hunt unit in the overall management area available for hunters to harvest, the mule deer inhabiting the Spruce Mountain study area represent approximately one-third of the overall metapopulation of this mule deer herd. Additionally, harvest rates of mule deer may not be entirely representative of changes in mule deer population size, as hunting success rates can vary with weather conditions, availability of male antlered deer, and changes in annual quota set by the state wildlife commission.

In general, mule populations in this study system and across Nevada peaked in the late 1980s and declined for several years in the early 1990s likely due to impacts from density dependence and compounding drought conditions (Wasley 2004). Many factors have resulted in declining mule deer populations across the western United State, including Nevada, however we contend that the short time frame of this study, lack of significant changes in forage abundance, weather conditions, or other factors, likely did not have the effect of changing mule deer distribution in this study area, but rather the introduction of elk and presence of elk, near the elk release site for at least 3 years post release, resulted in the changes we observed in our study.

Management Implications

Translocations of ungulates is a common occurrence not only in the western United States, but also in many parts of the world. Red deer (*Cervus elaphus*), fallow deer (*Dama dama*), sika (*Cervus nippon*), bighorn sheep (*Ovis canadensis*), and other species of ungulates have been moved to many areas often not well adapted to herbivory by large herbivores and without consideration of extant native species in the same area. The translocation of elk in our study system was ostensibly within the range limits of elk; however, this mountain range in northeastern Nevada was presumably devoid of elk prior to European settlement (Toweill and Thomas 1982) largely due to the lack of persistent water sources. In this instance, introduction of elk into critical winter range occupied by mule deer appears to have had detrimental effects on mule deer occupying this wintering range. Our study suggests that the introduction of a larger-bodied competitor into the range of smaller species caused shifts in selection of resources and changes in use of habitats to those of lower quality. Those habitats were widely considered to be important for maintenance of energy reserves and over-winter survival of mule deer in the Great Basin (Bishop et al. 2005, 2009). The observed shift in winter range use by mule deer appeared to be a direct result of the avoidance of elk as indicated by our distance to elk parameter estimate (mule deer avoided the elk release site during the four years of post-release monitoring). Mule deer appeared to make a trade-off in their selection of habitat by switching from mixed shrublands and pinyon-juniper cover types to a less palatable forage community (salt desert scrub). While mixed shrublands likely provide the nutritional requirements necessary for maintenance body fat reserves, pinyon-juniper is known to provide thermal cover to mule deer during the winter (Parker and Gillingham 1990; Cook et al. 1998; Bowyer and Kie 2009). Our study used a spatially analytical approach combined with resource selection functions to quantify observed patterns and changes in spatial distributions of a native ungulate following anthropogenic introduction of (in this instance) a nonindigenous species. Implications of this research have importance for conservationists and land managers seeking to introduce recreational opportunities without considering other competing species with similar niche requirements. We suggest that areas selected to receive translocations of ungulates be carefully evaluated prior to translocations or reintroductions to minimize negative impacts of those potential competitors on community structure. Our research may also provide the preliminary data and evidence for future studies exploring the role of changing habitat conditions and elk population increases on the distribution of mule deer in the Great Basin where resources such as forage, water, and thermal cover are highly limited.

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