## Research Article



# Effects of Distribution, Behavior, and Climate on Mule Deer Survival

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ABSTRACT Mule deer (Odocoileus hemionus hemionus) populations in North America are a valuable economic wildlife resource, with the managed harvest of this species reflecting societal values and recreational opportunities in many parts of the western United States. Managing mule deer populations while allowing for harvest requires an understanding of the species' population dynamics, including the specific factors associated with population change. We conducted a 7-year (2005-2012) study designed to investigate habitat use and survival of mule deer in eastern Oregon, USA. We used known-fate data for 408 adult female radiocollared mule deer to estimate monthly survival rates and to investigate factors that might affect these rates, including seasonal distribution, temporal effects (seasonal, annual, and trends across season and year), movement behavior, and local weather and regional climatic covariates. Variation in survival rates of female mule deer was best explained by an additive effect of migration behavior, differences in survival during the fall migration period compared to the rest of the annual cycle, and precipitation levels on winter ranges of individual deer. Estimates of annual survival were higher for migrants (0.81-0.82), compared to residents (0.76-0.77). Survival was lower for migrants and residents during fall migration (Oct-Nov) and higher amounts of winter precipitation increased survival of both groups. The results of our study suggest that migrating to potentially higher quality summer foraging areas outweighed the cost of traveling through unfamiliar habitats and energy expenditure associated with migration. © 2018 The Wildlife Society.

KEY WORDS migration, mule deer, *Odocoileus hemionus*, Oregon, population dynamics, survival, winter precipitation.

To sustainably manage mule deer (Odocoileus hemionus *hemionus*) populations while allowing for harvest requires an understanding of the species' population dynamics (Gordon et al. 2004), including the specific factors influencing population change. For ungulates in general, juvenile (<1 yr old) survival is highly variable and is the vital rate most commonly attributed to fluctuations in population size (White and Bartmann 1998, Gaillard et al. 1998). In contrast, adult female survival rates are generally characterized as high, exhibiting little temporal variation (Gaillard et al. 1998), and mule deer populations may rely more on high stable adult survival rates than other ungulate populations to prevent long-term population fluctuations (Forrester and Whittmer 2013). However, where survival rates for adult female mule deer have been quantified, they can vary temporally and spatially between populations (Nicholson et al. 1997, Unsworth et al. 1999, Bishop et al. 2005), and small changes in adult female survival of mule deer can have

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and Doak 2002). Thus, biotic and abiotic factors that increase variation in adult female survival rates can decrease mule deer population stability (Gaillard et al. 1998). Specific factors associated with temporal and spatial

major effects on the overall population growth rate (Morris

variation in adult mule deer survival rates include migration behavior (Nicholson et al. 1997), location of seasonal ranges (Bishop et al. 2005), and regional climate and local weather patterns (Monteith et al. 2011, Lendrum et al. 2014). Mule deer populations across the West contain individuals that migrate between seasonal ranges and those that do not, with migratory individuals typically more common in a population than those that do not migrate (Garrott et al. 1987, Brown 1992, Nicholson et al. 1997). The benefits of migration can include seasonal escape from predation or insect harassment (Fryxell et al. 1988, Hebblewhite and Merrill 2007) and the advantage of following seasonal food availability (Pettorelli et al. 2005, Lendrum et al. 2014) or other limiting resources (e.g., water; Murray 1995). However, mule deer that migrate must travel longer distances, and can be exposed to greater risks, such as predation or vehicle collisions associated with crossing highways (Nicholson et al. 1997).

In addition, the seasonal movement of individuals between summer and winter ranges can subject an ungulate population to varying climate or weather stresses during different parts of the annual cycle (Post and Stenseth 1999). In particular, winter precipitation (Bishop et al. 2005), winter severity (DeLgiudice et al. 2002), and midsummer drought (Brown et al. 2006) can be associated with variation in mule deer survival. Climate change models for the Pacific Northwest predict drier summers, and wetter autumns and winters (Mote and Salathé 2010) and this may increase the risk for large-scale wildfire in the western United States (Westerling et al. 2006); these are all changes that could affect mule deer at different stages of their life cycle (Post and Stenseth 1999).

The objective of our study was to estimate monthly survival rates for adult female mule deer in south-central Oregon and determine the spatial and temporal factors that affected mule deer survival. We hypothesized that survival rates for mule deer on our study area would vary in relation to 4 general factors: individual migration behavior, location and characteristics of seasonal ranges, winter weather patterns, and disturbance on seasonal ranges and during the hunting season. Specifically, we predicted decreased survival as the distance traveled between seasonal ranges increased because of an increase in migration costs (i.e., energy expenditure, risk of predation, or vehicle collision), particularly as migration routes generally included crossing between 1-3 highways. We predicted that survival rates would be negatively affected by higher winter severity because severe winter weather can make mule deer more susceptible to predation and starvation as temperatures decrease and precipitation increases (Nelson and Mech 1986, DeLgiudice et al. 2002). We predicted that deer with ranges that included the expanding urban area would have lower survival than deer with ranges outside because of higher exposure of human disturbance (Nicholson et al. 1997, Oliver and Kline 2012). Finally, we predicted that the disturbance of hunting (hunters on foot, sounds of firearms, increased vehicle use) would negatively affect females by increasing flight response time (Stankowich 2008), which could decrease time spent foraging or increase interactions with vehicles.

# STUDY AREA

The study area was located in south-central Oregon near the eastern slopes of the Cascade Range and extended into the High Lava Plains and the Basin and Range provinces (Franklin and Dyrness 1973). The study area ( $\sim$ 44,000 km<sup>2</sup>) primarily included lands under federal ownership administered by the United States Department of Agriculture Forest Service and United States Department of Interior Bureau of Land Management, with private land dispersed throughout. Although plant communities differed across the study area because of elevation and soil type (Franklin and Dyrness 1973), vegetation for a large portion of study area was typical of shrub-steppe ecosystems (low rainfall, natural grassland primary composed of sagebrush [*Artemisia* spp.]) with forested ecosystems at higher elevation. Shrub-steppe ecosystems are characterized by plant communities that

include sagebrush, antelope bitterbrush (*Purshia tridentata*), snowbrush (*Ceanothus velutinus*), rabbitbrush (*Chrysothamnus* sp.), fescue (*Festuca* spp.), and blue bunch wheatgrass (*Agropyron spicatums*). Forested ecosystems are characterized by plant communities that include ponderosa pine (*Pinus ponderosa*), western juniper (*Juniperus occidentalis*), Douglas fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*).

In addition to mule deer, the study areas supported wild populations of elk (*Cervus canadensis nelsoni*), pronghorn (*Antilocapra americana*), cougar (*Puma concolor*), black bear (*Ursus americanus*), and coyote (*Canis latrans*). Widespread livestock grazing (cattle) on private lands and through permit on federal lands administered by the Bureau of Land Management also occurred.

The climate in this region is described as having dry warm summers (Jun-Aug) with average July maximum temperatures of 27°C to 31°C, and cold winters (Dec-Feb) with average minimum January temperatures of  $-7^{\circ}$ C to  $-11^{\circ}$ C (PRISM Climate Group 2010). Annual precipitation ranged from 38 cm to 89 cm, usually in the form of snow (Franklin and Dyrness 1973), and the topography was relatively flat with gently rolling hills ranging in elevation from 587 m to 2,192 m. Soil types varied widely throughout the study area, mostly composed of pumice and ash, from the eruption of Mount Mazama over 8,000 years ago (Franklin and Dyrness 1973). Most of the area was administrated by the Bureau of Land Management (24%) or the United States Forest Service (44%) and the rest was privately owned (particularly at lower elevations). The human estimated population for the area was 254,000 people (U.S. Census Bureau 2010).

Oregon Department of Fish and Wildlife (ODFW) managed ungulate populations within the context of discretely bounded areas know as Wildlife Management Units (WMUs). The WMUs were created in 1958 to facilitate distribution of wildlife harvest levels across the state (Mace et al. 1995). State administrative boundaries within the study area included Klamath, Lake, and Deschutes counties (Fig. 1), and the Fort Rock, Interstate, Klamath Falls, Paulina, Metolius, Silver Lake, Sprague, Upper Deschutes, and Wagontire WMUs (ODFW 2003). The core study area included the Fort Rock, Sprague, Sliver Lake, and portions of Paulina, Wagontire, and Upper Deschutes WMUs. During the winter, some mule deer also occurred in Maury and Warner WMUs, north-central California, and west of the Cascade Mountain crest in McKenzie, Indigo, and Santiam WMUs.

# **METHODS**

### Capture and Handling

Research personnel from ODFW captured and radiocollared adult female mule deer from June 2005 to September 2011 (n = 456). Most deer were captured using helicopter net guns (75%; Barrett et al. 1982) with the rest captured via chemical immobilization with a rifle-fired dart (23%) or using panel or clover traps (2%; Clover 1954). We used a combination of Telazol (Zoetis, Kalamazoo, MI,



Figure 1. Location and core study area of the 408 adult female mule deer used in the known-fate survival analysis in south-central Oregon, USA, August 2005 to May 2012.

USA), xylazine, (Lloyd, Shenandoah, IA, USA), and ketamine (Bionichepharma, Galaway, Ireland) to chemically immobilize deer, with Tolazoline (Wildlife Pharmaceuticals, Windsor, CO, USA) used as an antagonist (Monteith et al. 2012). We aged (through dental examination; Erickson et al. 1970), ear-tagged, and sexed all deer captured (fawns, yearlings, adults), and radio-collared adult females. We handled all deer in accordance with protocols approved by ODFW for safe capture and handling and following recommendations of the American Society of Mammalogists (Sikes et al. 2011).

We attached global positioning system (GPS) radio-collars to adult females, with data either stored on board (3300S, Lotek, Newmarket, ON, Canada; n = 401), or downloaded remotely (4400S, Lotek; n = 55). We programmed GPS radio-collars to obtain locations every 4 hours except during fall and spring migration periods when we increased programmed location frequency to obtain a location every 90 minutes. The comprehensive location data stored on collars became available when the deer died, or once the radio-collar automatically detached from the deer 17 months after attachment. The GPS collars had a motion-sensitive sensor that caused a change in the transmitter's pulse rate if the transmitter was motionless for >4 hours (i.e., mortality signal). We investigated these mortality signals within 24-72 hours of detection and conducted necropsies if the carcass was present. We assigned each deer mortality to 1 of 8 causeof-death categories: cougar predation, coyote, illegal harvest, harvest, vehicle collision, disease, other (e.g., fence collisions, malnutrition or starvation, death during fawning), and unknown. We used a standardized protocol developed by ODFW to evaluate cause of death for every necropsy. We determined the cause of death by observing predator-specific wounds, concealment and location of the carcass, and consumption habits (Henne 1975, Wade and Bowns 1982). If it appeared that predation had occurred, we required a complete checklist of descriptive indications (i.e., bite marks, scat, tracks) at each site for a carcass to be assigned to a potential predator (cougar, coyote); otherwise we classified it as predator unknown. After we investigated a deer mortality, we collected the GPS collar and downloaded the collar location data into a geographic information system (GIS) database (ArcMap version 10.0, Environmental Systems Research Institute, Redlands, CA, USA).

#### **Explanatory Variables for Survival**

We estimated monthly survival rates for adult female mule deer from August 2005 through May 2012. We defined the mule deer annual cycle in terms of their biology with each year starting on 1 June, when most fawns are born (Speten 2014), and ending 12 months later on 31 May. We defined 4 seasons that reflected different stages of the mule deer life cycle: summer (1 Jun–30 Aug), fall (1 Sep–30 Nov), winter (1 Dec–28 Feb), and spring (1 Mar–31 May). We also identified spring (Apr and May) and fall (Oct and Nov) migration periods (Coe et al. 2015), and the hunting season (Aug–Oct) as potentially important sources of temporal variation in survival.

We plotted the GPS data for each individual deer to determine summer and winter ranges. We categorized locations as those that delineated seasonal ranges or those that reflected migration routes by examining distances and direction of sequential movements (Cupples and Jackson 2014). Each seasonal range was characterized by short movements (<3 km within 4 hr) conducted between winter and summer. We defined the beginning of the migration movement by the first movement (>3 km) outside the seasonal ranges without returning, and ended once the individual reached the new seasonal range (Thomas and Irby 1990). Once we determined each summer and winter location cluster and removed migration locations, we used spatial statistics in ArcMap version 10.0 to obtain the mean center of the seasonal range. We considered a deer to be migrating when the direction of movement was away from the mean center of one seasonal range in the direction of the other mean center seasonal range, outside of the cluster (Brown 1992). We also assigned each seasonal range center a WMU number associated with the WMU where it occurred. If a deer remained in one area the entire year then we categorized it as a resident deer and calculated a mean center using all location data. Because management and harvest pressure varied by WMU, we predicted that variation in survival could be explained by differences in WMUs where summer and winter seasonal ranges were located.

Oregon Department of Fish and Wildlife estimated mule deer herd composition annually for population trend information and hunting tag allocation (ODFW 2003). We identified groups of deer in our study based on fine-scale temporal location data from GPS collars (Cupples and Jackson 2014). We determined mule deer groups identified as herds by similarities in winter location, angle and distance of travel from winter location, and migration pathways (J. B. Cupples, ODFW, personal communication). We assigned each individual deer in our analysis to a herd group based on this characterization (Cupples and Jackson 2014).

To index human development in proximity to the seasonal ranges and migration pathways of mule deer, we used Wildland Urban Interface (WUI) geospatial data from Oregon Department of Forestry (http://www.oregon.gov/ odf/pages/fire/sb360/sb360.aspx, 27 May 2014). The WUI delineated areas where houses (urban, suburban, and sometimes rural areas) and undeveloped natural areas interface (Radeloff et al. 2005). We assigned each individual deer a binary value for each seasonal range depending on whether that range was inside (1) or outside (0) the WUI.

We considered an individual deer migratory if its seasonal ranges did not overlap (Brown 1992), whereas we categorized deer that had both winter and summer ranges in the same location as resident deer. If a deer died before we could determine its migratory status, we categorized it as unknown, so we had 3 categories associated with migration behavior and 2 dummy variables to code these categories (migratory: migrant = 1 and unknown = 0; unknown: migrant = 0 and unknown = 1; resident: migrant = 0 and unknown = 0). We estimated distance migrated by measuring the distance (km) between the seasonal range centers following the actual migration path.

We also compared our method of categorizing migration behavior with the results from a net squared displacement analysis to identify movement patterns of yearly trajectories of individual deer (Cagnacci et al. 2016). We derived migration parameters corresponding to resident, migrant, and nomadic (distance, timing, and duration of seasonal movements are random) behavior from a fixed effects model by fitting nonlinear models to each individual trajectory separately following Bunnefeld et al. (2011) and using the nls function in R (Cagnacci et al. 2016).

Deer-vehicle highway collisions are a concern to state agencies nationwide (Romin and Bissonette 1996, Coe et al. 2015). We used a Oregon state highways GIS layer from Oregon Department of Transportation land use development zones (2009) (http://www.oregon.gov/ODOT/TD/ TDATA/pages/gis/odotmaps.aspx, accessed 17 Aug 2014) to calculate the number of highways an individual deer must cross during fall or spring migration (range = 0-3) to reach its seasonal range (average traffic volume = 15,200 Annual Average Daily Traffic of all vehicles for 3 highways in study area from 2005–2012). In addition, we also calculated a third covariate combining the number of times a deer crossed a highway (i.e., number of highway crossings) during spring and fall migration (range = 0-6). We predicted that survival rates would decrease as the number of highways crossed or highway crossings increased because the risk of collision with a vehicle would be increased the more often a deer crossed a highway.

We obtained mean temperature and precipitation data for 2005–2012 from the PRISM maps for our study areas (PRISM Climate Group 2010). We calculated a winter

precipitation value (mm) by averaging the mean monthly precipitation (mm) for December, January, and February at 2 spatial scales: the individual's winter range and across the entire WMU assigned to each individual's winter range. The resolution of the PRISM data were similar in size to the winter seasonal ranges, so we used the precipitation value taken at the mean center point of the individual's winter range to determine the winter precipitation at the individual level. Because of the expansive area within each WMU (>5,000 km<sup>2</sup>), we used zonal statistic in ArcMap version 10.0 to calculate the mean monthly winter precipitation across each WMU for each year. We chose 2 different spatial scales (WMU and individual home range) to be able to detect different weather patterns and variability, while trying to eliminate bias of perceived ecological importance (Levin 1992). Deep snow can make deer more susceptible to predation and starvation; therefore, we predicted that winter survival rates would be negatively affected by higher winter precipitation at the WMU level and individual home range.

We used geospatial winter severity data developed by ODFW to index winter range conditions during December through February (Johnson et al. 2013). We calculated this index using precipitation from December to February and the average monthly minimum temperature and then standardized into a single metric (WSI = standardized precipitation—standardized temperature; Johnson et al. 2013) using PRISM models (PRISM Climate Group 2010). We calculated winter severity at 2 spatial scales: the individual's winter range and across the entire WMU assigned to each individual's winter range.

We used Palmer Drought Severity Index (PDSI; Palmer 1965) data (http://www.wrcc.dri.edu/wwdt/about.html, accessed 07 Jul 2014) to compare an index to soil moisture conditions across years on deer summer ranges. This standardized index is widely used to measure long-term drought intensity, and is based on evaporation, soil moisture, and temperature in past and current weather patterns (Palmer 1965). The PDSI values range from -6 to +6, with negative values indicating drier conditions (Palmer 1965). Ungulate survival was positively related to PDSI in other systems (Lawrence et al. 2004, Brown et al. 2006), suggesting that drought during summer can negatively affect female ungulate survival. We used the PDSI for August to determine if summer drought directly influenced summer survival, or if there were lag effects of drought that influenced fall survival at the individual summer range level (Table 1).

#### Adult Female Survival Analysis

We generated monthly survival estimates for adult female mule deer using known-fate models, with estimates and model selection statistics generated in Program MARK (White and Burnham 1999). This approach allowed for a staggered entry of marked deer, and the modeling of temporal variation and individual-specific covariates that we predicted would affect survival within a standardized model selection and multi-model inference framework (Murray 1995). We excluded from analysis deer whose collars failed prior to the data download process or that died within 14 days of capture because of the likelihood of capture myopathy (Chalmers and Barrett 1982).

We used an information-theoretic approach to evaluate models using Akaike's Information Criterion (AIC<sub>c</sub>); we considered models within 2  $\Delta$ AIC<sub>c</sub> to be competitive with the top model (Burnham and Anderson 2003). We also examined the 95% confidence intervals for slope coefficients (betas) and used the degree of interval overlap with zero to evaluate the direction and strength of model covariates.

To avoid a large *a priori* model set that would result from running every possible combination of all covariates, we used a sequential modeling approach that allowed us to evaluate covariate effects for specific types of covariates in singlefactor models and in combination with competitive models retained from a previous modeling stage. At each modeling stage, we also evaluated models that excluded covariates from the previous stage to be sure all the covariates in our top models were informative (Arnold 2010). This sequential approach generally results in the same model selection outcome as an all-possible combinations modeling approach, with the benefits of a much smaller model set and fewer models with uninformative parameters (Arnold 2010, Doherty et al. 2012). We began by building models that examined temporal covariates including year, season, migration period, and hunting season. We then tested the location covariates associated with individuals, including WMU location during the summer and winter, herd group membership, and proximity to human development (winter range present within WUI). We tested these first as single factor models and then combined them in models with temporal covariates from competitive models identified from the first modeling stage. We then tested movement parameters, including migration behavior, distance migrated, and number of highways crossed, singly and in conjunction with competitive models from the first 2 modeling stages. Finally, we tested whether monthly survival was associated with winter precipitation or winter severity at the WMU scale and also at the individual home range scale through the process outlined above. We included the most general model including separate estimates of survival for each month and year and the model with no effects for comparison at all modeling stages.

#### **Causes of Mortality**

We documented 157 female deaths over the course of the study, but because of logistical difficulties associated with recovering mortalities (inaccessible locations and limited personnel) a portion of the carcasses could not be investigated to determine cause of death; thus, we had 54% categorized as unknowns. Therefore, we present the proportion of mortalities assigned to various known-cause categories relative to proportion known to have died to provide some basic information on the causes of mortality and relative frequency of these events when cause of death was known for mule deer in our study. During this study, Oregon did not issue hunting tags for females in our study area and only 1 deer management permit was given to a landowner with a nuisance deer. We defined illegal harvest as

any deer that we found mortally wounded from an arrow or firearm inside and outside the hunting season. There was a small possibility that some legal harvest of female deer on tribal lands could have occurred within Oregon's archery and rifle season, and outside this season, so there is a potential that some of the females were unclaimed legal tribal harvest. However, considering that the locations of these mortalities fell outside tribal hunting areas (all but 2 were >48 km away), it was unlikely these deer represented legal tribal harvest. Therefore, we considered all female deer that were killed by archery or rifle to be illegal harvest.

#### RESULTS

We used GPS collar data for 408 adult female mule deer over 82 months (Aug 2005 to May 2012) to estimate monthly survival. Adult female survival was best modeled by the effect of migration behavior (did a deer migrate or not), the additive effect of the fall migration period (Oct-Nov), and the additive effect of winter precipitation at the level of the individual's winter range (Table 2). Only models including migration behavior had any model weight, and survival was positively associated with migration ( $\hat{\beta}_{migrant} = 0.556$ , SE = 0.252, 95% CI = 0.060 to 1.052) compared to deer that remained resident year-round, and resident deer had higher survival than unknowns ( $\beta_{unknown} = -1.719$ , SE = 0.325, 95% CI = -2.375 to -1.080). Survival decreased during fall migration for all deer ( $\beta_{\text{fall migration}} = -0.413$ , SE = 0.244, 95% CI = -0.892 to -0.064) compared to monthly survival during the rest of the year (Mar-Sep; Fig. 2). Contrary to

predictions, increased precipitation on an individual's winter range (Iwp) was associated with increased survival ( $\hat{\beta}_{Iwp} = 0.014$ , SE = 0.008, 95% CI = -0.002 to 0.031) during winter (Dec–Feb; Fig. 2). However, the effect of winter precipitation was weaker because 95% confidence intervals on the covariate coefficient slightly overlapped zero (<10% of the interval overlapped zero; Forsman et al. 2011; Fig. 3). Two other models were competitive ( $\leq 2 \Delta AIC_c$ ), but model weights were influenced primarily by the inclusion of either migration behavior or individual winter precipitation (Table 2).

We calculated annual survival rates from the best model including the effect of migration behavior, migration period, and winter precipitation ( $\hat{\beta}$  value across all deer each year) as the product of migratory months (Oct–Nov), winter months (Dec–Feb), and the rest of the year (Mar–Sep). We used a first-order Taylor expansion (i.e., the delta method; Cooch and White 2015:appendix B) to estimate standard errors for these estimates. Annual estimates of survival based on monthly estimates from the best model were approximately 0.82 for female migrants and 0.76 for residents (Fig. 4).

We characterized 75% of our individual deer as migratory, 16% as residents, and 9% with unknown migratory behavior. Our classification of deer migration behavior was consistent with results from the net squared displacement analysis, which characterized 73% of our individuals as migratory, 14% as resident, and 12% as nomadic. The estimated mean distance of migration between ranges for migratory deer from the net square displacement analysis was  $38 \pm 9.9$  (SD)

Table 1. Covariate categories, models run within each category, and the predicted direction of the effect associated with monthly survival rates of female mule deer in south-central Oregon, USA, 2005–2012.

category	Model and covariate acronyms	Description and predicted effects		
Temporal effects	YR×Mon	Survival (8) is fully time-dependent varying by month (Mon) and year (YR; biological year: Jun–May 2005–2012).		
	YR+Mon	S varies by month with an additive effect of year.		
	Mon	S varies between all monthly intervals within a year.		
		S is fixed through time (i.e., monthly interval estimates are equal).		
	YR	S varies by year.		
	T, Ln T, or TT	Monthly survival exhibits a linear (T), log-linear (lnT), or quadratic (TT) time trend within biological year		
	SEAS	S varies as a function of season (SEAS).		
	YR+SEAS	S varies with an additive effect of year in addition to seasonal variation.		
	SMig	S is negatively affected during the spring migration period only (spring: Apr-May).		
	FMig	S is negatively affected during the fall migration period only (fall: Oct-Nov).		
	FSMig	S is negatively affected during both migration periods.		
	FSMig+YR	S is negatively affected during both migration periods with an additive effect of year.		
	FSMig×YR	S is negatively affected during both migration periods with an interaction of year.		
Individual sumWMU		S varies as a function of summer Wildlife Management Unit.		
	winWMU	S varies as a function of winter Wildlife Management Unit.		
	Н	S varies as a function of herd group.		
	WUI	S is negatively affected when ranges fall within the Wildland Urban Interface.		
Movement	MU	S varies as a function of migratory behavior with 3 levels (migrant, resident, unknown),		
	D	S is negatively associated with the distance migrated between seasonal ranges.		
	HC	S is negatively associated with the number of highways crossed during migration.		
	TC	S is negatively associated with the times highways are crossed during migration.		
Environmental	Wpp	S is negatively associated with an increase in winter precipitation at the WMU scale.		
	Iwp	S is negatively associated with an increase in winter precipitation at the individual winter range scale.		
	Iws	S is negatively associated with an increase in winter severity at the individual winter range scale.		
	Wws	S is negatively associated with an increase in winter severity at the WMU scale.		
	Dr	S is negatively associated with an increase in drought severity during August.		

**Table 2.** Model selection results for the top 10 *a priori* models investigating survival probability (*S*) of radio-collared mule deer in south-central Oregon, USA, 2005–2012, relative to time effects, individual covariates, environmental covariates, and movement behavior. Models are ranked according to Akaike's Information Criterion adjusted for small sample sizes (AICc). Difference in AICc ( $\Delta$ AICc), Akaike weight ( $w_i$ ), number of parameters (*K*), and deviance are also listed for each model. Model set includes the intercept-only (null) model of constant survival over time, *S*(.), and the most general model with survival variation by season and year, *S*(t).

0			-		
Model <sup>a</sup>	AIC	$\Delta AIC_{c}$	$w_i$	K	Deviance
S(MU+FMig+Iwp)	1,018.84	0.00	0.31	5	1,008.83
S(MU+Iwp)	1,019.52	0.68	0.22	4	1,011.51
S(MU+FMig)	1,020.22	1.38	0.16	4	1,012.21
S(MU+FSprM)	1,021.33	2.49	0.09	5	1,011.31
S(MU+SprM+Iwp)	1,021.52	2.68	0.08	5	1,011.51
S(MU)	1,022.13	3.29	0.06	3	1,016.12
S(MU×FMig)	1,023.39	4.55	0.03	6	1,011.37
S(MU+SprM)	1,023.94	5.10	0.02	4	1,015.93
$S(MU \times SprM)$	1,025.74	6.90	0.01	6	1,013.72
S(MU×FSprM)	1,026.46	7.62	0.01	9	1,008.43
S(.)	1,072.32	53.48	0.00	1	1,070.32
S(t)	1,134.15	115.31	0.00	82	967.54

<sup>a</sup>Model notation: migration behavior (MU), migration season, fall only (FMig), individual home range precipitation (Iwp), migration season (FSprM), and migration season, spring only (SprM).

km and the mean residence time on summer range for these individuals was  $159 \pm 38$  days.

We determined cause of mortality for 73 of 157 radiocollared female mule deer that died during the study and the deaths of 84 other deer (54%) were categorized as unknown. The causes of mortality identified for females included predation, anthropogenic mortality (vehicle collision or fencing entanglement), illegal harvest, and natural mortality (fawning, disease, and starvation or malnutrition). Relative to the number that died, following unknown, the highest proportion of females died as a result of predation (18%), followed by anthropogenic mortality (14%), illegal harvest (11%), and natural mortality (3%; Table 3).



Figure 3. Estimates of monthly survival during winter, December–February (with 95% confidence limits) plotted against mean monthly winter precipitation for adult female mule deer in south-central Oregon, USA, 2005–2012. We derived survival estimates from the best approximating known-fate model including the additive effect of migration ( $\bar{x}$  across all migration categories, migrants, residents, and unknown), the fall migration time period, and individual total winter range precipitation (Dec–Feb).

#### DISCUSSION

We observed differences in monthly survival rates between migratory deer and resident deer and on average, migratory deer had 6% higher annual survival rate compared to residents. However, consistent with predictions regarding temporal variation in annual survival of adult females, we found very little model support for year-to-year variation in female survival rates within migration behavior categories. Annual survival rates for females in this study were lower for resident deer (0.76) than survival rates reported for adult females in other populations (0.85, Unsworth et al. 1999; 0.86, Bleich and Taylor 1998; 0.81, Bender et al. 2007; 0.91, Bishop et al. 2009). However, the weighted mean annual survival rate for adult females from values reported in the literature (n=21) over 30 years was 0.84 (CV=0.06; Forrester and Wittmer 2013), which was very similar to our annual estimates for migratory deer (0.82). The mean annual survival estimate for all females (residents, migrants, and unknowns) in this study across all years was  $0.79 \pm 0.02$  (SE),



**Figure 2.** Seasonal survival rate estimates and 95% confidence intervals for migratory and resident adult female radio-collared mule deer in south-central Oregon, USA, 2005–2012. Fall (Sep–Nov) had the lowest monthly survival and was constant across years. Each winter (Dec–Feb) had a different seasonal estimate because the individual winter precipitation was a time varying covariate (noted by last 2 digits of year). Spring and summer (Mar–Aug) also had constant survival across all years. We derived estimates from the best approximating known-fate model including the additive effect of migration (migrants, residents, and unknown), the fall migration period, and individual winter range precipitation (Dec–Feb,  $\bar{x}$  across all individuals each year).



Figure 4. Annual survival rate estimates and 95% confidence intervals for migratory and resident adult female radio-collared mule deer in south-central Oregon, USA, 2005–2012. We derived estimates from the best known-fate model including the additive effect of migration (migrants, residents, and unknown), the fall migration, and individual winter range precipitation (Dec–Feb;  $\bar{x}$  across all individuals each year).

which is still slightly lower than values reported for other populations (see Fig. S1, available online in Supporting Information).

Migration behavior represents a trade-off between the benefits of moving to higher quality habitat, which can ultimately increase reproductive success, compared to the potentially greater risk of predation or vehicle collision during the migration process while passing through unknown areas (Nicholson et al. 1997). Mule deer generally migrate from low elevations to a higher summer elevation for better foraging (D'Eon and Serrouya 2005, Monteith et al. 2011). Ranges used by mule deer in the summer can offer higher nutritional benefits in terms of quantity and quality than ranges at lower elevations used during the winter (Wallmo et al. 1977) and can be partly responsible for herd productivity (Julander et al. 1961). Deer that do not move to a different summer range (but remain on the same range year-round) make a risk-forage tradeoff, particularly if forage growing conditions are poor that year (Hebblewhite and Merrill 2009). One mechanism for partial migration (some individuals migrate; some stay on winter range year-round) in a population could be due to balancing densitydependence when resources are limited (Lundberg 1988). In addition, there can be a wide range of individual migration

**Table 3.** Proportion of female radio-collared mule deer attributed to cause of death from the full sample of deer and from a sample of deer for which cause of death was known in south-central Oregon, USA, 2005–2012. The sources of mortality include predation (cougar and coyote), anthropogenic (vehicle or fence), illegal harvest, natural (disease, malnutrition, fawning), and unknown (cause of mortality could not be determined).

Mortality	Proportion of	Proportion of deaths where cause
source	deaths	was known
Predation Anthropogenic Illegal harvest Natural Unknown	0.18 (29/157) 0.14 (22/157) 0.11 (17/157) 0.03 (5/157) 0.54 (84/157)	0.40 (29/73) 0.30 (22/73) 0.23 (17/73) 0.07 (5/73)

distances within a partially migratory mule deer population (Sawyer et al. 2006, Monteith et al. 2011, Sawyer and Kauffman 2011, Middleton et al. 2013, Jones et al. 2014), and the distance a deer migrates may therefore, influence an individual's overall fitness (Sawyer et al. 2016). For example, long-distance migrants (>150 km) can spend almost a third of their annual cycle on migration grounds, potentially increasing overall carrying capacity of the system as they take advantage of resources outside winter or summer ranges (Sawyer et al. 2016). The average distance migrated by mule deer in our study would classify our entire migratory population as short distance migrants following Sawyer et al. (2016; <50 km), and the time spent migrating averaged 26 days during fall and spring migration combined (Cupples and Jackson 2014). Thus, benefits gained from increased forage availability or quality on migration areas between seasonal ranges might be lower for deer in our study compared to longer-distance migrants, but they might also experience less travel-related anthropogenic mortality risk (road and fence crossings (Sawyer et al. 2016). In this study, the benefits of moving to a different seasonal range appeared to be worth the risk in terms of increased survival for our deer and was also evident in the high number of migratory (n = 316) compared to resident deer (n = 69) observed in the sample population.

Human disturbance as perceived by wildlife is difficult to quantify, and the parameter we developed specifically to quantify the effect of human disturbance on individual deer survival was not strongly supported. However, it may not have accurately represented the effect of development, land conversion, or vehicle traffic other studies have reported for large ungulates (Sawyer et al. 2006, Olson et al. 2014, Johnson et al. 2013). A recent study reported that the substantial increase in human development (resorts, homes, roads) led to an increase in habitat loss, disruption of migratory routes, and potentially increased stress on the mule deer population in the Bend, Oregon area (Coe et al. 2015). The continuous sprawling urbanization could also decrease habitat quality or overall carrying capacity, resulting in decreased survival for resident deer because of a lack of sufficient resources necessary for mule deer to meet their lifehistory needs (i.e., forage, cover, water).

In addition to a consistent difference in monthly survival throughout the year related to migration behavior, we also observed an additional difference in monthly survival during fall migration relative to other months in the year, consistent with observations for mule deer in southern California (Nicholson et al. 1997). However, the negative effect observed in this study was consistent for both migrants and residents (no support for an interaction), and only occurred during fall migration rather than both fall and spring migrations. There are 2 hypotheses that independently or in synergy might explain this finding. First, although female mule deer could not be legally harvested under the regulations in effect during this study, illegal harvest, or disturbance from legal harvest activities could negatively affect survival rates, and we might expect residents and shortdistance migrants to be affected similarly (Sawyer et al. 2016). In addition, competition for forage and changes in forest structure (Peek et al. 2002) on summer ranges may mean food resources are becoming limiting during October and November (Baker and Hobbs 1982). Food limitation at this time may increase the energetic challenge for females who are still nursing fawns (Wallmo 1981), thereby negatively affecting their survival regardless of migration behavior. In Rocky Mountain elk (Cervus canadensis nelsoni) the energetic demands of lactation, especially during summer and autumn, negatively affect mothers and calves (Cook et al. 2004). In northeastern Oregon, female Rocky Mountain elk will choose birthing site locations that favor nutritional quality and availability over predation risk because of the high energetic demands of parturition (Rearden et al. 2011). In addition, red deer (Cervus elaphus hispanicus) will metabolize body reserves while lactating if food availability is low (Landete-Castillejos et al. 2003), and Sika deer (Cervus nippon centralis) will not enter estrus unless there are enough resources for the energetic demands of parturition and rearing (Minami et al. 2012).

The positive relationship we observed between winter survival and precipitation (snow or rain) during winter was also consistent regardless of migration strategy (i.e., additive) and was contrary to our prediction. At lower elevations  $(\sim 1,525 \text{ m})$ , annual snowfall averages 90 cm (Franklin and Dryness 1973), which likely is not detrimental to mule deer survival (Hobbs 1989). We did not have a measure of snowfall included in the analysis, but annual winter precipitation during 2005-2012 was similar to the longterm average (1970-2004; see Fig. S2a, available online in Supporting Information). Average winter temperature for each year was near but often higher than freezing, suggesting that precipitation was mainly in the form of rain and not snow, and if it was in the form of snow it would not persist as long with warmer temperatures (see Fig. S2b, available online in Supporting Information). In New Mexico, a positive relationship between adult female survival and total precipitation from January to June was reported (Bender et al. 2007). An increase in precipitation led to better forage and in turn, to an increase in nutrition, and ultimately increased mule deer survival (Bender et al. 2007). It could be that forage is limited during winter on our study area, and that the increase in precipitation allowed for more forbs and grasses, which are preferred by mule deer (Bender et al. 2007). In ungulates, adult survival is the last demographic affected by resource limitations (Gaillard et al. 1998) and therefore it is difficult to observe differences year to year. However, survival was highest in winter 2010-2011 and it is apparent that the mean winter precipitation for 2010–2011 was above average compared to the 30-year average (see Fig. S1, available online in Supporting Information). In a shrub-steppe ecosystem, winters with higher precipitation likely result in more productive plant growth because plants use most of the available water earlier in the year (Mata-González et al. 2014).

Predation was the leading cause of known mortality for female mule deer in this study (40%), which is consistent with findings for other mule deer populations (Bleich and Taylor 1998, Robinson et al. 2002). However, the proportion of known mortalities attributed to anthropogenic (mainly vehicle collision) causes was second (30%), and illegal harvest (23%) the third leading cause of female mortality (Table 3). This is unexpected because Oregon hunting regulations did not allow for female deer harvest during this study. Competing risks like illegal harvest are often grouped together with other sources of mortality that are not significant enough to stand on their own as a separate category (Forrester and Wittmer 2013). Thus, it is unclear how prevalent illegal harvest is for females in other populations, but presumably it is low given it is rarely reported separately.

## MANAGEMENT IMPLICATIONS

It is important to maintain corridors and pathways for future mule deer movements given the current benefits of migration to annual female survival. Resident deer that had summer ranges in more urbanized areas had lower survival than the migrant deer that moved out of urban areas during the summer. If maintaining or increasing mule deer populations by increasing survival rates of resident female mule deer throughout the year is an important objective, then it is important for future development in this part of Oregon to consider avoiding deer migration routes and winter ranges.

In addition, our research suggests that female mule deer have lower survival during fall migration, a time when we documented mortality from illegal harvest and other humanrelated causes. More research is needed to confirm the sources of mortality important during this time period. However, if human activities are associated with these survival patterns, there is the potential for management, hunter education, and law enforcement actions to decrease these negative effects to the benefit of resident and migratory female mule deer populations.

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## LITERATURE CITED

- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.
- Baker, D. L., and N. T. Hobbs. 1982. Composition and quality of elk summer diets in Colorado. Journal of Wildlife Management 46:694–703.
- Barrett, M. W., J. W. Nolan, and L. D. Roy. 1982. Evaluation of a handheld net-gun to capture large mammals. Wildlife Society Bulletin 10:108–114.
- Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118–1124.
- Bishop, C. J., J. W. Unsworth, E. O. Garton, and Ransom. 2005. Mule deer survival among adjacent populations in southwest Idaho. Journal of Wildlife Management 69:311–321.
- Bishop, C. J., G. C. White, D. J. Freddy, B. E. Watkins, and T. R. Stephenson. 2009. Effect of enhanced nutrition on mule deer population rate of change. Wildlife Monographs 172:1–28.
- Bleich, V. C., and T. J. Taylor. 1998. Survivorship and cause-specific mortality in five populations of mule deer. Great Basin Naturalist 58:265–272.
- Brown, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. Journal of Wildlife Management 56:246–253.
- Brown, D. E., D. Warnecke, and T. McKinney. 2006. Effects of midsummer drought on mortality of doe pronghorn (*Antilocapra americana*). Southwestern Naturalist 51:220–225.
- Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.
- Burnham, K. P. and D. R. Anderson. 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, New York, New York, USA.
- Cagnacci, F., S. Focardi, A. Ghisla, B. van Moorter, E. H. Merrill, E. Gurarie, M. Heurich, A. Mysterud, J. Linnell, M. Panzacchi, R. May, T. Nygård, C. Rolandsen, and M. Hebblewhite. 2016. How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. Journal of Animal Ecology 85:54–68.
- Chalmers, G. A., and M. W. Barrett. 1982. Capture myopathy. Pages 84–94 in G. L. Hoff and J. W. Davis, editors. Noninfectious diseases of wildlife. Iowa State University Press, Ames, USA.
- Clover, M. R. 1954. A portable trap and catch-net. California Fish and Game 40:367–373.
- Coe, P. K., R. M. Nielson, D. H. Jackson, J. B. Cupples, N. E. Seidel, B. K. Johnson, S. C. Gregory, G. A. Bjornstrom, A. N. Larkins, and D. A. Speten. 2015. Identifying migration corridors of mule deer threatened by highway development. Wildlife Society Bulletin 39:256–267.
- Cook, R. C., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of northern Yellowstone elk. Journal of Mammalogy 85:714–722.
- Cupples, J. B., and D. H. Jackson. 2014. Comparison of mule deer distributions during winter and hunting seasons in south-central Oregon. Wildlife Technical Report. Oregon Department Fish and Wildlife, Portland, USA.
- DeLgiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. Journal of Wildlife Management 66:698–717.
- D'Eon, R. G., and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. Journal of Mammalogy 86:736–744.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. Journal of Ornithology 152:317–323.
- Erickson, J. A., A. E. Anderson, E. Medin, and D. C. Bowden. 1970. Estimating ages of mule deer: an evaluation of technique accuracy. Journal of Wildlife Management 34:523–531.
- Forrester, T. D., and H. U. Wittmer. 2013. A review of the population dynamics of mule deer and black-tailed deer *Odocoileus hemionus* in North America. Mammal Review 43:292–308.
- Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, D. R. Anderson, J. D. Nichols, J. E. Hines, J. B. Lint, R. J. Davis, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, S. A. Gremel, D. R. Herter, J. M. Higley, R. B. Horn, J. A. Reid, J. Rockweit, J. Schaberel, T. J. Snetsinger, and S. G. Sovern. 2011. Population demography of northern

spotted owls. Studies in Avian Biology 40. University of California Press, Berkeley, USA.

- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Portland, USA.
- Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131:781–798.
- Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.
- Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management 51:634–643.
- Gordon, I. J., A. J. Hester, and M. Festa-Bianchet. 2004. Review: the management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.
- Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.
- Henne, D. R. 1975. Domestic sheep mortality on a western Montana ranch. Thesis, University of Montana, Missoula, USA.
- Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101:3–39.
- Johnson, B. K., P. K. Coe, and R. L. Green. 2013. Abiotic, bottom-up, and top-down influences on recruitment of Rocky Mountain elk in Oregon: a retrospective analysis. Journal of Wildlife Management 77:102–116.
- Jones, J. D., M. J. Kauffman, K. L. Monteith, B. M. Scurlock, S. E. Albeke, and P. C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. Ecological Applications 24:1769–1779.
- Julander, O., W. L. Robinette, and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. Journal of Wildlife Management 25:54–60.
- Landete-Castillejos, T., A. García, J. A. Gómez, and L. Gallego. 2003. Lactation under food constraints in Iberian red deer *Cervus elaphus hispanicus*. Wildlife Biology 9:131–139.
- Lawrence, R. K., S. Demarais, R. A. Relyea, S. P. Haskell, W. B. Ballard, and T. L. Clark. 2004. Desert mule deer survival in southwest Texas. Journal of Wildlife Management 68:561–569.
- Lendrum, P. E., C. R. Anderson Jr, K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2013. Migrating mule deer: effects of anthropogenically altered landscapes. PLOS ONE 8:e64548.
- Lendrum, P. E., C. R. Anderson, K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2014. Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality. Mammalian Biology Zeitschrift für Säugetierkunde 79:369–375.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.
- Lundberg, P. 1988. The evolution of partial migration in birds. Trends in Ecology & Evolution 3:172–175.
- Mace, R. U., R. Denney, and R. Ingram. 1995. Big game history. Oregon Department Fish and Wildlife, Portland, USA.
- Mata-González, R., T. L. Evans, D. W. Martin, T. McLendon, J. S. Noller, C. Wan, and R. E. Sosebee. 2014. Patterns of water use by great basin plant species under summer watering. Arid Land Research and Management 28:428–446.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.
- Minami, M., N. Oonishi, N. Higuchi, A. Okada, and S. Takatsuki. 2012. Costs of parturition and rearing in female sika deer (*Cervus nippon*). Zoological Science 29:147–150.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and lifehistory characteristics. Ecosphere 2:1–34.
- Monteith, K. L., K. B. Monteith, J. A. Delger, L. E. Schmitz, T. J. Brinkman, C. S. Deperno, and J. A. Jenks. 2012. Immobilization of whitetailed deer with telazol, ketamine, and xylazine, and evaluation of antagonists. Journal of Wildlife Management 76:1412–1419.
- Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts, USA.

- Mote, P. W., and E. P. Salathé. 2010. Future climate in the Pacific Northwest. Climatic Change 102:29–50.
- Murray, M. G. 1995. Specific nutrient requirements and migration of wildebeest. Pages 231–256 in A. R. E. Sinclair, and P. Arcese, editors. Serengeti II: dynamics, management, and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.
- Nelson, M. E., and L. D. Mech. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471–474.
- Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.
- Oliver, M., and J. Kline. 2012. Seasonal neighbors: residential development encroaches on mule deer winter range in central Oregon.
- Olson, D. D., J. A. Bissonette, P. C. Cramer, K. D. Bunnell, D. C. Coster, and P. J. Jackson. 2014. Vehicle collisions cause differential age and sexspecific mortality in mule deer. Advances in Ecology 2014:article 971809.
- Oregon Department of Fish and Wildlife [ODFW]. 2003. Oregon's mule deer management plan. Oregon Department of Fish and Wildlife, Portland, USA.
- Palmer, W. C. 1965. Meteorological drought. Research Paper No. 45. U.S. Department of Commerce, Weather Bureau, Washington, D.C. USA.
- Peek, J. M., B. Dennis, and T. Hershey. 2002. Predicting population trends of mule deer. Journal of Wildlife Management 66:729–736.
- Pettorelli, N., A. Mysterud, N. G. Yoccoz, R. Langvatn, and N. C. Stenseth. 2005. Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. Proceedings of the Royal Society B: Biological Sciences 272:2357–2364.
- Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339.
- PRISM Climate Group. 2010. http://www.prism.oregonstate.edu. Accessed 18 Jun 2014.
- Radeloff, V. C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005. The wildland–urban interface in the United States. Ecological Applications 15:799–805.
- Rearden, S. N., R. G. Anthony, and B. K. Johnson. 2011. Birth-site selection and predation risk of Rocky Mountain elk. Journal of Mammalogy 92:1118–1126.
- Robinson, H. S., R. B. Wielgus, and J. C. Gwilliam. 2002. Cougar predation and population growth of sympatric mule deer and white-tailed deer. Canadian Journal of Zoology 80:556–568.
- Romin, L. A., and J. A. Bissonette. 1996. Deer: vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24:276–283.
- Sawyer, H. and M. J. Kauffman. 2011. Stopover ecology of a migratory ungulate. Journal of Animal Ecology 80:1078–1087.

- Sawyer, H., A. D. Middleton, M. M. Hayes, M. J. Kauffman, and K. L. Monteith. 2016. The extra mile: ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. Ecosphere 7: e01534.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.
- Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.
- Speten, D. A. 2014. Assessment of mule deer fawn survival and birth site habitat attributes in south-central Oregon. Thesis, Oregon State University, Corvallis, USA.
- Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159–2173.
- Thomas, T. R., and L. R. Irby. 1990. Habitat use and movement patterns by migrating mule deer in southeastern Idaho. Northwest Science 64:19–27.
- Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. Journal of Wildlife Management 63:315–326.
- U.S. Census Bureau. 2010. Population estimates. U.S. Census Bureau, Washington, D.C., USA. http://factfinder2.census.gov. Accessed 01 Jan 2017.
- Wade, D. A., and J. E. Bowns. 1982. Procedures for evaluating predation on livestock and wildlife. Texas Agricultural Extension Service, College Station, USA.
- Wallmo, O. C., editor. 1981. Mule and black-tailed deer of North America: a wildlife management institute book. First edition. University of Nebraska Press, Lincoln, USA.
- Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal of Range Management 30:122–127.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943.
- White, G. C., and R. M. Bartmann. 1998. Mule deer management—what should be monitored. Pages 104–118 in Proceedings of the 1997 Deer/Elk Workshop, Rio Rico, Arizona. Arizona Game and Fish Department, Phoenix, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

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## SUPPORTING INFORMATION

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