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Northern Yellowstone mule deer seasonal movement, habitat selection, and survival patterns

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ABSTRACT.—We determined the movement patterns and survival rates of 85 radio-marked adult female Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) wintering on the Northern Yellowstone Winter Range (NYWR). We assessed seasonal movement and distribution patterns and individual fidelity to those patterns, along with seasonal habitat selection and survival rates. Twenty-three percent of the deer were nonmigratory, remaining on the winter range year-round, and 77% were migratory, moving 10–104 km from winter to summer ranges. No deer switched between migratory and nonmigratory status. All migratory deer that were monitored for ≥ 2 years exhibited traditional movement patterns and utilized the same winter and summer ranges in all years. Mean winter and summer home range sizes for migratory deer were 1076 ha (SE 129) and 1527 ha (SE 249), respectively, and mean home range size for resident deer was 3100 ha (SE 902). There was a dichotomy in winter habitat use, with one group of deer selecting cultivated and grassland vegetation land cover classes and a second group of deer selecting shrubland and grassland vegetation land cover classes. A dichotomy in summer habitat use was evident between those deer selecting for unburned forest and avoiding all burned land cover classes and those deer selecting for moderate and high burn intensity land cover classes and avoiding unburned forest. We estimated annual mean survival at 0.813 (SE 0.028) and found no differences in survival rates among migratory deer, nonmigratory deer, or deer exhibiting differences in winter or summer habitat selection patterns.

RESUMEN.—Determinamos los patrones de desplazamiento y la tasa de supervivencia de 85 hembras adultas de ciervos mulos (*Odocoileus hemionus hemionus*), radio marcadas, que invernan al norte de Yellowstone Winter Range (NYWR, por sus siglas en inglés). Evaluamos los desplazamientos migratorios, la distribución y la fidelidad individual a tales patrones, junto con la selección de hábitat y las tasas de supervivencia en cada período estacional. El 23% de los ciervos no fueron migratorios, lo que significa que permanecieron en su ámbito invernal durante todo el año, mientras que el 77% restante fueron migratorios, desplazándose entre 10–104 km desde su ámbito invernal hasta el estival. Ningún ciervo cambió su estado migratorio a no migratorio o viceversa. Todos los ciervos migratorios que fueron monitoreados durante ≥ 2 años exhibieron patrones de desplazamiento tradicionales y utilizaron los mismos ámbitos de invierno y verano todos los años. El tamaño promedio del ámbito hogareño en invierno y verano de los ciervos migratorios fue de 1076 ha (EE. 129) y 1527 ha (EE. 249) respectivamente. Mientras que, el ámbito hogareño promedio de los ciervos residentes fue de 3100 ha (EE. 902). Se observó una dicotomía en el uso del hábitat durante el invierno, un grupo de ciervos eligió un tipo de cubierta vegetal cultivada/plantada y de vegetación herbácea/de pastizales, y un segundo grupo de ciervos que seleccionó un tipo de cubierta vegetal herbácea/de pastizales y de matorrales. Asimismo, durante el verano se observó una evidente dicotomía en el uso del hábitat, entre los ciervos que seleccionaron bosques no quemados y que evitaron todo tipo de cubierta vegetal quemada y aquellos ciervos que eligieron cubiertas vegetales quemadas (de intensidad moderada y alta) evitando los bosques no quemados. Estimamos la supervivencia media anual en 0.813 (EE. 0.028) y no encontramos diferencias entre las tasas de supervivencia de los ciervos migratorios, de los no migratorios, ni entre los ciervos que exhiben diferencias en los patrones de selección del hábitat durante el invierno y el verano.

Migration enables animals to exploit gradients in resources over heterogeneous regions. Among ungulates, seasonal movements between disjunct areas facilitate access to more abundant and higher-quality forage, which

may enhance a migrant's survival (Fryxell and Sinclair 1988, Berger 2004, Middleton et al. 2013). Mule deer (*Odocoileus hemionus hemionus*) are typically migratory in the Rocky Mountain region. They respond to seasonal

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variations in weather, forage quality, and forage availability by overwintering on lower-elevation shrub grassland steppes and moving to summer ranges at higher elevations characterized by a vegetative mosaic of meadows and coniferous forest (Wallmo and Regelin 1981). Summer and winter ranges may be separated by distances as small as 5 km (Pac et al. 1991) up to distances >140 km (Sawyer and Kauffman 2011). These seasonal movements often bring migrants into contact with conspecifics from other wintering areas, thereby enhancing the potential for transmission of diseases and parasites such as chronic wasting disease (CWD; Conner and Miller 2004). Segments of the mule deer herd wintering in the Gardiner Basin of the Northern Yellowstone Winter Range (NYWR) are known to migrate seasonally (Murie 1940, Houston 1982, Barmore 2003), but the migratory pathways and extent and distribution of summer ranges utilized are unknown. The summer ranges of mule deer from at least 8 additional wintering areas encompass portions of Yellowstone National Park (YNP; Singer and Mack 1993).

Low measures of fawn recruitment in 1989 (Singer 1991), as well as a decline in numbers of mule deer wintering in the Gardiner Basin portion of the NYWR in 1989 and 1990 (Lemke and Singer 1990, Singer 1991), raised concerns over the potential impacts of the 1988 drought and wildland fires across the Greater Yellowstone Area (GYA) on the abundance and survival of northern Yellowstone mule deer and highlighted the lack of information on the seasonal movement patterns and demographics of this herd. This decline was coincident with a widespread decline in mule deer abundance throughout much of Rocky Mountains in the early 1990s (Unsworth et al. 1999, Hefelfinger and Messmer 2003).

We initiated a study of northern Yellowstone mule deer to secure a basic understanding of the herd's ecological status. We assessed the seasonal movements of adult female mule deer wintering on the NYWR from 1993 to 1997 in order to determine the proportion that were resident or migratory, the migratory patterns, and the location and extent of summer ranges utilized. We evaluated habitat selection, with special emphasis on use of areas that were unburned or burned in the 1988 fires at a "mosaic of differing severities"

(Christensen et al. 1989, Turner et al. 1994). Given the 5-year interval between the 1988 fires and the onset of this study, our findings reflect the response of deer to postfire plant succession in burned areas. We simultaneously evaluated differences in survival rates relative to migratory status and differences in use of winter and summer habitats.

METHODS

Study Area

The study area encompassed the northern GYA, including portions of YNP, Gallatin (now Custer–Gallatin) and Targhee (now Caribou–Targhee) National Forests, and state and private lands in Wyoming, Montana, and Idaho (Fig. 1). The study area consisted of a winter range centered on the lowest-elevation areas of the NYWR and summer ranges extending over the Yellowstone Plateau and adjacent mountain ranges and broad river valleys, including all of the NYWR.

WINTER RANGE.—The winter distribution of female mule deer captured in this study was in the Gardiner Basin, which extends northerly from a southern limit marked by Mount Everts (2390 m) and Mammoth Hot Springs (2053 m) within YNP, Wyoming, to a mixture of public and privately owned lands along the Yellowstone River at the point where the river enters Yankee Jim Canyon near Dome Mountain (2995 m), Montana. The Gardiner Basin consisted of a relatively narrow floodplain divided by the Yellowstone River and foothills rising to rolling bench lands bounded by the mountains of the Absaroka Range to the east and the Gallatin Range to the west. These mountains varied in elevation from 2745 to 3400 m and were intersected by steep drainages flowing to the Yellowstone River.

Human activities throughout the winter range centered on the YNP headquarters and visitor facilities at Mammoth, Wyoming, and the community of <750 permanent residents of Gardiner, Montana. The year-round paved U.S. Route 89 paralleled the Yellowstone River through the Gardiner Basin.

The climate at Gardiner (1618 m), Montana, is characterized by short, warm summers and long, cold winters. During 1971–2000, a mean maximum monthly temperature of 26.1 °C occurred during July. A mean minimum

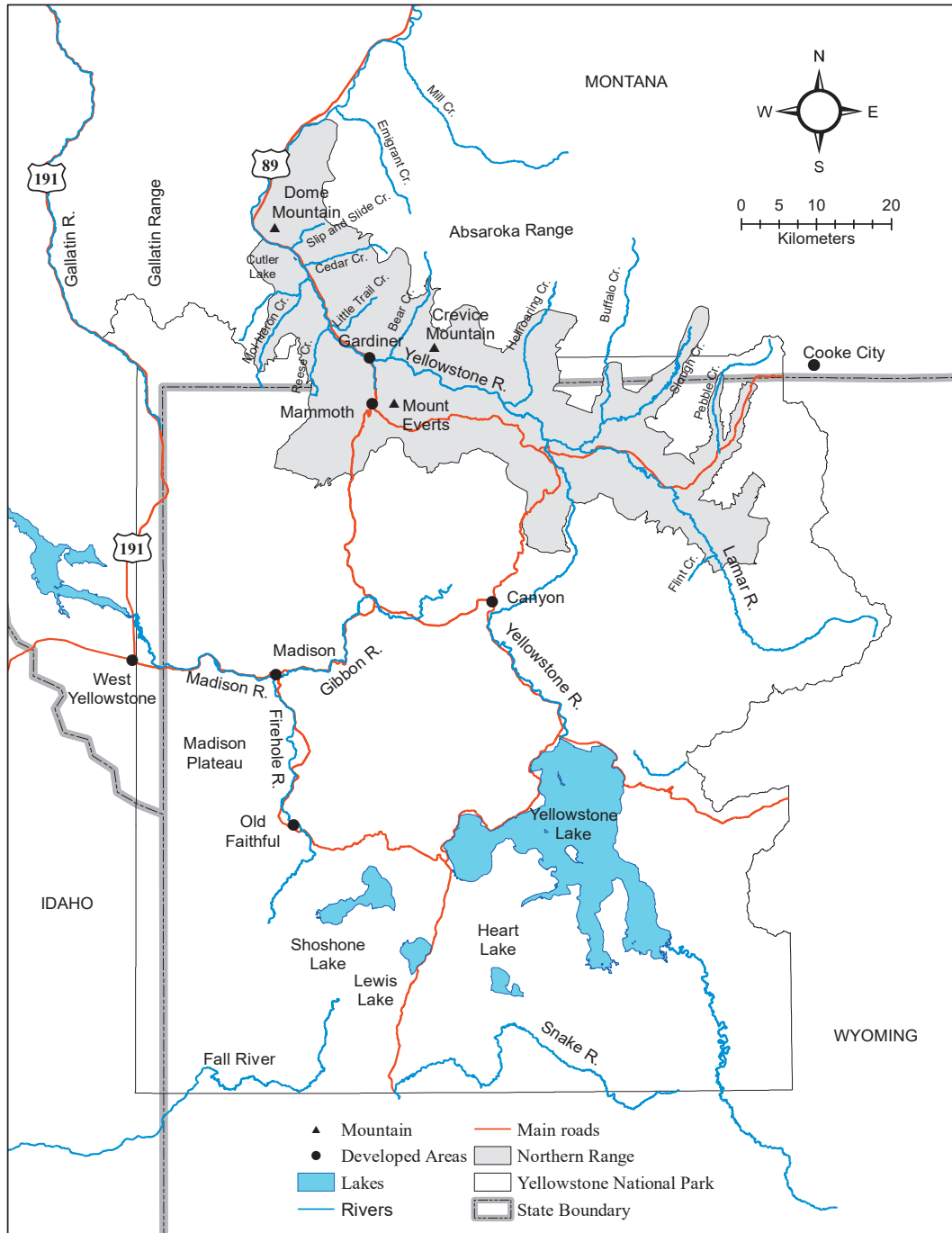


Fig. 1. Locations used in describing movements of female northern Yellowstone mule deer in the Greater Yellowstone Area, 1993–1997, including the Northern Yellowstone Winter Range (shaded).

monthly temperature of -7.2°C occurred in January during the same period (<https://wrcc.dri.edu>). Lower elevations were arid, with

mean precipitation from April to July averaging 11.1 cm (1985–2013). Much of the lower-elevation areas remained snow free for portions

of the winter, but higher-elevation areas were covered in snow throughout winter. Mean snow water equivalent (SWE) at Crevice Mountain (2510 m) was 9.4 cm. The area experienced a drought, with a below-average annual precipitation of 39.0 cm at Mammoth, Wyoming, for 5 of the 10 years between 1988 and 1997 (<https://wrcc.dri.edu>).

Lower elevations in the Gardiner Basin (<1850 m) supported open grassland dominated by Sandberg bluegrass (*Poa secunda*), fringed sage (*Artemisia frigida*), and sandwort (*Arenaria hookeri*), with abandoned agricultural fields on the west side of the Yellowstone River dominated by crested wheatgrass (*Agropyron cristatum*) within YNP and active agricultural fields planted to alfalfa (*Medicago sativa*) on private lands north of the park. Other lands <1850 m elevation on both sides of the Yellowstone River supported a grassland–sagebrush steppe characterized by big sagebrush (*Artemisia tridentata*) and rabbitbrush (*Ericameria nauseosa*), with an understory of Sandberg bluegrass and prairie junegrass (*Koeleria macrantha*; Boccadori et al. 2008). Areas between 1800 m and 2500 m in elevation were characterized by big sagebrush in association with Idaho fescue (*Festuca idahoensis*), prairie junegrass, and needle and thread (*Hesperostipa comata*) (Hoffman 1996). Forest cover, generally beginning at elevations >2500 m, was dominated by limber pine (*Pinus flexilis*) grading into Douglas-fir (*Pseudotsuga menziesii*) at higher elevations (Hoffman 1996).

Modeling suggested that mule deer wintering in the NYWR numbered 3000 in the 1980s (Mack and Singer 1993). Numbers of mule deer detected during late-winter aerial surveys ranged from 1600 in 1990 (Lemke and Singer 1990) to >2500 in 1992 (Lemke 1992). During the study period, antlered and antlerless mule deer north of YNP were subjected to an October–November hunting season.

SUMMER RANGES.—The extent of summer range unfolded during our study. Houston (1982) observed that NYWR mule deer moved to summer ranges at higher elevation within YNP, while Barmore (2003) noted only that mule deer from the NYWR summered in “mountain ranges bordering the winter range.” We found that summer range utilized by migratory mule deer included the 6660-km² Yellowstone Plateau, at a mean elevation of

2400 m, and adjacent north-to-south-trending Gallatin and Absaroka mountain ranges rising to 3000–4000 m within Wyoming, Montana, and Idaho. It includes a large portion of the GYA. At Yellowstone Lake, mean maximum temperature for July–August was 21.5 °C, and mean minimum temperature for November–April was –15 °C (2370 m, 1961–1990; <https://www.wrcc.dri.edu>). Precipitation occurred year-round, with a late-spring peak at lower elevations and a winter peak at higher elevations (Despain 1990).

Vegetation of the Yellowstone Plateau varies with underlying soils, elevation, gradient, precipitation, and temperature patterns (Despain 1990, Marston and Anderson 1991). Vegetation on andesitic soils, concentrated on the east and northeast of the Yellowstone Plateau at elevations between 1850 m and 2400 m, was characterized by Douglas-fir, juniper (*Juniperus* spp.), and aspen (*Populus tremuloides*). Whitebark pine (*Pinus albicaulis*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) commonly occurred at elevations >2700 m. Much of the central Yellowstone Plateau supports extensive areas of lodgepole pine (*Pinus contorta*) on rhyolitic soils at a mean elevation of 2500 m (Despain 1990).

The wildland fires that burned over the GYA in 1988 were similar in extent and intensity to fires that occurred between AD 1200 and AD 1500 (Millspaugh and Whitlock 1995), in the early 1700s, and in the mid-1800s (Romme and Despain 1989, Higuera et al. 2011). Wildland fire frequencies within the GYA vary by vegetative type. Low-elevation Douglas-fir stands tend to burn every 20–25 years, leading to open stands with a low tree density and an abundant understory (Houston 1973). Forest stands at higher elevations have historically burned once every 100–300 years, frequently as crown fires resulting in stand replacement (Despain 1990, Schoennagel et al. 2003). Approximately 5700 km² of the GYA burned in 1988 (Romme et al. 2011). Fire distribution varied unevenly across vegetative types, with some 25%–30% of the burns being canopy fires that created vegetative patterns differing markedly from those of unburned forest (Knight and Wallace 1989). Postfire succession following the 1988 fires also varied by vegetative type and fire intensity, with heterogeneity greater in vegetative structure rather

than in plant species richness or composition (Romme et al. 2011). Herbaceous and shrub species in burned conifer forest began above-ground growth 1–3 years postfire (Anderson and Romme 1991, Turner et al. 1997, 1999), and “biotic cover” approximated prefire levels by 1996 with only a minor “shift” away from perennial species toward annual and biennial species (Romme et al. 2011).

Mule deer winter and summer ranges overlapped with those of the northern Yellowstone elk (*Cervus elaphus*) and bison (*Bison bison*) herds, along with pronghorn antelope (*Antilocapra americana*) and bighorn sheep (*Ovis canadensis*). Mammalian predators active year-round included mountain lions (*Puma concolor*), coyotes (*Canis latrans*), and wolverines (*Gulo gulo*). Additionally, grizzly bears (*Ursus arctos*) and black bears (*U. americanus*) were active during spring, summer, and autumn. Mule deer were exposed to wolf predation in 1995–1997 following the wolf’s reintroduction to YNP in 1995 (Bangs and Fritts 1996).

Capture and Radio Marking

We sampled female mule deer within the Gardiner Basin from Slip and Slide Creek to Bear Creek drainages on the east side and from the vicinity of Cutler Lake south to the Reese Creek drainage on the west side of the Yellowstone River. Between 26 February 1993 and 2 March 1993, we captured 60 female mule deer ≥ 1 year old with a net-gun fired from a helicopter (Barrett et al. 1982, Krausman et al. 1985) and radio-marked each deer with standard VHF collars equipped with a motion (mortality) sensor (Model 315, Telonics, Inc., Mesa, AZ). In order to facilitate detection of radio-marked deer from the air, a 10 \times 15-cm section of colored vinyl material was fitted to the top of each radio collar. The vinyl colors denoted the side of the Yellowstone River (east or west) the wearer was captured on. The vinyl material was not visible from the ground. During March 1995, we used helicopter net-gunning to capture an additional 25 does ≥ 1 year old in the same area and fit them with similar VHF collars.

Movements

We followed movements and survival of radio-marked deer from March 1993 until August 1997 using standard aerial radio-telemetry techniques (Mech 1983, Mech et

al. 1998) to acquire the locations. We observed movements from a Piper PA-18 Super Cub (Piper Aircraft, Lock Haven, PA) or occasionally from a Christen Husky (Aviat Aircraft, Inc., Afton, WY) with a 2-element Yagi antenna fitted to a strut of each wing. The aircraft was flown at approximately 200 m above ground level at an air speed of 130 km/h. Deer location flights were scheduled for early morning hours to avoid turbulence associated with warming air temperatures over mountainous terrain. We plotted deer locations on 1:24,000 maps between March 1993 and January 1994 and thereafter utilized a Trimble Pathfinder Professional (Trimble Inc., Sunnyvale, CA) noncorrectable Global Positioning System (GPS) in the aircraft to determine deer locations. Mean error of locations was 88 m when the radio-collared deer was detected from the air and 137 m based upon radio signal alone (Olexa et al. 2000). We attempted to secure locations at approximately 10-d intervals when deer were on their summer or winter ranges and at approximately 2-d intervals as the estimated time of migration approached and once we determined that deer were migrating. We classified radio-marked deer that remained in the Gardiner Basin year-round as nonmigratory and deer that moved beyond the Gardiner Basin as migratory. We investigated locations of radio collars in mortality mode via ground telemetry to confirm the presence of carcasses or skeletal remains. We defined the onset of spring and fall migration as the date on which we detected directed movement beyond the winter or summer range, respectively. We estimated mean daily distance that deer moved during migration by averaging the recorded distances moved beyond the winter or summer home range between locations obtained ≤ 5 d apart.

Age Structure

We extracted an incisiform canine tooth from 28 of the deer captured in 1993 and a first incisor from 5 additional radio-marked deer at time of death. We extracted an incisiform canine tooth from 24 of the deer captured in 1995. We also obtained first incisors from female deer that were legally harvested in the Gardiner Basin during the fall 1994–1996 hunting seasons ($n = 76$). These teeth were provided by hunters to the Montana Department of Fish, Wildlife and Parks. We

TABLE 1. National Land Cover Database (NLCD) categories (Vogelmann et al. 2001) in the area of Montana, Wyoming, and Idaho used by female northern Yellowstone mule deer. Categories were reclassified for the analysis of habitat selection. Original categories with black lines in the revised classification were merged into more general categories in the revision.

Original NLCD classification	Revised NLCD classification
11 Water	11 Water
12 Ice/Snow	12 Ice/Snow
21 Low Intensity Residential	█
22 High Intensity Residential	20 Residential
23 Commercial/Industrial/Transportation	█
31 Bare Rock/Sand/Clay	31 Bare Rock/Sand/Clay
33 Transitional	33 Transitional
41 Deciduous Forest	█
42 Evergreen Forest	40 Forest (unburned)
43 Mixed Forest	█
51 Shrubland	51 Shrubland
71 Grassland	71 Grassland
81 Pasture/Hay	█
82 Row Crops	█
83 Small Grains	80 Cultivated
84 Fallow	█
85 Urban Grasses	█
91 Woody Wetlands	90 Wetlands
92 Herbaceous Wetlands	█

submitted all teeth for aging by dental annuli (Mattson's Laboratory, Milltown, MT; Low and Cowan 1963, Hamlin et al. 2000). We also calculated the age of capture for deer aged at the time of death.

Data Analyses

HOME RANGE SIZE.—We used the adehabitatHR package (Calenge 2006) in Program R (R Development Core Team 2016) to calculate bivariate normal kernel seasonal home ranges for migratory deer (≥ 20 locations for summer ranges and ≥ 20 locations for winter ranges) and annual home ranges for resident deer. The kernel method offers the least biased method, with no overestimate, of estimating home range size with < 20 relocations (Börger et al. 2006). We used the approach by Kie (2013) to calculate the bandwidth and used the smoothing parameter $h = 0.6 * h_{ref}$, where h_{ref} is the reference bandwidth which

determines the kernel functional shape and width (Kie 2013), for all animals after evaluating values $0.6-1.0 * h_{ref}$.

HABITAT AVAILABILITY AND DISTRIBUTION.—We buffered the winter distribution of radio-marked deer by 5 km and assessed the vegetation present and fire history within the resulting polygon. After excising the winter distribution polygon, we then repeated the process for summer distribution. We used the National Land Cover Dataset 1992 (NLCD, Vogelmann et al. 2001) and the Monitoring Trends in Burn Severity (MTBS, Eidenshink et al. 2007) data for our vegetation data. Mule deer used 19 of the 21 land cover classes in the NLCD. We combined these 19 land cover classes into 10 classes for our habitat selection analysis (Table 1). We found 10 wildfires that occurred from 1988 through 1997 in the MTBS within the area occupied by the radio-marked mule deer (Fig. 2). MTBS classified all areas within the perimeter of fires between 1988 and 1997 into 7 categories (0 = unburned, 1 = unburned to light severity, 2 = low severity, 3 = moderate severity, 4 = high severity, 5 = increased greenness, and 6 = no data). We used only categories 1–4 and added 100 to fire severity classes 1–4 to distinguish their classification from the NLCD land cover classes. Within our GIS, we stacked the fires from most recent to oldest. Finally, we stacked the composited wildfire map on top of the NLCD layer, again with the maximum classification.

HABITAT SELECTION.—We created winter and summer seasonal selective models by comparing the habitat categories within each deer's home range to available habitat categories (design II analysis; Thomas and Taylor 1990, Erickson et al. 1998, Manly et al. 2002). We determined that selection was significant when a selection ratio (w , the used proportion to available proportion of each habitat) differed significantly from 1 (White and Garrott 1990, Manly et al. 2002), as assessed with the adehabitatHS package (Calenge 2006) in program R. Selection for a habitat category was indicated when w differed from 1 and the lower limit of the confidence interval was > 1 . Avoidance of a habitat category was indicated when w differed from 1 and the upper limit of the confidence interval was < 1 . Use of a habitat category in proportion to its availability was indicated when the w confidence

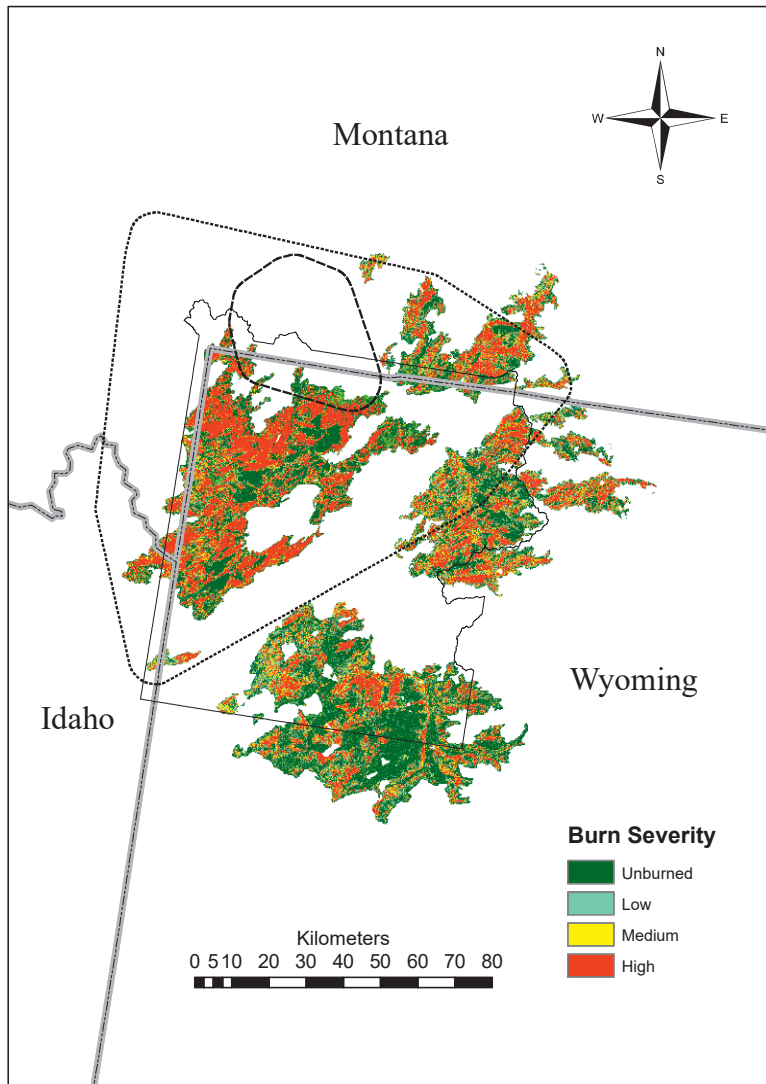


Fig. 2. Distribution and intensity of wildland fire perimeters across the Greater Yellowstone Area 1988–1997 and buffered winter (dashed line) and summer (dotted line) ranges of female northern Yellowstone mule deer against the boundary of Yellowstone National Park (solid black line) and states of Montana, Wyoming, and Idaho (gray lines). Unshaded areas are unburned outside a fire perimeter.

interval included 1 (White and Garrott 1990, Manly et al. 2002). We performed eigen-analysis of the selection ratios to examine the differences in selection of habitat types among deer (Calenge and Dufour 2006) noted during our radio tracking. The first axis of analysis explained most variation in habitat type selection when most deer selected the same habitat type, but multiple axes were created when habitat selection differed among deer (Calenge and Dufour 2006).

CAUSES OF MORTALITY.—We estimated the frequency of mortality by month for all radio-marked deer. Although we made no systematic effort to determine all causes of mortality observed in our sample of radio-marked deer, we documented and reported the proportion of radio-marked deer killed by vehicle collisions and hunters.

SURVIVAL RATES.—We used the known-fate model in program MARK (White and Burnham 1999) to estimate survival of radio-collared

deer. We constructed capture histories for each of quarter of a year (i.e., summer [June–August], fall [September–November], early winter [December–February], and late winter/spring [March–May]). We tested whether survival was influenced by the animal's age at initial capture or season of death, and whether the deer was resident ($n = 17$ deer) or migratory ($n = 56$ deer). We defined season as being either summer/fall (i.e., June–November) or winter/spring (i.e., December–May). Additionally, we tested whether survival differed between groups of deer distinguished by different habitat-selection patterns (e.g., selecting burned or unburned landscapes in summer and selecting cultivated or natural landscapes in winter).

We used an information-theoretical measure of model parsimony, Akaike's information criterion (AICc) (Akaike 1973), to select the most parsimonious model, and considered models differing by ≤ 2 AICc units from the selected model as potential alternatives (Burnham and Anderson 2002). We used Akaike weights (w_i) as an indication of support for each model. We tested for overdispersion by increasing \hat{c} up to 3 and found no change in the ranking models. We considered spurious models that had essentially the same deviance with the addition of the one parameter and with 95% confidence intervals overlapping zero (Burnham and Anderson 2002, Arnold 2010). We used the delta method (Seber 1982, Powell 2007) to convert the quarterly survival rate values for our null model, $S(\cdot)$, to annual survival rate values.

RESULTS

Movements

We determined the seasonal movement patterns of 73 adult female deer and classified the 56 (77%) summering beyond the Gardiner Basin as migrants and the 17 (23%) remaining within the Gardiner Basin year-round as residents. Some resident deer utilized disjunct but nearby ranges in winter and summer within the same drainage, while others maintained a continuous yearlong home range by shifting their distribution to higher elevations in summer. We were unable to determine the migratory status of 12 radio-marked deer that died prior to the onset of spring migration.

Migratory deer that wintered east of the Yellowstone River moved to the east to sum-

mer in the Hellroaring and Buffalo Creek drainages of the Yellowstone River, the Slough Creek and Flint Creek drainages of the Lamar River, and north of Cooke City (Fig. 3). Others moved northeast to summer in the Emigrant and Mill Creek drainages of the Yellowstone River, south to the upper Firehole River drainage, and northwest of Heart Lake. Four radio-marked deer wintering in the Slip and Slide drainage moved west to cross the Yellowstone River at peak spring runoff and crossed the Gallatin Mountain range to reach summer ranges west of the Gallatin Mountains. All 4 recrossed the mountains and river in autumn to return to winter range. Other deer wintering east of the Yellowstone River moved southwest to utilize summer ranges on the east and west sides of Shoshone Lake (Fig. 3).

Migratory deer wintering on the west side of the Yellowstone River moved mainly to the south and southwest to summer in the Gibbon and Madison River drainages and in areas between those drainages and the winter range. A single deer summered south of Lewis Lake, and another crossed the Continental Divide to summer in the upper Fall River drainage. A single radio-marked deer wintering in the Reese Creek drainage west of the Yellowstone River crossed the river to move east to summer range in the Pebble Creek drainage (Fig. 3). Individual deer movement patterns were invariant among the years that each deer was studied. Deer remained either migrant or resident in the Gardiner Basin throughout the life of the study. No migratory or resident deer with disjunct distributions remained on its summer range over winter. We detected no difference in movement routes utilized by individual migratory deer during the study. Additionally, there were no changes in the specific side drainages of the Yellowstone River utilized each winter or in the use of summer ranges among individual migratory deer. No migratory deer shifted to an alternate winter range.

The frequency of animal relocations allowed us to approximate the timing of migratory deer departure and arrival on winter and summer ranges. Migratory deer left their winter ranges from late April to early June, with most leaving from mid- to late May. Most deer reached summer ranges in late May and early June, although some deer were on summer ranges

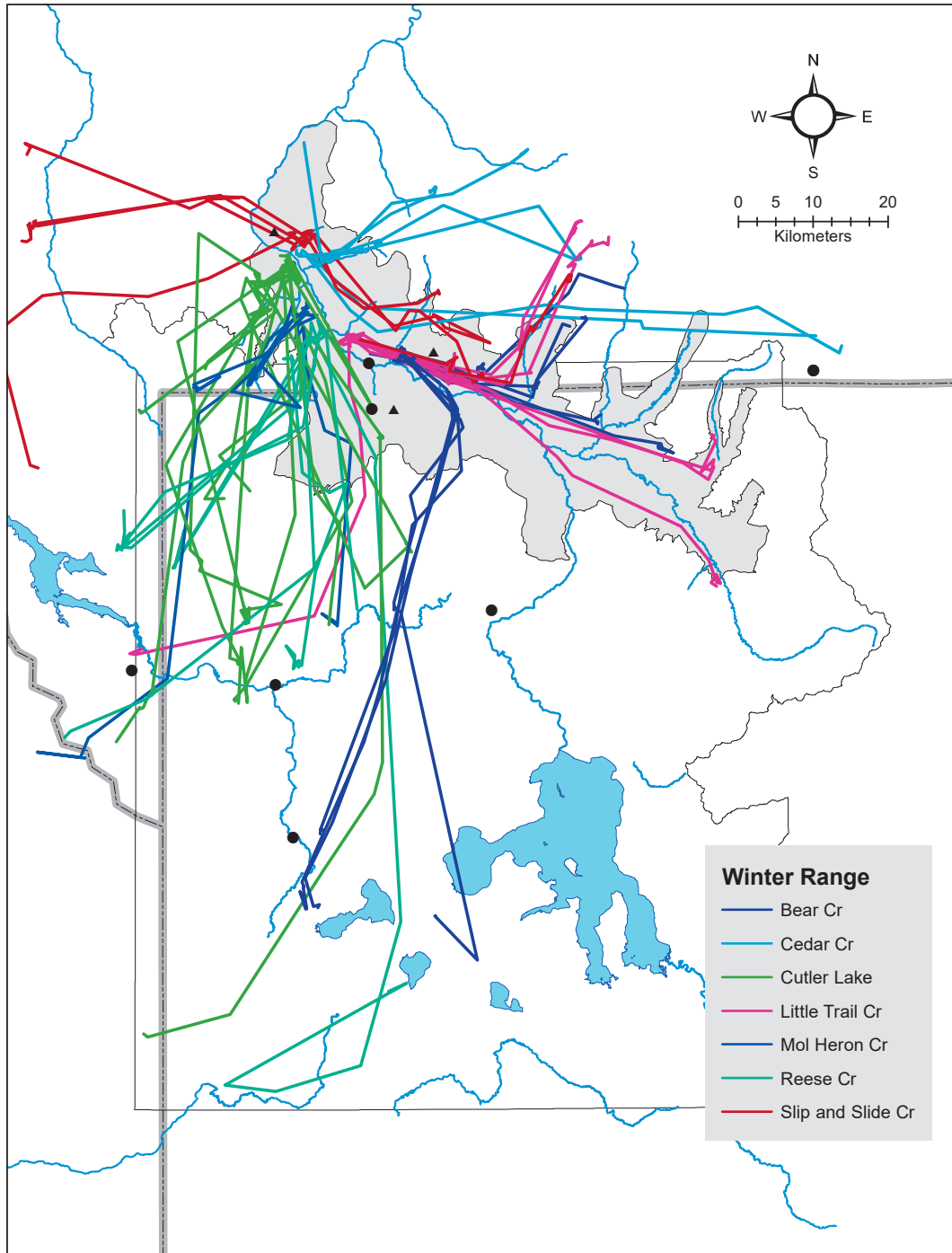


Fig. 3. Female northern Yellowstone mule deer seasonal movement patterns, 1993–1997. Radio-marked deer are color coded to the drainage in which they overwinter.

TABLE 2. Area and percent area of revised land cover classes present within the buffered winter and summer ranges of northern Yellowstone mule deer in Montana, Wyoming, and Idaho.

Revised land cover class	Winter range		Summer range	
	Area (km ²)	% Area	Area (km ²)	%Area
Water	5.8	0.5	131.2	1.3
Ice/Snow	0.7	0.1	5.0	0.1
Residential	1.0	0.1	5.0	0.1
Bare Rock/Sand/Clay	4.7	0.4	35.6	0.4
Transitional	6.7	0.5	101.8	1.0
Forest (unburned)	719.8	58.1	5908.5	57.2
Shrubland	215	17.4	982.6	9.5
Grassland	213.7	17.3	863.4	8.4
Cultivated	3.4	0.3	23.8	0.2
Wetlands	4.8	0.4	49.9	0.5
Low burn severity	6.3	0.5	342.7	3.3
Moderate burn severity	10.6	0.5	460.3	4.5
High burn severity	45.5	3.6	1423.8	13.8

by early May. Deer left their summer ranges from late September through mid- to late October in all years. Arrival on winter ranges was protracted, with most deer reaching winter ranges between mid-October and mid-November.

Migratory deer moved seasonally a mean of 42 km (SE 2.66, range 10–104 km) from the Gardiner Basin to summer ranges at a rate of <1 to 25 km/d (\bar{x} = 3.8 km/d, SD 4.22). Overall, migratory deer traveled between winter and summer ranges within 2–40 d (\bar{x} = 19.5 d, SD 10.6, n = 41).

HOME RANGE SIZE.—We determined the winter and summer home range sizes of 48 and 30 radio-marked deer, respectively, and the annual home ranges of 14 deer resident in the Gardiner Basin. Mean winter home range size was 1076 ha (SE 129) and mean summer home range size was 1527 ha (SE 249) for migratory deer. The mean annual home range size of resident deer was 3102 ha (SE 902). There was a weak relationship between number of relocations and size of winter home range for migratory deer (y = 13.238 x + 483.380, r^2 = 0.0904, $F_{1,46}$ = 4.569, P = 0.0378). The relationship between number of relocations and home range size was not significant for summer home range size of migratory deer (y = 16.979 x + 914.234, r^2 = 0.0244, $F_{1,28}$ = 0.701, P = 0.4095) or for annual home range size of resident deer (y = 12.913 x + 195.232, r^2 = 0.0112, $F_{1,12}$ = 0.136, P = 0.7186). Use of h_{ref} to estimate home range size leads to a positive bias in estimated home range size relative to true home range size and probability of type I or type II error (over- or

underestimating home range area), which declines with increased sample sizes (Kie 2013).

Habitat Availability and Selection

WINTER RANGE HABITAT AVAILABILITY AND SELECTION.—The buffered mule deer winter range of 1238 km² (Fig. 2) was >50% unburned forest, with shrubland and grassland landscape types each making up 18% of the area (Table 2). Cultivated lands made up 0.3% of the area, and the area within fire perimeters was <5% of the total. We assessed winter habitat selection for 50 radio-marked deer. A design II analysis revealed strong habitat selection by deer during winter (χ^2 = 336,040, df = 624, P < 0.01) and significant variation among deer in habitat selection (χ^2 = 137,035, df = 612, P < 0.01). An eigenanalysis revealed a dichotomy in habitat use between deer that had positive scores and those that had negative scores on the y -axis of the first factorial plane (Fig. 4). We censored a single deer outside of this pattern. We then examined winter habitat selection separately for those deer that were positive or negative on the y -axis, keeping all deer as individuals. Two habitat selection strategies were evident. Those deer that were positive on the y -axis selected for cultivated lands and grassland cover. (Table 3). Habitat selection was strong (χ^2 = 109,052, df = 216, P < 0.01) and varied among individual animals (χ^2 = 28,488, df = 204, P < 0.01). Those deer that were negative on the y -axis selected the shrubland and grassland land cover classes, and there was no evidence for selection or avoidance of cultivated lands. (Table 4).

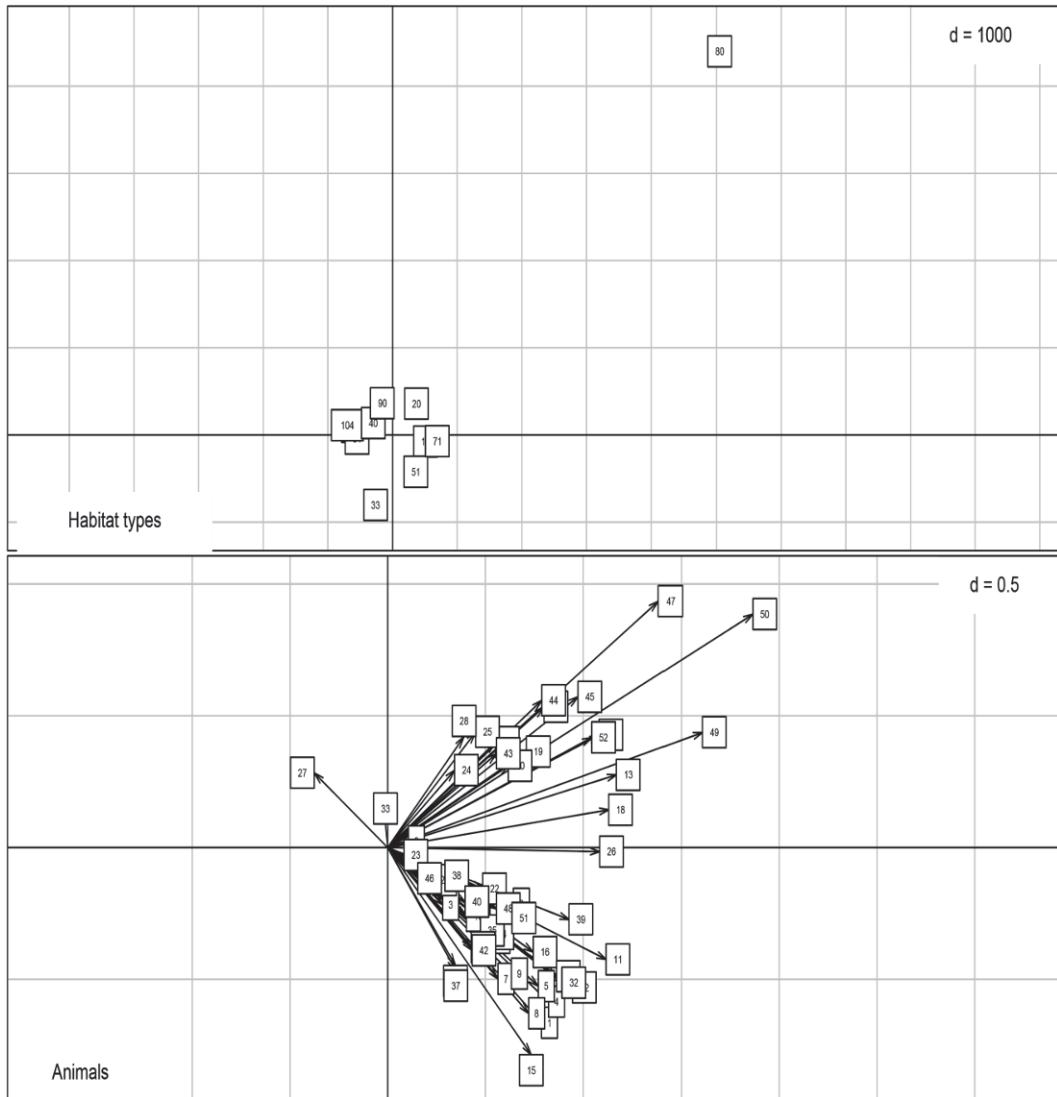


Fig. 4. Results of eigenanalysis of winter habitat selection ratios (design II; Manly et al. 2002) of female northern Yellowstone mule deer, 1994–1996 ($n = 50$). Habitat-type loading on the first 2 factorial axes (upper panel); individual animal scores on the first factorial plane (lower panel). The revised NLCD classification (upper panel) is given in Table 1.

Habitat selection was strong ($\chi^2 = 218,256$, $df = 384$, $P < 0.01$) and varied among individuals ($\chi^2 = 60,598$, $df = 372$, $P < 0.01$). Both groups avoided the land cover classes of ice/snow, bare rock, transitional, and all burn severities. The mean elevation of winter habitat utilized by deer with negative eigenvalues, which was 1966 m (SE 16.4), did not differ significantly from the mean elevation of winter habitat used by deer with positive

eigenvalues, which was 1914 m (SE 34.0) ($t = 1.3581$, $df = 28$, $P > 0.05$). Deer with positive eigenvalues on the y -axis showed a marked difference in winter distribution from those with negative values (Fig. 5).

SUMMER RANGE HABITAT AVAILABILITY AND SELECTION.—The buffered summer range covered an area of 10,334 km² (Fig. 2). Forest unburned since 1988 or with high to low burn severity made up 57.2% and 21.6% of the

TABLE 3. Estimated percent available, percent used, selection ratios (w_i , ordered highest to lowest), and 95% confidence intervals of revised land cover classes used by northern Yellowstone mule deer with eigenvalues ≥ 0 (design II; Manly et al. 2002), winters of 1994–1996.

Revised land cover class	% Available	% Used	w_i	95% Confidence interval	
				Lower limit	Upper limit
Cultivated	<0.01	0.03	12.05	6.86	17.23
Grassland	0.18	0.31	1.72	1.39	2.04
Residential	<0.01	0	1.69	0.38	3
Water	0.01	0.01	1.46	0.61	2.3
Wetlands	<0.01	0.01	1.23	0.44	2.03
Shrubland	0.18	0.17	0.94	0.82	1.05
Forest (unburned)	0.56	0.47	0.84	0.68	1
Ice/Snow	<0.01	0	0.08	-0.01	0.16
Bare Rock/Sand/Clay	<0.01	0	0.08	0.03	0.13
Transitional	0.01	0	0	0	0
Low burn severity	0.01	0	0	0	0
Moderate burn severity	0.01	0	0	0	0
High burn severity	0.04	0	0	0	0

TABLE 4. Estimated percent available, percent used, selection ratios (w_i , ordered highest to lowest), and 95% confidence intervals of revised land cover classes used by northern Yellowstone mule deer with eigenvalues < 0 (design II; Manly et al. 2002), winters of 1994–1996.

Revised land cover class	% Available	% Used	w_i	95% Confidence interval	
				Lower limit	Upper limit
Grassland	0.18	0.32	1.76	1.39	2.12
Shrubland	0.18	0.32	1.75	1.47	2.03
Water	<0.01	0.01	1.66	0.88	2.45
Transitional	0.01	0.01	1.54	-1.97	5.04
Cultivated	<0.01	0	1.11	-0.76	2.99
Residential	<0.01	0	0.9	-0.63	2.43
Forest (unburned)	0.56	0.34	0.61	0.47	0.75
Wetlands	<0.01	0	0.35	0.14	0.57
Bare Rock/Sand/Clay	<0.01	0	0.32	0.14	0.5
Ice/Snow	<0.01	0	0.12	0.01	0.23
Low burn severity	0.01	0	0	0	0
Moderate burn severity	0.01	0	0	0	0
High burn severity	0.04	0	0	0	0

buffered area, respectively (Table 2). All other land cover classes covered <10% of the area each. We assessed summer habitat selection for 36 radio-marked deer. There was evidence for strong habitat selection by deer during summer ($\chi^2 = 473,779$, $df = 432$, $P < 0.01$) and evidence that selection varied among deer ($\chi^2 = 450,602$, $df = 420$, $P < 0.01$). We used a design II eigenanalysis to evaluate habitat selection for migratory deer on the summer ranges. Scores on the first factorial plane revealed a dichotomy in land cover class use between deer with values < 0 and ≥ 0 on the x -axis (Fig. 6). We then examined summer habitat selection separately for deer based upon the x -axis grouping, keeping all deer as individuals. Two habitat selection strategies were evident. Those deer with x -axis values

≥ 0 showed positive selection for unburned forest and avoidance of all burn intensity land covers within the fire perimeters, cultivated lands, and water (Table 5). Habitat selection was strong ($\chi^2 = 254,986$, $df = 252$, $P < 0.01$) and varied significantly among animals ($\chi^2 = 117,529$, $df = 240$, $P < 0.01$). Selection or avoidance of other land cover classes was not significant. Those deer with x -axis values < 0 selected moderate and high burn intensity land cover classes and avoided unburned forest, wetlands, grasslands, water, and cultivated land cover types (Table 6). Habitat selection was strong ($\chi^2 = 218,793$, $df = 180$, $P < 0.01$) and varied among animals ($\chi^2 = 105,637$, $df = 168$, $P < 0.01$). The mean summer range elevation was 2007 m (SE 36.6) for deer with negative eigenvalues and 2226 m (SE 76.3) for

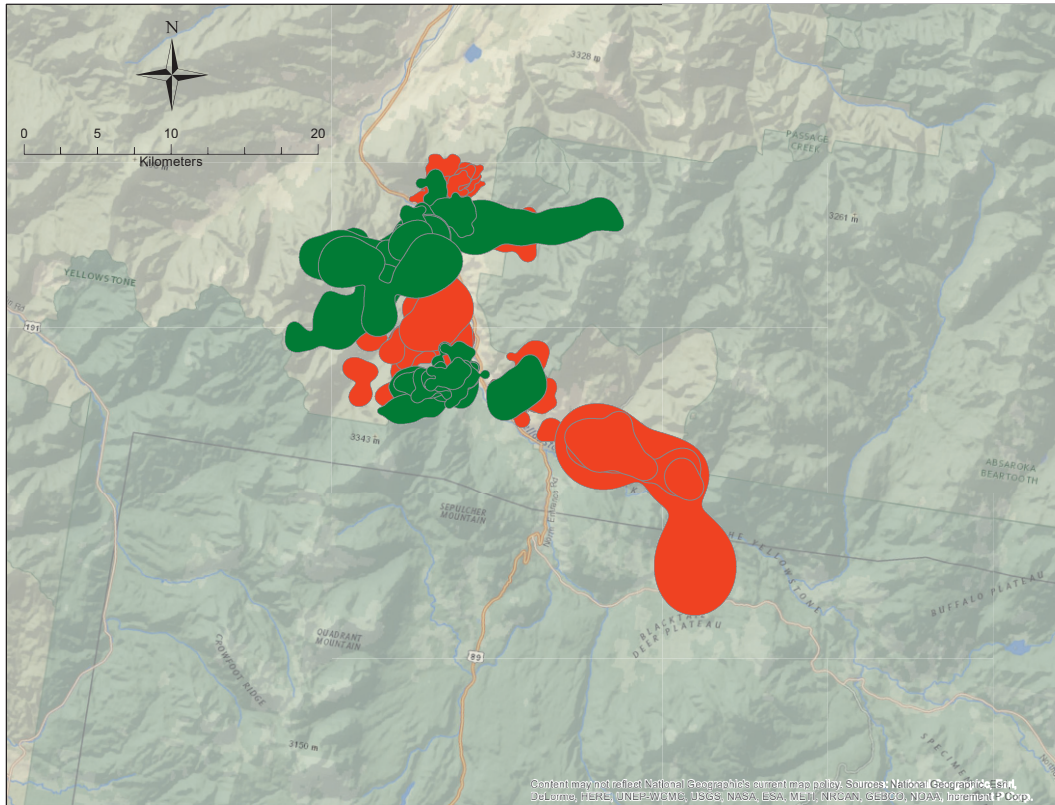


Fig. 5. Distribution of winter home ranges (≥ 20 locations each) of female northern Yellowstone mule deer in Montana and Wyoming. Home ranges with positive eigenvalues on the y -axis are shown in green and those with negative eigenvalues are shown in red. Solid line is Yellowstone National Park boundary.

deer with positive eigenvalues, a difference that was statistically significant ($t = -2.578$, $df = 20$, $P \leq 0.05$). The distribution of deer selecting or avoiding burned land cover classes was consistent with the distribution of wildland fires, most notably the distribution of those deer with home ranges in the area burned in the 1988 North Fork Fire across the Madison Plateau and the 1988 Hellroaring Fire (Fig. 7).

Age Structure, Causes of Mortality, and Survival Rates

AGE STRUCTURE.—The ages of female deer captured in 1993 and 1995 ranged from 1 to 13 years and the ages of harvested female deer ranged from 1 to 12 years, with deer ≥ 8 years old uncommon in both samples (Fig. 8). We compared differences between the samples with a chi-squared test after grouping deer ≥ 8 years old into a single age class for each

sample, owing to small sample sizes among older deer. There was no significant difference between the ages of captured and harvested deer ($\chi^2 = 4.54$, $df = 7$, $P = 0.716$).

CAUSES OF MORTALITY.—Fifty-five of the 85 radio-marked female deer died during this study. We classified the cause of death for 44 (83%) as unknown, as carcasses were unexamined or were not inspected in sufficient time to assess cause of death. Seven mortalities (13%) were roadkills, 2 (4%) were taken by hunters, and 1 was suspected to have been killed by poachers. The radio collar of an additional deer was found at a mountain lion kill site (Kerry Murphy, University of Idaho, personal communication). Mortalities occurred in all months of the year except September, with a clustering from April to August around a peak in June and with a second peak in October.

SURVIVAL RATES.—We estimated the mean annual survival rate at 0.813 (SE 0.028).

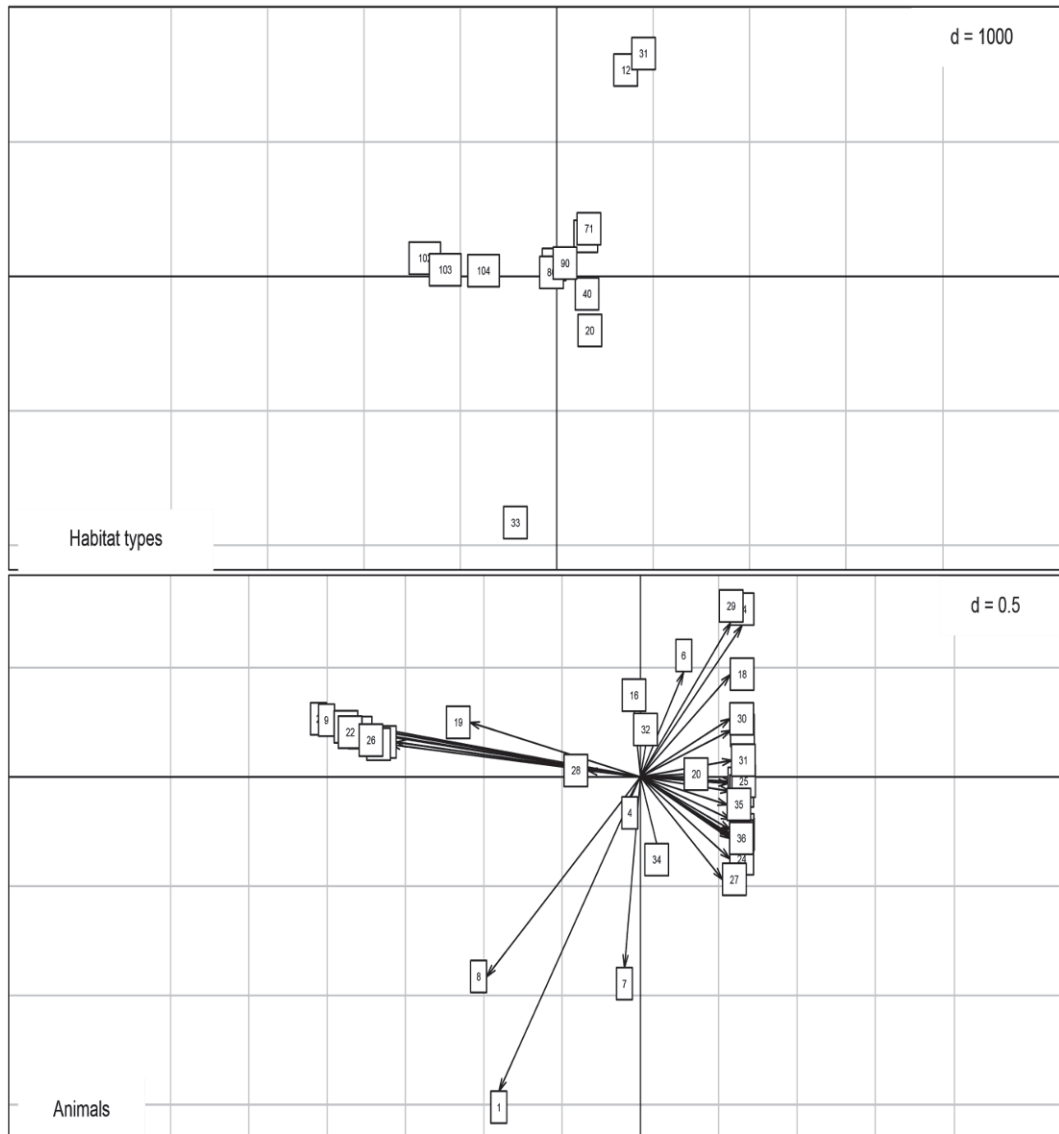


Fig. 6. Results of eigenanalysis of summer habitat selection ratios (design II; Manly et al. 2002) of female northern Yellowstone mule deer, 1993–1996 ($n = 36$). Habitat-type loading on the first 2 factorial axes (upper panel); individual animal scores on the first factorial plane (lower panel). The revised NLCD classification (upper panel) is given in Table 1.

Age-specific annual survival rates increased slightly from 0.771 (SE 0.072) among yearlings to >0.822 (SE 0.041) for 3 year olds before declining to 0.777 (SE 0.054) at 6 years and then beginning a precipitous decline to 0.094 (SE 0.177) at 11 years (Fig. 9). AICc showed that a quadratic model with Age + Age² was the best predictor of annual survival, perhaps indicating senility effects (Table 7). A model with Age alone fell within 2 units of the best

model (Table 7), but the age coefficient by itself was not statistically significant ($\beta = -0.118$, SE 0.077); hence, we concluded that the linear age model was not informative. We found no differences between the quarterly survival rates of migratory and nonmigratory deer, nor among those deer with differences in winter or summer habitat selection, with estimates of 0.95 to 0.96 for all categories (Table 8). AICc revealed that a model with Survival

TABLE 5. Estimated percent available, percent used, selection ratios (w_i , ordered highest to lowest), and 95% confidence intervals of revised land cover classes used by northern Yellowstone mule deer with eigenvalues ≥ 0 (design II; Manly et al. 2002), summers of 1993–1996.

Revised land cover class	% Available	% Used	w_i	95% Confidence interval	
				Lower limit	Upper limit
Bare Rock/Sand/Clay	<0.01	0.01	2.6	-2.2	7.4
Ice/Snow	<0.01	0	2.12	-2.32	6.57
Residential	<0.01	0	1.67	-1.3	4.64
Forest (unburned)	0.52	0.69	1.34	1.1	1.58
Shrubland	0.11	0.14	1.29	0.73	1.85
Grassland	0.09	0.11	1.18	0.38	1.98
Wetlands	0.01	0	0.73	-0.19	1.64
Transitional	0.01	0.01	0.59	-0.75	1.92
Water	0.01	0	0.18	-0.12	0.48
Low burn severity	0.04	0.01	0.16	-0.11	0.43
Moderate burn severity	0.05	0.01	0.14	-0.09	0.36
High burn severity	0.16	0.02	0.12	-0.1	0.33
Cultivated	<0.01	0	0.03	-0.04	0.1

TABLE 6. Estimated percent available, percent use, selection ratios (w_i , ordered highest to lowest), and 95% confidence intervals of revised land cover classes used by northern Yellowstone mule deer with eigenvalues < 0 (design II; Manly et al. 2002), summers of 1993–1996.

Revised land cover class	% Available	% Used	w_i	95% Confidence interval	
				Lower limit	Upper limit
Low burn severity	0.04	0.13	3.36	0.06	6.65
Moderate burn severity	0.05	0.15	3.07	1.18	4.96
Transitional	0.01	0.03	2.85	-1.83	7.53
High burn severity	0.15	0.33	2.13	1.2	3.05
Residential	<0.01	0	1.08	-1.13	3.3
Shrubland	0.11	0.08	0.76	0	1.5
Bare Rock/Sand/Clay	<0.01	0	0.74	-1.4	2.88
Ice/Snow	<0.01	0	0.61	-1.05	2.33
Forest (unburned)	0.52	0.25	0.48	0.07	0.89
Grassland	0.09	0.02	0.25	0.03	0.47
Wetlands	<0.01	0	0.16	-0.33	0.66
Water	0.01	0	0.04	-0.04	0.12
Cultivated	<0.01	0	0	0	0

alone was the best model, although there is some support for models including Range and Migratory Status or Range alone, as these models fell within 2 units of the best model, and the model with Season alone just exceeded a difference of 2 units from the best model with the same deviance (w_i ; Table 9). There is less support for models including Range * Migratory Status and Year, respectively (Table 9).

DISCUSSION

Seasonal Distribution

The general extent of northern Yellowstone mule deer winter range appears to be largely unchanged from the 1930s to the 1990s. The movement patterns and extent of potential

summer range overlap between 7 other mule deer herds with winter ranges adjacent to YNP are not well known (Singer and Mack 1993). Studies from Nevada suggest that overlap of summer ranges of mule deer from different winter ranges can be extensive (Gruell and Papez 1963). Additionally, migratory northern Yellowstone mule deer overlap the annual range of elk of the Madison herd (Craighead et al. 1972) and the summer ranges of the Jackson and Sand Creek elk herds (Singer and Mack 1993), and the Clark's Fork elk herd (Middleton et al. 2013). Northern Yellowstone mule deer and elk both utilize movement corridors between the Yellowstone River valley winter range and the Shoshone and Lewis Lakes area (White et al. 2010).

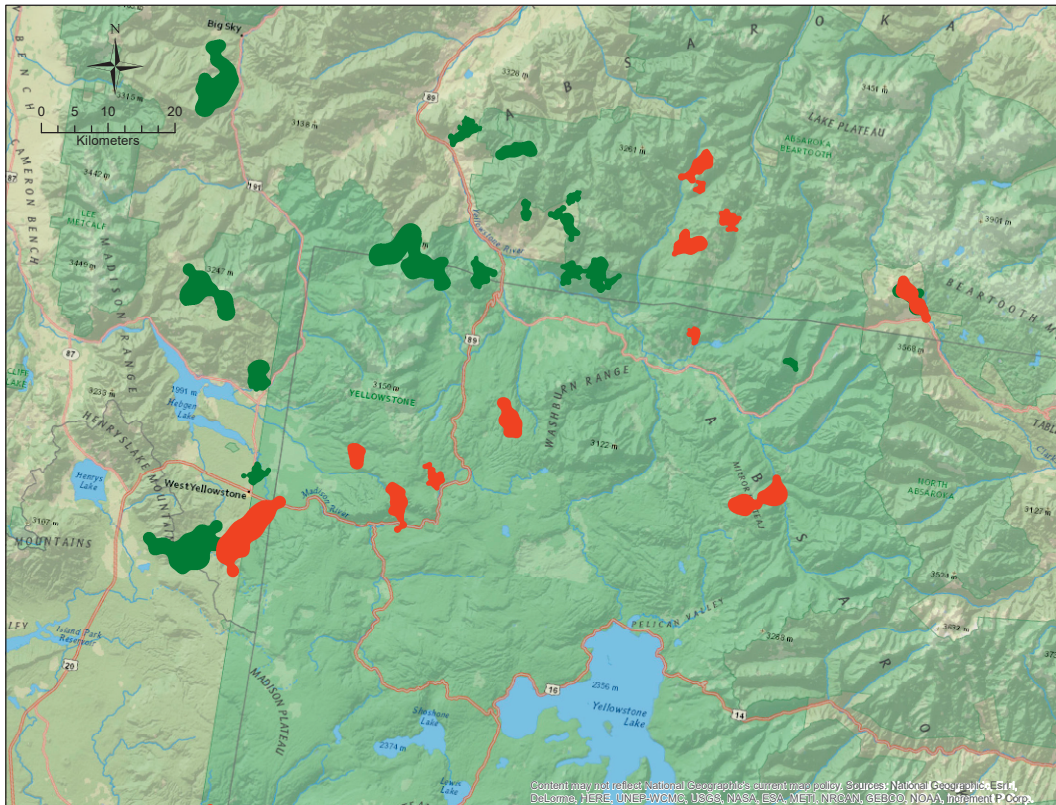


Fig. 7. Summer distribution of home ranges (≥ 20 locations each) of female northern Yellowstone mule deer in Montana, Wyoming, and Idaho. Home ranges with negative eigenvalues on the x -axis are shown in red and those with positive eigenvalues are shown in green. Solid line is Yellowstone National Park boundary.

Movements, Home Range Size and Habitat Selection

MOVEMENTS.—Our categorizing deer as nonmigrants is equivalent to Pac et al.'s (1991) identification of some mule deer in the nearby Bridger Mountains, Montana, as having “indistinct seasonal ranges” and “adjacent seasonal ranges.” Our classification of 77% of the deer wintering in the Gardiner Basin as migrants is very much like Pac et al.'s (1991) finding that 80% of the mule deer in the Bridger Mountains were migratory. The proportion of migrant mule deer in other populations along the Rocky Mountains ranges from 0% to 100% (Brown 1992, Conner and Miller 2004), with a higher proportion of migrants among deer herds utilizing higher-elevation winter ranges (Conner and Miller 2004).

Migratory mule deer utilized numerous movement routes between winter and summer ranges. Potential anthropogenic barriers

to migration with increased vehicle use in our study area included U.S. Route 89, which parallels the Yellowstone River within the Gardiner Basin, and U.S. Route 191, which parallels the Gallatin River and is traversed by deer summering west of the park's western boundary. The migratory routes of some deer cross the road network within YNP (Fig. 3).

The mean and wide range of distances mule deer moved between winter and summer ranges in this study are similar to the means and ranges reported for other mule deer populations in the Rocky Mountains (Thomas and Irby 1990, Pac et al. 1991, Brown 1992, Conner and Miller 2004, Sawyer et al. 2005, Lendrum et al. 2013). The mean daily distance moved in this study, 3.8 km, is similar to the 3.3 km/d reported for mule deer in northwestern Wyoming (Sawyer et al. 2005), although the maximum distance of 25 km/d that we recorded is considerably greater than

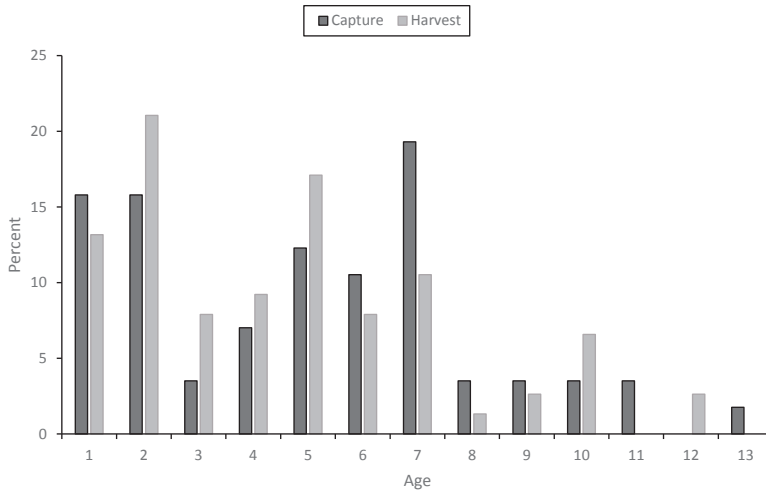


Fig. 8. Age structure of female mule deer live-captured on the Northern Yellowstone Winter Range (NYWR), Montana and Wyoming, 1993 and 1995, and legally harvested in Montana hunting district 314, including part of the NYWR, 1994–1996.

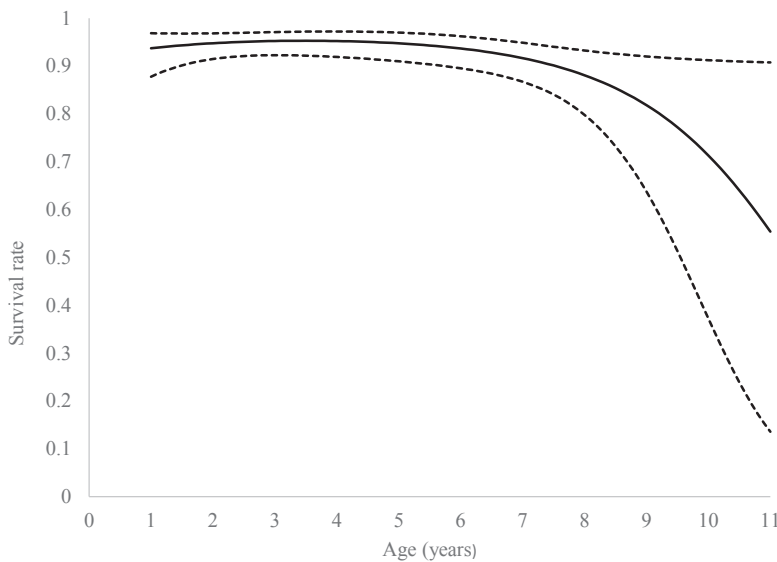


Fig. 9. Mean annual survival rates (solid line) of female northern Yellowstone mule deer ≥ 1 year old, 1993–1997. Dashed lines represent the standard error around the mean.

the 5 km/d recorded in that study (Sawyer et al. 2005) and reaches the lower limits of 20–50 km/d observed in Idaho (Thomas and Irby 1990). The 15-d median migratory time between winter and summer ranges, a mean of 42 km apart in our study, is intermediate between a median of 4 d to travel an average 46 km from winter to summer ranges (Len-

drum et al. 2014) and the 60–90 d for deer using stopover sites to travel 20–158 km (Sawyer et al. 2005). We relocated deer too infrequently to detect a pattern of use of stopover sites as reported for migratory mule deer in western Wyoming (Sawyer et al. 2005).

Our estimate of a late-April to mid-June onset of spring migration is similar to that of

TABLE 7. Candidate known-fate models to estimate annual survival rates of female northern Yellowstone mule deer, 1993–1997 ($n = 53$). The age models are compared with fully time-dependent, seasonal, and annual models. Models are listed in order of Akaike weights (w_i).

Model	AICc	Δ AICc	w_i	Parameters	Deviance
S(Age + Age ²)	213.62	0.00	0.47	3	207.57
S(Age)	214.23	0.60	0.35	2	210.20
S(Season)	216.54	2.92	0.11	2	212.51
S(Year)	217.37	3.74	0.07	4	209.27
S(Quarterly)	233.84	20.21	0.00	16	200.52

TABLE 8. Quarterly survival estimates for mule deer based on their migratory status, summer use of burned or unburned landscapes, and winter use of cultivated or natural vegetation.

Parameter	n	Class	Estimate	SE	95% Confidence interval	
					Lower limit	Upper limit
Migration status	73	Migratory	0.95	0.01	0.92	0.96
		Resident	0.95	0.01	0.91	0.98
Summer strategy	36	Burned	0.96	0.01	0.93	0.98
		Unburned	0.96	0.01	0.92	0.98
Winter strategy	50	Cultivated	0.96	0.01	0.93	0.97
		Natural	0.96	0.01	0.92	0.98

TABLE 9. Candidate known-fate models for estimating the effects of migration status and seasonal range on survival rates compared with quarterly and annual models of northern Yellowstone mule deer females, 1993–1997 ($n = 73$). Models are listed in order of Akaike weights (w_i).

Model	AICc	Δ AICc	w_i	Parameters	Deviance
S(.)	267.83	0.00	0.38	1	265.83
S(Range + Migrate)	269.37	1.54	0.17	3	263.34
S(Range)	269.76	1.92	0.14	2	265.74
S(Season)	269.84	2.01	0.14	2	265.83
S(Range * Migrate)	270.13	2.29	0.12	4	262.07
S(Year)	271.99	4.16	0.05	4	263.94
S(Quarterly)	399.82	131.99	0.00	14	371.20

mule deer elsewhere in the Rocky Mountains (Pac et al. 1991, Lendrum et al. 2014), but somewhat later than the early April to mid-April onset for other mule deer herds (Sawyer et al. 2005, Sawyer and Kauffman 2011, Monteith et al. 2011). Mule deer migrating 150–250 km began spring migration more than 3 weeks sooner than deer migrating <150 km (Sawyer et al. 2016). We were not able to ascertain the timing of fawning in our study; however, Lendrum et al. (2014) report pregnant migratory mule deer arriving on summer ranges prior to parturition. The median birth date for mule deer in the nearby Bridger Mountains, Montana, is June 26 (Pac et al. 1991), suggesting that pregnant deer in our study were on summer ranges prior to parturition.

The mid-October onset of fall migration exhibited by northern Yellowstone mule deer

is consistent with that of other mule deer herds throughout the mountains of western North America (Monteith et al. 2011). Mule deer in the nearby Bridger Mountains breed in mid-December (Pac et al. 1991), suggesting that migratory female deer in our study returned to winter range prior to the rut. Migratory northern Yellowstone mule deer departed their winter range and arrived on summer ranges later than did sympatric pronghorn antelope that wintered in the Gardiner Basin and had summer ranges along the Lamar and Yellowstone rivers (White et al. 2007). However, the timing of mule deer departure from summer ranges coincided with that of pronghorn antelope (White et al. 2007). Similarly, the onset of mule deer spring and fall migrations in this study was coincident with that of northern Yellowstone elk winter-

ing beyond the northern boundary of YNP (White et al. 2010).

HOME RANGE SIZE.—Mule deer home range size varies with habitat conditions, with smaller home ranges characterized by diverse and stable habitat conditions relative to larger home ranges, which have more simple and variable habitats (Mackie et al. 2003). Northern range adult female mule deer showed high philopatry to winter and summer ranges, as reported for mule deer elsewhere (Gruell and Papez 1963, Garrott et al. 1987, Wood et al. 1989, Brown 1992, Kucera 1992). However, Houston (1982) observed most mule deer on the NYWR moving north of the park boundary briefly during a harsh winter, indicating that philopatry may break down under severe conditions. The high philopatry to winter and summer ranges we detected suggests that adult females may be slow to abandon sites with habitat conditions transitioning from suitable to unsuitable or to colonize any sites with habitat conditions becoming suitable for deer. Subadult female mule deer move greater distances on summer ranges than do adult females (Garrott et al. 1987, Wood et al. 1989), possibly facilitating establishment of home ranges in areas of newly suitable habitat.

HABITAT SELECTION.—Temporal shifts in habitat selection are well documented in Rocky Mountain mule deer (Wallmo and Regelin 1981), but dichotomies in habitat selection in winter and summer ranges within a herd have not been reported previously. In our study, the dichotomy is attributable to disjunct habitat modification through human activities or wildland fires. Using the eigenanalysis allowed us to tease out the differences in habitat selection for both winter and summer ranges and avoid inappropriately treating our sample of deer as a uniform group. Activity patterns have been documented as influencing habitat selection in black-tailed deer (Bose et al. 2018), and diel patterns of habitat selection have been documented in elk (Roberts et al. 2017). Our study of northern Yellowstone mule deer did not address activity or diel patterns, but most of our telemetry locations of deer were obtained from shortly after dawn to early midday.

Winter range habitat selection: Our findings of mule deer selection for cultivated and grassland land cover types across a portion of the winter range and for shrubland and grassland land cover across the remainder of the winter

range are consistent with previous assessments of mule deer winter habitat selection (Barmore 2003) and winter diet (Singer and Norland 1994, Singer and Renkin 1995, Wambolt 1996, 1998). The high selection for cultivated lands is striking given its relative scarcity on the winter range (0.3%). Selection by mule deer for cultivated lands on winter range has been reported elsewhere (Thomas and Irby 1990, Anderson et al. 2012), with selection becoming greater as the proportion of cultivated land declined (Anderson et al. 2012). Similarly, wintering mule deer selection for *Artemisia*-dominated shrublands has been confirmed elsewhere (Oedekoven and Lindzey 1987, Anderson et al. 2012). Landscape classes avoided by the 2 divergent groups of deer included all burn intensities within the fire perimeter that covered <5% of the winter range. The mean >2000-m elevation of winter ranges of female mule deer in the Gardiner Basin was similar to the elevation of winter ranges of mule deer in the Bridger Mountains, Montana (Pac et al. 1991). Mule deer wintering in the Gardiner Basin utilized areas receiving more solar radiation than did elk or bighorn sheep (Keating et al. 2007), suggesting that mule deer are less capable of dealing with colder temperatures or deeper snow than these other species (Houston 1982), although snow depth was not measured directly (Keating et al. 2007).

Summer range habitat selection: The dichotomy of habitat selection among deer on summer ranges is attributable to differences in response to fire distribution, with the first group selecting for moderate and high burn intensity areas within the fire perimeters and the second group selecting against all intensities of burned area. This dichotomy largely reflects the difference in distribution of fires relative to deer home ranges. Use of burned areas by deer suggests an ability to persist in or exploit such areas 5 years postfire. Mean summer range elevations utilized by deer with positive and negative eigenvalues in our study (2007 m and 2226 m, respectively) indicate use of Douglas-fir-dominated forest occurring between 1850 and 2400 m on andesitic soils and use of lodgepole pine-dominated forest on rhyolitic soils. The mean summer range elevations were marginally higher than the mean winter range elevations, suggesting little delay in plant phenology on summer ranges

relative to winter ranges (Sawyer and Kauffman 2011). Mean northern Yellowstone mule deer summer range elevations are lower than the 2400-m to >3000-m elevation of mule deer summer range elsewhere in northwest Wyoming (Sawyer et al. 2005).

Deer demonstrated a dichotomy of summer range habitat selection, either avoiding all intensities of burned forest (Table 5) or selecting moderate or high burn intensity forest (Table 6) both in the Douglas-fir-dominated forest east and northeast of the Gardiner Basin and on the central Yellowstone Plateau lodgepole pine-dominated forest. This pattern reflects the distribution of burned forest across the summer range (Fig. 5). Those mule deer selecting moderate or high burn intensity forest had home ranges within the perimeter of recent forest fires, in contrast to those deer avoiding burned forest, which maintained home ranges outside the burned areas. We can only speculate on factors influencing mule deer selection for moderate or high burn intensity areas, given the paucity of information on prefire summer range conditions and deer habitat use in years prior to and immediately following the 1988 fires. Assessments of lodgepole pine forest 1–3 years postfire revealed a mosaic of unburned forest and various burn severities within 200 m of each other (Turner et al. 1994) and little difference in plant species distribution between unburned and burned forest, although plant species richness was lowest in crown fire areas (Turner et al. 1997). Vegetation within burned areas showed a trend back toward prefire plant community composition, particularly for perennial herbs, forbs, grasses and grasslike plants (Anderson and Romme 1991, Turner et al. 1997, 1999). However, shrub cover was greater in areas of light surface fires and lower in areas of greater fire intensity. In contrast, tree seedling cover, especially lodgepole pine seedling cover, was greatest in forest that burned with crown fires or severe surface fires (Tinker et al. 1994, Turner et al. 1997, Schoennagel et al. 2003). Model projections indicate that more frequent and larger wildland fires on the central Yellowstone Plateau over the next 600 years will result in a decrease in forest cover along with an increase in Douglas-fir abundance and a decrease in the abundance of lodgepole pine (Clark et al. 2017). We are unable to speculate on the impact of such

changes on summer use of the plateau by mule deer.

Age Structure, Causes of Mortality, and Survival

AGE STRUCTURE.—The paucity of female deer ≥ 8 years old in the northern Yellowstone herd is similar to the female deer age structure on the west slope of the Bridger Mountains, but dissimilar to that of female deer on the east slope of the Bridger Mountains, where a decline in the proportion of older deer does not occur until 12 years of age (Pac et al. 1991). Pac et al. (1991) attributed the difference in age structures to lower recruitment and higher survival among deer ≥ 1 year old on the west slope of the Bridger Mountains.

CAUSES OF MORTALITY.—We did not determine causes for most mortalities. However, the death of 13% of radio-marked deer due to automobile collisions over the 4 years of this study exceeds the 4% of the radio-marked females harvested by hunters. The loss of radio-marked females to automobile collisions was unexpected and suggests that deer-vehicle collisions are a potentially important mortality factor for female deer on the NYWR. In Montana, radio-marked deer were killed by automobile collisions along U.S. Route 89 in December, April, and May. Carcasses of non-marked deer were observed frequently along U.S. Route 89 south of Yankee Jim Canyon from November to May in all years.

SURVIVAL.—The marked decline in annual survival among female mule deer ≥ 6 years old detected in this study differs from the pattern on the east and west side of the Bridger Mountains, where there was little variation in age-specific survival among female mule deer until ≥ 10 years of age (Pac et al. 1991). Few female deer in this study survived beyond 10 years, but some female deer in the Bridger Mountains survived until they were 15 years old (Pac et al. 1991).

An annual survival rate of approximately 0.85 is common among female mule deer ≥ 1 year old across a large area of the U.S. Rocky Mountains (Unsworth et al. 1999) and elsewhere (Forrester and Wittmer 2013, Monteith et al. 2014). Changes in the abundance of predators or alternate prey may affect survival of mule deer associated with the NYWR in the future. Restoration of wolves (*Canis lupus*) to the GYA in 1995 (Bangs and Fritts 1996) and a

decline in northern Yellowstone elk numbers beginning in 1989 (Eberhardt et al. 2007) have the potential to destabilize mule deer demographics through either reduced interspecific competition for resources or prey-switching (Forrester and Wittmer 2013).

Management Implications

Northern Yellowstone mule deer utilize an extensive area for winter range, migratory pathways, and summer range. Much of the migratory network and summer range are on lands protected within YNP and Custer–Gallatin National Forest, including the Absaroka Beartooth wilderness zone, thereby reducing the possibility of disruption through human activities such as construction of rural housing, fencing, and energy extraction (Seidler et al. 2015) as documented in other herds within the region (Sawyer et al. 2005, 2009, Lendrum et al. 2012). However, those portions of the northern Yellowstone herd's migratory corridors and summer and winter ranges on private lands may be subject to changes in land use, particularly a rapid rate of rural residence construction since the time of this study, leading to habitat fragmentation (Gude et al. 2006, 2007). Some types of residential development may appear less disturbing to deer, as the owner's permanency may enable deer to adjust behaviorally (Lendrum et al. 2013). However, the nature of other human activities may have a marked effect on deer behavior, with deer known to avoid high levels of such activities (Sawyer et al. 2009, Wyckoff et al. 2018). Current levels of other human activities on private lands, such as agricultural practices, may be beneficial to deer, as demonstrated in our study by deer selecting cultivated lands in winter. Any potential increase in the volume or speed of traffic on U.S. Route 89 traversing the northern Yellowstone herd's winter range may result in an increase of the deer mortality due to deer–vehicle collisions documented in this study and elsewhere (Sawyer et al. 2012).

Our findings of some migratory deer selecting moderate and high burn intensity areas on summer range 5–9 years postfire may be indicative of the species' ability to respond to changes in landscape conditions and its flexibility in summer habitat selection. The lack of use of low burn intensity areas by the same group of deer, and avoidance of all burn intensity areas on summer range 5–9 years postfire

by a second group, suggests that the response of deer to fire modification of habitat on summer range may be long term. Additionally, the similarity in survival rates among deer utilizing burned or unburned summer range suggests no long-term detrimental effect of fire. The significance of the lack of selection by all deer of the relatively small areas of low to high burn intensity on the winter range is less clear.

Our study took place during a trend evident since 1948 of increasing annual precipitation and increasing minimum and maximum temperatures on the winter and summer ranges (Gonzalez 2012, Chang and Hansen 2015, Sepulveda et al. 2015). Such changes are predicted to increase the frequency and extent of fires (Westerling et al. 2011) and lead to shifts in the distribution and composition of plant communities (Littell et al. 2009, Hansen et al. 2015). Such changes may affect the GYA's ability to support mule deer at current levels, although deer have demonstrated flexibility in use of burned areas some 5 years postfire.

Potential overlap of northern Yellowstone mule deer summer ranges, with migratory deer herds wintering to the south and east of YNP, may indicate that the threat of chronic wasting disease (CWD) transmission to the northern Yellowstone herd is considerable (Conner and Miller 2004, Almborg et al. 2011). Models of CWD spread predict that CWD will enter the Yellowstone Plateau from the southeast (Almborg et al. 2011), where a CWD prevalence averaging 24% has caused a decline in mule deer numbers (DeVivo et al. 2017). Our data indicate that migratory northern Yellowstone mule deer could carry CWD from the southern Yellowstone Plateau to the NYWR and thereby transmit the disease throughout the herd's summer range. Additionally, CWD was detected to the north of YNP in 2017 (<http://fwp.mt.gov/news/news>), suggesting that deer moving to the east of NWYR could contact infected animals and thereby spread the disease throughout the herd's range.

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