

## SEASONAL MOVEMENTS AND HOME-RANGE USE BY FEMALE PRONGHORNS IN SAGEBRUSH-STEPPE COMMUNITIES OF WESTERN SOUTH DAKOTA

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Knowledge of seasonal movements by pronghorns (*Antilocapra americana*) within the easternmost extension of sagebrush-steppe communities is limited. Current hypotheses regarding movement patterns suggest that pronghorns initiate seasonal movements in response to severe winter weather, snowfall patterns, spatial and temporal variation in forage abundance, and availability of water. From January 2002 to August 2005, we monitored movements of 76 adult ( $\geq 1.5$  years) female pronghorns on 2 study areas (Harding and Fall River counties) in western South Dakota. We collected 8,750 visual locations, calculated 204 home ranges, and documented 17 seasonal movements. Eighty-four percent ( $n = 55$ ) of pronghorns were nonmigratory and 10% ( $n = 6$ ) were conditional migrators. Mean distance between summer and winter range was 23.1 km ( $SE = 2.8$  km,  $n = 13$ ). Five adult pronghorns (8%) dispersed a mean distance of 37.6 km ( $SE = 12.4$  km); of which 1 female moved a straight-line distance of 75.0 km. Winter and summer home-range size varied ( $P < 0.0001$ ) between study sites. Mean 95% adaptive kernel winter and summer home-range size of pronghorns was 55.5 and 19.7 km<sup>2</sup>, respectively, in Harding County and 127.2 and 65.9 km<sup>2</sup>, respectively, in Fall River County. Nonmigratory behavior exhibited by pronghorns was likely associated with minimal snow cover and moderate temperatures during winter 2002–2004. Variation in size of adult seasonal home ranges between sites was likely associated with differences in forage distribution and availability between regions.

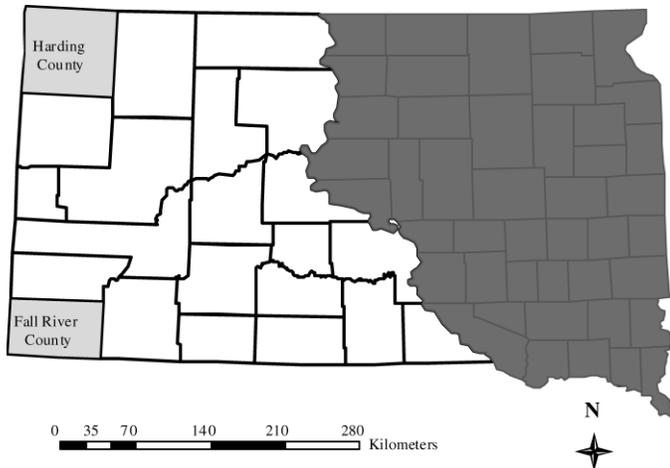
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Pronghorn (*Antilocapra americana*) populations are widely distributed throughout western South Dakota where mixed-grass prairie habitats characterize rangelands. Distribution of pronghorns in western South Dakota is within an eastward extension of sagebrush-steppe communities, including both big sagebrush (*Artemisia tridentata*) and silver sagebrush (*A. cana*)—Schroeder et al. 1999; Smith et al. 2004). In the northern part of pronghorn range, seasonal movements between traditional home ranges to which pronghorns return annually has previously been documented (Riddle 1990; Yoakum and O’Gara 2000). However, several studies have suggested that seasonal ranges were not traditional areas to which pronghorns returned annually, but rather that pronghorns migrated only as far as necessary to optimize effects of environmental conditions

(Barrett 1982; Pepper and Quinn 1965). Pronghorns are adapted to moving long distances to locate and use high-quality forage (O’Gara and Yoakum 2004); however, some populations may not exhibit migratory behavior (Boccardi and Garrott 2002) or move only short distances (i.e.,  $\leq 20$  km) between seasonal ranges (Cole 1956; Cole and Wilkins 1958; Hoskinson and Tester 1980). Kitchen and O’Gara (1982) indicated that pronghorn home-range size was variable and resulted from differences in habitat quality, population and group sizes, land-use history, and season. Consequently, previous reports of home-range size for adult pronghorns have varied widely and included estimates of 0.2 to 2,873 km<sup>2</sup> (Bates 2000; Canon 1993; Clemente et al. 1995; Hervert et al. 2005; Kitchen 1974).

Because of the difficulty of monitoring individuals adapted to moving long distances, empirical data documenting movement that occurs across landscapes are not available in many areas throughout the northern range of pronghorns, particularly within the easternmost extension of sagebrush-steppe communities. To our knowledge, the only seasonal

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**FIG. 1.**—Pronghorn (*Antilocapra americana*) study areas in western South Dakota, 2002–2005, were located in Harding and Fall River counties (shaded light gray). Thick black lines delineate county boundaries in western South Dakota. The dark gray shaded area encompasses eastern South Dakota and represents the area outside the current pronghorn range.

movements documented previously for female pronghorns within the easternmost expanse of sagebrush-steppe communities were those reported by West (1970), who documented movements >320 km by pronghorns in response to severe winters in western South Dakota. However, information on home-range use by female pronghorns has not been previously documented in sagebrush-steppe communities of western South Dakota. Thus, the primary objectives of our study were to determine seasonal movements (i.e., migration and dispersal) and home-range use by adult female pronghorns in western South Dakota and to infer differences in habitat quality based on differences in home-range size.

## MATERIALS AND METHODS

**Study areas.**—We conducted our study in 2 sites (Harding and Fall River counties) in western South Dakota. The landscape in western South Dakota was characterized by a mosaic of mixed-grass prairie interspersed with sagebrush (*Artemisia*) and patches of ponderosa pine (*Pinus ponderosa*) forest. Although pronghorns occur throughout western South Dakota, counties along the western border are within the sagebrush-steppe region of North America, and, thus, are most representative of habitats associated with pronghorns (Yoakum and O’Gara 2000).

Harding County encompassed an area of 6,940 km<sup>2</sup> in northwestern South Dakota (Fig. 1). Most of the land area in Harding County was treeless, semiarid rolling plains (Johnson 1988). The county was bordered by Butte County to the south, Perkins County to the east, North Dakota to the north, and Montana to the west. Land elevation ranged between 817 and 1,224 m above mean sea level (Johnson 1988). Harding County had a continental climate characterized by cold winters and hot summers, averaging  $-7^{\circ}\text{C}$  in winter and  $20^{\circ}\text{C}$  in summer. Annual precipitation averaged 37 cm and average seasonal

snowfall was 101 cm (Johnson 1988). Most farm or ranch land (88%) in Harding County was used for grazing sheep (*Ovis aries*) and cattle (*Bos taurus*) and 12% was used for cultivated crops, tame pasture (i.e., pastures planted primarily to cool-season exotic or introduced grass or legume species or both), or hay. Dominant grasses on the landscape included western wheatgrass (*Pascopyrum smithii*), prairie Junegrass (*Koeleria pyramidata*), buffalograss (*Buchloe dactyloides*), green needlegrass (*Nassella viridula*), and blue grama (*Bouteloua gracilis*). Silver sagebrush and big sagebrush were widely distributed throughout the county (Johnson 1988).

Fall River County encompassed an area of 5,071 km<sup>2</sup> in southwestern South Dakota (Fig. 1). The county was bordered by Custer County to the north, Shannon County to the east, Nebraska to the south, and Wyoming to the west. Land elevation ranged between 914 and 1,478 m above mean sea level (Kalvels 1982). Fall River County had a continental climate characterized by cold winters and hot summers, averaging  $-3^{\circ}\text{C}$  in winter and  $22^{\circ}\text{C}$  in summer. Annual precipitation averaged 42 cm and average seasonal snowfall was 107 cm (Kalvels 1982). Approximately 83% of farm and ranch land in Fall River County was grazed by livestock (primarily cattle) and 17% was used for cultivated crops, tame pasture, or hay (Kalvels 1982). Fall River County was located within the mixed-grass prairie region of western South Dakota and dominant grasses included western wheatgrass, buffalograss, green needlegrass, needleandthread (*Stipa comata*), sideoats grama (*Bouteloua curtipendula*), blue grama, and prairie Junegrass. Dominant overstory woody vegetation in Fall River County consisted of limited stands of ponderosa pine interspersed with small stands of quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*)—Kalvels 1982). Silver sagebrush and big sagebrush were limited in distribution throughout Fall River County. Plant nomenclature followed Larson and Johnson (1999) and Johnson and Larson (1999).

**Pronghorn captures.**—We captured adult female pronghorns ( $\geq 1.5$  years old) by net-gun deployed from a helicopter (Krausman et al. 1985) at sites in Harding and Fall River counties during 22–24 January 2002 and 18–19 February 2003, respectively. Each captured pronghorn was restrained, hobbled, blindfolded, and transported to nearby processing sites. We determined age for pronghorns based on incisor wear and replacement (Dow and Wright 1962). We ear-tagged, measured (chest and neck circumference and right rear foot length), assessed body condition, and radiocollared each pronghorn. We monitored rectal temperature continuously throughout the processing period as an indicator of physical stress, and released individuals if body temperature exceeded  $42^{\circ}\text{C}$ . Blood samples were collected from each pronghorn by venipuncture of the jugular vein for disease and genetic evaluation. Radiocollars (151 MHz; Telonics Inc., Mesa, Arizona; Advanced Telemetry Systems, Isanti, Minnesota) were attached to each captured pronghorn and were equipped with activity and mortality sensors that switched to mortality mode after the transmitter remained motionless for  $\geq 5$  h. Before release of pronghorns, we administered a 5-ml intramuscular injection of

a broad-spectrum antibiotic (Dual-Cillin; Phoenix Scientific, St. Joseph, Missouri) and removed blindfolds and restraint straps. We recorded total handling time for each pronghorn. We also recorded capture locations for each pronghorn using a global positioning system (Garmin International Inc., Olathe, Kansas). Our animal handling methods were approved by the Institutional Animal Care and Use Committee at South Dakota State University (approval number 02-A001) and followed guidelines for the care and use of animals approved by the American Society of Mammalogists (Gannon et al. 2007).

*Monitoring and radiotracking.*—We monitored each radio-collared animal for mortality 2 or 3 times per week from January 2002 to August 2005. We used a vehicle-mounted “null-peak” antenna system (Brinkman et al. 2002), handheld directional antennas (Telonics Inc.), or fixed-wing Cessna 182 aircraft to locate pronghorns. All individual pronghorns were radiotracked until they were visually observed; locations of individuals were then recorded as Universal Transverse Mercator coordinates using a handheld global positioning system. We visually located each pronghorn 1–3 times per week from February 2002 to February 2003 and monthly from March 2003 to August 2004 in Harding County. Radiocollared pronghorns were visually located 1–3 times per week from March 2003 to March 2005 and monthly from April to August 2005 in Fall River County, at which time fieldwork was terminated. We conducted field necropsies at death sites to determine cause of death. We classified deaths that occurred during capture operations as direct mortalities and deaths that occurred within 26 days postcapture as capture-related (Beringer et al. 1996). Annual mortality events also were documented and contributed to subsequent decreases in sample sizes across years during our study.

*Data analyses.*—We entered locations into a geographic information system, and analyzed them to determine home-range use and seasonal movements of female pronghorns. We used the Home Range Tools (HRT) Analysis Extension in ArcGIS 9.1 (Rodgers and Carr 1998) to calculate 95% summer and winter home ranges and 50% core areas. Adaptive kernel methods (Kie et al. 1996; Seaman et al. 1999) were used to calculate summer and winter home ranges. We generated home-range estimates using an ad hoc smoothing parameter ( $h_{ad\ hoc}$ ) by choosing the smallest increment of the reference bandwidth ( $h_{ref}$ ) that resulted in a contiguous 95% kernel home range (i.e.,  $h_{ad\ hoc} = 0.9 \times h_{ref}$ ,  $0.8 \times h_{ref}$ , etc.—J. G. Kie, Idaho State University, Pocatello, Idaho, pers. comm.). Kernel estimators are nonparametric and thus are not based on an assumption that the data conform to specified distribution parameters (Seaman et al. 1999).

We used the harmonic mean measure of an individual pronghorn's center of activity to determine the geographic center of seasonal ranges (Dixon and Chapman 1980); harmonic means were used because they are not sensitive to a pronghorn's location and enabled shifts in activity centers within seasonal ranges to be detected (Dixon and Chapman 1980). We used our geographic information system to measure the distance between center points of seasonal home ranges. Dispersal was defined as a permanent movement by an indi-

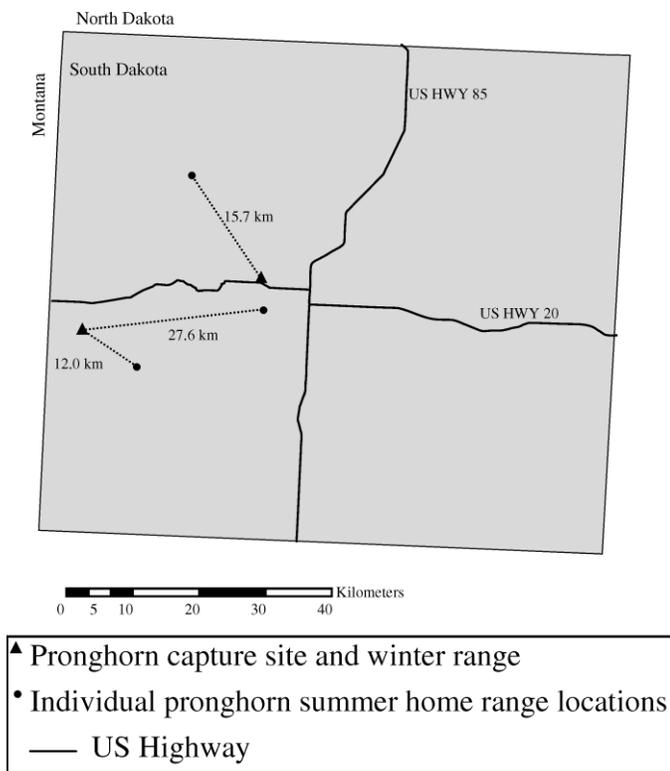
vidual from an established home range and establishment of a nonoverlapping home range elsewhere. We defined migration as seasonal movement between nonoverlapping winter and summer ranges, measured as linear distance between centers of seasonal home ranges (Brinkman et al. 2005). If we detected any overlap between summer and winter home ranges, we assumed migration did not occur. Pronghorns were classified as obligate migrators (Martinka 1967) if they migrated between established summer and winter home ranges during every migratory period. We classified pronghorns as conditional migrators if they made a minimum of 3 migrations between summer and winter home ranges, failed to migrate to a previously occupied winter home range, or migrated briefly ( $\leq 1$  month) to a winter home range during a single winter (Bruns 1977; Hoskinson and Tester 1980). Pronghorns were classified as residents if they never migrated (Boccardi and Garrott 2002). We defined spring migration as seasonal movement from winter to summer home range and fall migration as seasonal movement from summer to winter home range (Brinkman et al. 2005). A migration strategy (i.e., obligate, conditional, or permanent resident) was assigned only to individual pronghorns that were monitored through a minimum of 3 consecutive migratory periods (Brinkman et al. 2005). Because individuals in Harding County were not located frequently enough during 2003 and 2004 to calculate individual seasonal home-range size, we pooled locations from all individuals within this study site during these years in home-range analyses. Thus, we calculated summer 2003–2004 and winter 2003–2004 home-range size for Harding County and compared these estimates to 2002 seasonal home-range size estimates; our analyses were kept separate by study site.

We performed statistical analyses using SYSTAT (SYSTAT Software Inc., Richmond, California; Wilkinson 1990). Pronghorn migration distances, percentage of pronghorns migrating, and home-range sizes between seasons and years were compared using parametric *t*-tests and 2-factor analyses of variance. We set alpha at  $P \leq 0.05$  and used a Bonferroni correction factor to maintain experiment-wide error rates when multiple *t*-tests were performed (Neu et al. 1974).

## RESULTS

*Pronghorn capture mortalities.*—We captured and radio-collared 67 adult female pronghorns during January 2002 ( $n = 30$ ) and February 2003 ( $n = 37$ ) at 2 study sites in western South Dakota (Fig. 1). Because of relatively high capture mortality during January 2002, we captured and radiocollared 15 additional pronghorns during April 2002 in Harding County (i.e., northwestern South Dakota). Of 82 pronghorns captured, 12 (14.6%) died during helicopter capture operations; 5 deaths were caused by direct injuries sustained during captures and 7 deaths occurred within 26 days postcapture.

*Monitoring, home ranges, and seasonal movements.*—We collected 8,750 visual locations (4,824 in Harding County and 3,926 in Fall River County) from 76 adult female pronghorns in Harding ( $n = 39$ ) and Fall River ( $n = 37$ ) counties from February 2002 to August 2005. We monitored 15, 18, 15, 9,



**FIG. 2.**—Migration and dispersal distance and direction of radio-collared female pronghorns (*Antilocapra americana*;  $n = 3$ ) in Harding County, South Dakota, 2002–2005. Seasonal movements south of United States Highway 20 represented dispersal and new range establishment by 2 individuals. Seasonal movements north of United States Highway 20 represented migration by a single pronghorn between summer and winter home ranges during spring and fall 2002 migratory periods.

13, and 5 individual pronghorns through 6, 5, 4, 3, 2, and 1 migratory period(s), respectively, in Harding and Fall River counties. We calculated 204 individual home ranges during 6 seasonal range periods: winter 2002, summer 2002, winter 2003, summer 2003, winter 2004, and summer 2004; seasonal home ranges were calculated using a minimum of 25 and a mean of 38.3 ( $SE = 0.93$ ) telemetry locations. To avoid potential biases in the number of locations collected between individuals, study sites, and seasons, we attempted to distribute telemetry location efforts evenly between individuals, both spatially (study sites) and temporally (seasons). We calculated 26, 23, 12, and 7 seasonal home ranges for individual pronghorns during 4, 3, 2, and 1 seasonal range period(s), respectively. A decrease in sample sizes of pronghorns across years was due to mortality events of individual pronghorns throughout our study.

**Harding County migration and dispersal.**—We documented 4 seasonal movements by 3 of 36 pronghorns in Harding County during 2 migratory periods, spring and fall 2002. Of the 3 pronghorns that initiated seasonal movements, mean migration and dispersal distances were 15.7 ( $SE = 2.7$ ) and 19.8 ( $SE = 7.8$ ) km, respectively, and varied from 12.0 to 27.6

km (Fig. 2). Median departure date from winter to summer ranges by migratory and dispersing individuals was 8 April 2002 and varied from 14 March to 3 May; timing of 1 individual was unidentifiable. The single individual that migrated during the fall 2002 migratory period departed summer range on 1 October and arrived on winter range on 4 October; this individual also exhibited migratory behavior during the spring 2002 migratory period (Table 1). Surprisingly, we documented no additional migratory or dispersal movements by any individuals in Harding County during the remaining 5 migratory periods (spring 2003–spring 2005; Table 1). Nonmigratory pronghorns comprised  $\geq 92\%$  of the study population and 3–6% of our sample was classified as conditional migrators. Further, we documented no obligate migration by pronghorns in Harding County during our study (Table 1).

**Fall River County migration and dispersal.**—Similarly, we documented 13 seasonal movements by 7 of 27 pronghorns in Fall River County during 3 migratory periods: spring 2003–spring 2004 (Table 1). Thirteen seasonal movements (10 conditional migrations and 3 dispersal movements) by 7 pronghorns occurred during the spring 2003, fall 2003, and spring 2004 migratory periods (Table 1). Pronghorns that migrated during spring 2004 also exhibited migratory movements during the fall 2003 migratory period (Table 1). We documented no additional migratory or dispersal movements by any individuals in Fall River County during the remaining 2 migratory periods (fall 2004–spring 2005; Table 1). Mean migration and dispersal distances were 25.0 ( $SE = 3.3$ ) and 49.6 ( $SE = 17.6$ ) km, respectively. Migration and dispersal distances varied from 12.1 to 39.2 km and 15.7 to 75.0 km, respectively (Fig. 3). Median departure date from winter to summer ranges by migratory and dispersing individuals was 5 May 2003 and varied from 11 April to 30 May. Similarly, the median departure date from summer to winter ranges was 24 October 2003 and ranged from 10 October to 7 November. Nonmigratory pronghorns accounted for  $\geq 81\%$  of the Fall River County study population, whereas conditional migrators comprised 7–17%. Interestingly, we documented no obligate migration by pronghorns in Fall River County during our study (Table 1).

**Home range.**—We calculated seasonal home-range size of individual pronghorns using a minimum of 25 and a mean of 38.3 ( $SE = 0.934$ , range = 47,  $n = 230$ ) locations. We documented no difference ( $t \leq 0.966$ ,  $df = 57$ ,  $P \geq 0.338$ ) in winter 95% home-range size between 2002 ( $\bar{X} = 37.0$  km<sup>2</sup>,  $SE = 4.0$  km<sup>2</sup>,  $n = 33$ ) and 2003–2004 ( $\bar{X} = 38.5$  km<sup>2</sup>,  $SE = 4.7$  km<sup>2</sup>,  $n = 26$ ) in Harding County. Likewise, we documented no difference ( $t \leq 0.842$ ,  $df = 59$ ,  $P \geq 0.403$ ) in summer 95% home-range size between 2002 ( $\bar{X} = 15.4$  km<sup>2</sup>,  $SE = 1.8$  km<sup>2</sup>,  $n = 37$ ) and 2003–2004 ( $\bar{X} = 15.5$  km<sup>2</sup>,  $SE = 2.5$  km<sup>2</sup>,  $n = 24$ ) in Harding County. Mean winter 95% home-range size was similar ( $t \leq 1.538$ ,  $df = 49$ ,  $P \geq 0.133$ ) between 2003 ( $\bar{X} = 135.3$  km<sup>2</sup>,  $SE = 20.6$  km<sup>2</sup>,  $n = 24$ ) and 2004 ( $\bar{X} = 105.2$  km<sup>2</sup>,  $SE = 19.2$  km<sup>2</sup>,  $n = 23$ ) in Fall River County. Furthermore, we documented no differences ( $t \leq 1.017$ ,  $df = 39$ ,  $P \geq 0.315$ ) in mean summer home-range size between 2003 ( $\bar{X} = 71.2$  km<sup>2</sup>,

**TABLE 1.**—Seasonal movements of adult female pronghorns (*Antilocapra americana*) by study site, year, and season in western South Dakota, 2002–2005.

Study site <sup>a</sup>	Year	Season <sup>b</sup>	No. marked animals	No. nonmigrators <sup>c</sup>	No. obligate migrators <sup>d</sup>	No. conditional migrators <sup>e</sup>	No. dispersers <sup>f</sup>
HC	2002	Spring	36	33 (91.6)	0	1 (2.8)	2 (5.6)
		Fall	35	34 (97.1)	0	1 (2.9)	0
	2003	Spring	27	27 (100)	0	0	0
		Fall	26	26 (100)	0	0	0
	2004	Spring	24	24 (100)	0	0	0
		Fall	24	24 (100)	0	0	0
2005	Spring	24	24 (100)	0	0	0	
FRC	2003	Spring	27	22 (81.4)	0	2 (7.4)	3 (11.1)
		Fall	24	20 (83.3)	0	4 (16.7)	0
	2004	Spring	24	20 (83.3)	0	4 (16.7)	0
		Fall	24	24 (100)	0	0	0
	2005	Spring	21	21 (100)	0	0	0

<sup>a</sup> HC = Harding County; FRC = Fall River County.

<sup>b</sup> Spring migration was defined as seasonal movements by pronghorns from winter to summer home ranges; fall migration was defined as seasonal movement by pronghorns from summer to winter home ranges.

<sup>c</sup> Number (and percentages) of nonmigratory pronghorns.

<sup>d</sup> Number (and percentages) of obligate migrators.

<sup>e</sup> Number (and percentages) of conditional migrators.

<sup>f</sup> Number (and percentages) of dispersing pronghorns.

$SE = 13.5 \text{ km}^2$ ,  $n = 28$ ) and 2004 ( $\bar{X} = 56.5 \text{ km}^2$ ,  $SE = 15.5 \text{ km}^2$ ,  $n = 21$ ) in Fall River County.

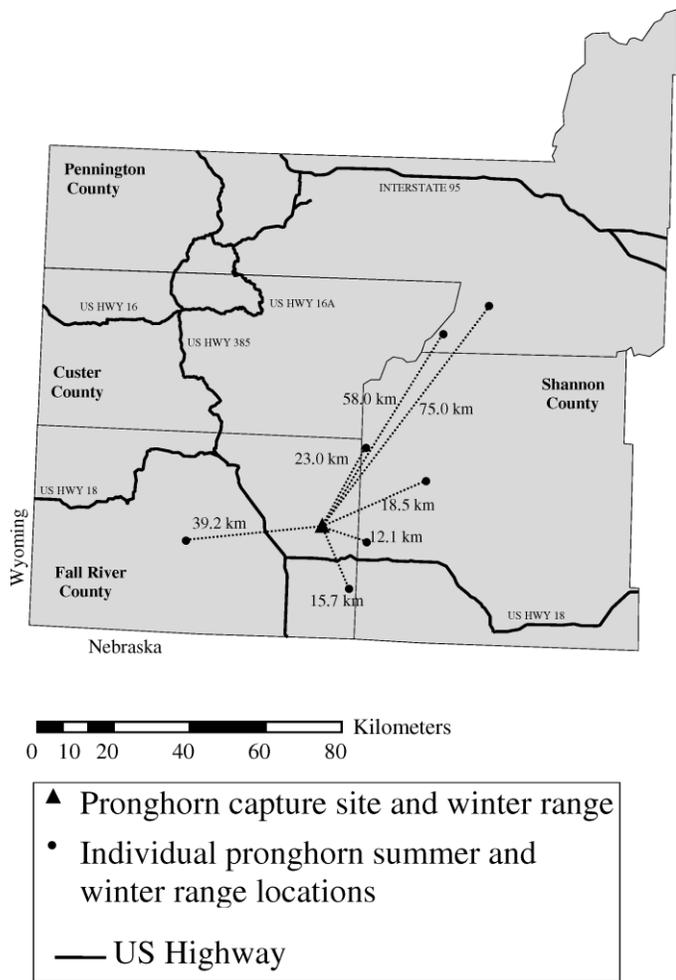
Mean winter home-range size varied significantly ( $t \geq 4.55$ ,  $df. = 60$ ,  $P < 0.001$ ) between study sites. Mean 95% and 50% winter home-range sizes were  $55.5 \text{ km}^2$  ( $SE = 9.4 \text{ km}^2$ ,  $n = 35$ ) and  $9.5 \text{ km}^2$  ( $SE = 1.6 \text{ km}^2$ ,  $n = 35$ ), respectively, for Harding County and  $127.2 \text{ km}^2$  ( $SE = 10.7 \text{ km}^2$ ,  $n = 27$ ) and  $21.3 \text{ km}^2$  ( $SE = 2.5 \text{ km}^2$ ,  $n = 27$ ), respectively, for Fall River County. Mean summer home-range size also varied significantly ( $t \geq 5.38$ ,  $df. = 65$ ,  $P < 0.001$ ) between sites. Mean 95% and 50% summer home-range sizes were  $19.7 \text{ km}^2$  ( $SE = 2.9 \text{ km}^2$ ,  $n = 39$ ) and  $3.3 \text{ km}^2$  ( $SE = 0.5 \text{ km}^2$ ,  $n = 39$ ) for Harding County and  $65.9 \text{ km}^2$  ( $SE = 9.0 \text{ km}^2$ ,  $n = 28$ ) and  $9.4 \text{ km}^2$  ( $SE = 1.1 \text{ km}^2$ ,  $n = 28$ ) for Fall River County (Fig. 4).

## DISCUSSION

Numerous studies have demonstrated that helicopter net-gunning is an efficient and safe method for capturing ungulates (Brinkman 2003; DelGiudice et al. 2001; White and Bartmann 1994). However, capture-related mortality rates for pronghorns in the present study were moderate to high (15%) compared to other ungulate net-gun captures (12% [Barrett et al. 1982], 10% [Firchow et al. 1986], 12% [Kock et al. 1987b], <3% [Kock et al. 1987a], and 15% [Krausman et al. 1985]). Unfavorable capture conditions (i.e., mild temperatures and lack of snow cover) and long transport distances (up to 14 km) to processing sites likely contributed to high capture-related mortalities. Further, most pronghorns were transported in multiples of 2 or more. Because exact times are unavailable, it is unknown how long captured pronghorns remained hobbled and blindfolded before being transported. However, failure to immediately transport individuals contributed to long handling times. Consequently, prolonged handling times and long

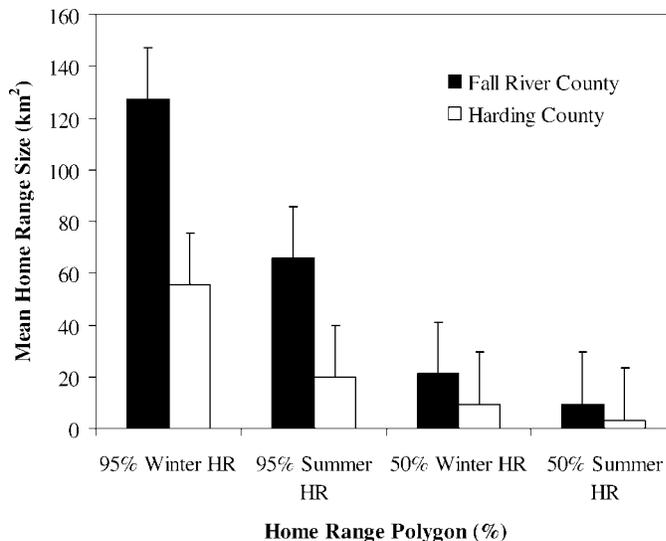
transport distances may have collectively predisposed individuals to fatal capture myopathy (Chalmers and Barrett 1982; Seal et al. 1978), and thus contributed to relatively high capture-related mortality rates. To this end, transporting pronghorns to processing sites has serious limitations. To minimize capture-related mortalities, we recommend that transporting individuals to processing sites should be minimized or if feasible, eliminated. Additionally, coordinating helicopter net-gun capture operations during favorable environmental conditions (i.e., cold temperatures and adequate snow cover) would provide the best situation for capture-related mortality to be controlled to acceptable levels (i.e., <5%—DelGiudice et al. 2005).

Pronghorns occupying the edge of the sagebrush-steppe biome in Harding and Fall River counties exhibited a mixture of migration strategies consisting of conditional migrators and permanent residents; our results indicated that pronghorn populations in our study sites were composed largely of permanent residents. Interestingly, obligate migration was not documented in any animals in the present study, which contrasts sharply with much of the previous literature. For instance, Martinka (1966) reported migratory movements of >160 km in Montana. Hoskinson and Tester (1980) documented obligate migration in pronghorn populations in southeastern Idaho and suggested that spring and autumn migrations were prompted by breakup of snow cover and moisture content of vegetation, respectively. Sawyer et al. (2005) documented the longest seasonal migrations (116–258 km) yet recorded for pronghorns and noted that movement data were consistent with migration patterns documented by Harper (1985), Segerstrom (1997), and Hoskinson and Tester (1980). In contrast, Boccadori and Garrott (2002) and Sievers (2004) described nonmigratory pronghorn populations in Yellowstone National Park and Wind Cave National Park, respectively.



**FIG. 3.**—Migration and dispersal distance of radiocollared female pronghorns (*Antilocapra americana*;  $n = 7$ ) in Fall River County, South Dakota, 2003–2005. Seasonal movements northward into Pennington County (58 km and 75 km) represented dispersal and new range establishment by 2 individuals during the spring 2003 migratory period. Seasonal movements northward and eastward into Shannon County were to summer (18.5 km and 23.0 km) and winter (12.1 km) ranges by 3 pronghorns during spring and fall 2003 migratory periods, respectively. Pronghorn movements south of United States Highway 18 represented dispersal and new permanent home-range establishment by a single individual during the spring 2003 migratory period. Pronghorn movements west of United States Highway 385 were between winter and summer home ranges by a single pronghorn during fall 2003 and spring 2004 migratory periods.

However, Sievers (2004) noted that constraints (i.e., fencing structures) placed on closed populations may limit migratory movements by pronghorns in response to changing environmental conditions. The likelihood of fencing structures limiting migratory movements by the free-ranging populations in the present study was minimal, yet individuals remained largely nonmigratory. Additionally, migratory movements by the animals in the present study consisted of short migration distances (12–39 km), suggesting that individuals migrated only as far as necessary to optimize effects of environmental



**FIG. 4.**—Mean seasonal home-range size for adult female pronghorns (*Antilocapra americana*) in Harding and Fall River counties, South Dakota, February 2002–August 2005. Harding County 95% and 50% summer and winter home-range estimates were calculated using radiotelemetry data obtained from 39 and 35 individual pronghorns, respectively. Similarly, Fall River County 95% and 50% summer and winter home-range estimates were calculated from telemetry data obtained from 28 and 27 individual pronghorns, respectively.

conditions (i.e., distribution of optimal forage [shrubs] and reduced snow depths).

Yoakum (2004) reported that winter movements by pronghorns were influenced primarily by snow depth and condition, noting that cumulative snow depths > 15 cm contributed to reduced forage availability and subsequent seasonal movements by pronghorns to lower elevations or alternative areas with reduced snow and greater available forage. Similarly, Hoskinson and Tester (1980) found that as cumulative snow depth increased (i.e., up to 13.3 cm), distance migrated by pronghorns also increased. Pyle (1973) reported that pronghorns avoided cumulative snow depths > 20 cm, yet pronghorns moved only as far as necessary to locate high-quality forage. To this end, Bruns (1977) hypothesized that pronghorns were opportunistic migrants and only exhibited migratory behaviors when prompted by severe environmental conditions. Interestingly, cumulative monthly snow depths and winter temperatures for Harding and Fall River counties averaged 15.4 cm and  $-5.8^{\circ}\text{C}$ , and 7.9 cm and  $1.1^{\circ}\text{C}$ , respectively (South Dakota Office of Climatology 2007), indicating that favorable winter conditions prevailed throughout our study. Our results are comparable to those of previous studies and further suggest that minimal cumulative snow depth and mild temperatures likely contributed to limited migratory behavior by pronghorns in the study populations.

Variation in seasonal home-range size between Harding and Fall River counties were notable. Winter and summer home ranges were 2.3 and 3.0 times smaller, respectively, in Harding County than in Fall River County. Unfortunately, we did not have sufficiently detailed data on quality and distribution of

food resources to test for regional effects on variation in pronghorn seasonal home-range size between study areas. Consequently, mechanisms influencing seasonal variation in home-range size remain speculative. Nevertheless, it is possible that fragmentation of winter rangelands or sustained drought conditions may have contributed to variation in pronghorn seasonal ranges in the study populations. For instance, winter rangelands were more fragmented and availability of shrubs (particularly sagebrush) more patchy in distribution in Fall River County than in Harding County (A. R. Lewis, Augustana College, Sioux Falls, South Dakota, pers. comm.). Jacques and Jenks (2007) also suggested that differences in habitat quality between Harding and Fall River counties likely contributed to differences in winter home-range sizes between yearling pronghorns. We suggest that fragmentation of winter rangelands and relatively more patchy distribution of shrubs (particularly sagebrush) between study sites contributed to limited spatial distribution and availability of winter forage in Fall River County. Consequently, pronghorns in Fall River County occupied larger winter home ranges compared to pronghorns in Harding County. Similarly, drought conditions persisted throughout our study, particularly in Fall River County, and may have reduced high-quality summer forage required by parturient female pronghorns. Subsequently, females may have used larger summer home ranges in Fall River County to meet increased energetic demands during parturition and fawn-rearing periods.

Spatial distribution of pronghorns across western South Dakota also may be influenced by global warming. Global mean surface temperatures have risen 0.6°C since the late 19th century (Intergovernmental Panel on Climate Change 2001), and global warming is expected to continue throughout the 21st century (O'Gara and Yoakum 2004). Elevated ambient temperatures, particularly during winter and spring, may affect pronghorns in 2 opposite ways. Global warming may enhance primary production and food availability for pronghorns throughout their geographic range. Alternatively, continued long-term drought conditions throughout shortgrass prairies and shrub-steppe communities may reduce food availability and contribute to subsequent declines in pronghorn survival across the geographic range of the species (O'Gara and Yoakum 2004). Jacques et al. (2006) hypothesized that an observed pronghorn population decline in Wind Cave National Park was associated with reduced food availability due to long-term drought conditions throughout western South Dakota. Long-term drought conditions may have contributed to site-specific differences in seasonal movements and home-range use by pronghorns in the populations in the present study via reduced precipitation in summer and reduced snow accumulation in winter.

Dispersal by yearling pronghorns (<1.5 years old) has been described in Idaho (Hoskinson and Tester 1980) and South Dakota (Jacques and Jenks 2007). To our knowledge, dispersal by adults has not previously been documented in pronghorn populations. Reasons for yearling dispersal have been described in the literature. For instance, Jacques and Jenks (2007) hypothesized that winter movements had selective advantages

to fawn and yearling pronghorns, and may have enabled individuals to rapidly colonize new or vacant habitats. Reasons for dispersal by adults are more speculative and may be associated with aggressive behavior among female social groups (Fairbanks 1994) or failure to successfully raise young (Testa et al. 2000; Welch et al. 2000; Wiseman et al. 2006).

We documented spring dispersal movements by 5 (8%) of 63 adult female pronghorns; estimated age of dispersers was 1.5 years ( $n = 3$ ), 2.5 years ( $n = 1$ ), and 3.5 years ( $n = 1$ ). The longest dispersal distance in this study (75 km) is the longest reported dispersal distance for adult pronghorns. Dispersal movements by 1.5-year-old females may have been associated with their inability to successfully raise fawns. For instance, 1 female gave birth to twins on 26 June 2002 during extreme drought conditions, and, consequently, both fawns were found dead on 28 June 2002 within 0.40 km of the birth site. The remaining 2 females were unsuccessful at producing fawns. Fairbanks (1994) noted that among social groups of pronghorns in north-central Colorado, older females exhibited higher rates of aggression than younger females. Therefore, 1.5 year-old females without fawns may have lacked environmental triggers to exhibit behaviors to defend summer ranges. To avoid confrontation with older, aggressive females rearing fawns, 1.5-year-old females in our study may have dispersed.

Explanations for dispersal by older-aged ( $\geq 2.5$  years) females are more complex. It is possible that dispersal movements by older-aged adults may have been away from areas where they lost fawns to predation. For instance, we observed 3.5- and 2.5-year-old females with 2 fawns during late May 2003. Interestingly and within 24 h of our detecting their fawns, both females initiated long-distance movements without fawns. For instance, the 3.5-year-old female initiated 2 consecutive long-distance movements (39 km) between the southern border of Fall River County along the Nebraska border into northeastern Shannon County (Fig. 3) over a 6-day time period; total distance traveled was approximately 156 km. The 2.5-year-old female initiated a single long-distance movement (18 km) between the eastern border of Fall River County along the Shannon County border into west-central Shannon County (Fig. 3) over a 3-day time period; total distance traveled was approximately 37 km. Consequently, we observed no fawns with either of these individuals throughout the remaining summer months. We acknowledge that because only 2 adults exhibited such movement patterns, reliability of our results and inferences are likely limited. However, our results support previous research by Wiseman et al. (2006), who found that female pronghorns that successfully weaned fawns in previous years exhibited birth-site fidelity, whereas females that experienced a fawn mortality event in the previous year were more likely to change birth sites in subsequent years. Additionally, Testa et al. (2000) suggested that following loss of calves to predation, parturient female moose (*Alces alces*) may have avoided birth sites that year, especially if predation occurred nearby while calves were young. During our study, it is possible that dispersal movements by adult females were away from areas where they experienced fawn mortality events

to alternative areas where they were subsequently located throughout the remaining summer months.

Our findings illustrate the complexity of spatial and temporal variation in seasonal movements and home-range use by pronghorns at the eastern edge of their range, and suggest the need for further studies of similar populations. Of particular interest are the effects of global warming, habitat fragmentation, forage quality, and interspecific competition for food resources on seasonal movements and home-range use by pronghorns occurring at the easternmost extension of sagebrush-steppe communities. Future investigations evaluating mechanisms that trigger adult dispersal behavior also may be warranted.

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### LITERATURE CITED

- BARRETT, M. W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. *Journal of Wildlife Management* 46:991–1002.
- BARRETT, M. W., J. W. NOLAN, AND L. D. ROY. 1982. Evaluation of a hand-held net-gun to capture large mammals. *Wildlife Society Bulletin* 10:108–114.
- BATES, S. 2000. Preliminary results from a radiotelemetry study of pronghorn antelope at Dugway Proving Ground, Utah. *Proceedings of the Biennial Pronghorn Antelope Workshop* 17:42–44.
- BERINGER, J., L. P. HANSEN, W. WILDING, J. FISCHER, AND S. L. SHERIFF. 1996. Factors affecting capture myopathy in white-tailed deer. *Journal of Wildlife Management* 60:373–380.
- BOCCADORI, S. J., AND R. A. GARROTT. 2002. Effects of winter range on a pronghorn population in Yellowstone National Park. *Proceedings of the Biennial Pronghorn Antelope Workshop* 20:114.
- BRINKMAN, T. J. 2003. Movement and mortality of white-tailed deer in southwest Minnesota. M.S. thesis, Department of Wildlife and Fisheries Sciences, South Dakota State University, Brookings.
- BRINKMAN, T. J., C. S. DEPERNO, J. A. JENKS, B. D. HAROLDSON, AND J. D. ERB. 2002. A vehicle-mounted radio-telemetry antenna system design. *Wildlife Society Bulletin* 30:256–258.
- BRINKMAN, T. J., C. S. DEPERNO, J. A. JENKS, B. D. HAROLDSON, AND R. G. OSBORN. 2005. Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. *Journal of Wildlife Management* 69:1099–1111.
- BRUNS, E. H. 1977. Winter behavior of pronghorns in relation to habitat. *Journal of Wildlife Management* 41:560–571.
- CANON, S. K. 1993. Fawn survival and bed-site characteristics of Trans-Pecos pronghorn. Ph.D. dissertation, Texas Tech University, Lubbock.
- CHALMERS, G. A., AND M. W. BARRETT. 1982. Capture myopathy. Pp. 84–94 in *Noninfectious diseases of wildlife* (G. L. Hoff and J. W. Davis, eds.). Iowa State University, Ames.
- CLEMENTE, F., R. VALDEZ, J. L. HOLECHEK, P. J. ZWANK, AND M. CARDENAS. 1995. Pronghorn home range relative to permanent water in southern New Mexico. *Southwestern Naturalist* 40:38–41.
- COLE, G. F. 1956. The pronghorn antelope. Its range use and food habits in central Montana with special reference to alfalfa. Montana Fish and Game Department and Montana State College Agriculture Experiment Station Technical Bulletin 516:1–63.
- COLE, G. F., AND B. T. WILKINS. 1958. The pronghorn antelope. Its range use and food habits in central Montana with special reference to wheat. Montana Fish and Game Department Technical Bulletin 2:1–39.
- DELGIUDICE, G. D., B. A. MANGIPANE, B. A. SAMPSON, AND C. O. KOCHANNY. 2001. Chemical immobilization, body temperature, and post-release mortality of white-tailed deer captured by Clover trap and net-gun. *Wildlife Society Bulletin* 26:1147–1157.
- DELGIUDICE, G. D., B. A. SAMPSON, D. W. KUEHN, M. C. POWELL, AND J. FIEBERG. 2005. Understanding margins of safe capture, chemical immobilization, and handling of free-ranging white-tailed deer. *Wildlife Society Bulletin* 33:677–687.
- DIXON, K. R., AND J. A. CHAPMAN. 1980. Harmonic mean measure of animal activity areas. *Ecology* 61:1040–1044.
- DOW, S. A., AND P. L. WRIGHT. 1962. Changes in mandibular dentition associated with age in pronghorn antelope. *Journal of Wildlife Management* 26:1–18.
- FAIRBANKS, W. S. 1994. Dominance, age, and aggression among female pronghorn, *Antilocapra americana* (family: Antilocapridae). *Ethology* 97:278–293.
- FIRCHOW, K. M., M. R. VAUGHAN, AND W. R. MYTTON. 1986. Evaluation of the hand-held net gun for capturing pronghorns. *Journal of Wildlife Management* 50:320–322.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- HARPER, H. A. 1985. A review and synthesis of existing information on the history, migration routes, and wintering areas of pronghorn that summer in Grand Teton National Park. Grand Teton National Park, Moose, Wyoming.
- HERVERT, J. J., J. L. BRIGHT, R. S. HENRY, L. A. PIEST, AND M. T. BROWN. 2005. Home-range and habitat-use patterns of Sonoran pronghorn in Arizona. *Wildlife Society Bulletin* 33:8–15.
- HOSKINSON, R. L., AND J. R. TESTER. 1980. Migration behavior of pronghorn in southeastern Idaho. *Journal of Wildlife Management* 44:132–144.
- INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE. 2001. Climate change 2001: the scientific basis. Pp. 105 in *A contribution of working groups I, II, and III to the third assessment report of the Intergovernmental Panel on Climate Change* (R. T. Watson and the Core Writing Team, eds.). Cambridge University Press, Cambridge, United Kingdom.
- JACQUES, C. N., AND J. A. JENKS. 2007. Dispersal of yearling pronghorns in western South Dakota. *Journal of Wildlife Management* 71:177–182.
- JACQUES, C. N., J. D. SIEVERS, J. A. JENKS, C. L. SEXTON, AND D. E. RODDY. 2006. Evaluating diet composition of pronghorns in Wind Cave National Park, South Dakota. *Prairie Naturalist* 38:239–250.

- JOHNSON, J. R., AND G. E. LARSON. 1999. Grassland plants of South Dakota and the Northern Great Plains. South Dakota Agricultural Experiment Station, Brookings, South Dakota.
- JOHNSON, W. F. 1988. Soil survey of Harding County, South Dakota. United States Department of Agriculture, Soil Conservation Service, Washington, D.C.
- KALVELS, J. 1982. Soil survey of Fall River County, South Dakota. United States Department of Agriculture, Soil Conservation Service, Washington, D.C.
- KIE, J. G., J. A. BALDWIN, AND C. J. EVANS. 1996. CALHOME: a program for estimating animal home ranges. *Wildlife Society Bulletin* 24:342–344.
- KITCHEN, D. W. 1974. Social behavior and ecology of the pronghorn. *Wildlife Monographs* 38:1–96.
- KITCHEN, D. W., AND B. W. O'GARA. 1982. Pronghorn, *Antilocapra americana*. Pp. 960–972 in *Wild mammals of North America: biology, management, and economics* (J. A. Chapman and G. A. Feldhammer, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- KOCK, M. D., R. K. CLARK, C. E. FRANTI, D. A. JESSUP, AND J. D. WEHAUSEN. 1987a. Effects of capture on biological parameters in free-ranging bighorn sheep (*Ovis canadensis*): evaluation of normal, stressed and mortality outcomes and documentation of postcapture survival. *Journal of Wildlife Diseases* 23:652–662.
- KOCK, M. D., D. A. JESSUP, R. K. CLARK, C. E. FRANTI, AND R. A. WEAVER. 1987b. Capture methods in five subspecies of free-ranging bighorn sheep: an evaluation of drop-net, drive-net, chemical immobilization and the net-gun. *Journal of Wildlife Diseases* 23:634–640.
- KRAUSMAN, P. R., J. J. HERVERT, AND L. L. ORDWAY. 1985. Capturing deer and mountain sheep with a net-gun. *Wildlife Society Bulletin* 13:71–73.
- LARSON, G. E., AND J. R. JOHNSON. 1999. Plants of the Black Hills and Bear Lodge Mountains. South Dakota Agricultural Experiment Station, Brookings, South Dakota.
- MARTINKA, C. J. 1966. The international antelope herd. *Montana Wildlife* July:28–30.
- MARTINKA, C. J. 1967. Mortality of northern Montana pronghorn in a severe winter. *Journal of Wildlife Management* 31:159–164.
- NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization–availability data. *Journal of Wildlife Management* 38:541–545.
- O'GARA, B. W., AND J. D. YOAKUM. 2004. Pronghorn ecology and management. Wildlife Management Institute, Washington, D.C.
- PEPPER, G. W., AND R. QUINN. 1965. 1965 antelope population trend survey in Saskatchewan. Wildlife Branch Saskatchewan Department of Natural Resources, Regina, Saskatchewan, Canada.
- PYLE, W. H. 1973. Range vegetation characteristics, fall and winter habitat utilization, food habits and behavior of pronghorn antelope on the Piapot winter range, Piapot, Saskatchewan. Ph.D. dissertation, University of Saskatchewan, Regina, Saskatchewan, Canada.
- RIDDLE, P. 1990. Wyoming antelope status report—1990. *Proceedings of the Biennial Pronghorn Antelope Workshop* 14:24.
- RODGERS, A. R., AND A. P. CARR. 1998. HRE: the Home Range Extension for ArcView. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
- SAWYER, H., F. LINDZEY, AND D. MCWHIRTER. 2005. Mule deer and pronghorn migration in western Wyoming. *Wildlife Society Bulletin* 33:1266–1273.
- SCHROEDER, M. A., J. R. YOUNG, AND C. E. BRAUN. 1999. Sage grouse (*Centrocercus urophasianus*). Number 425 in *The birds of North America* (A. Poole and F. Gill, eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.
- SEAL, U. S., M. E. NELSON, L. D. MECH, AND R. L. HOSKINSON. 1978. Metabolic indicators of habitat differences in four deer populations. *Journal of Wildlife Management* 42:746–754.
- SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- SEGERSTROM, T. B. 1997. The history and status of pronghorn that summer in Jackson Hole in the upper Gros Ventre River drainage. Great Plains Wildlife Institute, Jackson, Wyoming.
- SIEVERS, J. D. 2004. Factors influencing a declining pronghorn population in Wind Cave National Park, South Dakota. M.S. thesis, South Dakota State University, Brookings.
- SMITH, J. T., L. D. FLAKE, K. F. HIGGINS, AND G. D. KOBRIGER. 2004. History of greater sage-grouse in the Dakotas: distribution and population trends. *Prairie Naturalist* 36:213–230.
- SOUTH DAKOTA OFFICE OF CLIMATOLOGY. 2007. South Dakota climate and weather. [http://climate.sdstate.edu/climate\\_site.climate.htm](http://climate.sdstate.edu/climate_site.climate.htm). Accessed 12 October 2007.
- TESTA, J. W., E. F. BECKER, AND G. R. LEE. 2000. Movements of female moose in relation to birth and death of calves. *Alces* 36:155–162.
- WELCH, I. D., A. R. RODGERS, AND R. S. MCKINLEY. 2000. Timber harvest and calving site fidelity of moose in northwestern Ontario. *Alces* 36:93–103.
- WEST, D. R. 1970. Effects of prolonged deep snow and cold winters on pronghorn mortality and reproduction in South Dakota. *Proceedings of the Biennial Pronghorn Antelope Workshop* 4: 41–49.
- WHITE, G. C., AND R. M. BARTMANN. 1994. Drop nets versus helicopter net guns for capturing mule deer fawns. *Wildlife Society Bulletin* 22:248–252.
- WILKINSON, L. 1990. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois.
- WISEMAN, P. A., M. D. CARLING, AND J. A. BYERS. 2006. Frequency and correlates of birth-site fidelity in pronghorns (*Antilocapra americana*). *Journal of Mammalogy* 87:312–317.
- YOAKUM, J. D. 2004. Habitat characteristics and requirements. Pp. 409–445 in *Pronghorn ecology and management* (B. W. O'Gara and J. D. Yoakum, eds.). Wildlife Management Institute, Washington, D.C.
- YOAKUM, J. D., AND B. W. O'GARA. 2000. Pronghorn. Pp. 559–577 in *Ecology and management of large mammals in North America* (S. Demarais and P. R. Krausman, eds.). Prentice Hall, Inc., Upper Saddle River, New Jersey.

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