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Female survival rates in a declining white-tailed deer population

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and Leslie A. Rice*

Abstract Our objective was to identify seasonal and annual survival rates, in the context of habitat and other environmental conditions, necessary to identify ultimate causes of proximate mortality for white-tailed deer (*Odocoileus virginianus*) in the central Black Hills. From 1993 to 1996, we monitored radiocollared female ($n=73$) white-tailed deer in the central Black Hills of South Dakota and Wyoming. Natural mortality (i.e., from coyotes [*Canus latrans*], dogs, malnutrition, sickness, and unknown causes) ($n=44$, 71%) was the primary cause of female mortality, followed by harvest ($n=14$, 22.6%) and accidental causes (i.e., road kill and drowning) ($n=4$, 6.5%). More females died in spring ($n=33$, 53.2%) than in fall ($n=14$, 22.6%), winter ($n=9$, 14.5%), or summer ($n=6$, 9.7%). For the entire study period (1993–1996), survival rate for female white-tailed deer was 10.4%. Annual survival rates of females ranged from 50.3 to 62.1% and were similar among years ($P=0.743$). Intraseasonal survival rates for females differed between winter ($P=0.003$) and spring ($P=0.014$), whereas summer ($P=0.073$) and fall ($P=0.404$) were similar. High spring mortality of females was related to poor forage conditions on winter range and limited escape cover throughout the central Black Hills. We recommend the use of management techniques that promote overstory and understory plant diversity, such as aspen (*Populus tremuloides*) regeneration and prescribed burns, to improve the habitat in this region.

Key words Black Hills, mortality, *Odocoileus virginianus*, population decline, survival, white-tailed deer

Numbers of white-tailed deer (*Odocoileus virginianus*) in the central Black Hills have declined since the middle 1970s (Griffin et al. 1992, Griffin 1994). Population status has been documented by a decline in hunter success (McPhillips and Rice 1991), deer reproductive success (Rice 1984, Hauk 1987, McPhillips 1990), and fawn survival (Rice 1979). Griffin et al. (1992) reported that most management agencies believe habitat deterioration is the primary cause of population decline in the Black Hills. Rice (1984) concluded that, compared to other regions of South Dakota, reproductive potential of white-tailed deer was least in the Black

Hills, primarily due to low-availability and poor-quality forage.

Knowledge of survival rates and temporal and spatial patterns of mortality is essential to understand and manage white-tailed deer populations (Caughley 1976, DeYoung 1989, Dusek et al. 1992, Stussy et al. 1994). We investigated survival rates and cause-specific mortality factors for a declining white-tailed deer herd in the central Black Hills of South Dakota from January 1993 to December 1996. Our objective was to examine seasonal and annual survival rates, in the context of habitat and other environmental conditions, necessary to

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identify ultimate causes of proximate mortality for white-tailed deer in the central Black Hills. Because deer in the central Black Hills are migratory, factors affecting survival and cause-specific mortality differ with forage, reproductive condition (i.e., lactation vs. gestation), and habitat conditions on winter and summer range. Hence, we hypothesized that survival rates and cause-specific mortality would vary relative to ranges occupied by female white-tailed deer.

Study area

The Black Hills is an isolated mountainous area in western South Dakota and northeast Wyoming that extends approximately 190 km north to south and 95 km east to west (Petersen 1984). Elevation ranges from 973–2,202 m above mean sea level (Orr 1959, Turner 1974). Annual temperatures are typical of a continental climate and range from 5–9°C with extremes of –40 to 44°C (Thilenius 1972). Mean annual precipitation ranges from 45–66 cm (Orr 1959) and yearly snowfall may exceed 254 cm at higher elevations (Thilenius 1972).

The central Black Hills study area (43° 52' N to 44° 15' N, 104° 07' W to 103° 22' W) was composed of separate winter and summer ranges used by migratory white-tailed deer (DePerno 1998, Griffin et al. 1995, 1999) and included Pennington and Lawrence counties of South Dakota and Crook and Weston counties of Wyoming. Public land within the study area was managed by the United States Department of Agriculture Forest Service—Pactola, Harney, and Elk Mountain Ranger Districts—primarily for timber production and livestock grazing (1 June–31 October).

Overstory vegetation on winter range was largely homogeneous and consisted of ponderosa pine (*Pinus ponderosa*) interspersed with small stands of quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) (McIntosh 1949, Thilenius 1972, Richardson and Petersen 1974, Hoffman and Alexander 1987). Species common to the understory on winter range included snowberry (*Symphoricarpos albus*), spiraea (*Spiraea betulifolia*), serviceberry (*Amelanchier alnifolia*), woods rose (*Rosa woodsii*), bearberry (*Arctostaphylos uvaursi*), and cherry (*Prunus* spp.). Dominant overstory vegetation on summer range consisted of stands of ponderosa pine and white spruce (*Picea glauca*) interspersed with small

stands of quaking aspen (McIntosh 1949, Thilenius 1972, Richardson and Petersen 1974, Hoffman and Alexander 1987).

Understory vegetation on summer range was represented by Oregon grape (*Berberis repens*), juniper (*Juniperus communis*), bearberry, snowberry, spiraea, and serviceberry. In the Black Hills, white-tailed deer occur sympatrically with mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and livestock. Mountain lions (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and dogs are the primary predators of deer in this region. Deer are harvested throughout the Black Hills during overlapping archery and rifle hunting seasons.

Methods

We captured 480 white-tailed deer during February and March, 1993–1996 (Griffin et al. 1999) using modified, single-gate Clover traps (Clover 1956) baited with fresh alfalfa hay. We captured deer on 4 trap sites located northeast, northwest, and west of Hill City, South Dakota, on the McVey Burn deer winter range (DePerno 1998; Griffin et al. 1995, 1999). Adult and yearling females ($n=73$) were fitted with radiocollars (Telonics Inc., Mesa, Ariz.; Lotek Engineering, Inc., Ontario, Canada), eartagged, aged, and released. All methods used in this research were approved by an Institutional Animal Care and Use Committee at South Dakota State University.

We visually located individual radiocollared deer from the ground, one to 3 times/week, from July 1993 to July 1996. We attempted to determine the timing of radiocollared deer mortality to the nearest day. When possible, we determined cause of death from field necropsy and evidence of tracks and other signs of predation (White et al. 1987). Radiocollared deer were legal game and hunters were requested to return collars of harvested deer and report the day and location of kill. Mortality was categorized as harvest (i.e., hunter kill), natural (i.e., coyotes, dogs, malnutrition, sickness, and unknown causes), and accidental (i.e., road kill and drowning).

We calculated survival rates using the Kaplan-Meier procedure (Kaplan and Meier 1958) modified for a staggered entry design (Pollock et al. 1989) for the following 3-month periods (seasons): January–March (winter), April–June (spring), July–September (summer), and October–December (fall).

Table 1. Cause-specific, seasonal mortality for female white-tailed deer in the central Black Hills, South Dakota and Wyoming, 1993-1996.

Cause of mortality	Winter ^a	Spring	Summer	Fall	Totals
Harvest	0	0	1	13	14
Natural	8	30	5	1	44
Accidental	1	3	0	0	4
Totals	9	33	6	14	62

^a Number of radiocollared white-tailed deer that died.

Survival rates were calculated by sex, year, and season and compared using Program CONTRAST (Hines and Sauer 1989); alpha was set at $P \leq 0.05$. A Bonferroni correction factor was used to maintain the experiment-wide error rate when we performed multiple chi-square tests (Hopkins and Gross 1970, Neter and Wasserman 1974, Neu et al. 1974).

Results

More females died in spring ($n=33$, 53.2%) than in fall ($n=14$, 22.6%), winter ($n=9$, 14.5%), or summer ($n=6$, 9.7%; Table 1); spring deaths coincided with late winter (March), early spring (April), spring (May), and late spring (June) snowstorms (Midwest Climate Information System 1998). When seasons were combined, natural mortality ($n=44$, 71.0%) was the primary cause of female deaths followed by harvest ($n=14$, 22.6%) and accidental ($n=4$, 6.5%) causes (Table 1). Natural causes accounted for most female mortality in winter ($n=8$, 88.9%), spring ($n=30$, 90.9%), and summer ($n=5$, 83.3%), whereas hunting ($n=13$, 92.9%) was the main cause of female mortality in fall (Table 1). Annual female mortality ranged from 33 to 46% (Table 2). When accidental mortality was combined with natural mortality, approximately 30% of radiocollared females died from natural causes and 10% were harvested each year (Table 2).

Overall (1993-1996), survival rate of female white-tailed deer was 0.10. Female annual survival rates ranged from

0.50 to 0.62 and were similar among years ($\chi^2_3 = 1.241$, $P=0.743$, Table 2). However, female survival rates varied intraseasonally (e.g., winter 1993-96); survival rates differed across winters ($\chi^2_3 = 13.915$, $P=0.003$) and springs ($\chi^2_3 = 10.616$, $P=0.014$, Figure 1). Winter survival was less in 1994 than in 1993 ($\chi^2_1 = 10.541$, $P=0.001$) and spring survival was greater in 1994 than in 1996 ($\chi^2_1 = 7.736$, $P=0.005$). Survival rates were similar across summers ($\chi^2_3 = 6.976$, $P=0.073$) and falls ($\chi^2_3 = 2.922$, $P=0.404$, Figure 1).

Within years, seasonal survival rates (e.g., 1993 winter vs 1993 spring) differed for females in 1993 ($\chi^2_3 = 9.418$, $P=0.024$) and 1996 ($\chi^2_3 = 14.981$, $P=0.002$, Figure 2).

In 1993, females had greater survival rates in winter than spring ($\chi^2_1 = 17.955$, $P < 0.001$) or fall ($\chi^2_1 = 7.256$, $P=0.007$), and greater survival rates in summer than spring ($\chi^2_1 = 17.955$, $P < 0.001$) or fall ($\chi^2_1 = 7.256$, $P=0.007$, Figure 2). Survival rates during 1994 ($\chi^2_3 = 4.366$, $P=0.225$) and 1995 ($\chi^2_3 = 6.936$, $P=0.074$, Figure 2) were similar. In 1996, females had greater survival rates in winter ($\chi^2_1 = 11.782$, $P=0.001$) and summer ($\chi^2_1 = 10.867$, $P=0.001$) than spring (Figure 2).

Discussion

In the central Black Hills, mortality of female white-tailed deer resulted primarily from natural ($n=44$, 71.0%), harvest ($n=14$, 22.6%), and accidental ($n=4$, 6.5%) causes (Table 1). Although causes of mortality were similar to those in other studies reported for female white-tailed deer, natural mortality rates observed in the central Black Hills (71%, Table 1) were greater than in other studies

Table 2. Survival rates and harvest, natural, and total mortality for female white-tailed deer in the central Black Hills, South Dakota and Wyoming, 1993-1996.

Sex	Year	Number at-risk ^a	Mortality			Survival rate	Confidence interval (95%)	Variance
			Harvest (%)	Natural (%) ^b	Total (%)			
Female	1993	41	4 (10)	11 (27)	15 (37)	0.6207	± 0.1391	0.0050
	1994	42	2 (5)	12 (29)	14 (33)	0.5786	± 0.1367	0.0049
	1995	42	4 (10)	13 (31)	17 (41)	0.5747	± 0.1414	0.0052
	1996	35	4 (11)	12 (34)	16 (46)	0.5031	± 0.1554	0.0063
	Annual Mean	40	4 (10)	12 (30)	16 (40)	0.5693		

^a Number of radiocollared white-tailed deer at the beginning of the monitoring period.

^b Includes natural (i.e., coyotes, dogs, malnutrition, sickness, and unknown causes) and accidental causes (i.e., drowning and road kill).

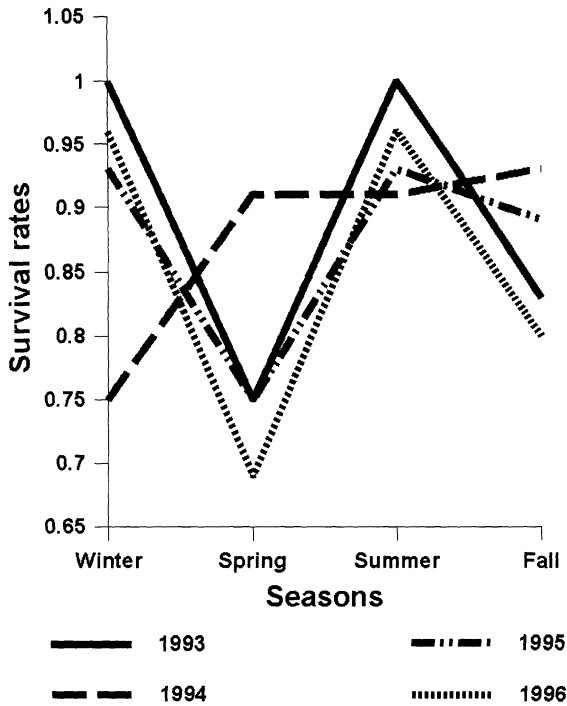


Figure 1. Intraseasonal (e.g., winter 1993–96) survival rates of female white-tailed deer in the central Black Hills, South Dakota and Wyoming, 1993–1996.

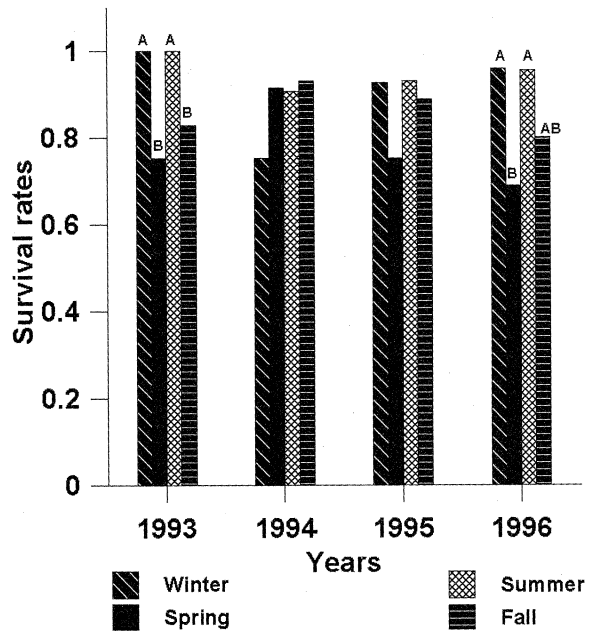


Figure 2. Survival rates of female white-tailed deer within years (e.g., 1993 winter vs. 1993 spring) in the central Black Hills, South Dakota and Wyoming, 1993–1996. Different letters within years denote significance at $P \leq 0.05$.

(12%–52%, Nelson and Mech 1986, Dusek et al. 1989, Van Deelen et al. 1997, Whitlaw et al. 1998). Furthermore, annual mortality of fawn white-tailed deer in the central Black Hills was 65%, with natural mortality accounting for 76%; male fawns had greater mortality (77%) than female fawns (48%, Benzon 1998).

Annual survival rates of female white-tailed deer ($\bar{x} = 56.93$, Table 2) in the central Black Hills were less than average survival rates reported elsewhere for female white-tailed deer (65%–80%, Gavin et al. 1984, Fuller 1990, Nixon et al. 1991, Whitlaw et al. 1998), black-tailed deer (74%–82%, McNay and Voller 1995, McCorquodale 1999), or mule deer (67%–88%, White and Bartmann 1983, Hamlin and Mackie 1989, Unsworth et al. 1999, Grassel 2000). In northern latitudes, winter is typically identified as the season when most natural deaths occur (Mautz 1978a). However, in our study, natural mortality of females was greatest in spring. Survival rates from 1993 to 1996 (0.10, Table 2) indicated that turnover of females occurred approximately every 4–5 years.

Data from this study indicated that females were especially susceptible to mortality during winter and spring. Female white-tailed deer must be able

to replace subcutaneous fat lost while lactating in summer and during fat catabolism in winter (Mautz 1978b). During March, females typically are in the third trimester of pregnancy and experience an increased metabolic rate that coincides with lengthened daylight hours (Verme and Ullrey 1984). If females are stressed nutritionally from poor-quality forage in fall and winter and if spring forage is inadequate or unavailable because of early spring snowstorms (Coblentz 1970, Osborn and Jenks 1995), females likely will be more susceptible to natural mortalities. In the central Black Hills, Hippensteel (2000) documented that pine consumption increased during early spring snowstorms in 1995. Females on a low nutritional plane tend to give birth to fawns that weigh less, are stunted skeletally, and have lower postnatal survival compared to fawns from mothers on a high nutritional plane (Verme 1963). Furthermore, females in poor physical condition may reduce parental care, in the form of defense of young against predators, which may contribute to greater fawn mortality (Smith 1987).

Mortality during summer and fall was 9.7% and 22.6%, respectively (Table 1). Other studies have suggested that survival of adult female white-tailed deer was relatively high throughout the summer months (90–100%, Dusek et al. 1989, Van Deelen et

al. 1997, Whitlaw et al. 1998, Grassel 2000). Interestingly, no natural mortality occurred for a non-hunted female white-tailed deer herd in the grassland-shrub complex of the Missouri River Breaks region of South Dakota (Grassel 2000). In the central Black Hills, poor-quality habitat on summer range likely contributed to the natural mortality observed in this study. Grass and forbs composed <30% of ground cover, shrubs composed <21% of ground cover, and 48% was litter (DePerno 1998). Furthermore, tall shrub/sapling densities and habitats dominated by deciduous cover (<12%) are limited on summer range in the central Black Hills (DePerno 1998). In the central Black Hills, the high fawn mortality (Benzon 1998) supports the conclusion that grass, forb, and shrub forages are lacking on summer range (DePerno 1998). Similarly, other researchers have noted that vegetation production, through its impact on nutritional condition and hiding cover, may be an important source of fawn mortality (Knowlton 1976, Robinette et al. 1977, Salwasser et al. 1978, Hamlin et al. 1984).

Other ungulates (e.g., cattle and elk) may be contributing to deer decline by competing for forage (Jenks et al. 1996, Hippensteel 2000), diminishing quality of habitat through consumption and trampling (Loft et al. 1987), and the length of time they spend on summer and winter grazing allotments. Jenks et al. (1996) documented that under intense cattle-stocking rates white-tailed deer consumed 49% conifer, which was significantly greater than diets of deer on unstocked areas. Additionally, they determined that dietary overlap was high between deer and cattle and ranged from 14–35%, depending on season. Also, cattle may impact white-tailed deer by increasing deer home ranges (Loft 1988), amount of time spent feeding (Kie et al. 1991), and reducing hiding and thermal cover (Loft et al. 1987) and ultimately fawn survival (Smith 1982). Furthermore, evidence suggests that under intense stocking regimes, cattle may be better competitors for available forage and may cause deer to forage in areas that contain vegetation of lesser nutritional value (Crawford 1984, Kie et al. 1991). Hippensteel (2000) noted that approximately 40% of white-tailed deer diets on winter range in the central Black Hills were composed of ponderosa pine and that dietary overlap between deer and elk was 49% in the central Black Hills. Low to moderate cattle regimes may be beneficial

to elk and deer (Skovlin et al. 1968). However, high dietary overlap between deer and elk, high pine consumption by deer (Hippensteel 2000), and length of cattle grazing (i.e., livestock grazing occurs from 1 June to 31 October) suggest that the cattle grazing regime presently practiced in the Black Hills is excessive and incompatible with reversing or stabilizing the decline of the white-tailed deer herd in the central Black Hills.

On winter range, aspen stands represent <5% of the available habitat; understory shrubs and forbs (i.e., bearberry, juniper, and snowberry) represent <30% of available ground cover (DePerno 1998). These data, coupled with 57% litter cover, strongly suggest that forage is relatively unavailable in this region of the Black Hills. Furthermore, >90% of the forest stands in the central Black Hills lack significant understory vegetation (DePerno 1998) and approximately 40% of white-tailed deer diets for winter range in the central Black Hills are composed of ponderosa pine (Hippensteel 2000). Coblenz (1970) reported that 7.6 cm of snow reduced the herbaceous forage in white-tailed deer diets from 63.4 to 0%. Consequently, poor-quality habitat and limited availability of deciduous and shrub habitats (DePerno 1998) likely interact with early spring snowstorms (Hippensteel 2000) to further limit diet diversity and increase energy expenditures for maintenance and locomotion (Parker et al. 1984).

Because hunter success (McPhillips and Rice 1991), deer reproductive success (Rice 1984, Hauk 1987, McPhillips 1990, Hippensteel 2000), and fawn survival (Rice 1979) have not increased with herd reductions, carrying capacity of habitat for deer in the central Black Hills has likely declined concomitantly. Mackie et al. (1990) reported that continued reductions of populations by hunting did not result in compensatory increases in survival and reproduction, but rather continued population declines. Researchers have noted that populations on ranges with low forage diversity, homogenous habitat, poor habitat conditions (e.g., limited availability of forage within the central Black Hills; DePerno 1998), and low recruitment (e.g., in the central Black Hills; Rice 1979, 1984; Hauk 1987; McPhillips 1990) may exhibit little ability to compensate and hunting may quickly become additive. However, when habitat conditions are good and recruitment is high, population potential for compensatory mortality is high (Hobbs 1989, Baldassarre and Bolen 1994).

Management implications

Because reproductive and recruitment rates (Rice 1979, 1984; Hauk 1987; McPhillips 1990; Hippensteel 2000) have not increased with herd reductions, carrying capacity has likely declined in the central Black Hills. This decline is in part responsible for reduced survival of female white-tailed deer in this region. The long-term decrease and low productivity affecting the central Black Hills deer herd is related directly to the quantity, quality, and type of forage biomass available (DePerno 1998). Sieg and Severson (1996) hypothesized that white-tailed deer densities in the Black Hills have been reduced due to the regeneration of ponderosa pine stands, prevention of natural fires, and elimination of man-made fires. The present trend toward dominance by ponderosa pine is detrimental not only to timber production, through overcrowding of trees, but also to wildlife (Richardson and Petersen 1974). Absence of fire has substantially increased ponderosa pine while hindering new growth with negative consequences for habitat diversity (Richardson and Petersen 1974, Sieg and Severson 1996).

In forested landscapes where agricultural habitats are limited, it is crucial to consider management practices that promote overstory and under-story diversity. Historically, fire was the primary natural disturbance in the central Black Hills; now it is largely absent from this system (Richardson and Petersen 1974, Sieg and Severson 1996). Moreover, addition of livestock grazing likely imposes a disturbance that has changed the dynamics of habitat regeneration; the consequences are an apparent reduction in habitat capability for white-tailed deer in the central Black Hills. The obvious choices are to accept a continued reduction in deer populations or to change management practices (e.g., aspen regeneration, controlled burns, reduce/eliminate livestock) in a manner that favors white-tailed deer populations.

The high spring mortality observed during this study is likely the primary reason for the long-term decline of white-tailed deer in the central Black Hills. Although it seems that deer harvest may be acting additively on the population, this is likely a consequence of diminished habitat capabilities, which are expressed as reduced natality and greater natural mortality. We hypothesize that poor quality and quantity of forage on winter range and limited escape cover (DePerno 1998) are responsible for the high spring mortality and low reproduc-

tion of deer in the central Black Hills. Harvest management techniques, although important to population survival, are relatively minor compared to the effects of habitat management on white-tailed deer herds. We recommend that habitat management techniques such as aspen regeneration and prescribed burns be used to improve the habitat base in the central Black Hills. Also, we recommend that the Forest Service re-evaluate its current grazing allotment system (e.g., number of cattle and length of time) as it relates to forage availability for wild cervids in the central Black Hills.

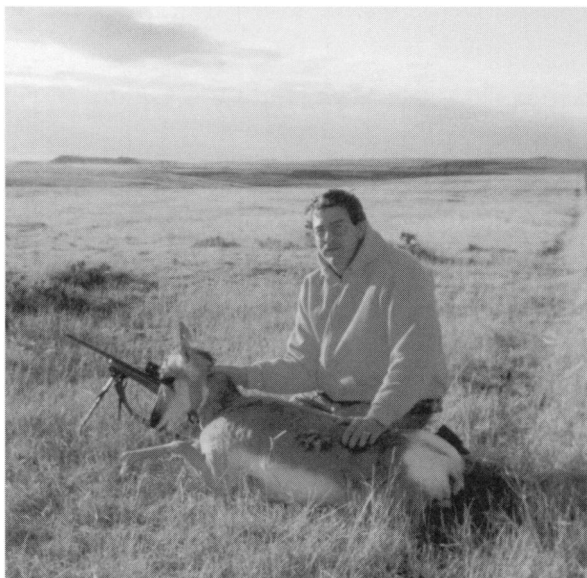
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