

VARIANCE IN SURVIVAL OF YOUNG MULE DEER IN THE SIERRA NEVADA, CALIFORNIA

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Survival rates of young ungulates have not been studied intensively, but are thought to be more variable than those of adults. Survival rates of young potentially are important factors in the dynamics of populations of mule deer, *Odocoileus hemionus*, and other large herbivores. We estimated survival among four cohorts of mule deer from birth to 3 years-of-age that inhabited the Sierra Nevada of eastern California. For males and females combined, survival from birth to 6 months was low ($\bar{x} = 27.9 \pm 6.8$ [SD]%), and differed among cohorts. Annual survival from 6 months to 3 years-of-age was variable (range 80.4 - 90.6%), but survivorship functions did not differ among cohorts. Proportion of mortality of young attributable to predation (55%) was markedly less than reported for adult females elsewhere in the Sierra Nevada (87%), and proportion of mortalities resulting from vehicle collisions (27%) was markedly higher than elsewhere in that range (4%). Our results are consistent with the notion that temporal variation in mortality of young is an important component of variation in the population dynamics of mule deer and beg the question of whether top-down or bottom-up processes regulate populations of those ungulates in arid, unpredictable environments.

INTRODUCTION

Mule deer, *Odocoileus hemionus*, are among the most abundant and conspicuous large mammals in North America. Mule deer are highly prized game animals, are important indicators of ecosystem health (Loft 1998a, Kie and Czech 2000, Mackie et al. 2003), and have tremendous economic and aesthetic value (Loft¹ 1998b). Moreover, management of mule deer populations can be controversial and result in mistrust of those charged with the conservation and management of that resource (Freddy et al. 2004).

Populations of mule deer fluctuate over time (Mackie et al. 2003), and populations throughout western North America appear to have undergone substantial changes during the past 50 years (Workman and Low 1976, Longhurst et al. 1976, Mackie et al. 2003). Mule deer populations are subject to the influences of nutrient availability, competition with other herbivores, accidents, predation, disease, and climate, and those factors have been subjects of numerous investigations. There is general agreement that no single cause can be invoked to explain the dynamics of mule deer populations (Bleich and Taylor 1998), and causes of contemporary population declines (Mackie et al. 2003) remain speculative and controversial (Gill² 2001). Indeed, specific, detailed, investigations are required to evaluate factors that may regulate populations of those large herbivores (Hornocker 1976, Knowlton 1976, Connolly 1981, Mackie et al. 2003).

Temporal variation in survival is an important fitness component among large herbivores (Gaillard et al. 2000), and is an important factor in the population dynamics of mule deer and white-tailed deer, *Odocoileus virginianus* (Short 1979). Four demographic parameters (juvenile survival, fecundity of young females, fecundity of adult females, and adult survival) can be expected to change with shifts in population density (Eberhardt 1977, Gaillard et al. 2000). Among those parameters, variation in post-weaning survival generally is high; variation is markedly lower, however, for yearling survival among ungulates inhabiting temperate environments (Gaillard et al. 2000), such as those occupied by mule deer. Nevertheless, survival of offspring remains highly variable within and among populations of large herbivores (Gaillard et al. 1998). Because most investigators have not separated survival rates of young animals from those of older adults, there is limited information available on variation for that fitness component (Gaillard et al. 2000).

Adult female survival generally is characterized by high survivorship and low yearly variation, regardless of causes of mortality (Gaillard et al. 2000). Because of the paucity of information related to factors affecting the demographics of mule deer from post-weaning through yearling stages, we examined survivorship and cause-specific

¹Loft, E. R. (editor). 1998b. An assessment of mule and black-tailed deer habitats and populations in California. California Department of Fish and Game, U.S. Bureau of Land Management, and U.S. Forest Service, Sacramento, California, USA.

²Gill, R. B. 2001. Declining mule deer populations in Colorado: reasons and responses. Colorado Division of Wildlife Special Report 77, Denver, Colorado, USA.

mortality for young up to 3 years-of-age. Our purpose was to estimate survival rates of young mule deer and test the hypotheses that survival rates differ (1) between males and females within years, and (2) among young born during different years for animals from 6 months to 3 years-of-age. Finally, we report causes of mortality for animals that died during our investigation.

STUDY AREA

We conducted research on a population of mule deer that inhabited Round Valley (37°24'N, 118°34'W), Inyo and Mono counties, California, during winter (Kucera³ 1988), but that migrated long distances northward and westward to summer ranges (Kucera 1992). Mule deer occurred in Round Valley from approximately 15 October through 15 May, and inhabited summer ranges the remainder of the year.

Round Valley is extremely arid as a result of the rainshadow cast by the Sierra Nevada, an immense mountain range oriented in a north-south direction that forms the western boundary of that winter range. Mean (\pm SD) annual precipitation at the Bishop airport (37°22'N, 118°25'W; 1,340 m) is 13.3 (\pm 7.0) cm, and approximately 75% of total precipitation occurs between November and March (Fig. 1); potential evapotranspiration in Round Valley is 66.8 cm (Kucera 1992). January is the coldest month (\bar{x} = 0.9 [\pm 2.6] °C), and night-time temperatures frequently are $<$ -15° C during winter (Kucera 1992). Climatological conditions in Round Valley are similar to those on other winter ranges occupied by mule deer in the eastern Sierra Nevada (Bleich and Taylor 1998).

Vegetation in Round Valley is representative of the western Great Basin, and conforms to the sagebrush belt described by Storer and Usinger (1968); dominant shrubs that figure importantly in mule deer ecology during winter include bitterbrush, *Purshia glandulosa*; big sagebrush, *Artemisia tridentata*; blackbrush, *Coleogyne ramosissima*; desert peach, *Prunus andersonii*; and rabbitbrush, *Chrysothamnus nauseosum* (Kucera³ 1988, Kucera 1992, Kucera 1997; Pierce et al. 2000a, Pierce et al. 2000b, Pierce et al. 2004).

Summer ranges occur on both sides of the Sierra crest at elevations from 2,200 to $>$ 3,600 m (Kucera³ 1988). Vegetation zones (Storer and Usinger 1968) on summer ranges include the sagebrush; Jeffrey pine, *Pinus jeffreyi*; lodgepole pine, *Pinus murryana* - red fir, *Abies magnifica*; subalpine; and alpine belts (Kucera 1992). Summer ranges west of the Sierra crest are more mesic than the Round Valley winter range (Fig. 1), and average annual precipitation at Huntington Lake, California (37°22'N, 119°13'W; 2,260 m) near the center of the summer range is 101.2 (\pm 38.3) cm. Mean annual temperature at Huntington Lake (7.1 [\pm 1.0] °C) is substantially lower than at Bishop (13.3 [\pm 0.5] °C).

Use of winter range by livestock is light and occurs in Round Valley largely when deer are not present. Livestock grazing on summer ranges varies from none in remote areas to heavy in easily accessible areas east of the Sierra crest (Kucera 1992). Grizzly bears, *Ursus arctos*, which formerly occurred west of the Sierra crest, have been

³Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California. Ph.D. Dissertation, University of California, Berkeley, California, USA.

extirpated (Storer and Tevis 1955), but areas used by migratory mule deer support an otherwise full complement of native carnivores including mountain lions, *Puma concolor*, coyotes, *Canis latrans*, and bobcats, *Lynx rufus* (Pierce et al. 2000a, Pierce et al. 2000b). Black bears, *Ursus americanus*, are common on summer ranges west of the Sierra crest, but are encountered infrequently in the eastern Sierra Nevada (Wildlife Programs Branch⁴ 2004).

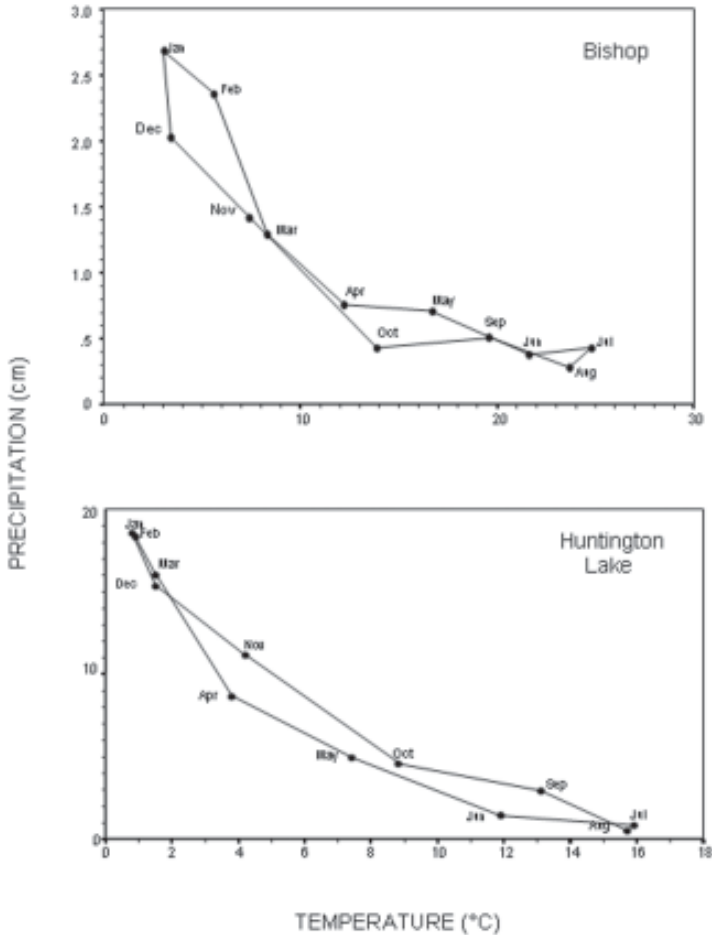


Fig. 1. Climographs (1948 - 2004) for Huntington Lake, California, located near the center of summer ranges used by migratory mule deer west of the Sierra Crest and for Bishop, California, located immediately east of the Round Valley winter range. Scales for both the ordinate and abscissa differ between the two climographs.

⁴Wildlife Programs Branch. 2004. 2003 annual bear take report. California Department of Fish and Game, Sacramento, California, USA (available at: <http://www.dfg.ca.gov/hunting/bear/pdfs/beartk2003.pdf>).

METHODS

To determine fetal rates during the second trimester of pregnancy, we performed necropsies on females ≥ 1 -year-of-age that were randomly selected from the population during March 1993-1996 (Kucera 1997). We used those data to estimate population-level birth rates (i.e., the number of young expected to be born/100 females for each birth cohort).

We used a hand-held net gun (Krausman et al. 1985) to capture mule deer fawns (young-of-the-year, 6-8 months-of-age) in Round Valley. We distributed our capture efforts across the winter range (Pierce et al. 2000a, Pierce et al. 2000b, Pierce et al. 2004) to ensure that collars were distributed homogeneously across the winter range, and not concentrated in any particular area. Each year, we captured male and female fawns and placed expandable collars that incorporated a mortality sensor (Bleich and Pierce 1999) on them in approximately equal proportions. Fawns were captured during January and March 1994-1997; during 1994-1996, fawns also were captured in March to bring the marked cohort back to the total number collared 2 months earlier. In 1997, logistical constraints dictated that animals were captured only in March.

We monitored the status of each collared deer from the ground on a daily basis from 15 October through 15 May (winter), then every other week using aerial telemetry the remainder of the year (summer). When we received a mortality signal during winter we attempted to locate the animal immediately (almost always within 24 hours) to ascertain date and cause of death. During summer, we attempted to locate the dead animal as quickly as possible, and again determined cause of death. Animals for which date of death could not be ascertained were assigned a date midway between when they were last known to have been alive and when the mortality signal was first detected (Bleich and Taylor 1998). We recorded sources of mortality as species-specific predation, other natural causes, anthropogenic causes, or undetermined. For animals killed by predators, we used the criteria of Shaw (1983) or Woolsey (1985), or relied on our own experience, to identify the species responsible.

We calculated confidence intervals for the number of expected births and for estimates of "recruitment" at 6 months-of-age following the method of Riney (1956). We estimated early survival of fawns for each cohort by dividing the results of aerial surveys conducted in January following their birth (when those young deer were approximately 6 months old, and expressed as young/100 females) by the expected birth rates (expressed as neonates/100 females) and multiplying by 100. We used *G*-tests (Zar 1984) to compare fetal rates among years for females sampled during March, to compare recruitment rates the following January, and to determine if differences existed in proportion of mortalities between males and females by season. We used a goodness-of-fit test (Zar 1984) to determine if proportion of deaths during summer and winter differed from expectation. We used the Kaplan-Meier (1958) procedure, as modified by Pollock et al. (1989) for staggered entry of telemetered animals, to determine monthly and annual survival rates (Bleich and Taylor 1998). To compare survivorship functions, we used the log-rank test (Cox and Oakes 1984) as modified by Pollock et al. (1989). We calculated the most conservative chi-square statistic presented by

Pollock et al. (1989) to enhance the probability that any differences detected between survivorship functions were real (Bleich and Taylor 1998). We adopted $\alpha = 0.10$ as our threshold for statistical significance.

RESULTS

Fetal rates during March (Table 1) ranged from 147/100 females to 182/100 females, but did not differ among years ($G = 0.237$, $P = 0.971$, $DF = 3$). Recruitment rates during January following the year of birth varied from 35.2 young/100 females to 63.0 young/100 females, and did differ among years ($G = 52.850$, $P < 0.001$, $DF = 3$). Percentage of young expected to be born each year and that survived until 6 months-of-age ranged from 22.6 to 37.0 (Table 1).

Table 1. Expected birth rates and 95% confidence intervals (as estimated from fetal rates during the second trimester of pregnancy), recruitment rates and 95% confidence intervals at 6 months-of-age (as estimated from aerial surveys), and proportion of fawns that survived to 6 months-of-age for offspring born to females that used the Round Valley winter range, Inyo and Mono counties, California, 1993-1996.

Year of birth	Sample size ¹	Expected births/100	Sample size ²	Young/100 at 6 months	Survival to 6 months (%)
1993	28	156 ± 94	446	35.2 ± 6.5	22.6
1994	25	147 ± 92	468	33.5 ± 6.5	22.8
1995	34	170 ± 96	373	63.0 ± 7.0	37.0
1996	20	182 ± 136	547	53.2 ± 7.7	29.2
Mean ± SD		164 ± 15.4		46.2 ± 14.3	27.9 ± 6.8

¹ Number of females in necropsy sample used to estimate expected births/100 .

² Number of females in aerial sample used to estimate young/100 at 6 months-of-age.

We placed radio collars on 109 young mule deer (48 males, 61 females) during January 1994 through March 1997. Juveniles captured in January were ~6 months-of-age, and those captured in March were ~8 months-of-age, assuming a birth date of 1 July (Jones⁵ 1954). We monitored those deer for a total of 2,499 telemetry-months; monitoring was terminated on the third birthday (i.e., 1 July following 3 full years of life) of each cohort.

Thirty-three telemetered deer (30.3%) died during our investigation and we determined cause of death for 22 (66.7%) of those individuals. Small sample sizes precluded statistical comparisons of causes of death between males and females within years, or making comparisons among years. Among deer for which cause of death could

⁵Jones, F. L. 1954. The Inyo-Sierra deer herds: a final area report. California Department of Fish and Game, Sacramento, USA.

be determined, mortality factors included predation (by mountain lions, coyotes, and bobcats), drowning, and dystocia (Fig. 2). Human-caused deaths were attributed to legal harvest, poaching, and collisions with vehicles (Fig. 2).

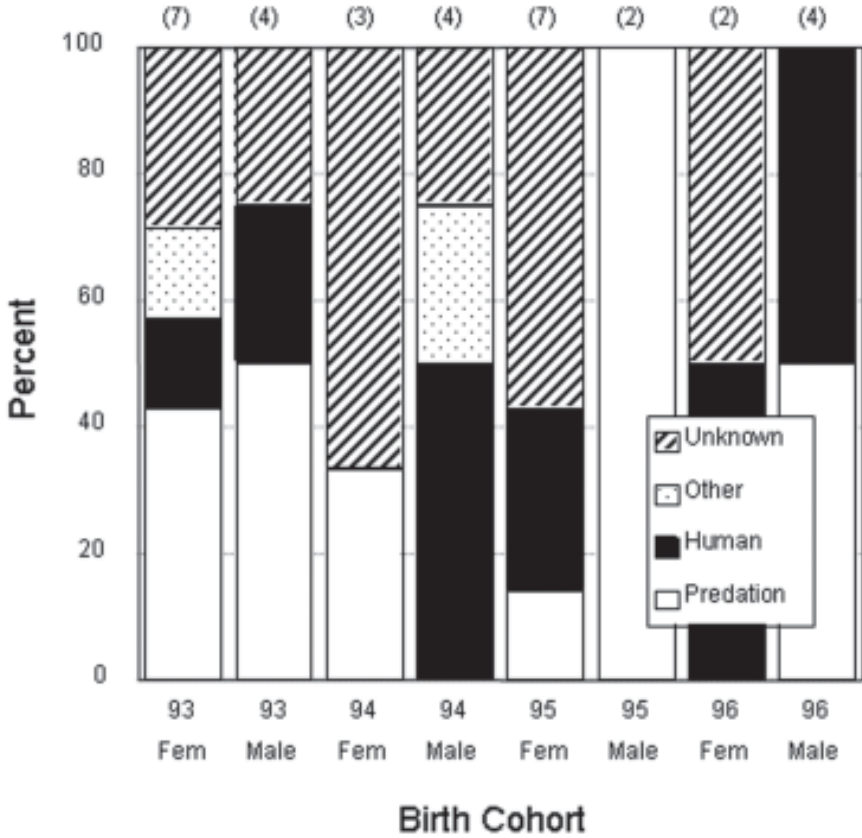


Fig. 2. Proportion of mortality attributed to natural and anthropogenic causes for young mule deer of both sexes and alive at 6 months-of-age. Cause-specific mortality was determined through the third full year of life, terminating with the 3rd birthday for young born to females that wintered in Round Valley, Inyo and Mono counties, California, 1993-1996. Sample sizes are shown parenthetically above the bars.

The proportion of deaths that occurred during summer ($n = 15$) and winter ($n = 18$) did not differ from expected ($G = 0.062, P = 0.804, DF = 1$), and mortality of males (8 in summer, 6 in winter) and females (7 in summer, 12 in winter) did not differ by season ($G = 1.345, P = 0.246, DF = 1$). Animals for which cause of death could not be assigned with certainty were distributed about equally between summer ($n = 5$) and winter ($n = 6$).

Survivorship of males and females born during our investigation (Table 2) did not differ from 6 through 36 months-of-age for any cohort; annual survival rates ranged from 0.804 to 0.906 (Table 3). Because no intersexual differences were detected, we combined males with females from each cohort (i.e., animals born in 1993, 1994, 1995, 1996), and compared survivorship among deer born in each of the 4 years; again, no differences existed in survivorship functions (Table 4).

Table 2. Proportions (and standard errors) of young female and male mule deer alive at 6 months-of-age and that remained alive at ages of 1 year, 2 years, and 3 years that were born to females that winter in Round Valley, Inyo and Mono counties, California, 1993-1996. Survivorship was calculated using the method of Kaplan and Meier (1958), as modified for staggered entry of animals by Pollock et al. (1989). No difference ($P > 0.10$) existed between survivorship of female and male fawns for any birth year.

Age	Year of birth							
	1993		1994		1995		1996	
	F	M	F	M	F	M	F	M
1 Year	0.7857 (0.0120)	0.9167 (0.0058)	0.9333 (0.0039)	0.9167 (0.0058)	0.8824 (0.0061)	0.8182 (0.0135)	0.8333 (0.0116)	0.9231 (0.0055)
2 Years	0.6349 (0.0164)	0.7550 (0.0156)	0.8711 (0.0070)	0.8333 (0.0116)	0.7647 (0.0106)	0.8182 (0.0152)	0.8333 (0.0116)	0.8462 (0.0100)
3 Years	0.5556 (0.0196)	0.6667 (0.0185)	0.8089 (0.0096)	0.6667 (0.0185)	0.5882 (0.0142)	0.8182 (0.0152)	0.8333 (0.0116)	0.8462 (0.0184)

Table 3. Sample sizes and estimated survival rates of four cohorts of mule deer (males and females combined) from 6 to 36 months-of-age that were born to females that wintered in Round Valley, Inyo and Mono counties, California, 1993-1996.

Year of birth	Deer (N)	Telemetry-months	Monthly survival	Monthly survival (variance)	Annual survival
1993	26	573	0.982	0.00004	0.804
1994	29	736	0.991	0.000021	0.906
1995	29	610	0.987	0.00002	0.853
1996	25	580	0.990	0.00002	0.886

Table 4. Pairwise comparisons of survivorship functions for young mule deer (males and females combined) born to females that wintered in Round Valley, Inyo and Mono counties, California, 1993-1996. Chi-square statistics are shown above the diagonal; probabilities that survivorship functions differed are shown below the diagonal. For all comparisons, degrees of freedom = 1.

Year of birth	1993	1994	1995	1996
1993	-----	2.052	0.574	0.845
1994	> 0.10	-----	0.462	0.305
1995	> 0.25	> 0.25	-----	0.137
1996	> 0.25	> 0.50	> 0.75	-----

DISCUSSION

We contend that one of the greatest obstacles to better understanding population dynamics of large herbivores is the scarcity of long-term field investigations utilizing marked animals, and that the paucity of results from such investigations limits the use of scientific approaches to conserve those animals. Further, incomplete knowledge of age-specific survival rates hampers efforts to manage populations of large mammals. In an attempt to decrease that void, we addressed the issue of temporal variation in survivorship among four cohorts of mule deer for the initial 3 years of life.

Survival of fawns to 6 months-of-age largely represents “pre-weaning” survival, as defined by Gaillard et al. (2000), and such data are uncommon. We calculated survival rates through the first 6 months of life (Table 1) from ratios of expected birth rates (based on fetal rates estimated for the population during late gestation) and recruitment rates derived from aerial surveys. Thus, our results are subject to potentially large sampling error because ratios can change as a function of changes in the numerator or denominator (McCullough 1994), either of which can be affected by visibility bias (Gaillard et al. 2000) or by heterogeneous distributions across the landscape (Bowyer 1984, Bleich et al. 1997).

Visibility bias in Round Valley likely is minimal because cover is sparse and structure of vegetation is open (Pierce et al. 2004), and adult survival is high (Pierce et al. 2000b). Thus, despite the potential shortcomings associated with the use of ratio data, our results are consistent with the widely held notions that most mortality among ungulates occurs during the first months of life (Bowyer et al. 1998, Gaillard et al. 2000), and that mortality rates during that period are substantial (Ricca et al. 2002) and vary temporally (Gaillard et al. 2000). Indeed, estimated mortality during the first 6 months of life ranged from 63.0 to 77.4% (Table 1), and was comparable to that for other populations of mule deer reported by Salwasser et al. (1978), Hamlin and Mackie⁶ (1989), Hamlin et al. (1984),

⁶Hamlin, K. L., and R. J. Mackie. 1989. Mule deer in the Missouri River Breaks, Montana: a study of population dynamics in a fluctuating environment. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

and Pac et al.⁷ (1991).

Body condition of females likely plays a significant role in early survival of offspring (Gaillard et al. 2000, Keech et al. 2000). We were unable to determine causes of death during the pre-weaning period, but annual differences in body condition of females (Kucera 1997, Pierce et al. 2000b) indicate maternal condition could have played a role in pre-weaning survival rates. Precipitation is an important factor influencing quantity and quality of vegetation available to herbivores (Noy-Meir 1973, Wehausen and Hansen 1988), both of which can have profound influences on maternal condition and, ultimately, recruitment (Wallmo et al. 1977, Hobbs and Swift 1985). During our study, years characterized by high recruitment followed periods of below-normal (1994) and above-normal (1995) precipitation on winter range, and precipitation on summer range was above normal. Where predators are common, predation is often the primary source of pre-weaning mortality (Linnell et al. 1995), but it is not always independent of maternal care (Gaillard et al. 2000). Clearly, the role of precipitation and its influences on female body condition, juvenile survival and, ultimately, the dynamics of this population warrant further investigation. Moreover, downward trends in habitat quality (perhaps linked to anthropogenic influences including urbanization, or fire suppression, grazing practices, recreational use, and other wildland management strategies; Loft¹ 1998b) have important implications for maternal condition and, ultimately, for survival of young. Clearly, the importance of these factors cannot be underestimated.

Among mule deer from 6 months to 3 years-of-age, mortality was divided about evenly between natural and anthropogenic causes (Fig. 2); unfortunately, however, interpretation of these results was confounded by our inability to ascertain cause of death for all animals that died. Proportions of mortality attributable to specific causes differed markedly from those reported by Bleich and Taylor (1998) for mule deer elsewhere in the Sierra Nevada, where predation was the primary cause of death (83%) for adult females, and mountain lions and coyotes were the most important predators. Pierce et al. (2000b) reported that mountain lions preyed selectively on adult females and young < 1 year-of-age of both genders in Round Valley. Coyotes did not select young deer, but did prey selectively on adult females (Pierce et al. 2000b).

Only male deer are legally hunted in eastern California; when deaths resulting from legal harvest ($n = 2$) were ignored, predation accounted for 55% of mortality in our study. Although predation was an important cause of death for young mule deer, anthropogenic causes were nearly equal in importance (Fig. 2). Differences in the proportion mortalities attributed to predation in Round Valley and other populations in the eastern Sierra Nevada may be attributable to temporal differences in mountain lion densities (which vary with densities of mule deer [Pierce et al. 2000a]), as well as the large proportion of road-kills (27%) among deaths we investigated (Fig. 2) when compared to that (4%) reported by Bleich and Taylor (1998). The proportion of deaths attributable to anthropogenic causes among deer in Round Valley can only be expected to increase with destruction of winter ranges and constriction of migration corridors (Kucera and

⁷Pac, D. F., R. J. Mackie, and H. E. Jorgensen. 1991. Mule deer population organization, behavior and dynamics in a Rocky Mountain environment. Montana Department of Fish, Wildlife, and Parks, Helena, Montana, USA.

McCarthy 1988), both of which will increase vehicle traffic.

Survivorship functions for young deer exhibited substantial variation, but did not differ between males and females (Table 2) or among the four cohorts of mule deer (Table 4). Our failure to detect differences may have been a function of sample size. Average monthly survivorship for all cohorts was ≥ 0.982 , but annual survivorship ranged from 0.804 to 0.906 (Table 3). Nevertheless, those values are remarkably high when compared to those for adults elsewhere in the eastern Sierra Nevada (0.643 - 0.884; Bleich and Taylor 1998) and other parts of California (0.813 [Schaefer et al. 2000], $\sim 0.60 - 0.80$ [Nicholson et al. 1997]). Gaillard et al. (2000) compiled information on age-specific survival of mule deer, and reported that annual survival of "prime age" females ranged from 0.673 (White and Bartmann 1983) to 0.923 (Pojar 1981). When combined with information summarized by Gaillard et al. (2000), our results serve further to illustrate variability in survival rates among young ungulates.

Logistical constraints dictated that we not capture deer in January 1997, and we caught deer only in March of that year. Deer captured in March were, of course, alive the preceding January. Still, it is possible that the cohort of young born in 1996 experienced a higher rate of mortality during January and February 1997 than did the other three cohorts during their initial winters. If that occurred, our estimates of survival for young born in July 1996 would be biased upward. Sex-specific survivorship for young collared during March 1997 was, however, similar to values obtained during other years (Table 2). Thus, we surmise any biases associated with collaring deer in March, rather than January, 1997 were minimal and unlikely to have affected outcomes of our analyses.

Information on age-specific cohort survival is potentially useful in developing conservation and management programs, particularly as they relate to harvest management. Little information is available on post-weaning survival and yearling survival generally is not estimated separately from adult survival (Gaillard et al. 2000). In this paper, we estimated survival rates of mule deer that had achieved an age of 6 months through their 3rd birthday. That period included post-weaning survival, yearling survival, and survival through the 2nd year of life. Survival rates varied among years, but did not differ statistically; nevertheless, failure to detect a statistically significant difference does not undermine the potential biological significance of temporal variation in survival rates of young animals. Survival rates among these cohorts also were similar to those reported for "prime-age females" from throughout the range of mule deer, but markedly higher than survival rates for mule deer from other parts of California and, in particular, from five populations in the eastern Sierra Nevada. Whether interannual differences in climate, regional differences in predation pressure, nutritional differences, anthropogenic influences, or a combination of these were important factors explaining that variation is uncertain, and warrants further inquiry.

Information contained herein can be useful in refining population models, and adds to our general knowledge of variances associated with fitness components (Gaillard et al. 2000). Further, it emphasizes the need for detailed analyses of the relationships between climate, predators, and prey to more fully understand how those factors interact to drive the dynamics of ungulate populations. Cause of death is of general

interest; however, little understanding of the relative importance of mortality factors is gained if mortality is compensatory rather than additive.

Temporal variation in survivorship of young mule deer, when considered in the context of effects of climate, habitat quality, and risk of predation on survival of adult animals (Pierce et al. 2000*a*, 2000*b*, 2004) begs the question of whether top-down or bottom-up processes regulate this deer population. That subject is best addressed over a continuum of ecological conditions involving both prey and predators (Pierce⁸ 1999), and emphasizes the importance of long-term investigations an understanding the dynamics of ungulate populations. We concur with Gaillard et al. (2000) that increased cooperation between universities and government agencies is desirable to fully realize the potential of long-term monitoring of marked individuals, and urge administrators to recognize the importance of those collaborative efforts. Indeed, we wonder why resource agencies appear to not recognize the value of long-term data sets and their implications for management of ungulate populations. Ultimately, those endeavors have tremendous value in conserving the complex systems of which large herbivores are such important components.

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