

# DESERT MULE DEER SURVIVAL IN SOUTHWEST TEXAS

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**Abstract:** We studied population structure and limiting factors within a desert mule deer (*Odocoileus hemionus eremicus*) population in Brewster County of the Trans-Pecos Region in Texas, USA. We estimated and compared annual survival and pregnancy rates from March 1990–February 1993 for 121 adult (>33 months old) male and female, 61 subadult (21–33 months old), and 77 young (8–20 months old) deer. Variation in weather patterns (i.e., drought) was associated with—if not causative of—annual variation in survival patterns. Adult female and young survival had the strongest correlation with drought. Pregnancy status of young ( $\leq 1.5$  yr) and old ( $\geq 6.5$  yr) deer appeared most affected by drought. Seasonal periods of natural stress differed for adult sex classes, with most female mortalities occurring during months associated with parturition and lactation, and most male natural stress losses occurring during late winter and early spring. The major mortality sources were hunting and natural stressors for adult males, natural stressors and predation for adult females, and predation and natural stressors for young. Subadult mortalities were too few to identify significant mortality agents. The significance of natural stress-related survival and fecundity impacting herd productivity and stability warrants further consideration of poorly understood causative mechanisms. Ideally, replicated treatment areas would be used to address compensatory and additive mortality issues relative to predator abundance, harvest, and natural-stress losses.

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For decades, populations of western mule deer (*Odocoileus hemionus*) have undergone considerable fluctuations in size (Julander and Low 1976, Hurley and Unsworth 1998, Kie and Czech 2000), and the Trans-Pecos population is no exception (Cantu and Richardson 1997). A regional decline of the Trans-Pecos desert mule deer population occurred from 1965 to 1975 (Connolly 1981). The unpredictability of population changes raised concerns about the management of this valuable resource (Clark 1989). High rates of fawn mortality had been documented in this area due to predation and natural stress (Dickinson et al. 1980, Leopold 1984), but survival and mortality information on

the adult segment of the population was sparse. Cause-specific mortality data can help managers evaluate the need for predator-control programs. In addition, timing of natural mortality can be used to identify stressful periods for the population.

Our objectives were to estimate desert mule deer survival rates by sex–age class, evaluate differences in survival rates by sex–age class among years, determine annual cause-specific mortality rates, examine age-specific pregnancy rates between years, and generate and test plausible hypotheses to explain apparent differences. We tested the following null hypotheses: annual survival rates did not vary by sex–age class, year, or sex–age class  $\times$  year interaction; cause-specific mortality rates did not vary within or among years; and age-specific pregnancy rates did not differ between years.

## STUDY AREA

Our 34,500-ha study area consisted of the Elephant Mountain Wildlife Management Area (EMWMA) and surrounding private properties in Brewster County of southwest Texas, USA. Elevations ranged from 1,160 to 1,880 m. The cli-

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mate was warm and semi-arid, with a strong seasonal component. Precipitation averaged 34 cm annually (U.S. Department of Commerce 1994).

Dominant vegetation types were desert grassland (73%), mixed prairie (13%), loamy bottomland (8%), and desert shrub (6%). Common grasses and forbs included cane bluestem (*Bothriochloa saccharoides*), gramas (*Bouteloua* spp.), leather-weed croton (*Croton pottsii*), and succulent cacti (*Opuntia* spp., *Yucca* spp.; Hatch et al. 1990). Acacia (*Acacia* spp.), creosote bush (*Larrea tridentata*), and juniper (*Juniperus* spp.) were common woody species (Hatch et al. 1990).

Potential predators of desert mule deer in our study area included mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), and coyote (*Canis latrans*). Predator control efforts, such as trapping and hunting, occurred on the EMWMA and surrounding properties, although they were reduced during our study because of human safety concerns.

## METHODS

### Drought Index

We compiled monthly Palmer Drought Severity Index (PDSI; Palmer 1965) data from March 1989 through February 1993 from locations across the Trans-Pecos (National Climatic Data Center, Ashville, North Carolina, unpublished data). The PDSI was calculated from numerous measures associated with precipitation, soil moisture, temperature, and evaporation. We examined drought index differences among years using the Cox and Stuart (1955) test of trend (Conover 1980:133).

### Field Procedures

We used net guns from helicopters and baited drop-nets to capture and radiocollar deer in February–March of 1990 and March of 1991. We collected blood from all deer at time of capture and used serum progesterone assays to assess pregnancy status. Body mass, hind-foot length, and body length were measured. We estimated ages of captured deer using cementum analyses of the third premolar (Matson Labs, Milltown, Montana, USA). We classified radiomarked deer as young (8–20 months old), subadults (21–33 months old), and adults (>33 months old) for survival analyses. We moved deer into the next age class on the 1 March anniversary date. Crews monitored radiomarked deer daily from February 1990 through February 1992, and 4–6 times weekly during March–May 1992. Radiocollars were checked 1–2 days per week from June 1992

through February 1993 by EMWMA personnel. When a mortality signal was confirmed, we located the animal and performed a field necropsy (Wade and Bowns 1982). We searched for indirect evidence of predation within a 200-m radius of the mortality site (Ballard et al. 1979). Causes of mortality were determined after assessing evidence from necropsies and site searches. At least 3 convergent lines of indirect evidence (e.g., tracks, drags, burial mounds, etc.) in the absence of direct proof were required to classify cause of mortality as predator-caused death.

### Data Analysis

We used analysis of variance (ANOVA) to test for annual differences in body mass among years. Daily and annual survival rates were estimated with MICROMORT software (Heisey and Fuller 1985). We tested daily rate equality among months using generalized chi-square procedures (Sauer and Williams 1989). We combined months that had statistically equivalent survival rates into periods of equal survival, from which we estimated annual rates. We used chi-square tests (Sauer and Williams 1989) to investigate rate equality among years and sex–age classes during 1990–1991 and 1991–1992. During the third year, we only compared rates of subadults, adult males, and adult females because young were absent from 1992–1993 samples. We constructed contrasts between rates using Bonferroni z-tests when chi-square tests indicated rate non-homogeneity (Sauer and Williams 1989). Given small sample sizes for comparisons within age classes or years, we considered  $P \leq 0.10$  to be statistically significant to increase power of tests. We therefore relied more heavily on capture methods to yield representative samples of the population being tested.

We used MICROMORT to estimate rates for 5 causes of mortality: predation, natural stressors, accidents, harvest (legal and illegal), and unclassified (insufficient evidence of any other cause). Animals succumbing to natural stressors included deer dying of natural processes, such as disease, old age, or malnutrition, that exhibited no evidence of predation during necropsy. Although animals that succumbed to natural stressors displayed no evidence of predation, this did not imply that animals claimed by predation (or other causes) were unaffected by natural stressors. We excluded animals potentially dying of capture myopathy during the first 15 days post-capture (Bartsch et al. 1977). We evaluated number of deaths among mortality categories and

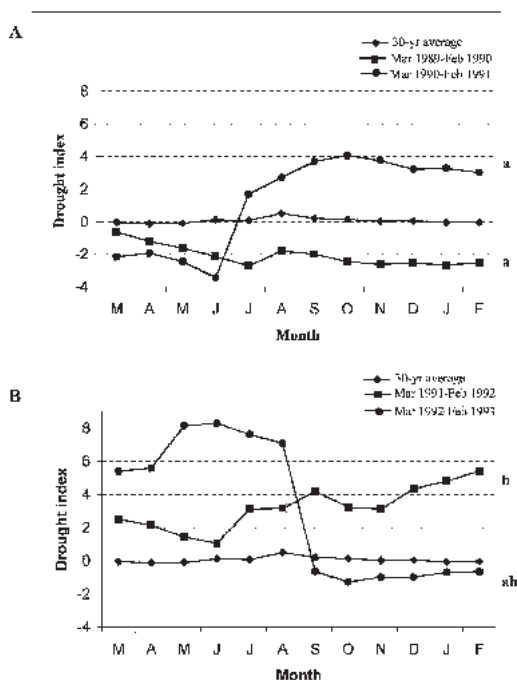


Fig. 1. Annual variation of Palmer Drought Severity Index (<-1 is drought; >1 is wet) in the Trans-Pecos region of southwestern Texas, USA, during (A) Mar 1989–Feb 1991 and (B) Mar 1991–Feb 1993, with a 30-year average (1959–1988). Differences in trends among years are indicated by differing letters ( $P < 0.10$ ).

years using both chi-square (Steel and Torrie 1980) and Bonferroni  $z$ -tests. We summarized and compared the number of deaths in each mortality category that occurred among years using chi-square analyses; cause-specific mortality rates were tested directly with  $z$ -tests. We pooled data to improve test power, when appropriate.

Personnel from EMWMA provided predator-removal numbers from the EMWMA. While we did not test effects of predator control, we reported control effort and success so that mortality and survival results could be interpreted in light of predator-control information.

**RESULTS**

We captured 60 adults (31 females [F], 29 males [M]), 12 subadults (7 F, 5 M), and 30 young (15 F, 15 M) deer during February–March 1990 and 35 adults (21 F, 14 M), 6 subadults (3 F, 3 M), and 47 young (23 F, 24 M) during March 1991. The 1992–1993 sample consisted of 73 adults (51 F, 22 M) and 32 subadults (15 F, 17 M) that survived the 1990–1991 and 1991–1992 seasons.

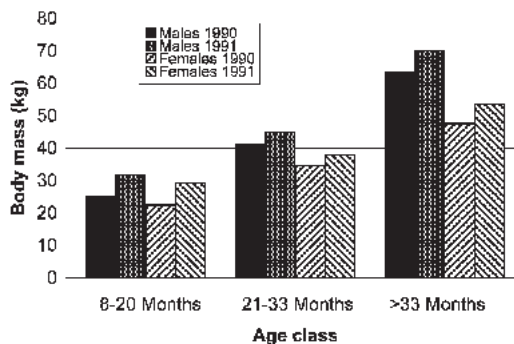


Fig. 2. Annual variation in body mass of all age-gender classes for desert mule deer captured during Feb–Mar 1990 and Mar 1991 in the Trans-Pecos region of southwestern Texas, USA. Body mass measures within age-gender classes with different letters were different between years ( $P < 0.10$ ).

The trend of monthly PDSI values during 1989–1990 was below the long-term ( $n = 65$ ) average ( $P < 0.05$ ), while in 1991–1992, values consistently exceeded the average ( $P < 0.05$ ; Fig. 1). Trends during other years were normal ( $P > 0.05$ ). The trend during 1991–1992 differed from that of 1990–1991 ( $P < 0.05$ ). While PDSI values during 1989–1990 generally were lower than those during 1990–1991, difference in trend was not significant ( $P = 0.15$ ).

Body mass was higher during 1991 than 1990 for all sex-age classes except subadults ( $P < 0.10$ ; Fig. 2). While differences of approximately the same magnitude as those observed for other classes existed for subadult deer, sample sizes lowered power of the test for that age class.

Pregnancy rates were higher in 1991 than in 1990 for all age classes of deer (fawns: 13% [ $n = 23$ ] in 1991 vs. 0% [ $n = 15$ ] in 1990; 1.5 yr olds: 67% [ $n = 3$ ] vs. 0% [ $n = 7$ ]; 2.5–5.5 yr olds: 100% [ $n = 14$ ] vs. 95% [ $n = 20$ ]; and  $\geq 6.5$  yr olds: 100% [ $n = 7$ ] vs. 73% [ $n = 11$ ]). About 10% of serum samples from males that were included as controls tested within the range of progesterone values associated with pregnancy. We assumed that any positive biases that may have occurred among doe samples did so at equal rates between years, and we thus considered annual comparisons valid.

Of 180 deer monitored from 1990 to 1993, 84 survived to 28 February 1993, 76 died, and 20 were censored (Table 1). Of those censored, 3 were collected for humane reasons, 2 lost radiocollars, 1 lost its radiocollar and was confirmed killed during the 1991 hunting season, and we lost contact with the remaining 14. Of those 14 animals, 2 were

Table 1. Annual survival, cause-specific mortality, and number (*n*) of radiomarked desert mule deer dying during Mar 1990–Feb 1993 at Elephant Mountain Wildlife Management Area and surrounding properties in Brewster County, Texas, USA. Similar survival rates within a year are identified by same letters ( $P < 0.10$ ).

Age–sex class	<i>n</i>	Days	Rate	90% CI	Mortality											
					Predation		Stressors		Accidents		Unclassified		Harvest			
					Rate	<i>n</i>	Rate	<i>n</i>	Rate	<i>n</i>	Rate	<i>n</i>	Rate	<i>n</i>		
Mar 1990–Feb 1991	95	26,216														
8–20 month	26	6,200	0.53A	0.39 to 0.72	0.16	4	0.08	2	0.04	1	0.12	3	0.08	2		
21–33 month	10	3,147	0.89B	0.74 to 1.00	0.11	1	0.00	0	0.00	0	0.00	0	0.00	0		
Adult bucks	28	8,637	0.75BC	0.62 to 0.90	0.00	0	0.07	2	0.00	0	0.04	1	0.15	4		
Adult does	31	8,232	0.59AC	0.45 to 0.75	0.14	4	0.21	6	0.07	2	0.00	0	0.00	0		
Mar 1991–Feb 1992	148	47,294														
8–20 month	46	13,775	0.75A	0.65 to 0.87	0.09	4	0.09	4	0.07	3	0.00	0	0.00	0		
21–33 month	19	6,814	0.95B	0.87 to 1.00	0.00	0	0.00	0	0.00	0	0.00	0	0.05	1		
Adult bucks	38	11,086	0.54C	0.42 to 0.70	0.08	3	0.13	5	0.03	1	0.00	0	0.21	7		
Adult does	45	15,619	0.91B	0.84 to 0.98	0.05	2	0.02	1	0.02	1	0.00	0	0.00	0		
Mar 1992–Feb 1993	105	34,521														
21–33 month	32	10,869	0.93A	0.86 to 1.00	0.07	2	0.00	0	0.00	0	0.00	0	0.00	0		
Adult bucks	22	6,688	0.80B	0.67 to 0.96	0.10	2	0.05	1	0.00	0	0.00	0	0.05	1		
Adult does	51	16,964	0.88AB	0.81 to 0.96	0.02	1	0.04	2	0.02	1	0.04	2	0.00	0		

harvested during 1991–1992 hunting seasons, 1 was confirmed alive by multiple sightings, and the fates of the remaining 11 were unknown.

Our data did not indicate sex-specific variation for survival of young or subadult deer ( $P > 0.10$ ), so we pooled sexes within age class. Most losses of 8–20-month-old deer during 1990–1991 occurred during spring and winter, while rates appeared more variable during 1991–1992. Survival of subadults remained relatively constant among seasons and years, although small sample sizes during 1990–1991 and 1991–1992 probably reduced power of statistical tests. Nevertheless, subadult survival was the highest and most constant of all age classes. Although survival for adult deer varied among years, seasonal patterns within gender were similar. Marked decreases in survival of adult males occurred during fall, coinciding with harvest, and during late winter–early spring. Adult females had lowest survival from late spring through early fall of all years, with high survival on both sides of the timespan. However, seasonal variation in daily survival rates of adult females was clearly evident only during 1990–1991, and was noted in only 1 month during 1992–1993.

We observed differences in annual survival rates among classes within years and within classes among years (Table 1). We did not find statistical differences in cause-specific mortalities and therefore report only apparent differences. Predation- and natural-stress-related deaths were more numerous than other causes in all years, each claiming 23 deer (Table 1). Of the 23 predation-related losses, 19 were attributed to mountain

lions. From 1991–1992 to 1992–1993, natural-stressor mortalities decreased at a higher rate than did predation-related mortalities (Fig. 3). Harvest was the third most significant cause of mortality, affecting only males and primarily adults. Accidents accounted for a small portion of mortality causes. Accidental and unclassified mortalities numbered fewer than predation, stress, or harvest losses.

We detected no cause-specific mortality rate differences among sex–age classes or years ( $P > 0.25$ ). In an effort to increase power of comparisons, we pooled data across years for adult male and subadult deer based on the lack of significant

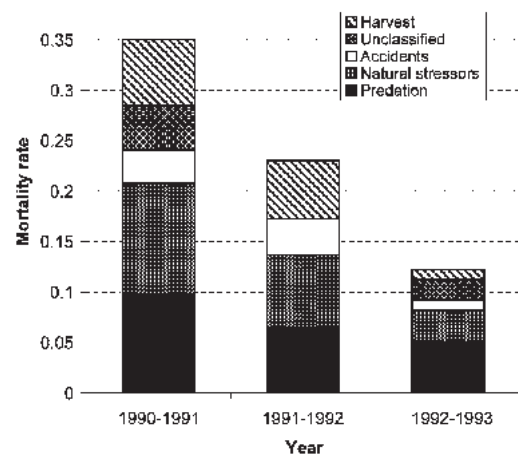


Fig. 3. Annual cause-specific mortality rates for radiomarked desert mule deer in Brewster County, Texas, USA, during Mar 1990–Feb 1993. Number of animals dying from each cause is shown to the side of corresponding bars. Data were pooled across age–gender classes.

variation among years. Cause-specific mortality rates were similar ( $P > 0.25$ ) for subadults. However, for adult males, harvest rates exceeded mortality rates due to natural stressors ( $P < 0.10$ ), predation ( $P < 0.05$ ), or accidents ( $P < 0.001$ ) during our 3-year study period. Overall, natural stressors ( $n = 9$ ) and predation ( $n = 7$ ) accounted for most adult female mortalities, while predation ( $n = 8$ ) and natural stressors ( $n = 6$ ) took the majority of young deer (Table 1).

Four mountain lions were removed from EMWMA during 1990–1993, and at least 9 lions also were removed from areas surrounding EMWMA (J. Kilpatrick, Texas Parks and Wildlife Department, personal communication). Of the 4 mountain lions captured on EMWMA during 1990–1993, we know that at least 2 killed radiomarked deer.

## DISCUSSION

We chose to extend the “fawn” class to 1 year post-capture because dangers associated with being young (i.e., learning costs and dispersal) likely were disproportionately high for that age class (Geist 1981). The significantly higher survival of 21–33-month-old versus 8–20-month-old mule deer during our 1990–1991 and 1991–1992 seasons generally corroborated our a priori age classification on the basis of life history. Actual fawn survivorship (0–12 months) would have been significantly lower due to lower survival during months 0–6. Pittman (1987) estimated Trans-Pecos mule deer fawn (0–12 months) survival at 42%, which is 14–33% lower than our estimates for 8–20-month-old deer. Therefore, our data are not easily compared with studies that estimate fawn survival from zero to 12 months-of-age. Low survival rates of our young age class were not surprising when compared to other studies that considered mule deer 0–20 months-of-age (Neal 1990, Bartmann et al. 1992, Unsworth et al. 1999).

Predation and natural stressors were the most significant mortality causes for young deer. Low survival of young during spring and winter of 1990–1991, affecting both old fawns and yearlings, may have been directly and indirectly caused by drought. Desert mule deer fawn survival is a function of density-dependent (Bartmann et al. 1992, White and Bartmann 1998) and density-independent factors such as rainfall and subsequent plant density that provides forage, thermal cover, and escape-hiding cover (Smith and LeCount 1979, Leopold and Krausman 1991, Tull et al. 2001). Secondary evidence implicated predation as a possible cause of death in all cases

of unclassified death for young deer during 1990–1991. Therefore, the true predation rate for 8–20-month-old deer during 1990–1991 probably was between 0.16 and 0.27. Similar to other studies (McCulloch and Brown 1986, Neal 1990, Bleich and Taylor 1998), mountain lions were the main predator of young deer, accounting for 7 of 8 predation-related losses.

Once deer were 21 months old, they had high survival. Subadult deer had the highest survival rate of all classes in all years and least variability among years (Table 1). Most deaths of 21–33-month-old deer in our study (3 of 4) were attributed to predation, although sample sizes were too limited to conclude statistical significance.

In the adult age class, males had lower survival than females, as reported for other hunted deer populations (McCulloch and Brown 1986, Horejsi et al. 1988). Harvest was the most important cause of mortality for adult males over the 3-year period. This pattern was most evident during 1990–1991 and 1991–1992. Three radiomarked males whose radiocollars had failed were harvested during 1992–1993, indicating that harvest may have been the most important cause of mortality during that year had those deer been included in the sample. Stress-related deaths for adult males occurred mainly during February–March, the period just following the rut and post-rut periods (Kucera 1978, Pittman 1987). The most stressful period for Trans-Pecos desert mule deer has been estimated as mid-January through mid-March (Russ and Bone 1992). Increased activity associated with mate searching (Relyea and Demarais 1994), coupled with reduced nutrient reserves associated with the periods following the rut (Anderson et al. 1972), and seasonal lows in forage quality and quantity (U.S. Department of Agriculture, Alpine, Texas, unpublished data) may have combined to cause severe nutritional stresses for adult males during this period.

In contrast to previous studies of desert mule deer (Short 1981, Russ and Bone 1992), we found that late spring and summer months generally were the most critical periods for adult females in the EMWMA population. Also, the variability in annual survival rates of adult females was an exception to the findings of Gaillard et al. (2000) and was attributable to the differences in natural stressor-related mortalities among years. Low survival of adult females and young during 1990–1991 likely was due to lingering drought effects (Table 1, Fig. 1). Short-term drought apparently reduced deer populations in Arizona, USA

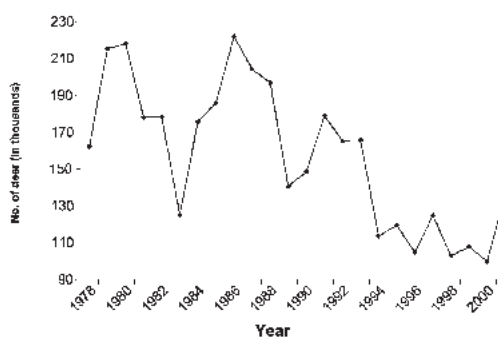


Fig. 4. Annual population estimates of desert mule deer in the Trans-Pecos region of southwestern Texas, USA, 1978–2001.

(Anthony 1976). Vegetation response occurred too late to provide quality forage for females during May–September 1990. For Trans-Pecos mule deer, the May–July period coincides with the latter stages of pregnancy, while the subsequent 2–3 months are associated with lactation (Pittman 1987). Nutrient demands associated with gestation typically resulted in lowest female body fat amounts during late spring and early summer (Anderson et al. 1972). Demands associated with lactation may be as high as 2.3 times the basal metabolic rate of adult females (Wallmo et al. 1977). Pregnancy rates also were generally lower during 1990–1991 than 1991–1992, particularly in young and old deer. Furthermore, fecundity probably was reduced because pregnant females likely absorbed or aborted fetuses in efforts to survive the nutritionally stressful drought period. Body mass paralleled survival and reproductive patterns between 1990–1991 and 1991–1992, strongly implicating the drought as the proximate mechanism contributing to lowered body mass, reproduction, and survival for adult females.

Natural stressors, predation, and harvest were the most important mortality causes impacting the EMWMA herd. Desert mule deer in New Mexico, USA, also showed high nonpredation mortality during any given year (Humphreys and Elenowitz 1989, Humphreys 1993). Environmental resistance likely was a partial explanation for the high nonpredation mortality we observed, given that variations in Trans-Pecos weather coincided closely with variations in body condition, survival, and pregnancy. Environmental resistance is traditionally based and more easily demonstrated where carrying capacity is stable or relatively unchanging. Variable Trans-Pecos weather produces dynamic changes in habitat and for-

age quantity and quality. In turn, habitat offering ample forage, cover, and water may stimulate deer population growth via high survival and fecundity during favorable conditions. When drought conditions return, lowered survival and fecundity follow, resulting—presumably—from drought-induced vegetation and environmental changes during poorer conditions. These “switch-over” conditions (from drought to favorable or vice versa) may occur among or within the same annual periods, such as during 1990–1991 and 1992–1993 (Fig. 1). The switch-over during 1992–1993 began a period of drought that has continued nearly unabated through May 2002, as the mean monthly PDSI value from September 1992 through February 2002 is equal to  $-2.03$  (90% CI:  $\pm 0.40$ ; U.S. Department of Commerce 2002). During this time, the Trans-Pecos mule deer population declined to historical lows, with an increase ( $\lambda = 1.36$ ,  $r = 0.31$ ) occurring between 2000 and 2001, despite relatively low fawn survival in 2000 during a period of severe drought (Fig. 4; Bone 2001). Switch-overs and time lags probably are characteristic of Trans-Pecos mule deer ecology.

Predation also was an important mortality cause, with mountain lions responsible for at least 83% of all predation-related mortalities. We confirmed that radiomarked deer were killed by 2 of the 4 lions removed from EMWMA. Although we could not directly attribute deer losses to other mountain lions removed from the area, the timing and proximity of many of the predation-related deer losses implicated that those lions may have been responsible. Based on these facts, predation would have likely persisted at somewhat higher levels in the absence of predator-control efforts. The fact that lion-related losses occurred—even when some level of control was in place—emphasized the problematic nature of predator-control efforts in eliminating deer losses. Predation by mountain lions likely will persist even when control efforts are in place because mountain lions in this part of the Trans-Pecos tend not to have established territories and are thus primarily transient (J. Kilpatrick, Texas Parks and Wildlife Department, personal communication).

## RESEARCH AND MANAGEMENT IMPLICATIONS

Based on our study, predation and weather-induced environmental resistance would be excellent candidates for future, long-term investigations of mortality compensation in Trans-Pecos desert

mule deer. Replicated studies, using management units or noncontiguous, large ranches as replicates within each treatment could be used to discern compensatory and additive mortality from predation, harvest, and natural stressors. Each study area should contain no fewer than 30–40 radiomarked deer in each sex–age class of interest; 40–50 deer would be more conservative, allowing for high losses of deer and radiocollar failure.

Our results could not predict the outcome of increased or decreased levels of predator (lion) control on this deer herd. If escape–hiding cover is a limiting factor (Tull et al. 2001) due to land use, management practices, environmental conditions, or a combination, then predator control may succeed in raising recruitment rates. However, if the deer population exists near its range carrying capacity and hunter harvest is unable to compensate for lowered predation rates, this may not be a desirable outcome, or recruitment may not increase at all (Cantu and Richardson 1997, Ballard et al. 2001). If forage quality and quantity are not limiting factors, then predator control may increase herd productivity based on feeding behavior and the perceived availability of resources (Altendorf et al. 2001). Predator control must be economically justifiable (Cantu and Richardson 1997, Ballard et al. 2001).

Management of ungulate populations that have increased to levels that are suddenly overabundant after environmental conditions degrade is difficult because weather, time lags, and switch-overs are difficult to predict. A stable population of predators may buffer against a sudden overabundance of deer given a rapid decline in habitat quality. A policy that recognizes both the concerns of conservationists and land managers, such as listing mountain lions as a game animal, may provide adequate control of mountain lions while at the same time allow for their continued existence.

When a deer population is regulated by density-dependent factors, increased harvest can increase fawn survival (Bartmann et al. 1992). Losses of apparently prime adult males during late winter and early spring represented a group of animals that may have been “predisposed” to death but were not harvested. Harvesting such animals would be desirable if field identification of these individuals, perhaps by antler size, is logistically possible. High natural-stress-related losses of adult females during periods of both poor and favorable environmental conditions may have been indicative of a population existing at or over range carrying capacity. Antlerless deer

harvests in this case are justifiable (Cantu and Richardson 1997) and may increase adult survival and early recruitment, but caution must be taken during the hunt because orphaned fawns may have lower rates of survival (Giuliano et al. 1999). Our data indicated high survival of 21–33-month-old desert mule deer. We felt that some room was available for harvest in this age class if an overall desirable age structure could be maintained. In this arid environment, harvest of spike yearlings when nutritional conditions are favorable can increase potential for large-antler genetics (Cantu and Richardson 1997). If environmental conditions improve habitat for only a short time, allowing the population to increase during this period would be unnecessary.

The variability of natural-stress-related mortality in young and adult female classes during both poor and favorable range conditions may be a significant factor in the population dynamics of mule deer in this region, but specific causative mechanisms remain poorly understood and consequently unmanageable. More survival and fecundity data could be used for sensitivity analyses and modeling techniques to determine which age-specific demographic parameters are most important for population growth in light of limiting environmental factors and other sources of mortality. Managing for a particular parameter could prove to be possible.

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