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Condition, survival, and productivity of mule deer in semiarid grassland-woodland in east-central New Mexico

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Abstract: Mule deer (*Odocoileus hemionus*) are an economically important species to wildlife enterprises throughout New Mexico and the western United States, but populations are declining, limiting recreational and revenue potential to private and public wildlife managers. We documented body condition, survival, production of fawns, and trends in population size of a declining mule deer population on the Corona Range and Livestock Research Center (CRLRC), a multiple-use research ranch in east-central New Mexico owned by New Mexico State University. Mule deer females were in poor condition, characterized by accrual of little body fat or lean tissue (muscle mass) reserves. Annual female survival was 0.42, 0.78, and 0.71 during 2006 to 2008 and was related to poor body condition and precipitation. Survival of females was positively related to precipitation from January to June and April to June, seasons that coincide with conception-parturition and late gestation in deer. Survival also was positively related to increasing lean tissue (muscle) reserves. Malnutrition was the most common cause of death for adult females (n = 13 of 22). Fawn survival to weaning was positively related to increasing size of females, but not to any measure of seasonal or annual precipitation. Low survival and low productivity resulted in the CRLRC deer population declining from 539 to 191 during 2005 to 2008. Poor condition of deer was the result of both seasonal drought and a lack of quality forage. While drought will always decrease productivity of mule deer populations, survival may be maintained by managing for more drought-tolerant forage, which limit population declines during droughts.

Key words: mule deer, precipitation, survival, New Mexico

Wildlife enterprises are increasingly important to ranch income in the western United States, and, thus, management practices that facilitate economically important species, such as mule deer (*Odocoileus hemionus*), are important for optimal management of private ranches in New Mexico and throughout the West. However, mule deer populations throughout New Mexico have declined significantly since the 1980s, paralleling declines throughout the West (Carpenter 1998, Bender et al. 2007*a*). Declines in mule deer have been attributed to many factors, including changes in plant communities (Urness et al 1971, Sowell et al. 1985), drought (Anthony 1976, Bender et al. 2007*a*, *b*), competition with or displacement by elk (*Cervus elaphus*; Lindzey et al. 1997), and predation (Ballard et al. 2001). Ultimately, it is how these and other factors influence the likelihood of survival and reproduction of individual deer that determines how populations respond. Only recently have studies documented fundamental factors affecting mule deer survival and productivity, including rigorous assessments of underlying factors that influence susceptibility of individual deer to mortality, including *a priori* body condition (Bender et al. 2007*a*, *b*; Lomas and Bender 2007; Hoenes 2008; Bishop et al. 2009; Bender 2010).

In the arid Southwest, trends in mule deer populations are frequently attributed to precipitation patterns; deer increase during wet periods and decline during dry ones (McKinney 2003, Lawrence et al. 2004). In arid environments, precipitation has a strong effect on plant production and nutritional quality, and, consequently, on deer populations (Smith and LeCount 1979, McKinney 2003, Marshall et al. 2005). Thus, precipitation and other environmental factors affect deer through resource acquisition, which is ultimately manifested in individual body condition. In

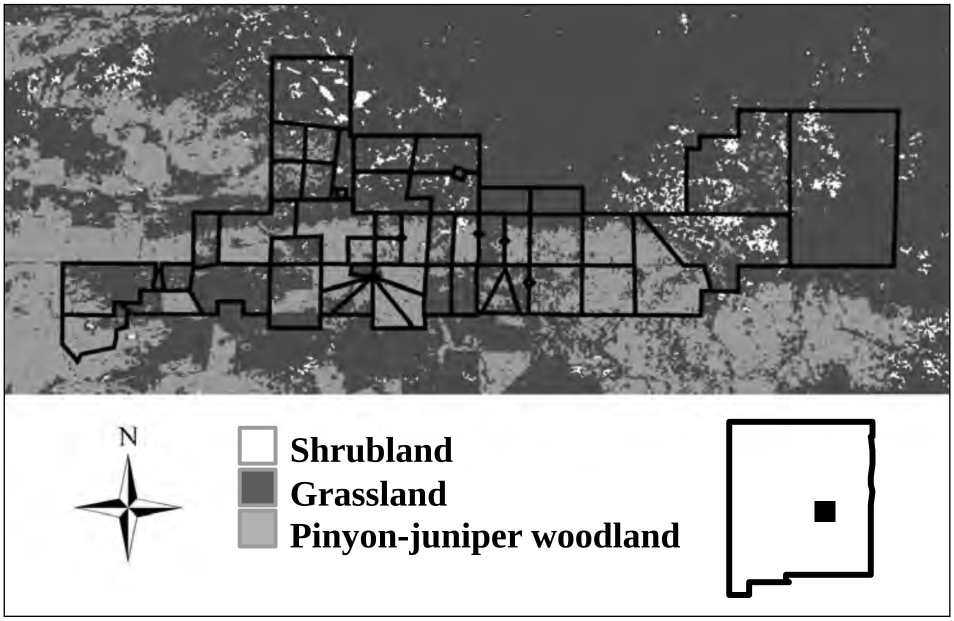

Figure 1. Location, pastures, and primary classes of vegetation on the Corona Range and Livestock Research Center, east-central New Mexico.

turn, body condition can affect virtually every survival and reproductive parameter of deer (Clutton-Brock et al. 1982, Verme and Ullrey 1984, Wakeling and Bender 2003, Bender et al. 2006, Bender et al. 2007*a*, Lomas and Bender 2007, Bishop et al. 2009). Therefore, individual animal condition is a valuable tool to collate population health (Mautz 1978, Franzmann 1985, Bender et al. 2006).

Adult female survival has the greatest effect on the rate of increase of deer populations (Gaillard et al. 2000), and nutritional condition can affect survival of adult female cervids (Bender et al. 2007*a*, Bender et al. 2008, Bender and Piasecke 2010). Thus, knowledge of both these demographics is prerequisite to understanding the importance of any proximate mortality factor thought to be limiting mule deer populations. Hence, our goal was to determine relations among condition, survival, and productivity of adult female mule deer on the Corona Range and Livestock Research Center (CRLRC), a multiple-use research ranch owned and operated by New Mexico State University. Our specific objectives included, to determine: (1) survival rates of adult female mule deer, (2) causes of mortality of adult female mule deer, (3) production and recruitment of fawns, (4) population rates of increase of mule deer, (5) nutritional condition of adult female mule deer, and (6) to relate the condition of deer and factors that may affect the condition to survival and productivity of deer.

Study area

The CRLRC is an 11,290-ha working-ranch laboratory located approximately 22.5 km east of Corona, New Mexico (34° 15′ 36″ N, 105° 24′ 36″ W; Figure 1). It has an average elevation of 1,900 m and a mean annual precipitation of 40 cm, most of which occurs during July and August as high-intensity, short-duration convectional thunderstorms. Topography is mostly rolling, with steep (30 to 75% slope) mesa sides and rock outcrops limited to the extreme southwest. Vegetation is composed mostly of perennial grassland, with scattered sparse to dense pinyon pine (*Pinus edulis*) and 1-seed juniper (*Juniperus monosperma*) woodlands and few shrublands (Figure 1). Predominant grasses are blue grama (*Bouteloua gracilis*), wolftail (*Lycurus phleoides*), threeawns (*Aristida* spp.), sideoats grama (*B. curtipendula*), and sand dropseed (*Sporobolus cryptandrus*).

Methods

We captured and fit ≥1.5-year-old female mule deer with mortality-sensitive radio collars (Advanced Telemetry Solution, Asanti, Minn.), in early December 2005 to 2007 and April 2006 to

2007. Deer were captured by aerial net-gunning or darting from a Bell JetRanger 206B helicopter using 1.5 to 1.8 mg of carfentanil citrate and 50 to 75 mg of xylazine hydrochloride per deer. Deer were aged as yearling or adult by tooth wear and tooth replacement (Robinette et al. 1957) and treated with antibiotics, vitamin E-selenium, vitamin B, and an 8-way Clostridium bacterin to help alleviate capture stress. Following processing, the immobilants were antagonized with naltrexone and tolazoline.

Health and condition

We measured the thickness of subcutaneous rump fat at its thickest point immediately posterior to the cranial process of the tuber ischium (pin bone; MAXFAT) using a SonoVet 2000 portable ultrasound with a 5-mHz probe. Approximate body fat (BF) was estimated using BF = 5.68 + 5.93 × MAXFAT (cm; Stephenson et al. 2002). Because the above equation can predict body fat down only to 5.7% (Stephenson et al. 2002), we also used a rump body-condition score (rBCS) to predict body fat, where BF = 3.444 × rBCS – 0.746 ($r^2 = 0.83$; $n = 27$; Bender et al. 2007*a*). This relationship was derived from Rocky Mountain mule deer (*O. h. hemionus*) captured in north-central and east-central New Mexico (Bender et al. 2007*a*) and allowed determination of levels of BF below levels where subcutaneous fat is fully catabolized. We estimated rBCS by palpating the sacral ridge and soft tissue of the rump near the base of the tail and scored measurements on a scale of 1 to 5 in intervals of 0.25, where 1 = emaciated and 5 = obese (Cook 2000, Bender et al. 2007*a*).

We measured the depth of the longissimus dorsi (loin) muscle at the thickest part between the twelfth and thirteenth ribs (LOIN) and determined a withers body condition score (wBCS; Bender et al. 2007*a*) by measuring the amount of the sacral ridge discernable immediately posterior to the shoulder hump to index catabolism of lean muscle tissue. Last, we measured body mass or heart girth (GIRTH) of captured deer to index overall size. We compared condition indices among years using ANOVA (Zar 1996), specifically testing the year × lactation interaction for adult females because of the known negative impacts of lactation on condition (Wakeling and Bender 2003, Hoenes 2008). For this and all subsequent tests, we used $\alpha = 0.10$ as our level of significance because of the inherent variation in field studies.

Survival and causes of mortality

We located radio-collared mule deer 1 to 2 times per week and determined survival rates using the Kaplan-Meier estimator, modified for staggered-entry of individuals (Pollock et al. 1989). We compared annual survival estimates using Z-tests (Pollock et al. 1989). We excluded any mortality that occurred ≤30 days post-capture from analyses because we were unable to rule out capture-related stress in deer deaths (Berringer et al. 1996).

We determined causes of death following Bender et al. (2007*a*). We considered the proximate cause of mortality to be the ultimate cause unless femur marrow fat levels were <12%. Femur marrow fat <12% is indicative of acute starvation (Ratcliffe 1980); thus, deer below this threshold were classed as malnutrition mortalities regardless of proximate cause of death.

We used logistic regression (Hosmer and Lemeshow 1989) to model survival of individual deer as a function of condition and seasonal precipitation (see below). We modeled effects of lactation status, MAXFAT, BF, rBCS, wBCS, LOIN, and GIRTH (Table 1; body mass and girth were strongly linearly related; L. Bender, unpublished data) on the probability of an individual deer surviving the subsequent 12 months following assessment of condition. This allowed us to assess the effects of individual condition at or near the annual peak of condition in late autumn (early December) on subsequent survival through the following year (January to December), that is, effects of *a priori* condition on deer survival.

We also modeled the effects of precipitation on the probability of a deer surviving through the following year. We used precipitation data collected from 3 automated and 7 manual weather stations distributed across CRLRC. We summed annual precipitation (e.g., total amount received from January through December) and cumulative precipitation during each of 4 seasons based on biological relevance to mule deer (Bender et al. 2007*a*, Hoenes 2008, Bender and Piasecke 2010). These seasons included: (1) conception-parturition (January to June), when deer attempt to minimize overwinter loss of body condition and later require increased nutritional quality as the fetus begins to grow (Wakeling and Bender 2003; precipitation during this period has been strongly linked to survival in cervids [Bender et al. 2007*a*, Hoenes 2008, Bender and Piasecke 2010]); (2) late gestation-parturition (April to June) when nutritional requirements of deer increase greatly (Wakeling and Bender 2003); (3) lactation (July to September), the period of greatest nutritional demand on females (Wakeling and Bender 2003); and (4) post-lactation (October to December), when females need to recover energy reserves prior to winter. We determined a grand mean among all sites and used (1) totals from the nearest station for each individual deer home range (L. Bender et al., unpublished data) and (2) the grand mean of all sites in analyses of precipitation effects on survival and lactation.

Productivity and population rate of increase

We determined lactation status of each captured female by presence or absence of milk in the udder from December 2005 to 2007. Mammary tissue still secreting milk indicates nursing by a fawn within 3 to 11 days, and, thus, survival of fawns to that point (Bender et al. 2002). Consequently, lactation is evidence of production and survival of ≥1 fawn through autumn, and, thus, is a valid index of population productivity (Hoenes 2008, Bender and Piasecke 2010). We determined variances around proportions lactating using the normal approximation and compared proportions lactating annually using Fischer's exact tests (Zar 1996). We also used logistic regression (Hosmer and Lemeshow 1989) to model the probability of a female lactating as a function of annual and seasonal precipitation during that year and size of the female. Precipitation was defined as described above for survival modeling.

We determined fawn:adult female (F:D) ratios by helicopter counts during April 2005 to 2008 and by ground surveys and surviving fawns-at-heel (Hoenes 2008) in May 2009. For aerial surveys, we surveyed the entire study area throughout the day and recorded sizes and composition of all deer social groups; we categorized deer as fawns, adult (≥1.5-years-old) females, or adult males. We determined SEs for F:D ratios following Czaplewski et al. (1983) and compared F:D ratios annually, using Fischer's exact tests (Zar 1996). We determined the maximum potential finite rate of population increase (γ) using $\gamma = S_D + ½ \times F{:}D$, where S_D = annual survival rate of adult females (White and Bartmann 1998). We calculated SEs for estimates of γ using parametric bootstrapping (Bender et al. 1996).

Last, we used aerial survey data from April 2005 to 2008 to estimate population size of mule deer on CRLRC by correcting the number of deer observed for group size and 2 levels of activity (moving or not moving [i.e., bedded, standing]) using an aerial sight-bias model developed for grassland-woodland habitats of New Mexico (Bender 2006).

Results

Condition and survival

We captured or recaptured and assessed for condition 52 adult mule deer (46 individually radio-collared) from December 2005 to 2007. Numbers of radio-collared deer annually from 2006 to 2008 were 18, 27 and 19 females, respectively. Although lactating females were consistently in poorer condition than dry females for most condition indices each year (Table 1), no indices of condition varied among females by year × lactation status ($F_{5,46} \leq 1.10$; $P \geq 0.38$), likely because all females were in extremely poor condition each year (Table 1), and, consequently, sample sizes of lactating females were low (3 to 4 annually).

Annual survival of adult females was lower ($Z \geq 1.63$; $P \leq 0.10$) in 2006 (0.42; SE = 0.14; n = 16) than in 2007 (0.78; SE = 0.08; n = 22) or 2008 (0.71; SE = 0.11; n = 19); survival in 2007 and 2008 did not differ ($Z = 0.57$; $P = 0.57$; Table 2). Malnutrition was the most common cause of death for females (n = 13 of 22) over all years, followed by unknown (6), predation (2), and unknown-nonpredation (1).

Thickness of the loin muscle (LOIN: $\chi^2 = 3.7$; $P = 0.06$; $n = 52$) was the only condition variable related to female survival (all others $\chi^2 < 2.1$; $P > 0.14$). Odds ratios indicated that probability of surviving increased 5.7× (95% CI = 1.0–34.1) for each 1-cm increase in loin muscle thickness.

Survival of adult females was positively associated with cumulative precipitation during the conception–parturition ($\chi^2 = 3.7$; $P =$

Table 1. Mean and SE of condition indices for lactating and dry adult female mule deer at the peak of condition in late autumn on the Corona Range and Livestock Research Center, New Mexico.

		Dry females		Lactating females	
Year	Index[1]	$\bar{x}$	SE	$\bar{x}$	SE
2005	rBCS	2.21	0.20	1.88	0.13
	wBCS	3.27	0.24	3.31	0.28
	MAXFAT	0.23	0.10	0	0
	LOIN	3.64	0.15	3.81	0.12
	GIRTH	87.3	1.1	87.3	0.5
	BF	7.06	0.59	5.68	0.35
2006	rBCS	2.22	0.13	1.83	0.08
	wBCS	3.71	0.92	3.58	0.30
	MAXFAT	0.17	0.08	0	0
	LOIN	3.68	0.08	3.70	0.15
	GIRTH	87.6	1.0	88.7	2.7
	BF	6.69	0.48	5.61	0.23
2007	rBCS	2.10	0.26	1.67	0.33
	wBCS	3.58	0.21	3.58	0.17
	MAXFAT	0.28	0.12	0	0
	LOIN	3.94	0.09	3.67	0.09
	GIRTH	89.2	0.9	84.0	1.0
	BF	7.32	0.73	4.99	1.15

[1]rBCS = rump body condition score; wBCS = withers body condition score; MAXFAT = maximum subcutaneous rump fat thickness (cm); LOIN = depth of the longissimus dorsi muscle (cm); GIRTH = heart girth (cm); and BF = approximate body fat (%).

0.05; n = 52) and the late gestation–parturition periods (χ^2 = 4.3; P = 0.04; n = 52) as recorded at the weather station nearest the home range. Probability of a female surviving the year increased 1.3× (95% CI = 1.0 to 1.6) and 1.5× (95% CI = 1.1–2.3), respectively, for each 2.5-cm increase in precipitation during these periods. Conversely, probability of survival was negatively related to cumulative precipitation during the lactation (χ^2 = 7.5; P < 0.01; n = 52; odds ratio = 0.7 [95% CI = 0.5–0.9]) and post-lactation (χ^2 = 10.2; P < 0.01; n = 52; odds ratio = 0.2 [95% CI = 0.1–0.5]) periods.

Similarly, probability of survival of adult females was positively related to precipitation during conception–parturition (χ^2 = 3.8; P = 0.05; n = 52) and the late gestation to parturition periods (χ^2 = 4.3; P = 0.04; n = 52) as averaged across all rain gauges on CRLRC. Odds ratios indicated that probability of a female surviving the year increased 1.3× (95% CI = 1.0–1.7) and 1.6× (95% CI = 1.1 to 2.4), respectively, for each 2.5 cm increase in precipitation during these periods. Conversely, probability of survival was again negatively related to cumulative precipitation during the lactation (χ^2 = 8.8; P < 0.01; n = 52; odds ratio = 0.8 [95% CI = 0.6–0.9]) and post-lactation (χ^2 = 10.4; P < 0.01;

n = 52; odds ratio = 0.3 [95% CI = 0.2–0.6]) periods when averaged across all rain gauges.

Productivity and population rate of increase

Proportions of females lactating at capture were similar (Fischer's exact P = 0.75) among 2005 (0.25; SE = 0.11; 4/16), 2006 (0.15; SE = 0.08; 3/20), and 2007 (0.19; SE = 0.09; 3/16; Table 2). Probability of a female lactating was not related to any measure of seasonal or annual precipitation ($\chi^2 \leq 2.7$; $P \geq 0.10$; n = 52), but was positively related to GIRTH ($\chi^2 = 3.5$; $P = 0.06$; n = 52). Probability of a female lactating increased approximately 1.9× (95% CI = 0.9 to 4.4) for each 2.5 cm increase in GIRTH.

April to May F:D ratios varied (Fischer's exact $P < 0.001$) among years from 9 ± 4 to 45 ± 5 (Table 2). Annual rate of increase of mule deer on CRLRC derived from annual survival rates and F:D ratios predicted annual decreases in population size of 47, 17, and 16% for 2006 to 2008, respectively (Table 2). Sightability corrected population estimates of mule deer were n = 539, 397, 318, and 191 for April 2005 to 2008, respectively.

Discussion

Good nutrition allows deer to accrue more body fat and muscle mass, which increases individual probability of survival (see above; Bender et al. 2007*a*, Bender et al. 2008, Bishop et al. 2009, Bender and Piasecke 2010). Conversely, nutritionally stressed deer are more susceptible to disease, parasitic infection, and predation (Dixon and Herman 1945, Longhurst and Douglas 1953, Ballard et al. 2001, Bender et al. 2007*a*, Lomas and Bender 2007, Bender 2010). Adult female mule deer on CRLRC were able to accrue only 33 to 50% of the levels of body fat that mule deer are capable of accruing (Oliver 1997), and poor condition of deer on CRLRC compromised survival and reproduction (Table 2). Mean body fat levels on CRLRC (lactating females = 5.4%; dry females = 7.0%) were also generally lower than levels previously seen in northcentral New Mexico (dry females = 8.1%; Bender et al. 2007*a*) and in the San Andres Mountains of southcentral New Mexico (lactating females = 6.1%; dry females = 9.2%; Hoenes 2008, Bender 2010). Moreover, both probability of survival and lactation also showed dependence of deer upon lean muscle tissue, as opposed to more readily mobilized fat reserves, further reflecting the poor condition of deer on CRLRC (Bender et al. 2007*a*, Bender et al. 2008, Bender 2010).

Adult female survival on CRLRC in 2006 was 0.42, the lowest recorded among contemporary mule deer studies. Most mortality was due to malnutrition (i.e., 13 of 22 = 59% of adult female deaths). Only Lawrence et al. (2004) in Texas (0.59), Bender et al. (2007*a*) in northcentral New Mexico (0.63), and Bleich and Taylor (1998) in California (0.64) found similarly low survival in at least 1 year of their studies, which Lawrence et al. (2004) and Bender et al. (2007*a*) attributed to drought and poor foraging environments. We similarly found a strong relationship between late winter-spring precipitation and mule deer survival on CRLRC, where the probability of a deer surviving increased approximately 1.3 to 1.6× for each 2.5 cm increase in precipitation. Precipitation during late winter-spring (January to June) and spring (April to June) was well below normal on CRLRC in 2006: 3.5 cm and

Table 2. Survival of adult female mule deer, proportions of adult females that were lactating in late-autumn, fawns per adult female in early spring (April–May), and annual finite rate of population increase (λ) for mule deer on the Corona Range and Livestock Research Center, 2005–2009.

	Survival		Proportion lactating		Fawns/ female[1]		λ	
Year	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
2005	n/a		0.25	0.11	0.29	0.07	n/a	
2006	0.417	0.141	0.15	0.08	0.22	0.05	0.53	0.07
2007	0.783	0.083	0.19	0.09	0.09	0.04	0.83	0.09
2008	0.705	0.109	n/a		0.27	0.08	0.84	0.12

[1]Sample sizes = 369, 169, 163, and 93, 2005–2008, respectively.

3.4 cm, respectively, as compared to norms of 13.2 cm and 8.1 cm, respectively. This low precipitation, in combination with poor body condition the previous autumn (females ≤7.1% BF; Table 1), led to the extremely high mortality in 2006, as well as low recruitment of fawns in both 2006 and 2007 (Table 2). High mortality associated with low precipitation during the conception-parturition season (January to June) has previously been documented in both mule deer (Bender et al. 2007*a*, Lomas and Bender 2007) and elk (Bender and Piasecke 2010) populations in arid New Mexico habitats.

While adult female survival on CRLRC in 2007 (0.78) and 2008 (0.71) was also lower than levels typically seen in mule deer, survival was not compromised to the extent seen in 2006 and was comparable to other mule deer studies in New Mexico that found adult female survival ranging from 0.74 to 0.91 (Bender et al. 2007*a*, Hoenes 2008, Bender 2010). Precipitation during late winter-spring (January to June) and spring (April to June) was higher in both 2007 (16.9 cm and 12.0 cm, respectively) and 2008 (5.1 cm and 4.8 cm, respectively), contributing to the higher survival in these years. Although the below-normal precipitation likely lowered survival rates in 2008, survival remained above 2006 levels because the seasonal drought was not as severe, and many of the most vulnerable deer (i.e., older) likely were lost in 2006 (L. Bender, unpublished data).

Adult survival is the last demographic impacted by resource limitations (Gaillard et al. 2000), and, consequently, impacts are infrequently observed in free-ranging herbivores. Thus, the low survival seen on CRLRC (0.42, 0.78, 0.71; Table 2) and the magnitude of malnutrition-related mortality (13 of 22 = 59% of deaths and 4 of 4 = 100% of deaths from a limited number of radio-collared adult males due to malnutrition [L. Bender, unpublished data]) highlight the magnitude of nutritional limitation faced by mule deer on CRLRC, even in years of near normal precipitation. The pattern of mortality further illustrates this; most mortality occurred in spring and summer (April to August), including 18 of 22 deaths, of which 9 of 18 were from malnutrition. Energy requirements of females increase greatly during the last trimester of gestation and remain high throughout lactation (Verme and Ullrey 1984, Wakeling and Bender 2003), which begins approximately in April on CRLRC. Deer, thus, require foods of higher nutritional quality during this period, and precipitation is needed to initiate growth of annual forbs and woody browse species preferred by deer (McKinney 2003, Marshall et al. 2005, Hoenes 2008). Low precipitation results in a lack of early phenology forage during this period. Consequently, lack of precipitation during this period leads to extreme nutritional stress because of the high energy demands of deer to nourish the growing fetus and recover body reserves depleted over winter (Verme and Ullrey 1984, Wakeling and Bender 2003). Lack of green forage contributed to the high mortality of adult females seen on CRLRC, especially in 2006, with the high losses to malnutrition during this period likely representing loss of deer that would have managed to survive under normal precipitation patterns, but whose resources were too depleted to survive any longer without significant spring green-up. Such a pattern in malnutrition-related losses is likely to occur only in mule deer populations that are severely nutritionally stressed (Lawrence et al. 2004, Bender et al. 2007*a*). Above normal precipitation during the summer lactation period (July to September; 32.5 cm as compared to a norm of 19.1 cm) in 2006 was unable to compensate, in terms of deer survival, for the lack of precipitation during January to June. This resulted in the negative relationship between post-parturition precipitation and adult female survival on CRLRC. This further illustrates that the timing of precipitation is of greater importance than the total amount with respect to survival and productivity of mule deer populations in arid environments (Bender et al. 2007*a*, Lomas and Bender 2007, Hoenes 2008).

Female condition in December 2006 and 2007 was similar to that in 2005 (Table 1), but adult survival increased, whereas, population productivity remained low (Table 2). Mule deer still faced a challenging nutritional environment, as evidenced by their poor condition and productivity (Tables 1 and 2); these challenges resulted in a declining deer population (n = 539, 397, 318, and 191 for April 2005 to 2008, respectively). However, these limitations did not affect adult female survival to the degree seen in 2006, corroborating that resource limitations act on populations by sequentially affecting body condition, juvenile fecundity and survival, adult fecundity, and, lastly, adult survival (Gaillard et al. 2000, Bender et al. 2006). Increased precipitation during late winter-spring in 2007 and 2008 was apparently enough to allow adult survival to rebound.

Malnutrition was the most common cause of death of both adult female and male mule deer on CRLRC. Although other factors (e.g., predation) killed deer, they were minor, similar to other highly nutritionally stressed populations of mule deer in New Mexico (Bender et al. 2007*a*, Hoenes 2008, Bender 2010). Survival of adult females was best predicted by measures of lean muscle reserves on CRLRC, similar to survival of extremely nutritionally stressed elk in the Pacific Northwest (Bender et al. 2008), likely because nutritional limitations allowed little accrual of body fat (Bender et al. 2008). Data from CRLRC clearly indicate that mule deer faced a limited foraging environment, and, consequently, were in very poor condition. In turn, poor body condition resulted in high levels of malnutrition-related mortality and decreased population productivity, as the probability of a female lactating in autumn (i.e., survival of ≥1 fawn to that point) also declined as size (GIRTH, which itself is a product of nutrition and condition; Piasecke 2006) decreased.

Low adult survival and poor fawn production (Table 2) predicted population declines of 16 to 47% annually from 2006 to 2008, on CRLRC (Table 2). These demographics-based predictions were corroborated by annual population estimates from helicopter surveys, which were corrected for visibility bias (Bender 2006); observed annual declines were 20 to 40% for April 2005–2006 to 2007–2008, respectively. The ultimate cause of declining mule deer numbers was limited nutrition, as evidenced by extremely low adult body condition (Table 1) and dependent demographics (Table 2); condition, in turn, was limited by seasonal precipitation and composition of extant vegetation communities, which lacked high-quality deer forages (L. Bender et al., unpublished data). Because of the ecological and economic importance of mule deer on CRLRC, habitat factors that limit forage quantity or quality for mule deer need to be identified and addressed, or the deer population will likely continue to decline (L. Bender et al., unpublished data). Relatedly, mule deer foods (primarily deciduous or evergreen shrubs) that are less impacted by lack of seasonal precipitation during the critical conception-parturition period (January to June; Marshall et al. 2005, Hoenes 2008) need to be managed for or established to limit adult female mortality during this period. While productivity of mule deer will likely always be limited during drought years because of the lack of high-quality nutrition provided by annual forbs (Hoenes 2008), maintaining high adult survival during droughts can limit the magnitude of population declines (Bender et al. 2007*a*, Bender 2010) and, thus, allow much faster recovery of populations during periods of increased productivity.

Management implications

Environmental conditions on CRLRC resulted in mule deer being unable to accrue significant amounts of body fat or other reserves, which limited productive potential of this population and predisposed deer to mortality. Two factors were responsible for poor deer condition. First, seasonal drought and limited nutrition resulted in poor deer condition, as evidenced by the significant effect of precipitation on female survival. Even given near-normal precipitation, however, mule deer were unable to accrue high levels of BF or other reserves (Table 1) and showed an annual rate of increase of only 0.84 (SE = 0.12), or a 16% decline on CRLRC (Table 2). Thus, composition of plant communities was the second principal factor limiting the quality of food available for mule deer on CRLRC (Bender et al. 2010). Forbs and particularly palatable shrubs are rare on CRLRC. Management practices have emphasized maintaining healthy grasslands which are dominated by perennial grasses that are of limited nutritional and cover value to mule deer (Bender et al. 2007*b*, Hoenes 2008). Thus, significant habitat enhancements will be necessary to get the CRLRC population growing at levels mule deer can achieve (>25% annually). Consequently, specific habitat attributes that affect condition of mule deer on CRLRC need to be identified to develop informed management strategies to increase survival and productivity of mule deer on the CRLRC.

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