Factors influencing survival of desert mule deer in the greater San Andres Mountains, New Mexico

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Abstract: Mule deer numbers have declined precipitously in the San Andres Mountains of southcentral New Mexico. To assess reasons for population declines, we monitored condition, survival, and causes of mortality for a range of 37 to 64 radio-collared, $\geq$1.5-year-old female mule deer annually, and a range of 14 to 31 radio-collared, $\geq$1.5-year-old male mule deer annually from 2003 to 2009, and modeled environmental factors affecting survival. We found annual survival rates of 0.74 to 0.86 for females and 0.74 to 0.92 for males, rates that were similar among years within sexes. Causes of mortality for 50 radio-collared females and 22 radio-collared males included predation (13 females, 2 males), accidents (4 females, 1 male), malnutrition (13 females, 7 males), disease (6 females, 2 males), unknown-not-predation (3 females, 6 males), unknown (11 females, 3 males), and harvest (0 females, 1 male). Condition of females varied among years and was poor in most years (i.e., lactating females had <7% body fat). Probability of survival of individual females was most closely related to indices of muscle and body mass in late autumn at the annual peak of condition, whereas probability of survival of individual males was unrelated to size or condition. Probability of survival of individuals of either sex was not related to any index of condition or size at the seasonal low of condition in late-winter, lactation or pregnancy status, geographic location, or any measure of annual or seasonal precipitation. Mean annual survival rates of both males and females were negatively correlated to total precipitation during July to September (primary lactation period), but female survival was positively correlated to total precipitation from January to June (conception–parturition). Ratios of fawns to adult females during April 2005 to 2010 ranged from 31 to 57 fawns/100 adult females, and maximum potential rates of increase (λ) showed a significant positive rate of increase only in 2004 and 2005 (P [λ > 1.0] $\geq$ 0.937). Potential rates of increase of mule deer in the greater San Andres Mountains were limited by production and survival of fawns, rather than adult mortality.

Key words: body condition, human–wildlife conflicts, mule deer, New Mexico, survival

Desert mule deer (*Odocoileus hemionus crooki*) populations have declined throughout the Southwest, including the greater San Andres Mountain region (SAM) of southcentral New Mexico. Declines in mule deer in the SAM have been substantial; historically, the SAM supported annual hunts for both male and female mule deer, with an average of 676 deer harvested annually from 1955 to 1983 (Taylor and Burkett 1997). This level of historical harvest was greater than the most recent total population estimate of 500 to 600 deer (L. Bender, unpublished data).

Declines in the number of mule deer in the SAM since the 1980s may have been influenced by a variety of factors that affected either deer survival or productivity (Logan and Sweanor 2001, Hoenes 2008). Most variation in annual rate of increase in ungulate populations is related to production and survival of juveniles

(Gaillard et al. 2000). However, population rate of growth is most sensitive to adult female survival, and any change in female survival will result in a much greater effect on population growth than will a comparable change in any other demographic (Gaillard et al. 2000). Hence, an understanding of female survival is needed to identify the importance of factors potentially limiting population growth.

Because of the importance of adult female survival to population growth, we assessed survival and factors affecting survival of $\geq$1.5-year-old mule deer to determine whether survival was limiting deer population performance in the SAM. Our goal was to determine whether habitat conditions (as expressed through condition of deer), precipitation, or direct mortality factors, such as predation or disease, were resulting in poor survival of mule deer in the SAM. We also

wanted to contrast survival and environmental influences affecting survival between males and females to see whether any limitations detected were applicable to all deer in the SAM. Our specific objectives included (1) size and nutritional condition of mule deer, (2) annual survival rates, (3) cause-specific mortality rates, (4) influences of condition at the seasonal peak in autumn and seasonal low in late-winter on deer survival, (5) influences of annual and seasonal precipitation on deer survival, (6) recruitment of fawns in the SAM, and (7) population potential rates of increase.

Study area

The greater San Andres Mountains area (SAM) encompass ~11,000 km^2 (approximately 165 km north to south and 64 km east to west), including joint use and management areas of San Andres National Wildlife Refuge (SANWR), White Sands Missile Range (WSMR), the National Air and Space Administration's White Sands Test Facility, and the U.S. Department of Agriculture Jornada Experimental Range (Figure 1). The SAM and surrounding terrain include playas, rugged mountain peaks, canyons, rolling grasslands, sand dunes, lava flows, and scattered springs and ponds (Muldavin et al. 2000). Precipitation averages 200 to 350 mm annually, with the bulk of moisture occurring as short, intense rainstorms from July through September. Snowfall averages <100 mm, is short-lived, and occurs only at high elevations. Temperatures of the area range from –23° to 41° C. Three principal seasons occur in the study area: warm-wet (July to October); cool-dry (November to February); and warm-dry (March to June).

Major vegetation communities of the SAM include semidesert grassland, Chihuahuan desert scrub, and Great Basin conifer woodland (Muldavin et al. 2000). Vegetation is typical of the Chihuahuan desert shrublands and grasslands with characteristic plant species, including grama grasses (*Bouteloua* spp.), dropseeds (*Sporobolus* spp.), bristlegrass (*Setaria leucopila*), soaptree yucca (*Yucca elata*), banana yucca (*Yucca baccata*), Mormon tea (*Ephedra* spp.), creosotebush (*Larrea tridentata*), tarbush (*Flourensia cernua*), mesquite (*Prosopis glandulosa*), and 4-wing saltbush (*Atriplex canescens*). Pinyon (*Pinus edulis*)-juniper
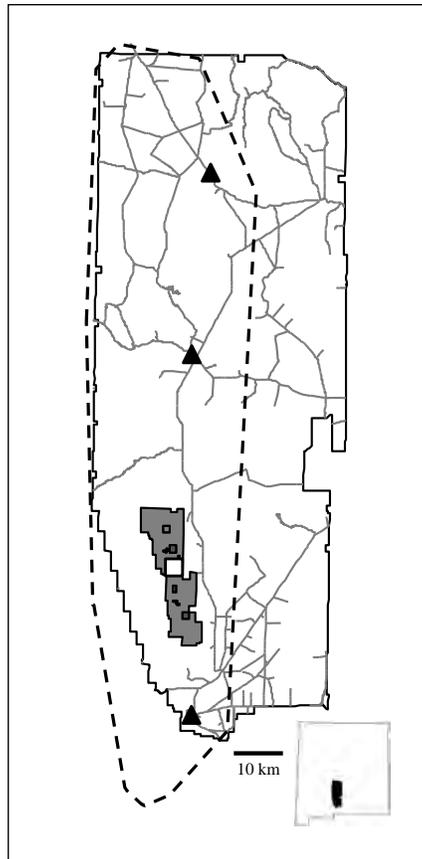

Figure 1. Location of the 6,100 km^2 San Andres Mountains mule deer study area (dashed line) in association with White Sands Missile Range (solid line) and San Andres National Wildlife Refuge (SANWR; dark inset), south-central New Mexico. Also shown are weather stations (▲; □ = average of 4 stations from SANWR) used to measure precipitation totals.

(*Juniperus* spp.) woodlands occur in the higher elevations in association with mountain mahogany (*Cercocarpus montanus*) and oak (*Quercus* spp.) shrublands.

Mule deer numbers in the study area, as estimated by aerial sight bias surveys, ranged from 0.30 to 0.97 deer/km^2 in the higher density portions of our study area (L. Bender, unpublished data), as compared to estimates extrapolated from modeling by Logan and Sweanor (2001) of ≤2.3 deer/km^2 during the 1990s. Other large herbivores present included oryx (*Oryx gazella gazella*; <0.10/km^2), desert bighorn (*Ovis canadensis mexicanus*; approximately 50 to 100 individuals annually, associated mainly with the 232 km^2 SANWR), and javelina (*Pecari tajacu*; numbers unknown but uncommon). Predators of mule deer included

cougars (*Puma concolor*), coyotes (*Canis latrans*), bobcat (*Felis rufus*), and golden eagles (*Aquila chrysaetos*). Some cougar control occurred on or adjacent to SANWR (approximately 3.8% of our 6,092-km^2 study area) during our study, with 1, 4, 3, 3, 0, and 1 cougars removed during 2004, 2005, 2006, 2007, 2008, and 2009, respectively. Population estimates for cougars were available only for SANWR, where minimum densities of resident adults were 0.9, 1.3, 1.7, 1.7, 1.7, and 2.2 cougars/100 km^2 for 2004, 2005, 2006, 2007, 2008, and 2009, respectively (L. Bender, unpublished data). These densities were similar to densities estimated by Logan and Sweanor (2001) for areas with (0.8 to 2.1 adults/km^2) or without (0.9 to 2.0 adults/km^2) some degree of cougar control during the 1980s and 1990s in the SAM.

Methods
Deer capture and locations

We captured deer by aerial darting or net-gunning from an OH-58 or Bell 206B Jet Ranger helicopter each December during 2003 to 2007, and April 2004 to 2008. Captured deer were distributed uniformly throughout the study area, although some areas had few collars because of extreme low densities of deer encountered. We immobilized deer using 1.5 to 1.8 mg carfentanil citrate and 50 to 75 mg xylazine hydrochloride per deer, blindfolded deer to minimize stress during handling, and injected them with penicillin G procaine, vitamin B, MUSE (vitamin E and selenium), and an 8-way *Clostridium* bacterin. We aged deer based on tooth wear and replacement or cementum annuli counts (Robinette et al. 1957, Hamlin et al. 2000). We fit deer with mortality-sensitive radio collars (Advanced Telemetry Solutions, Asanti, Minn.), marked deer with unique small and large numbered, color-coded ear tags, and recorded geographic location of capture using a handheld GPS. We also performed tonsilar biopsies (Wolfe et al. 2002) on >95% of deer handled to assess prevalence of chronic wasting disease. Upon completion of processing, we antagonized immobilants with naltrexone and tolazoline or atipamezole and released individuals after they recovered.

Nutritional condition and size

We collected multiple indices of nutritional condition and size of captured deer, including subcutaneous fat thickness at the rump (MAXFAT), approximate body fat (BF), depth of the longissimus dorsi (loin) muscle (LOIN), rump body condition scores (rBCS) and withers body condition scores (wBCS), girth, and body mass. We measured MAXFAT at its thickest point immediately posterior to the cranial process of the tuber ischium (pin bone) using a SonoVet 2000 portable ultrasound with a 5-mHz probe. We estimated BF of females only (only females were used in development of predictive equations; Stephenson et al. 2002) using BF = 5.68 + 5.93 × MAXFAT (cm; Stephenson et al. 2002). The above equation can predict body fat down to only 5.7% and only when MAXFAT is present (Stephenson et al. 2002); therefore, we used rBCS (Bender et al. 2007*a*) to predict body fat when MAXFAT was absent, where BF = 4.014 × rBCS – 2.021 (r^2 = 0.81; n = 39; L. Bender, unpublished data). These relationships were derived from desert mule deer captured in south-central New Mexico 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 inch intervals of 0.25, where 1 = emaciated and 5 = obese (Cook 2000, Bender et al. 2007*a*).

We measured LOIN at the thickest point between the twelfth and thirteenth ribs and determined wBCS (Cook 2000, 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. We also measured body mass to the nearest kg using a spring scale and heart girth (cm) immediately posterior to the shoulder hump 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).

We determined lactation status in late-autumn by presence or absence of milk in the udder at capture (Bender et al. 2002) and assessed pregnancy status from late-winter captures using serum progesterone (Weber et al. 1982) or pregnancy-specific placental protein B (BioTracking, Moscow, Ida., USA).

Survival and causes of mortality

We monitored radio-collared mule deer ≥ 1 times/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 (Beringer et al. 1996).

We performed a field necropsy on all mortalities or removed the carcass for a lab necropsy to determine cause of death, following Bender et al. (2004). We collected biological samples to help differentiate proximate from ultimate causes of mortality, including femurs, pharyngeals, mandible, fecal and rumen samples, and a sample of each major organ (i.e., heart, liver, lungs). We considered the proximate cause of mortality the ultimate cause unless femur marrow fat level was <12%. Femur marrow fat <12% is indicative of acute starvation (Ratcliffe 1980, Depperschmidt et al. 1987). Any deer mortalities exhibiting these levels were classified as experiencing malnutrition regardless of proximate cause of death. We calculated annual cause-specific mortality rates using the approach of Heisey and Fuller (1985).

We used logistic regression (Hosmer and Lemeshow 1989) to model survival of individual deer as a function of condition, size, reproductive status, and seasonal and annual precipitation (see below). We modeled effects of MAXFAT, BF, rBCS, wBCS, LOIN, mass, and girth on the probability of an individual deer surviving the subsequent 9 to 12 months following assessment of condition in early December or late March. This allowed us to assess the effects of individual condition at or near the annual peak of condition in late autumn (early December) and the seasonal low in late winter (late March to early April) on subsequent survival through the following year (January to December or April to December), i.e., effects of *a priori* condition on deer survival. Because of the known negative effect of lactation on condition (Verme and Ullrey 1984, Wakeling and Bender 2003, Hoenes 2008), we also modeled survival of individual females as a function of lactation and pregnancy status the previous autumn.

Lastly, we calculated a distribution variable (LAT × LONG in UTMs) to test for differences in geographic distribution of mule deer in the SAM on survival. We modeled each index separately because interpretation of multivariate models of differing condition indices is unintuitive due to uncertainty in differential rates of fat and lean tissue catabolism; all indices were related, even though each indexed a slightly different combination of fat and lean tissue reserves; and we were interested in the comparative effects of fat, protein reserves, and size only.

We also modeled the effects of precipitation on the probability of a deer surviving through the following year as above. We used precipitation data collected from 3 sites on WSMR and from 4 weather stations on SANWR. Because of their close proximity of these sites, we averaged the values from SANWR and used the resultant mean with the 3 WSMR values to calculate average precipitation across the study area (Figure 1).

To relate precipitation patterns to deer survival, we summed annual precipitation (e.g., total amount received from January throuth December of year$_t$) and cumulative precipitation during each of 4 seasons based on biological relevance to mule deer (Bender et al. 2007*a*, Hoenes 2008). These seasons included: (1) conception to parturition (January to June), when deer attempt to minimize overwinter condition loss and later require increased nutritional quality as the fetus and antlers begin 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 to 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 and increased requirements of males for antler growth (Wakeling and Bender 2003); and (4) post-lactation (October to December), when females need to recover energy reserves prior to winter and males experience the greatly increased energy demands associated with the rut. We modeled each season separately because of high correlations among seasonal and annual measures of precipitation, and we were interested in which specific season(s)

had the strongest relationships to survival. Lastly, we used Pearson's correlations (Zar 1996) to identify relationships between annual and seasonal precipitation and mean annual survival rates of mule deer.

Productivity and potential population dynamics

We determined sex and age composition of the mule deer population in the SAM from helicopter counts in April 2005 to 2010. Surveys covered >90% of the study area. We classified all observed deer as adult male, adult female, or fawn; we further differentiated adult males by number of antler points. We determined variances around ratios following Czaplewski et al. (1983). We did not conduct composition surveys in April 2009.

We estimated maximum potential finite rate of population increase (λ) using $\lambda = \hat{S}_F + \frac{1}{2} \times$ F/D, where $\hat{S}_F$ = estimated annual survival rate of adult females and F/D = fawn/adult female ratio in April (White and Bartmann 1998). We used parametric bootstrapping to calculate annual probabilities that $\lambda > 1$ following Bender and Hall (2004).

Results

Deer captures

We captured 445 deer that were $\geq$1.5 years old. Of these, 226 deer were unique individuals and 219 deer were recaptures, with 153 individual females and 73 individual males handled $\geq$1 time. We captured 34, 60, 34, 51, and 48 deer during December 2003, 2004, 2005, 2006, and 2007, respectively, and 32, 50, 45, 48, and 43 deer during April 2004, 2005, 2006, 2007, and 2008, respectively. We fit 169 individual deer (55 males and 114 females) with radio collars from December 2003 to April 2008, and monitored between 37 to 64 females and 14 to 31 males annually from 2004 to 2009.

Nutritional condition

Condition indices of both females and males were highly variable among years during late autumn (Table 1). For females, rBCS ($F_{4, 151} = 4.6$; $P < 0.01$), wBCS ($F_{4, 130} = 5.2$; $P < = 0.01$), MAXFAT ($F_{4, 151} = 2.2$; $P = 0.07$), BF ($F_{4, 151} = 4.0$; $P < 0.01$), LOIN ($F_{4, 127} = 4.6$; $P < 0.01$), and girth ($F_{4, 135} = 2.2$; $P = 0.07$) varied among years, whereas mass ($F_{1, 27} = 0.7$; $P = 0.40$) did not. Approximate BF of

lactating females ranged from 5.1% (SE = 0.2) to 6.7% (SE = 0.4) annually, while dry females ranged from 7.0% (SE = 1.1) to 11.1% (SE = 0.5) annually from 2003 to 2007. For males, rBCS ($F_{4, 60} = 3.8$; $P < 0.01$), wBCS ($F_{3, 52} = 2.6$; $P = 0.06$), MAXFAT ($F_{3, 53} = 2.7$; $P = 0.06$), and LOIN ($F_{3, 52} = 10.2$; $P < 0.01$) varied among years, whereas girth ($F_{4, 57} = 0.9$; $P = 0.47$) did not. Too few measures of mass were available to analyze for males.

Condition indices of females were variable among years in late-winter (Table 1). For females, rBCS ($F_{4, 71} = 7.6$; $P < 0.01$), wBCS ($F_{3, 52} = 5.5$; $P < 0.01$), MAXFAT ($F_{4, 70} = 2.1$; $P = 0.09$), BF ($F_{4, 71} = 7.9$; $P < 0.01$), LOIN ($F_{4, 69} = 2.3$; $P = 0.07$), and girth ($F_{4, 64} = 3.6$; $P = 0.01$) varied among years; insufficient estimates of mass were available for analysis. In contrast, for males only LOIN ($F_{4, 26} = 4.3$; $P < 0.01$) and wBCS ($F_{3, 32} = 9.9$; $P < 0.01$) varied among years (Table 1). MAXFAT ($F_{4, 29} = 0.8$; $P = 0.52$), rBCS ($F_{4, 27} = 1.6$; $P = 0.21$) and girth ($F_{4, 26} = 1.1$; $P = 0.36$) were similar among years, and insufficient estimates of mass were available for analysis of males.

Survival

Annual survival of females ranged from 0.740 (SE = 0.059) to 0.863 (SE = 0.052) and was similar ($Z \leq 1.56$, $P \geq 0.12$) among years (Table 2). Annual survival of males ranged from 0.744 (SE = 0.100) to 0.842 (SE = 0.080) (Table 3), and similarly did not vary among years ($Z \leq 1.18$; $P \geq 0.24$). Annual survival rates did not differ ($Z \leq 1.05$; $P \geq 0.29$) between sexes in any year.

Cause-specific mortality

We documented mortalities of 50 females and 22 males, and were able to definitively determine cause of death (or eliminate some potential causes such as predation) for 43 females and 20 males. Mule deer died from a variety of factors in the SAM (Tables 2 and 3), including predation (males = 9%; females = 26%; all cougar predation), malnutrition (males = 32%; females = 26%; of these, no male and 3 of 7 female mortalities were proximately attributable to cougar predation); accidents (males = 9%; females = 8%; includes deer–vehicle collisions, drowning, and wound trauma from rutting), disease (males = 5%; females = 12%; includes pneumonia, complications with parturition, and 2 cases of chronic wasting disease); unknown (males = 14%; females =

Table 1. Range of indices of condition and size for female and male mule deer during late-autumn (December) and late winter–early spring (early April) in the greater San Andres Mountains of south-central New Mexico, 2003–2008.

| | Female mule deer | | | | Male mule deer | | | |
| | December | | April | | December | | April | |
Index	Population	Individuals	Population	Individuals	Population	Individuals	Population	Individuals
rBCS	2.23–2.77	1.50–4.00	1.53–2.23	1.25–3.25	3.47–4.35	1.75–5.00	1.69–2.04	1.25–2.50
wBCS	2.63–3.88	2.00–4.75	3.43–4.05	2.00–4.50	4.13–4.43	3.50–5.00	2.83–4.00	1.75–4.50
MAXFAT	0.14–0.44	0.0–1.8	0.00–0.12	0.0–1.0	1.64–2.24	0.0–3.1	0.00–0.08	0.0–0.6
BF	5.1–11.1	2.1–18.8	4.7–7.1	3.0–11.6	–	–	–	–
LOIN	3.20–3.95	3.0–4.2	3.31–4.00	2.5–4.3	4.17–4.58	3.7–4.9	3.74–4.46	3.3–4.9
Girth	86.1–89.6	77–102	84.5–90.7	79–98	99.6–106.0	88–123	86.8–96.7	87–107
Mass	120–125	100–156	–	92–142	–	180–200+	–	121–170

Table 2. Annual survival and cause-specific mortality rates of female mule deer in the greater San Andres Mountains, 2004–2009.

| Year | Number of females | Cause of death | | | | | | Survival | SE |
		Malnutrition	Predation	Accident	Disease	Unknown	Unknown-not predation		
2004	43	0.044	0.024	0.0	0.025	0.026	0.025	0.863	0.052
2005	57	0.021	0.061	0.019	0.021	0.060	0.0	0.829	0.051
2006	64	0.061	0.085	0.039	0.059	0.045	0.0	0.740	0.059
2007	48	0.068	0.046	0.0	0.0	0.047	0.024	0.825	0.055
2008	48	0.070	0.069	0.0	0.022	0.047	0.0	0.804	0.058
2009	37	0.056	0.0	0.050	0.0	0.067	0.071	0.774	0.086

Table 3. Annual survival and cause-specific mortality rates of male mule deer in the greater San Andres Mountains, 2004–2009.

Year	Number of males	Cause of death							Survival	SE
		Malnutrition	Predation	Accident	Disease	Unknown	Unknown-not predation	Harvest		
2004	19	0.0	0.056	0.059	0.0	0.0	0.053	0.0	0.842	0.080
2005	25	0.045	0.045	0.0	0.0	0.0	0.0	0.0	0.911	0.059
2006	31	0.0	0.0	0.042	0.044	0.091	0.050	0.0	0.792	0.082
2007	25	0.044	0.0	0.0	0.0	0.0	0.089	0.053	0.824	0.081
2008	21	0.159	0.0	0.0	0.0	0.067	0.050	0.0	0.744	0.100
2009	14	0.0	0.0	0.0	0.0	0.0	0.083	0.0	0.917	0.151

22%; of these, 2 of 3 males and 7 of 11 females had insufficient evidence remaining to detect likely cause of death); unknown-not-predation (males = 27%; females = 6%); and harvest (males = 5%; females = 0%).

For females, only predation in 2006 (annual rate of mortality = 0.09), malnutrition in 2008 (annual mortality rate = 0.07), and unknown-not predation in 2009 (annual mortality rate = 0.07) showed annual cause-specific mortality rates of ≥0.07 in any single year (Table 2). The highest cause-specific mortality rate varied annually, and included malnutrition (2 of 5 years), predation (2 of 5 years), and unknown-not predation (1 of 5 years). For males, only malnutrition in 2008 (annual mortality rate = 0.16), unknown-not-predation in 2007 (annual mortality rate = 0.09) and 2009 (annual mortality rate = 0.08), and unknown in 2006 (annual mortality rate = 0.09) showed annual cause-specific mortality rates of >0.07 in any single year (Table 3). The highest annual cause-specific mortality rates for males similarly varied annually, and included unknown-not-predation (2 of 5 years), malnutrition (2 of 5 years), and accidents, predation, and unknown (each 1 of 5 years; predation and malnutrition each had the highest rate in 2005).

Condition and survival

The probability of individual female mule deer surviving from January to December was related to wBCS ($\chi^2 = 3.3$; $P = 0.07$; $\beta = 0.908$ [SE = 0.498]), LOIN ($\chi^2 = 3.8$; $P = 0.05$; $\beta = 1.83$ [SE = 0.94]), and mass ($\chi^2 = 2.8$; $P = 0.09$; $\beta = 0.063$ [SE = 0.037]) when measured during the peak of accrual in late-autumn. Probability of a deer surviving increased approximately $2.5 \times$ (95% CI = 1.0 to 6.6) for each 1-unit increase in wBCS, $6.2 \times$ (95% CI = 1.0 to 38.9) for each 1-cm increase in LOIN, and approximately $1.1 \times$ (95% CI = 1.0 to 1.2) for each 1-kg increase in mass. No other condition variables ($P \geq 0.27$) were related to female survival from January to December. Similarly, no indices of size or condition of female deer in late winter were related ($P \geq 0.14$) to survival through the following year (i.e., April to December). Neither lactation status ($P \geq 0.28$), pregnancy status ($P \geq 0.98$), nor geographic distribution ($P \geq 0.33$) was related to survival of individual adult females during either period.
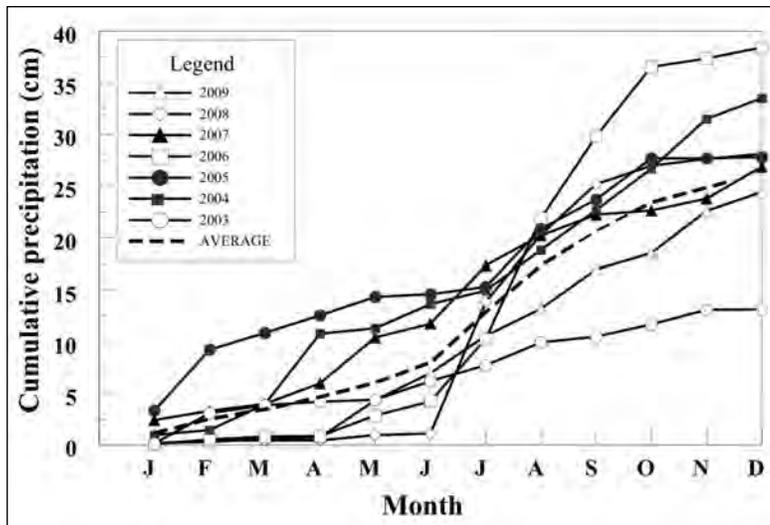
Figure 2. Cumulative precipitation the San Andres Mountains received beginning in January through each month, 2003–2009. Also shown is the 10-year mean (---).

Survival of males was not related to any index of condition or size, regardless of whether measured the previous late autumn ($P \geq 0.13$) or in late winter ($P \geq 0.21$). Survival of males also was not related to geographic location during either period ($P \geq 0.21$).

Precipitation

Total annual and seasonal precipitation was highly variable during our study (CV = 17.3 to 116.4; Table 4, Figure 2). No measures of annual or seasonal precipitation were related to the probability of survival of individual males ($P \geq 0.17$) or females ($P \geq 0.18$). Annual mean male survival rate was negatively correlated with July to September cumulative precipitation ($r = -0.801$; $P = 0.06$). Annual mean female survival rate was similarly negatively correlated with July to September precipitation ($r = -0.829$; $P = 0.04$), but was positively correlated with cumulative precipitation from January to June ($r = 0.771$; $P = 0.07$). No other seasonal or annual precipitation totals were correlated with mean survival rates for either sex ($P > 0.11$).

Productivity and potential population dynamics

Maximum estimates of the finite rate of population increase were 1.07, 1.11, 0.89, 1.07, and 0.94 for 2004, 2005, 2006, 2007, and 2009, respectively (Table 5). Estimates of λ exceeded 1.0 only in 2 of 5 years (2004 and 2005). We

could not estimate λ for 2008 because we lacked fawn/doe ratio data for that year (Table 5).

Discussion

We found that survival of females was related to condition, specifically, measures that mostly (wBCS) or solely (LOIN) indexed lean muscle tissue or size (mass). Similar patterns have been seen in mule deer in east-central New Mexico (Bender et al. 2011) and in nutritionally stressed elk (*Cervus elaphus*) in the Pacific Northwest (Bender et al. 2008), with the dependence on lean tissue attributed to nutritional limitations allowing little accrual of body fat (Bender et al. 2008). We found that females in the SAM were able to accrue only <7% BF (lactators) or ≤11% BF (dry females), well below levels (>23% BF; Oliver 1997) mule deer are capable of accruing. Additionally, ≥26% of female deaths were related to malnutrition in the SAM, further illustrating the poor condition of female deer. Thus, the dependence of females on lean muscle tissue for survival reflected the poor overall condition of females in the SAM (Torbit et al. 1985). Habitat conditions were exerting a strong limiting effect on population performance of mule deer in the SAM (Hanks 1981, Gaillard et al. 2000) and predisposing females to mortality, regardless of the proximate cause of death. In turn, poor condition of female mule deer in the SAM was a consequence of poor quality forage in their home ranges and seasonal drought (Hoenes 2008, Bender 2010).

Conversely, males were able to accrue substantially more subcutaneous body fat and other reserves than were females in each year (Table 1), and survival of individual males was not related to any measure of condition or size. The lack of a relationship between condition and survival indicates no predisposition to mortality among males in the SAM (i.e., survival was independent of condition given the range of condition we observed). Males and females

Table 4. Mean, SE, and coefficient of variation (CV) of annual and seasonal precipitation (cm) in the greater San Andres Mountain area, 2004–2009.

Season	Mean	SE	CV
January–March	3.43	1.63	116.4
April–June	5.28	1.34	62.4
January–June	8.70	2.23	62.8
July–September	14.72	3.21	53.5
October–December	6.37	1.25	48.2
Annual	29.84	2.10	17.3

showed different habitat-use patterns in the SAM (Hoenes 2008, Bender 2010), and males are able to benefit more nutritionally from poorer quality diets than females because they possess a larger rumeno-reticulum and have lower

causes of mortalities of mule deer. Females showed greatest mortality (48%) during the late-gestation through lactation period (Figure 3), a time of greatly increased nutritional stress when females need to both recover condition lost over winter and provide for the nutritional requirements of their rapidly growing fetus and, following parturition, fawn (Verme and Ullrey 1984, Wakeling and Bender 2003). Moreover, 25% of total female mortality in this period was due to malnutrition. In the SAM, this period begins prior to the onset of the summer monsoon, so the probability of early phenology forage is low (Kemp 1983, Hoenes 2008) as deer enter late-gestation and early-lactation. Bender et al. (2007a) and Bender et al. (2011), similarly, saw high mortality of adult females in north-central and east-central New

Table 5. Annual survival, fawns/100 adult females (F/D), number of deer counted during April, sex, age composition surveys, estimated finite population rate-of-increase (λ), and probability that the finite rate of population increase exceeds one (P > 1.0) and thus indicates an increasing population of mule deer in the greater San Andres Mountains, 2004–2009.

Year	S	SE	F/D	SE	Number counted	λ	P > 1.0
2004	0.84	0.05	43	4	143	1.07	0.937
2005	0.83	0.05	57	5	147	1.11	0.979
2006	0.74	0.06	31	4	142	0.89	0.034
2007	0.83	0.06	49	5	184	1.07	0.885
2008	0.80	0.06	–	–	–	–	–
2009	0.77	0.09	34	5	118	0.94	0.248

energetic requirements per unit of body mass (Short 1963, Hanley 1997). Thus, while females were predisposed to mortality by low condition, males were apparently able to use areas that allowed accrual of sufficient reserves to not affect their likelihood of dying. Furthermore, differences in habitat influences on survival of male and female mule deer in the SAM went beyond precipitation, as survival models for individuals of both sexes were unaffected by annual or seasonal precipitation (see below) despite a positive association between seasonal precipitation and deer condition (Hoenes 2008, Bender 2010). Similar to females, however, no single mortality factor strongly proximately impacted survival of males (Tables 2 and 3).

The ultimate influence of condition on survival was also reflected in the timing and

Mexico, respectively, when precipitation early in this period (late gestation–early lactation) was below normal, which they attributed to nutritionally-exhausted females being unable to meet the increased energy demands of late-gestation or lactation without early phenology forage stimulated by precipitation. Previously in the SAM, Logan and Sweanor (2001) also saw significantly reduced female survival (normal precipitation = ≥0.83; drought = ≤0.76) and male survival (normal precipitation = ≥0.81; drought = ≤0.62) associated with drought during the lactation period.

Conversely, males showed greatest mortality during the conception–late-gestation period (59%; Figure 3). This period immediately follows the rut, when energy reserves of males are at their lowest (Mautz 1978, Wakeling and

Bender 2003) and little early phenology forage is available in Chihuahuan desert habitats (Kemp 1983). Thus, timing of mortality of males in the SAM was primarily associated with their seasonal low in condition following the rut and winter, similar to patterns seen in most ungulate populations (excluding hunting harvest; Mautz 1978). Because adult sex ratios are high (>60 to 70/100; L. Bender, unpublished data) and population densities are low (<1 deer/km^2; L. Bender, unpublished data) in the SAM, competition during the rut is likely intense. This, combined with small amounts of green forage availability during mid- to late winter (Kemp 1983, Hoenes 2008), resulted in males dramatically declining in condition from late autumn to late winter (Table 1). Although males were in better condition than females in late-autumn, they emerged from winter in poorer condition than females (Table 1). Consequently, the proportion of deaths due to malnutrition tended to be higher in males than females (0.54 versus 0.33) in this period, as well as being higher than the proportion of malnutrition-related mortality in all other seasons (0.00) for males. This significant loss of condition to near-starvation levels from late-autumn to late-winter may have also contributed to the lack of any relationship between condition, size, and survival seen in males in the SAM.

Despite low condition, annual female survival (0.74 to 0.86) was comparable to estimates obtained from stable or increasing mule deer populations (0.78 to 0.86; White et al. 1987, Humphreys and Elenowitz 1988, Bartmann et al. 1992, Unsworth et al. 1999), including results from the 1980s and 1990s in the SAM (0.83 to 0.92; Logan and Sweanor 2001). Similarly, annual male survival (0.74 to 0.92) was similar to previous data from the SAM (0.81 to 0.90; Logan and Sweanor 2001) and higher than rates seen elsewhere (McCorquodale 1999, Patterson et al. 2002, Lawrence et al. 2004), although these studies dealt with harvested populations that experienced much higher hunting pressure. Demographics of large herbivores respond to resource limitations through a predictable process, and adult survival is the last parameter affected by declining condition (Gaillard et al. 2000). Females in the SAM were in slightly better condition (Table 1) than were other populations where adult female survival dropped precipitously, such as in north-central New Mexico (BF of dry females = 6.8%; survival = 0.63 [Bender et al. 2007*a*]) and east-central New Mexico (BF of lactating females = 5.0%; BF of dry females = 6.7%; survival = 0.42 [Bender et al. 2011]). Because each of these study areas experienced comparable drought conditions as the SAM during >50% of the study periods, the differences between impacts seen in north-central and east-central New Mexico and the SAM were likely a result of other extant habitat conditions, particul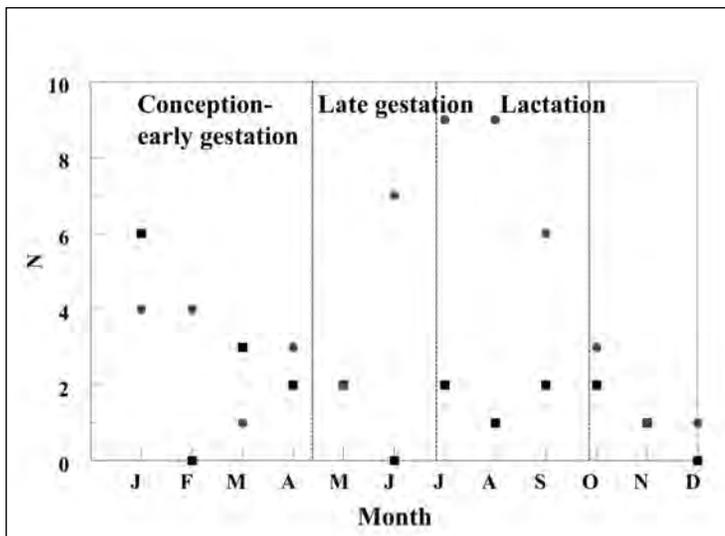arly forage quantity and composition (Hoenes 2008). Although much of it is in late seral stages, browse in the SAM is far more abundant than in the north-central and east-central New Mexico ranges noted above (Bender et al. 2007*b*, Hoenes 2008; L. Bender, unpublished data). This browse component may have buffered the effects of drought by keeping female condition above levels where significantly high levels of mortality (i.e., survival <0.63) were seen elsewhere (Bender et al. 2007*a*, Bender et al. 2011).

The importance of vegetation community composi-

Figure 3. Annual distribution of deaths of adult female (●) and male (■) mule deer in the greater San Andres Mountains area of south-central New Mexico, 2003–2009.

tion was further illustrated by the lack of relationships between probability of survival of individual mule deer and precipitation in the SAM, which contrasts with most previous work in arid Southwest environments (Logan and Sweanor 2001, Lawrence et al. 2004, Bender et al. 2007*a*). For example, Bender et al. (2007*a*) found that probability of survival of females in north-central New Mexico decreased 1.3 to 2.7 times for each 1 cm decrease in precipitation during the annual, winter, or mid- to late-gestation periods. Similarly, probability of female survival increased 1.3 to 1.5 times for each 2.54 cm increase in precipitation from January to June and April to June in east-central New Mexico (Bender et al. 2010). Forbs and other herbaceous vegetation are less tolerant of seasonal drought than are woody shrubs (Marshall et al. 2005, Hoenes 2008), and the dependence of mule deer on these more drought-vulnerable forages likely made these other populations more vulnerable to seasonal drought than were mule deer in the SAM.

However, in contrast to our results, Logan and Sweanor (2001) found significantly reduced survival of both female (≤0.76) and male (≤0.62) mule deer during drought years in the SAM, which they attributed ultimately to effects of drought on forage and water availability. Although seasonal precipitation was highly variable during our study (Figure 2), the SAM did not experience 3 successive years of severe drought during the same biological season (lactation) as during the study of Logan and Sweanor (2001). Precipitation likely has a much stronger influence on mule deer survival if it occurs in multiple successive years during biological seasons of high nutritional demand, such as late-gestation and lactation. Alternatively, densities of mule deer were much higher during the 1980s and early 1990s (>2 deer/km²; Logan and Sweanor 2001) than during our study (<1.0 deer/km²), which may have resulted in much stronger density-dependent effects from drought on per capita forage availability and consequently greater impacts on mule deer survival in the SAM.

Moreover, Logan and Sweanor (2001) documented cougar predation as the primary cause of mortality during drought (and non-drought) years, whereas we found condition-related mortality, including malnutrition,

to be the primary mortality factor affecting SAM deer during most years. Despite high proximate mortality due to predation during low-survival drought years (males, ≥0.28 versus ≤0.19; females, ≥0.23 versus ≤0.12; Logan and Sweanor 2001), Logan and Sweanor (2001) concluded that cougar predation was at least partially compensatory because of presumed low condition of deer due to drought. Our data support this conclusion; we found predation rates (males, ≤0.06 and 0.00 in 4 of 6 years; females, ≤0.09 and 0.00 in 1 of 6 years; Tables 2 and 3) consistently lower than those of Logan and Sweanor (2001) despite comparable cougar densities (see Study area) and much lower deer densities, which should have resulted in increased cougar predation rates if predation was independent of deer condition. Instead, we found mule deer survival was not strongly influenced by any direct mortality factor, such as predation, and that survival of females was strongly related to condition across widely varying annual and seasonal precipitation totals.

Despite the lack of a relationship between survival of individual mule deer and any measure of annual or seasonal precipitation in the SAM, precipitation did affect mean annual survival of adult females at the population level. Mean annual survival rate of females was positively correlated with cumulative precipitation from conception to parturition (January to June), similar to results seen in north-central New Mexico (Bender et al. 2007*a*) and east-central New Mexico (Bender et al. 2010). In arid environments, such as the Chihuahuan desert, the relationship between precipitation and population performance of deer is usually strong (Smith and Lecount 1979, Ginnett and Young 2000, McKinney 2003, Heffelfinger et al. 2006, Bender et al. 2007*a*, Hoenes 2008, Marshal et al. 2008). Deer depend on precipitation to initiate new growth of forage, which they need to meet the increased energetic requirements of late gestation, lactation, and antler growth. Throughout our study, the SAM experienced highly variable annual and seasonal precipitation, although years of well-above normal annual precipitation (2004, 2006) suggest that the poor condition seen in females was a result of extant forage conditions being unable to meet gestation

Figure 4. Mule deer in the San Andres Mountains.

and lactation requirements (Hoenes 2008) but adequate to sustain relatively stable annual rates of survival.

However, timing of precipitation, particularly as it relates to key life processes of mule deer (i.e., conception, late gestation, lactation), has a greater influence on survival (Bender et al. 2007*a*). In both north-central and east-central New Mexico, low survival was seen only during years when cumulative precipitation from conception to parturition (approximately January to June) was much below normal (Bender et al. 2007*a*, Bender et al. 2011). Similarly, in the SAM, annual female survival was ≥0.83 during years when cumulative precipitation from January to June was above normal, and ≤0.80 when precipitation during this period was below normal (Table 5, Figure 2). Moreover, the proportion of female deaths due to malnutrition (0.32 versus 0.22) tended to be higher in these drought years. Similarly, fawn recruitment was lowest in 2006 (31 fawns/100 adult females) and 2009 (34 fawns/100 adult females), years of below normal precipitation for the January to June period (Figure 2). Thus, drought conditions during January to June had some overall negative impact on adult survival in the SAM, as well as negative impact on fawn recruitment (Hoenes 2008), similar to patterns seen elsewhere in New Mexico (Lomas and Bender 2007, Bender et al. 2007*a*, Bender 2011). However, the impact of seasonal drought on survival of females did not approach the magnitude of impact seen elsewhere in New

Mexico (Bender et al. 2007*a*, Bender et al. 2010) likely because of a more abundant and diverse browse community in the SAM (Bender et al. 2007*b*, Hoenes 2008).

In contrast to the positive relationship with precipitation during conception to parturition, mean annual survival rates of females and males were negatively related to cumulative precipitation from July to September, the period of primary lactation, antler growth, and plant production in the SAM. Conversely, Logan and Sweanor (2001) found deer survival in the SAM to be positively correlated with precipitation during the June to September period in the 1980s and 1990s. During our study, the wettest July to September periods tended to follow the driest January to June periods (Figure 2), so this pattern was at least partially attributable to higher mortality resulting from the dry January to June. Mule deer were highly stressed leaving the January to June period, and even significantly greater than normal precipitation from July onward was unable to increase deer survival or productivity (Bender et al. 2007*a*, Hoenes 2008). It is also possible that the rapid change in plant phenology with the onset of abundant precipitation following drought in the January to June period may have resulted in too rapid a change in diet quality for stressed deer to adapt to (Wakeling and Bender 2003). Such rapid changes in diet quality can lead to enterotoxemia and other imbalances in the digestive system, increasing mortality (Rideout 2003, Wakeling and Bender 2003). Lastly, mule deer densities were much lower during our study than during the Logan and Sweanor (2001) study, and this may have lowered the relative importance of density-dependent effects of precipitation during the primary plant growing season (June to September) on forage quantity during our study as compared to Logan and Sweanor (2001).

Because survival of adult mule deer in the SAM was comparable to levels seen in stable or increasing populations of mule deer (White et al. 1987, Bartmann et al. 1992, Unsworth et al. 1999, Bender et al. 2007*a*), our data indicated that the deer population in the SAM was limited by production and survival of fawns (Table 5; Hoenes 2008). Fawn recruitment ratios seen in April 2005 to 2010 (Table 5) allowed a positive rate of population increase in only two of 5

years, despite adult survival being adequate for population growth (White et al. 1987, Bartmann et al. 1992, Unsworth et al. 1999, Gaillard et al. 2000). Environmental conditions were also only able to provide for low rates of increase in the SAM mule deer population (i.e., 2004 = 7% and 2005 = 11%), rates that were far below levels that mule deer populations are capable of attaining (Heffelfinger et al. 2003). Demographics from the SAM indicate that given average annual female survival (0.81) and assuming a 1:1 fawn sex ratio, the deer population needs to recruit ≥38 fawns/100 adult females to maintain population levels, similar to estimates derived by Logan and Sweanor (2001) for the SAM during the 1980s and 1990s (37 to 39 fawns/100 does needed for positive population growth). Even this relatively low level of production was seen in only three of 5 years in the SAM (Table 5), illustrating that the primary limitation on population growth was low fawn survival, not adult survival. In turn, Hoenes (2008) found that production and survival of fawns in the SAM was related to body condition of females, which in turn was related to vegetative attributes of female home ranges and seasonal precipitation (Hoenes 2008).

Management implications

Female mule deer in the SAM were predisposed to mortality by poor condition, a result of limited availability of high-quality forage, which was exacerbated by periodic drought during the conception to parturition period (Hoenes 2008). Previously, Logan and Sweanor (2001) similarly concluded that mule deer in the SAM were ultimately limited by forage and precipitation, rather than direct mortality factors, such as predation, although their inferences were limited because they did not assess *a priori* condition of deer and their postmortem indices were qualitative and potentially of limited validity (Cook et al. 2001). Availability and quality of forage plays a significant role in condition, ovulation, prenatal nutrition, gestation, and postpartum survival of fawns (Verme and Ullrey 1984, Lomas and Bender 2007, Hoenes 2008, Bishop et al. 2009). In the SAM, management practices including prescribed fire and mechanical thinning of tree and shrub canopies could increase the quality and quantity of browse and forbs

species that mule deer need to accrue higher levels of condition for increased survival and reproductive rates. Precipitation can also positively influence survival and productivity (Hoenes 2008), but weak relationships with individual survival indicate that increased precipitation alone cannot compensate for limited forage availability, particularly browse. Similarly, management actions aimed at mitigating any single mortality factor are unlikely to affect deer survival in the SAM because of low cause-specific mortality rates associated with any single mortality factor and the predisposition associated with poor condition. Because densities of other large herbivores are low in the SAM, competition is also likely having little effect on deer condition and, thus, survival (Hoenes and Bender 2010).

Managers also need to realize that condition of adult males and females can vary substantially in the same area. Many assessments of deer habitat quality are based on condition indices of harvested males, and these may poorly reflect condition of (and, thus, habitat quality for) females, as seen in the SAM. Such assessments can lead to mistaken impressions of habitat quality for mule deer and, thus, faulty population or habitat management strategies. Measures that increase condition of females are needed to increase population performance, and these habitat prescriptions need to focus on areas used by females to have positive responses.

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