Factors influencing survival and productivity of pronghorn in a semiarid grass-woodland in east-central New Mexico

Louis C. Bender, Department of Extension Animal Sciences and Natural Resources, New Mexico State University, Las Cruces, New Mexico 88001, USA

Jon C. Boren, Associate Dean and Director, Cooperative Extension Service, New Mexico State University, Las Cruces, New Mexico 88001, USA

Heather Halbritter, Extension Animal Sciences and Natural Resources, New Mexico State University, Las Cruces, New Mexico 88001, USA

Shad Cox, Corona Range and Livestock Research Center, New Mexico State University, Corona, New Mexico, USA

Abstract: Pronghorns (*Antilocapra americana*) are an important source of revenue and recreation for property managers throughout New Mexico, but have been declining in number. We documented body condition, survival, production of fawns, and trends in population size of pronghorns on the Corona Range and Livestock Research Center (CRLRC), a working research ranch and wildlife enterprise located in east-central New Mexico, from 2006 through 2011. Accrual of all indices of condition and size of both adult female and adult male pronghorns was positively associated with precipitation during June to July, August to September, and annually. Annual survival rates of females (0.33 to 0.78) and males (0.63 to 0.89) were highly variable on CRLRC. Survival of individuals was not related to any measure of condition or size taken the prior autumn. Survival of adult females was related to reproductive status the previous year; females that had successfully weaned >1 fawn the previous year were 0.11 times less likely to survive. Malnutrition was the most common cause of mortality (nine of 22 females; seven of 15 males), followed by suspected plant toxicities and enterotoxaemia (nine of 22 females) and harvest (six of 15 males). Most adult female mortality (73%) occurred after parturition and prior to weaning when energy demands are greatest on adult females; females that successfully weaned >1 fawn accrued significantly less condition by autumn. Survival of fawns was related to maternal condition, and fawn:adult female ratios were positively correlated with cumulative precipitation during late gestation and parturition. Low survival of adult females and fawns has resulted in the CRLRC pronghorn population declining from a minimum of 136 individuals to 66 from 2005 to 2011. Timing and causes of mortality highlight a strong nutritional limitation faced by lactating females related to the most energetic costs of reproduction being borne prior to the onset of summer monsoonal precipitation. The poor timing of reproduction to precipitation (and, thus, to forage phenology) in the southwestern United States will likely always limit productivity and survival of pronghorn relative to northern populations.

Key words: condition, habitat, human–wildlife conflicts, New Mexico, pronghorn

Pronghorn (*Antilocapra americana*) populations on the Corona Range and Livestock Research Center (CRLRC), a multiple-use research ranch and wildlife enterprise owned and operated by New Mexico State University, have declined from a minimum count of 136 pronghorn in 2004 to 66 by 2011. Similar declines are occurring in adjacent areas of southern New Mexico and west Texas (Brown et al. 2006, Simpson et al. 2007). Declines in pronghorn represent a loss of ecological diversity, recreational opportunity, and revenue for landowners and state agencies. Reasons for declines on CRLRC currently are unknown. However, pronghorn are sensitive to many environmental variables because they require

a high-quality diet due to their small rumeno-reticular volume (Hofmann 1985) and, thus, are sensitive to even small changes in plant communities or precipitation. Additionally, pronghorns have higher reproductive investment than other North American ungulates (Byers 1997), yet, have a reproductive season that is poorly timed to plant phenology patterns in the arid and semiarid environments of the Southwest.

Most previous studies have identified precipitation, winter severity, and coyote predation as key nonhuman variables affecting pronghorn populations (O'Gara 2004*a, b*; O'Gara and Shaw 2004; Brown et al. 2006; Simpson et al. 2007; Brown and Conover
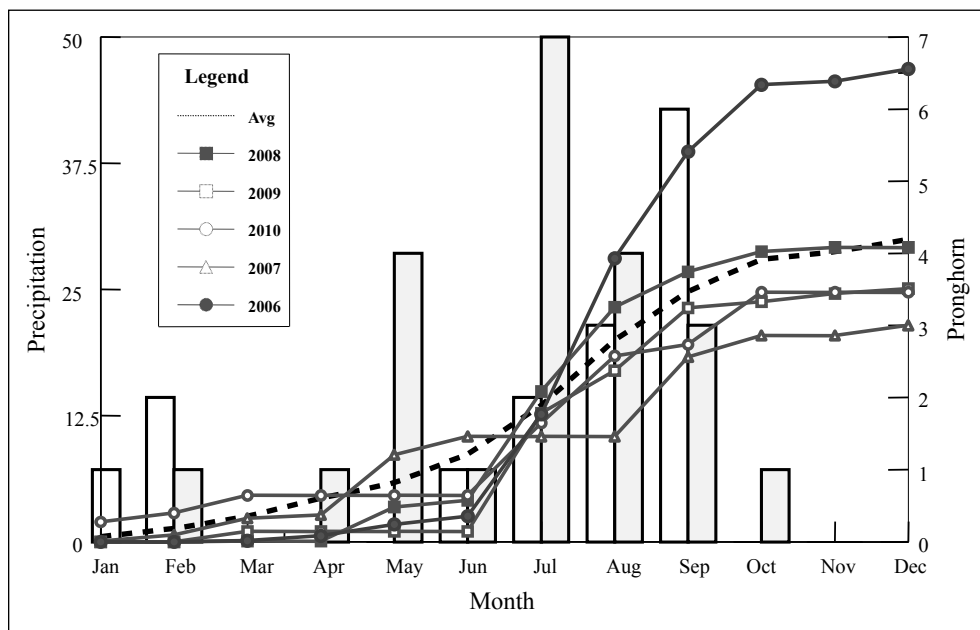
Figure 1. Mean and annual cumulatie precipitation (cm) on the Corona Range and Livestock Research Center, east-central, New Mexico. Also shown is the number of male (open bar) and female (shaded bar) mortalities of pronghorns observed for each month, 2006 to 2010, inclusive.

2011). In arid southwestern environments, precipitation in particular has been related to long-term trends in pronghorn population size and productivity (deVos and Miller 2005, Brown et al. 2006, Simpson et al. 2007, McKinney et al. 2008), likely through effects on plant production and nutritional quality (Brown et al. 2002; McKinney 2003; Yoakum 2004*a*; Marshall et al. 2005; McKinney et al. 2008). Thus, precipitation and other environmental factors affect pronghorn through resource acquisition, which is ultimately manifested in individual body condition. In turn, body condition can affect survival and reproduction of ungulates (Wakeling and Bender 2003; Bender et al. 2006; Bender et al. 2007*a*, 2011, 2012; Lomas and Bender 2007; Dunn and Byers 2008), including predisposing to proximate mortality factors, such as predation and disease (O'Gara and Shaw 2004; Brown et al. 2006; Bender et al. 2007*a*, 2011, 2012; Lomas and Bender 2007).

To our knowledge no studies of pronghorn dynamics have included direct assessments of underlying individual factors that influence survival or productivity, such as *a priori* body condition (*sensu* Bender et al. 2011). Adult female survival has the greatest effect on

population rate of increase (Gaillard et al. 2000), and precipitation and nutritional condition of individuals can affect survival of ungulates (Bender et al. 2007*a*, 2011, 2012; Brown et al. 2006) and population productivity (Lomas and Bender 2007; Simpson et al. 2007; McKinney et al. 2008; Bender et al. 2011, 2012) in the arid Southwest. Thus, knowledge of both of these demographics is prerequisite to understanding the importance of any proximate mortality factor thought to be limiting pronghorn populations. Hence, our goal was to determine factors affecting population trends of pronghorn on the CRLRC. Our specific objectives were to determine: survival rates and causes of mortality of adult female and male pronghorns; production and recruitment of fawns and population rates of increase; and the relationships among survival, productivity, condition, and precipitation for pronghorns on the CRLRC.

Study area

The CRLRC (34° 15′ 36″ N, 105° 24′ 36″ W) is an 11,290-ha working ranch laboratory owned and operated by New Mexico State University. Located approximately 22.5 km east of the

Figure 2. A pronhorn stands on the valley floor of the Corona Range and Livestock Research Center, New Mexico. (*Photo courtesy M. Weisenberger*)

village of Corona, New Mexico, the CRLRC has an average elevation of 1,900 m; mean annual precipitation across the facility is 40 cm, most of which occurs in July and August as high-intensity, short-duration convectional thunderstorms. Topography consisted of valley floors (0 to 5% slope), gently sloping uplands (2 to 15% slope), steep (30 to 75% slope) mesa sides, and rock outcrops (Figure 2). Vegetation is composed of perennial grassland with an overstory of sparse to dense pinyon pine (*Pinus edulis*) and 1-seed juniper (*Juniperus monosperma*) woodlands. Predominant grasses are blue grama (*Bouteloua gracilis*), wolftail (*Lycurus phleoides*), threeawns (*Aristida* spp.), sideoats grama (*Bouteloua curtipendula*), and sand dropseed (*Sporobolus cryptandrus*).

Methods

We captured and fitted 71 ≥1.5-year-old pronghorns (39 females, 32 males) with mortality-sensitive radio collars (Advanced Telemetry Systems, Isanti, Minn.) in early-December 2005 to 2007 and in early April 2006 to 2007. Pronghorns were captured by both aerial net-gunning or darting from a Bell JetRanger 206B helicopter using carfentanil citrate and xylazine hydrochloride as immobilants. Pronghorns were aged as yearling or adult by tooth wear and replacement (Dow and Wright 1962) and treated with antibiotics, vitamin E and selenium, vitamin B, and an 8-way *Clostridium* bacterin. Following processing, the immobilants were antagonized with naltrexone and tolazoline.

Condition

We measured subcutaneous fat thickness at the rump at its maximum thickness along a line between the spine at its closest point to the *tuber coxae* (hip bone) and the *tuber ischii* (pin bone) using a SonoVet 2000 portable ultrasound with a 5-mHz probe. We also used a rump body condition score (rBCS; Bender et al. 2007*a*) and estimated rBCS by palpating the ischial ligamentand soft tissue 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).

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. We scored wBCS in the same intervals as rBCS (Cook 2000). Last, we measured heart girth (cm) to index overall size. We compared condition indices among years using MANOVA (Morrison 1990), specifically testing the year × lactation interaction for adult females because of the known negative impacts of lactation on condition and using only year for males. We tested the effect of seasonal and annual precipitation (see below) on accrual of

condition using a MANOVA for each season individually because of limited sample size.

Survival and causes of mortality

We monitored radio-collared pronghorns 1 to 2 times per week and determined survival rates for the June to May biological year 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 deaths (Berringer et al. 1996).

We determined causes of death following the methods of Bender et al. (2011). 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, Depperschmidt et al. 1987); thus, pronghorn below this threshold were classed as malnutrition mortalities regardless of proximate cause of death.

Because we were interested in survival through a specific period rather than time-to-death (Hosmer et al. 2008), we used logistic regression (Hosmer and Lemeshow 1989) to model survival of individual pronghorn as a function of condition and seasonal precipitation (see below). We modeled effects of lactation

Table 1. Mean indices of condition and size for adult female and male pronghorn in late-autumn 2005 to 2007, on the Corona Range and Livestock Research Center, New Mexico.

Index[a]	Females			Males		
	2005	2006	2007	2005	2006	2007
rBCS	2.9 ± 0.2 A	3.3 ± 0.2B	2.4 ± 0.1C	3.2 ± 0.2	3.2 ± 0.1	2.7 ± 0.2
wBCS	3.8 ± 0.1 A	4.2 ± 0.1 B	4.0 ± 0.1 A	3.9 ± 0.1 A	4.1 ± 0.1 B	3.8 ± 0.1 A
Fat	0.9 ± 0.2 A	1.1 ± 0.1 A	0.3 ± 0.1 B	1.1 ± 0.2	0.8 ± 0.2	0.5 ± 0.2
Loin	3.4 ± 0.2 A	3.7 ± 0.1 B	3.7 ± 0.1 B	3.8 ± 0.1 A	3.8 ± 0.1 A	4.0 ± 0.1 B
Girth	91.9 ± 0.9A	92.8 ± 0.7 A	88.6 ± 0.8 B	91.9 ± 1.1	95.2 ± 0.8	92.4 ± 1.0
N	22	12	16	9	20	12

[a]rBCS = rump body condition score; wBCS = withers body condition score; Fat = maximum subcutaneous rump fat thickness (cm); Loin = depth of the longissimus dorsi muscle (cm); and Girth = heart girth (cm).

Table 2. Odds ratios of costs of lactation on accrual of condition and size indices (Lactation; females only) and correlations between indices of condition and seasonal and annual precipitation for pronghorn. Significant (*P* < 0.10) relationships in boldface.

Sex	Index	Precipitation season					
		Lactation	Conception-parturition	Gestation	Lactation	Post-lactation	Annual
Female	rBCS	**0.26**	**-0.28**	**-0.26**	**0.45**	**0.49**	**0.47**
	wBCS	0.28	**-0.36**	**-0.27**	**0.51**	**0.35**	**0.31**
	Fat	**0.19**	-0.15	-0.20	**0.39**	**0.49**	**0.49**
	Loin	0.78	**-0.24**	-0.20	0.15	0.14	0.09
	Girth	0.87	-0.18	**-0.33**	**0.39**	**0.58**	**0.54**
Male	rBCS	–	-0.06	-0.25	0.16	**0.28**	0.26
	wBCS	–	**-0.38**	**-0.52**	**0.51**	**0.50**	**0.48**
	Fat	–	0.07	-0.18	0.08	0.22	0.21
	Loin	–	-0.16	0.11	0.13	0.13	0.21
	Girth	–	**-0.34**	**-0.37**	**0.40**	**0.35**	**0.34**

Table 3. June to May survival of adult female and male pronghorns, female fawns per adult female in early spring (April to May), annual finite rate of population increase (λ), and probability that $\lambda > 1$ for pronghorns on the Corona Range and Livestock Research Center, 2006–2007 to 2010–2011. Also shown are minimum population counts, 2004–2005 through 2010–2011.

Year	Female survival		Male survival		$\frac{1}{2} \times$ Fawns/female		λ		N
	Mean	SE	Mean	SE	Mean	SE	Mean	$P (\lambda > 1)$	
2004	–	–	–	–	–	–	–	–	136
2005	–	–	–	–	–	–	–	–	126
2006	0.33	0.06	0.63	0.09	0.07	0.01	0.40	0.00	–
2007	0.70	0.09	0.84	0.08	0.16	0.02	0.86	0.05	83
2008	0.75	0.10	0.83	0.09	0.11	0.01	0.87	0.07	–
2009	0.75	0.13	0.66	0.13	0.06	0.01	0.81	0.07	63
2010	0.78	0.14	0.89	0.11	0.09	0.01	0.98	0.16	66

Table. 4. Causes of death of pronghorn on the Corona Range and Livestock Research Center, east-central New Mexico, 2006 to 2011.

Cause	Females	Males
Malnutrition	9	7
Enterotoxaemia	5	0
Other digestive system imbalances	4	0
Predation	1	0
Harvest	0	6
Unknown, not predation	2	0
Unknown	1	2
Total	22	15

status, fat, rBCS, wBCS, loin, and girth on the probability of an individual pronghorn 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 (i.e., early December) on subsequent survival through the following year (January to December). That is, we monitored the effects of *a priori* condition on pronghorn survival.

We also modeled the effects of precipitation on the probability of a pronghorns 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 (i.e., total amount received from January through December) and cumulative precipitation

during each of 4 seasons based on biological relevance to pronghorns on CRLRC (*sensu* Bender et al. 2011). These seasons included: (1) conception to early gestation (winter; October to March), when pronghorns attempt to minimize overwinter condition loss and later require increased nutritional quality as fetuses begin to develop; (2) late gestation to parturition (March to May), when nutritional requirements increase because of the rapidly developing fetuses; (3) primary lactation (June to July), the period of greatest nutritional demand on females; and (4) post-lactation (August to September), when females need to recover energy reserves prior to winter and the rut, and males enter the rut. We used totals from the nearest station for each individual pronghorn's home range in analyses of precipitation effects.

Productivity and population rate of increase

We determined lactation status of each captured female by presence or absence of milk or clear fluid in the udder or successful weaning of ≥ 1 fawn by radio-collared females (Bender et al. 2002). To assess the cost of lactation on accrual of condition, we used logistic regression (Hosmer and Lemeshow 1989) to model the probability of a female lactating in autumn on condition and size indices of the female that autumn (Piasecke and Bender 2011). To

assess factors affecting fawn survival through weaning, we used logistic regression (Hosmer and Lemeshow 1989) to model the probability of a female lactating or radio-collared females with fawn(s)-at-heel as a function of annual and seasonal precipitation during that year and condition and size indices of the female the previous autumn. Precipitation was defined as described above for survival modeling.

We determined fawn:adult female ratios by helicopter counts in April 2005 to 2008 and by ground surveys and surviving fawns-at-heel (Bender et al. 2011), May 2009 to 2011. For aerial surveys, we surveyed the entire study area throughout the day and recorded sizes and composition of all pronghorn social groups; we categorized pronghorns as fawn (≤1 year old), adult (≥1.5 years old) female, or adult male. We determined SEs for fawn:adult female ratios following Czaplewski et al. (1983). We determined the maximum potential finite rate of population increase (λ) using $\lambda = S_D + \frac{1}{2} \times$ fawn:adult female, where S_D = annual survival rate of adult females (White and Bartmann 1998). We calculated the probability that $\lambda > 1.00$ using parametric bootstrapping (Bender et al. 1996).

Results

We captured and recaptured and assessed for condition 71 individual adult pronghorns (39 females and 32 males) from December 2005 to 2007. We had 30, 27, 19, 14, and 12 radio-collared females, and 26, 22, 19, 16, and 11 radio-collared males for survival analysis annually from 2006 to 2010.

Condition

Indices of condition and size varied annually for female ($F_{5,42}$ = 6.06, P = 0.0003) and male ($F_{5,33}$ = 5.58, P = 0.0008) pronghorns (Table 1). Female pronghorn showed significant annual variation ($F_{2,45} \geq 3.08$, $P \leq 0.06$) in all indices of condition and size, whereas males showed annual variation in indices of lean (muscle) reserves (wBCS, loin; $F_{2,36} \geq 2.94$; $P \leq 0.07$) but less variation in indices that mostly indexed readily mobilized fat reserves or size (rBCS and fat: $F_{2,36} \leq 2.06$; $P \geq 0.14$) (Table 1). Condition of both females ($F_{5,42} \geq 4.90$; $P \leq 0.001$) and males ($F_{5,33} \geq 3.37$; $P \leq 0.01$) was related to precipitation on CRLRC (Table 2). For males, the most consistent

and strongest relationships were seen with wBCS and girth, which emphasize lean muscle tissue and size (Table 2). Females showed these same relationships, but precipitation was also related to indices of more immediately mobilized reserves (fat, rBCS), as well (Table 2). For both sexes, these indices were positively correlated with increasing precipitation during the lactation (June to July) and post-weaning (August–September) periods, as well as total annual precipitation.

Accrual of rBCS (χ^2 = 4.62; P = 0.03) and fat (χ^2 = 5.71; P = 0.02) of females was negatively related to successfully raising a fawn through autumn (Table 2), whereas loin thickness, girth, and wBCS were not ($\chi^2 \leq 1.28$; $P \geq 0.26$). Lactating females were able to accrue only approximately 20% of the indices that measure more readily mobilized reserves (fat, rBCS) as were dry females.

Survival

Annual survival of adult females ranged from 0.33 to 0.78 and varied among years; survival in 2006 was lower (Z $\geq$ 2.92; $P \leq 0.002$) than all other years, which were similar (Z $\leq$ 0.50; $P \geq 0.31$). Survival of adult males (0.63 to 0.89) was lower in 2006 (Z $\geq$ 1.57; $P \leq 0.06$) than all other years except 2009 (Z = 0.19; P = 0.43). All other years were similar (Z $\leq$ 1.18; $P \geq 0.12$; Table 3). Survival of adults was not related to any measure of condition or size (females: $\chi^2 \leq 1.99$; $P \geq 0.16$; males $\chi^2 \leq 1.85$; $P \geq 0.17$). Survival of adult females was negatively related to reproductive status the previous year (χ^2 = 4.83; P = 0.03). Odds ratios indicated that females that had successfully raised a fawn the previous year were 0.11 (95% CI = 0.014–0.79) times less likely to survive. Survival of individuals was not related to either seasonal or annual precipitation (females: $\chi^2 \leq 2.44$; $P \geq 0.12$); males: $\chi^2 \leq 1.78$; $P \geq 0.18$). Annual survival rate of adult females was not correlated with seasonal or total precipitation ($P \geq 0.14$), while annual survival rate of adult males was positively correlated with winter (October to March) precipitation (r = 0.90; P = 0.04; all others: $P \geq 0.19$).

Mortality

The most common causes of mortality of pronghorns on the CRLRC were malnutrition (9

of 22 females and 7 of 15 males), enterotoxaemia, and other digestive imbalances (including possibly locoweed [*Astragalus* spp.]-associated nitrate poisoning, ketosis, and rumen acidosis; 9 of 22 females), and harvest (6 of 15 males; Table 4). Most adult female (16 of 22 mortalities = 73%; Fischer's exact $P = 0.01$) mortality occurred after parturition and prior to weaning; 9% (2 of 22) occurred prior to parturition and 18% (4 of 22) after weaning (Figure 1). Pattern of nonharvest mortality of males differed (Fisher's exact $P = 0.06$); 44% (4 of 9) occurred prior to parturition and 56% (5 of 9) after parturition and prior to weaning (Figure 1).

Productivity and population rate of increase

Survival of fawns was related to maternal fat ($\chi^2 = 2.83$; $P = 0.09$) and wBCS ($\chi^2 = 2.71$; $P = 0.10$) the autumn prior to birth; no other indices of size or condition were significant ($\chi^2 \geq 0.72$; $P \geq 0.39$). Similarly, the number of fawns weaned was related to maternal wBCS ($F_{1,42} = 3.69$; $P = 0.06$) and fat ($F_{1,42} = 2.78$; $P = 0.10$) during the autumn prior to birth, but no other indices of size or condition ($F_{1,42} \leq 2.10$; $P \geq 0.15$). Survival of fawns was not related to reproductive success of the dam the previous year ($\chi^2 = 0.02$; $P = 0.88$) or to seasonal or total precipitation ($\chi^2 \leq 0.19$; $P \geq 0.66$), but fawn:adult female ratios were correlated positively with precipitation from late gestation–parturition ($r = 0.97$; $P = 0.006$; all others: $P \geq 0.17$).

Finite rate of increase ranged from 0.40 to 0.98 and indicated a >90% probability of declining in 4 of 5 years (Table 3). Low rate of increase was driven by both low adult female survival and low fawn:adult female ratios (range = 0.12 to 0.32; Table 3). The demographic-based rates paralleled minimum counts that showed pronghorn population declining from a minimum of 136 individuals to 66 from 2005 to 2011 (Table 3).

Discussion

Low survival of females and low productivity resulted in the CRLRC pronghorn population declining from a minimum of 136 to 66 from 2005 to 2011. Observed fawn:adult female ratios were <32/100, which is significantly below the productive potential of pronghorn populations. The maximum potential rate of increase can theoretically approach 200% annually because female pronghorns characteristically produce twin fawns (Byers 1997, O'Gara 2004*b*). However, fawn mortality can be high (O'Gara 2004*a, b*; O'Gara and Shaw 2004; Jacques et al. 2007), particularly when populations are resource stressed due to strong density-dependence, low precipitation, or other environmental influences (O'Gara and Shaw 2004, Byers 2006, Brown et al. 2002, McKinney et al. 2008, Dunn and Byers 2008). On the CRLRC, fawn survival was positively associated with condition of adult females; successfully weaning a fawn(s) decreased probability of survival of females the following year; and female condition was positively associated with precipitation during and after lactation. All of these relationships relate to the degree of resource stress (i.e., quantity and quality of available forage) experienced by dams and fawns during late gestation and lactation (O'Gara 2004*b*). Moreover, these relationships also are affected by the timing of the reproductive cycle of pronghorns with respect to precipitation patterns seen in the arid environments of southern New Mexico. Pronghorns on the CRLRC fawn in mid- to late May, approximately 1 to 2 months prior to the onset of the summer monsoonal precipitation. This results in pronghorn females facing the most energetically challenging phases of reproduction (late gestation and lactation) with little probability of early phenology forage being available (Hoenes and Bender 2012). Although this situation affects most ungulates in the Southwest to some degree (Hoenes 2008, Bender et al. 2011, 2012), the extreme parental investment seen in pronghorns (i.e., fetuses and neonates comprise a greater proportion of adult body mass than any other North American ungulate; Byers 1997) likely exacerbates this nutritional stress. Consequently, accrual of condition suffers, which, in turn, decreases fawn survival. Further, adult survival may decrease, as well (deVos and Miller 2005, Brown et al. 2006, Dunn and Byers 2008), particularly during years characterized by low precipitation during late gestation and lactation. Such years also are likely to see extremely high mortality of fawns, because production and survival of juveniles are impacted by resource stress prior to survival of adults (Gaillard et al.

2000). Thus, the poor timing of reproduction of pronghorns to plant phenology suggests that pronghorn populations in the Southwest may seldom be as productive as populations in more northern habitats (McKinney et al. 2008). This is particularly relevant, given that low precipitation during late gestation and lactation is relatively common in the arid Southwest; for example, precipitation during gestation was below the long-term average in 4 of 5 years of our study (range = 0.23 to 0.76 of average) and precipitation during lactation was below average in 2 of 5 years (range = 0.24 to 0.93 of average; Figure 1).

Timing of mortality of adult females further illustrates this quandary. Most (73%) pronghorn mortality occurred during lactation and was related to malnutrition (50%) or enterotoxcemia and other digestive imbalances (31%), highlighting the nutritional stress associated with lactation in ungulates in general (Piasecke and Bender 2011) and pronghorns in particular (O'Gara 2004*b*). Because parturition occurs approximately 1 to 2 months prior to the onset of the summer monsoon on the CRLRC, this nutritional cost is elevated by the absence of early phenology forage during late gestation and lactation, resulting in seasonally high mortality rates of female pronghorns if spring and summer precipitation is below normal (Brown et al. 2006) as also seen with mule deer on the CRLRC (Bender et al. 2011). This nutritional cost may have been magnified if females successfully weaned a fawn(s) the previous year because they may have entered late gestation and lactation in poor condition (Dunn and Byers 2008). High reproductive investment in the face of uncertain precipitation patterns contributes to the increased vulnerability of female pronghorns following successful recruitment of a fawn(s) on CRLRC (Dunn and Byers 2008).

Precipitation during late gestation and early lactation may mitigate some survival and reproductive costs. The positive correlation between fawn:adult female ratios and precipitation during late gestation probably reflected the benefit to condition that females receive from precipitation during this time. The positive relationships between readily mobilized reserves (i.e., fat) and precipitation in females, but not survival and precipitation,

suggest that precipitation during late gestation and early lactation (prior to the onset of the summer monsoons) can decrease condition loss associated with reproduction to a limited degree, although not enough to consistently enhance female survival. Overall, pronghorns exist on a tenuous nutritional basis in arid southwestern ranges (deVos and Miller 2005), and this was exacerbated by the poor timing between reproduction and precipitation. Consequently, survival and productivity of pronghorns in these habitats will likely always be well below the species potential (McKinney et al. 2008). Management practices that provide early phenology forage in late spring, such as late winter burns (Bender 2011), targeted cattle grazing of grasslands during early spring (Pollack 2007), and establishment or enhancement of shrublands or forage plots (Wilson et al. 2010), may enhance pronghorn habitat by providing access to higher quality forage at the onset of nutritional needs for reproduction in mid- to late March.

A wet summer following a dry spring can result is an abrupt change in diet quality for herbivores; such changes can result in digestive toxicities, such as enterotoxaemia (Rideout 2003), that result from a rapid proliferation of pathogenic bacteria in the digestive tract, particularly in individuals that are immunocompromised due to inadequate nutrition (O'Gara and Shaw 2004, National Research Council 2007). The high mortality rate associated with enterotoxaemia in females seen on the CRLRC during summer months was indicative of this. Less clear, however, was the increased vulnerability to other digestive imbalances or plant toxicoses seen in females but not males. Because lactating females have an increased drive to forage (Piasecke and Bender 2011), they may be more likely to feed on species, such as locoweed, which may be the most abundant green forb available during spring and early summer of low-precipitation years. Undernutrition during late pregnancy and lactation also can result in digestive imbalances such as ketosis in livestock, and abrupt transition from high fiber to highly digestible carbohydrate diets can result in rumen acidosis (National Research Council 2007).

In contrast, survival of males was higher

than females on the CRLRC (although this was significant in only 2006; Table 3), and the annual pattern of male mortality differed from females. Males do not face the same energetic challenges that females do in late spring to early summer, and, thus, males were not as adversely affected by the timing of precipitation. Although malnutrition mortality was still high during summers (4 of 7 nonharvest deaths), males also died of malnutrition during mid- and late winter in the CRLRC (3 of 7 nonharvest pronghorn deaths), with the latter likely influenced by rutting expenditures in autumn. Harvest was the other primary cause of male mortality on CRLRC (6 of 15 total deaths), similar to other hunted populations (O'Gara 2004, Kolar et al. 2012).

Previous work hypothesized that reproduction had no cost to pronghorns, unless accompanied by extreme climatic events (Byers 1997, 2006; Dunn and Byers 2008). Our data show that reproduction has a cost to pronghorns; lactation to weaning decreased a female's likelihood of survival the subsequent year; and accrual of body condition by autumn for lactating pronghorns was less, which decreased the likelihood of survival of her subsequent litter. Compared to previous work, our results were likely influenced by the timing of reproduction in pronghorns in the arid Southwest with respect to precipitation patterns discussed above. Long-term positive correlations between size of southwestern pronghorn populations and fawn:adult female ratios with precipitation (Brown et al. 2006, Simpson et al. 2007, McKinney et al. 2008) illustrate the importance of precipitation-induced forage (and possibly cover) for fawn recruitment. The positive effect of precipitation during lactation on condition of females seen on the CRLRC similarly highlights this relationship. While reproduction may not have strong costs to females in more mesic, productive habitats, in arid southwestern habits the costs include decreased condition of lactating females, lowered likelihood of successfully weaning their subsequent litter, and decreased survival.

Management implications

Sufficient seasonal precipitation appears to be the driver of pronghorn survival and productivity on the CLRC and in the Southwest. On the CRLRC and similar shortgrass prairie-Chihuahuan desert habitats, seasonal drought may be compensated for by management practices that provide early phenology forage in late spring and early summer, coincident with the reproductive process of pronghorns. Early phenology forage during this time may decrease severe undernutrition during late gestation and lactation, as well as lessen the severity of dietary changes associated with the onset of the summer monsoon. Forage enhancements that could contribute more favorable forage during this period include late winter burns (Bender 2011), targeted cattle grazing of grasslands during early spring (Pollack 2007), and establishment or enhancement of shrublands or forage plots (Wilson et al. 2010). For wildlife enterprises, supplemental feeding may accomplish the same effect with an appropriate suitable ration (Yoakum 2004). Short of extensive feeding, however, we are unsure of the magnitude of benefit pronghorns may receive from these activities. Thus, activities short of extensive feeding may not enhance nutrition sufficiently to compensate for dry spring and early summer conditions, and, thus, have little overall effect on pronghorn productivity (or survival) during drought years. Management actions, such as those listed above, may increase productivity during average or above average precipitation years, however, accelerating recovery of populations lowered by frequent drought.

Acknowledgments

Literature cited

Bender, L. C. 2011. Burning for big game. Circular 657. Cooperative Extension Service, New Mexico State University, Las Cruces, New Mexico, USA.

Bender, L. C., J. Boren, H. Halbritter, and S. Cox. 2011. Condition, survival, and productivity of mule deer in semiarid grassland-woodland in east-central New Mexico. Human–Wildlife Interactions 5:276–286.

Bender, L. C., E. Carlson, S. M. Schmitt, and J. B. Haufler. 2002. Production and survival of elk (*Cervus elaphus*) calves in Michigan. American Midland Naturalist 148:163–171.

Bender, L. C., B. D. Hoenes, and C. L. Rodden. 2012. Factors influencing survival of desert mule deer in the greater San Andres Mountains, New Mexico. Human–Wildlife Interactions 6:245–260.

Bender, L. C., L. A. Lomas, and J. Browning. 2007*a*. Condition, survival, and cause-specific mortality of mule deer in north-central New Mexico. Journal of Wildlife Management 71:1118–1124.

Bender, L. C., L. A. Lomas, and T. Kamienski. 2007*b*. Habitat effects on condition of doe mule deer in north-central New Mexico. Rangeland Ecology and Management 60:277–284.

Bender, L. C., G. J. Roloff, and J. B. Haufler. 1996. Evaluating confidence intervals for habitat suitability models. Wildlife Society Bulletin 24:347–352.

Berringer, J., L. P. Hansen, W. Wildling, J. Fischer, and S. L. Sheriff. 1996. Factors affecting capture myopathy in white-tailed deer. Journal of Wildlife Management 60:373–380.

Brown, D. E., and M. R. Conover. 2011. Effects of large-scale removal of coyotes and pronghorn and mule deer productivity and abundance. Journal of Wildlife Management 75:876–882.

Brown, D. E., W. F. Fagan, R. Lee, H. G. Shaw, and R. B. Turner. 2002. Winter precipitation and pronghorn survival in the Southwest. Proceedings of the Biennial Pronghorn Workshop 20:115–122.

Brown, D. E., D. Warnecke, and T. McKinney. 2006. Effects of midsummer drought on mortality of doe pronghorn (*Antilocapra americana*). Southwestern Naturalist 51:220–225.

Byers, J. A. 1997. American pronghorn: social adaptations and ghosts of predators past. University of Chicago Press, Chicago, Illinois, USA.

Byers, J. A. 2006. Are pronghorn vital rates affected by habitat quality? Proceedings of the Biennial Pronghorn Workshop 22:27–39.

Cook, R. C. 2000. Studies of body condition and reproductive physiology in Rocky Mountain elk. Thesis, University of Idaho, Moscow, Idaho, USA.

Czaplewski, R. L., D. M. Crowe, and L. L. McDonald. 1983. Sample sizes and confidence intervals for wildlife population ratios. Wildlife Society Bulletin 11:121–128.

Depperschmidt, J. D., S. C. Torbit, A. W. Alldredge, and R. D. Deblinger. 1987. Body condition indices for starved pronghorns. Journal of Wildlife Management 51:675–678.

deVos, J. C., Jr., and W. H. Miller. 2005. Habitat use and survival of Sonoran pronghorn in years with above-average rainfall. Wildlife Society Bulletin 33:35–42.

Dow, S. A., Jr., and P. L. Wright. 1962. Changes in mandibular dentition associated with age in pronghorn antelopes. Journal of Wildlife Management 26:1–18.

Dunn, S. J., and J. A. Byers. 2008. Determinants of survival and fecundity through a population bottleneck in pronghorn (*Antilocapra americana*). Journal of Mammalogy 89:1124–1129.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Hoenes, B. D. 2008. Identification of factors limiting desert mule deer populations in the Greater San Andres Mountains of southcentral New Mexico. Thesis, New Mexico State University, Las Cruces, New Mexico, USA.

Hoenes, B. D., and L. C. Bender. 2012. Factors influencing foraging habitats of desert mule deer in the greater San Andres Mountains, New Mexico. Southwestern Naturalist 57:370–379.

Hofmann, R. R. 1985. Digestive physiology of the deer – their morphophysiological specialization and adaptation. Pages 393–407 *in* P. F. Fennessy and K. R. Drew, editors. Biology of deer production. Royal Society of New Zealand, Auckland, New Zealand.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. Wiley, New York, New York, USA.

Hosmer, D. W., S. Lemeshow, and S. May. 2008. Applied survival analysis: regression modeling of time-to-event data. Wiley, Hoboken, New Jersey, USA.

Jacques, C. N., J. A. Jenks, J. D. Sievers, D. E. Roddy, and F. G. Lindzey. 2007. Survival of pronghorns in western South Dakota. Journal of Wildlife Management 71:737–743.
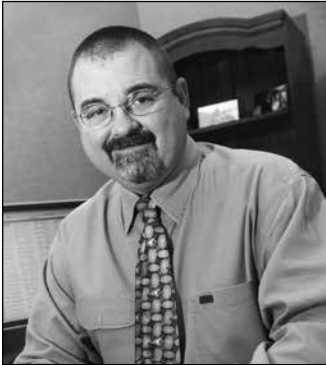
Kolar, J. L., J. J. Millspaugh, T. W. Mong, and B. A. Stillings. 2012. Survival and cause-specific mortality of pronghorn in southwestern North Dakota. American Midland Naturalist 167:164–173.

Lomas, L. A., and L. C. Bender. 2007. Survival and cause-specific mortality of mule deer fawns in northcentral New Mexico. Journal of Wildlife Management 71:884–893.

Marshall, J. P., P. R. Krausman, and V. C. Bleich. 2005. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology and Management 58:360–365.

McKinney, T. 2003. Precipitation, weather, and mule deer. Pages 219–237 in J. C. deVos Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Logan, Utah, USA.

McKinney, T., D. E. Brown, and L. Allison. 2008. Winter precipitation and recruitment of pronghorns in Arizona. Southwestern Naturalist 53:319–325.

Morrison, D. F. 1990. Multivariate statistical methods. McGraw-Hill, New York, New York, USA.

National Research Council. 2007. Nutritional, and metabolic diseases, ailments, and modifiers. Pages 220–231 in Nutrient requirements of small ruminants. National Academies Press, Washington, D.C., USA.

O'Gara, B. W. 2004a. Mortality factors. Pages 379–408 in B. W. O'Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. Wildlife Management Institute and University of Colorado Press, Boulder, Colorado, USA.

O'Gara, B. W. 2004b. Reproduction. Pages 275–298 in B. W. O'Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. Wildlife Management Institute and University of Colorado Press, Boulder, Colorado, USA.

O'Gara, B. W., and H. G. Shaw. 2004. Predation. Pages 337–378 in B. W. O'Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. Wildlife Management Institute and University of Colorado Press, Boulder, Colorado, USA.

Piasecke, J. R., and L. C. Bender. 2011. Patterns in the costs of lactation to body condition of free-ranging Rocky Mountain elk (*Cervus elaphus nelsoni*) populations. Pages 95–111 in V. K. Gupta and A. K. Verma, editors. Animal Diversity, Natural History, and Conservation. Volume 1. Daya, New Delhi, India.

Pollak, E. 2007. Evaluation of low-stress herding and supplement placement to modify cattle distribution and improve pronghorn habitat. Thesis, New Mexico State University, Las Cruces, New Mexico, USA.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7–15.

Ratcliffe, P. R. 1980. Bone marrow fat as an indicator of condition in roe deer. Acta Theriologica 25, 26:333–340.

Rideout, B. A. 2003. Clostridial diseases in all taxa. Pages 712–718 in M. E. Fowler and R. E. Miller, editors. Zoo and wild animal medicine. Saunders, St. Louis, Missouri, USA.

Simpson, D. C., L. A. Harveson, C. E. Brewer, R. A. Walser, and A. R. Sides. 2007. Influence of precipitation on pronghorn demography in Texas. Journal of Wildlife Management 71:906–910.

Wakeling, B. F., and L. C. Bender. 2003. Influence of nutrition on mule deer biology and ecology. Pages 93–116 in J. C. deVos Jr., M. R. Conover, and N. E. Headrick, editors. Mule deer conservation: issues and management strategies. Jack H. Berryman Institute Press, Logan, Utah, USA.

White, G. C., and R. M. Bartmann. 1998. Mule deer management—what should be monitored? Pages 104–120 in J. C. deVos Jr., editor. Proceedings of the 1997 deer/elk workshop. Arizona Department of Game and Fish, Phoenix, Arizona, USA.

Wilson, R. R., P. R. Krausman, and J. R. Morgart. 2010. Forage enhancement plots as a tool for Sonoran pronghorn recovery. Journal of Wildlife Management 74:236–239.

Yoakum, J. D. 2004. Foraging ecology, diet studies, and nutrient values. Pages 447–502 in B. W. O'Gara and J. D. Yoakum, editors. Pronghorn: ecology and management. Wildlife Management Institute and University of Colorado Press, Boulder, Colorado, USA.

LOUIS C. BENDER is a senior research scientist with Extension Animal Sciences and Natural Resources at New Mexico State University. He received his Ph.D. and M.S. degrees in wildlife from Michigan State University and his B.S. degree in wildlife from the University of Montana. His research and management programs emphasize ungulate and large carnivore populations and habitat, integrated wildlife and livestock habitat management, and wildlife enterprises in the Southwest and Mexico.

HEATHER HALBRITTER is a terrestrial biologist in the northeast region for the Colorado Division of Wildlife. She has a B.S. degree in biology from State University of New York–Brockport and received an M.S. degree in wildlife biology from New Mexico State University. She has spent most of her career working on various ungulate research and management projects and has a strong interest in livestock–wildlife conflicts.

JON C. BOREN earned his bachelor's and master's degrees in wildlife ecology and his doctoral degree in range science from Oklahoma State University before coming to New Mexico State University in 1996 as an assistant professor and extension wildlife specialist. He was selected as associate dean and director of the New Mexico Cooperative Extension Service in 2009. He has investigated wildlife and livestock interactions through scientific studies on rangelands and forests in New Mexico, developed innovative and cost effective methods to cope with problems from wildlife damage, and developed teaching materials to use in natural resource educational curricula. He conducts educational programs for youth in 4-H, FFA, and the public school system.

SHAD COX is the superintendent of New Mexico State University's Corona Range and Livestock Research Center (CRLRC). He graduated from New Mexico State University in 1994 with a B.S. degree in animal science and an M.S. degree in reproductive physiology and toxicology in 2000. He has lived and worked on the CRLRC for 17 years. He spends his leisure time insuring extracurricular opportunities for youth in agriculture.