10-2010

Factors influencing long-term population dynamics of pronghorn (*Antilocapra americana*): evidence of an Allee effect

Justin D. Hoffman
McNeese State University, jhoffman@mcneese.edu

Hugh H. Genoways
University of Nebraska - Lincoln, h.h.genoways@gmail.com

Rachel R. Jones
University of Nebraska - Lincoln

Factors influencing long-term population dynamics of pronghorn (*Antilocapra americana*): evidence of an Allee effect

Justin D. Hoffman,* Hugh H. Genoways, and Rachel R. Jones

Department of Biological and Health Sciences, McNeese State University, Lake Charles, LA 70609, USA (JDH)
University of Nebraska State Museum, University of Nebraska, Lincoln, NE 68588, USA (HHG)
School of Natural Resources, University of Nebraska, Lincoln, NE 68583, USA (RRJ)

* Correspondent: jhoffman@mcneese.edu

Populations of pronghorn (*Antilocapra americana*) are subjected to multiple forms of density-dependent and density-independent regulation. Little is known about the combined effects of these variables across multiple populations throughout the landscape. The objectives of this study were to examine long-term trends in density and recruitment in pronghorn and to assess how different forms of regulation influence these trends. We used multiple density-dependent and density-independent explanatory variables in a model selection process to explain variation in pronghorn density and July fawn : doe ratios from 1955 to 1993 in 4 pronghorn management units in Nebraska. We also investigated levels of density-dependent feedback in each management unit. Examination of long-term population trends suggested that pronghorn populations in Nebraska exhibited an Allee effect (inverse density dependence), in which population growth decreases as density decreases. We suggest that variation in rangeland condition and presence of adequate forage could explain the presence of the Allee effect. Both density-dependent and density-independent variables affected pronghorn populations, with density of cattle, spring precipitation, abundance of winter wheat, and hunting harvest most important for explaining fluctuations in pronghorn densities. Snow depth and density of cattle best explained yearly July fawn : doe ratios. The importance of each factor was variable across the different management units. Management objectives aimed at improving access to and abundance of food resources during times when rangeland condition is poor could prevent drastic declines in pronghorn populations. DOI: 10.1644/09-MAMM-A-257.1.

Key words: Allee effect, *Antilocapra americana*, density dependence, density independence, Nebraska, pronghorn, recruitment, regulation

Population regulation in ungulates has received considerable attention in the scientific literature. The general consensus is that populations can be regulated through either density-dependent or density-independent factors, with few studies investigating the combined effects of these factors (Sæther 1997). Common forms of density-dependent regulation include forage limitation (Kie et al. 1980; Skogland 1986), disease (Shrauder 1984), and predation (Wittmer et al. 2005), whereas density-independent regulation typically involves the effects of climatic variables on populations (Post and Stenseth 1998). In populations in which density dependence is the dominant form of regulation, a negative relationship between density and population growth commonly is observed (Gotelli 1998).

When densities fall to low levels, however, some populations experience inverse density dependence. Inverse density dependence occurs when a decrease in population density (or size) facilitates a decrease in the population growth rate. This situation is commonly referred to as the Allee effect (Allee 1931). Stephens et al. (1999) defined the Allee effect as ''a positive relationship between any component of individual fitness and either number or density of conspecifics.'' Allee effects have multiple conservation implications for natural populations because even slight increases in mortality can cause dramatic collapses in populations and increase probabilities of extinction (Courchamp et al. 1999). Also, populations operating under an Allee effect might exhibit a critical density below which the likelihood of extinction is high (Lande 1998). Although rarely considered in many previous studies of population dynamics, Allee effects are more common in natural populations than previously thought (Kramer et al. 2009; Morris 2002; Stephens and Sutherland 1999).

www.mammalogy.org

Regulation of pronghorn (*Antilocapra americana*) populations has been noted in several studies with examples of both density-dependent and density-independent factors affecting populations. Availability of resources is a commonly cited density-dependent factor contributing to the regulation of pronghorn populations. For instance, vegetation is an important resource for pronghorn, providing forage (Aoude and Danvir 2002) and protection from predation and inclement weather (Yoakum 2004). Removal of native vegetation for agriculture can have a negative effect on pronghorn (Yoakum 2004), although some crops, such as winter wheat, might provide an important food source during the winter months (Hepworth 1970; Torbit et al. 1993). The regulatory effects of livestock on pronghorn populations have been noted in the literature; however, debate exists about the relationship of their effect. Some research indicates that livestock, specifically cattle, directly compete with pronghorn for preferred forage (Autenrieth 1984; Hailey et al. 1966; Hervert et al. 2001), other studies suggest no such effect (Roebuck 1982), and some indicate that livestock might be beneficial to pronghorn by stimulating plant growth through their grazing activities (Danvir 2000; Loeser et al. 2005). Much of the effect that cattle have on pronghorn populations can be related to grazing intensity and rangeland condition (Campbell 1970). Finally, hunting harvests long have been used by wildlife agencies to regulate pronghorn populations (O'Gara 2004).

Severe winter weather and drought are the 2 most likely density-independent factors that impact pronghorn (O'Gara 2004). Deep snow can restrict access to preferred forage, leading to malnutrition and in some cases starvation (West 1970). Low temperatures can cause pronghorn to seek protective cover. However, increased snow depths can cause pronghorn to experience difficulties in accessing proper shelter (Yoakum 2004). Drought conditions resulting from low winter snowfall and spring precipitation have been correlated with low pronghorn densities and recruitment (Brown et al. 2006; Simpson et al. 2005). These studies suggest that low amounts of precipitation and subsequent drought conditions will affect pronghorn populations indirectly through available forage and cover by decreasing vegetation growth and diversity.

Pronghorn once were abundant throughout Nebraska, but due to subsistence and sport hunting and land-use changes, their populations began declining until only a few herds persisted in portions of northwestern Nebraska by the early 1900s (Jones 1964). Consequently, pronghorn were protected from harvest in Nebraska in 1907. Pronghorn populations responded favorably to the lack of hunter harvest, and in 1953 a hunting season was reestablished in areas of western Nebraska. Although the overall population of pronghorn in Nebraska has increased since the early 1900s, the historic activities of humans have resulted in small populations of pronghorn restricted to certain regions of the state. Much of the pronghorn habitat in western Nebraska has been converted to agricultural fields consisting mostly of corn, soybeans, and wheat (Hiller et al. 2009). Lands that were not cultivated and support native prairie often are used for livestock grazing. Further, areas in western Nebraska are located in the western Great Plains and are subject to severe summer droughts and harsh winter storms.

Most studies of processes that regulate pronghorn populations have focused on a single population, and results are used to develop management plans across multiple populations and differing habitat conditions. Little is known regarding the role of different factors in regulating adjacent populations of pronghorn that exist in a heterogeneous landscape (Smyser et al. 2006). If populations experience different forms of regulation, using the same criteria to manage all pronghorn populations might not be appropriate. This is especially important when recommending harvest limits. Without knowing the mechanisms that regulate populations of pronghorn, implementing certain harvest objectives could have undesirable or detrimental effects (Kohlmann 2004). Knowledge about mechanisms that regulate populations of mammals is vital for sound management and conservation planning.

The objective of this study was to investigate the roles of density-dependent and density-independent factors in regulating multiple populations of pronghorn using long-term data on population density and recruitment (hereafter referred to as July fawn : doe ratios) across 4 pronghorn management units (PMUs) in Nebraska. These units consist of a diverse matrix of habitats and environmental conditions. Therefore, we expected that factors important in regulating pronghorn density and recruitment would vary across populations, with both density-dependent and density-independent variables providing significant predictions.

MATERIALS AND METHODS

Populations of pronghorn were monitored through aerial line transect surveys in western Nebraska beginning in 1955. Locations of surveys corresponded to 4 established PMUs: Sioux, Box Butte, Garden, and Banner (Fig. 1). In most cases only a portion of the PMU was surveyed, except in the Garden PMU (Table 1). The Sioux PMU is located in extreme northwestern Nebraska and encompasses the northern quarter of Sioux County and the northwestern corner of Dawes County. This unit consists mostly of native prairie and small areas of agricultural land and forested habitat (Table 1). The Box Butte PMU is located in portions of Box Butte, Sioux, Morrill, and Scotts Bluff counties. The predominant land cover for this unit is similar to the Sioux PMU with native prairies being most abundant; however, more agricultural land is present (Table 1). The Garden PMU is located primarily within Garden and Morrill counties and parts of western Grant, Arthur, Box Butte, Sheridan, and Keith counties. This unit is dominated by Sandhills prairie habitat. Only small amounts of agriculture are present in the Garden PMU (Table 1). The Banner PMU consists of the western halves of Banner and Kimball counties and a small portion of southern Scotts Bluff County. The Banner PMU includes more
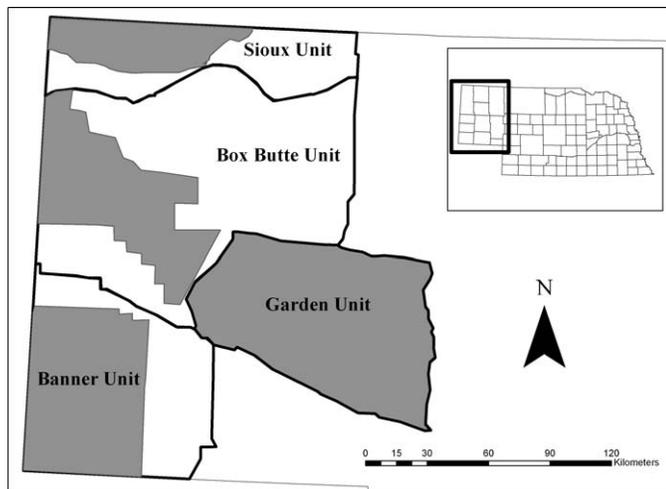
FIG. 1.—Locations of 4 pronghorn management units in western Nebraska that were surveyed during 1955–1993. Bold lines indicate unit borders. Shaded areas correspond to survey areas within each unit.

agricultural land than any other PMU surveyed, but western shortgrass prairie characterizes >40% of the area (Table 1).

The predominant landscape in this region has changed little over the course of the survey period, especially with respect to cultivation. Hiller et al. (2009) showed that the greatest rate of increase in conversion of native prairie to agricultural land happened from 1865 to 1930. From 1930 to the present the amount of cropland in Nebraska has remained relatively stable, with small annual fluctuations. The general topography for western Nebraska is rolling hills, with some areas of steep relief and a maximum elevation of approximately 1,500 m (Jones 1964). We believe that these survey units represent independent pronghorn populations because all of the survey units are separated by a matrix of paved highways and fences. Artificial barriers such as fences and highways can severely restrict pronghorn movements (Deblinger et al. 1984; Ockenfels et al. 1992; Yoakum 2004), so we believe movement of individuals among our survey units is minimal.

Transects were established within each PMU and surveyed once during July of each year using a fixed-wing aircraft. Typically, surveys were conducted on the same day(s) during each year, weather permitting. These days included 9 July for the Sioux PMU; 10, 12, and 13 July for the Box Butte PMU; 13, 15, and 17 July for the Garden PMU; and although exact dates were not available for the Banner PMU, surveys in this unit were conducted during July. Surveying was conducted at 15–30 m above ground level. Transects were located between 2.4 and 4.8 km apart. Two observers counted the number of male, female, and juvenile pronghorn observed within 0.40 km on either side of the midline of the transect. From these data the density of pronghorn and the ratio of fawns per 100 does per sample unit were calculated (Fig. 2). Density was calculated by dividing the number of pronghorn observed by the total transect area. We summarized the results of these surveys for each PMU and presented population data collected during 1955–1993 for Sioux, Box Butte, and Garden PMUs, and 1964–1993 for the Banner PMU. Although aerial surveys continued beyond 1993, we chose to exclude post-1993 data from the analysis because of changes in the locations of surveys and absence of surveys during certain years for some units. Unfortunately, no corrections for sightability or estimates of error for density or fawn : doe ratios were calculated. We assumed that the relative consistency in the survey methodology over the years minimized the effects these had on our results. Finally, it should be noted that July fawn : doe ratios provide only an index of pronghorn recruitment that can be influenced markedly by multiple variables. July fawn : doe ratios represent the best long-term data on reproduction by pronghorn in Nebraska.

To determine potential causes of the fluctuation in pronghorn density and July fawn : doe ratios, we collected data on several density-dependent and density-independent variables. Density-independent data consisted of climate variables taken from the High Plains Regional Climate Center (http://www.hprcc.unl.edu/). Locations of the climate stations were variable with respect to locations of the survey areas, but we collected data from the station that was closest to the center of each survey area. Winter temperature (Win_t) was calculated from the average minimum temperature from January and February of each survey year. We used this variable to represent the physiological challenges of pronghorn to low winter temperatures. Spring precipitation (Spring_p) was calculated as the average rainfall from April

TABLE 1.—Landscape characteristics for 4 pronghorn management units (PMUs) in western Nebraska, with total area given in parentheses. Average annual precipitation was calculated during 1955–1993 for the Sioux, Box Butte, and Garden PMUs and during 1964–1993 in the Banner PMU. These dates correspond to years when pronghorn surveys were conducted in each unit. Ranges for average annual precipitation are given in parentheses. Data on land cover were extracted from the Nebraska Gap Analysis Program (GAP; http://www.calmit.unl.edu/gap/) for each PMU.

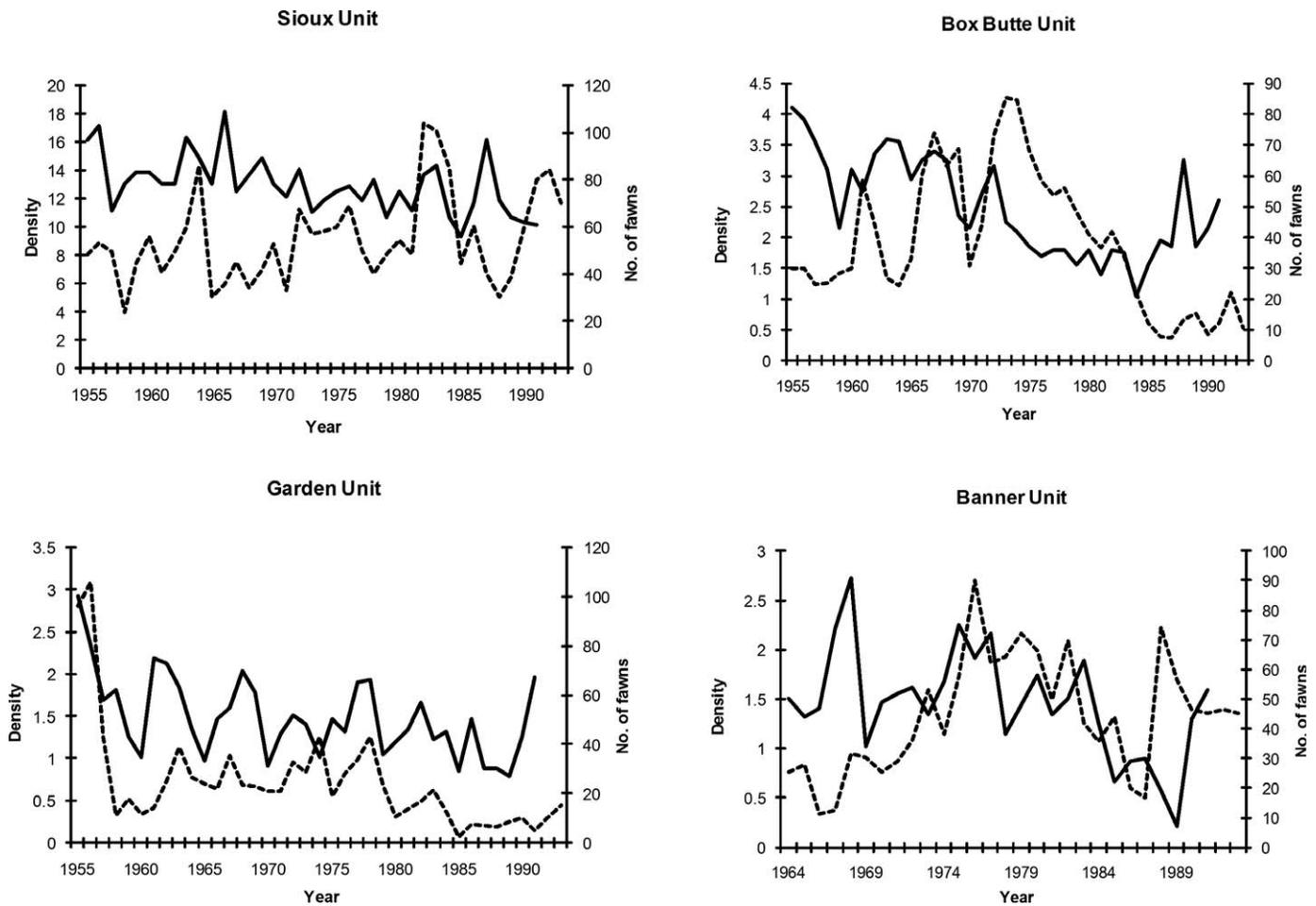|	Sioux PMU (4,574 km^2)	Box Butte PMU (13,688 km^2)	Garden PMU (7,705 km^2)	Banner PMU (7,652 km^2)
Area surveyed (km^2)	1,691	5,148	7,705	4,131
Average annual precipitation (cm)	42.6 (28.6–58.9)	39.8 (15.4–58.6)	43.6 (27.0–67.6)	36.4 (24.4–59.8)
Western shortgrass prairie (%)	69	48	20	43
Agricultural land (%)	10	23	6	44
Pine forest (%)	6	—	—	—
Sandhill upland prairie (%)	5	19	64	8
Mixed-grass prairie (%)	4	—	—	—
Tallgrass prairie (%)	—	3	5	—

Fig. 2.—Population trends of pronghorn for 4 pronghorn management units in western Nebraska based on aerial surveys conducted annually during July from 1955 to 1993. Solid lines indicate the estimated number of fawns per 100 does. Dashed lines indicate the estimated density of pronghorn per square kilometer.

to June of each survey year, and snow depth (Snow_d) was averaged from October of the previous year to April of the survey year.

Density-dependent variables used to account for variation in annual pronghorn density and July fawn : doe ratios included the percentage of actively cultivated ground (Ag), percentage of winter wheat (Wheat), average number of cattle per square kilometer (Cattle), and harvest of pronghorn during the previous year (Harvest). Data on percent cultivated ground, percent winter wheat, and density of cattle were available only at the county level. Also, data on pronghorn harvest were available for the entire PMU, not just the survey area. Because of these discrepancies, a correction was performed on each data set that represented the proportion of the survey areas that fell within each county. This correction consisted of multiplying the amount of cultivated ground (Ag and Wheat) and cattle density (Cattle) per county by the proportion of the survey area that existed in each county. We then summed the values for all the counties that were present in each PMU. All data on cultivated ground and number of cattle per county were downloaded from the National Agricultural Statistics Service (http://www.nass.usda.gov/). Data on the overall

number of pronghorn harvested were corrected in a similar fashion by multiplying the total number of pronghorn harvested in a PMU by the proportion of unit that was surveyed.

We used a model selection approach to investigate fluctuations in pronghorn density and July fawn : doe ratios (Burnham and Anderson 2002). Sixteen candidate models were determined a priori based on our knowledge of pronghorn population dynamics. A subset of the candidate models was constructed using only density-dependent variables, another subset was constructed with density-independent variables, and a final subset of candidate models consisted of both density-dependent and density-independent variables. Two sets of analyses were conducted, 1 for each response variable, pronghorn density and July fawn : doe ratios, using the same candidate models. Before constructing candidate models, we generated a correlation matrix for all explanatory variables to test for multicollinearity. We used a conservative correlation estimate (Leathwick et al. 2005) where any variables with $r^2 > 0.5$ were considered correlated and not included in the same model. Candidate models included various combinations of density-dependent variables,

density-independent variables, and combinations of both density-dependent and density-independent variables. We included a global model that consisted of all noncorrelated variables. Finally, we included a null model (''response = [1]'') that predicts that pronghorn density and July fawn : doe ratios are random with respect to all variables. All statistical analyses were performed using R (2.9.2) statistical software (R Development Core Team 2008).

When the response variable was density, models were fit to the data using a generalized linear model with a Gaussian link function, and Akaike's information criterion (AIC) was used to evaluate model fit. When the response variable was July fawn : doe ratio, we used a quasi-Poisson link function to account for overdispersion in the count data (Burnham and Anderson 2002). We calculated quasi-AIC (QAIC) values for the model predicting July fawn : doe ratios to determine the best-fit model. Each response variable (density and July fawn : doe ratio) was log-transformed to satisfy the assumption of normality before being fit to the data. The model with the lowest AIC value was considered the best-approximating model, and models with ΔAIC < 2 were considered significant and equally supported (Burnham and Anderson 2002). We calculated Akaike model weights (ws) for each significant model to represent the probability of best fit among all other candidate models (Burnham and Anderson 2002). In situations in which more than 1 candidate model was equally supported, we performed model averaging on the coefficient estimates for each significant model (ΔAIC < 2). The average coefficient estimate, *SE*, 95% confidence intervals, and relative importance of the parameter also were calculated. This approach allowed us to use all significant models for inference.

Finally, we performed a generalized cross-validation exercise to determine whether our models reasonably fit the data. This consisted of calculating the calibration slope for the best-fit model in each PMU. Calibration refers to the agreement between predicted and observed probabilities of the response variable. Measures of model calibration include the spread, or the slope, of a regression line. The calibration slope characterizes the departure of the curve from a line with a slope equal to 1. Models with good calibration have a slope = 1, whereas models with slopes > 1 or < 1 indicate either an overestimation or underestimation of the predictive values, respectively (Pearce and Ferrier 2000). We randomly extracted 10 subsets of the original data ($n = 10$) with replacement for each model to predict pronghorn density and July fawn : doe ratios. These predictions then were regressed against the observed values and calibration slopes were recorded. Student *t*-tests were performed to test the hypothesis that calibration slope was significantly different from 1.

We investigated density-dependent feedback for each unit by calculating the logarithmic per capita rate of change in density (r_t):

$$r_t = \log\left(\frac{X_{t+1}}{X_t}\right),$$

where X is the population density. Following Liebhold and Bascompte (2003), we fit a linear regression model with the per capita rate of change as the response variable and pronghorn density as the explanatory variable. We calculated a critical population threshold (d) by dividing the negative intercept (a) by the slope (b) of a linear regression line: $d = -a/b$. This represents the density of pronghorn when rate of change is 0. When populations are experiencing an Allee effect and $X > d$, populations are expected to increase, and when $X < d$, it is assumed that populations will decrease and have a higher probability of extinction without management intervention.

RESULTS

We observed variation in several measures of pronghorn demographics throughout western Nebraska. The average density for the Sioux PMU from 1955 to 1993 was 9.1 pronghorn/km^2 (range = 3.9–17.3 pronghorn/km^2; Fig. 2), which resulted in an average estimated population size of 1,909 pronghorn (range = 400–4,364 pronghorn) for this time period. The average July fawn : doe ratio for the Sioux PMU was 78 fawns : 100 does (range = 56–109 fawns : 100 does). In the Box Butte PMU pronghorn densities peaked in 1967 at approximately 4.3 pronghorn/km^2 (Fig. 2) but declined in succeeding years and never recovered despite increasing trends in reproductive success during the mid to late 1980s. Average density of pronghorn in the Box Butte PMU was 1.9 pronghorn/km^2 (range = 0.37–4.26 pronghorn/km^2), with an average estimated population size of 1,591 pronghorn (range = 288–3,272 pronghorn) from 1955 to 1993, and the average number of fawns per 100 does was 50 (range = 21–82 fawns per 100 does). Populations of pronghorn in the Garden PMU showed overall decreasing trends in density and reproductive success (Fig. 2). Highest levels of density and recruitment were observed in 1955 and 1956, after which both experienced sharp declines. The average density of pronghorn in the Garden PMU was 0.6 pronghorn/km^2 (range = 0.1–1.2 pronghorn/km^2), and the average estimated population size was 613 pronghorn (range = 78–1,404 pronghorn). The average July fawn : doe ratio was 50 fawns : 100 does (range = 27–100 fawns : 100 does). The Banner PMU was the most variable unit with regard to population trends (Fig. 2). Data for this unit were collected from 1964 to 1993. Overall trends in density and July fawn : doe ratios showed an initial increase until approximately 1980, after which populations began to decline. After 1988, populations appeared to be recovering to higher levels. Average density of pronghorn in the Banner Unit was 1.3 pronghorn/km^2 (range = 0.3–2.7 pronghorn/km^2), and the average estimated population size was 809 pronghorn (range = 232–1,664 pronghorn). The average July fawn : doe ratio was 48 fawns : 100 does (range = 7–91 fawns : 100 does).

Our results indicated that both density-dependent and density-independent variables explained annual variation in pronghorn density among PMUs. One model (Spring_p + Snow_d + Cattle) provided the most support (i.e., no other

TABLE 2.—Akaike information criterion (AIC) scores, differences in AIC score between the *i*th and top-ranked model (ΔAIC), Akaike weights (w_i), and number of variables (k) for models predicting the density of pronghorn in Nebraska for 4 pronghorn management units (PMUs). Only models with ΔAIC < 2 are reported.

Model variables	AIC	ΔAIC	w_i	k
Sioux PMU				
Spring_p + Snow_d + Cattle	181.5	0	0.59	4
Box Butte PMU				
Harvest + Wheat	95.24	0	0.73	3
Garden PMU				
Harvest	7.86	0	0.42	2
Harvest + Wheat	8.13	0.27	0.37	3
Cattle + Harvest	9.84	1.99	0.16	3
Banner PMU				
Wheat + Cattle + Win_t +				
S pring_p + Snow_d + Harvest	44.46	0	0.32	7
Ag + Wheat + Cattle	44.60	0.14	0.30	4
Harvest + Wheat	45.56	1.10	0.18	3

models had ΔAIC < 2) in explaining fluctuations in pronghorn density in the Sioux PMU (Table 2). It also possessed a good fit to the data with a calibration slope of 0.99 ($P > 0.05$). These results suggest that pronghorn density was higher during years of higher spring precipitation and when higher densities of cattle were present in the study area. Parameter estimates indicated that snow depth was not a significant variable (Table 3). In the Box Butte PMU 1 model (Harvest + Wheat) best explained annual fluctuations of pronghorn density (Table 2), with a calibration slope of 0.98 ($P > 0.05$). Both variables were significant and indicated that higher pronghorn densities were observed during years when more cultivated ground was planted to winter wheat and when pronghorn harvest during the previous year was high (Table 3). Three models were considered to fit the data for the Garden PMU (Table 2). The top model (Harvest) had a calibration slope equal to 1.4 ($P > 0.05$). Results of model averaging among all significant models indicated that the previous year's harvest was the most important variable for explaining pronghorn density, and higher pronghorn densities were correlated with higher harvest during the previous year (Table 3). Finally, 3 models were equally supported for explaining variation in pronghorn density in the Banner PMU (Table 2), with the top model (Global model) having a calibration slope of 1.2 ($P > 0.05$). Model averaging across all significant models determined that the percentage of cultivated ground planted to wheat was the only significant variable (Table 3). These results also suggested that a positive relationship existed between the amount of wheat present in the Banner PMU and pronghorn density.

Pronghorn recruitment in Nebraska appeared to be most influenced by winter snow depths and density of cattle. In the Sioux PMU 2 models were equally supported in explaining annual variations in July fawn : doe ratios (Table 4); however, the null model was among the significant models, which indicates that the variables used did not predict variation in

TABLE 3.—Parameter estimates, *SE*s, and 95% confidence limits (lower confidence limit [*LCL*] and upper confidence limit [*UCL*]) for models that predict pronghorn density for 4 pronghorn management units (PMUs) in Nebraska. Parameter estimates were averaged across models with ΔAIC < 2 for the Garden and Banner PMUs, and relative importance values are reported. Model averaging was not applied to the Sioux and Box Butte PMUs because no models were within 2 AIC points of the top model. Significant variables are in boldface type.

	Estimate	*SE*	Relative importance	*LCL*	*UCL*
Sioux PMU					
(Intercept)	−8.308	4.862	—	−17.839	1.221
Cattle	**1.019**	**0.309**	—	**0.414**	**1.625**
Spring_p	**1.024**	**0.501**	—	**0.042**	**2.007**
Snow_d	0.038	0.170	—	−0.295	0.372
Box Butte PMU					
(Intercept)	−2.640	1.665	—	−5.906	0.624
Harvest	**0.004**	**0.001**	—	**0.002**	**0.006**
Wheat	**0.885**	**0.381**	—	**0.138**	**1.632**
Garden PMU					
(Intercept)	0.137	0.388	—	−0.640	0.914
Harvest	**0.003**	**0.001**	**0.95**	**0.002**	**0.007**
Wheat	0.517	0.087	0.37	−0.121	0.225
Cattle	−0.001	0.003	0.16	−0.008	0.007
Banner PMU					
(Intercept)	2.030	3.110	—	−4.140	8.200
Wheat	**0.148**	**0.049**	**0.80**	**0.047**	**0.249**
Cattle	−0.128	0.152	0.62	−0.431	0.175
Harvest	−0.002	0.002	0.50	−0.007	0.002
Snow_d	0.001	0.003	0.32	−0.006	0.008
Spring_p	0.005	0.012	0.32	−0.019	0.030
Win_t	0.003	0.007	0.32	−0.010	0.017
Ag	−0.067	0.079	0.30	−0.223	0.089

July fawn : doe ratios any better than chance. Further, none of the other variables in the best-fit models were significant (Table 5). In the Box Butte PMU 2 models fit the data equally well (Table 4). The calibration slope for the best-fit model (Spring_p + Snow_d + Cattle) was 1.3 ($P > 0.05$). When the coefficients were averaged across both models, snow depth and density of cattle were the only 2 significant variables, and both exhibited a negative relationship with fawn : doe ratios (Table 5). Thus, lower July fawn : doe ratios were observed during years with higher densities of cattle and greater snow depths. In the Garden PMU 3 models possessed equal support for predicting July fawn : doe ratios (Table 4). Similar to the Box Butte PMU, the top model possessed a good fit to the data with a calibration slope of 1.3 ($P > 0.05$). Density of cattle was the only significant variable once coefficients were averaged across all significant models (Table 5). Again, July fawn : doe ratios tended to be higher with lower cattle densities. Finally, the global model was the best-fit model in the Banner Unit (Table 4) and possessed a calibration slope of 1.5 ($P > 0.05$). July fawn : doe ratios were larger during years with higher cattle densities and lower snow depths (Table 5).

In all PMUs pronghorn density was related significantly and positively to per capita rate of change (Fig. 3). Calculation of

TABLE 4.—Quasi-Akaike information criterion (QAIC) scores, differences in QAIC score between the ith and top-ranked model (ΔQAIC), quasi-Akaike weights (w_i), and number of variables (k) for models predicting July fawn : doe ratios of pronghorn in Nebraska for 4 pronghorn management units (PMUs). Only models with ΔQAIC < 2 are reported.

Model variables	QAIC	ΔQAIC	w_i	k
Sioux PMU				
Null	172.52	0.00	0.336	2
Cattle + Harvest	173.24	0.72	0.234	4
Box Butte PMU				
Spring_p + Snow_d + Cattle	163.45	0.00	0.362	5
Win_t + Spring_p + Snow_d + Cattle	163.55	0.10	0.344	6
Garden PMU				
Spring_p + Snow_d + Cattle	178.44	0.00	0.230	5
Cattle + Harvest	179.04	0.60	0.170	4
Ag + Wheat + Cattle	179.64	1.19	0.126	5
Banner PMU				
Wheat + Cattle + Win_t +				
Spring_p + Snow_d + Harvest	131.63	0.00	0.533	8

model parameters suggested that each PMU possessed a critical density threshold (d). As population densities fell below d, the per capita rate of change was negative. In the Sioux PMU the density threshold was 8.6 pronghorn/km^2, the Box Butte PMU had a threshold of 2.2 pronghorn/km^2, the Banner PMU threshold was 1.3 pronghorn/km^2, and the Garden PMU had a critical threshold value of 0.7 pronghorn/km^2.

DISCUSSION

Examination of our data shows that as pronghorn density decreased, the per capita rate of change in population density also decreased. These results suggest that an Allee effect was present in populations of pronghorn in western Nebraska. The effect was especially evident in the Sioux and Garden PMUs, for which the slopes of the curves began to decrease more rapidly at lower densities. This effect was not as prominent in the Box Butte and Banner PMUs. The presence of a strong Allee effect in the Sioux PMU, and especially the Garden PMU, could be the result of the quality of habitat in these areas compared to the Box Butte and Banner PMUs. First, our modeling results suggested that pronghorn density in the Sioux PMU is correlated positively with both density-dependent and density-independent variables (cattle density and spring precipitation) that could directly affect the quality and quantity of available forage. During periods when spring precipitation and cattle grazing are low, densities of pronghorn might decrease because these factors stimulate growth of forbs. Also, the primary habitat in the Garden PMU is Sandhill upland prairie (Table 1). This habitat type is dominated by tall and midsized grass species and might not possess an adequate amount of preferred forage or suitable habitat to support dense populations of pronghorn. For instance, several hundred pronghorn were released into similar habitat in Cherry, Rock,

TABLE 5.—Parameter estimates, *SE*s, and 95% confidence limits (lower confidence limit [*LCL*] and upper confidence limit [*UCL*]) for models that predict July fawn : doe ratios ratios for 4 pronghorn management units (PMUs) in Nebraska. Parameter estimates were averaged across models with differences in quasi-Akaike information criterion (ΔQAIC) < 2 for the Sioux, Box Butte, and Garden PMUs, and relative importance values are reported. Model averaging was not applied to the Banner PMU because no models were within 2 QAIC points of the top model. Significant variables are in boldface type.

	Estimate	*SE*	Relative importance	*LCL*	*UCL*
Sioux PMU					
(Intercept)	4.71	0.61	—	3.510	5.910
"1"	—	—	0.336	—	—
Cattle	−1.06	0.60	0.234	−2.250	0.120
Harvest	0.04	0.06	0.234	−0.080	0.160
Box Butte PMU					
(Intercept)	6.010	0.520	—	4.980	7.040
Cattle	**−0.110**	**0.020**	**0.71**	**−0.150**	**−0.080**
Snow_d	**−0.050**	**0.020**	**0.71**	**−0.100**	**−0.010**
Spring_p	0.010	0.040	0.71	−0.080	0.090
Win_t	−0.023	0.044	0.34	−0.078	0.095
Garden PMU					
(Intercept)	4.520	0.430	—	3.680	5.350
Cattle	**−0.040**	**0.020**	**0.52**	**−0.780**	**−0.003**
Snow_d	−0.003	0.026	0.23	−0.055	0.048
Spring_p	0.080	0.045	0.23	−0.009	0.168
Harvest	0.000	0.000	0.17	−0.001	0.003
Wheat	0.110	0.100	0.12	−0.085	0.310
Ag	−0.015	0.013	0.12	−0.042	0.012
Banner PMU					
(Intercept)	0.600	0.910	—	−1.210	2.380
Cattle	**0.180**	**0.060**	—	**0.050**	**0.300**
Snow_d	**−0.080**	**0.020**	—	**−0.130**	**−0.030**
Spring_p	−0.070	0.080	—	−0.220	0.080
Harvest	−0.001	0.000	—	−0.002	0.001
Win_t	−0.001	0.020	—	−0.050	0.050

and Brown counties from 1958 to 1961. These populations were surveyed approximately 10 years later during 1966–1971 (Suetsugu 1971) and showed similar densities ($\bar{X}$ = 0.8 pronghorn/km^2) to the Garden PMU ($\bar{X}$ = 0.7 pronghorn/km^2) during the same time period (this study). In the Banner and Box Butte PMUs the presence of agricultural crops, especially winter wheat, might explain the weaker Allee effect. In the Sioux and Garden PMUs, where the Allee effects were strongest, a notable lack of agricultural ground was present compared to the Box Butte and Banner PMUs. During periods when food resources (i.e., forbs) were low, such as during a drought or severe winter, populations in the Box Butte and Banner PMUs likely had better access to food resources compared to populations in Sioux and Garden PMUs. Our modeling results support this contention because the amount of winter wheat was a significant variable for pronghorn density in the Box Butte and Banner PMUs but not in the Garden or Sioux PMUs. Pronghorn density is related directly to the abundance of food (Aoude and Danvir 2002; Yoakum 2004), and as forage becomes scarcer, population levels are expected to decrease.
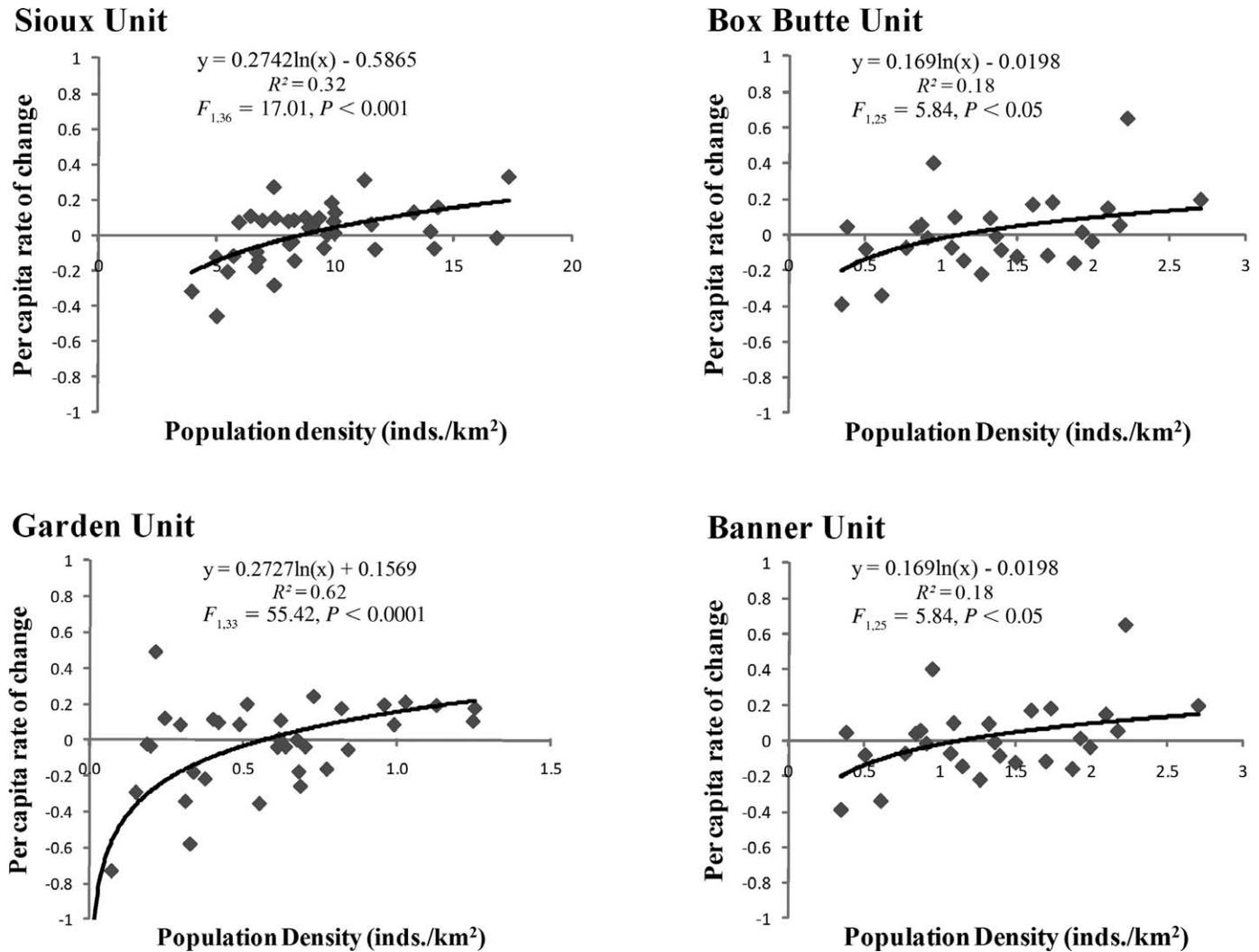
Sioux Unit

$y = 0.2742\ln(x) - 0.5865$
$R^2 = 0.32$
$F_{1,36} = 17.01, P < 0.001$

Box Butte Unit

$y = 0.169\ln(x) - 0.0198$
$R^2 = 0.18$
$F_{1,25} = 5.84, P < 0.05$

Garden Unit

$y = 0.2727\ln(x) + 0.1569$
$R^2 = 0.62$
$F_{1,33} = 55.42, P < 0.0001$

Banner Unit

$y = 0.169\ln(x) - 0.0198$
$R^2 = 0.18$
$F_{1,25} = 5.84, P < 0.05$

Fig. 3.—Logarithmic per capita rate of change relative to pronghorn density for 4 pronghorn management units in western Nebraska during 1955–1993. Linear equations and lines are provided for the regression models that best fit the data.

During our survey period years existed when pronghorn populations fell below the critical density thresholds. When this happens, the probability of extinction for a population increases (Courchamp et al. 1999). During no time did pronghorn become extinct from any of the survey units, even if they existed at critically low population densities. We suggest that gradual increases in range condition could explain the recovery of pronghorn populations from these low levels.

When population size is reduced beyond a critical threshold, individuals become exposed to several factors that could facilitate an Allee effect, including inbreeding, mate limitation, higher rates of predation due to a relative increase in abundance of predators, demographic stochasticity, and reduction in cooperative defense (Kramer et al. 2009; Lande 1998). Cooperative defense might be most pertinent to pronghorn because it involves each individual of the population remaining vigilant for potential predation. O'Gara (2004) suggested that pronghorn form herds primarily for protection from predators. Lipetz and Bekoff (1982) showed that as herd size increased, the proportion of pronghorn that

were vigilant decreased. They hypothesized that this was due to an increase in awareness and detection of predators, which allowed individuals to spend more time feeding and resulted in greater overall fitness for individuals in the herd. For pronghorn in Nebraska the reduction in population densities below the critical threshold following years of poor habitat quality could lead to a loss of antipredator strategies. Murray Berger and Conner (2008) suggested that the low densities of pronghorn and higher densities of coyotes in Grand Teton National Park might contribute to the presence of an Allee effect in that population.

Based on our modeling results, pronghorn density is subjected to both density-dependent and density-independent forms of regulation. We hypothesize that the condition of the rangeland, specifically the availability of suitable forage, was primarily responsible for fluctuations in pronghorn density. For instance, the vegetative condition of pronghorn habitat ultimately might determine long-term trends in population numbers (O'Gara 2004; Yoakum 2004), so that prolonged periods of poor habitat quality could maintain low densities of

pronghorn. Aoude and Danvir (2002) reported that pronghorn density remained low in areas where forbs were less abundant. After increasing the forb abundance in these areas through mechanical manipulation, they observed an increase in pronghorn density. Groups of females with young tend to select habitats rich in forbs during the summer (Danvir 2000). Simpson et al. (2005) suggested that lower precipitation on pronghorn rangeland led to a decrease in habitat quality and pronghorn abundance.

In the Sioux Unit the density of cattle and amount of spring precipitation were both significant variables. Spring precipitation commonly has been associated with higher pronghorn densities (Brown et al. 2006; Simpson et al. 2005; Yoakum 2004). Rangelands that receive more precipitation typically produce higher diversities of forbs (Goldberg and Turner 1986), which are the preferred diet of pronghorn (Yoakum 1990). Lack of nutritious forage because of low amounts of precipitation can result in higher mortality rates for both fawns and adults (Bright and Hervert 2005). Higher densities of cattle also could lead to improved forage on pronghorn rangelands. The grazing activities of domestic cattle have been shown to increase forb diversity (Loeser et al. 2005). Also, little evidence can be found that the diets of cattle and pronghorn overlap, suggesting that competition for food resources likely is minimal (Yoakum 2004). The amount of winter wheat was identified as a significant variable in both the Box Butte and Banner PMUs. Winter wheat is an important food source for pronghorn during the winter when other resources are limited (Dunn and Byers 2008; Hepworth 1970; West 1970).

Hunter harvest during the previous year was positively and significantly related to pronghorn density in both the Garden and Box Butte PMUs. We believe that the significance of this variable in these 2 units was due to the closure of the hunting seasons during portions of the survey. In the Garden PMU the pronghorn hunting season was closed during 1958–1959, 1961, and 1987–1991, and in the Box Butte PMU hunting was suspended during 1958–1960 and 1987–1991. No pronghorn were harvested during these times because the Nebraska Game and Parks Commission documented a declining trend in the densities of pronghorn for these 2 units. Although no pronghorn were being removed from the population by hunters, densities still remained low. We suggest that the several years during which no hunting occurred in these units biased the data, resulting in a significant relationship between harvest and pronghorn density that is not indicative of a typical density-dependent effect. Further, in the Sioux and Banner PMUs pronghorn hunting season was not suspended during the survey, and subsequently harvest was not determined to be a significant variable.

Similar to the regulation of pronghorn density, we found that both density-dependent and density-independent factors best described annual variation in July fawn : doe ratios in western Nebraska, with density of cattle and snow depth being the best predictors. In the Box Butte and Garden PMUs July fawn : doe ratios decreased as cattle density increased. The

higher intensity of grazing could have reduced the amount of adequate cover available to protect fawns from inclement weather and predation (Autenrieth 1984; Barrett 1978). Also, when cattle are present, pronghorn females tend to relocate their fawning sites to less favorable habitats (McNay and O'Gara 1982). High snow depths best explained decreases in July fawn : doe ratios for the Box Butte and Banner PMUs. Heavy winter snow can restrict access to favorable forage resulting in malnutrition in adults, which could result in the doe either aborting her fetus or producing underweight fawns (Danvir 2000; O'Gara 2004). Lower birth weights among pronghorn have been correlated to higher fawn mortality (Fairbanks 1993). One result that was surprising was that higher cattle densities were correlated positively with higher July fawn : doe ratios in the Banner PMU, which was opposite of the results from the Box Butte PMU. It is unclear to us how higher densities of cattle would result in higher July fawn : doe ratios. One explanation could be that when more cattle are present, a need arises for ranchers to provide more supplemental feed (i.e., alfalfa hay), especially during severe winters. Forty-four percent of the Banner PMU has been converted to agriculture, which is twice as much as any other PMU in western Nebraska. This could result in relatively small patches of native grassland available for grazing, and cattle in these areas might require additional feed to compensate for the minimal pastureland. These additional resources inadvertently could provide supplemental forage for pronghorn, resulting in more healthy adults. Each year the Nebraska Game and Parks Commission receives several reports from ranchers in this area of pronghorn feeding on hay bales that were initially set out for cattle during the winter (Jeff D. Hoffman, pers. comm.). More research is needed, however, to confirm these results. Finally, none of our variables adequately explain July fawn : doe ratios in the Sioux PMU, suggesting that other unexplained factors influence pronghorn recruitment in this region.

Our results have several implications for the management of pronghorn. For example, pronghorn management plans should include calculations of critical density thresholds for individual PMUs. Our results indicate that Allee effects can be present in pronghorn populations and should be considered when developing management and conservation programs. As population density falls below these thresholds, the per capita rate of change becomes negative and the population faces a greater chance of extinction. As population densities approach the critical threshold, these areas should receive management priority for population recovery. Further, our modeling results suggested that factors explaining pronghorn density and July fawn : doe ratios differed among local populations and consisted of both density-dependent and density-independent variables. Knowing the underlying causes of annual fluctuations in these 2 population parameters and how those causes interact will help to maintain populations at desired levels for different management units. We suggest that developing management plans that consider local variation in landscape characteristics and rangeland quality will be most helpful for

wildlife managers. Specifically, implementing programs aimed at improving quality of forage during periods of drought or when availability of other forage (i.e., winter wheat) is low will reduce the loss in population numbers and improve reproductive output. Also, working with landowners to alter grazing patterns, especially during times when the quality of rangeland is low, could benefit pronghorn populations. Finally, our results illustrate the importance of investigating factors that regulate pronghorn at local scales. Although some factors (i.e., cattle density) might benefit pronghorn in 1 management unit, the same factor might be deleterious to pronghorn in an adjacent unit. Knowing how local populations of pronghorn respond to annual fluctuations in density-dependent and density-independent variables will provide the basis for more sound management plans.

ACKNOWLEDGMENTS

LITERATURE CITED

ALLEE, W. C. 1931. Animal aggregations: a study in general sociology. University of Chicago Press, Chicago, Illinois.

AOUDE, A., AND R. E. DANVIR. 2002. Using range manipulations to increase pronghorn production and abundance in Utah sagebrush steppe. Proceedings of the Pronghorn Antelope Workshop 20:124–134.

AUTENRIETH, R. E. 1984. Little lost pronghorn fawn study—condition, habitat use, and mortality. Proceedings of the Pronghorn Antelope Workshop 11:49–70.

BARRETT, M. W. 1978. Pronghorn fawn mortality in Alberta. Proceedings of the Pronghorn Antelope Workshop 8:429–444.

BRIGHT, J. L., AND J. J. HERVERT. 2005. Adult and fawn mortality of Sonoran pronghorn. Wildlife Society Bulletin 33:43–50.

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.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference. 2nd ed. Springer-Verlag Inc., New York.

CAMPBELL, R. B. 1970. Pronghorn, sheep, and cattle range relationships in Carter County, Montana. M.S. thesis, Montana State University, Missoula.

COURCHAMP, F., T. CLUTTON-BROCK, AND B. GRENFELL. 1999. Inverse density dependence and the Allee effect. Trends in Ecology & Evolution 14:405–410.

DANVIR, R. E. 2000. Environmental and density-dependent effects on a northern Utah pronghorn population. Proceedings of the Pronghorn Antelope Workshop 17:36–41.

DEBLINGER, R. D., A. W. ALLDREDGE, AND L. SASLAW. 1984. Migratory patterns of pronghorn in the Red Desert, Wyoming. Proceedings of the Pronghorn Antelope Workshop 11:90–91.

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.

FAIRBANKS, W. S. 1993. Birthdate, birthweight, and survival in pronghorn fawns. Journal of Mammalogy 74:129–135.

GOLDBERG, D. E., AND R. M. TURNER. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. Ecology 67:695–712.

GOTELLI, N. J. 1998. A primer of ecology. 2nd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

HAILEY, T. L., J. W. THOMAS, AND R. M. ROBINSON. 1966. Pronghorn die-off in Trans-Pecos Texas. Journal of Wildlife Management 30:488–496.

HEPWORTH, J. L. 1970. Winter wheat utilization by pronghorn antelope in northwestern Nebraska. Proceedings of the Pronghorn Antelope Workshop 4:6–9.

HERVERT, J. J., J. L. BRIGHT, L. A. PIEST, M. T. BROWN, AND R. S. HENRY. 2001. Sonoran pronghorn recovery: habitat enhancements to increase fawn survival. Proceedings of the Pronghorn Antelope Workshop 19:19–27.

HILLER, T. L., L. A. POWELL, T. D. McCOY, AND J. J. LUSK. 2009. Long-term agricultural land-use trends in Nebraska, 1866–2007. Great Plains Research 19:225–237.

JONES, J. K., JR. 1964. Distribution and taxonomy of mammals of Nebraska. University of Kansas Publications, Museum Natural History 16:1–356.

KIE, J. G., D. L. DRAWE, AND G. SCOTT. 1980. Changes in diet and nutrition with increased herd size in Texas white-tailed deer. Journal of Range Management 33:28–34.

KOHLMANN, S. G. 2004. Population dynamics and modeling. Pp. 645–674 in Pronghorn ecology and management (B. W. O'Gara and J. D. Yoakum, eds.). University Press of Colorado, Boulder.

KRAMER, A. M., B. DENNIS, A. M. LIEBHOLD, AND J. M. DRAKE. 2009. The evidence for Allee effects. Population Ecology 51:341–354.

LANDE, R. 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. Oikos 83:353–358.

LEATHWICK, J. R., D. ROWE, J. RICHARDSON, J. ELITH, AND T. HASTIE. 2005. Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Freshwater Biology 50:2034–2052.

LIEBHOLD, A., AND J. BASCOMPTE. 2003. The Allee effect, stochastic dynamics, and the eradication of alien species. Ecology Letters 6:133–140.

LIPETZ, V. E., AND M. BEKOFF. 1982. Group size and vigilance in pronghorns. Zeitschrift für Tierpsychologie 58:203–216.

LOESER, M. R., S. D. MEZULIS, T. D. SISK, AND T. C. THEIMER. 2005. Vegetation cover and forb responses to cattle exclusion: implications for pronghorn. Rangeland Ecology and Management 58:234–238.

McNAY, M. E., AND B. W. O'GARA. 1982. Cattle–pronghorn interactions during the fawning season in northwestern Nevada. Pp. 593–606 in Wildlife–livestock relationships symposium (J. M. Peek and G. D. Dalke, eds.). Forest, Wildlife and Range Experiment Station, University Idaho, Moscow.

MORRIS, D. W. 2002. Measuring the Allee effect: positive density dependence in small mammals. Ecology 83:14–20.

MURRAY BERGER, K., AND M. M. CONNER. 2008. Recolonizing wolves and mesopredator suppression of coyotes: impacts on pronghorn population dynamics. Ecological Applications 18:599–612.

OCKENFELS, R. A., C. L. DOROTHY, AND J. D. KIRKLAND. 1992. Mortality and home range of pronghorn fawns in central Arizona. Proceedings of the Pronghorn Antelope Workshop 15:78–92.

O'GARA, B. W. 2004. Mortality factors. Pp. 379–394 in Pronghorn ecology and management (B. W. O'Gara and J. D. Yoakum, eds.). University Press of Colorado, Boulder.

PEARCE, J., AND S. FERRIER. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

POST, E., AND N. C. STENSETH. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. Journal of Animal Ecology 67:537–543.

R DEVELOPMENT CORE TEAM. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. Accessed 1 June 2009.

ROEBUCK, C. M. 1982. Comparative food habits and range use of pronghorn and cattle in the Texas Panhandle. M.S. thesis, Texas Tech University, Lubbock.

SÆTHER, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology & Evolution 12:143–149.

SHRAUDER, P. A. 1984. Appalachian mountains. Pp. 331–344 in White-tailed deer: ecology and management (L. K. Halls, ed.). Stackpole Books, Harrisburg, Pennsylvania.

SIMPSON, D. C., L. A. HARVESON, C. E. BREWER, R. E. WALSER, AND A. R. SIDES. 2005. Influence of precipitation on pronghorn demography in Texas. Journal of Wildlife Management 71:906–910.

SKOGLAND, T. 1986. Density dependent food limitation and maximal production in wild reindeer herds. Journal of Wildlife Management 50:314–319.

SMYSER, T. J., A. F. REEVE, AND E. O. GARTON. 2006. Evaluation of pronghorn population productivity relative to broad-scale habitat variables in Wyoming (1978–2003). Proceedings of the Pronghorn Antelope Workshop 22:41–52.

STEPHENS, P. A., AND W. J. SUTHERLAND. 1999. Consequences of the Allee effect for behavior, ecology, and conservation. Trends in Ecology & Evolution 14:401–405.

STEPHENS, P. A., W. J. SUTHERLAND, AND R. P. FRECKLETON. 1999. What is the Allee effect. Oikos 87:185–190.

SUETSUGU, H. 1971. Surveys and management of antelope. Job Completion Report, March 1, 1970 to February 29, 1971, Nebraska Game and Parks Commission, Pittman-Robertson Project W-15-R-27:64–84.

TORBIT, S. C., R. B. GILL, A. W. ALLDREDGE, AND J. C. LIEWER. 1993. Impacts of pronghorn grazing on winter wheat in Colorado. Journal of Wildlife Management 57:173–181.

WEST, D. R. 1970. Effects of prolonged deep snow and cold winters on pronghorn mortality and reproduction in South Dakota. Proceedings of the Pronghorn Antelope Workshop 4:41–47.

WITTMER, H. U., A. R. E. SINCLAIR, AND B. N. MCLELLAN. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144:257–267.

YOAKUM, J. D. 1990. Food habits of the pronghorn. Proceedings of the Pronghorn Antelope Workshop 14:102–111.

YOAKUM, J. D. 2004. Habitat characteristics and requirements. Pp. 409–445 in Pronghorn ecology and management (B. W. O'Gara and J. D. Yoakum, eds.). University Press of Colorado, Boulder.