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PRONGHORN POPULATION IRRUPTIONS

Title:

IRRUPTIVE POPULATION DYNAMICS IN YELLOWSTONE PRONGHORN

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Abstract. Irruptive population dynamics appear to be widespread in large herbivore populations, but there are few empirical examples from long time series with small measurement error and minimal harvests. We analyzed an 89-year time series of counts and known removals for pronghorn (*Antilocapra americana*) in Yellowstone National Park of the western United States during 1918-2006 using a suite of density-dependent, density-independent, and irruptive models to determine if the population exhibited irruptive dynamics. Information-theoretic model comparison techniques strongly supported irruptive population dynamics (Leopold model) and density dependence during 1918-1946, with the growth rate slowing after counts exceeded 600 animals. Concerns about sagebrush (*Artemisia spp*.) degradation led to removals of >1,100 pronghorn during 1947-1966 and counts decreased from approximately 700 to 150. The best models for this period (Gompertz, Ricker) suggested culls replaced intrinsic density-dependent

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mechanisms. Contrary to expectations, the population did not exhibit enhanced demographic vigor soon after the termination of the harvest program, with counts remaining between 100-190 animals during 1967-1981. However, the population irrupted (Caughley model with a 1-year lag) to a peak abundance of approximately 600 pronghorn during 1982-1991, with a slowing in growth rate as counts exceeded 500. Numbers crashed to 235 pronghorn during 1992-1995, perhaps because important food resources (e.g., sagebrush) on the winter range were severely diminished by high densities of browsing elk, mule deer, and pronghorn. Pronghorn numbers remained relatively constant during 1996-2006, at a level (196-235) lower than peak abundance, but higher than numbers following the release from culling. The dynamics of this population supported the paradigm that irruption is a fundamental pattern of growth in many populations of large herbivores with high fecundity and delayed density-dependent effects on recruitment when forage and weather conditions become favorable after range expansion or release from harvesting. Incorporating known removals into population models that can describe a wide range of dynamics can greatly improve our interpretation of observed dynamics in intensively-managed populations.

Keywords: Antilocapra americana; *density dependence; large herbivores; logistic growth; time series.*

INTRODUCTION

A dominant paradigm in managing large herbivores is that populations increase to peak abundance following introduction to a new range, crash to a lower abundance, and then increase to a carrying capacity lower than peak abundance (Leopold 1943, Riney 1964, Caughley 1970, McCullough 1997, Forsyth and Caley 2006). Caughley (1979) argued a similar, but lesser, irruptive dynamic was likely for populations released from harvesting because the herbivore had been in the system for some time and some food has already been removed; thus, the potential to overshoot carrying capacity was reduced. Pronounced fluctuations in population size are not uncommon in ungulates and have been related to changes in food availability, disease or parasite infestation, and predator numbers (e.g., Sinclair 1979, Bergerud 1983, Leader-Williams 1988, Fryxell et al. 1991). In one of the most detailed studies of demography and dynamics in a naturally regulated population of mammals, the Soay sheep (*Ovis aries*) population of Hirta in the St. Kilda archipelago of the United Kingdom showed a marked and persistent pattern of irregular irruptions and population crashes, sometimes increasing or declining by more than 60% in a year (Clutton-Brock et al. 1997, Clutton-Brock and Pemberton 2007). Forsyth and Caley (2006) also found some evidence to support the widespread existence of irruptive dynamics, including greater magnitude of irruptions in herbivores introduced to a new range than those released from harvesting. However, they lamented the paucity of empirical examples from long time series (>20 years) with small measurement error and minimal harvests and encouraged the consideration of irruptive models in future studies of large-herbivore dynamics.

Managers of Yellowstone National Park in the western United States culled >1,100 pronghorn (*Antilocapra americana*) during 1947-1968 due to concerns about sagebrush (*Artemisia sp.*) degradation (Houston 1982). A moratorium on culling was instituted in 1969 when numbers decreased to <200 and there were concerns about apparent isolation and reductions in the quantity and quality of available winter range (Cole 1971, Scott 2004). Since that time, pronghorn numbers have exhibited periods of relative stability for 10-15 years, punctuated by rapid, dramatic fluctuations in numbers (Keating 2002). Understanding these dynamics is essential for developing feasible management strategies to conserve this population that retains one of only two pronghorn migrations remaining in the greater Yellowstone region, but faces a serious risk of extirpation (National Research Council 2002, White et al. 2007).

We evaluated the time series of counts and known removals for Yellowstone pronghorn during 1918-2006 using competing model formulations that described a wide range of dynamics to determine if the complex dynamics of this population were best characterized by irruptive models. We also evaluated if pronghorn numbers had decreased below a critical density threshold where the instantaneous rate of increase would likely continue to decrease, thereby increasing the likelihood of extirpation (i.e., Allee effect; Courchamp et al. 1999). While our work did not explicitly examine the effects of climate on the population, results provided significant insights regarding irruptive population dynamics and model formulations for large herbivores. Our analyses incorporated known removals of pronghorn into population models to obtain a more accurate measure of annual variation in the population growth rate. Thus, the results also have direct applicability to intensively-managed populations of large herbivores.

STUDY AREA

Yellowstone pronghorn inhabited foothills, mountain slopes, and valley bottoms along the Gardiner, Lamar, and Yellowstone Rivers in the northern portion of Yellowstone National Park, Wyoming, and adjacent areas of Montana (Boccadori 2002). The climate was characterized by short, cool summers and long, cold winters with a mean annual temperature of 1.8 C. Mean annual precipitation varied from 25-35 cm as elevation increased from 1,500 m in river drainages to 2,400 m on mountains. Average snow-water equivalents (amount of water in snow) ranged from 2-30 cm along this elevation gradient, with relatively severe winters occurring in 1949, 1962, 1969, and 1997 (Farnes et al. 1999). There were periods of severe to extreme drought in northwestern Wyoming during 1930-1936, 1952-1960, 1974-1980, 1987-1994, and 1998-2005 (Palmer Drought Severity Index, National Climatic Data Center).

The lower-elevation habitat used by pronghorn was primarily open grassland-sagebrush steppe with interspersed upland grasslands, wet meadows, old agricultural fields (e.g., crested wheatgrass *Agropyron cristatum*) and pastures, agricultural fields on private land (alfalfa *Medicago sativa*), and non-vegetated areas (Boccadori 2002, Savage 2005). Dominant plant species included big sagebrush, bluebunch wheatgrass (*Elymus spicata*), Idaho fescue (*Festuca idahoensis*), greasewood (*Sarcobatus vermiculatus*), prairie junegrass (*Koeleria macrantha*), rabbitbrush (*Chrysothamnus* spp.), and Sandberg bluegrass (*Poa secunda*). Coniferous forests of Douglas fir (*Pseudotsuga menziesii*, Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) were interspersed at higher elevations (Savage 2005). Large-scale fires during 1988 burned approximately 30% of the pronghorn summer range, but none of the winter range (Scott and Geisser 1996).

The pronghorn range supported a diverse predator complex, including grizzly bears (*Ursus arctos*), black bears (*U. americanus*), mountain lions (*Puma concolor*), coyotes (*Canis latrans*), and, after 1995, wolves (*Canis lupus*). Wolf and bear predation on pronghorn adults and fawns was low (Mattson 1997, Smith 2005). However, coyote predation was a significant limiting factor for Yellowstone pronghorn, contributing to substantial fawn mortality, decreased recruitment, and some adult mortality (Byers 2002, National Research Council 2002, Scott 2004).

METHODS

Counts during late December to mid-April were conducted from the ground during 1918-1955, by helicopter during 1956-1968, and by airplane during 1969-2005 (Houston 1982, Singer and Norland 1994, Keating 2002, Barmore 2003, Scott 2004). We conducted 11 aerial counts during 2002-2006 and used logistic regression models to evaluate the detection of marked pronghorn (Samuel et al. 1987). A 2-covariate model with group size and range (summer, winter) received the most support ($AIC_c = 120.0$, $w_i = 0.67$), but a 1-covariate model with range was also supported ($\Delta AIC_c = 1.48$, $w_i = 0.32$). These models indicated the predicted detection of pronghorn was high (89%) on the winter range and approximated 100% for groups >5 (Appendix A).

Multiple counts (2-6) per year were conducted during 1969-1972, 1976, 1987-1992, and 1997-1998 and we used the single highest count each winter to estimate abundance. No counts were conducted during 1919-1921, 1926-1928, 1943, 1950, 1958-60, and 1994, while counts were deemed "poor" during 1934, 1942, 1982, and 2004 (Keating 2002). We used Eberhardt's (1987) polynomial models to estimate counts for years of no and poor counts because we needed successive population estimates to evaluate the effects of removals during all years. More than 1,100 pronghorn were culled within the park during 1947-1968 due to concerns about sagebrush degradation (Houston 1982). In addition, approximately 190 pronghorn depredating alfalfa fields adjacent to the park were harvested during autumn 1985-2002 (Montana Fish, Wildlife, and Parks, unpublished data).

We conducted regression analyses comparing the relative change in total population size ($r_t = ln\ n_{t+1} - ln\ n_t$) to the natural logarithm of the count ($ln\ n_t$), to identify significant break-points in density-related effects, assess the effects of removals during 1947-1968 on population dynamics, and evaluate if there was a positive relationship between population growth rate and density

(Courchamp et al. 1999, Piepho and Ogutu 2003). We also evaluated the change in total population size using a suite of density-independent, density-dependent, and irruptive models. A population with no limiting factors may grow according to the stochastic growth equation (i.e., perturbed exponential growth),

$$n_{t+1} = n_t \exp(a + \sigma\varepsilon) \tag{1}$$

where ε and σ represent the stochastic contribution from noise and unmodeled processes. Alternatively, the population may grow according to a random-walk model,

$$n_{t+1} = n_t \exp(\varepsilon) \tag{2}$$

where population growth rate is uncorrelated with population size. The stochastic Gompertz model takes a density-dependent form:

$$n_{t+1} = n_t \exp(a + b \ln n_t + \sigma\varepsilon). \tag{3}$$

where a represents population growth rate without the influence of density and b represents the strength of density dependence. A population is said to exhibit a density-dependent response if b differs significantly from zero (Zeng et al. 1998, Jacobson et al. 2004). In contrast, the stochastic Ricker model assumes exponential density dependence:

$$n_{t+1} = n_t \exp(a + bn_t + \sigma\varepsilon). \tag{4}$$

The most commonly used model for understanding the dynamics of large herbivore populations is the θ-logistic (Turchin 2003):

$$n_{t+1} = n_t \exp(r_m[1 - (n_t/K)^{\theta}]) \tag{5}$$

where r_m is the intrinsic rate of increase, K is the carrying capacity, and θ is the shape parameter influencing the form of density dependence. The delayed-logistic model (Hutchinson 1948) describes a time delay (T) in the effect of abundance on the population's growth rate:

$$n_{t+1} = n_t \exp(r_m[1 - (n_{t-T}/K)^{\theta}]). \tag{6}$$

The θ-logistic only generates irruptive dynamics when $r_m > 2$ (May 1981), which has not been observed for large herbivores (Sinclair 1996). Also, the delayed-logistic does not capture the crash and subsequent increase in abundance following an irruption. Thus, Forsyth and Caley (2006) developed a new irruptive model by adding a term (S) to the θ-logistic model that afforded affords more flexibility in fitting the model to data by allowing changes in carrying capacity over time ("Leopold model"):

$$n_{t+1} = \{n_t \exp[r_m(1 - [n_t/(K + S(1 - t/t_K))]^{\theta})] \text{ for } t \leq t_K \text{ and } n_t \exp[r_m(1 - [n_t/K]^{\theta})] \text{ for } t > t_K\} \quad (7)$$

They also produced a variant of this model by adding a time lag, T, to increase the magnitude of the population crash and attain a post-crash equilibrium via dampening oscillations ("Caughley model"):

$$n_{t+1} = \{n_t \exp[r_m(1 - [n_{t-T}/(K + S(1 - t/t_K))]^{\theta})] \text{ for } t \leq t_K \text{ and } n_t \exp[r_m(1 - [n_{t-T}/K]^{\theta})] \text{ for } t > t_K\} \quad (8)$$

We fit models with the response variable n_{t+1} to data from 3 periods (1918-1946, 1947-1968, 1969-2006) based on changes in management policies, sampling methodology and error, and removal rates. The 1918-1946 period included intensive husbandry (feeding, fencing/herding, predator control), few removals, counts from the ground, and numerous missing or poor counts. Husbandry ceased in 1935 and pronghorn were allowed to increase their distribution and abundance. The 1947-1968 period included sizable culls and translocations from the park that were irregularly spaced over time, ground and helicopter counts, and several missing counts. The 1969-2006 period included a moratorium on culling inside the park, relatively small harvests outside the park, airplane counts, and the restoration of wolves in 1995-1996.

Annual population estimates, n_t, were generally expressed as $n_t = n_t' + C_t$, where n_t' refers to the number of counted individuals, C_t the number of removals, and t the annual index ($t = 1, 2, \ldots, N-1$). In 1940, 1941, 1954, and 1957, however, we expressed the population estimate as $n_t =$

$n_t' - C_t$ because removals occurred after a December count. We assumed all error was lognormally distributed and observational (i.e., process error was not modeled separately). We estimated θ for the θ-logistic and delayed-logistic models, but set $\theta = 1$ for remaining models. We examined time lags up to 10 years ($T = 1, 2, \ldots, 10$) for the delayed-logistic and Caughley models. Owing to convergence problems while using t_K as a parameter, we examined data for each period and set t_K at the approximate year in which population dynamics changed from that described by the Leopold (or Caughley) model to the θ-logistic (or delayed-logistic) model. We also constrained r_m within biologically sensible values (Forsyth and Caley 2006). We used program R version 2.3.1 (R Development Core Team 2006) to fit models and estimate parameter coefficients. We used Akaike's Information Criterion corrected for small sample size (AIC$_c$) as model-selection criterion (Burnham and Anderson 2002). In addition, we conducted exploratory modeling to re-fit the best model for 1969-2006 to the periods 1976-2006 and 1981-2006 to see if the fit improved when the time series started at, or near, the beginning of the exponential growth period.

RESULTS

Counts of pronghorn increased from approximately 250 to >600 during 1918-1932, but then decreased to approximately 400 by 1935 during a severe drought (Fig. 1). The relative change in total population size (r_t) was not significantly related to the natural logarithm of the count ($ln\ n_t$) during this period of intense husbandry ($R^2 = 0.05$, $P = 0.36$; 95% CI for slope: -0.31, 0.12; Fig. 2). Counts then increased to a high of 811 pronghorn during 1936-1946, after husbandry ceased and pronghorn were allowed to expand their distribution. There was a significant negative relationship ($R^2 = 0.53$; $P = 0.01$; slope: -1.26, -0.21) between r_t and $ln\ n_t$ after pronghorn counts consistently exceeded 600 animals. Data provided considerable support for the Leopold model during 1918-1946 ($\text{AIC}_c = 348.21$, $w_i = 0.23$), which produced significant estimates of $r_m = 0.49$ (95% CI = 0.14, 0.83; $P = 0.008$), $K = 691$ (594, 788; $P < 0.001$), and $S = -426$ (-627, -225; $P = 0.001$; Fig. 3). There was also support for the Ricker ($\Delta\text{AIC}_c = 1.18$; $w_i = 0.13$) and Gompertz ($\Delta\text{AIC}_c = 1.75$, $w_i = 0.10$) models, though parameter estimates slightly overlapped zero (Ricker: $\hat{a} = 0.24$ [-0.01, 0.49; $P = 0.06$], $\hat{b} = -0.00037$ [-0.00077, 0.00004; $P = 0.07$]; Gompertz: $\hat{a} = 1.16$ [-0.22, 2.54; $P = 0.10$], $\hat{b} = -0.18$ [-0.40, 0.04; $P = 0.10$]).

Counts of pronghorn decreased from approximately 700 to <200 during 1947-1968 due to at least 8 culls of 32-258 pronghorn (Fig. 1). There was no relationship between r_t and $ln\ n_t$ ($R^2 = 0.02$, $P = 0.52$; slope: -0.37, 0.19; Fig. 2) during the most intense period of culling between 1947-1961, which also included sustained drought during 1953-1961. Annual rates of increase remained high (0.1-0.3) during 1947-1968, after accounting for culls, with the exception of 1958-1962 when rates were negative, apparently in response to a reduction in carrying capacity. There was an apparent density-dependent relationship between r_t and $ln\ n_t$ ($R^2 = 0.79$, $P = 0.008$; slope: -2.0, -0.52) during 1962-1968, with counts remaining between 120-190. Data provided considerable support for the Gompertz model during 1947-1968 ($\text{AIC}_c = 268.59$, $w_i = 0.545$, Fig. 3), which produced significant estimates of $\hat{a} = 2.86$ (0.92, 4.81; $P = 0.006$) and $\hat{b} = -0.51$ (-0.84, -0.18; $P = 0.004$). Also, there was support for the Ricker model ($\Delta\text{AIC}_c = 1.21$; $w_i = 0.30$), though parameter estimates slightly overlapped zero ($\hat{a} = 0.34$ [-0.06, 0.73; $P = 0.09$], $\hat{b} = -0.0012$ [-0.0021, 0.0002; $P = 0.02$]). Many of the delayed-logistic and Caughley time lag models did not converge to biologically meaningful parameter estimates.

There was an apparent density-dependent relationship between r_t and $ln\ n_t$ ($R^2 = 0.68$, $P = 0.001$; slope: -2.1, -0.8) during 1969-1981 and counts remained between 102-165 even though no pronghorn were culled (Figs. 1 and 2). These years were characterized by a severe drought during 1974-1980 and an increase in counts of sympatric elk from 4,000 to 16,000 (Houston 1982). Pronghorn numbers irrupted to >594 during 1982-1991 and there was a significant negative relationship between r_t and $ln\ n_t$, after counts exceeded 500 pronghorn ($R^2 = 0.62$, $P = 0.007$; slope: -0.8, -0.2). There was a precipitous decrease in counts from 536 to 235 pronghorn during 1992-1995. Counts remained between 196-235 during 1996-2006 and the relationship between r_t and $ln\ n_t$ was not significant ($R^2 = 0.25$, $P = 0.12$; slope: -1.2, 0.2; Fig. 2). Data provided considerable support for the Caughley model with a time lag of 1 year during 1969-2006 ($\mathrm{AIC_c} = 399.99$, $w_i = 0.21$), which produced significant estimates of $r_m = 0.18$ (0.05, 0.31; $P = 0.007$), $K = 177$ (54, 300; $P = 0.006$), and $S = 1049$ (165, 1933; $P = 0.02$; Fig. 3). There was also support for the Caughley time lag 5 ($\Delta\mathrm{AIC_c} = 1.47$; $w_i = 0.10$), Caughley time lag 8 ($\Delta\mathrm{AIC_c} = 1.89$; $w_i = 0.08$), and delayed-logistic time lag 5 models ($\Delta\mathrm{AIC_c} = 1.98$; $w_i = 0.08$). Confidence intervals did not span zero for parameters r_m and K in the Caughley models with a 5-year lag ($r_m = 0.49$ [0.14, 0.83; $P = 0.007$], $K = 691$ [594, 788; $P < 0.001$], $S = -426$ [-627, -225; $P = 0.20$]) and an 8-year lag ($r_m = 0.20$ [0.05, 0.345; $P = 0.01$], $K = 254$ [154, 355; $P < 0.001$], $S = -83$ [-354, 189; $P = 0.54$]). Only K was significant in the delayed-logistic model with a 5-year lag ($r_m = 0.19$ [-0.39, 0.78; $P = 0.51$], $K = 293$ [154, 433; $P < 0.001$], $\theta = 1.00$ [-2.31, 4.31; $P = 0.54$]).

The exploratory models for 1976-2006 and 1981-2006 progressively improved the fit of the Caughley time lag 1 model compared to the a priori 1969-2006 model (Fig. 3). Confidence intervals did not span zero for parameters r_m, K, and S in the Caughley time lag 1 model for the 1976-2006 period ($r_m = 0.24$ [0.09, 0.39; $P = 0.003$], $K = 199$ [86, 311; $P = 0.001$], $S = 763$ [187, 1338; $P = 0.01$]) and the 1981-2006 period ($r_m = 0.31$ [0.14, 0.48; $P < 0.001$], $K = 217$ [118, 316; $P < 0.001$], $S = 554$ [186, 922; $P = 0.005$]).

DISCUSSION

The dynamics of the pronghorn population in Yellowstone National Park support the paradigm that irruption is a fundamental and natural pattern of growth in populations of large herbivores with high fecundity and delayed density-dependent effects on recruitment when forage and weather conditions become favorable after range expansion or release from harvesting (Caughley 1979, Clutton-Brock et al. 1997, Forsyth and Caley 2006). Irruptive population dynamics were supported in population models for Yellowstone pronghorn during the time periods when park managers did not conduct intensive culling. The Leopold model, which predicts an irruption followed by a gradual decline to carrying capacity (Forsyth and Caley 2006), received the most support during the period of husbandry and range expansion from 1918-1946. However, we could not evaluate the population crash and post-crash dynamics because intense culling began in 1947. Thus, it is possible an oscillatory Caughley or delayed-logistic model would have better described the dynamics if they had continued uninterrupted.

The Gompertz model was highly supported during 1947-1968, suggesting that culling acted in place of a density-dependent mechanism. A moratorium on culling was instituted in 1969 when numbers decreased to <200 and there were concerns about apparent isolation and reductions in the quantity and quality of available winter range (Cole 1971, Scott 2004). There is typically enhanced demographic vigor after the termination of control measures because the reduction in density increases per capita resources and, in turn, the fecundity and survival of survivors (Caughley and Sinclair 1994). However, Yellowstone pronghorn did not exhibit irruptive dynamics immediately after their release from culling and counts remained between 100-190 animals until 1981. Houston (1982) speculated that culling during 1947-1968 reduced the population from one resource-limited stable state to a lower state maintained by natural predation (primarily coyotes), incidental human predation (vehicle strikes), and dispersal. We found some evidence for this reduction (Fig. 2) and the low population growth rates at low densities, high pregnancy rates, and high predation in summer (O'Gara 1968, Houston 1982, Barmore 2003) support increased predation rather than a per capita decrease in food availability or predation-sensitive foraging as the causal factor during 1968-1980 (Wittmer et al. 2005). There was no evidence the rate of decline increased at lower densities (e.g., inverse density dependence).

The Caughley time lag 1 model received the most support during the period of protection following culling (1969-2006), characterizing a population irruption and subsequent crash. Thus, our findings convincingly showed that if a population is reduced and held at low abundances by continued removals, then there is a potential for the population to irrupt if removals cease and other conditions such as food quality and quantity and weather events are favorable. Explanations proposed for the irruption to a peak abundance of approximately 600 pronghorn during 1982-1991 included favorable weather and forage conditions, increased predator harvest outside the park, and increased irrigated cropland outside the park (Singer and Norland 1994, Scott 2004). However, none of these explanations have been strongly supported by other studies and the precise factors driving this increase in abundance remain unknown (Keating 2002). There was evidence of a density-related slowing in growth rate as counts exceeded 500, but density had a relatively weaker effect on growth during 1982-1994 ($\hat{b} = -0.49$) than 1969-1981 ($\hat{b} = -1.45$); suggesting an increase in per capita resources during the latter period. We need a better understanding of changes and renewal rates in food supplies to interpret these dynamics (Caughley 1976).

There was some indication the crash in pronghorn numbers during 1992-1995 was related to diminished food resources on the winter range. Intense browsing associated with the exponential growth in elk numbers from 4,000 to >19,000 during 1969-1988 contributed to a significant decrease in sagebrush on the pronghorn winter range, which was the major component of pronghorn diets and has high protein content during winter (Singer and Norland 1994, Singer and Renkin 1995, Wambolt and Sherwood 1999). The percent composition of sagebrush in the winter diets of pronghorn based on microhistological examination of feces decreased from approximately 70% during 1985-1988 (Singer and Norland 1994) to <10% during 2000-2001 (Boccadori 2002). Conversely, the percent composition of less-palatable rabbitbrushes (*Chrysothamnus* spp.) increased from approximately 5% to 60% during the same time periods. Pronghorn numbers have remained relatively constant after the crash during 1992-1995, at a level lower (200-235) than peak abundance (600), but higher than numbers following the release from culling (100-190). Additional monitoring is necessary to determine if the population has reached a stable equilibrium or is in a period of a dampened oscillation as predicted by the Caughley model (Forsyth and Caley 2006).

These results support other studies indicating irruptive behavior in large herbivore populations (e.g., Boyd 1981, Leader-Williams 1988, Peterson 1999). For example, Clutton-Brock et al. (1997) concluded that the high fecundity and rapid development of Soay sheep enabled them to evade density-dependent effects on recruitment until numbers exceeded carrying capacity by a substantial margin, subsequently triggering overcompensatory mortality in all age classes. While the irruptions and subsequent crashes in Yellowstone pronghorn occurred over larger temporal scales, the population appears to have been influenced by both bottom-up and top-down processes during the 1918-1946 and 1969-2006 periods during which minimal or no removals occurred. Yellowstone pronghorn have high fecundity, with most does >2 years old twinning each year (O'Gara 1968, Byers 2002). The irruption during 1982-1991 was spurred by high recruitment (80 fawns per 100 does) during 1982 and 1986, while recruitment decreased precipitously to 8-22 fawns per 100 does during the crash from 1992-1995 (Yellowstone Center for Resources, unpublished data).

Because the primary goal of this research was to determine whether the Yellowstone pronghorn population exhibited irruptive dynamics, examining the effects of climate, food availability, and predation was beyond the scope of this work. Also, evaluating a full suite of models that consider climate, food availability, and predation effects dating back to 1918 is problematic because data on coyote abundance in Yellowstone is incomplete and rigorous annual measures of forage biomass are not available. Data on large-scale climate variability is available for a portion of the 1969-2006 period, but preliminary analyses suggest climate played only a supporting role in affecting pronghorn population dynamics. Therefore, any future work in attempting to elucidate mechanisms that influenced Yellowstone pronghorn may have to rely solely on partial data to describe a complex phenomenon.

Our exploratory modeling exercise indicated the fit and predictive capability of irruptive models was sensitive to the date of origin for the time series. The Caughley time lag 1 model fit poorly when data included the period of relative stability in counts during 1969-1980. However, fit improved remarkably when the time series was constrained to begin in 1981, at the start of the period of exponential growth (Fig. 3). This sensitivity is supported by examinations of irruptive model fits to time series of data from other ungulate species (Forsyth and Caley 2006:301). Thus, we suggest that these irruptive models are most applicable for data sets that document immediate irruptions in the population, but not a period of extended stability prior to the irruption.

The apparent reduction in carrying capacity for Yellowstone pronghorn following the crash in abundance during 1992-1995 is worrisome because this population faces a serious risk of extirpation (National Research Council 2002:83). Though there is no evidence the population is below a critical density threshold where a positive relationship between growth rate and density would increase their likelihood of extinction (Courchamp et al. 1999), the quantity and quality of the winter range has diminished substantially since the 1960s and migration routes to historic wintering habitat outside the park have been fragmented by development, fencing, and other land-use practices (Singer and Renkin 1995, Caslick 1998, Scott 2004, Wagner 2006). The National Park Service has developed plans in conjunction with restoration experts to re-establish native vegetation dominated by big sagebrush/bluebunch wheatgrass to areas on the winter range once tilled for agriculture and now supporting invasive alien species. Park personnel are also working with the U.S. Forest Service, State of Montana, private landowners, and conservation organizations to improve connectivity between the park and historic winter ranges to the north. Similar problems and remedial actions are facing managers of migratory ungulates worldwide (Schaller 1988, Berger 2004, Thirgood et al. 2004, Johnson et al. 2005, Hebblewhite et al. 2006).

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APPENDIX A

A description of the development and results of sightability analyses from aerial counts of pronghorn in Yellowstone National Park is available in ESA's Electronic Data Archive: *Ecological Archives* xxxx-xxx-xx.

Figure Legends

FIG. 1. Counts (circles) and removals (bars) of pronghorn during 1918-2006 in and near Yellowstone National Park

FIG. 2. Observed population growth rates and predicted trends for pronghorn in and near Yellowstone National Park during (a) 1918-1946, (b) 1947-1968, and (c) 1969-2006.

FIG. 3. Observed and predicted abundances of pronghorn in and near Yellowstone National Park during 1918-2006. Predicted abundances were determined from the best approximating a priori and/or exploratory models during (a) 1918-1946, (b) 1947-1968, and (c) 1969-2006.

Figure 1.

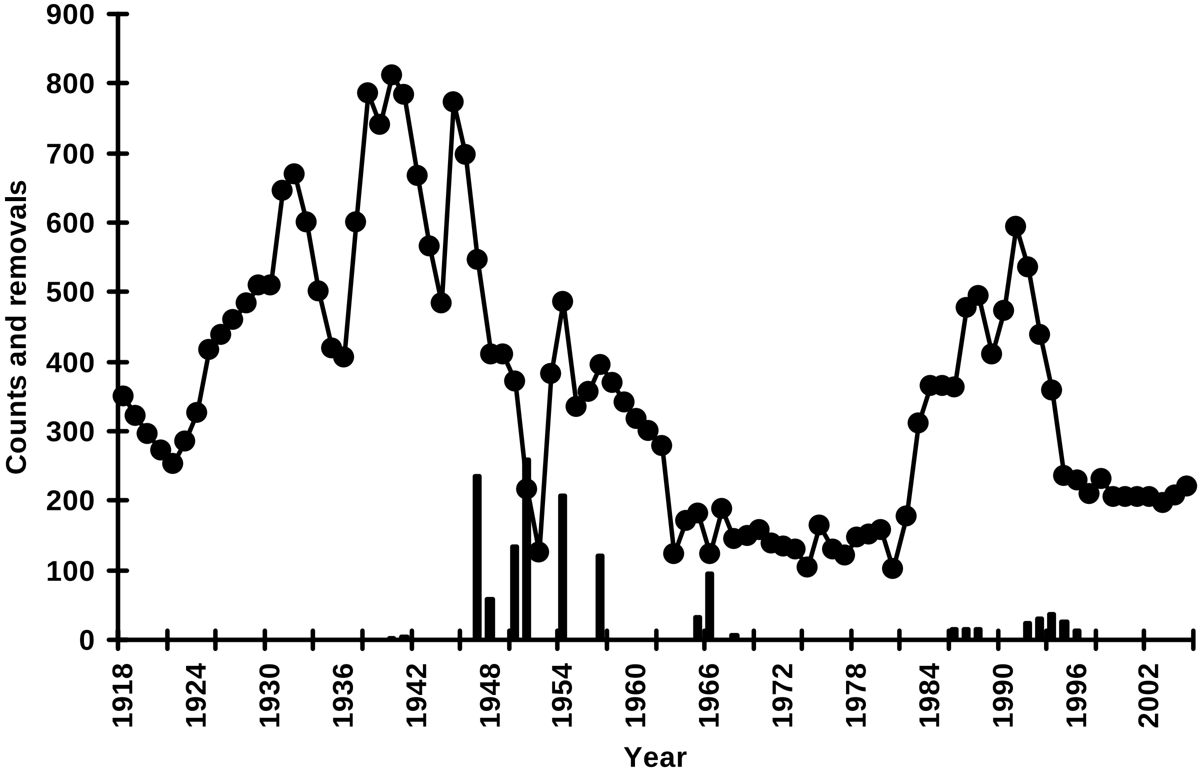
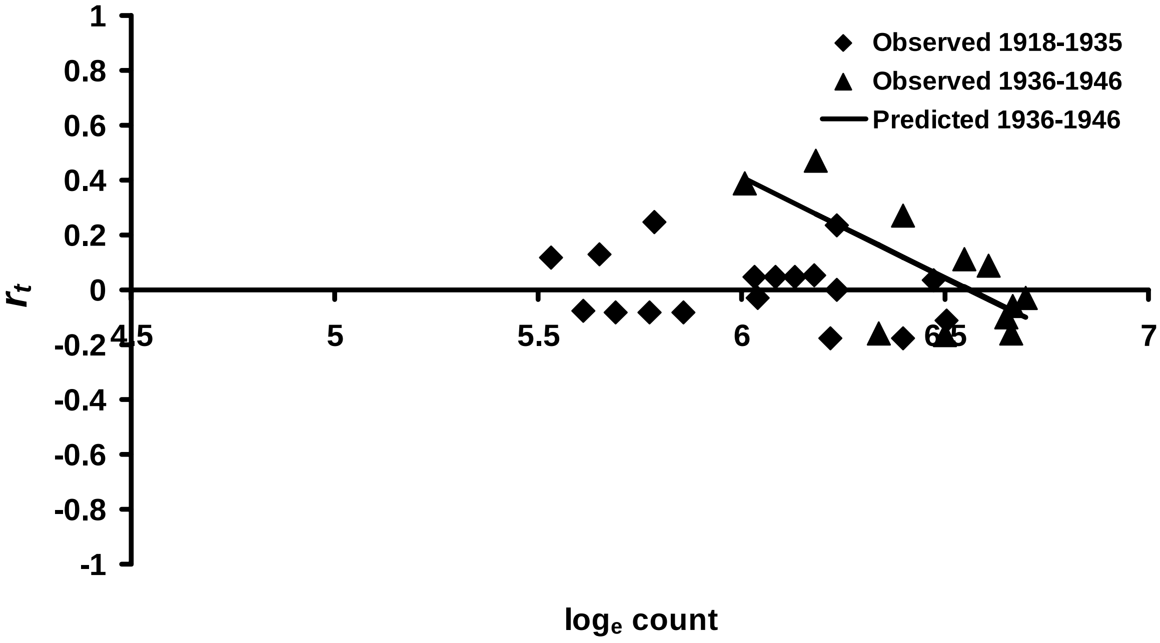
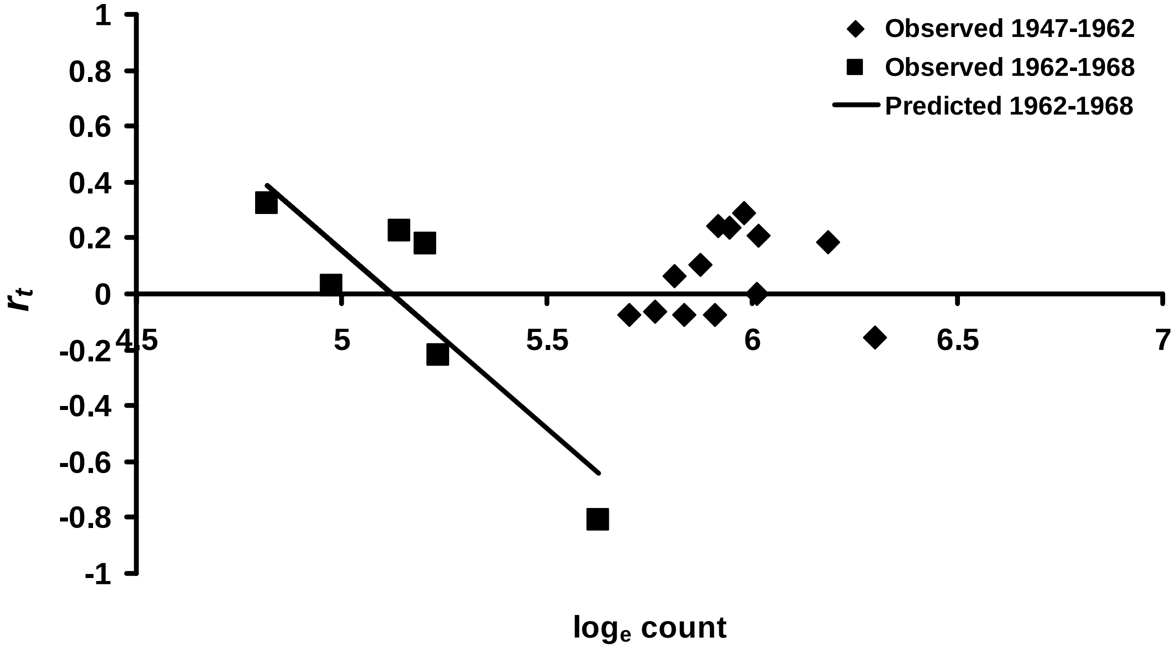

900
800
700
600
500
400
300
200
100
0
Counts and removals
1918
1924
1930
1936
1942
1948
1954
1960
1966
1972
1978
1984
1990
1996
2002
Year

Figure 2.



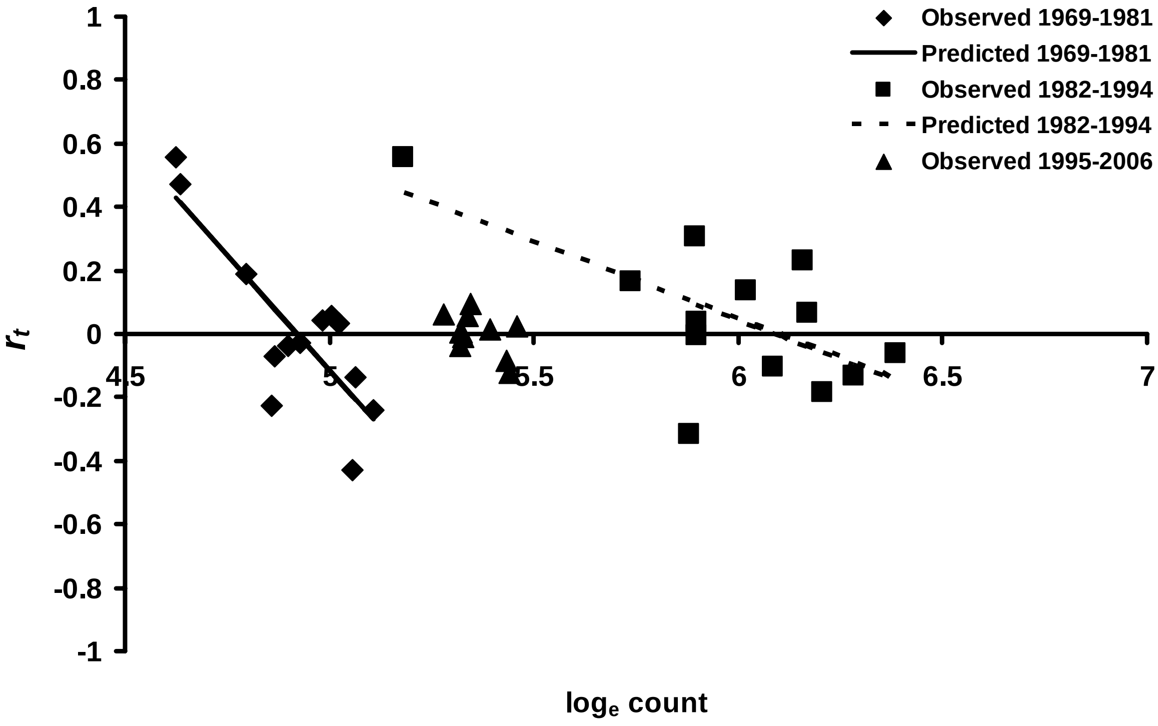
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
r_t
4.5
5
5.5
6
6.5
7
◆ Observed 1918-1935
▲ Observed 1936-1946
Predicted 1936-1946
log$_e$ count

(a)



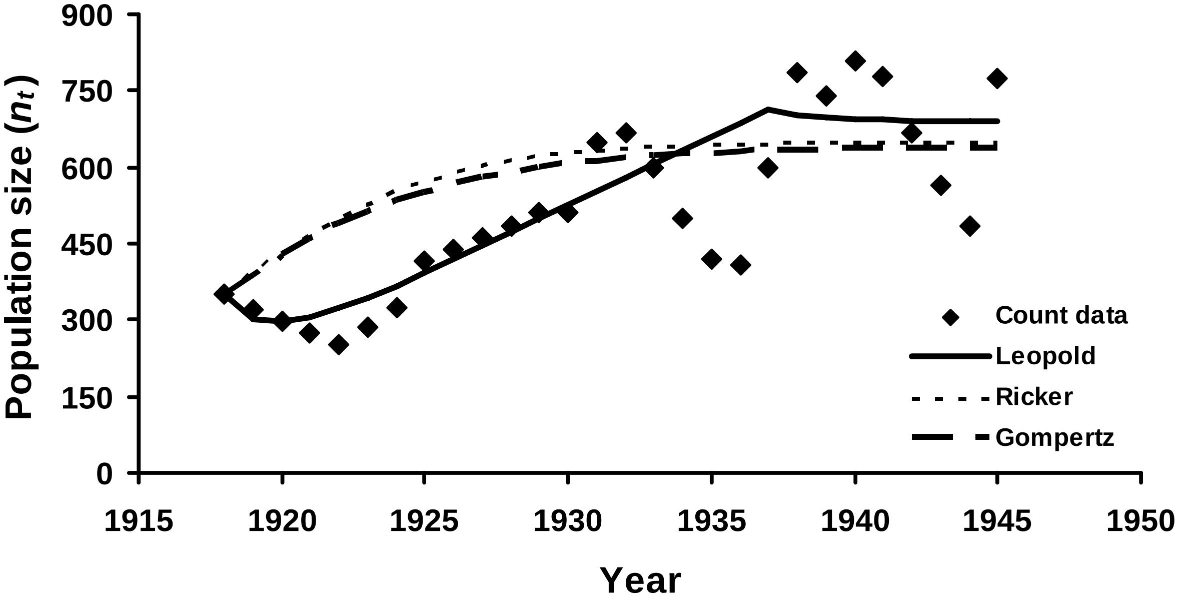
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
r_t
4.5
5
5.5
6
6.5
7
◆ Observed 1947-1962
■ Observed 1962-1968
Predicted 1962-1968
log$_e$ count

(b)

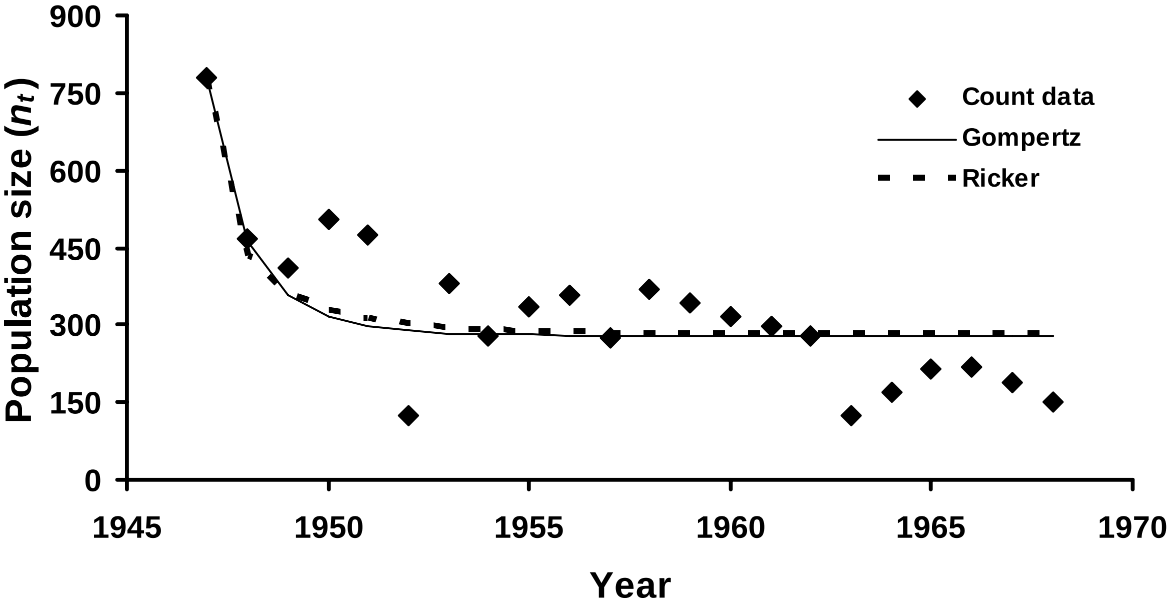

1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
r_t
4.5
5
5.5
6
6.5
7
$\log_e$ count
Observed 1969-1981
Predicted 1969-1981
Observed 1982-1994
Predicted 1982-1994
Observed 1995-2006

(c)

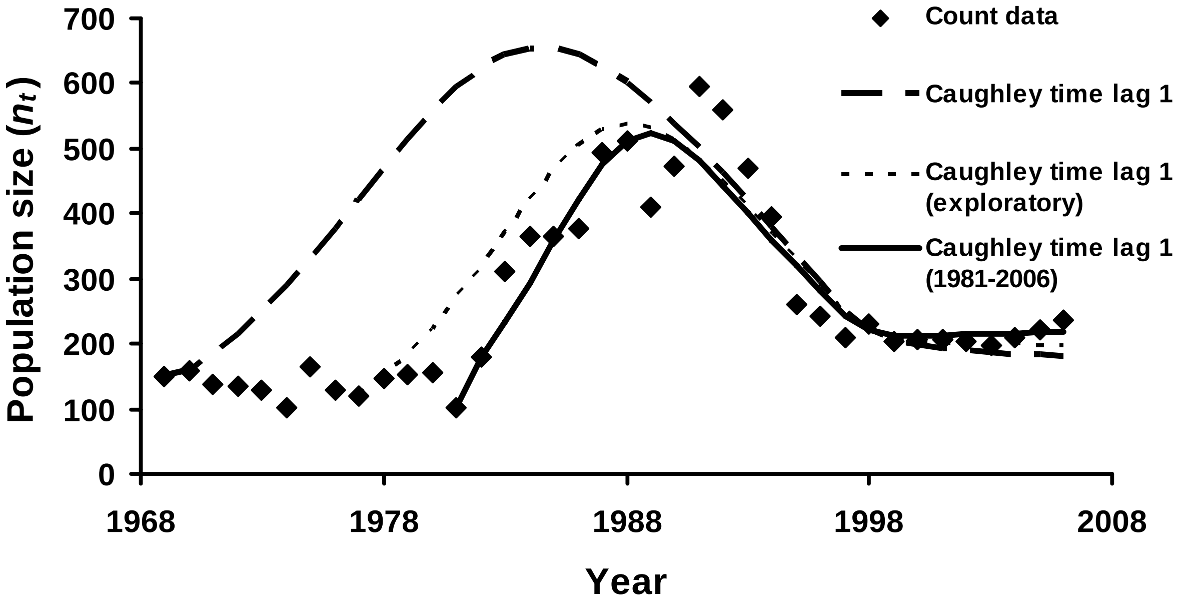
Figure 3.


900
750
600
450
300
150
0
Population size (n_t)
1915
1920
1925
1930
1935
1940
1945
1950
Year
Count data
Leopold
Ricker
Gompertz

(a)


900
750
600
450
300
150
0
Population size (n_t)
1945
1950
1955
1960
1965
1970
Year
Count data
Gompertz
Ricker

(b)


Population size (n_t)
700
600
500
400
300
200
100
0
1968
1978
1988
1998
2008
Year
◆ Count data
Caughley time lag 1
Caughley time lag 1 (exploratory)
Caughley time lag 1 (1981-2006)

(c)

APPENDIX A. Development and results of sightability analyses from aerial counts of pronghorn in Yellowstone National Park (Ecological Archives xxxx-xxx-xx).

Yellowstone pronghorn are typically counted by a single observer in an airplane during late March or early April when animals are concentrated on their winter range between Mammoth, Wyoming, and Mol Heron Creek, Montana, on the west side of the Gardner and Yellowstone Rivers. During some years, however, pronghorn begin migrating over Mt. Everts to their summer ranges several weeks early owing to mild late-winter conditions and early vegetation green-up. If pronghorn begin migrating prior to the count, then it is necessary to survey both the winter and summer ranges of pronghorn, which extend between Mol Heron Creek, Montana, and Mt. Norris in the upper Lamar Valley, Wyoming.

The detection of pronghorn varies among counts due to factors that influence an observer's ability to sight animals, such as snow cover, vegetation cover, group size, animal behavior, and observer experience. We suspected the detectability of pronghorn, especially those in groups of <10 animals, would be lower on the 244-km^2 summer range compared to the 30-km^2 winter range and 27-km^2 northern portion of Mt. Everts. We conducted 11 counts of Yellowstone pronghorn during 2002-2006 using a Super Cub airplane (Montana Aircraft, Bozeman) to fly transects across the winter and summer ranges. Observed pronghorn were considered on the summer range if they were located east of a straight line with endpoints at the confluence of Blacktail Deer Creek and the Yellowstone River and the confluence of Lava Creek with the Gardner River. We recorded group size, range (summer or winter), and other ancillary information. Immediately after each count, the pilot/observer team used telemetry to locate radio-collared pronghorn and determine if each group containing at least one radio-collared pronghorn was observed during the original count.

We developed logistic regression sightability models of the form, $y = exp(u) / (1 + exp(u))$, where y is the sighting probability, and u is the regression equation of covariates (x_i) expressed as $u = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n$. We defined covariates for the size of each group (GROUPSIZE) detected or missed and an indicator variable for the range (RANGE = 1 for winter range; RANGE = 0 for summer range) on which the group was located. Using the covariates GROUPSIZE and RANGE, we developed three competing models consisting of all possible combinations of covariate main effects. We fit models and estimated parameter coefficients using logistic regression techniques in R version 2.3.1. Ninety-five percent confidence bands for sightability estimates were determined using the Delta Method. We selected the top approximating models using Akaike's Information Criterion corrected for small sample size (AIC_c).

In total, 103 of 128 groups with radio-collared pronghorn were detected, including 32 of 48 groups on the summer range and 71 of 80 groups on the winter range. Group size varied between 1-61 animals (9.9 ± 0.7, mean ± SE), with a range of 1-27 animals (9.9 ± 0.9) on the summer range and 1-61 animals (9.9 ± 1.1) on the winter range. The two-covariate model (GROUPSIZE + RANGE) received the most support ($AIC_c = 120.0$, $w_i = 0.67$) and contained a significant RANGE covariate indicating a higher probability of sighting groups on the winter range (Table A1). This model also contained a positive GROUPSIZE covariate, though 95% confidence intervals slightly overlapped zero. The one-covariate RANGE model also received some support ($\Delta AIC_c = 1.48$, $w_i = 0.32$). The one-covariate GROUPSIZE model received little support ($\Delta AIC_c = 7.70$, $w_i = 0.01$).

Using the two covariate model, predicted sightability increased from 0.83-0.99 and 0.53-0.97 on the winter and summer ranges, respectively, as group size increased from 1-50 (Figs. A1 and A2). Predicted sightability was 0.89 and 0.67 on the winter and summer ranges, respectively, using the one covariate RANGE model.

TABLE A1. Model selection output of sightability models for pronghorn in Yellowstone National Park during 2002-2006 with the regression model structure, parameter estimates, 95% lower and upper confidence limits, ΔAIC_c value, and Akaike weight (w_i).

Model Structure	**ΔAIC_c**	**w_i**
$u = \beta_0 + \beta_1(GROUPSIZE) + \beta_2(RANGE = WINTER)$	0.000	0.667
$\beta_0 = 0.036\ (-0.910, 0.981)$		
$\beta_1 = 0.070\ (-0.011, 0.150)$		
$\beta_2 = 1.459\ (0.507, 2.411)$		
$u = \beta_0 + \beta_1(RANGE = WINTER)$	1.475	0.319
$\beta_0 = 0.693\ (0.087, 1.299)$		
$\beta_1 = 1.372\ (0.446, 2.299)$		
$u = \beta_0 + \beta_1(GROUPSIZE)$	7.696	0.014
$\beta_0 = 0.924\ (0.195, 1.653)$		
$\beta_1 = 0.055\ (-0.017, 0.128)$		

FIG. A1. Predicted sightability from the two-covariate model (GROUPSIZE + RANGE) for the winter and summer ranges of pronghorn in Yellowstone National Park during 2002-2006.

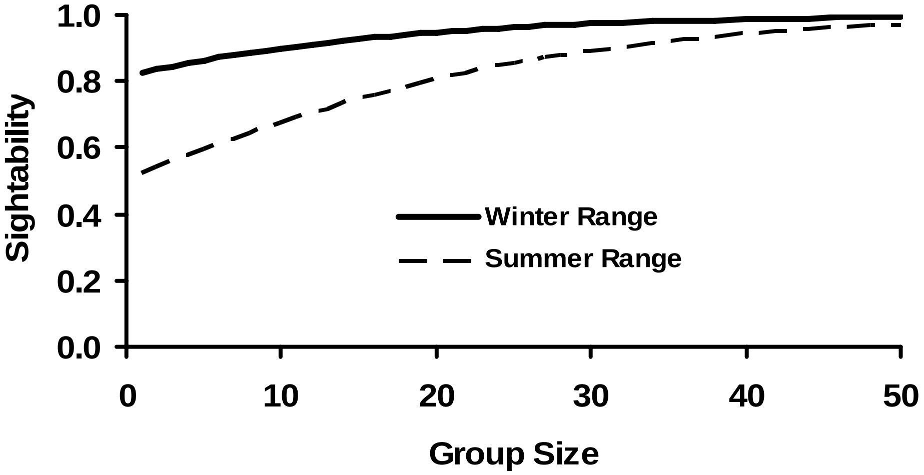


FIG. A2. Predicted sightability with 95% confidence bands from the two-covariate model (GROUPSIZE + RANGE) for the winter and summer ranges of pronghorn in Yellowstone National Park during 2002-2006.