

**IDAHO DEPARTMENT OF FISH AND GAME**

**Steven M. Huffaker, Director**

**Completion Report**



**THE INFLUENCE OF HABITAT VARIABLES ON PRONGHORN  
RECRUITMENT**

July 1, 2002 to June 30, 2005

By:

Tim Smyser  
Graduate Student  
University of Idaho

E. O. Garton  
Professor of Wildlife Resources  
University of Idaho

Peter Zager  
Principal Wildlife Research Biologist

September 2005  
Boise, Idaho

RESPONSE OF PRONGHORN (*Antilocapra americana*)  
POPULATIONS TO HABITAT CONDITIONS  
WITH  
MODIFICATION TO SURVEY METHODS

A Thesis

Presented in Partial Fulfillment of the Requirements for the  
Degree of Master of Science  
with a  
Major in Wildlife Resources  
in the  
College of Graduate Studies  
UNIVERSITY OF IDAHO

by

Timothy J. Smyser

Major Professor: Edward O. Garton, Ph.D.

## TABLE OF CONTENTS

ABSTRACT .....	1
PAIRED OBSERVER EVALUATION OF PRONGHORN LINE TRANSECT SURVEYS .....	2
INTRODUCTION .....	2
STUDY AREA .....	3
METHODS .....	5
Survey Methods .....	5
Analysis.....	6
RESULTS .....	8
DISCUSSION .....	11
CONCLUSIONS.....	13
POPULATION PRODUCTIVITY AND PRONGHORN NUTRITION DURING LACTATION	13
INTRODUCTION .....	13
STUDY AREA .....	15
METHODS .....	17
Forage Quality .....	17
Aerial Survey Methods .....	18
Analysis.....	18
RESULTS .....	19
DISCUSSION .....	20
EVALUATION OF PRONGHORN POPULATION PRODUCTIVITY RELATIVE TO BROAD-SCALE HABITAT VARIABLES IN WYOMING .....	22
INTRODUCTION .....	22
STUDY AREA .....	24
METHODS .....	25
Data Acquisition .....	25
Analysis.....	26
RESULTS .....	26
DISCUSSION .....	27
CONCLUSIONS.....	29
ACKNOWLEDGMENTS .....	30
LITERATURE CITED .....	30

## TABLE OF CONTENTS (Continued)

### LIST OF TABLES

Table 1. Pronghorn density ( $\hat{D}$ ) and abundance ( $\hat{N}$ ) estimates from distance analysis, Huggins' closed capture, and logistic regression approaches for Kemmerer and Pinedale, Wyoming, June 2004 .....	42
Table 2. Pronghorn density ( $\hat{D}$ ) and abundance ( $\hat{N}$ ) estimates from distance analysis, Huggins' closed capture, and logistic regression approaches for Camas Prairie and Eastern Owyhee, Idaho, August 2003.....	42
Table 3. Huggins' closed capture models evaluated using program MARK for pronghorn sight-resight surveys conducted in Kemmerer and Pinedale, Wyoming, June 2004.....	43
Table 4. Huggins' closed capture models evaluated in program MARK for pronghorn sight-resight surveys conducted in Camas Prairie and Eastern Owyhee, Idaho, August 2003 .....	43
Table 5. Logistic regression models evaluated for pronghorn population abundance surveys conducted in Kemmerer and Pinedale, Wyoming, June 2004 .....	44
Table 6. Logistic regression models evaluated for pronghorn herd composition surveys conducted in Camas Prairie and Eastern Owyhee, Idaho, August 2003.....	44
Table 7. Linear regression models evaluating relationship between the fecal indicators, fecal nitrogen (FN) and fecal 2,6 diaminopimelic acid (DAPA), and pre-harvest fawn:doe ratios (f:d).....	45
Table 8. Models of fawn:doe ratios z-score transformed by herd unit evaluated with linear regression to assess the influence of the temporally variable habitat characteristics .....	45
Table 9. Parameter estimates and the associated magnitude of response for the best regression model relating z-score transformed fawn:doe ratios to annually varying habitat variables .....	46
Table 10. Competing regression models to predict average pronghorn fawn:doe ratios from the 44 herd units encompassing Wyoming .....	46
Table 11. Parameter estimates and magnitude of effects associated with the 3 competing regression models used to predict average pronghorn fawn:doe ratios from the 44 herd units in Wyoming.....	47

### LIST OF FIGURES

Figure 1. Study populations within the state of Idaho .....	37
Figure 2. Mean fecal nitrogen values for pronghorn across the lactation season for 5 sites in Idaho .....	38

**TABLE OF CONTENTS (Continued)**

Figure 3. Mean pronghorn fecal diaminopimelic acid (DAPA) values across the lactation season for 5 sites in Idaho .....39

Figure 4. Pronghorn fawn:doe ratios from 5 sites in Idaho .....40

Figure 5. Pronghorn fawn:doe ratios from 5 sites in Idaho .....41

## COMPLETION REPORT STATEWIDE WILDLIFE RESEARCH

**STATE:** Idaho

**JOB TITLE:** Pronghorn Recruitment at the Population Scale

**STUDY NAME:** Pronghorn Recruitment vs. Habitat Variables

**PERIOD COVERED:** July 1, 2002 to June 30, 2005

### ABSTRACT

Valid population estimates are an essential element for understanding of population dynamics and effective management. Distance sampling, line transect methods are commonly used for pronghorn (*Antilocapra americana*) population estimation throughout the West. Line transect surveys will produce unbiased estimates if 3 key assumptions can be met: 1) groups directly on the line are always detected; 2) groups are detected at their initial location, prior to moving in response to the observer; and 3) distances to groups are measured accurately. However, comparison of pronghorn line transect estimates to those generated through quadrat sampling indicates line transects underestimate population abundance. This negative bias suggests observers do not satisfy the first assumption. We, therefore, used independent paired observers to evaluate the frequency of missed detections on the line. Paired observers also allowed us to evaluate the influence of variables beyond distance on the probability of detection. Our evaluation indicated line transect methods used in pronghorn surveys underestimate population abundance by as much as 18%. Paired observer analysis methods demonstrated here were able to reduce bias and improve precision by addressing other sources of detection heterogeneity without requiring additional survey effort.

Predators, specifically coyotes (*Canis latrans*), are often thought to greatly limit pronghorn populations, yet few studies have investigated nutritional constraints for pronghorn. Research must address the effects of nutrition on population dynamics before conclusions regarding the role of predation can be reached. We assessed nutrition during lactation from 5 disjunct populations in Idaho through analysis of fecal nitrogen (FN) and 2,6 diaminopimelic acid (DAPA); we related nutritional condition to population productivity as assessed through fawn:doe ratios. Both fecal indicators showed a positive relationship with population productivity, although the null model outperformed those incorporating nutritional indices. Comparison of our observations to other studies employing these fecal indicators suggested some populations in Idaho are nutritionally limited.

Fine-scale studies have identified factors influential in pronghorn population dynamics, although application of these factors to broad temporal and spatial scales has limited utility. Density-dependent nutritional constraints may regulate pronghorn populations and serve to unify many of these fine-scale processes. We used fawn:doe ratios collected from the 44 herd units in Wyoming from 1978-2003 to assess the response of population productivity to broad-scale habitat variables selected to reflect nutritional condition. We evaluated 2 sets of models to: 1) examine the response of productivity to annually varying precipitation patterns and population densities and

2) contributions of habitat characteristics to inherent differences between herd units in productivity. Relationships between fawn:doe ratios and habitat conditions generally reflected a pattern of density-dependent growth characteristics and a positive population response with increasing levels of range productivity.

## **PAIRED OBSERVER EVALUATION OF PRONGHORN LINE TRANSECT SURVEYS**

Distance sampling is used to estimate the density of several taxa including pronghorn. Line transect surveys produce unbiased estimates of density if key assumptions are met, including that all clusters on the line are detected. We conducted aerial line transects for pronghorn in Wyoming and Idaho using independent paired observers to evaluate the ability of observers to satisfy this assumption. Enumerating groups as both detected and missed enabled evaluation of the data as a sight-resight survey and construction of a logistic regression sightability model. Independent paired observers identified failures to detect all groups within the nearest band; violations were particularly prominent from the rear seat of the aircraft (12 out of 58 groups missed in the nearest distance band) contributing to a negative bias in density estimates. Sight-resight and sightability model estimates presented here correct for this bias while improving the precision of estimates associated with pronghorn line transect estimates.

### **Introduction**

Effective management of animal populations requires valid estimates of abundance and the rate of population change. Line transect sampling has been used for density estimation in a variety of species such as Pacific and common loons (*Gavia pacifica* and *G. immer*; Quang and Becker 1997), marine mammals (Borchers et al. 1998), mule deer (*Odocoileus hemionus*; Koenen et al. 2002), marbled murrelets (*Brachyramphus marmoratus*; Mack et al. 2002), woodpeckers (Nielsen-Pincus 2005), and pronghorn (Johnson et al. 1991). The accuracy of line transect estimates depend on the ability of the field protocols to meet 3 critical assumptions, listed in order of importance: 1) clusters of individuals directly on the line are always detected; 2) clusters are detected at their initial location, prior to moving in response to the observer; and 3) distances to clusters are measured accurately (Buckland et al. 2001). For application to pronghorn from an aerial platform, Johnson et al. (1991) and Guenzel (1997) simplified the measurement of distance off the line to place clusters (detected groups of  $\geq 1$  adult pronghorn) into 4 distance bands (from 'A', nearest to 'D', farthest). Given the above ground level at the time of detection, the distance band in which the pronghorn cluster was detected can be converted to an estimated distance off the line. Simplification of distance measurement requires modifying the first assumption: that a very high proportion of clusters within the first distance band are detected. Missed groups within the nearest distance band will result in a near proportional bias in the density estimate (Guenzel 1997).

Pronghorn are an ideal species for aerial line transect monitoring because they largely occupy open habitats and sightability is believed to be primarily influenced by the distance from the aircraft. However, comparison of quadrat sampling to line transect estimates indicates that pronghorn line transects underestimate population abundance. This negative bias suggests observers do not detect all groups of pronghorn within the nearest distance band (Pojar and Guenzel 1999).

To ensure compliance with the assumption that all clusters within the nearest distance band are recorded, observers must focus their attention on the ‘A’ band (Guenzel 1997). Aerial surveys are a dynamic activity, however, and a number of external factors can lead to violations of this critical assumption. First, fixed-wing aircraft travel at a high rate of speed such that groups must be identified, counted, and placed into the appropriate distance band within a short period of time. This sequence of actions requires the observer to divert attention away from the line following each detection and direct it toward the identified group; the mental processing of groups detected in outer distance bands provides an opportunity for groups in the nearest distance band to go undetected. Second, observers develop a search image to detect the object of interest. For example, in pronghorn surveys, observers may cue on the contrast of the white rump and underbelly to the light brown coat or vegetated background. Different body postures of individuals relative to the passing aircraft may distort the search image (i.e., bedded pronghorn conceal their white rump and underbelly) and lead to a failure of detection. Third, landscapes encountered during typical surveys differ in both spectral reflectance and complexity. The color signature of a pronghorn may be more pronounced against some backgrounds than others; additionally, complex landscapes pose more opportunities to conceal individuals and challenge the observer with extraneous visual information to decipher. Survey protocol and animal activity patterns also require flights early and late in the day when low sun angles can limit optimal viewing. Finally, due to the configuration of the seats, struts, and windows within the aircraft, objects falling within the nearest distance band are in the viewable area for a shorter duration than objects in outer distance bands. These external factors as well as observer variability and/or fatigue may contribute to clusters within the nearest distance band going undetected.

Recent work in line transect theory has sought to eliminate the first assumption by modeling the probability of detection as a function of additional explanatory variables (Quang and Becker 1996, Borchers et al. 1998). A methodology employing paired observers has proven to be effective for estimating probability of detection while allowing for incorporation of additional covariates into a sightability model (Graham and Bell 1989, Johnson et al. 1991, Potvin et al. 2004). Such a paired observer arrangement has been successfully applied to surveys of a number of taxa (Antarctic minke whales [*Balaenoptera bonarensis*], Borchers et al. 1998; marbled murrelets, Mack et al. 2002; polar bears [*Ursus maritimus*], Manly et al. 1996; song birds, Kissling and Garton, in press; and white-tailed deer [*Odocoileus virginianus*], Potvin et al. 2004) improving population estimates over those generated from traditional distance sampling.

When Johnson et al. (1991) first presented a protocol for pronghorn population monitoring, they asserted that, if key assumptions could be met, line transect estimates would be unbiased. Applying a paired observer approach to an established pronghorn survey protocol, we sought to rigorously test the assumption that all clusters are detected within the nearest distance band. Additionally, enumerating groups as both observed and missed provided the opportunity to evaluate the influence of additional group characteristics such as cluster size, activity class (bedded, standing, running), cover type, and aircraft seat position on the probability of detection.

### **Study Area**

Two series of flights were conducted representing the breadth of pronghorn surveys conducted from a fixed-wing aircraft; flights carried out in Wyoming were standard population abundance,

line transect surveys, while flights conducted in Idaho incorporated line transect methodologies with pre-harvest herd composition surveys. The first of the population abundance surveys were conducted in Lincoln and Sweetwater counties, northwest and southeast of the town of Kemmerer, Wyoming, in the general area of 41° 32' - 42° 58' latitude and 109° 46' - 110° 35' longitude (referred to as Kemmerer). The areas surveyed were typical of sagebrush winter habitats in western Wyoming that sustain a limited residential population. Other habitats encountered were classified by biologists as winter or transitional range. Average annual precipitation for the area was 25.0 cm (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Kemmerer, Wyoming 1948-2004). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) was the dominant vegetation community in the study area, accounting for 64% of the total land area (Wyoming GAP Analysis 1996). Desert scrub communities composed another 17% of the area. Limited amounts (<5%) of the study area supported aspen (*Populus tremuloides*) stands, mountain big sagebrush (*A. t. vaseyana*), greasewood flats (*Sarcobatus vermiculatus*), and riparian zones. Irrigated agriculture accounted for <2% of the area.

Additional abundance flights were conducted in Sublette County, north of the town of Pinedale, Wyoming, in the general area of 109° 50' - 110° 23' longitude and 42° 10' - 43° 11' (referred to as Pinedale). Habitats encountered represent summer range that seasonally supports higher densities of pronghorn. The study area was dominated by mountain big sagebrush communities composing 58% of the total area (Wyoming GAP Analysis 1996). A mixture of aspen, lodgepole (*Pinus contorta*), and spruce/fir (*Picea engelmanni/Abies lasiocarpa*) stands were the second most prevalent habitat type (15%) with irrigated crops a close third (13%). The remainder of the study area was a mix of shrub-dominated riparian, Wyoming big sagebrush, and dryland agriculture. Similar habitats with a mix of brush, grassland, and agricultural interface are common within the eastern third of Wyoming. Average annual precipitation for the area was 27.4 cm (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Pinedale, Wyoming 1948-2004).

Pre-harvest composition flights were conducted in 2 populations in Idaho. The first of these flights covered portions of Camas and Elmore counties, near the towns of Fairfield and Hill City (referred to as Camas Prairie). The general area was 43° 13' - 43° 23' latitude and 114° 22' - 115° 11' longitude. This area supported a migratory pronghorn population, largely subsidized by agricultural forage during the spring, summer, and fall seasons. The majority (52%) of the study area was under agricultural cultivation of which 81% was dryland and 19% was irrigated agriculture. Alfalfa was the dominant crop (54% of cultivated area) followed by barley (13%), and grass hay (11%) in addition to pasture or Conservation Reserve Program lands (17%; Kinder 2004). Perennial grass (21% of the study area) and Wyoming and basin big sagebrush (*A. t. tridentate*; 18%) persisted on Bureau of Land Management and state held lands (Scott et al. 2002). Average annual precipitation for the area was 38.2 cm with a periodicity of dry summers and wet winters (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Fairfield Ranger Station, Idaho 1948-2004).

The second set of composition flights in Idaho was conducted in Owyhee and Twin Falls counties, and included the small towns of Three Creek and Roseworth (referred to as Eastern

Owyhee). The general area of flights was 41° 59' - 42° 23' latitude and 114° 44' - 115° 37' longitude. Habitats were typical of xeric native and exotic range. Stands of basin and Wyoming big sagebrush were the dominant cover types accounting for >60% of the study area (Scott et al. 2002). Perennial grasses composed another 25% of the area with the remaining area a mix of low sagebrush (*Artemisia arbuscula*), bitter brush (*Pershia tridentate*), and rabbit brush (*Chrysothamnus* spp.) communities (Scott et al. 2002). Average annual precipitation was 32.8 cm with a periodicity characterized by hot, dry summers with precipitation spread evenly through the fall, winter, and spring (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Three Creek 1940-1987). Pronghorn population densities tended to be lower in the Eastern Owyhee site relative to the Camas Prairie site.

## Methods

### Survey Methods

Paired observer methods were incorporated into both spring population abundance surveys and pre-harvest composition surveys. Population abundance surveys in Wyoming were conducted on 16-17 June 2004, within the seasonal timeframe of maximal dispersion and highest uniformity in pronghorn group size (Guenzel 1997). Flights were conducted between sunrise and 1030 to maximize the number of individuals not bedded. Transect lines were spaced at >1 minute latitude or longitude intervals to provide adequate coverage of the survey area while avoiding the detection of the same group on adjacent transects. Composition flights in Idaho were conducted on 6-7 August 2003. Flights were conducted between sunrise and 1100 and between 1800 and sunset. Flight lines were spaced at >0.5 minute intervals to provide adequate coverage for herd composition estimates. Survey lines were oriented both east-west and north-south to capture the breadth of lighting conditions encountered during typical surveys.

Surveys followed the protocol described in Guenzel (1997) with the modifications listed below. All transects were conducted by observers experienced in pronghorn line transect surveys in a Maule 5 aircraft with window and door modifications to increase visibility. A Global Positioning System was used for transect and ferry navigation. Under traditional survey protocols, as each cluster of pronghorn is detected, the group size and distance band in which the group lies is recorded. Observers were able to consistently delineate the geographic center of detected groups to 1 of 4 distance bands by aligning tape on the window with dowel rods fitted to the dual strut of the aircraft. The use of a radar altimeter during flights enabled conversion from the distance band in which each group was detected to an estimated distance off the line.

Important alterations to the established methodology included: 1) both observers were seated on the right side of the aircraft; 2) the activity class (bedded, standing, or running) of each group detected was recorded; and 3) whether the group was detected by the front, rear, or both observers was recorded. Under traditional pronghorn survey protocol, observers relay group detection to the pilot for data recording as the group is encountered. Under the paired observer arrangement, observers delayed indicating cluster detection until the group had passed out of the viewable area for both observers. At this point, an observer would announce to the pilot that a group had been detected. Following the listing of the group characteristics, the other observer would then indicate whether the group had been detected by the front, rear, or both observers.

For the population abundance surveys, an opaque cloth was hung between the 2 observers to prevent the possible transfer of visual cues; interviews of observers following composition surveys suggested transfer of visual cues did not occur. If the activity class of a pronghorn cluster was not consistent among all individuals within the group, the cluster was defined as having the activity class deemed most easily detected (favoring running to standing and standing to bedded). The chief objectives of these protocol modifications were to evaluate the ability of observers to detect all individuals within the nearest distance band and the influence of group characteristics on the probability of detection. Therefore, in the rare instances in which observers disagreed on either distance band or group size, differences were reconciled prior to data entry.

## **Analysis**

Given the sight-resight and line transect nature of the collected data, there were a number of appropriate analysis options. We applied a traditional distance analysis, a mark-recapture analysis, and a logistic regression as these methods represent tools with which managers and biologists are familiar, that can easily be applied to this and other similar data sets, and that provide a population estimate with a measure of variability. Because group size, dispersion, and landscape greenness differed dramatically between spring abundance surveys and fall composition surveys, the 2 data sets were analyzed independently.

### *Distance Analysis*

We used program DISTANCE (Thomas et al. 2004) to model a detection function, using the key functions and series expansions available to describe a relationship between detection and distance off the line. To evaluate the influence of seat, independent abundance estimates were calculated for the front and rear observers (sampling fraction = 0.5). Observations were also pooled across observers to simulate tandem surveys with observers seated on opposite sides of the aircraft (sampling fraction = 1). Aircraft currently used for pronghorn surveys limit the number of observers to 2. Therefore, the pooling approach represents the quality of estimate that might be expected had the 2 observers been seated on opposite sides of the aircraft as is directed under current survey protocol. A single detection function was modeled for each survey type with population estimates derived by site. Preliminary analysis of group covariates in the alternative population estimation methods indicated that probability of detection differed between the Kemmerer and Pinedale sites. For this reason, we conceptually incorporated a 'site' variable by developing a unique detection function for each of the population abundance survey sites.

Information-theoretic methods using Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) were used to evaluate competing models. We ranked the models based on  $\Delta AIC_c$  and calculated the Akaike weights ( $w_i$ ) for each model given the suite of candidate models (Anderson et al. 2000). In the event that one of the modeling options available under program DISTANCE was not clearly the best (Akaike weights  $\geq 0.90$ ) model, then a multi-model inference approach was used in which density estimates were averaged across models and the variance associated with the estimate takes into account model uncertainty. Such an approach provides better precision and reduces bias in the prediction of population size (Anderson et al. 2000, Burnham and Anderson 2002).

## Mark-Recapture

The second method for density estimation used Huggins' (1989, 1991) analysis method for capture-recapture within a closed population with heterogeneous capture probabilities. Manly et al. (1996) demonstrated that the Huggins' analysis was applicable to paired-observer, line transect contexts in which detection on the line was less than perfect. This method relaxes the first assumption of distance sampling, that groups on the line are always detected while requiring other assumptions: groups do not move in response to the aircraft prior to detection and the distance of groups from the transect line has a uniform distribution. In accord with Manly et al. (1996), we treated both distance and group size as covariates while we added the categorical variables, activity and site. The Huggins' (1989, 1991) closed capture model with 2 capture occasions incorporated in program MARK (White and Burnham 1999) provided an efficient means to build and evaluate competing models. Emulating Manly et al. (1996), we constructed 9 competing models, sequentially increasing in complexity. Our most reduced model had a single intercept and distance parameter for both seats. The next model allowed a unique intercept for each seat while maintaining a single distance parameter. We followed this pattern of first introducing a variable as a single parameter and then allowing a unique parameter for each seat in the ensuing models. The order in which variables were added to the set of competing models was intercept, distance, group size, activity, and site. Therefore, after estimating the probability of detection for each observed group, the abundance of the surveyed area was estimated as:

$$\hat{N}_1 = \sum_{i=1}^n g_i / \{ \hat{P}_{i1} + \hat{P}_{i2} - \hat{P}_{i1}\hat{P}_{i2} \}$$

where  $\hat{P}_{ij}$  is the estimated probability of detection for group  $i$  from seat  $j$ ,  $g_i$  is the size of the  $i$ th group, and  $n$  is the number of groups observed.

One limitation of program MARK was that abundance and associated variance estimates were calculated for the number of groups. Estimating the abundance of individuals required multiplying the probability of detection for group  $i$  by the number of individuals in group  $i$ . In multiplying by group size, we must account for variation in the probability of detection associated with group size. Given that larger groups are more likely to be observed than smaller groups (Drummer and McDonald 1987, Otto and Pollock 1990), we used our  $AIC_c$  best model to predict the true distribution of group sizes. Therefore, in multiplying the model variance estimated by program MARK by our estimated group size variance, the variance of the population abundance estimate became:

$$v(\bar{xy}_i) = \bar{x}^2 v(\bar{y}_i) + \bar{y}_i^2 v(\bar{x}) - v(\bar{y}_i)v(\bar{x}) \quad (\text{Goodman 1960})$$

where  $\bar{x}$  is the estimated mean of group size corrected for size bias, and  $\bar{y}_i$  is the estimated group abundance for site  $i$ . Likewise,  $v(\bar{x})$  is the estimated variance of mean group size corrected for size bias and  $v(\bar{y}_i)$  is the variance associated with the group abundance estimate.

## *Logistic Regression*

The unique characteristics of each group identified (i.e., distance off the line, group size, activity level, and site) introduced heterogeneity into the probability of detection (Huggins 1989, Alho 1990). Logistic regression has proven to be an efficient method to incorporate such variables in modeling the probability of detection when groups can be classified as both missed and detected (Steinhorst and Samuel 1989, Alho 1990). In an independent paired observer arrangement, groups detected by a given observer create trials for the opposing observer. For example, groups detected by the front observer were either detected (success) or missed (failure) by the rear observer. Evaluating the successes and failures of both observers, we used logistic regression to model a correction factor as a function of the covariates associated with the observed groups (Proc LOGISTIC, SAS Institute 1999). A global model and 10 reduced models were estimated for the variables observer position (seat), distance off the line, group size, activity class, site, and the interaction terms of observer position and distance off the line (seat×distance) and group size (seat×group size). Preliminary analysis of the activity covariate indicated that the difference in the probability of detection between bedded and standing was greater than the difference between standing and running. Therefore, we reclassified our activity variable to reflect 2 categorical activity levels: bedded versus standing or running. A parallel suite of competing models was evaluated with results presented independent of models incorporating 3 activity levels.

To verify that analysis with logistic regression was appropriate for our data, we used a Hosmer-Lemeshow goodness-of-fit test to evaluate the null hypothesis against the global model. Variables were screened for collinearity. The model set was evaluated with  $AIC_c$  in pursuit of the most parsimonious model (Anderson et al. 2000). Similarly here, we ranked the models based on  $\Delta AIC_c$  and calculated the Akaike weights ( $w_i$ ) for each model given the suite of candidate models (Anderson et al. 2000). In the event that no  $w_i$  was  $>0.90$ , we used a multi-model inference approach (Anderson et al. 2000, Burnham and Anderson 2002). Densities were estimated for each transect by applying the correction factor to observations from each seat independently. Estimates were then averaged across observers to determine the density estimate for each transect. We calculated the sample variance within sites, treating transects as independent estimates of density.

## **Results**

In the population abundance flights, observers detected 266 unique groups of pronghorn; 51 pronghorn groups were detected at the Kemmerer site, while 215 groups were detected at the Pinedale site. These groups represented 439 adult individuals with group sizes ranging from 1 to 13 individuals (Kemmerer  $\bar{x} = 1.65$ ,  $SD = 1.80$ ; Pinedale  $\bar{x} = 1.65$ ,  $SD = 1.52$ ). Of the groups identified, 46 were located in the A band (0-25m), 39 in the B band (25-50m), 78 in the C band (50-100m), and 103 in the D band (100-200m), representing estimated distances off the line ranging from 9 to 370 meters. Fifty-seven groups were characterized as bedded, 161 groups were standing, and 48 groups were running. Independent paired observers identified violations of the assumption that all groups within the nearest distance band were detected; of the 46 groups detected within the 'A' band, 45 were observed from the front seat while only 36 were observed

from the rear seat. Assuming complete detection within the 'A' band, such missed detections have the potential to negatively bias density estimates.

In the composition flights, observers detected 41 unique groups of pronghorn representing 442 individuals; 24 groups were detected at the Camas Prairie site, while 17 groups were detected at the Eastern Owyhee site. Observed group sizes ranged from 1 to 45 individuals (Camas Prairie  $\bar{x} = 11.25$ ,  $SD = 12.57$ ; Eastern Owyhee  $\bar{x} = 9.59$ ,  $SD = 7.07$ ). Of the groups identified, 6 were located in the A band, 5 in the B band, 16 in the C band, and 14 in the D band, representing estimated distances off the line ranging from 12 to 203 meters. Six groups were classified as bedded, 26 groups were standing, and 9 groups were running. As in the population abundance flights, independent paired observers identified violations of the assumption that all groups within the nearest distance band were detected during composition flights; of the 6 groups detected within the 'A' band, only 4 were detected by the rear observer while all 6 groups were detected by the front observer. Again, such missed detections have the potential to negatively bias density estimates from the rear seat.

### *Distance Analysis*

In accord with standard survey protocol (Guenzel 1997), we used distance sampling methods incorporated into DISTANCE (Thomas et al. 2004) for abundance estimation. Estimates from DISTANCE are uncorrected for known groups missed within the 'A' band. Of the 4 key functions used to model the probability of detection for all observers by survey type, no analysis produced a clear  $AIC_c$  best model. Therefore, a model-averaging approach was used for all density estimates. From the population abundance surveys analyzed with a single detection function across sites, the abundance estimate for the Kemmerer site derived from the front seat observer was 88 (SE = 24.3) individuals in the 97.8 km<sup>2</sup> surveyed area (Table 1). For the rear seat, the estimated abundance in the Kemmerer area was 70 (SE = 22.4) individuals in the surveyed area. Simulating observers on both sides of the aircraft, the abundance estimate for the Kemmerer area was 78 (SE = 21.8) in the area surveyed. In the Pinedale area, the estimated abundance from the front seat was 375 (SE = 62.6) individuals in the 70.6 km<sup>2</sup> area surveyed (Table 1). From the rear seat, the estimated abundance was 334 (SE = 52.1) individuals. For both seats combined in the Pinedale area, the estimated abundance was 352 (SE = 51.3) individuals.

Incorporating unique detection functions for each site, abundance estimates increased for the front observer and decreased for the rear observer. The abundance estimate for the Kemmerer site from the front seat observer increased to 101 (SE = 39.2) individuals (Table 1). The corresponding estimate from the rear observer decreased to 63 (SE = 25.8) individuals. The estimate varied little for the simulated dual observers with an estimated abundance of 81 (SE = 27.3) individuals. At the Pinedale site, the abundance estimate from the front seat decreased with the incorporation of a unique detection function to 375 individuals (Table 1). The abundance estimate from the rear seat increased to 344 individuals (Table 1). Again, the abundance estimates from the simulated dual observer remain nearly unchanged at 348 individuals (SE = 50.7).

From the composition surveys, the estimated abundance from the front observer for the Camas Prairie site was 383 (SE = 181.8) individuals in the 147.6 km<sup>2</sup> area surveyed (Table 2).

Estimated abundance from the rear seat for the Camas Prairie area was 370 (SE = 176.2) individuals. Simulating observers on both sides of the aircraft, the estimated abundance for the Camas Prairie area was 375 (SE = 144) individuals. For the Eastern Owyhee area, estimated abundance from the front observer was 229 (SE = 106.7) individuals in the 177.5 km<sup>2</sup> area surveyed (Table 2). The abundance estimate from the rear seat was 265 (SE = 124.8) individuals. With observations analyzed simulating observers on both sides of the aircraft, the abundance estimate was 241 (SE = 86.7) individuals.

The much greater sample size of groups from the population abundance surveys provided a better opportunity to address biases associated with seat position. Clearly, an uncorrected distance analysis of observations from the rear seat is negatively biased due to the substantial proportion of missed clusters in the A band. Estimates derived from the rear seat with unique detection functions for each site were 38% below those from the front seat for the Kemmerer site and 6% below those for the Pinedale site, which roughly corresponds with the frequency of missed groups in the 'A' band (3 of 10 in Kemmerer and 7 of 36 in Pinedale). Combining observations across observers serves to average this bias but does not eliminate it. Estimates derived from the simulated dual observers were 20% below those for the front observer in the Kemmerer site and 5% below those for the front in the Pinedale site.

### *Mark-Recapture*

Evaluation of the population abundance surveys with Huggins' closed capture models failed to select a single AIC<sub>c</sub> best model, but identified 4 models with  $\Delta AIC_c$  values between 0 and 2. The remaining 5 models had  $\Delta AIC_c$  scores between 3.42 and 7.00 (Table 3). Accordingly, we took a multi-model inference approach, calculating a weighted average for estimated abundances across all models. For the Kemmerer area, the estimated abundance was 96 (SE = 13.6) individuals for the 97.8 km<sup>2</sup> area surveyed (Table 1). In the Pinedale site, the estimated abundance was 366 (SE = 21.4) individuals for the 70.6 km<sup>2</sup> area surveyed (Table 1).

From the composition surveys, model selection again failed to select a single best model although we identified model 1 and model 2 as competing models (Table 4). Because the distance parameters evaluated in these models occur throughout the suite of candidate models, a model-averaging approach was taken. In the Camas Prairie, the estimated abundance was 502 (SE = 90.1) individuals for the 147.6 km<sup>2</sup> area surveyed (Table 2). In the Eastern Owyhee site, the estimated abundance was 206 (SE = 39.3) individuals for the 177.5 km<sup>2</sup> area surveyed (Table 2).

### *Logistic Regression*

The Hosmer-Lemeshow goodness-of-fit test provided little evidence to suggest that a logistic response function did not fit either of the data sets (population abundance  $X^2 = 6.30$ ,  $P = 0.61$ ; composition  $X^2 = 7.05$ ,  $P = 0.53$ ). No pairwise comparisons of covariates indicated significant correlation ( $P > 0.05$ ). Therefore, examination of the global and reduced models with logistic regression was appropriate. Multiple competitive models were identified in both analyses (Tables 5 and 6). The best model from the Wyoming abundance surveys incorporated the variables distance, group size, activity, and site although all variables are incorporated for

density estimation with a multi-model inference approach. The abundance derived from the logistic regression sightability model for the Kemmerer site was 101 (SE = 19.9) individuals for the 97.8 km<sup>2</sup> surveyed area (Table 1). For the Pinedale site, the abundance estimate was 369 (SE = 63.6) individuals for the 70.6 km<sup>2</sup> surveyed area (Table 1).

Independent analysis of composition surveys produced an estimated abundance for Camas Prairie of 334 (SE = 1511) individuals for the 147.6 km<sup>2</sup> area surveyed (Table 2). The estimated abundance for the Eastern Owyhee area was 174 (SE = 836) individuals for the 177.5 km<sup>2</sup> area surveyed (Table 2).

## Discussion

The paired observer evaluation of current line transect survey protocol identified violations of the assumption that all groups are detected within the nearest distance band. In our trial, front seat observers nearly satisfied this assumption, detecting 45 of 46 groups observed in population abundance surveys and 6 of 6 in composition surveys. The high frequency of 'A' band detections by the front observer was sufficient to produce density estimates equivalent to unbiased sight-resight estimates. Detections from the rear seat fell off dramatically, detecting 36 of 46 groups from the population abundance surveys and 4 of 6 of the groups from the composition surveys. These missed detections contributed to a negative bias in distance sampling estimates; estimates derived from the rear observer were 64% and 94% of those derived from the front observer for the Kemmerer and Pinedale sites, respectively. Comparison of estimates from the rear seat to those derived from the paired observer methods were 62% and 94% for Kemmerer and Pinedale, respectively. Pooling observations across observers simply averages rather than ameliorates this bias. This study further demonstrated that the precision of estimates was not greatly compromised, and in some cases was improved, by shifting the second observer to the right side of the aircraft. Bias of the magnitude observed from the rear seat and the precision of alternative methods warrant application of paired observer methods for population estimation.

Our results demonstrated that by incorporating the methods used in population abundance surveys, composition surveys can also produce a population estimate. The high variance in group size limits the quality of the estimate; however, even an imprecise estimate may represent increased knowledge in some management situations. Because of the limited group sample size and high variance in population estimates associated with composition surveys, our discussion emphasizes results from the abundance surveys.

A simple solution that reduces bias associated with distance sampling while maintaining established protocol is to estimate a seat-specific correction factor associated with the frequency of missed clusters on the line. Continued paired observer testing will resolve whether the realized bias associated with the rear seat is a common problem plaguing current surveys or simply an artifact of small sample size and/or observer bias. A seat-specific correction factor could be incorporated into traditional distance analysis with the subtle modification of analyzing seats independently. While a correction factor for clusters missed on the line will reduce bias caused by violations of this assumption, other analysis methods demonstrated here offer the potential to improve precision by correcting for additional sources of detection heterogeneity.

Population estimates from Huggins' closed capture models both reduced bias associated with observed covariates and had the greatest precision based on standard errors. Huggins' closed capture models express variance for a homogeneous landscape rather than considering variation in density among surveyed transects. This method appears to be a viable approach for continued population monitoring, although future work should consider whether variance estimates derived from sight-resight analyses adequately express estimate uncertainty from transect surveys.

Logistic regression proved to be a viable method for incorporating detection heterogeneity into estimates of abundance. To employ a logistic regression for future population estimation, the model should be constructed across the range of habitat characteristics, survey conditions, and observer experience encountered in routine management surveys. The greatest benefit of using logistic regression for population estimation is that following model construction and validation, agencies could return to tandem surveys with observers seated on opposing sides of the aircraft, using the logistic sightability model rather than a distance analysis approach to estimate abundance.

The models developed in both the logistic regression and mark-recapture analyses correct for detection heterogeneity as a function of seat position, distance, group size, activity, and site. Conceivably, a pronghorn cluster that is easy to detect for the front observer because of characteristics beyond the addressed covariates is similarly easy to detect for the rear observer. It is possible that variables yet unquantified, such as lighting conditions or observer experience, introduce uncorrected detection heterogeneity into pronghorn surveys. Alho (1990), addressing similar issues, simulated population estimates under a regime in which only half the variables contributing to detection heterogeneity could be perceived by the observer. Estimates under these conditions were slightly negatively biased (Alho 1990). Similarly, should our global model be inadequate to fully describe group heterogeneity, precision could be improved by incorporating additional meaningful variables.

Evaluating covariates used in the logistic models indicated that the difference in the probability of detection between bedded and standing was more substantial than between standing and running. While the models with 2 activity levels proved to be more powerful, parsimonious models, simplifying activity level had little impact on population estimates (Table 1). Continued model development should consider both categorical delineations of activity as larger data sets and will have greater power to resolve the increases in the probability of detection associated with running.

While anecdotal evidence at the conclusion of flights prompted the incorporation of a site variable, both the logistic and mark-recapture analysis demonstrated its importance in estimating the probability of detection. Our distance analysis, with a single detection function applied across sites, failed to consider these important differences. The subsequent distance analysis, incorporating a unique detection function for each site, further corroborated the importance of the site variable with the dramatic changes in density estimates. Introducing a unique detection function for each site, we predicted that density estimates from the Kemmerer site would increase while estimates from the Pinedale site would decrease. This pattern was observed for estimates from the front observer but the opposite trend was realized for the rear observer.

Distance sampling estimates are derived from a detection function, which in this case, is a line fit to 4 distance bands identified from the aircraft. The use of coarse distance classes rather than a continuous distance measurement prevents a smooth fit of a curve to the observations. We believe that it is variation in the distance sampling estimate, caused by limitations of coarse distance classes, that caused rear seat distance estimates to respond counter to predictions.

Our results support the continued inclusion of a site or cover type variable as a source of detection heterogeneity although alternative methods are needed for application to more than 2 landscapes. One solution to appropriately address between-site variability on a broader scale is to develop a subjective scoring method incorporating greenness and landscape complexity. This measure could be assessed on the site level, or based on the viewing frame when groups are detected. We recommend such a subjective score might most appropriately be included at the conclusion of individual transects, balancing the tradeoff between capturing much of the variability on the landscape and yet allowing for reasonable data recording in the field.

### **Conclusions**

Our assessment of pronghorn line transect surveys with independent paired observers corroborated the conclusions of the quadrat sampling and line transect comparisons (Pojar and Guenzel 1999): pronghorn line transect estimates underestimate population abundance. The substantial bias identified here warrants reevaluating survey methodology. While distance sampling estimates from the front seat are unbiased, the precision of estimates can be improved through the incorporation of other variables important for detectability (group size, group activity, and cover type). Reducing bias and improving precision through the use of a sightability model or sight-resight method will allow for more responsive management action.

### **POPULATION PRODUCTIVITY AND PRONGHORN NUTRITION DURING LACTATION**

Predators, specifically coyotes, are often thought to limit pronghorn populations, yet few studies have investigated the potential role of nutritional constraints. We assessed lactation season nutrition for 5 populations in Idaho through analysis of FN and DAPA. We related nutritional condition to population productivity as assessed through fawn:doe ratios. Regression models relating fawn:doe ratios to fecal indicators were evaluated with AIC<sub>c</sub>. The null model outperformed those models incorporating fecal indicator values although the model including a weighted FN value explained 48% of the variation in productivity. Comparison of our observations to other studies employing these fecal indicators suggested that some populations in Idaho are nutritionally limited.

### **Introduction**

Simple predator-prey models provide a theoretical framework under which predators hold prey below environmental carrying capacity (see review in Berryman 1992). Incorporating alternative prey items into these models provides a reasonable extension to ungulate systems. Such models predict that the bolstering of predator densities with alternative prey items will lead to greater reductions in the abundance of primary and secondary prey species (Seip 1992, Pech et al. 1995).

Empirical examples in which predators in single or multi-prey systems strongly limit or regulate prey abundance can be drawn from various ungulate systems (moose [*Alces alces*], Van Ballenberghe and Ballard 1994; caribou [*Rangifer tarandus*], Seip 1992).

It has been hypothesized that predators, most commonly coyotes, similarly maintain pronghorn populations below carrying capacity through high rates of fawn predation (Trainer et al. 1983). Predation was the proximate cause of mortality for  $\geq 54\%$  of radio-marked fawns from O’Gara and Shaw’s (2004) summary of 18 neonatal telemetry studies representing 995 fawns. Of this predation, 67% was caused by coyotes. Dunbar et al. (1999) concluded that coyote predation contributes additively to fawn mortality as coyotes kill “apparently regardless of fawn health.”

Corroborative evidence for the hypothesis that predators limit pronghorn populations can be drawn from the success of coyote eradication programs in eliciting positive population responses. A predator removal program on the Anderson Mesa herd in Arizona increased fawn:doe ratios at weaning to 57:100 in years with predator treatment from 31:100 in years  $\geq 4$  years post-coyote control (Smith et al. 1986). Improved recruitment following coyote removal was accompanied by increased abundance as the herd grew 136% (Smith et al. 1986). Similar positive population responses have been observed elsewhere (southeast Oregon, Willis 1988; National Bison Range, Montana, O’Gara and Malcolm 1988, Byers 1997b; west Texas, Canon 1993).

While the evidence for predator control of pronghorn populations may superficially appear overwhelming, more complex habitat interactions may be occurring. A widespread conclusion from ungulate population studies is that forage-limited, density dependence controls populations (i.e., caribou, Post and Klein 1999; elk [*Cervus elaphus*], Singer et al. 1997; mule deer, Pojar and Bowden 2004, Bishop et al. 2005; white-tailed deer, Patterson et al. 2002). Reduced juvenile survival is among the first population parameters to respond to resource limitation (Eberhardt 1977) and is a common characteristic of stable or declining pronghorn populations (O’Gara and Shaw 2004). Stress caused by forage resource limitation may be revealed through increased predation rates, particularly on young, vulnerable age classes (Bishop et al. 2005).

As in other ungulate systems, a growing body of evidence suggests processes other than simply fawn predation drive pronghorn recruitment and population abundance. Forage-limited density dependence has been shown to regulate pronghorn populations through fawn survival in shrubsteppe habitats of Utah (Aoude and Danvir 2004). Through experimental habitat manipulations designed to augment summer forage, Aoude and Danvir (2004) were able to increase recruitment and population abundance. Similarly, recruitment into this population as well as Arizona populations was negatively associated with population size (O’Gara and Shaw 2004). A more careful look at the role of predators in fawn survival suggests predation is at least partially compensatory. The nutritional condition of gravid females as they enter the winter affects both the gestation length and birth weight of the ensuing fawn crop; gestation length increased and birth weight decreased from wet to dry years (Byers and Hogg 1995). Relating these observations to population processes, heavier fawns at birth had a greater probability of survival to weaning (Fairbanks 1993). Similarly, fawns born during the peak fawning period realized higher survival rates to weaning (Gregg et al. 2001). Therefore, poor nutritional

condition, which prolongs gestation, may perturb birth synchrony and lead to increased predation risk.

Nutritional condition likely continues to influence fawn survival after birth through a cascade of ecological interactions. Pronghorn fawns depend on a hiding strategy to avoid predators during their first weeks of life (Byers 1997a). Fawns grow rapidly during this period (Martin and Parker 1997) as they transition from hiders to followers. The response of fawn growth rates to a range of both natural and artificial levels of energy and protein intake suggests nutrition rather than physiology constrains fawn development (Martin and Parker 1997). Poor forage quality may depress milk production by lactating does, thereby reducing fawn growth rates and prolonging the period in which fawns remain vulnerable to terrestrial predators.

Researchers have identified nutritional limitation within pronghorn herds (Dunbar et al. 1999) and strong differences in forage conditions between herds (Trainer et al. 1983), and yet attributed poor recruitment or population declines to coyote predation (Trainer et al. 1983, Dunbar et al. 1999). While these factors likely interact in shaping population processes, research must address potential contributions from nutrition before conclusions regarding the role of predation can be reached. We sought to explore the relationship between lactation season nutrition and pronghorn recruitment in populations within the shrubsteppe bioregion. Five populations across the state of Idaho were selected to represent the breadth of pronghorn habitat and observed population productivities. Our objectives were to: 1) evaluate nutritional condition across the lactation season and 2) explore the relationship between nutrition and population-level productivity. We used fecal indicators to quantify changes across the lactation season and differences among populations. We evaluated the relationship between these indices of nutritional condition and population recruitment as assessed through post-weaning aerial surveys.

## Study Area

This study was conducted in 5 disjunct pronghorn populations throughout southern and southeastern Idaho. The Eastern Owyhee study site typified resident pronghorn populations persisting in desert habitats. The area fell within Owyhee and Twin Falls counties defined on the east by Salmon Falls Creek, the west by the Bruneau/Jarbridge Canyons, and the south by the Nevada border and the foothills of the Jarbridge Mountains (Figure 1). To the north, we truncated the Eastern Owyhee study area at 42° 36' because cheat grass (*Bromus tectorum*) increased in dominance and pronghorn densities decreased precipitously beyond that line. According to Idaho's GAP analysis classification (Scott et al. 2002), stands of basin and Wyoming big sagebrush (*Artemisia tridentata tridentata* and *A. t. wyomingensis*) were the dominant cover types accounting for >60% of the study area. Perennial grasses composed another 25% of the area with the remaining area a mix of low sagebrush, bitter brush, and rabbit brush communities. Eastern Owyhee was a multi-use landscape with much of the area grazed by cattle and sheep for at least part of the year. The towns of Roseworth and Three Creek fell within the study area, of which Roseworth had a limited amount of irrigated agriculture (<3% of the Eastern Owyhee study area). Many of the wet meadows in the area were fenced and hayed in July and August. Average annual precipitation was 32.8 cm (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Three Creek, Idaho 1940-1987). The precipitation regime was characterized by hot, dry summers with precipitation spread evenly through fall, spring, and

winter. The mean monthly low temperature in January was  $-11.4^{\circ}\text{C}$  with a mean monthly maximum temperature in July of  $30.1^{\circ}\text{C}$ .

The second study site, the Camas Prairie, was selected to characterize migratory pronghorn persisting largely on agricultural lands through the summer months. The Camas Prairie study area was bounded to the north by the Soldier Mountains (Sawtooth National Forest) and to the south by the Bennett Hills. The majority of the study area fell within Camas County with a small portion in Elmore County (Figure 1). The towns of Fairfield and Hill City fell within the study area. Camas Prairie was heavily roaded, bisected by state highways 20 and 46 with secondary roads established along most section lines. The majority (52%) of the study area was under agricultural cultivation, of which 81% was dryland and 19% was irrigated agriculture. Alfalfa was the dominant crop (54% of agricultural area) followed by barley (13%), and grass hay (11%) in addition to pasture or Conservation Reserve Program lands (17%; Kinder 2004). Perennial grass (21% of the study area) and basin and Wyoming big sagebrush communities (18%) persisted in Bureau of Land Management and state-held lands. Average annual precipitation for the area was 38.2 cm with a periodicity of dry summers and wet winters (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Fairfield Ranger Station, Idaho 1948-2004). The mean low monthly temperature in January was  $-14.9^{\circ}\text{C}$  with a mean high monthly temperature in July of  $29.7^{\circ}\text{C}$ .

The third study site was the Little Wood area characterizing migratory pronghorn on native shrubsteppe range. This foothills habitat was bordered to the north by the Pioneer Mountains and to the south by the eastern expanses of the Big Desert. The study area fell within Blaine County (Figure 1). Local ranches grazed cattle, sheep, and horses throughout the area. Basin and Wyoming big sagebrush was the dominant vegetation type covering 73% of the study area. Agricultural lands accounted for 6% of the study area and irrigated alfalfa was available to pronghorn. The remainder of the study area was composed of mountain big sagebrush, perennial grasslands, and bitter brush. Average annual precipitation for the area was 32.6 cm characterized by dry summers with precipitation spread evenly throughout the remainder of the year (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Picabo, Idaho 1958-2004). The mean low temperature in January was  $-13.7^{\circ}\text{C}$  and the mean high temperature in July was  $30.2^{\circ}\text{C}$ .

Two populations inhabiting mountain valley habitats were included in the study. These migratory populations likely over-wintered together on the Big Desert (Hoskinson and Tester 1980), but were isolated by the Lemhi Mountain Range during the summer. The first, encompassing the Lemhi and Birch Creek Valleys, fell within Lemhi County (Figure 1). Low sagebrush was the dominant vegetation community, comprising 51% of the study area. Mountain, basin, and Wyoming big sagebrush accounted for another 40% of the study area. The area had limited agriculture (4%) and interspersed forest stands (4%). Average annual precipitation for the area was 20.1 cm (National Oceanic and Atmospheric Administration, Western Regional Climate Center, Leadore, Idaho 1965-2004). The mean low monthly temperature in January was  $-15.7^{\circ}\text{C}$  with a mean high monthly temperature in July of  $29.1^{\circ}\text{C}$ .

The second mountain valley habitat fell within the Little Lost and Pahsimeroi valleys in Custer and Butte counties (Figure 1). Mixed stands of mountain big sagebrush and low sagebrush dominated the study area (>60%). Basin and Wyoming big sagebrush accounted for 23% of the study area. Patches of Douglas fir (*Pseudotsuga menziesii*) and subalpine fir persisted in higher, mesic microsites. Agriculture accounted for <2% of the total land area. Average annual precipitation for the area was 21.1 cm (National Oceanic and Atmospheric Administration, Western Regional Climate Center, May, Idaho 1948-2004; Howe, Idaho 1948-2004). The mean low temperature in January was -14.0° C and the mean high temperature in July was 30.1° C.

## Methods

### Forage Quality

Pronghorn are highly mobile and selective feeders, such that the relative abundance of preferred food items on the landscape does little to reflect the ability of pronghorn to meet their dietary requirements (Byers 1997a). Therefore, we used 2 fecal indicators, FN and DAPA, to depict the response of populations to the nutritional environment, incorporating elements of both forage abundance and competition. The utility of FN and fecal DAPA has been demonstrated through feeding trials with captive pronghorn (Robinson 2001) and applied to free-ranging pronghorn to track changes in seasonal diet quality (Dunbar et al. 1999, Dennehy 2001, Hansen et al. 2001), to compare diet quality between populations (Hansen et al. 2001) and to evaluate differences in diet associated with social dominance (Dennehy 2001). Robbins et al. (1987) caution that FN is not a precise indicator of either dietary nitrogen content or dry matter digestibility, as this nutritional metric lacks the ability to distinguish contributions from dietary crude protein content, non-digested fiber-bound protein, metabolic fecal protein (MFN), and tannin-bound protein. The protein-precipitating effects of tannins in some forage items can greatly inflate nitrogen levels observed in feces and distort the relationship between FN and protein and energy available to the herbivore (Robbins et al. 1987). However, with a large portion of pronghorn summer diets composed of generally high-protein, low-tannin forbs (Hansen et al. 2001), FN is seasonally an appropriate metric of diet quality and energy intake.

Fresh fecal samples were collected from groups of pronghorn throughout the lactation season (24 May-30 Jul) in 2004. Groups were observed from roads using spotting scopes and binoculars. We monitored groups until defecation was observed, at which time an individual remaining at the road would direct a second observer to the location of the fecal sample using 2-way radios. Each study site was visited during five 2-week sampling periods (time rotations). Within each sampling period, we spatially segregated fecal samples in order to avoid resampling the same group and to obtain a representative sample of the entire population. Groups, but not necessarily individuals, were potentially resampled in subsequent 2-week intervals. Using a latex glove, pellets were deposited in resealable plastic (Eastern Owyhee, Camas Prairie, and Little Wood) or paper (Birch Creek and Pahsimeroi) bags. Given the correlation in plant communities encountered by a group foraging together, we considered the group our sampling unit. Therefore, in the event that more than a single sample was located from a group site, additional pellet groups were bagged independently and equal weights were homogenized in the laboratory. For the purposes of chemical fecal analysis, a composite sample produces a value equal to the mean of the represented individuals (Jenks et al. 1989). Samples were stored frozen (Eastern Owyhee,

Camas Prairie, and Little Wood) or air-dried (Birch Creek and Pahsimeroi) until laboratory analysis. All samples were transferred to paper bags, dried in a drying oven at 40° C for 2 days or until dry, and ground prior to analyses.

Samples were sent to Washington State University's Wildlife Habitat Lab for chemical analysis. Fecal nitrogen was extracted according to the Kjeldahl method and DAPA was extracted according to Nelson and Davitt (1984) with values expressed as oven-dry weights.

### **Aerial Survey Methods**

Herd composition surveys were conducted from 28 July-11 August in a Bell 47 Soloy with a pilot and 2 observers experienced in pronghorn aerial surveys. Flights were conducted before noon to maximize the proportion of individuals not bedded. Detectability of groups was improved by the common response of groups to run with the approach of the low flying helicopter. For each population, the extent of the inhabited area was delineated and divided into search subunits. With the assistance of an onboard Global Positioning System for navigation, rough transects were flown within each subunit in an effort to census each population. For large groups, classification of bucks and fawns was divided between observers. In all other groups, the observers reached a consensus on group composition.

While fawn:doe ratios represent the additive effect of both fecundity and survival, ratios are an appropriate measure of pronghorn population productivity. Pregnancy rates have been shown to be uniformly high across pronghorn populations (O'Gara 2004a) with the exception of years following severe winters (Barrett 1982), conditions not observed during the timeframe of our study.

### **Analysis**

We used multivariate analysis of variance (MANOVA) to evaluate differences in FN and DAPA between study sites, time rotations, and the interaction of study site and time rotations (Proc GLM, SAS Institute 1999). Where statistical differences were identified with MANOVA, we used canonical variables to quantify the influence of each response variable on the significant outcome. Subsequent analysis of variance (ANOVA) and Tukey's pairwise comparisons were used to identify between site differences with an alpha value of 0.05 (Proc GLM, SAS Institute 1999).

We conducted 2 sets of multiple regression analyses to evaluate the relationship between pronghorn population productivity and nutritional plane (Proc REG, SAS Institute 1999). Large mammal population dynamics are influenced by the integration of environmental conditions over a long time period (Picton 1984), and fawns remain vulnerable until weaning. Therefore, we evaluated the relationship between fawn:doe ratios and the nutritional conditions experienced through the entire lactation season, using a grand mean from the 5 sampling rotations. Assuming nutrition has a constant importance for fawn survival from birth to weaning may be an oversimplification of biological processes. Protein and energy demands on a lactating mother change over a short time period; energy demands decrease from a high of 141.7 KJ/kg/day during the first 2 weeks of lactation to 22.3 KJ/kg/day at 74 days post-parturition (Martin 1995).

Therefore, to depict the relative importance of observed nutritional levels, we averaged milk energy expenditure over 2-week intervals to correspond with our sampling frame, and weighted observed fecal values accordingly. We then evaluated the relationship between fawn:doe ratios and the grand mean from the 5 weighted sampling periods.

For each set of regression analyses, we used an information theoretic approach employing  $AIC_c$  to evaluate 3 competing models (FN, DAPA, FN + DAPA) against a null, intercept-only model (Burnham and Anderson 2002).

## Results

Significant differences in nutrition were identified across sites with the multivariate test (Wilks' Lambda = 0.5571,  $P < 0.0001$ ). Differences were attributable to variation by site in both FN and DAPA (CAN1  $F = 25.40$ ,  $P < 0.0001$ , CAN2  $F = 6.29$ ,  $P = 0.0004$ ). Significant differences were also identified across time rotations (Wilks' Lambda = 0.8330,  $P < 0.0001$ ); these differences were attributable to the general decline in FN values across the lactation season (CAN1  $F = 7.15$ ,  $P < 0.0001$ , CAN1 =  $1.4684*FN - 0.5791*DAPA$ ; CAN2  $F = 1.28$ ,  $P = 0.2817$ ). The statistically significant interaction term (Wilks' Lambda = 0.8377,  $P = 0.0083$ ) indicated FN values varied independently by site across time rotations (CAN1  $F = 1.73$ ,  $P = 0.0083$ , CAN1 =  $1.1862*FN + 0.2936*DAPA$ ; CAN2  $F = 1.10$ ,  $P = 0.3597$ ).

Fecal nitrogen values varied between sites and generally declined through the lactation season (Figure 2). Subsequent univariate tests on the FN response variable identified the interaction term as being significant and the full model was used for further comparisons ( $F = 12.81$ ,  $P < 0.0001$  Type III SS site\*time  $P = 0.0023$ ). Pairwise comparisons, correcting for site-specific changes over time, identified a number of significant differences between sites. Fecal nitrogen values observed in the Camas Prairie were significantly greater than all other sites. Fecal nitrogen values from the Little Wood population were greater than those from the Pahsimeroi and Eastern Owyhee populations, similar to the Birch Creek population, and less than the Camas Prairie population. Fecal nitrogen values from the Birch Creek population were greater than the Pahsimeroi and Eastern Owyhee populations, similar to the Little Wood population, and less than the Camas Prairie population. No difference was detected between the Pahsimeroi and Eastern Owyhee populations, both having FN scores significantly lower than all other populations.

Diaminopimelic acid levels showed similar, although less pronounced, trends (Figure 3). In the univariate test, the interaction term approached statistical significance ( $F = 3.57$ ,  $P < 0.001$ , Type III SS site\*time  $P = 0.0838$ ) and, therefore, the full model was used for between-site comparisons to adjust for unequal sample sizes across sampling rotations. Pairwise comparisons between sites indicated DAPA values for Eastern Owyhee were significantly lower than Birch Creek, Camas Prairie, and Little Wood sites and similar to Pahsimeroi. No other statistical differences were detected.

In our regression analysis of population productivity against fecal indicator values, evaluation of both the simple and weighted regression models identified the null model as the  $AIC_c$  'best' model with  $\Delta AIC_c$  scores greater than 3 for the next competing model (Table 7). In both model

sets, our second best model incorporated FN with R-square values of 46% and 48% for the simple and weighted regression models, respectively (Figure 4). The relationship with DAPA was not as strong, with R-square values of 16% and 13% for the simple and weighted regression models, respectively (Figure 5). Weighting observations to reflect changes in energy expenditures of lactating does generally improved the quality of our models; AIC<sub>c</sub> values decreased and R-square values increased from the simple regressions to the weighted regressions. Regression analysis suffered from a lack of power. A retrospective power analysis conducted on the weighted FN model suggested a minimum of 10 sites would have been necessary to identify a statistically significant slope parameter at the 0.05 level.

## Discussion

Our study demonstrated FN and DAPA are well suited to resolve both statistical and biological differences among pronghorn populations and changes across the lactation season. Across sites, FN generally declined through the lactation season. As preferred forage items senesce with the progression of the lactation season, pronghorn might switch to high-tannin sagebrush, which would decouple FN and digestible energy and protein. We did not observe this hypothesized FN spike, indicating FN was an appropriate metric to evaluate pronghorn nutrition throughout the lactation season. Diaminopimelic acid values did not show a strong trend across the lactation season, although the pattern of between-site differences observed in FN was generally reflected in DAPA.

Both FN and DAPA have unique ranges for different ungulate species and may vary with forage types. By placing our observations in the context of other studies, we gain perspective and can begin to qualitatively characterize Idaho's pronghorn summer range. Fecal nitrogen and DAPA were used by Hansen et al. (2001) to quantify nutritional condition of pronghorn at Sheldon National Wildlife Refuge and Hart Mountain National Antelope Refuge, Oregon, during the summers of 1994 and 1995. Mean FN values observed across the lactation season in Oregon were similar to native range sites in Idaho. Alternatively, DAPA values in Oregon were substantially greater than any of the sites observed in Idaho. Similarly, DAPA values observed from females at the National Bison Range, Montana, in 1996 (Dennehy 2001) were substantially greater than those observed in Idaho, and comparable to values observed in Oregon. The ability to draw meaningful inference from FN and DAPA values will continue to improve with the application of these tools to free-ranging pronghorn across similar habitats and seasonal timeframes.

Within the observed distribution of DAPA values, the tight clustering of the Birch Creek, Camas Prairie, Little Wood, and Pahsimeroi populations suggests that these populations are able to obtain similar levels of digestible energy. In contrast, DAPA values from Eastern Owyhee were the lowest recorded in pronghorn and were significantly lower than other sites in Idaho. Recruitment into the Eastern Owyhee population could be energetically limited.

In the Birch Creek, Eastern Owyhee, Little Wood, and Pahsimeroi sites, we observed an increase in DAPA levels between the fourth (6-18 Jul) and fifth (19-30 Jul) sampling rotation. We believe this late-season spike was caused by changes in foraging behavior associated with senescence of preferred forage items. Pronghorn responded to the curing of forage items in late summer by

concentrating activity around more mesic habitats. At the Little Wood site, pronghorn groups were observed at higher frequencies in the available irrigated alfalfa and wet meadows with the progression of the growing season. In Eastern Owyhee, our most heterogeneous site, most of the groups identified from aerial surveys in August were associated with wet meadow habitats; the median distance from detected groups to the nearest wet meadow was 2.8 km (T. J. Smyser, unpublished data).

Fecal nitrogen and DAPA levels generally showed similar patterns among populations across the sampling frame. Deviations in this pattern were observed at the Birch Creek and Little Wood sites within the fifth time rotation as FN remained stable or declined and DAPA values increased. Fecal nitrogen and DAPA are unique tools to assess diet quality, and the decoupling of FN and DAPA may be caused by individuals foraging on more digestible items with lower protein values or decreased contributions to FN from MFN, plant-bound protein, or tannin-bound protein. Further, while we observed increases in DAPA between the fourth and fifth sampling rotation within these sites, evaluating this improvement within the range of observed DAPA levels suggests that the increases may have little biological significance.

With protein demands of ungulates in the peak of lactation at 5 times those of maintenance levels (Spalinger 2000), it is likely that the low values of FN observed in some populations are potentially limiting fetal growth and dam milk production. We believe that the failure to identify a strong relationship between the observed fecal indicators and productivity was likely a result of the limited sample size and not a lack of relationship. The ability of the weighted FN model to explain 48% of the variation in recruitment rate offers support for the hypothesis of summer range limitation.

Weighting observations in a biologically meaningful way improved the quality of our models. The weighting scheme we used highlights the challenges of milk production while minimizing the importance of fawns obtaining an increasing proportion of energy from herbaceous food items. The simple linear regression model provided an important counterbalance to the weighted models by emphasizing the importance of late-summer nutrition in recognition of the sustained vulnerability of fawns until weaning. The concentration of mortality events within the first 3 weeks of life (Beale and Smith 1973, Bodie and O’Gara 1980, Trainer et al. 1983, Barrett 1984, Dunbar et al. 1999) suggests nutritional difference may have the greatest effects early in the fawn’s life or during gestation. Because of the preponderance of early mortality and high protein and energy demands of late gestation, future research may find it prudent to broaden the sampling frame to include the third trimester of gestation. A weighting scheme could easily be extended to consider the energy and protein demands associated with rapid fetal growth.

Our minimal data set limited analysis to linear regression. Given that the relationship between dietary protein and apparent digestibility is curvilinear (Robbins 1983), it is likely that the relationship between nutritional plane and recruitment is similarly non-linear. Above threshold levels, fetal growth and milk production are likely limited by the behavioral and physiological constraints of the dam. Additional improvements in diet quality above these thresholds have diminishing returns. It is not known whether the nutritional condition experienced within any of our study sites had reached a level of physiological limitation, although the substantially greater

metrics of nutritional quality observed elsewhere (NBR, Dennehy 2001; Oregon, Hansen et al. 2001) suggested that lactating mothers would seek out a higher-quality diet if available.

While our data offers some support for the hypothesis that the quality of summer range limits pronghorn populations, it is not sufficient to refute the importance of other mortality factors such as predation. As growing fawns take on adult proportions, they enter a speed refuge at about 45 days of age with the ability to evade most terrestrial predators (Byers 1997a). Nutrition likely interacts with predation within this window of fawn vulnerability as high nutrition ushers fawns rapidly into an adult survival class while poor nutrition prolongs the risk to predation (Martin and Parker 1997). Understanding the biological mechanisms at work on the landscape will improve with the continued assessment of fecal indicators across levels of habitat quality, net primary productivity, and various intensities of inter- and intra-specific competition. The true influence of nutrition on population parameters is likely to increase with understanding of the interaction between nutritional level, fawn growth rates, the attainment of adult running speeds, and associated predation risk.

## **EVALUATION OF PRONGHORN POPULATION PRODUCTIVITY RELATIVE TO BROAD-SCALE HABITAT VARIABLES IN WYOMING**

Intensive studies of pronghorn populations have identified a number of factors that contribute to population dynamics but few have strong effects beyond the local scale or function in a regulatory manner. We used fawn:doe ratios collected from the 44 herd units in Wyoming from 1978-2003 to assess the influence of broad scale habitat variables on population productivity. We evaluated 2 sets of models to: 1) examine the response of productivity to annually varying habitat characteristics and 2) contributions of habitat characteristics to inherent differences between herd units in productivity. The annually varying habitat model identified positive relationships between fawn:doe ratios and previous growing season precipitation, fall precipitation, and previous season's population growth potential. Fawn:doe ratios were negatively related to winter precipitation and growing season precipitation. For contributions to inherent differences between herd units, fawn:doe ratios were negatively associated with fall precipitation and positively associated with growing season precipitation.

### **Introduction**

Most efforts to understand population processes focus on intense studies of local populations (Bomar 2000). Results from these local populations are then extrapolated across landscapes and occasionally synthesized with other studies to frame concepts of population regulation. Fine-scale studies of pronghorn have yielded several complementary and competing hypotheses regarding the mechanisms that regulate populations. Disease (Beale and Smith 1973, Trainer et al. 1983, Dunbar et al. 1999), trace mineral deficiencies (Bodie and O'Gara 1980, Stoszek et al. 1980), severe winter weather (Martinka 1967, Barrett 1982), predation (Smith et al. 1986, O'Gara and Malcolm 1988, Willis 1988, Canon 1993, Byers 1997a, O'Gara and Shaw 2004), and nutrition (Hess 1999, Kohlman et al. 1999, Aoude and Danvir 2004, O'Gara and Shaw 2004) have all been shown to contribute to population processes at fine scales. Under typical environmental conditions, adult pronghorn have high survival and pregnancy rates (Byers 1997a). For this reason, much of the research on pronghorn population dynamics has focused on

fawn survival as a population parameter sensitive to environmental conditions (Eberhardt 1977) and important for the persistence of populations.

The incidence of disease can be an important component in the regulation of wildlife populations; however, with low rates of disease reported from pronghorn populations, it is unlikely that pathogens contribute strongly to broad-scale processes (O’Gara 2004b). Investigating the infection rate of fawns at Hart Mountain National Antelope Refuge, Oregon, concurrent with a population decline, Dunbar et al. (1999) found 2% of marked fawns died as a result of pasteurellosis. Other studies have found similarly low rates of fawn mortality attributable to disease (Beale and Smith 1973, 5% mortality attributable to disease; Trainer et al. 1983, 2% mortality attributable to disease).

Trace element deficiencies have also been implicated in poor fawn survival in a limited number of studies (Bodie and O’Gara 1980, Stoszek et al. 1980). A subset of radio-marked fawns in the Pahsimeroi Valley, Idaho, demonstrated symptoms consistent with those of weak calf syndrome, a condition documented in domestic livestock. Associated symptoms include hemorrhages, edema, atrophic thymus gland, enlarged lymph nodes, and susceptibility to secondary bacterial enteritis (Bodie and O’Gara 1980). These symptoms in pronghorn fawns were accompanied by pathologically low levels of selenium (Stoszek et al. 1980). While selenium deficiencies may be important within the Idaho batholith (Robbins 1993, Bomar 2000) or other local habitats, it is unlikely that trace-element deficiencies play a major role in regulating pronghorn populations throughout their range.

Because of their sensitivity to snow accumulations, pronghorn populations are susceptible to catastrophic losses during severe winters. High snow accumulations and below normal temperatures can result in population losses in excess of 60%, as deep snows restrict access to winter forage causing individuals to perish from starvation (Martinka 1967, Barrett 1982). Poor recruitment often follows severe winters because of high rates of fetal absorption and the poor condition in which females leave the winter range (Barrett 1982). Catastrophic winter mortality and reduced recruitment occurs as access to food resources becomes limited by snow depth rather than density-dependent processes such as intra-specific competition. Therefore, while extreme winter conditions may cause catastrophic population losses, such a density-independent mechanism cannot regulate population abundance.

Predation is frequently implicated in heavy losses of pronghorn fawns. Predation was the proximate cause of mortality for  $\geq 54\%$  of radio marked fawns from O’Gara and Shaw’s (2004) summary of 18 neonatal telemetry studies representing 995 fawns. The importance of predation in pronghorn populations is corroborated by the positive population responses elicited following predator control (Smith et al. 1986, O’Gara and Malcolm 1988, Willis 1988, Canon 1993, Byers 1997a). While fawn predation is an important driving factor in population dynamics, the effects of predation can vary greatly both spatially and temporally. Coyote densities can vary across fine spatial scales with dramatically different impacts on local pronghorn populations (Trainer et al. 1983). Additionally, the impact of a constant coyote population may vary from one year to the next with the abundance of alternative prey items (Hamlin et al. 1984). Spatial and temporal

variability in the intensities of coyote predation prohibits using coyote densities to guide broad-scale management action.

While fine-scale studies have identified factors influential in pronghorn population response, application of these factors to broad temporal and spatial scales has limited utility. Density-dependent forage limitation has been hypothesized to regulate pronghorn populations (Aoude and Danvir 2004, O’Gara and Shaw 2004) and may function to unify many of these fine-scale processes. Further, environmental variables that influence nutrition such as climatic conditions, soil composition, and vegetation characteristics, may function on broader spatial and temporal scales. Aoude and Danvir (2004), working in the shrubsteppe habitats of Utah, suggested that summer forage quality was the mechanism limiting pronghorn populations in a density-dependent manner. On a broader scale, declines in fawn:doe ratios with increasing population size, as documented in this Utah population (Aoude and Danvir 2004) and throughout Arizona (O’Gara and Shaw 2004), provide corroborative evidence for density-dependent regulation. While predation is undoubtedly an important mortality factor, susceptibility to predation may be the response of an environmental cascade driven by nutrition. The nutritional condition of gravid females as they enter the winter affects both the gestation length and birth weight of the ensuing fawn crop; gestation length increased and birth weight decreased from wet to dry years (Byers and Hogg 1995). Relating these observations to population processes, heavier fawns at birth had a greater probability of survival to weaning (Fairbanks 1993). Similarly, fawns born during the peak fawning period realized higher survival rates to weaning (Gregg et al. 2001). Therefore, poor nutritional condition, which prolongs gestation, may perturb birth synchrony and lead to increased predation risk. Nutritional condition likely continues to influence fawn survival after birth. The response of fawn growth to a range of both natural and artificial levels of energy and protein intake suggests nutrition rather than physiology constrains the rate of development (Martin and Parker 1997). Poor forage quality may depress the milk production of lactating does, thereby reducing fawn growth rates and prolonging the period in which fawns remain vulnerable to terrestrial predators (Martin and Parker 1997).

If pronghorn population dynamics are regulated by density-dependent factors associated with nutrition rather than localized predation levels or stochastic factors such as winter severity, then broad-scale patterns should link habitat quality with population productivity. Our objective was to evaluate the response of population productivity to nutritionally-focused habitat variables at broad scales appropriate for management. At the scale of the herd unit, our goals were to evaluate the relationship between population productivity as assessed through fawn:doe ratios and 1) temporally variable habitat characteristics and 2) stable habitat characteristics that differed among herd units.

## **Study Area**

This study spanned the state of Wyoming, encompassing the 44 pronghorn herd units defined by the Wyoming Game and Fish Department (WGFD) for the purposes of population management. The study area excluded populations within Yellowstone and Grand Teton National Parks as management is out of the jurisdiction of WGFD. Within delineated herd units, managers subjectively classified habitat as unsuitable, crucial, spring/summer/fall, winter, winter/yearlong, and yearlong. Our spatial analysis excluded habitats classified as unsuitable habitat. Annual

average precipitation (1980-1997) within herd units ranged from 25.2 cm to 72.1 cm with precipitation generally increasing with elevation (Thornton et al. 1997). Irrigated and dryland agriculture (7%) was scattered throughout the state with concentrations in the southeast (Wyoming GAP Analysis 1996).

## Methods

### Data Acquisition

We evaluated fawn:doe ratios as our measure of population productivity relative to spatially and temporally explicit habitat variables. Fawn:doe ratios represent the additive effect of both fecundity and survival; however, pregnancy rates have been shown to be uniformly high across pronghorn populations (O’Gara 2004a). Therefore, differences observed in population productivity likely emphasize differences in fawn survival. Fawn:doe ratios were collected through aerial and ground surveys conducted by WGFD as part of routine population monitoring from 1978-2003. The relationship between fawn:doe ratios and habitat characteristics were assessed through 2 unique model sets intended to identify: 1) the response of fawn:doe ratios to annually varying habitat characteristics and 2) habitat conditions that contribute to inherent differences in population productivity.

Models evaluating annual fawn:doe ratios (1979-2003) were composed of the temporally dynamic variables: previous year’s fall precipitation (fall [Aug-Nov]), previous winter’s precipitation (winter [Dec-Feb]), growing season precipitation (grow [Mar-Jul]), previous year’s growing season precipitation [grow(-1)], population growth potential (potential), previous year’s growth potential [potential(-1)], and the z-score transformation of the previous year’s total harvest (harvest). To estimate herd-unit precipitation, we constructed a weighted average based on the inverse of distance from the herd unit centroid to the 5 nearest weather stations (National Oceanic and Atmospheric Administration, Western Regional Climate Center). Additional weather stations were incorporated when data from the nearest 5 were inadequate. Months with >5 missing days of precipitation data were eliminated from weighted averages. Growth potential was defined as: average population estimate - current population estimate / average population estimate. Population estimates were derived from a combination of line transect population estimates and population modeling conducted by WGFD (Reeve et al. 2003). Total harvest values were those published by WGFD (Reeve et al. 2003).

Averaging all available fawn:doe ratios from 1978-2003 for each herd unit, we evaluated herd-unit productivity relative to the spatially distinct habitat characteristics: average fall precipitation (fall [1980-1997]), average winter precipitation (winter [1980-1997]), average growing season precipitation (grow [1980-1997]), range production (production), per capita range production (forage), and the proportion of the herd unit not delineated as yearlong habitat (habitat). Precipitation data were obtained at a resolution of 1 km<sup>2</sup> from Thornton et al. (1997). We characterized annual potential production of range forage (lbs/acre) based on the composition of soil types assuming normal precipitation using STATSGO data (<http://www.ncgc.nrcs.usda.gov>). To represent forage availability to the individual, we divided range productivity by the average density of pronghorn over the study period. To express potential benefits of seasonal migration,

our final variable considered the proportion of the herd unit delineated by game managers as not “yearlong” habitat.

## **Analysis**

We used regression models to assess the response of population productivity to annual variation in precipitation and population densities. To isolate the response of population productivity to annual variation in habitat quality from inherent differences in recruitment potential among herd units, we used z-score transformations of annual fawn:doe ratios by herd unit as our response variable. For instance, we subtracted the mean fawn:doe ratio (1978-2003) for herd unit 202 from the observed 1979 ratio for this herd unit, and then divided the difference by the standard deviation of fawn:doe ratios for herd unit 202. We used an information theoretic approach applying AIC to evaluate a fully-parameterized, main-effects model, and 7 reduced models. The predictor variable ‘potential’ is based on population abundance and, therefore, will be strongly auto-correlated with the time-lagged growth potential variable. For this reason, we did not include both measures of growth potential in either our global or reduced models.

To assess the influence of stable habitat characteristics on population productivity, we used linear regression (Proc REG, SAS Institute 1999) to relate spatially explicit habitat characteristics to fawn:doe ratios averaged over the study period (1978-2003). Prior to model construction, we used the variance inflation factor to screen variables for collinearity. Because of the high collinearity of the fall precipitation variable with growing season and winter precipitation, we eliminated it from the fully parameterized model. We used AIC to evaluate the fully parameterized model, 4 reduced models, and a null model.

## **Results**

For the temporally variable models, 1,080 observed fawn:doe ratios were available from 25 years of surveys across 44 herd units. Evaluation of competing models with an information theoretic approach identified the model incorporating the variables fall, winter, grow, grow(-1), and potential(-1) (Model 1) as the AIC best model (Tables 9 and 10). This model explained 11% of the variation in the data (Table 8). The  $\Delta$ AIC score for the next competing model was  $>16$ , indicating there was little support for alternative models. From this best model, the time-lagged potential growth variable was the strongest variable with a predicted magnitude of 1.72 from the lowest to the highest growth potential (Table 9). Fawn:doe ratios were positively associated with fall precipitation (magnitude = 0.88), with a weak positive relationship to the time-lagged growing season precipitation (magnitude = 0.16; Table 9). Winter precipitation was negatively related with fawn:doe ratios (magnitude = -0.45) as was growing season precipitation (magnitude = -0.73; Table 9).

From the analysis of stable habitat characteristics, averaged fawn:doe ratios from the 44 herd units were normally distributed (Shapiro-Wilk = 0.96,  $P$  = 0.14, Skewness = -0.07). The average ratio was 0.68 fawns per doe (SD = 0.13) with a range from 0.44 to 0.88 fawns per doe.

The model including the variables fall precipitation and growing season precipitation was the AIC best model (Model 1; Table 10). The  $\Delta$ AIC scores from the 2 univariate models evaluated

(range production and habitat) indicated that these models should be considered competitive models (Table 10). Model 1 identified a negative relationship between fawn:doe ratios and fall precipitation with predicted fawn:doe ratios decreasing 0.31 fawns:doe from the wettest to driest herd units (Table 11). The second variable, growing season precipitation, was positively related with fawn:doe ratios, although the effects were not as strong as fall precipitation (magnitude = 0.16; Table 11). In the range productivity model (Model 3; Table 10), population productivity was positively related with range productivity, as herd units with the most productive rangelands were predicted to produce 0.13 greater fawns:doe than the least productive herd units (Table 11). The habitat model (Model 2; Table 10) identified a positive relationship with the proportion of habitat designated as yearlong habitat, such that herd units composed of 100% yearlong habitat were predicted to have 0.11 greater fawns:doe than those herd units with no yearlong habitat (Table 11).

### **Discussion**

Evaluation of temporally varying habitat characteristics identified a model inclusive of variables related to forage availability and carrying capacity. The positive associations between fawn:doe ratios and both the previous growing season precipitation and fall precipitation highlights the importance of female pre-winter condition on fawn survival (Byers and Hogg 1995, Danvir 2000). Summer and fall forage conditions are important for determining the status of females as they enter the winter season during which much of gestation occurs (Robbins 1993). The positive relationships identified between population productivity and precipitation are likely caused by the effects of summer and fall rains to delay the seasonal decline in protein and energy of forage items (Smith and Malechek 1974) or induce a fall green-up of seasonally important grasses (Pyrah 1987). Similarly, Byers and Hogg (1995) identified a positive relationship between fall precipitation (Jul-Oct) and birth weight and gestation length, 2 measures sensitive to available energy with impacts on fawn survival (Fairbanks 1993, Gregg et al 2001).

Our model identified a negative relationship associated with winter precipitation and fawn:doe ratios. Spring forb abundance which is important to meet the protein and energy demands of late gestation and lactation, may be closely tied with winter precipitation (Smith and Lecount 1979). These benefits of winter precipitation appear to be offset in the high plains habitats of Wyoming by the energetic stresses and mobility limitation associated with snow accumulations. Deep snows limit access to winter forage resources and severe winter conditions may cause catastrophic population losses and high rates of fetal absorption (Martinka 1967, Barrett 1982).

Growing season precipitation was negatively related to fawn:doe ratios in our selected model and throughout all models evaluated. Given the positive relationship identified between forb abundance and population response (Aoude and Danvir 2004), we expected herd units to respond positively with increasing levels of growing season precipitation due to the link between forb biomass and precipitation. While wetter springs may translate to greater forb abundance in the summer, small-bodied fawns on the open plains are susceptible to death by exposure in cold, wet environments within the first weeks of life (Ellis 1970). Additionally, with the majority of fawn mortality occurring during the first 3 weeks of life (Beale and Smith 1973, Bodie and O'Gara 1980, Trainer et al. 1983, Barrett 1984, Dunbar et al. 1999), much of the season's fawn mortality may occur before the potential benefits of growing season precipitation have emerged.

Finally, the strongest variable in our model was the time-lagged growth potential variable. The strength of both growth potential variables throughout the evaluated models indicated that pronghorn populations responded in a density-dependent manner. The strength of models inclusive of the time-lagged growth potential variable relative to the current growth potential variable (Table 8) suggested that conditions prior to conception and through gestation had a stronger influence on fawn survival than pronghorn abundance at birth. If females are able to manipulate their reproductive energy output in response to population levels, conceivably they would cue to the previous year's population level. Alternatively, some of the benefits of abundant resources in a population below carrying capacity may be offset by the benefits of predator-swamping in a higher density population (Linnell et al. 1995).

Evaluation of stable habitat characteristic models yielded a model similarly incorporating precipitation variables, although the trends were different than those observed in the annual variation analysis. Fall precipitation was the most influential variable in the selected model with fawn:doe ratios decreasing with increasing precipitation levels. This outcome was surprising given the positive association demonstrated in the annual variation analysis and conclusions drawn in other studies (Byers and Hogg 1995, Danvir 2000). The negative relationship may be a limitation of our seasonal delineations of precipitation variables as late fall precipitation may come in the form of snow. Alternatively, fall precipitation may be correlated with some other habitat gradient not incorporated in this analysis. Growing season precipitation was positively associated with fawn:doe ratios. While this trend is opposite of that identified in the annual variation analysis, the outcome falls in accord with our predictions given the positive associations between precipitation, forb abundance, and population productivity.

Two univariate models were identified as competitive models. The first identified a positive relationship between fawn:doe ratios and forage biomass production based on soil conditions in a "normal precipitation year." This variable showed a close positive correlation with growing season precipitation, supporting the connection from precipitation to forb abundance to population productivity. Further, the strength of this model supports the hypothesis of nutritional limitation regulating population dynamics.

The second univariate model identified a positive relationship between the proportion of habitat in a herd unit classified as yearlong habitat and population productivity. Seasonal migrations (Hoskinson and Tester 1980, Berger 2004) may allow populations to utilize seasonably unsuitable habitats that provide more abundant forage resources during times of suitability. For example, snow accumulations may force pronghorn to vacate some habitats, but snow melt subsequently contributes to increased forb abundance through the spring and summer months. Similarly, dense sagebrush may form in habitats too dry to support populations through the fawning season, although such areas may provide crucial access to forage through the winter. Based on this rationale, we predicted pronghorn that are able to capitalize on seasonably unsuitable habitats may realize higher levels of forage abundance. The opposite trend was observed in the data as herd units with higher proportions of yearlong habitats were more productive than herd units dependent upon seasonal habitats. The lower productivity associated with those herd units with reduced amounts of yearlong habitat may reflect the costs associated with migration. Alternatively, there is a general cline in yearlong habitats across the state of

Wyoming, with the highest proportions in the northeast declining to the southwest. The positive association along this gradient of yearlong habitats may reflect the response to some other environmental cline.

Both the analysis of annual habitat variation and the analysis of stable habitat characteristics failed to identify strong relationships between habitat conditions and population productivity. The strength of the identified relationships may be limited by a number of factors pervasive throughout our analyses. First, fawn:doe ratios are inherently noisy data, susceptible to fluctuations in the age distribution of the female population. A strong fawn crop in year 1 may depress fawn:doe ratios in year 2 because of the low reproductive potential of yearlings, even if conditions remain ideal. Additionally, large-bodied ungulates integrate environmental variables over a long period of time (Picton 1984). Population productivity may, therefore, reflect the interaction of habitat characteristics over the past several years rather than an immediate response to current conditions. Second, variables used in the modeling exercise may fail to accurately characterize conditions on the landscape. For example, characterizing herd unit precipitation through a weighted average of adjacent weather stations may fail to accurately capture the response of landscapes to variation in precipitation or the importance of spatial and temporal variability in precipitation. The challenges associated with simplifying landscapes to single values are exacerbated by a third factor, the habitat selection capabilities of pronghorn. Selection within a heterogeneous landscape further decreases the connection between habitat conditions assessed at the scale of the herd unit and the way in which habitat conditions are perceived by the individual. For example, highly mobile pronghorn are capable of responding to localized weather events or selecting habitats that are more mesic because of soil conditions or elevation in an otherwise dry landscape. Finally, population processes may indeed occur at a finer scale than the herd unit. Populations may function independently across the landscape responding uniquely to local conditions. Population response at the scale of the herd unit is then simply the sum of these stochastic interactions. It is likely that a combination of these factors limited the strength of the relationships between population productivity and environmental conditions.

## **Conclusions**

While we failed to identify a model capable of strongly predicting population productivity, our models highlight the positive relationship between range productivity and population response. Our assessment of annually varying habitat characteristics identified a model incorporating variables that depict the condition in which females enter the winter. Further, the strength of both the time-lagged and current growth potential variables indicated that pronghorn populations are under some form of density-dependent regulation.

Distilling landscape heterogeneity for the purposes of regression analysis necessitates an oversimplification of natural processes. The strength of our models likely would be improved had this averaging process reflected habitat use rather than habitat availability. Continued incorporation of biological data into competing models will allow managers to better understand biological processes.

## ACKNOWLEDGMENTS

I would like to thank my committee: Drs. E. Oz Garton, Janet Rachlow, and John Byers. It has been an extraordinary opportunity to work with such brilliant individuals on a project that integrated their unique areas of expertise. Oz, thanks for your encouragement, unbelievable availability, wisdom, and guidance throughout my time here. I would like to thank Idaho Department of Fish and Game, the University of Idaho, and Wyoming Game and Fish Department for financial support. A special thanks to so many individuals at IDFG that went beyond reasonable expectations to assist me in this project: Mark Hurley, Randy Smith, Bruce Palmer, Tom Keegan, Dave Musil, Doug Megargle, Terry Gregory, Greg Wooten, Mike Scott, and many others. I am truly grateful for your assistance. Also Rich Guenzel, at WGF, thank you for your guidance throughout the entirety of the project.

A special thanks to the Oz Family and fellow graduate students. It has been a pleasure to work in this diverse lab with such a supportive and intelligent group of people. Special thanks to Jay Shepherd for his patience and guidance.

Thank you to my field assistants. Kelsey Hall, your jovial spirit and hard work made 10 weeks of poop collection fun. Amy Rosso, thanks again and I am grateful for your help. Thanks to Jim Juza and Julie Mao for your assistance with fecal collection in the mountain valley habitats.

A warm thanks to my family. Leslie, you have been a tremendous support. Thank you for your patience, kindness, and love. Skip and Cheryl, thank you for your unwavering support and love.

## LITERATURE CITED

- ALHO, J. M. 1990. Logistic regression in capture-recapture models. *Biometrics* 46:623-635.
- ANDERSON, D. R., K. P. BURNHAM, AND W. L. THOMPSON. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912-923.
- AOUDE, A., AND R. E. DANVIR. 2004. Using range manipulations to increase pronghorn carrying capacity. *Pronghorn Antelope Workshop Proceedings* 20:124-135.
- BARRETT, M. W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. *Journal of Wildlife Management* 46:991-1002.
- \_\_\_\_\_. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. *Journal of Wildlife Management* 48:542-550.
- BEALE, D. M., AND A. D. SMITH. 1973. Mortality of pronghorn antelope fawns in western Utah. *Journal of Wildlife Management* 37:343-352.
- BERGER, J. 2004. The last mile: How to sustain long-distance migration in mammals. *Conservation Biology* 18:320-331.

- BERRYMAN, A. A. 1992. The origins and evolution of predator-prey theory. *Ecology* 73:1530-1535.
- BISHOP, C. J., J. W. UNSWORTH, AND E. O. GARTON. 2005. Mule deer survival among adjacent populations in southwest Idaho. *Journal of Wildlife Management* 69:311-321.
- BODIE, W. L., AND B. W. O'GARA. 1980. Description of "weak fawn syndrome" in pronghorn antelope. *Pronghorn Antelope Workshop Proceedings* 9:59-70.
- BOMAR, L. K. 2000. Broad-scale patterns of elk recruitment in Idaho: Relationships with habitat quality and effect of data aggregation. Thesis, University of Idaho, Moscow, USA.
- BORCHERS, D. L., W. ZUCCHINI, AND R. M. FEWSTER. 1998. Mark-recapture models for line transect surveys. *Biometrics* 54:1207-1220.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. *Introduction to distance sampling*. Oxford University Press, New York, USA.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer-Verlag, Inc., New York, New York, USA.
- BYERS, J. A. 1997a. *American pronghorn: social adaptations and the ghosts of predators past*. The University of Chicago Press, Illinois, USA.
- \_\_\_\_\_. 1997b. Mortality risk to young pronghorns from handling. *Journal of Mammalogy* 78:894-899.
- \_\_\_\_\_, AND J. T. HOGG. 1995. Environmental effects of prenatal growth rate in pronghorn and bighorn: further evidence for energy constraints on sex-biased maternal expenditure. *Behavioral Ecology* 6:451-457.
- CANON, S. K. 1993. *Fawn survival and bed-site characteristics of Trans-Pecos pronghorn*. Dissertation, Texas Tech University, Lubbock, USA.
- DANVIR, R. E. 2000. Environmental and density-dependent effects on a northern Utah pronghorn population. *Pronghorn Antelope Workshop Proceedings* 17:36-41.
- DENNEHY, J. J. 2001. Influence of social dominance rank on diet quality. *Behavioral Ecology* 12:177-181.
- DRUMMER, T. D., AND L. L. McDONALD. 1987. Size bias in line transect sampling. *Biometrics* 43:13-21.
- DUNBAR, M. R., R. VELARDE, M. A. GREGG, AND M. BRAY. 1999. Health evaluation of a pronghorn antelope population in Oregon. *Journal of Wildlife Diseases* 35:496-510.

- EBERHARDT, L. L. 1977. "Optimal" management policies for marine mammals. *Wildlife Society Bulletin* 5:162-169.
- ELLIS, J. E. 1970. A computer analysis of fawn survival in the pronghorn antelope. Dissertation, University of California, Davis, USA.
- FAIRBANKS, W. S. 1993. Birthdate, birth weight, and survival in pronghorn fawns. *Journal of Mammalogy* 74:129-135.
- GOODMAN, L. 1960. On the exact variance of products. *Journal of the American Statistical Association* 55:708-713.
- GRAHAM, A., AND R. BELL. 1989. Investigating observer bias in aerial survey by simultaneous double-counts. *Journal of Wildlife Management* 53:1009-1016.
- GREGG, M. A., M. BRAY, K. M. KILBRIDE, AND M. R. DUNBAR. 2001. Birth synchrony and survival of pronghorn fawns. *Journal of Wildlife Management* 65:19-24.
- GUENZEL, R. J. 1997. Estimating pronghorn abundance using aerial line transect sampling. Wyoming Game and Fish Department, Cheyenne, USA.
- HAMLIN, K. L., S. J. RILEY, D. PYRAH, A. R. DOOD, AND R. J. MACKIE. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *Journal of Wildlife Management* 48:489-499.
- HANSEN, M. C., J. D. YOAKUM, W. H. PYLE, AND R. G. ANTHONY. 2001. New strategies for pronghorn food habit studies. *Pronghorn Antelope Workshop Proceedings* 19:71-94.
- HESS, M. L. 1999. Density dependent summer pronghorn survival rates in the northwestern Great Basin-revisited. *Pronghorn Antelope Workshop Proceedings* 18:107.
- HOSKINSON, R. L., AND J. R. TESTER. 1980. Migration behavior of pronghorn in southeastern Idaho. *Journal of Wildlife Management* 44:132-144.
- HUGGINS, R. M. 1989. On the statistical analysis of capture experiments. *Biometrika* 76:133-140.
- \_\_\_\_\_. 1991. Some practical aspects of conditional likelihood approach to capture experiments. *Biometrics* 47:725-732.
- JENKS, J. A., D. M. LESLIE, JR., R. L. LOCHMILLER, M. A. MELCHORS, AND W. D. WARDE. 1989. Effect of compositing samples on analysis of fecal nitrogen. *Journal of Wildlife Management* 53:213-215.
- JOHNSON, B. K., F. G. LINDZEY, AND R. J. GUENZEL. 1991. Use of aerial line transect surveys to estimate pronghorn populations in Wyoming. *Wildlife Society Bulletin* 19:315-321.

- KINDER, C. A. 2004. Camas County Situation Summary. University of Idaho Camas County Extension Office, Fairfield, USA.
- KISSLING, M. L., AND E. O. GARTON. In Press. Estimating detection probabilities from point count surveys: a combination of distance and double observer sampling. *Auk*.
- KOENEN, K. K. G., S. DEStEFANO, AND P. R. KRAUSMAN. 2002. Using distance sampling to estimate seasonal densities of desert mule deer in a semidesert grassland. *Wildlife Society Bulletin* 30:53-63.
- KOHLMAN, S. G., D. G. WHITTAKER, M-J. HEDRICK. 1999. Density dependence in Great Basin pronghorn: implications for adaptive harvest management. *Pronghorn Antelope Workshop Proceedings* 18:103.
- LINNELL, J. D. C., R. AANES, AND R. ANDERSEN. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* 1:209-222.
- MACK, D. E., M. G. RAPHAEL, AND J. L. LAAKE. 2002. Probability of detecting marbled murrelets at sea: effects of single versus paired observers. *Journal of Wildlife Management* 66:865-873.
- MANLY, B. F. J., L. L. McDONALD, AND G. W. GARNER. 1996. Maximum likelihood estimation for the double-count method with independent observers. *Journal of Agricultural, Biological, and Environmental Statistics* 1:170-189.
- MARTIN, S. K. 1995. Characteristics of lactation and neonatal growth in pronghorn antelope (*Antilocapra americana*). Thesis, University of Wyoming, Laramie, USA.
- \_\_\_\_\_, AND K. L. PARKER. 1997. Rates of growth and morphological dimensions of bottle-raised pronghorns. *Journal of Mammalogy* 78:23-30.
- MARTINKA, C. J. 1967. Mortality of northern Montana pronghorns in a severe winter. *Journal of Wildlife Management* 31:159-164.
- NELSON, J. R., AND B. B. DAVITT. 1984. A regional cooperative DAPA research and development program. Pages 146-163 in R. W. Nelson, editor. *Proceedings of the western states and provinces elk workshop*. Alberta Fish and Wildlife Department, Edmonton, Canada.
- NIELSEN-PINCUS, N. 2005. Nest site selection, nest success, and density of selected cavity-nesting birds in northeast Oregon with a method for improving the accuracy of density estimates. Thesis, University of Idaho, Moscow, USA.
- O'GARA, B. W. 2004a. Reproduction. Pages 275-298 in B. W. O'Gara and J. D. Yoakum, editors. *Pronghorn ecology and management*. University Press of Colorado, Boulder, USA.

- \_\_\_\_\_. 2004b. Mortality Factors. Pages 379-407 in B. W. O’Gara and J. D. Yoakum, editors. Pronghorn ecology and management. University Press of Colorado, Boulder, USA.
- \_\_\_\_\_, AND J. MALCOLM. 1988. Pronghorn fawn mortality related to limited coyote control on the National Bison Range. Pronghorn Antelope Workshop Proceedings 13:61-70.
- \_\_\_\_\_, AND H. G. SHAW. 2004. Predation. Pages 337-377 in B. W. O’Gara and J. D. Yoakum, editors. Pronghorn ecology and management. University Press of Colorado, Boulder, USA.
- OTTO, M. C., AND POLLOCK, K. H. 1990. Size bias in line transect sampling: a field test. *Biometrics* 46:239-245.
- PATTERSON, B. R., B. A. MACDONALD, B. A. LOCK, D. G. ANDERSON, AND L. K. BENJAMIN. 2002. Proximate factors limiting population growth of white-tailed deer in Nova Scotia. *Journal of Wildlife Management* 66:511-521.
- PECH, R. P., A. R. E. SINCLAIR, AND A. E. NEWSOME. 1995. Predation models for primary and secondary prey species. *Wildlife Resources* 22:55-64.
- PICTON, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. *Journal of Applied Ecology* 21:869-879.
- POJAR, T. M., AND D. C. BOWDEN. 2004. Neonatal mule deer fawn survival in west-central Colorado. *Journal of Wildlife Management* 68:550-560.
- \_\_\_\_\_, AND R. J. GUENZEL. 1999. Comparison of fixed-wing line transect and helicopter quadrat pronghorn surveys. *Proceedings of the Pronghorn Antelope Workshop* 18:64-68.
- POST, E., AND D. R. KLEIN. 1999. Caribou calf production and seasonal range quality during a population decline. *Journal of Wildlife Management* 63:335-345.
- POTVIN, F., L. BRETON, AND L-P. RIVEST. 2004. Aerial surveys for white-tailed deer with double-count technique in Quebec: two 5-year plans completed. *Wildlife Society Bulletin* 32:1099-1107.
- PYRAH, D. B. 1987. American pronghorn antelope in the Yellow Water Triangle, Montana. Montana Department of Fish, Wildlife, and Parks, Helena, USA.
- QUANG, P. X., AND E. F. BECKER. 1996. Line transect sampling under varying conditions with application to aerial surveys. *Ecology* 77:1297-1302.
- \_\_\_\_\_, AND \_\_\_\_\_. 1997. Combining line transect and double count sampling techniques for aerial surveys. *Journal of Agricultural, Biological, and Environmental Statistics* 2:230-242.

- REEVE, A. F., F. G. LINDZEY, AND S. H. ANDERSON. 2003. Pronghorn populations in Wyoming 1978-2001. Wyoming Cooperative Fish and Wildlife Research Unit, Laramie, USA.
- ROBBINS, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, USA.
- \_\_\_\_\_. 1993. Wildlife feeding and nutrition. Second edition. Academic Press, San Diego, California, USA.
- \_\_\_\_\_, T. A. HANLEY, A. E. HAGERMAN, O HJELJORD, D. L. BAKER, C. C. SCHWARTZ, AND W. W. MAUTZ. 1987. Role of tannins in defending plants against ruminants: Reduction in protein availability. *Ecology* 68:98-107.
- ROBINSON, M. L. 2001. Effects of diet quality on behavior and fecal nitrogen, diaminopimelic acid, and cortisol: An experimental study on a captive group of pronghorn (*Antilocapra americana*). Thesis, University of Idaho, Moscow, USA.
- SAS INSTITUTE INCORPORATED. 1999. SAS/STAT user's guide. Version 8. SAS Institute Incorporated, Cary, North Carolina, USA.
- SCOTT, J. M., C. R. PETERSON, J. W. KARL, E. STRAND, L. K. SVANCARA, AND N. M. WRIGHT. 2002. A Gap Analysis of Idaho: Final Report. Idaho Cooperative Fish and Wildlife Research Unit, Moscow, USA.
- SEIP, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Canadian Journal of Zoology* 70:1494-1503.
- SINGER, F. J., A. HARTING, K. K. SYMONDS, AND M. B. COUGHENOUR. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *Journal of Wildlife Management* 61:12-25.
- SMITH, A. D., AND J. C. MALECHEK. 1974. Nutritional quality of summer diets of pronghorn antelopes in Utah. *Journal of Wildlife Management* 38:792-798.
- SMITH, R. H., AND A. LECOUNT. 1979. Some factors affecting survival of desert mule deer fawns. *Journal of Wildlife Management* 43:657-665.
- \_\_\_\_\_, D. J. NEFF, N. G. WOOLSEY. 1986. Pronghorn response to coyote control-a benefit:cost analysis. *Wildlife Society Bulletin* 14:226-231.
- SPALINGER, D. E. 2000. Nutritional ecology. Pages 108-139 in S. Damarais and P. R. Krausman, editors. *Ecology and Management of Large Mammals in North America*. Prentice Hall, Upper Saddle River, New Jersey, USA.
- STEINHORST, R. K., AND M. D. SAMUEL. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. *Biometrics* 45:415-425.

- STOSZEK, M. J., H. WILLMES, H. L. JORDAN, AND W. B. KESSLER. 1980. Natural trace mineral deficiency in native pronghorn antelope populations. Pronghorn Antelope Workshop Proceedings 9:71-74.
- THOMAS, L., J. L. LAAKE, S. STRINDBERG, F. F. C. MARQUES, S. T. BUCKLAND, D. L. BORCHERS, D. R. ANDERSON, K. P. BURNHAM, S. L. HEDLEY, J. H. POLLARD, AND J. R. B. BISHOP. 2004. Distance 4.1. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, United Kingdom. <http://www.ruwpa.st-and.ac.uk/distance/>
- THORNTON, P. E., S. W. RUNNING, AND M. A. WHITE. 1997. Generating surfaces of daily meteorology variables over large regions of complex terrain. *Journal of Hydrology* 190:214-251.
- TRAINER, C. E., M. J. WILLIS, B. P. KEISTER, JR., AND D. P. SHEEHY. 1983. Fawn mortality and habitat use among pronghorn during spring and summer in southeastern Oregon, 1981-1982. Wildlife Resource Report 12. PR Projects W-70-R-11, Job 6 and W-77-R-1-3, Jobs 1-3. Oregon Department of Fish and Wildlife, Portland, USA.
- VAN BALLEMBERGHE, V., AND W. B. BALLARD. 1994. Limitation and regulation of moose populations: the role of predation. *Canadian Journal of Zoology* 72:2071-2077.
- WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study Supplement* 46:120-138.
- WILLIS, M. J. 1988. Impacts of coyote removal on pronghorn fawn survival. Pronghorn Antelope Workshop Proceedings 13:60.
- WYOMING GAP ANALYSIS. 1996. Land Cover for Wyoming. University of Wyoming, Spatial Data and Visualization Center, Laramie, USA.



Figure 1. Study populations within the state of Idaho were geographically isolated from one another through the lactation season. Study sites were selected to represent the breadth of pronghorn habitat types and population productivities encountered in Idaho.

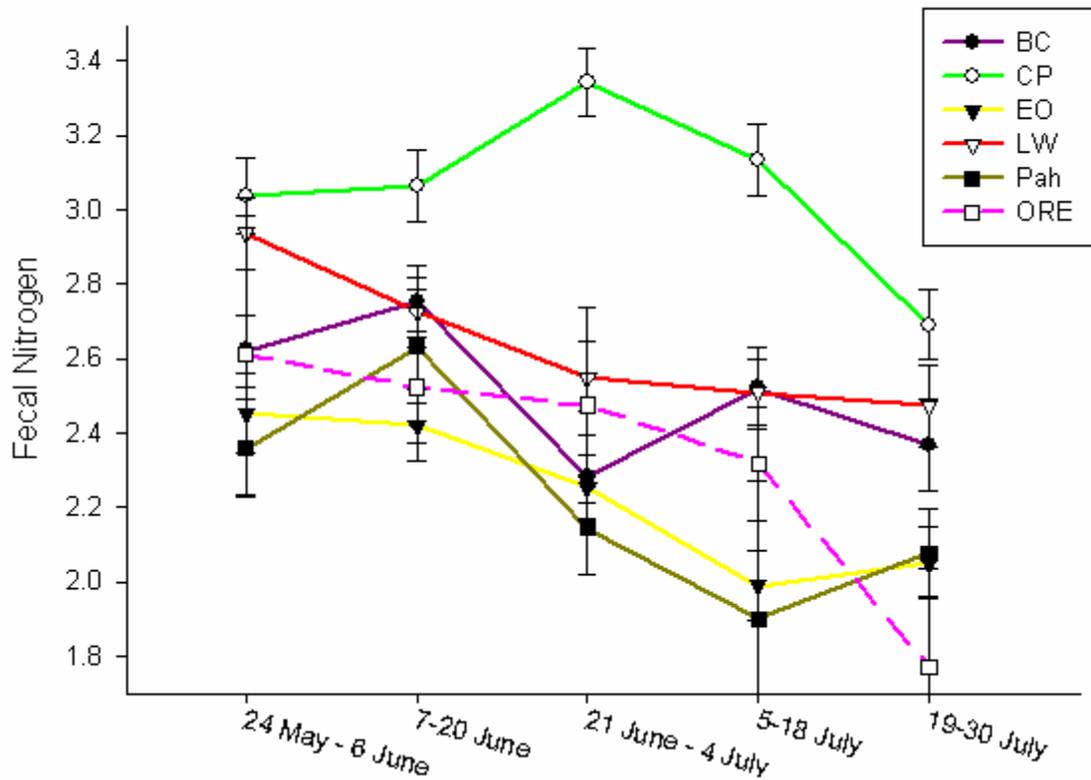


Figure 2. Mean fecal nitrogen values for pronghorn across the lactation season for 5 sites in Idaho: Birch Creek (BC), Camas Prairie (CP), Eastern Owyhee (EO), Little Wood (LW), Pahsimeroi (Pah) and 1 site from Oregon (ORE; Sheldon National Wildlife Refuge and Hart Mountain National Wildlife Refuge; Hansen et al. 2001). Error bars depict standard error.

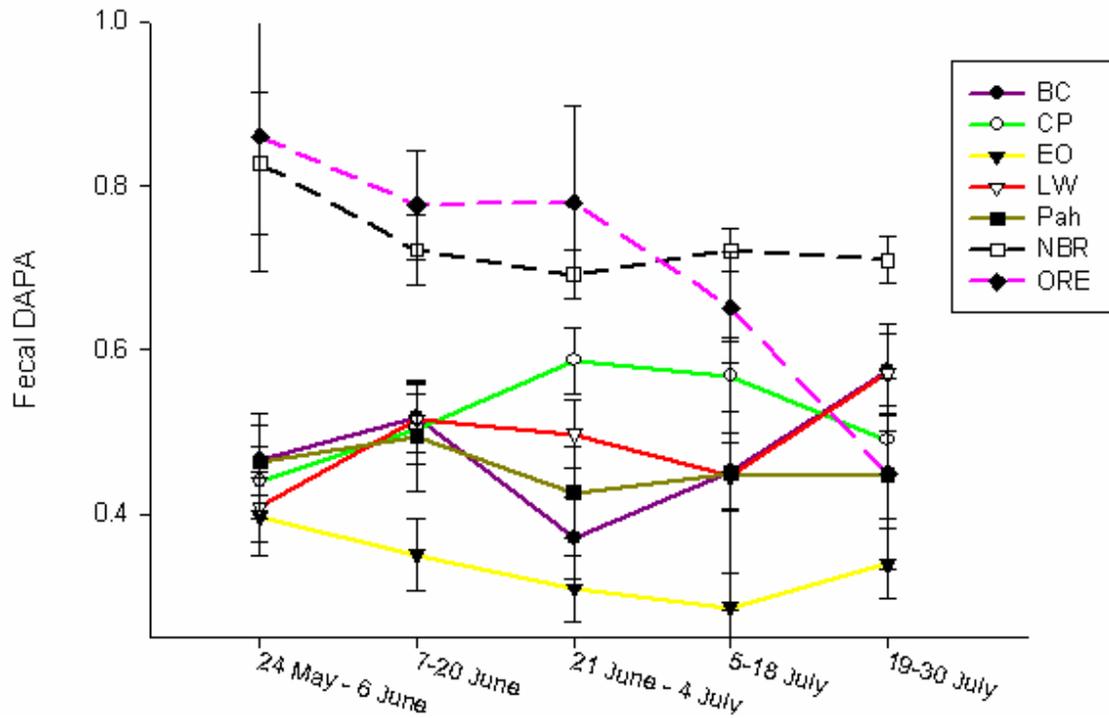


Figure 3. Mean pronghorn fecal diaminopimelic acid (DAPA) values across the lactation season for 5 sites in Idaho: Birch Creek (BC), Camas Prairie (CP), Eastern Owyhee (EO), Little Wood (LW), Pahsimeroi (Pah), 1 site from Oregon (ORE, Sheldon National Wildlife Refuge and Hart Mountain National Wildlife Refuge; Hansen et al. 2001), and 1 site from Montana (NBR, National Bison Range; Dennehy 2001). Error bars depict standard error.

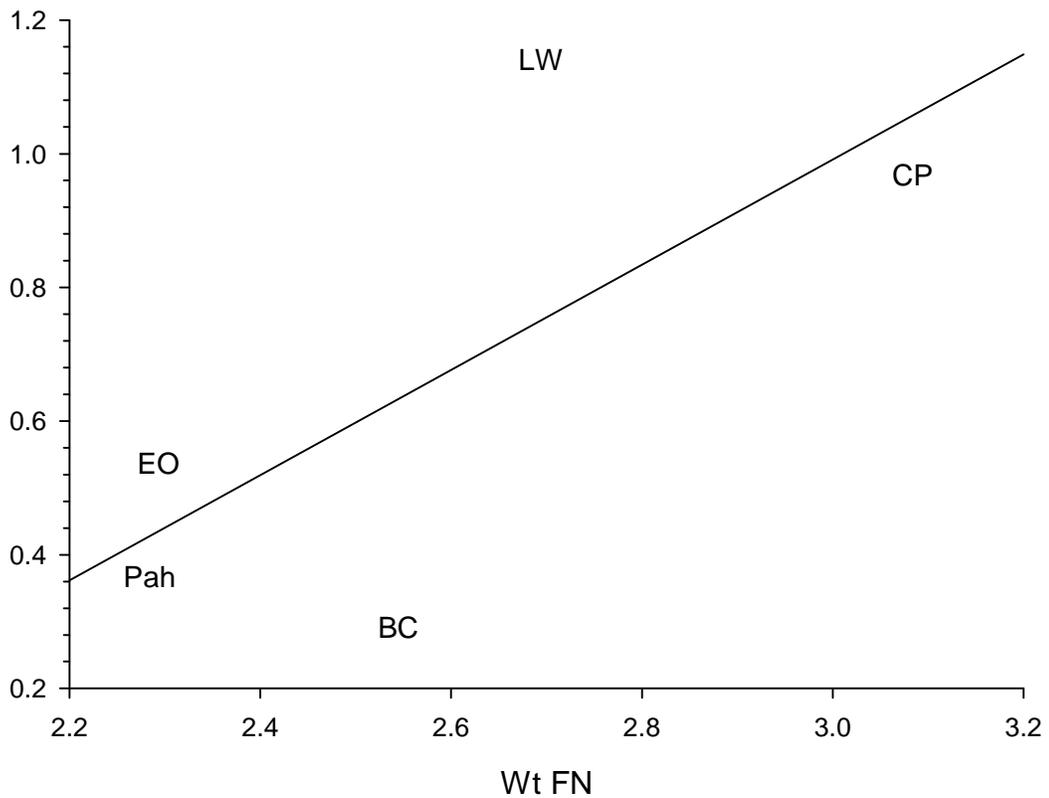


Figure 4. Pronghorn fawn:doe ratios from 5 sites in Idaho [Birch Creek (BC), Camas Prairie (CP), Eastern Owyhee (EO), Little Wood (LW), and Pahsimeroi (Pah)] relative to weighted mean fecal nitrogen (FN) values from the lactation season. Values (Wt FN) were weighted to reflect changes in milk energy expenditures by lactating does (Martin 1995).

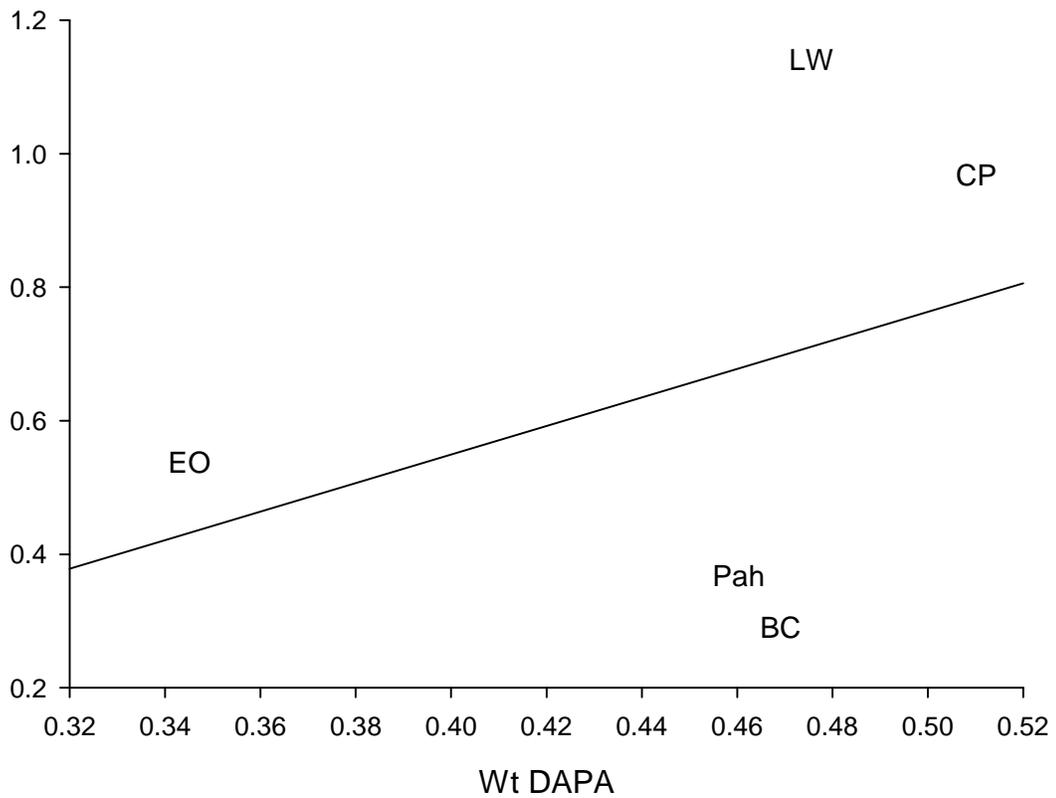


Figure 5. Pronghorn fawn:doe ratios from 5 sites in Idaho [Birch Creek (BC), Camas Prairie (CP), Eastern Owyhee (EO), Little Wood (LW), and Pahsimeroi (Pah)] relative to weighted fecal diaminopimelic acid (DAPA). Values (Wt DAPA) were weighted to reflect changes in milk energy expenditures by lactating does (Martin 1995).

Table 1. Pronghorn density ( $\hat{D}$ ) and abundance ( $\hat{N}$ ) estimates from distance analysis, Huggins' closed capture, and logistic regression approaches for Kemmerer and Pinedale, Wyoming, June 2004. Estimates were generated from line transect population abundance surveys conducted by paired independent observers. Abundance represents the estimated number of individuals in the surveyed area. The first distance analysis method used a single detection function across sites while the second used unique detection functions for the 2 sites. The first logistic regression used 3 activity classes (bedded/standing/running) while the second used only 2 activity classes (bedded versus standing/running).

Analysis	Kemmerer				Pinedale			
	D (km <sup>2</sup> )	SE	<i>n</i>	SE	D (km <sup>2</sup> )	SE	<i>n</i>	SE
Distance (front)	0.900	0.25	88	24.3	5.310	0.89	375	62.6
Distance (rear)	0.716	0.23	70	22.4	4.734	0.74	334	52.1
Distance (both)	0.800	0.22	78	21.8	4.985	0.73	352	51.3
Huggins' closed capture	0.986	0.14	96	13.6	5.167	0.30	366	21.4
Logistic (3 activity classes)	1.034	0.20	101	19.9	5.217	0.90	369	63.6
Logistic (2 activity classes)	1.038	0.20	101	20.0	5.200	0.90	367	63.4
Distance (front*site)	1.037	0.40	101	39.2	5.189	0.88	367	61.8
Distance (rear*site)	0.643	0.25	63	25.8	4.865	0.77	344	54.5
Distance (both*site)	0.826	0.28	81	27.3	4.935	0.72	348	50.7

Table 2. Pronghorn density ( $\hat{D}$ ) and abundance ( $\hat{N}$ ) estimates from distance analysis, Huggins' closed capture, and logistic regression approaches for Camas Prairie and Eastern Owyhee, Idaho, August 2003. Estimates were generated from line transect composition surveys conducted by paired independent observers. Abundance represents the estimated number of individuals in the surveyed area.

Analysis	Camas Prairie				Eastern Owyhee			
	D (km <sup>2</sup> )	SE	<i>n</i>	SE	D (km <sup>2</sup> )	SE	<i>n</i>	SE
Distance (front)	2.592	1.23	383	181.8	1.290	0.60	229	106.7
Distance (rear)	2.503	1.19	370	176.2	1.490	0.70	265	124.8
Distance (both)	2.541	0.97	375	143.8	1.358	0.49	241	86.7
Huggins' closed capture	3.401	0.61	502	90.1	1.165	0.22	207	39.3
Logistic (3 activity classes)	2.263	10.24	334	1511.2	0.985	4.70	175	835.8

Table 3. Huggins' closed capture models evaluated using program MARK for pronghorn sight-resight surveys conducted in Kemmerer and Pinedale, Wyoming, June 2004. Data were gathered through paired observers independently detecting groups. Models were composed of combinations of the variables intercept (Int), distance from the flight line (Dist), group size (Size), activity level of group ([bedded, standing, running] Act), and study site (Site). The suite of models incorporated both single parameters across seat position and unique parameters for the front and rear seats (represented by 'F' and 'R', respectively).

Model	Variables	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
1	Int, Dist	427.61	3.43	0.05
2	IntF, IntR, Dist	428.63	4.45	0.03
3	IntF, IntR, DistF, DistR	428.11	3.93	0.04
4	IntF, IntR, DistF, DistR, Size	424.24	0.06	0.29
5	IntF, IntR, DistF, DistR, SizeF, SizeR	426.07	1.89	0.12
6	IntF, IntR, DistF, DistR, SizeF, SizeR, Act	427.61	3.43	0.05
7	IntF, IntR, DistF, DistR, SizeF, SizeR, ActF, ActR	431.18	7.00	0.01
8	IntF, IntR, DistF, DistR, SizeF, SizeR, ActF, ActR, Site	424.18	0.00	0.30
9	IntF, IntR, DistF, DistR, SizeF, SizeR, ActF, ActR, SiteF, SiteR	426.14	1.96	0.11

Table 4. Huggins' closed capture models evaluated in program MARK for pronghorn sight-resight surveys conducted in Camas Prairie and Eastern Owyhee, Idaho, August 2003. Data were gathered through paired observers independently detecting groups. Models were composed of combinations of the variables intercept (Int), distance from the flight line (Dist), group size (Size), activity level of group ([bedded, standing, running] Act), and study site (Site). The suite of models incorporated both single parameters across seat position and unique parameters for the front and rear seats are represented by 'F' and 'R', respectively.

Model	Variables	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
1	Int, Dist	121.82	0.00	0.63
2	IntF, IntR, Dist	123.89	2.07	0.23
3	IntF, IntR, DistF, DistR	126.04	4.22	0.08
4	IntF, IntR, DistF, DistR, Size	127.19	5.37	0.04
5	IntF, IntR, DistF, DistR, SizeF, SizeR	129.19	7.37	0.02
6	IntF, IntR, DistF, DistR, SizeF, SizeR, Act	132.14	10.31	0.00
7	IntF, IntR, DistF, DistR, SizeF, SizeR, ActF, ActR	134.58	12.75	0.00
8	IntF, IntR, DistF, DistR, SizeF, SizeR, ActF, ActR, Site	136.65	14.83	0.00
9	IntF, IntR, DistF, DistR, SizeF, SizeR, ActF, ActR, SiteF, SiteR	139.14	17.32	0.00

Table 5. Logistic regression models evaluated for pronghorn population abundance surveys conducted in Kemmerer and Pinedale, Wyoming, June 2004. Detected groups were classified as either detected or missed through paired observer independently detecting groups. Models were composed of combinations of the predictor variables: distance from the flight line (Dist), group size (GrSz), activity level of group ([bedded, standing, running] Act), study site (Site), observer position ([Front, Rear] Seat), and the interaction terms of seat position and distance (Dist\*Seat) and seat position and group size (GrSz\*Seat).

Model	Variables	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
1	Dist	409.40	14.63	0.00
2	Dist, GrSz	403.88	9.11	0.00
3	Seat, Dist, GrSz	404.89	10.12	0.00
4	Dist, GrSz, Act, Site	394.77	0.00	0.40
5	Seat, Dist, GrSz, Act, Site	395.78	1.01	0.24
6	Seat, Dist, GrSz, Act, Site, Dist*Seat	396.69	1.92	0.15
7	Seat, Dist, GrSz, Act, Site, GrSz*Seat	397.61	2.84	0.10
8	Seat, Dist, GrSz, Dist*Seat, GrSz*Seat	407.09	12.32	0.00
9	Seat, Dist, GrSz, Act, Dist*Seat, GrSz*Seat	407.99	13.22	0.00
10	Seat, Dist, GrSz, Site, Dist*Seat, GrSz*Seat	399.24	4.47	0.04
Global	Seat, Dist, GrSz, Act, Site, Dist*Seat, GrSz*Seat	398.71	3.94	0.06

Table 6. Logistic regression models evaluated for pronghorn herd composition surveys conducted in Camas Prairie and Eastern Owyhee, Idaho, August 2003. Detected groups were classified as either detected or missed through paired observer independently detecting groups. Models were composed of combinations of the predictor variables: distance from the flight line (Dist), group size (GrSz), activity level of group ([bedded, standing, running] Act), study site (Site), observer position ([Front, Rear] Seat), and the interaction terms of seat position and distance (Dist\*Seat) and seat position and group size (GrSz\*Seat).

Model	Variables	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
1	Dist	79.17	0.00	0.48
2	Dist, GrSz	80.19	1.02	0.29
3	Seat, Dist, GrSz	82.22	3.05	0.10
4	Dist, GrSz, Act, Site	83.46	4.29	0.06
5	Seat, Dist, GrSz, Act, Site	85.48	6.31	0.02
6	Seat, Dist, GrSz, Act, Site, Dist*Seat	87.07	7.90	0.01
7	Seat, Dist, GrSz, Act, Site, GrSz*Seat	87.42	8.25	0.01
8	Seat, Dist, GrSz, Dist*Seat, GrSz*Seat	86.04	6.87	0.02
9	Seat, Dist, GrSz, Act, Dist*Seat, GrSz*Seat	87.59	8.42	0.01
10	Seat, Dist, GrSz, Site, Dist*Seat, GrSz*Seat	87.48	8.31	0.01
Global	Seat, Dist, GrSz, Act, Site, Dist*Seat, GrSz*Seat	88.94	9.77	0.00

Table 7. Linear regression models evaluating relationship between the fecal indicators, fecal nitrogen (FN) and fecal 2,6 diaminopimelic acid (DAPA), and pre-harvest fawn:doe ratios (f:d). Simple regression models evaluated the relationship between mean fecal values across the lactation season (24 May-30 Jul) while the weighted regression emphasized observed fecal values relative to milk energy expenditure by lactating does (Martin 1995). Fecal samples were collected from 5 sites in Idaho: Birch Creek, Camas Prairie, Eastern Owyhee, Little Wood, and Pahsimeroi, during 2004.

	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Regression equation	R-square
Simple regression				
Null	-7.59	0.00	f:d = 0.66	0.00
FN	-3.98	3.60	f:d = -1.22 + 0.74*FN	0.46
DAPA	-1.77	5.82	f:d = -0.30 + 2.12*DAPA	0.16
FN DAPA	15.79	23.37	f:d = -1.13 + 0.93*FN - 1.24*DAPA	0.48
Weighted regression				
Null	-7.59	0.00	f:d = 0.66	0.00
FN	-4.21	3.38	f:d = -1.37 + 3.94*FN	0.48
DAPA	-1.60	5.98	f:d = -0.31 + 10.69*FN	0.13
FN DAPA	15.38	22.97	f:d = -1.19 + 5.12*FN - 8.71*DAPA	0.52

Table 8. Models of fawn:doe ratios z-score transformed by herd unit evaluated with linear regression to assess the influence of the temporally variable habitat characteristics: fall precipitation (Fall), winter precipitation (Winter), growing season precipitation (Grow), previous year's growing season precipitation [Grow(-1)], population growth potential (Potential), previous year's population growth potential [Potential(-1)], and previous falls z-score transformation of total harvest (Harvest). The response of 1,080 estimates of fawn:doe ratios collected from the 44 pronghorn herd units throughout the state of Wyoming between 1979 and 2003 were used in the analysis.

Model	Variables	AIC	ΔAIC	R-square
1	Fall, Winter, Grow, Grow(-1), Potential(-1)	-222.70	0.00	0.11
2	Fall, Grow(-1), Potential(-1)	-205.88	16.82	0.10
3	Potential(-1)	-199.55	23.15	0.09
4	Fall, Winter, Grow, Grow(-1), Potential	-138.92	83.78	0.04
5	Fall, Grow, Potential	-137.71	84.99	0.04
6	Fall, Winter, Grow, Grow(-1), Potential, Harvest	-136.94	85.76	0.04
7	Fall, Winter, Grow, Grow(-1)	-131.40	91.30	0.03
8	Potential	-111.07	111.63	0.01

Table 9. Parameter estimates and the associated magnitude of response for the best regression model relating z-score transformed fawn:doe ratios to annually varying habitat variables. Variables included in the model were fall precipitation (Fall), winter precipitation (Winter), growing season precipitation (Grow), growing season precipitation from the previous year [Grow(-1)], and population growth potential from the previous year [Potential(-1)]. Magnitude is expressed as the estimated response of z-score transformed fawn:doe ratios to the range of values encountered for a given predictor variable.

Model	Regression equation
1	fawn:doe ratio = 0.00526 + 0.0942*Fall - 0.107*Winter - 0.0463*Grow + 0.0101*Grow(-1) + 0.803*Potential(-1)
Magnitude of effects	
Fall	0.88
Winter	-0.45
Grow	-0.73
Grow(-1)	0.16
Potential(-1)	1.72

Table 10. Competing regression models to predict average pronghorn fawn:doe ratios from the 44 herd units encompassing Wyoming. Habitat variables included in the models were: average fall precipitation (Fall), average winter precipitation (Winter), average growing season precipitation (Grow), range production based on soil type (Production), range production expressed on a per capita basis (Forage), and the proportion of habitat designated as not yearlong habitat (Habitat).

Model	Variables	AIC	ΔAIC	R-square
1	Fall, Grow	-183.89	0.00	0.15
2	Habitat	-183.31	0.58	0.10
3	Production	-182.06	1.83	0.07
Null		-180.75	3.13	0.00
4	Winter, Grow, Production, Forage, Habitat	-179.47	4.42	0.27
5	Forage	-178.98	4.90	0.01

Table 11. Parameter estimates and magnitude of effects associated with the 3 competing regression models used to predict average pronghorn fawn:doe ratios from the 44 herd units in Wyoming. Models were composed of the variables: average fall precipitation (Fall), average growing season precipitation (Grow), range production based on soil type (Production), and the proportion of habitat designated as not yearlong habitat (Habitat). Magnitude is expressed as the estimated response of fawn:doe (f:d) ratios to the range of values encountered for a given predictor variable.

Model	Regression equation	Magnitude
1	$f:d = 0.734 - 0.022*Fall + 0.00942*Grow$	Fall = -0.309    Grow = 0.162
2	$f:d = 0.538 + 0.000137*Production$	Production = 0.135
3	$f:d = 0.742 - 0.105*Habitat$	Habitat = -0.105

Submitted by:

*Tim Smyser*

---

Graduate Student, University of Idaho

*Peter Zager*

---

Principal Wildlife Research Biologist