



Effects of winter range on a pronghorn population in Yellowstone National Park  
by Sylvanna Jean Boccadori

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management

Montana State University

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Abstract:

The only population of pronghorn antelope (*Antilocapra americana*) in Yellowstone National Park (YNP) has showed a recent drop in numbers from over 500 animals in the early 1990's to <240 animals since 1995. Concern for the long-term sustainability of this herd led to an examination of the effects that the winter range has on the habitat use and demographics of this population. Radio-telemetry data were collected on instrumented adult does from June 1999 through August 2001. While all pronghorn congregated on the winter range from December through March, there were 2 distinct segments to this population based on migratory strategy: a resident herd that remained on the winter range year-round and a herd that migrated to higher valleys within the Park during the summer. There was evidence of migration north of YNP as well. The current winter range is located within the northern range of YNP, just west of Gardiner, Montana. A portion of it lies outside the Park on private, Forest Service, and conservation easement lands. Results from logistic regression showed that pronghorn selected for cover and elevation on the winter range and selected among cover types. Rabbitbrush (*Chrysothamnus* spp.) and greasewood (*Sarcobatus* spp.) cover types were used more than grassland, while big sagebrush (*Artemisia tridentata* spp.) types were avoided. Observational data did not show one cover type being used more for feeding and bedding than other cover types. Microhistological analysis of fecal pellets showed that the majority of pronghorn winter diet was comprised of browse, with rabbitbrush being the most prevalent woody species. Due to heavy browsing by ungulates over the past century, serai species such as rabbitbrush have dominated on the winter range while the vigor of the sagebrush community has declined. Adult doe survival probabilities and fawn: doe ratios for non-migratory pronghorn were lower than those for migratory pronghorn. An evaluation of the relationship between adult mortality and recruitment showed that during this study the resident herd was draining the population while the migratory herd was the source of the limited recruitment that occurred.

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Fish and Wildlife Management

MONTANA STATE UNIVERSITY  
Bozeman, Montana

May 2002

N378  
B6309

APPROVAL

of a thesis submitted by

Sylvanna J. Boccadori

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

Dr. Robert A. Garrett

Robert A. Garrett  
(Signature)

May 13, 2002  
Date

Approved for the Department of Ecology

Dr. Jay J. Rotella

Jay Rotella  
(Signature)

5/14/02  
Date

Approved for the College of Graduate Studies

Dr. Bruce McLeod

Bruce R. McLeod  
(Signature)

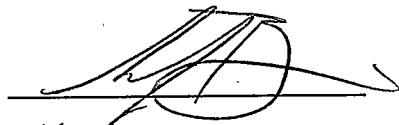
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## ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to the following individuals and organizations for their contributions to my study: Dr. Robert Garrott, for his sincerity and effectiveness as an academic mentor; Dr. Carl Wambolt and Dr. Lynn Irby for their assistance and critical review of this thesis; Wendy Clark and other members of the Northern Yellowstone Cooperative Wildlife Working Group for putting concerns for the Yellowstone pronghorn back on the radar; folks who helped me in the field, especially Kate Nittinger, Jeremy Zimmer, and Tris Hoffman; Glenn Plumb from Yellowstone National Park for his continued support in numerous ways throughout this project; Kim Keating for the gift of time and his knowledge of logistic regression; the staff and personnel of Yellowstone National Park for logistic support; Yellowstone Park Foundation and the National Park Service for funding this project; Steve Hess, for invaluable peer support; and Dan Tyers, for being the ultimate role model as a biologist with integrity. I would especially like to give thanks to my sister, Bobbye Kopec, and my husband, Andy Knight, for all the comic relief and support they provided me throughout this project.

## TABLE OF CONTENTS

LIST OF TABLES.....	vi
LIST OF FIGURES.....	vii
ABSTRACT.....	viii
1. INTRODUCTION.....	1
2. STUDY AREA.....	5
3. METHODS.....	8
Capture and Telemetry.....	8
Pronghorn Distribution.....	10
Winter Range Vegetation.....	12
Winter Range Use.....	14
Demography .....	21
4. RESULTS.....	23
Pronghorn Distribution.....	23
Winter Range Vegetation.....	27
Winter Range Use.....	31
Demography.....	39
5. DISCUSSION.....	42
LITERATURE CITED.....	52
APPENDICES.....	58
APPENDIX A.....	59
Cover Type Descriptions.....	60

## LIST OF TABLES

Table	Page
1. Candidate list of <i>a priori</i> models of pronghorn winter habitat use.....	17
2. Top <i>a priori</i> models ranked by $\Delta AIC_c$ values.....	32
3. Details of the best approximating model for pronghorn habitat selection.....	34
4. Pronghorn winter diet.....	37
5. Diet in April for migratory and non-migratory pronghorn.....	38

**LIST OF FIGURES**

Figure	Page
1. Population counts and estimates 1900 – 2001.....	2
2. Map of the annual pronghorn range.....	6
3. Map of sampling zones within the study area.....	9
4. Julian calendar of pronghorn movement between consecutive relocations.....	24
5. Pronghorn movement patterns by year.....	25
6. Map of pronghorn seasonal ranges.....	26
7. Overlap in individual winter ranges between consecutive years.....	26
8. Vegetation cover map of pronghorn winter range.....	28
9. Resource selection map of pronghorn use of the winter range.....	35
10. Pronghorn activity within each cover type.....	36
11. Number of fawns per doe during summer and early winter.....	40
12. Number of fawns per doe during summer months by migratory status.....	40

**ABSTRACT**

The only population of pronghorn antelope (*Antilocapra americana*) in Yellowstone National Park (YNP) has showed a recent drop in numbers from over 500 animals in the early 1990's to <240 animals since 1995. Concern for the long-term sustainability of this herd led to an examination of the effects that the winter range has on the habitat use and demographics of this population. Radio-telemetry data were collected on instrumented adult does from June 1999 through August 2001. While all pronghorn congregated on the winter range from December through March, there were 2 distinct segments to this population based on migratory strategy: a resident herd that remained on the winter range year-round and a herd that migrated to higher valleys within the Park during the summer. There was evidence of migration north of YNP as well. The current winter range is located within the northern range of YNP, just west of Gardiner, Montana. A portion of it lies outside the Park on private, Forest Service, and conservation easement lands. Results from logistic regression showed that pronghorn selected for cover and elevation on the winter range and selected among cover types. Rabbitbrush (*Chrysothamnus* spp.) and greasewood (*Sarcobatus* spp.) cover types were used more than grassland, while big sagebrush (*Artemisia tridentata* spp.) types were avoided. Observational data did not show one cover type being used more for feeding and bedding than other cover types. Microhistological analysis of fecal pellets showed that the majority of pronghorn winter diet was comprised of browse, with rabbitbrush being the most prevalent woody species. Due to heavy browsing by ungulates over the past century, seral species such as rabbitbrush have dominated on the winter range while the vigor of the sagebrush community has declined. Adult doe survival probabilities and fawn: doe ratios for non-migratory pronghorn were lower than those for migratory pronghorn. An evaluation of the relationship between adult mortality and recruitment showed that during this study the resident herd was draining the population while the migratory herd was the source of the limited recruitment that occurred.

## INTRODUCTION

Habitat characteristics of critical winter range strongly influence the distribution and population dynamics of wild ungulate herds (Bayless 1969, Ryder and Irwin 1987, Ferguson and Messier 2000). The demographics and distribution of pronghorn antelope (*Antilocapra americana*) in Yellowstone National Park are thought to be driven in large part by conditions on the winter range.

The pronghorn population in YNP is a remnant of a larger herd that historically numbered in the thousands (Skinner 1922). This herd once moved freely throughout the Yellowstone valley as it migrated between spring and summer ranges in YNP and lower-elevation winter range in the valley north of the park (Houston 1982). In the past century the herd has been heavily influenced by fencing of private land and hunting in the lower Yellowstone Valley, management practices in YNP including reduction and feeding programs, and land use practices on private property adjoining YNP (Barmore 1980). As a result the Yellowstone herd has been relatively isolated since the 1920's at the upper extreme of its historic winter range and the overall population size greatly reduced from its historic numbers (Barmore 1980, Keating 2002, unpubl. report). The population size has fluctuated greatly throughout the past century (Fig. 1). Some of the fluctuation can be attributed to inconsistent counting methods and anecdotal reports, especially during the first half of the century (Keating 2002, unpubl. report). Since the 1960s, the herd has experienced lengthy periods of

relatively low yet stable population size, despite human influences imposed on the herd during that time. There have been several factors and events suggested as contributors to the increasing trend in population size from the mid-1980's to the early 1990's, but there has been no conclusive explanation (Keating 2002, unpubl. report). The condition of habitat on this critical winter range, given the limited size of this area and lack of open access to former winter range north of the park, has been suggested as a major driver of Yellowstone pronghorn distribution and demographics.

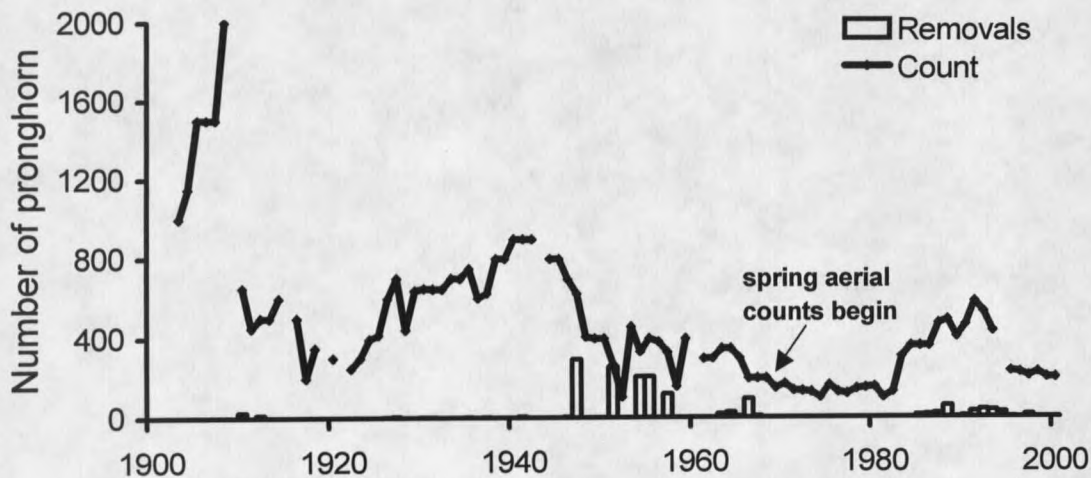


Fig. 1. Counts and estimates of pronghorn and the total number of known annual removals of pronghorn from 1900 –2001 in Yellowstone National Park, Wyoming. Data are from Barmore 1980, unpublished YNP report.

Current pronghorn winter range has been greatly altered from its condition prior to European settlement. For over a century, the area currently occupied by

pronghorn during the winter months has been heavily affected by human settlement and land use (Keating 2002, unpubl. report). Major habitat changes resulted from mining just north of the park boundary, and grazing and agriculture both in and out of YNP (Houston 1982). Historical evidence and recent studies indicate a significant decline of sagebrush on the pronghorn winter range (Houston 1982, Singer and Renkin 1995, Wambolt 1996, Wambolt and Sherwood 1999), which may impact ungulates that rely on sagebrush habitat to meet their nutritional needs. The decline in sagebrush communities has been linked in part to increasing elk numbers following YNP's decision in 1968 to minimize intervention and allow weather and outside-the-park hunting and land uses to influence elk population dynamics (i.e., "natural regulation") (Houston 1982). Additionally, elk have responded to a late hunt in Montana (mid-December through February) on national forest land north of YNP by staying within the park boundaries, resulting in large herds sharing the same area as pronghorn. As a result of these prolonged impacts on the winter range, seral species such as rabbitbrush have become more prevalent in the plant community while the quantity of sagebrush has been greatly reduced (Hoffman and Wambolt 1996).

Because effective planning for pronghorn conservation in YNP requires knowledge of how pronghorn ecology is influenced by the landscape, I sought to determine the influence of the winter range on the overall health of the population. My objectives were to 1) describe seasonal movement patterns and distributional shifts in the population, 2) describe current patterns of habitat use on the winter range and interpret these patterns of use within the scope of

historic changes that have occurred, and 3) associate patterns of seasonal landscape use with assessments of adult female survival and recruitment.

## STUDY AREA

The study was conducted on the northern Yellowstone winter range (NYWR) of YNP as described by Barmore (1980) and Houston (1982). The NYWR is approximately 100,000 ha in size and includes the upper Yellowstone and Lamar Valleys. It lies between 1,500 and 2,400 m elevation and approximately 83% of the area is within the boundary of YNP (Houston 1982). The study focused on that portion of the NYWR where pronghorn winter, which lies between Mammoth Hot Springs in the park to the Devils Slide area 4 km north of the park, along the Yellowstone River (Fig. 2). A large portion of this area is known as the Boundary Line Area, which is located on ancient mudflows that are high in clay and low in fertility. Soils in the rest of the area are derived from glacial debris of andesitic and sedimentary origin. The faunal complex in this area includes elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), as well as coyote (*Canis latrans*), gray wolf (*Canis lupus*), grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), and mountain lion (*Felix concolor*).

The climate of the study area is characterized by long, cold winters and short, cool summers. Mean temperatures for the winter periods, December 1 – March 31, of the study (-0.3 and -2.3°C during 1999 – 2000 and 2000 – 2001, respectively) were slightly warmer than or similar to the 1971 – 2000 base period average ( $\bar{x}$  = -2.3°C). Precipitation during each winter period (4.98 and 3.38 cm during 1999 – 2000 and 2000 – 2001, respectively) was also slightly lower than

the 1971 – 2000 base period average ( $x = 5.98$  cm). Weather data were obtained from the climatological station (CLIM) in Gardiner, Montana. Coughenour (1991) reported 27.9 cm of annual precipitation at Gardiner, Montana. Half of the precipitation is received as snow although peak moisture is received in spring and early summer (Farnes 1991). This area is relatively snow -free and, therefore, accessible for ungulate foraging throughout winter.

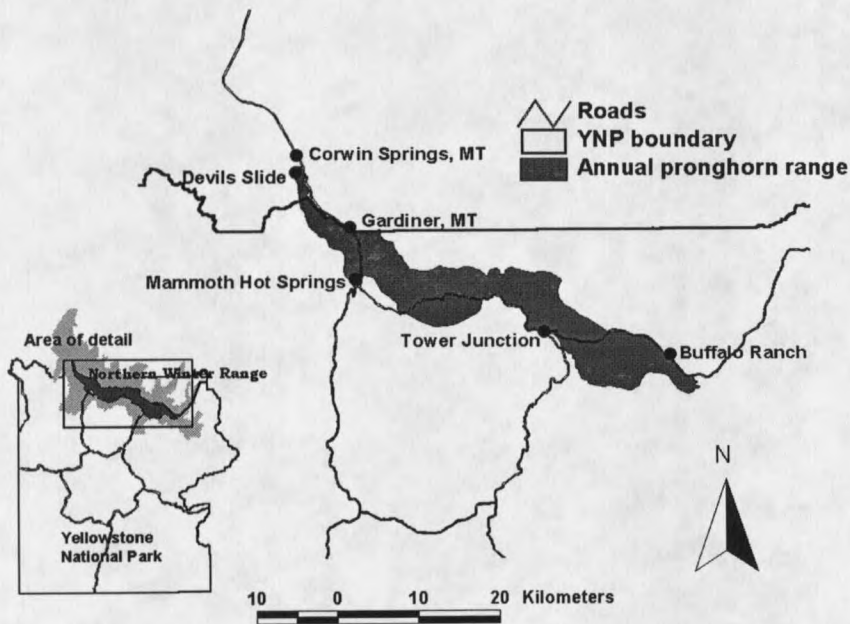


Fig. 2. Location of the annual pronghorn range in Yellowstone National Park, Wyoming. The study focused primarily on the pronghorn winter range, which extends from Mammoth Hot Springs to Devils Slide.

The study area is predominantly of the Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)/bluebunch wheatgrass (*Agropyron spicatum*) habitat type, interspersed with current and former agricultural lands and small areas of

riparian habitats. Current overstory vegetation is dominated by Wyoming big sagebrush, basin big sagebrush (*Artemisia tridentata tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*C. viscidiflorus*), and greasewood (*Sarcobatus vermiculatus*). The understory is dominated by Sandberg bluegrass (*Poa secunda*), Idaho fescue (*Festuca idahoensis*), prairie junegrass (*Koeleria macrantha*), bluebunch wheatgrass, and planted crested wheatgrass (*Agropyron cristatum*). Agricultural fields on private land within the winter range are planted in alfalfa (*Medicago sativa*).

## METHODS

Capture and Telemetry

Pronghorn were captured using a net gun in late winter when the population was congregated on their winter range. Captures occurred in February 1999 and March 2000. Efforts were made to distribute captures throughout the winter range. Ages of does, as determined by tooth wear at the time of capture, ranged from 1 to 8+ years. Captures were carried out by contract helicopter personnel specializing in wildlife capture and handling and in accordance with protocols established and approved by the National Park Service (NPS). All captured pronghorn were fitted with radio collars equipped with mortality sensors.

Instrumented animals were tracked diurnally from the ground during June 1999 – August 2001. Tracking was more intensive during winter and spring, and less intensive during summer. Due to lack of field personnel, no tracking occurred during fall migration (September and October). During winter, a restricted randomization design was used to sample instrumented animals. The range occupied by pronghorn during winter was divided into 5 sampling areas (Fig. 3). The order in which each area was sampled was randomly selected and all instrumented pronghorn occupying an area were located in random order before sampling occurred in another area. The entire winter range was sampled  $\geq 2$  times per week. A restricted randomization design was also used during spring migration. However, sampling areas were enlarged to encompass the entire

pronghorn range, and instrumented animals were sampled  $\geq 1$  time per week. While animals were on their summer ranges, sampling priority was given to instrumented does with fawn(s), then instrumented does without fawn(s).



Figure 3. Map of the current pronghorn winter range showing sampling sections.

Tolerance of pronghorn to human presence allowed homing techniques to be employed. Field personnel used ground-tracking procedures and a receiver with a 3-element folding Yagi antenna to locate instrumented animals. Locations were confirmed visually using a 15 x 60 spotting scope and 7 x 35 mm binoculars at distances of 30 – 150 m. Fidelity to certain areas indicated that observer presence did not significantly alter distributions.

For each sighting, the animal location was plotted to the nearest 50 m on a 1:24,000 U.S. Geological Survey (USGS) topographical map using the Universal Transverse Mercator (UTM) grid system. The location of the instrumented animal

was classified into 1 of 7 vegetation cover types according to the type that the animal was first observed in (grass, old fields, grass-sagebrush mix, sagebrush, rabbitbrush, greasewood, other). If the instrumented animal was associated with other pronghorn, then group size, age composition (fawn/adult) and sex composition (male/female) of the group were recorded. When young animals were unable to be distinguished definitively as fawns, they were counted as adults and their sex recorded. A "group" consisted of individuals within 100 m of each other or that acted in a collective manner (Medcraft and Clark 1986). If the animal(s) was undisturbed by the observer, then initial activity (feeding, traveling, bedded, or other) of the instrumented animal and each member of its group was recorded. Identities of any additional instrumented animals in the group were recorded. Opportunistic sightings of groups without an instrumented animal were treated in the same manner as groups with instrumented animals and the same information was recorded. Relocations of 2 fawns that were radio-tagged for a concurrent study of fawn survival were also treated opportunistically and information was gathered in the same manner as for instrumented adults.

### Pronghorn Distribution

Season dates were defined by pronghorn movement patterns. Dates were determined by plotting the distance traveled between consecutive relocations of each instrumented animal against the day of the Julian calendar on which the latter relocation occurred. Because of the timing of data collection, the Julian calendar for this study extended from 18 November – 25 August. Consistency of

movement between years was determined by plotting, for each year, the average distance traveled in 2-week intervals against the last day of the interval on the Julian calendar.

I used the ArcView® (ESRI 1998) Geographic Information System (GIS) to map pronghorn winter and summer ranges by aggregating across years all relocation points occurring within the respective seasons. Relocations were obtained from instrumented animals, ear-tagged fawns, observations of non-instrumented pronghorn, and aerial survey locations gathered by YNP biologists during their annual pronghorn spring census. Reynolds and Laudré (1990) found that  $\geq 4$  hours between consecutive animal locations was needed to attain independence for estimation of pronghorn home ranges and daily movements. To minimize autocorrelation among relocations from an individual, 1 of the 2 points defining any sampling interval  $\leq 4$  hours was randomly selected and censored from the data set. I used the Animal Movement extension (Hooge and Eichenlaub 1997) in ArcView® to estimate the population's collective home range for each season using the fixed kernel method with least squares cross validation (LSCV) and a 95% isopleth (Seaman and Powell 1996). I then clipped the home range polygon along geographic boundaries and along boundaries with unlikely pronghorn habitat so that the final map represented known pronghorn range as determined by animal sightings.

I estimated individual winter and summer home-range sizes for each instrumented animal using the same methods as those used for the range maps and clipped each to the appropriate season range map. Winter home ranges

were constructed for each individual by year. Fidelity on the winter range was assessed by calculating the percent overlap of each individual's home range for consecutive winters. Due to small summer data sets, all summer relocation data were pooled for each individual before constructing the summer home range and after plotting relocations for each summer to assess that individual's fidelity on the summer range. I classified instrumented pronghorn as either migratory or non-migratory. Individual summer ranges of migratory pronghorn were distinct from the population's winter range, while summer ranges of non-migratory pronghorn overlapped the winter range. I compared average summer home range size by migratory group using the 2-sample *t* test.

#### Winter Range Vegetation

To more accurately relate pronghorn use to current vegetation I constructed a vegetation cover map for the winter range by modifying an existing vegetation map originally constructed for a Cumulative Effects Model (CEM) for grizzly bears in the Greater Yellowstone ecosystem (GYE) (Mattson and Despain 1985). Dixon (1997) gives details of how the CEM map was constructed. Cover types used in the mapping represent those that are most common on the winter range. Cover patches were mapped from the ground by hand-drawing representative polygons on topographical maps. Polygon size was constrained by a 0.6 ha minimum mapping resolution. Inclusions of less than 20% of a mapped polygon were ignored unless they could clearly be broken into polygons at least 0.6 ha in size. I then clipped the geo-referenced CEM map to the winter range map and

edited the polygons of this clipped layer to reflect the polygons drawn onto the topographical maps. Fenced areas and permanent bodies of water within the winter range were designated unavailable to pronghorn and the polygons removed from the winter range. I assessed the accuracy of the digital vegetation cover map by comparing cover types recorded for ground-based relocations to cover types derived from the digital classification for those relocations. Similarities and differences within each cover type were tabulated and percentages of agreement recorded.

I surveyed the vegetation on the pronghorn winter range to describe the composition of each cover type. Sampling occurred during June 2001, when grasses had set seed and most forbs had flowered. I stratified the pronghorn winter range by cover type, then sampled 2 – 5 patches of each type. At each sampling site, a 30-m line transect was laid out and 10 20 x 50 cm quadrats were placed at 3-m intervals along the transect. Within each quadrat, I estimated frequency of occurrence and percent canopy coverage of grasses, sedges, forbs, cacti, and half-shrubs (Daubenmire 1959). Transects were laid along elevational gradients where possible. Cover classes used were: 0 – 5%, 5 – 25%, 25 – 50%, 50 – 75%, 75- 95%, and 95 – 100%. I used the midpoint for each cover class in calculating average canopy coverage for each plant species within each cover type. Plant species with the largest average canopy cover were considered the dominant species for that cover type. I used the line intercept method (Canfield 1941) along the 30-m transect to determine percent shrub canopy coverage. I considered shrub canopy intercept to be continuous if canopy openings were  $\leq 3$

cm. Live and dead shrub canopy intercepts were measured. A plumb bob accurately assessed intercepts on slopes or when the line was elevated due to shrubs. Measurements for Wyoming and basin big sagebrush were aggregated.

### Winter Range Use

I used maximum likelihood logistic regression (Afifi and Clark 1990) to model winter habitat selection by adult pronghorn does (SYSTAT 1996). Because I was interested in how the current winter range affects the Yellowstone pronghorn, modeling was done within the bounds of the population's winter home range. Modeling used the binary response of an observed location of use (1) versus locations of randomly selected points (0) (Agresti 1996). I generated random points with ArcView using the Animal Movement extension (Hooge and Eichenlaub 1997) to draw from within the bounds of the pronghorn winter range an equal number of random points as use points.

Potential explanatory variables that I considered included cover type, solar radiation, slope, and elevation. Cover was determined from the digital vegetation map of the winter range. Because solar radiation influences microsite conditions with respect to temperature, snow depth, and vegetation, it was used as a potential explanatory variable in habitat use analysis. An index of solar radiation was obtained from a digital layer created by the U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, Montana. Solar radiation was indexed (SRI) as a function of slope, aspect, and latitude. The index is

obtained as (Keating, USGS Northern Rocky Mountain Science Center, pers. commun.):

$$\text{SRI} = \cos\phi \cos\beta + \sin\phi \sin\beta \cos\gamma$$

where:

$\phi$  = latitude, north positive (degrees)

$\beta$  = slope of the surface measured in degrees from the horizontal position

$\gamma$  = surface aspect or azimuth angle measured as the number of degrees clockwise from south (instead of north) so that east is positive and west is negative. In this application, south is 0 degrees, westerly aspects range between 0 and -180 degrees, and easterly aspects range between 0 and +180 degrees. The transformation from the usual range of 0 to 360 degrees is calculated simply as  $180 - \text{aspect}$ .

Index values are greatest for south-facing moderate slopes and least for steep, northern aspects. Slope and elevation were derived from a 10-m digital elevation model (DEM) of the GYE (Spatial Analysis Center, YNP, Wyoming). To make elevation units more biologically meaningful and set the minimum elevation on the study area as the reference elevation for logistic regression analyses, I re-scaled values to a unit size of 100 m and subtracted the minimum elevation value for the study area from each value. Slope was in units of 1 degree.

I employed model selection to analyze pronghorn habitat use data. Prior to analyzing the empirical data, I reviewed the literature to develop qualitative hypotheses about pronghorn habitat use. I incorporated these hypotheses into statistical models for analyzing the empirical data. The importance of *a priori* model development in data analysis, as opposed to analyzing data by iteratively searching the data for relationships has been formalized by Burnham and

Anderson (1998). As per Franklin et al. (2000), I tested 2 forms of the continuous variables when translating ideas into statistical models: a linear and a quadratic form. The linear form of the variable appeared in the model as  $\beta_1 (x_1)$  and the quadratic form as  $\beta_1 (x_1) + \beta_2 (x_1^2)$ .

The different model structures corresponded to different predictions about the relationship between odds of use and the covariates. A linear structure was equivalent to assuming that probability of use changed with the covariate in a strict logistic fashion, while a quadratic structure was equivalent to assuming that probability of use peaked at some intermediate value of the covariate. Cover type,  $C$ , was treated as a categorical variable (Hosmer and Lemeshow 1989), with each of  $C - 1$  design variables corresponding to a different cover type. The  $C$ th cover type was the "reference" type (Hosmer and Lemeshow 1989), which in this study was the grassland cover type.

I compared 25 models (Table 1). I hypothesized that on a cascading scale pronghorn use patterns on the winter range are primarily a function of cover type, followed by elevation, solar radiation, and slope (models 1 - 15). I also hypothesized that elevation alone was the sole driver of pronghorn use patterns (models 16 -17), that use of the winter range was a function solely of solar radiation (models 18 -19), and that winter range use was influenced by elevation and solar radiation regardless of slope and cover (models 20 - 23). Lastly, I hypothesized that cover and solar radiation were the main drivers of landscape use, regardless of slope and elevation (models 24 -25). Models containing

quadratic terms represented alternative hypotheses regarding the relationship of pronghorn use to those variables. Although slope was expressed in the algorithm

Table 1. *A priori* models concerning effects of vegetation cover type (C2 –C7), elevation (E), solar radiation (S), and slope (L) on pronghorn use of the population's winter range in Yellowstone National Park, Wyoming. Cover is a categorical variable with 6 design variables and a reference type (grassland). The design variable representation is: C2 = old fields, C3 = grass-sagebrush mix, C4 = sagebrush, C5 = rabbitbrush, C6 = greasewood, and C7 = other.

Model	Model structure
1) Cover	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7)$
2) Cover+Elev	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E)$
3) Cover+Elev+Elev <sup>2</sup>	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(E^2)$
4) Cover+Elev+SRI	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(S)$
5) Cover+Elev+SRI+SRI <sup>2</sup>	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(S) + \beta_9(S^2)$
6) Cover+Elev+Elev <sup>2</sup> +SRI	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(E^2) + \beta_9(S)$
7) Cover+Elev+Elev <sup>2</sup> +SRI+SRI <sup>2</sup>	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(E^2) + \beta_9(S) + \beta_{10}(S^2)$
8) Cover+Elev+SRI+Slope	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(S) + \beta_9(L)$
9) Cover+Elev+SRI+Slope+Slope <sup>2</sup>	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(S) + \beta_9(L) + \beta_{10}(L^2)$
10) Cover+Elev+SRI+SRI <sup>2</sup> +Slope	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(S) + \beta_9(S^2) + \beta_{10}(L)$
11) Cover+Elev+SRI+SRI <sup>2</sup> +Slope+ +Slope <sup>2</sup>	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(S) + \beta_9(S^2) + \beta_{10}(L) + \beta_{11}(L^2)$
12) Cover+Elev+Elev <sup>2</sup> +SRI+SRI <sup>2</sup> + +Slope	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(E^2) + \beta_9(S) + \beta_{10}(S^2) + \beta_{11}(L)$
13) Cover+Elev+Elev <sup>2</sup> +SRI+SRI <sup>2</sup> + Slope +Slope <sup>2</sup>	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(E^2) + \beta_9(S) + \beta_{10}(S^2) + \beta_{11}(L) + \beta_{12}(L^2)$
14) Cover+Elev+Elev <sup>2</sup> +SRI+Slope	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(E^2) + \beta_9(S) + \beta_{10}(L)$
15) Cover+Elev+Elev <sup>2</sup> +SRI+Slope+ Slope <sup>2</sup>	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(E) + \beta_8(E^2) + \beta_9(S) + \beta_{10}(L) + \beta_{11}(L^2)$
16) Elev	$\beta_0 + \beta_1(E)$
17) Elev+Elev <sup>2</sup>	$\beta_0 + \beta_1(E) + \beta_2(E^2)$
18) SRI	$\beta_0 + \beta_1(S)$
19) SRI+SRI <sup>2</sup>	$\beta_0 + \beta_1(S) + \beta_2(S^2)$
20) Elev+SRI	$\beta_0 + \beta_1(E) + \beta_2(S)$
21) Elev+SRI+SRI <sup>2</sup>	$\beta_0 + \beta_1(E) + \beta_2(S) + \beta_3(S^2)$
22) Elev+Elev <sup>2</sup> +SRI	$\beta_0 + \beta_1(E) + \beta_2(E^2) + \beta_3(S)$
23) Elev+Elev <sup>2</sup> +SRI+SRI <sup>2</sup>	$\beta_0 + \beta_1(E) + \beta_2(E^2) + \beta_3(S) + \beta_4(S^2)$
24) Cover+SRI	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(S)$
25) Cover+SRI+SRI <sup>2</sup>	$\beta_0 + \beta_1(C2) + \dots + \beta_6(C7) + \beta_7(S) + \beta_8(S^2)$

for SRI, I also included it as a potential explanatory variable independent of SRI because the variables may represent 2 distinct biological meanings: in the SRI it influences solar radiation, while by itself it is used to indicate physical or behavioral limits of the species.

A critical problem in analyzing empirical data is selecting an appropriate model that is supported by the biology of the situation, by the data, and that has enough parameters to avoid bias, but not so many that precision is lost (Burnham and Anderson 1992). Because of small sample size, I used a bias-corrected version of Akaike's Information Criterion,  $AIC_c$  (Burnham and Anderson 1998) as the basis for objectively ranking models and selecting an appropriate "best approximating" model based on minimum  $AIC_c$  (Burnham and Anderson 1998). In this study,  $n$  was the number of instrumented animals from which use data were obtained. Models were ranked and compared based on  $\Delta AIC_c$ , with the most parsimonious model having the lowest value (Lebreton et al. 1992, Burnham and Anderson 1998). In general, models within 1-2  $AIC_c$  units of the selected model were considered competing models.

Standard logistic regression procedures may underestimate variance from the best model because data exhibited a cluster-correlated structure (i.e., repeated observations of the same individuals were not strictly independent). When true variance in the data set is greater than the nominal variance of the model, overdispersion occurs (Lebreton et al. 1992). Consequently, I used bootstrapping (Efron and Tibshirani 1993) to test coefficients by resampling the data set with replacement and repeating the model fitting procedure for the best model. For

each bootstrap iteration, the original set of 26 animals was resampled with replacement to generate a new set of 26 animals. Records for each animal in this new set were then resampled with replacement to generate bootstrap sets of use points for those animals. The number of use points in the new set for each animal was equal to the number in the original data set for that animal. Additionally, a new set of random points for each iteration was generated by resampling with replacement from the original set of random points. For each iteration, a set of 1,715 random points was drawn. This was the same number used in the standard regression analysis. One thousand bootstrap iterations were run. The resulting coefficients were accumulated and variances determined using the percentile method (Efron and Tibshirani 1993).

I used the ArcView map calculator to generate a 30-m grid resource selection model of the winter range based on the parameter estimates from the logistic regression model. Following Manly et al. (1993), I used the following equation to estimate the resource selection function (RSF) value for each pixel:  $RSF = \exp(\beta_1 X_1 + \dots + \beta_i X_i)$ . The map represents the ratio of odds of pronghorn use for each grid cell compared to a reference cell of grassland type at the minimum elevation in the winter range, and with  $SRI = 0$  and  $slope = 0$ .

I used behavioral data from observations of pronghorn groups to quantify pronghorn activity within each cover type. I tallied the total number of pronghorn observed in each cover type, then calculated the proportion of pronghorn engaged in each activity within that cover type.

Botanical composition of pronghorn diets was determined by microscopic examination of fresh fecal material (Sparks and Malachek 1968). Fecal pellets were collected on a weekly basis from January through March 2000 and 2001 on the winter range and on a weekly basis from the winter range and along migration routes in April 2000. Pellet piles were sampled soon after snowfalls and in areas known to have been recently used by pronghorn to ensure that pellets would reflect recent dietary intake. One pellet per pile was collected. Monthly composites were assembled containing 12 pellets each. Composite samples were oven-dried at 70° Celsius and ground to 1-mm size in a Wiley Mill.

Diet composition for individual composites was determined using microhistological techniques and frequency conversions described by Sparks and Malachek (1968). Analysis was conducted at the Composition Analysis Laboratory, Fort Collins, Colorado. Five slides were prepared from each composite using the method developed by Sparks and Malachek (1968). Slides were analyzed by examining 20 fields from each slide for a total of 100 fields per composite sample. Presence of plant species was determined by identification of epidermal cell tissue fragments (Sparks and Malachek 1968). Fragments were identified to genus with the exception of big sagebrush (*Artemisia tridentata*), fringed sage (*Artemisia frigida*) and winterfat (*Cerotoides lanata*). No adjustments for differential digestibility were included, and highly digestible species such as big sagebrush, and to a lesser degree other shrubs, may be underestimated. Monthly means were calculated for January, February, and March based on 3 samples per month in 2000, and 2 samples per month in 2001. Means were

expressed as percent relative density and pooled to yield 3 independent replications. In April 2000, 1 sample of 12 pellets was collected from non-migratory pronghorn on the winter range, and 1 sample was collected along travel routes of migrating pronghorn.

### Demography

I used group composition data from observations of instrumented does and opportunistic sightings to calculate the proportion of fawns per doe. Fawn:doe ratios for the population were constructed by month for June through January, except for September through mid-November when no tracking was conducted. After January all fawns were counted as adults. Fawn:doe ratios for June – August were also calculated by migratory status. Due to mixing on the winter range, I was unable to calculate ratios by migratory status November – January. I used the Kaplan-Meier product limit estimator (Kaplan and Meier 1958, White and Garrott 1990) to estimate survival probabilities ( $\hat{S}$ ) and Clopper – Pearson 95% confidence intervals (Clopper and Pearson 1934, Johnson et al. 1993) for the migratory and non-migratory subpopulations. To eliminate bias induced by capture-related mortality, I used only does that lived  $\geq 3$  months beyond capture. I tested for differences between groups' survival probability functions using a normal approximation for the test for 2 proportions (Sokal and Rohlf 1981). I evaluated the relationship between adult mortality and recruitment (Ockenfels 1994) by migratory group by multiplying mean female fawn recruitment in August by adult doe mortality rates. To do this, I partitioned mean

fawn ratios by assuming a 45 females: 55 males ratio at birth (Hailey 1979), and I used (1-survival probability) to derive the mortality rates.

## RESULTS

Pronghorn Distribution

Thirty adult does were radio instrumented in 1999, and 5 additional does were instrumented in 2000. During the study 3,001 relocations were obtained with a mean of 86 per individual. Sixty-six percent of the observations were gathered during winter, 18% during spring, and 16% during summer. Twenty-two animals were monitored for  $\geq 1$  year and 16 for  $\geq 2$  years. Seven animals died before monitoring began, 9 were monitored until their death, and the remaining 19 were monitored until the study terminated in August 2001. The percentage of female pronghorn monitored, relative to the estimated number of adult females in the study area, ranged between 20 and 24% during the study. No transmitter failed during the study, and no collars or transmitters were lost.

I stratified pronghorn activity into 3 categories for analysis: winter and summer activity, and spring migration. Spring migration was considered to have occurred when the collective distance traveled between consecutive relocations showed a substantial increase (Fig. 4). For this study, spring migration was defined as activity occurring from 1 April to 31 May. Winter activity was defined as activity occurring from 1 December to 31 March, with summer activity occurring from 1 June to 31 August. Movement patterns were consistent between years (Fig. 5).

A total of 1,819 relocations were available to construct the winter range map; 1,798 of these were collected during ground surveys and 19 during aerial

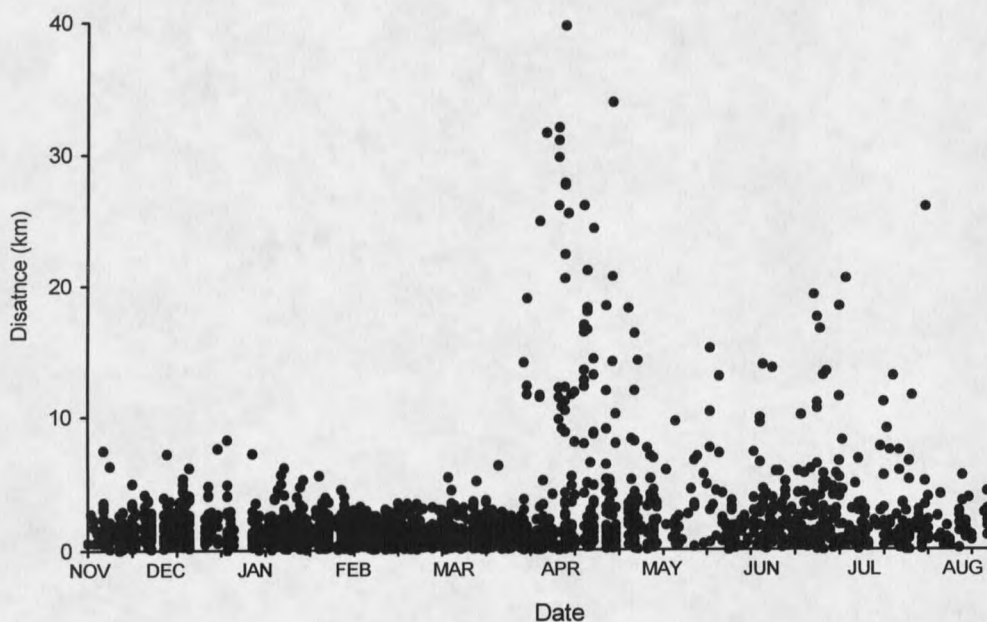


Fig. 4. Distance between consecutive relocations of instrumented pronghorn in Yellowstone National Park, Wyoming. Data collected June 1999 – August 2001.

surveys. Forty relocations (2.2% of the total) were censored because these points represented individuals that either arrived late or left early from, the core winter range. The final winter range map was constructed using 1,779 relocations and defined an area of approximately 22 km<sup>2</sup>. Winter range elevation extended from 1,500 – 1,850 m. Approximately 86% of the area was within the boundary of the park. The remaining 14% was within national forest, private, or conservation easement lands.

The summer database contained 438 relocation points; all were collected from ground surveys and used in map construction. The summer range was 240 km<sup>2</sup>, between 1,560 – 2,200 m elevation, and contained completely within the YNP boundary (Fig. 6). Because not all animals migrated from the winter range,

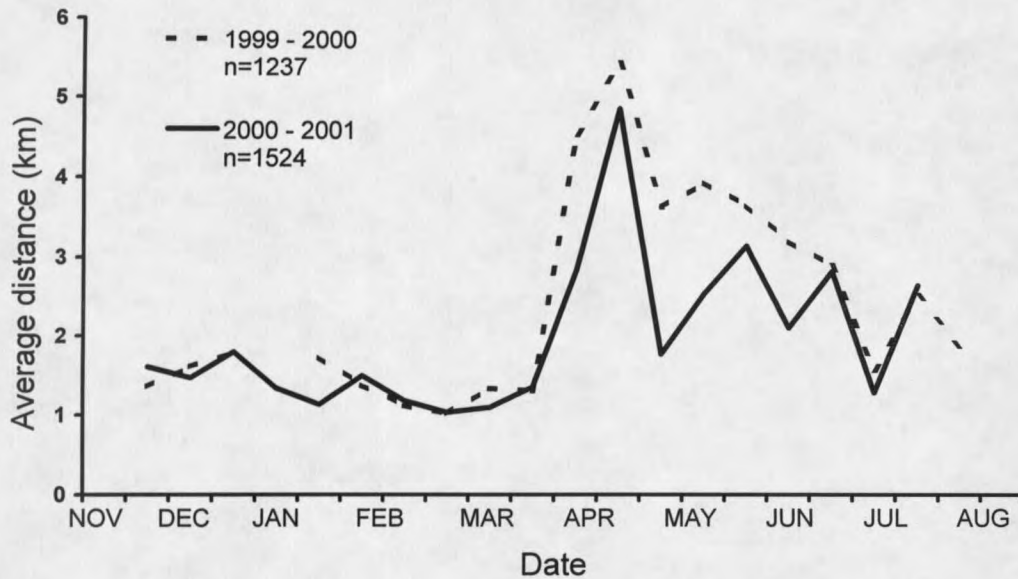


Fig. 5. Average bimonthly distances by year between consecutive relocations of instrumented pronghorn in Yellowstone National Park, Wyoming. Data collected November 1999 – August 2001.

instrumented pronghorn was  $10.9 \pm 0.4 \text{ km}^2$  ( $\bar{x} \pm \text{SE}$ , range = 3.9 – 15.6  $\text{km}^2$ ).

Thirteen of the 16 instrumented animals that were alive for both winters of the study showed  $\geq 51\%$  overlap in their home ranges between years, demonstrating fidelity to winter range areas (Fig. 7).

Average summer home range size for instrumented pronghorn was  $37.2 \pm 6.4 \text{ km}^2$  (range = 7.4 – 95.6  $\text{km}^2$ ). Sixty-five percent of the instrumented pronghorn were migratory and 31% were non-migratory. Except for 1 doe that displayed both movement strategies during the study, instrumented does showed consistency in strategy between years and in their home range locations on the summer range.

Average summer home range size for migratory animals was  $43.1 \pm 6.9 \text{ km}^2$

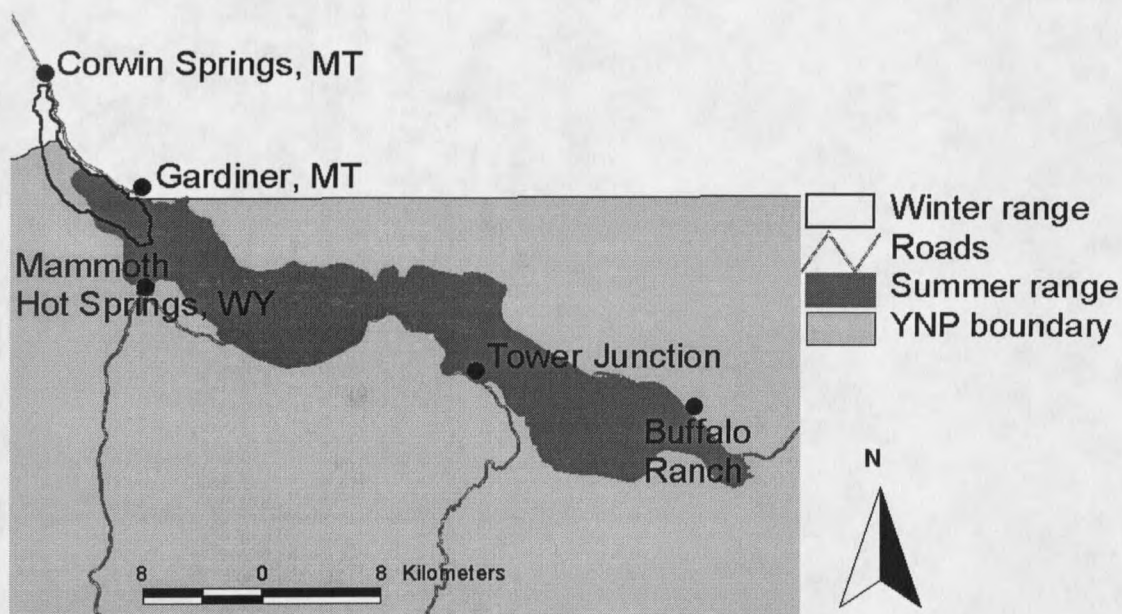


Fig. 6. Seasonal ranges of pronghorn in Yellowstone National Park, Wyoming. Overlap exists between the summer and winter range because not all animals migrate off the winter range in the summer.

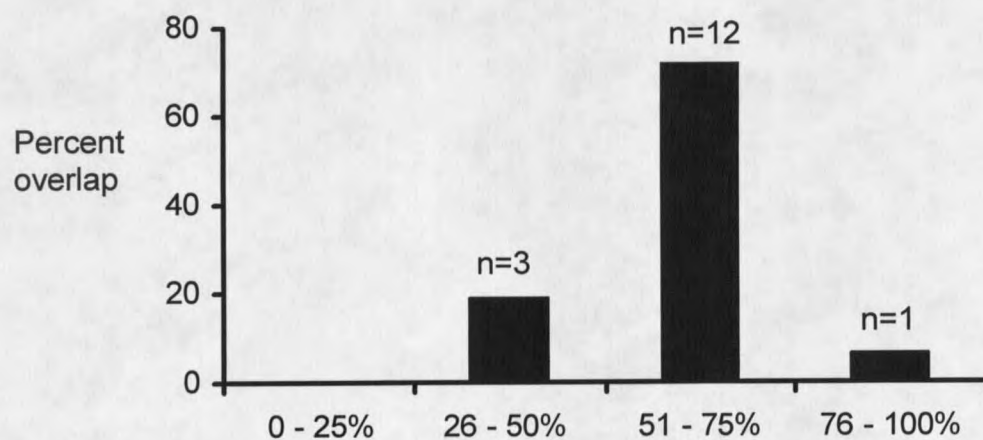


Fig. 7. Percent overlap in individuals' winter home ranges between consecutive years.

(range = 7.4 – 95.6 km<sup>2</sup>) and  $13.9 \pm 3.1$  km<sup>2</sup> (range = 7.4 – 22.1 km<sup>2</sup>) for non-migratory animals. I tested the hypothesis that summer home range size for migratory does was greater than for non-migratory does. There was strong evidence to support this hypothesis ( $HR_{\text{mig}} - HR_{\text{non}} = 29.2$ , where HR is average summer home range size by group; *t*-test;  $P < 0.001$ , *df* = 17). One of the instrumented migratory does spent the 1999 – 2000 winter on the population's winter range with a home range size of 12.3 km<sup>2</sup>, then traveled approximately 25 km north of the winter range onto private land where she remained for the duration of the study. The size of her home range on private land was 2.8 km<sup>2</sup>.

#### Winter Range Vegetation

The cover map of the current pronghorn winter range showed that 40% of the range was comprised of the grassland type (Fig. 8). Old fields, grass-sagebrush, sagebrush, rabbitbrush, and greasewood types comprised 16, 11, 25, 4, and <1 percent of the total winter range, respectively. The rabbitbrush cover type had the greatest percent canopy cover of herbaceous plants relative to the other types on the winter range (23.3% versus 8.8 – 17.8%, respectively). Grass-sagebrush, sagebrush, rabbitbrush, and greasewood types each had 8, 14, 15, and 17 percent live shrub canopy cover, respectively. Agreement between cover type assignment from ground-based relocations and cover type derived from the digital classification of each relocation on the cover map of the winter range was 73% for rabbitbrush and 88 – 100% for the other 6 cover types.

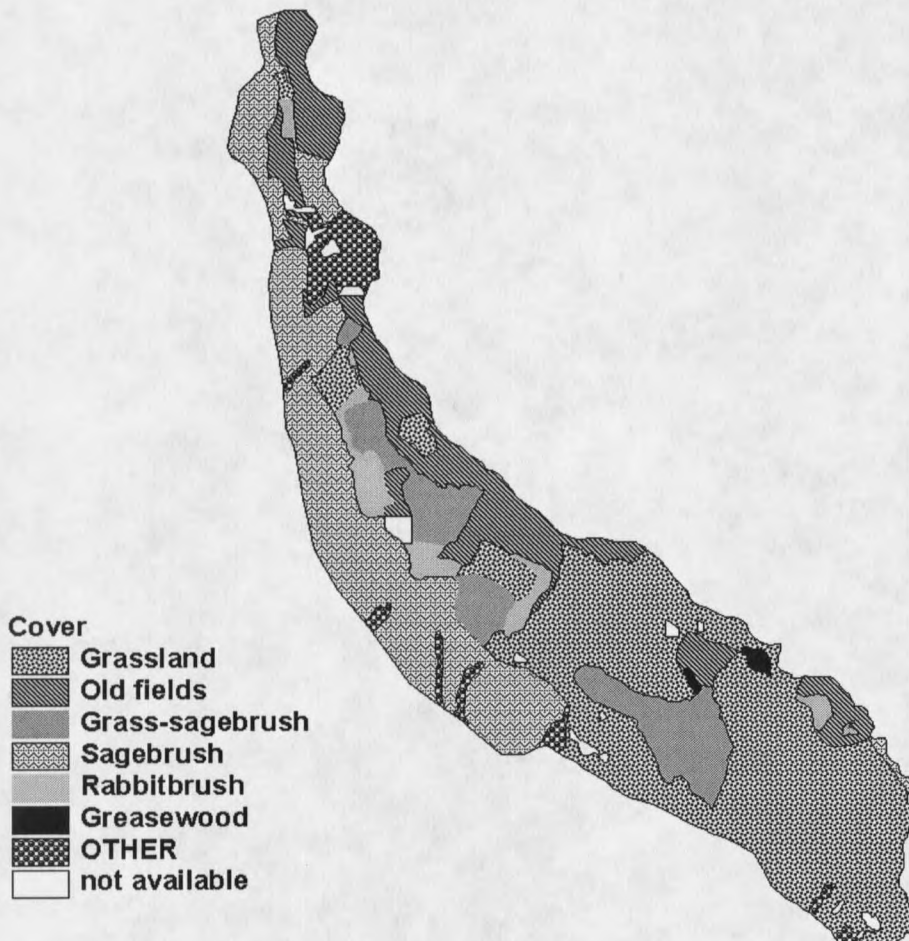


Fig. 8. Cover map of the current pronghorn winter range in Yellowstone National Park, Wyoming.

Descriptions of each cover type are as follows. Dominant species were those that had the greatest canopy coverage for that cover type, while plants with the highest frequency were those that appeared in the sample quadrats most often. Details of vegetation and percent canopy cover and frequency by cover type are in Appendix A.

- *Grasslands*. This type occurred on any slope and exposure below 1,850 m. Dominant grass species were Sandberg bluegrass, Idaho fescue, prairie junegrass, and bluebunch wheatgrass. Other dominant species were prickly pear cactus (*Opuntia polyacantha*), fringed sage, alyssum (*Alyssum desertorum*), and sandwort (*Arenaria hookeri*). Most frequent species were Sandberg bluegrass, fringed sage, and sandwort. Herbaceous plant cover was low (8.8%) relative to other cover types and a moderate to high proportion of ground surface was bare soil, gravel, or rock. This cover type comprised 40% of the current winter range.

- *Old fields/current pasture*. Old fields were cultivated and/or irrigated prior to park acquisition in 1932. This category also includes an area within the park that had been planted in alfalfa during the early 1900's. Current pastureland lies outside the north boundary of the park on private land. These 2 types were combined because the vegetation structure and plant types were similar. Both occur below 1,650 m on level terrain. The dominant grass species was crested wheatgrass, with some annual wheatgrass (*Agropyron triticeum*) and alyssum. The most frequent species was crested wheatgrass (97.5% frequency). Herbaceous plant cover was moderate (17.8%) relative to other cover types. This cover type comprised 16% of the current winter range.

- *Grassland-sagebrush mix*. This type occurred between 1,500 and 1,850 m elevation. The overstory was dominated by Wyoming big sagebrush, with varying amounts of rubber rabbitbrush and green rabbitbrush (0.2 – 4.5% cover). The understory was dominated by Sandberg bluegrass, prairie junegrass, annual wheatgrass and alyssum. The most frequent species were Sandberg bluegrass

and prairie junegrass. Total herbaceous canopy cover was moderate (15.8%) relative to other cover types. Shrub canopy cover was low (8.1%) relative to other shrub cover types; 1.6% of the canopy was comprised of dead sagebrush, and 1% of dead rubber rabbitbrush. This cover type made up 11% of the current winter range.

- *Sagebrush*. This category occurred between 1,500 and 1,850 m elevation within and out of the Park. The overstory was dominated by basin big sagebrush and Wyoming big sagebrush. The understory was dominated by Sandberg bluegrass, prairie junegrass, and bluebunch wheatgrass; these species also were the most frequent. Live shrub canopy cover was among the highest (14.1%) relative to other shrub cover types; 3.5% of the canopy was comprised of dead sagebrush. Herbaceous plant cover was moderate (17.6%) relative to other cover types. This cover type comprised 25% of the current winter range.

- *Rabbitbrush*. This type occurred below 1,650 m elevation on level terrain and was characterized by areas where rubber rabbitbrush and green rabbitbrush were the dominant overstory shrubs. The understory was dominated by crested wheatgrass, alyssum, dandelion (*Taraxacum officinale*), and stickseed (*Lappula redowskii*). The most frequent herbaceous species were crested wheatgrass, alyssum, and stickseed. Shrub canopy cover was among the highest (15.0%) relative to other shrub cover types; 6.6% of the canopy was comprised of dead rabbitbrush species. Herbaceous plant cover was high (23.3%) relative to other cover types. This cover type comprised 4% of the current winter range.

- *Greasewood*. This category occurred below 1,650 m elevation on level terrain. Greasewood was the dominant overstory shrub. The understory was dominated by annual wheatgrass and Sandberg bluegrass. The most frequent herbaceous species were annual wheatgrass, Sandberg bluegrass, and alyssum. Shrub canopy cover was among the highest (17.0%) of the other shrub cover types; 6.7% of the canopy was comprised of dead greasewood. Herbaceous plant cover was moderate (15.2%) relative to other cover types. This cover type comprised <1% of the current winter range.
- *OTHER*. This category includes current agricultural fields planted in alfalfa, riparian areas, and Douglas fir (*Pseudotsuga menzeisii*) patches. Combined, these areas make up 4.3% of the current winter range.

### Winter Range Use

Results from model selection showed that Yellowstone pronghorn selected for cover type, solar radiation, elevation, and slope (Table 2). The quadratic variable for slope did not appear in the most highly ranked models. The top model included quadratic terms for SRI and elevation, in addition to linear terms for cover type variables and slope. All 7 models containing cover type and the quadratic term for elevation were included in the top models. Candidate models that did not contain this combination had extremely large  $\Delta AIC_c$  values (209.2 – 533.1).

Although objective model selection found  $C+S+S^2+E+E^2+L$  to be the most parsimonious model, *a posteriori* examination showed that SRI and slope were

Table 2. Results of the regression model of the factors influencing pronghorn winter range use in Yellowstone National Park. The top 7 models are ranked by  $\Delta AIC_c$  value with the lowest being the most parsimonious.  $n = 26$  for all models. McFadden's rho-squared,  $\rho^2$ , is the amount of variation explained by the model.  $K$  is the number of estimable parameters. Letters correspond to those in Table 1, where  $C$  represents the 6 design variables for cover type,  $S$  is solar radiation,  $E$  is elevation, and  $L$  is slope.

Model	$\rho^2$	$K$	$AIC_c$	$\Delta AIC_c$
$C+S+S^2+E+E^2+L$	0.119	12	4227.98	0.00
$C+S+S^2+E+E^2$	0.118	11	4236.01	8.03
$C+S+E+E^2$	0.116	10	4239.47	11.49
$C+S+E+E^2+L$	0.117	11	4241.10	13.13
$C+S+S^2+E+E^2+L+L^2$	0.120	13	4241.54	13.57
$C+S+E+E^2+L+L^2$	0.118	12	4241.98	14.01
$C+E+E^2$	0.112	9	4252.77	24.79

correlated ( $P < 0.001$ ,  $r^2 = 0.44$ ), but SRI was more variable with higher values of slope, and contained more explanatory power than slope. Diagnostics also showed correlation between SRI and elevation ( $P < 0.001$ ,  $r^2 = 0.09$ ), with solar radiation decreasing with increasing elevation. These results may be due to the fact that the pronghorn winter range lies within the foothills of the Gallatin Mountain Range and the predominant aspect of the study area was north-facing. Furthermore, there is an order of magnitude increase in  $|\beta_i|$  for the SRI variables in a model with cover and elevation compared to a model with just the SRI

variables, suggesting that the significance of solar radiation might be a spurious result. The addition of SRI and  $SRI^2$ , and slope, to the model  $C+E+E^2$  only added a marginal amount to the McFadden's  $\rho^2$  value (0.006 and 0.001, respectively); the cover variables contributed 0.063 while  $E+E^2$  added 0.058 to McFadden's  $\rho^2$  value. Because of these findings from a *posteriori* examination and because cover and the quadratic term for elevation were found in all the top models, I chose  $C+E+E^2$  as the best approximating model of winter habitat selection.

I then applied bootstrap procedures to provide more reliable estimates of standard error for this model, reducing the effect of cluster-correlation within the data. The coefficients and 95% confidence intervals for this model support selection for cover and among cover types, and support a non-linear relationship between pronghorn habitat use and elevation (Table 3). Odds ratios indicated that rabbitbrush and greasewood cover types were selected in greater proportion than the reference grassland type, while less selection was shown for sagebrush and other cover types, including current agricultural fields planted in alfalfa. Because the 95% confidence interval for the coefficients spanned zero, there was no evidence of selection for grass-sagebrush mix or old fields at  $\alpha = 0.05$  relative to grassland cover. Since sagebrush cover also has decidedly negative odds, this suggests that pronghorn generally avoided cover types containing sagebrush relative to grass and the other cover types. Fine scale spatial heterogeneity may have been driving selection in mixed areas. Because historical agricultural practices had occurred on the lower end of the winter range, the old fields type was found to be correlated with elevation ( $P < 0.001$ ,  $r^2$

Table 3. Estimated coefficients and 95% confidence intervals for variables in a model of pronghorn use of the winter range in Yellowstone National Park, 1999 – 2001. Odds ratios and 95% confidence intervals are also given for the cover type variables. Confidence intervals were constructed using a bootstrap procedure to account for overdispersion. Grassland cover type was used as the reference type.

Variable	Estimated Coefficients	95% C.I.		Odds Ratio	95% C.I.	
		Lower	Upper		Lower	Upper
Intercept	-1.26	-1.79	-0.63			
C2 Old fields	0.26	<0.00	0.53	1.30	1.03	1.64
C3 Grass-sage	-0.28	-0.59	0.04	0.76	0.60	0.96
C4 Sagebrush	-1.20	-1.77	-0.74	0.30	0.24	0.37
C5 Rabbitbrush	0.78	0.40	1.20	2.18	1.59	2.97
C6 Greasewood	1.62	0.65	3.26	5.07	1.94	13.21
C7 Other	-2.40	-15.96	-1.27	0.09	0.04	0.23
Elevation	3.18	2.18	4.16			
Elevation <sup>2</sup>	-1.30	-1.63	-0.96			

= 0.15). The coefficient and 95% confidence interval for elevation were positive while those for elevation<sup>2</sup> were negative, indicating that pronghorn use reaches its maximum at intermediate elevations within the winter range while upper and lower elevations were used least. I used the variables from the logistic regression model to produce a resource selection map of pronghorn use of the winter range (Fig. 9).

Results from pronghorn activity observations did not show any 1 cover type being most important for feeding or bedded activities. Within all cover types except "other", the largest proportion of pronghorn observed were engaged in feeding (55 – 64%), followed by bedded (27 – 40%) (Fig. 10). Within the "other" cover type, 61% of pronghorn were traveling. Between cover types, the proportions of pronghorn seen feeding and bedded were evenly distributed.

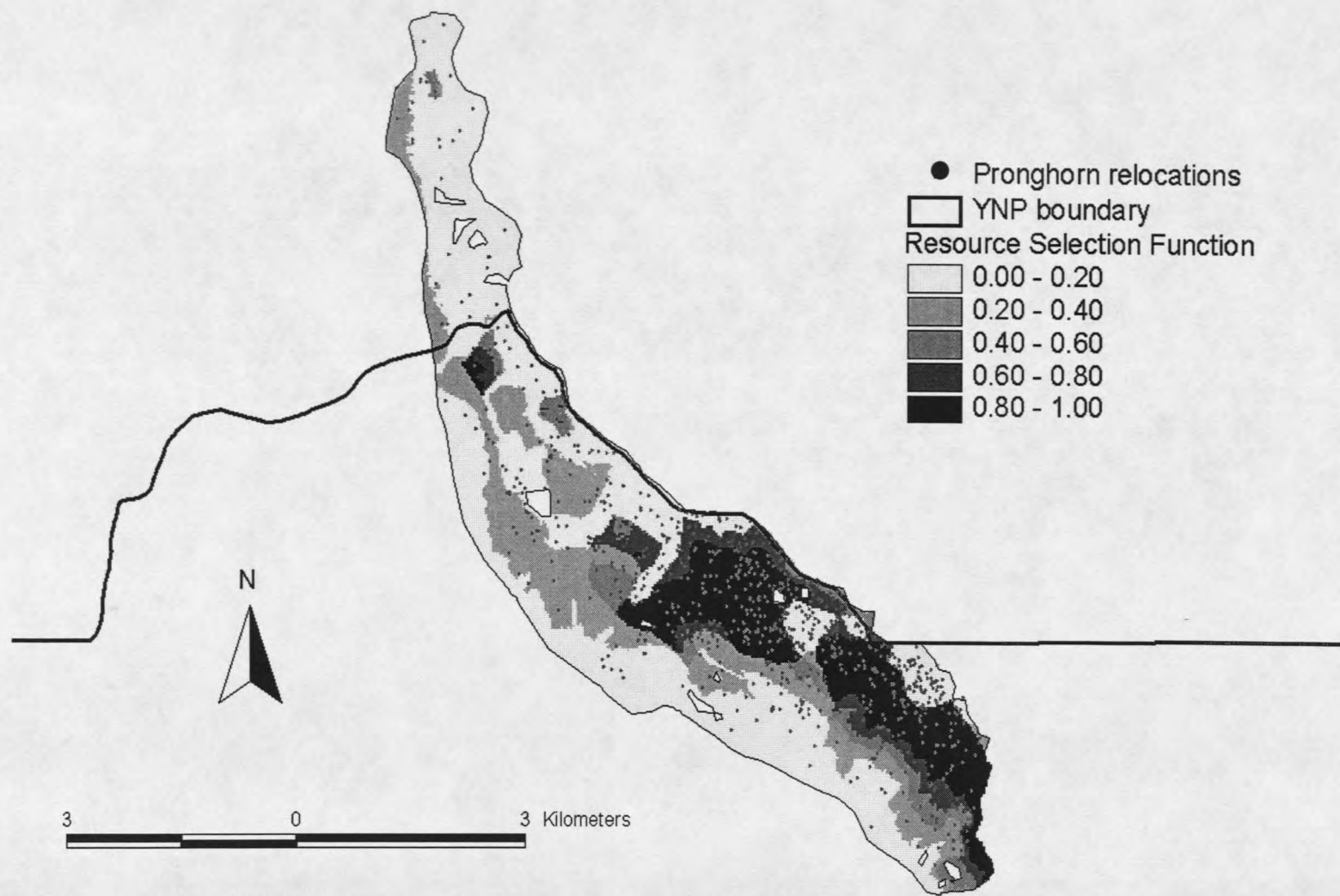


Fig. 9. Map of resource selection by pronghorn on the winter range in YNP based on parameters of a logistic regression model. Darker shading indicates greater odds of use relative to a reference cell of grassland cover at the minimum elevation of the winter range. Areas not available to pronghorn are defined polygons outlined in black.

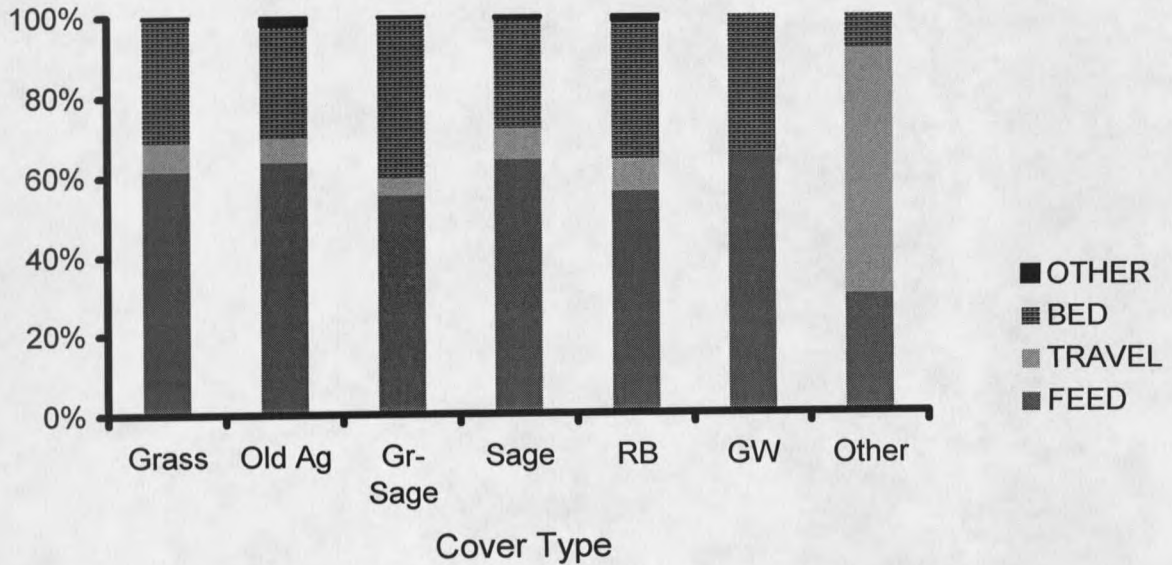


Fig.10. Total number of pronghorn seen within each cover type broken down into the proportion of pronghorn engaged in each of 4 activities.

Results from microhistological analysis suggest that when feeding, pronghorn are selecting at a finer scale than cover type. During the winter pronghorn in the study area fed primarily on woody species (Table 4). The major forage items in the winter diet included four woody taxa, rabbitbrush, Gardner saltbush (*Atriplex gardneri*), winterfat, and Rocky Mountain juniper (*Juniperus scopulorum*). Two forb taxa, granite gilia (*Leptodactylon pungens*) and bladderpod (*Lesquerella* spp.) were consistently utilized. No graminoid taxa were consistently utilized during the winter. In April, fecal samples indicated that the non-migratory segment of the population fed on fewer graminoids and more forbs and woody taxa than did the migratory segment of the herd (Table 5). The majority of the diets for both segments were comprised of graminoids. The major graminoid

Table 4. Summary of food items making up  $\geq 1\%$  of the overall diet of pronghorn in winter 2000 and 2001 in Yellowstone National Park based on microhistological analysis of fecal sample composite. Each composite had 12 fecal pellets. Monthly percentages represent the average percent from 3 composites for 2000 and 2 composites for 2001. Winter percentages are cumulative values based on 5 composites per month.

Food item	Jan	Feb	Mar	Winter
<b>Graminoids</b>				
<i>Agropyron</i> spp.			3	1
<i>Bouteloua gracilis</i>	tr <sup>a</sup>	tr	2	1
<i>Poa</i> spp.		tr	1	tr
<i>Oryzopsis hymenoides</i>	tr	tr	3	1
Identifiable minor grasses <sup>b</sup>	tr	tr	2	1
Total graminoids	tr	tr	11	4
<b>Forbs</b>				
<i>Eriogonum caespitosum</i>	1	tr		tr
<i>Leptodactylon pungens</i>	2	3	2	2
<i>Lesquerella</i> sp.	1	1	3	2
Identifiable minor forbs <sup>c</sup>	1	1	tr	1
Total forbs	5	5	5	5
<b>Shrubs and trees</b>				
<i>Artemisia frigida</i>	7	4	2	4
<i>Artemisia tridentata</i>	4	3	2	3
<i>Atriplex gardneri</i>	6	8	6	7
<i>Chrysothamnus</i> spp.	58	67	62	62
<i>Cerotoides lanata</i>	9	5	4	6
<i>Juniperus scopulorum</i>	6	6	5	6
<i>Salix</i> spp.	tr	tr	1	tr
Identifiable minor shrubs and trees <sup>d</sup>	1	tr		tr
Total shrubs and trees	92	93	82	88

<sup>a</sup> <1% of diet.

<sup>b</sup> Graminoids contributing <1% to the total winter diet including *Bromus* spp., *Festuca* spp., and *Phleum* spp.

<sup>c</sup> Forbs contributing <1% to the total winter diet including *Antennaria* spp., *Aster* spp., *Astragalus* spp., *Cerastium* spp., *Descurania* spp., *Oenothera* spp., *Suaeda* spp., and *Taraxacum* spp.

<sup>d</sup> Shrubs and trees contributing <1% to the total winter diet including *Shepherdia-Eleagnus* spp., *Pinus* spp., and *Pseudotsuga* spp.

items used included wheatgrasses (*Agropyron* spp.), grama grass (*Bouteloua gracilis*), and Indian ricegrass (*Oryzopsis hymenoides*).

Table 5. Summary of food items making up  $\geq 1\%$  of the April diet of pronghorn in 2000 in Yellowstone National Park based on microhistological analysis of fecal samples. Each sample was a composite of 12 fecal pellets.

Food item	Non-migratory	Migratory
<b>Graminoids</b>		
<i>Agropyron</i> spp.	17	37
<i>Bouteloua gracilis</i>	22	20
<i>Poa</i> spp.		2
<i>Oryzopsis hymenoides</i>	12	16
Identifiable minor grasses <sup>a</sup>	3	tr <sup>b</sup>
Total graminoids	54	75
<b>Forbs</b>		
<i>Aster</i> spp.	2	
<i>Eriogonum caespitosum</i>	2	2
<i>Leptodactylon pungens</i>	4	6
<i>Lesquerella</i> spp.	19	
<i>Lupinus</i> spp.		3
Total forbs	27	11
<b>Shrubs and trees</b>		
<i>Alnus</i> sp.		6
<i>Artemisia fringida</i>		2
<i>Chrysothamnus</i> spp.	4	4
<i>Cerotoides lanata</i>	9	
Identifiable minor shrubs and trees <sup>c</sup>	3	tr
Total shrubs and trees	16	12

<sup>a</sup> Graminoids contributing <1% to the April diet including *Aristida* spp., *Bromus* spp., *Carex* spp., and *Juncus* spp.

<sup>b</sup> <1% of diet.

<sup>c</sup> Shrubs and trees contributing <1% to the April diet including *Berberis* spp., *Juniperus* spp., *Pseudotsuga* spp., and *Salix* spp.

Demography

Group composition data from all years of the study were pooled to calculate fawn:doe ratios. Small sample sizes precluded examination of ratios at a finer scale. The low fawn:doe ratio for June was due to the fact that Yellowstone pronghorn usually begin fawning after the middle of that month. The mean number of fawns per doe was 0.38 and 0.32 in July and August, respectively. Means dropped substantially in the early winter months where the number ranged between 0.04 – 0.07 (Fig. 11). The low ratio in November may have been biased downward due to observer inexperience the first year of the study. During July and August, the mean number of fawns per doe was consistently higher for the migratory segment of the population (0.40 and 0.41, respectively) than for the does that remained on the winter range (0.22 and 0.15, respectively) (Fig. 12). The fawn:doe ratios for the non-migratory segment dropped in the first months of life, while ratios for the migratory segment remained relatively constant.

During the tracking period, there were 9 instrumented doe mortalities. Seven mortalities occurred on the winter range; 3 occurred during winter and 4 occurred in late spring. The other 2 mortalities occurred on the summer range in late spring. Adult pronghorn doe survival probability for the non-migratory segment of the population was 0.29 (0.05 – 0.69, n=7) while the survival probability for the migratory segment was 0.87 (0.61 – 0.98, n=15). Small sample sizes resulted in large confidence intervals which were skewed, since survival probabilities were assumed to be binomially distributed. While 95% confidence intervals were not

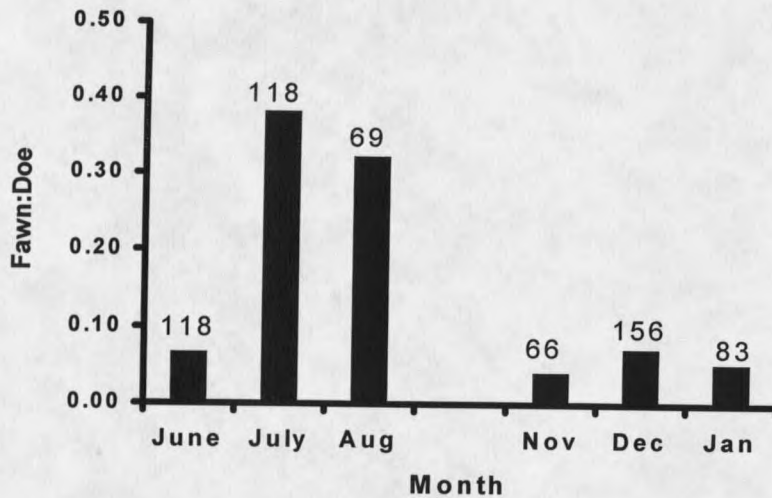


Fig.11. Mean number of pronghorn fawns per doe by month in Yellowstone National Park, Wyoming. Data were collected June 1999 – August 2001 with the exception of September and October of each year, and pooled across years. N = the number of groups used to calculate fawn:doe ratios.

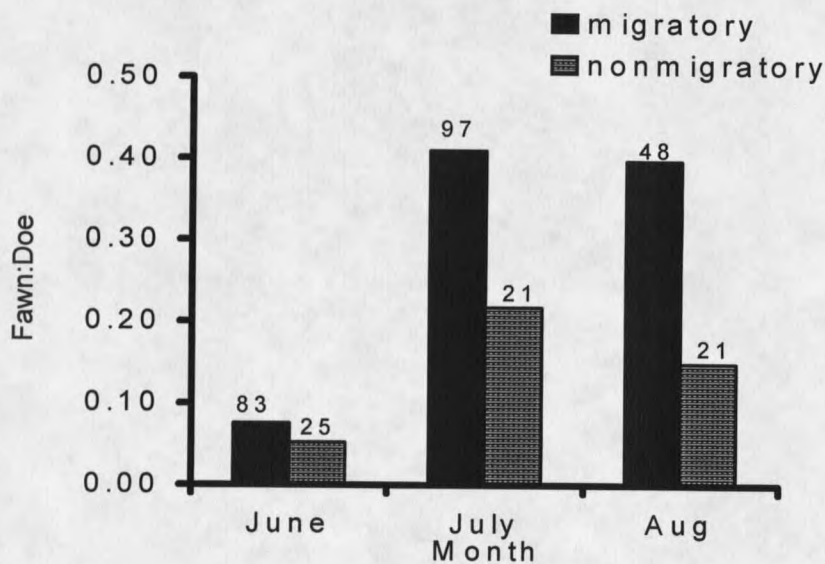


Fig.12. Mean number of fawns per doe for the pronghorn population in Yellowstone National Park, Wyoming, based on migratory status. Data collected 1999 – 2001 and pooled across years. N = number of groups used to calculate fawn:doe ratios.

exclusive, given that overlap occurred in the tails only of the intervals, this suggests a strong difference in survival does exist between the 2 segments of the population. I was interested in testing the hypothesis that the survival probability for the migratory segment of the population was greater than that of the non-migratory segment. There was strong evidence to support this hypothesis ( $S_{\text{mig}} - S_{\text{non}} = 0.58$ ; Test for 2 proportions; normal approximation  $P < 0.001$ ).

Mean fawn recruitment for the migratory and non-migratory segments in August were 0.40 and 0.15, respectively. Estimated female fawn recruitment for the migratory group was 0.18 female fawns:doe ( $0.40 \times 0.45 = 0.18$ ). Migratory adult female mortality ( $1 - 0.87 = 0.13$ ) was 0.05 less than female fawn recruitment. For the non-migratory group, estimated female fawn recruitment was 0.07 ( $0.15 \times 0.45 = 0.0675$ ). Non-migratory female mortality ( $1 - 0.29 = 0.71$ ) exceeded female fawn recruitment (0.07) by 0.64.

## DISCUSSION

All Yellowstone pronghorn congregate on the winter range during December through March, confirming this as critical range. Pronghorn showed a more restricted distribution than in the past, when use of areas to the east of the Yellowstone and Gardner Rivers had been documented (Barmore 1980). However, some apparently permanent emigration from the study area to the lower Yellowstone valley still occasionally occurred. Habitats outside YNP sustained the largest groups observed on the winter range during this study. Use of these areas during critical times of winter has been documented (Murie 1940, Singer 1988), and it has been suggested that habitats outside the park are vital to the maintenance of the herd, especially during winters of heavy snow (Barmore 1970).

During winter I found pronghorn selected for rabbitbrush and greasewood cover types at intermediate elevations. Pronghorn did not select for old fields, cover types where sagebrush is common, or various other cover types that occur in small amounts on the winter range, including alfalfa fields on private land. Other studies of pronghorn populations in the shrub-steppe biome have documented the importance of big sagebrush to pronghorn in winter (Severson and May 1967, Sundstrom et al. 1973). In the Yellow Water Triangle in central Montana, Bayless (1969) found that vegetation types dominated by sagebrush, primarily big sage, received more use in winter by pronghorn than other vegetation types, including greasewood. Pronghorn in southeastern Montana and

northern Wyoming used the big sagebrush vegetation type significantly more often than expected in winter (Amstrup 1978).

There have been 2 former habitat selection studies done on the Yellowstone pronghorn. Barmore (1980) conducted a study in the late 1960's when the population size was estimated at 100 – 125 animals. In the late 1980's, Singer and Norland (1994) repeated the earlier study. The pronghorn herd at that time had increased to approximately 500 animals. Both studies found that Yellowstone pronghorn selected for xeric grassland; sagebrush and old fields were avoided during the late 1960's (Barmore 1980), and no selection for sagebrush was shown in the late 1980's (Singer and Norland 1994). While some differences exist in the vegetation types considered between the 2 former studies and my study (i.e., I combined xeric and mesic grassland types into 1 grassland type, considered rabbitbrush and greasewood types, and had a sagebrush type distinct from sagebrush-grassland), I also found that pronghorn avoided sagebrush types. This continued selection against a plant type that is highly important to other pronghorn populations may reflect the declining quality of sagebrush habitat on the northern Yellowstone winter range.

Observations of pronghorn activity did not show any cover type to be most important for feeding or bedding. Most pronghorn observed within each cover type were found to be feeding, followed by bedded, and the percentage of pronghorn engaged in both of these activities was evenly distributed among cover types. The exception was the "other" category for cover type, which

included current agricultural fields and wooded areas; most pronghorn observed in these areas were traveling.

I believe that bias was low with respect to detecting pronghorn activity, given the openness of the vegetation on the winter range. Where visibility was poor, as in dense sagebrush, it was poor for determining all activities. The fact that most observations were of feeding or bedded pronghorn is not surprising. Byers (1997) found that pronghorn on the National Bison Range in western Montana spent approximately 80% of their time devoted to either feeding or bedding. Bruns (1977) reported that feeding and bedding followed each other with "monotonous regularity."

A possible explanation for the lack of apparent importance of one cover type for feeding is that none of the cover types on the winter range are extremely productive, as evidenced by the low percent canopy cover of herbaceous plants and shrubs (9.8 – 38.3%). Rabbitbrush and greasewood types had a larger combined percent canopy cover for herbaceous plants and shrubs than any other cover type. Rabbitbrush had the highest percent canopy cover for forbs (12.0%), and greasewood the highest percent shrub canopy cover (17%). Sagebrush type had 14.1% shrub canopy cover. It is unlikely that even the most productive cover type on the winter range can support sustained feeding by pronghorn; therefore, they must meet their nutritional needs from a combination of cover types.

Another potential explanation is that Yellowstone pronghorn select for individual plant types rather than cover type communities. Pronghorn are selective feeders (Dirschl 1963, Schwartz and Nagy 1976, Schwartz et al. 1977,

Byers 1997). Aside from rabbitbrush, other components of the pronghorn winter diet were detected in slight amounts or not at all in the vegetation sampling I conducted on the winter range. Although the purpose of the sampling was descriptive rather than statistical, a sampling scheme was employed to provide an adequate representation of vegetation within each cover type. Therefore, I believe that pronghorn were selecting for plants that are not abundant on the winter range and were selecting on a finer scale than cover type.

A comparison of the current winter diet of Yellowstone pronghorn to former dietary studies of this population lends further evidence of declining habitat condition on the winter range (Murie, 1940, O'Gara 1968, Barmore 1969, Singer and Norland 1994). The current study showed pronghorn in YNP consumed more rabbitbrush than any other plant species from January through March. During the 1930's, Murie (1940) found that big sagebrush was the staple winter food of pronghorn. Rabbitbrush and greasewood were eaten but were less palatable than sagebrush. Barmore (1969) found the Yellowstone pronghorn winter diet, as determined by rumens collected in 1965 – 1966, to be comprised mainly of big sagebrush with very little rabbitbrush. During the winter of 1965 – 1966, levels of big sagebrush utilization were generally higher than for other browse species on the same sites (O'Gara 1968). Regarding the pronghorn winter range, O'Gara (1968) noted that "a high percentage of big sagebrush on the lower elevations are severely decadent." Singer and Norland (1994) found that sagebrush consumption increased over that reported by Barmore (1980) while rabbitbrush consumption was low for both periods.

Although different techniques were employed to assess the food habits of Yellowstone pronghorn, comparisons between these studies can be made. Both rumen and microhistological analyses have the same bias: underrepresentation of forbs and overrepresentation of browse and grass (Anthony and Smith 1974, Smith and Shandruk 1979). Underrepresentation of forbs is less critical during winter, when plants are dormant (Vavra et al. 1978); all of these studies considered winter diets. It is apparent from the food habit studies done on Yellowstone pronghorn over the past 60+ years that a major shift in dietary components has occurred. This may reflect the continuing decline in habitat conditions on the winter range.

Winter diets of Yellowstone pronghorn differed from those of other pronghorn populations in similar habitats. Food habit studies from pronghorn populations in the shrub-steppe biome similarly found that browse species were the dominant component of winter antelope diets (Cole and Wilkins 1958, Severson and May 1967). However, big sagebrush was the most important shrub in the diets of these other populations (Bayless 1969, Medcraft and Clark 1986). While other studies have shown high consumption of rabbitbrush species in the fall (Amstrup 1978, Cole and Wilkins 1958), no study to date has shown a high proportion of winter diet being comprised of rabbitbrush, as I found in the Yellowstone pronghorn diet.

The successional pattern of the pronghorn winter range habitat provides an explanation for the results from the habitat use - and food habits analyses of this study. The pronghorn winter range is Wyoming big sagebrush/bluebunch

wheatgrass habitat type in secondary succession due to decades of intense browsing. Long-term herbivory has led to a significant decline in the quantity and quality of sagebrush plants (Wambolt and Sherwood 1999). Browsed sagebrush plants on the winter range were found to have thinner leaves, and lower shrub production and seedhead number than sagebrush plants that had been protected from herbivory in an exclosure erected on the winter range in 1957 (Hoffman and Wambolt 1996). Low seedhead numbers may result in stands having difficulty regenerating over the long term (Hoffman and Wambolt 1996). Sprouting shrubs, such as rabbitbrush, sustain prolonged herbivory better than non-sprouters, such as sagebrush (Wambolt and Sherwood 1999). Also, rabbitbrush is known to often benefit when associated species are preferred forages and are over-utilized (Young and Evans 1978). On the pronghorn winter range the dominant big sagebrush has been reduced from intense browsing, thereby providing the subdominant sprouting shrubs an opportunity to increase (Wambolt and Sherwood 1999).

Demographics of the Yellowstone pronghorn, as indexed by recruitment and adult mortality, provide further support that conditions on the winter range may be adversely affecting the population. Summer and early winter fawn:doe ratios for Yellowstone pronghorn during the period of this study were slightly lower than those reported during 1938 – 1970 in YNP (Barmore 1980). They were substantially lower than fawn:doe ratios reported for other populations (Beale and Smith 1970, Mitchell 1980, Pyrah 1987). Factors which can affect the number of fawns in the population include productivity of the breeding does, age structure of

the herd, and fawn mortality. While this study did not address age structure, an assessment of such would assist in better understanding the dynamics of the population. Productivity of Yellowstone pronghorn during the period 1965 – 1966, measured as the fetus:doe ratio, was 1.96 (O’Gara 1968). Productivity in 1999 – 2001, measured as fawns:doe at birth, was  $\geq 1.8$  (J. Byers, University of Idaho, unpubl. data). Studies of fetus:doe ratios among pronghorn indicate that 200:100 can be considered the potential maximum ratio (O’Gara 1969). Therefore, productivity does not appear to be a contributing factor to low recruitment in this herd.

Summer and early winter fawn:doe ratios suggest that fawn mortality is a primary contributor to low recruitment. Low fawn survival in this herd has been a concern since at least the mid 1960’s (O’Gara 1968). Summer fawn survival in YNP during the period 1938 - 1970 was lower in Yellowstone than in other population (Barmore 1980). The substantial birth-to-winter fawn mortality from the earlier period, which was consistently high regardless of population levels (O’Gara 1968) agrees with findings from this study. A substantial drop in summer to winter fawn:doe ratios has been reported for other pronghorn populations as well (Beale and Smith 1970). Fawn mortality appears to be a driving process in the dynamics of the Yellowstone pronghorn population and it is recommended that a better understanding of this process be pursued.

Coyotes have been linked to the majority of fawn mortalities during this study (J. Byers, University of Idaho, unpubl. data). While differences in predator densities between the winter and summer ranges may be driving the difference in

localized recruitment throughout the population, there has been no research done on this topic to date. Several inferences can be drawn that relate poor habitat conditions on the winter range to low recruitment to the does that remain on the winter range to fawn. During this study, heavy adult mortality occurred right before or soon after parturition. On a previous study conducted in YNP, health indices indicated that adult pronghorn does were in poorest condition in May (O'Gara 1968). Given this, and the fact that all pronghorn receive their nutrition from the winter range during winter, vegetation on the winter range may not be providing the animals with enough reserves to fully meet nutritional demands in the last trimester of pregnancy.

Lack of appropriate vegetation structure for safe fawn bed sites might also contribute to low recruitment from the non-migratory group. The importance of shrub cover for pronghorn fawns is well documented (Pyrah 1987, Barrett 1984, Alldredge et al. 1991). Proper concealment for the neonate is essential to its survival, especially during the first few weeks of life (Lent 1974). On the winter range, adequate shrub cover for fawn bed sites is limited. This might make it easier for predators to locate unguarded fawns. Additionally, it is reasonable to expect that given the sparse vegetation on the winter range, does have longer feeding bouts and thus are away from their fawns for longer periods of time, leaving them unprotected. While predator density on the winter range is unknown, there is strong support to link poor demographic performance of the Yellowstone pronghorn population with inadequate habitat on the winter range that leaves weakened adults and little hiding cover for fawns.

This study found that the Yellowstone pronghorn population is comprised of a migratory group and a resident group. In this study 65% of the instrumented pronghorn were migratory and 31% were non-migratory, but an unbiased estimate of the proportion of migratory versus non-migratory adult does would depend on a truly random sample of the population. There have been records of pronghorn summering on the winter range since 1905 (Hofer 1905), and previous reports recognize 2 migratory behaviors in this population (Skinner 1922, Barmore 1980). However, this is the first study that conclusively recognizes individuals with respect to migratory behavior and establishes that there are 2 distinct groups to the Yellowstone pronghorn herd.

The Yellowstone pronghorn population can be viewed within the framework of a source – sink dynamic (Pulliam 1988). Habitat quality on the winter range is a driving force behind this dynamic. If habitat quality is a measure of the importance of habitat in maintaining a certain population, then habitat quality should be defined in terms of the survival and production characteristics of that population (Van Horne 1983). In this study, fawns born on the winter range were found to suffer higher mortality during the summer than fawns born off the winter range. Recruitment and adult mortality rates strongly suggest that the non-migratory segment is a sink to the overall population, while the migratory segment is the source for what limited recruitment to the population is occurring (Pulliam 1988).

Two areas warrant further research. I recommend that they be studied within the source-sink framework. First, the quality and quantity of food items in the

pronghorn diet should be assessed during all 4 seasons. Second, demographic vital rates should continue to be monitored, including fawn production and survival, causes of fawn and adult mortality, coyote densities on the winter range, age structure of the herd, and recruitment to the population. Lastly, I recommend that YNP explore ways to improve habitat conditions on the winter range and to work with other agencies and private landowners to make travel out of Yellowstone along historic migration routes a viable option for pronghorn.

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APPENDICES

APPENDIX A

COVER TYPE DESCRIPTIONS

Table 6. Species composition, percent average canopy cover by Daubenmire plots for herbaceous and half-shrub species and from line intercepts for shrubs, and percent frequency for cover types on the winter range for a pronghorn antelope population in Yellowstone National Park. Data collected June 2001.

## Cover Type 1: Grassland

	% Cover	% Frequency
<b>Grasses</b>		
<i>Poa secunda</i>	2.2	52.5
<i>Festuca idahoensis</i>	0.9	22.5
<i>Koeleria macrantha</i>	0.8	18.8
<i>Agropyron spicatum</i>	0.7	16.2
<i>Carex stenophylla</i>	0.2	8.8
<i>Agropyron triticeum</i>	0.1	3.8
<i>Sitanion hystrix</i>	0.1	2.5
Total	5.0	
<b>Forbs</b>		
<i>Alyssum desertorum</i>	1.0	10.0
<i>Arenaria hookeri</i>	0.8	27.5
<i>Aster scopulorum</i>	0.2	7.5
<i>Antennaria dimorpha</i>	0.2	7.5
<i>Townsendia hookeri</i>	0.2	1.2
<i>Allium spp.</i>	0.1	5.0
<i>Lomatium triternatum</i>	0.1	2.5
<i>Phacelia heterophylla</i>	t	1.2
Total	2.6	
TOTAL HERB. CANOPY COVER	7.6	
<b>Cacti</b>		
<i>Opuntia polyacantha</i>	1.2	18.8
<b>Half-Shrubs</b>		
<i>Artemisia frigida</i>	1.0	28.8
Total	1.0	
TOTAL SHRUB CANOPY COVER	1.0	

## Cover Type 2: Old Fields/ Current Pastureland

	% Cover	% Frequency
<b>Grasses</b>		
<i>Agropyron cristatum</i>	14.3	97.5
<i>Agropyron triticeum</i>	0.8	20.0
<i>Stipa comata</i>	0.2	1.2
<i>Poa secunda</i>	0.1	2.5
Total	15.4	
<b>Sedges</b>		
<i>Carex stenophylla</i>	0.2	3.75
Total	0.2	
<b>Forbs</b>		
<i>Alyssum desertorum</i>	1.5	15.0
<i>Lappula redowskii</i>	0.4	17.5
<i>Salsola iberica</i>	0.2	2.5
<i>Camelina microcarpa</i>	0.1	2.5
<i>Descurainia sophia</i>	t	1.2
Total	2.2	
TOTAL HERB. CANOPY COVER	17.8	
<b>Cacti</b>		
<i>Opuntia polyacantha</i>	t	1.2
<b>Half-Shrubs</b>		
<i>Artemisia frigida</i>	0.3	6.2
Total	0.3	
TOTAL SHRUB CANOPY COVER	0.3	

## Cover Type 3: Grassland – Sagebrush Mix

	% Cover	% Frequency
<b>Grasses</b>		
<i>Poa secunda</i>	4.0	51.2
<i>Festuca idahoensis</i>	2.1	22.5
<i>Koeleria macrantha</i>	1.8	22.5
<i>Agropyron triticeum</i>	1.7	18.8
<i>Agropyron cristatum</i>	0.7	3.8
<i>Agropyron spicatum</i>	0.6	12.5
<i>Stipa comata</i>	0.2	11.25
<i>Agropyron smithii</i>	0.1	5.0
<i>Bromus tectorum</i>	0.1	2.5
Total	11.3	
<b>Sedges</b>		
<i>Carex stenophylla</i>	t	1.2
Total	t	
<b>Forbs</b>		
<i>Alyssum desertorum</i>	1.2	18.8
<i>Taraxacum officinale</i>	0.5	11.2
<i>Antennaria dimorpha</i>	0.4	5.0
<i>Achillea millefolium</i>	0.3	5.0
<i>Arenaria hookeri</i>	0.2	10.0
<i>Lupine spp.</i>	0.2	2.5
<i>Phacelia heterophylla</i>	0.2	2.5
<i>Polygonum bistortoides</i>	0.2	1.2
<i>Aster scopulorum</i>	0.2	6.2
<i>Lewisia rediviva</i>	0.2	8.8
<i>Lomatium triternatum</i>	0.1	5.0
<i>Astragalus miser</i>	0.1	3.8
<i>Lappula redowskii</i>	0.1	3.8
<i>Tragopogon dubius</i>	0.1	2.5
<i>Descurainia sophia</i>	0.1	2.5
<i>Allium spp.</i>	t	1.2
<i>Camelina microcarpa</i>	t	1.2
<i>Castilleja longispica</i>	t	1.2
<i>Eriogonum caespitosum</i>	t	1.2
Total	4.1	

TOTAL HERB. CANOPY COVER 15.4

Cacti

*Opuntia polyacantha* 0.4 3.8

Half-Shrubs

*Artemisia frigida* 0.4 10.0

*Cerotoides lanata* 0.1

Total 0.5

Shrubs

*Artemisia tridentata wymoingensis* 5.2

*Chrysothamnus viscidiflorus* 1.5

*Chrysothamnus nauseosus* 0.8

*Sarcobatus vermiculatus* 0.1

Total 7.6

TOTAL SHRUB CANOPY COVER 8.1

## Cover Type 4: Sagebrush

	% Cover	% Frequency
<b>Grasses</b>		
<i>Poa secunda</i>	5.9	57.5
<i>Koeleria macrantha</i>	3.3	32.5
<i>Agropyron spicatum</i>	2.2	28.8
<i>Agropyron cristatum</i>	1.0	7.5
<i>Agropyron smithii</i>	0.3	5.0
<i>Festuca idahoensis</i>	0.3	6.2
<i>Stipa comata</i>	0.1	3.8
<i>Bromus tectorum</i>	t	1.2
Total	13.1	
<b>Sedges</b>		
<i>Carex stenophylla</i>	0.6	6.2
Total	0.6	
<b>Forbs</b>		
<i>Alyssum desertorum</i>	0.9	16.2
<i>Comandra umbellata</i>	0.2	2.5
<i>Arenaria hookeri</i>	0.2	7.5
<i>Phacelia heterophylla</i>	0.1	5.0
<i>Astragalus miser</i>	0.1	2.5
<i>Lewisia rediviva.</i>	0.1	3.8
<i>Lappula redowskii</i>	0.1	2.5
<i>Arenaria congesta</i>	t	1.2
<i>Tragopogon dubius</i>	t	1.2
<i>Camelina microcarpa</i>	t	1.2
<i>Descurainia sophia</i>	t	1.2
Total	1.7	
TOTAL HERB. CANOPY COVER	15.4	
<b>Cacti</b>		
<i>Opuntia polyacantha</i>	2.2	8.8
<b>Half-Shrubs</b>		
<i>Artemisia frigida</i>	0.8	11.2

Total	0.8
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## Shrubs

<i>Artemisia tridentata</i> spp. <sup>ii</sup>	11.7
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<i>Chrysothamnus nauseosus</i>	0.9
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<i>Chrysothamnus. viscidiflorus</i>	0.7
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Total	13.3
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TOTAL SHRUB CANOPY COVER 14.1

## Cover Type 5: Rabbitbrush

	% Cover	% Frequency
<b>Grasses</b>		
<i>Agropyron cristatum</i>	6.5	46.2
<i>Agropyron triticeum</i>	1.1	12.5
<i>Bromus inermis</i>	0.9	10.0
<i>Bromus tectorum</i>	0.8	12.5
<i>Poa secunda</i>	0.7	21.25
<i>Stipa comata</i>	0.5	2.5
Total	10.5	
<b>Sedges</b>		
<i>Carex stenophylla</i>	0.8	8.8
Total	0.8	
<b>Forbs</b>		
<i>Alyssum desertorum</i>	9.1	57.5
<i>Taraxacum officinale</i>	1.5	11.2
<i>Lappula redowskii</i>	1.2	42.5
<i>Camelina microcarpa</i>	0.1	5.0
<i>Descurainia sophia</i>	0.1	2.5
<i>Draba nemorosa</i>	t	1.2
<i>Lewisia rediviva</i>	t	1.2
<i>Lomatium triternatum</i>	t	1.2
<i>Salsola iberica</i>	t	1.2
<i>Tragopogon dubius</i>	t	1.2
Total	12.0	
TOTAL HERB. CANOPY COVER 23.3		
<b>Shrubs</b>		
<i>Chrysothamnus naseosus</i>	12.7	
<i>Chrysothamnu viscidiflorus</i>	2.2	
<i>Artemisia tridentata</i> spp.	0.1	
Total	15.0	
TOTAL SHRUB CANOPY COVER 15.0		

## Cover Type 6: Greasewood

	% Cover	% Frequency
<b>Grasses</b>		
<i>Agropyron triticeum</i>	7.2	36.7
<i>Poa secunda</i>	3.4	26.7
<i>Agropyron cristatum</i>	1.6	18.3
<i>Sitanion hystrix</i>	0.9	1.7
<i>Festuca idahoensis</i>	0.4	1.7
Total	13.5	
<b>Forbs</b>		
<i>Alyssum desertorum</i>	1.1	20.0
<i>Descurainia sophia</i>	0.1	3.3
<i>Arenaria hookeri</i>	0.1	1.7
<i>Lappula redowskii</i>	0.1	1.7
<i>Lomatium triternatum</i>	0.1	1.7
<i>Antenaria dimorpha</i>	0.1	1.7
Total	1.6	
TOTAL HERB. CANOPY COVER	15.1	
<b>Cacti</b>		
<i>Opuntia polyacantha</i>	0.1	5.0
<b>Shrubs</b>		
<i>Sarcobatus vermiculatus</i>	16.4	
<i>Chrysothamnus nauseosus</i>	0.3	
<i>Artemisia tridentata</i> spp.	0.3	
Total	17.0	
TOTAL SHRUB CANOPY COVER	17.0	

<sup>i</sup> <1% canopy cover.

<sup>ii</sup> Sagebrush subspecies were not measured separately.

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