

An assessment of the risk of inter-specific transmission of Brucella abortus from bison to elk on the Madison-Firehole winter range

by Matthew Joseph Ferrari

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University
© Copyright by Matthew Joseph Ferrari (1999)

Abstract:
Brucella abortus, a bacterium which causes disease in livestock, wildlife, and humans, has become the target of a large scale eradication program in the wild species of the Greater Yellowstone area. An understanding of the spatial and temporal associations of bison {Bison bison) and elk (Cervus elaphus), the two major vertebrate hosts, is essential in assessing the risk of inter-specific transmission and the long term efficacy of proposed management scenarios to eradicate the disease. The Madison-Firehole drainage of Yellowstone National Park supports high densities of elk and bison during the winter and spring when B. abortus can be shed by females through birth or abortion. I utilized 4,526 telemetry locations of cow elk collected between 1991-1998 and conducted 30 ground censuses of bison between 1997-1998 to assess the distribution and spatial and temporal associations of elk and bison on the winter range. The Madison-Firehole bison winter range is entirely contained within the winter range used by elk. Elk and bison, which normally display significant spatial separation, were found to have high levels of association on the winter range. Increasing snow pack increased the density of bison on the winter range as bison moved into the Madison-Firehole from the Hayden Valley summer range, and deep snow restricted elk to the valley bottoms. Range overlap varied between 53 and 76% (ANOVA, $P = 0.09$) and tended to increase from December to May. The percent of radiolocations in which instrumented cow elk were, ≤100m of bison was 13-30% between April and May, 1991-1998, the peak time of bison calving. Regression analysis indicated that snow water equivalent, a measure of snow depth and density, was positively correlated with elk/bison association and was the strongest predictor of association ($P < 0.0001$). Despite close association between the two species, a sample of 73 adult cow elk indicated that the prevalence of seropositive animals in the Madison-Firehole was not significantly different ($P > 0.05$) from other elk populations that do not associate closely with bison. However the seroprevalence in the Madison-Firehole was lower ($P < 0.05$) than the seroprevalence in populations associated with winter feeding operations. Thus we conclude that the close contact between bison and elk during the winter and spring does not result in increased levels of disease exposure in elk.

AN ASSESSMENT OF THE RISK OF INTER-SPECIFIC TRANSMISSION OF *BRUCELLA ABORTUS* FROM BISON TO ELK ON THE MADISON-FIREHOLE WINTER RANGE

by

Matthew Joseph Ferrari

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY-BOZEMAN
Bozeman, Montana

February 1999

© COPYRIGHT

by

Matthew Joseph Ferrari

1999

All Rights Reserved

N378
F4123

APPROVAL

of a thesis submitted by

Matthew Joseph Ferrari

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.

Robert A. Garrott — (Signature) — 2/1/1999 (Date)

Approved for the Department of Biology

Ernest R. Vyse — (Signature) — 2/1/99 (Date)

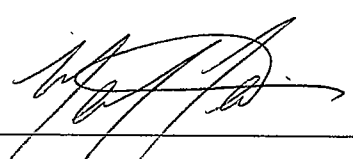
Approved by the College of Graduate Studies

Bruce R. McLeod — (Signature) — 2-4-99 (Date)

STATEMENT OF PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Montana State University-Bozeman, I agree that the Library shall make it available to borrowers under rules of the Library.

I have indicated my intention to copyright this thesis by including a copyright notice page, copying is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for permission for extended quotation from or reproduction of this thesis in whole or in parts may be granted only by the copyright holder.

Signature 

Date FEB 1, 1999

ACKNOWLEDGEMENTS

This research was funded by the National Park Service. Serologic testing was conducted by the Montana Department of Fish, Wildlife, and Parks. Equipment was donated by Polaris Industries, Inc., Polaris West, and Tubbs Snowshoe Co. Immobilizing drugs were donated by Lloyd Laboratories. I would like to thank J. McDonald, G. Pavellas, R. Jaffe, D.D. Bjornlie, A.C. Pils, S. Hess, and M. Bjorklund for assistance with field data collection; R. Abbeglen and National Park Service staff, and S. Carsley and Yellowstone Alpen Guides for logistical support; J. Mack and W. Clark of the National Park Service for logistical support, information on the study area , and reviewing the study proposal; N. Anderson of Montana Fish, Wildlife, and Parks for conducting serologic tests; K.E. Aune of Montana Fish, Wildlife, and Parks for advice on serology and reviewing the manuscript; B. Smith and S.G. Smith of Wyoming Game and Fish, and D. Hunter of Idaho Fish and Game for providing data on elk serology outside of Yellowstone; P.J. Gogan for providing data on bison serology, and reviewing the manuscript; T. Heilmann and B. Wilmer for providing GIS models and technical support; R. Boik for assistance and advice on statistical analysis; and L.R. Irby, A.V. Zale for reviewing the manuscript; and R.A. Garrott for criticism, advice, and support throughout the project.

TABLE OF CONTENTS

Page

INTRODUCTION 1

STUDY AREA 6

METHODS 9

RESULTS 16

DISCUSSION 29

REFERENCES CITED 35

APPENDIX 42

LIST OF TABLES

Table Page

1. Areas (ha) of habitat types and topographic attributes for the areas delimited as elk and bison winter ranges in the Madison-Firehole region of YNP. Percentages are presented as percent composition of the respective species winter range. 17

2. Mean number of bison counted in the Madison, Gibbon, and Firehole River drainages during ground censuses conducted during the winters of 1996-97 and 1997-98. Three total ground censuses were conducted each month. Only two surveys were conducted in December 1997..... 20

3. The percent of monthly elk telemetry locations collected on the Madison-Firehole winter range, YNP, in which collared elk were ≤100m from the nearest bison. Mean and standard deviation (S) are presented for each month..... 22

4. Results from first order autoregression models of association between elk and bison on the Madison-Firehole winter range, YNP from 1991-94 and 1996-98..... 23

5. Sero-prevalence rates for anitbodies to *B. abortus* in 21 elk populations (males and females) in Wyoming, Montana, and Idaho. Prevalence rates are presented as 95% Clopper-Pearson confidence intervals. Populations are characterized by contact with bison and use of winter feedgrounds..... 27

LIST OF FIGURES

Figure Page

1. Map of the Madison-Firehole study area, YNP, with elk and bison winter ranges highlighted.....7

2. Total bison counted during tri-monthly ground censuses of the Madison-Firehole study area, YNP, conducted during the winters of 1996-97 and 1997-98.....19

3. The relationship between the percent of monthly elk telemetry locations in which the collared animal was ≤100m from the nearest bison (association) and the average daily measurement of centimeters of water in the snow pack (snow water equivalent) at the Madison Plateau automated SNOTEL site (elev. 2362) for each month between December and May 1992-98 (excluding the winter of 1994-95).....24

4. The relationship between the percent of montly elk telemetry locations in which the collared animal was ≤100m from the nearest bison (association) and the mean monthly bison census total from tri-monthly ground censuses conducted on the Madison-Firehole winter range, YNP, between January -May 1997 and December 1997-May 1998.....25

ABSTRACT

Brucella abortus, a bacterium which causes disease in livestock, wildlife, and humans, has become the target of a large scale eradication program in the wild species of the Greater Yellowstone area. An understanding of the spatial and temporal associations of bison (*Bison bison*) and elk (*Cervus elaphus*), the two major vertebrate hosts, is essential in assessing the risk of inter-specific transmission and the long term efficacy of proposed management scenarios to eradicate the disease. The Madison-Firehole drainage of Yellowstone National Park supports high densities of elk and bison during the winter and spring when *B. abortus* can be shed by females through birth or abortion. I utilized 4,526 telemetry locations of cow elk collected between 1991-1998 and conducted 30 ground censuses of bison between 1997-1998 to assess the distribution and spatial and temporal associations of elk and bison on the winter range. The Madison-Firehole bison winter range is entirely contained within the winter range used by elk. Elk and bison, which normally display significant spatial separation, were found to have high levels of association on the winter range. Increasing snow pack increased the density of bison on the winter range as bison moved into the Madison-Firehole from the Hayden Valley summer range, and deep snow restricted elk to the valley bottoms. Range overlap varied between 53 and 76% (ANOVA, $P = 0.09$) and tended to increase from December to May. The percent of radiolocations in which instrumented cow elk were ≤100m of bison was 13-30% between April and May, 1991-1998, the peak time of bison calving. Regression analysis indicated that snow water equivalent, a measure of snow depth and density, was positively correlated with elk/bison association and was the strongest predictor of association ($P < 0.0001$). Despite close association between the two species, a sample of 73 adult cow elk indicated that the prevalence of seropositive animals in the Madison-Firehole was not significantly different ($P > 0.05$) from other elk populations that do not associate closely with bison. However the seroprevalence in the Madison-Firehole was lower ($P < 0.05$) than the seroprevalence in populations associated with winter feeding operations. Thus we conclude that the close contact between bison and elk during the winter and spring does not result in increased levels of disease exposure in elk.

INTRODUCTION

Attempts to manage disease in free ranging animals are complicated by the uncertainty inherent in wild populations. Information on population numbers, mechanisms and rates of infection, and the complexity of natural systems are, at best, estimates and confound not only attempts to mitigate disease problems, but also the ability to judge the success of management efforts (Wobeser 1994). The ability of wildlife to harbor infectious agents is of particular concern in the case of diseases that have the potential to infect humans or livestock (Laughlin et al. 1989). Disease eradication has been successful in wildlife populations on a regional basis, but implementation requires detailed information on the disease agent, the environment, and the disease hosts and their interactions with each other (Wobeser 1994).

The bison of Yellowstone National Park have recovered from less than 50 animals at the turn of the century (Meagher 1973) to 4200 in July 1994 (National Park Service 1998). Some of Yellowstone's bison are infected with *Brucella abortus*, a bacterium that causes disease in livestock and humans, and recent increases in the bison population and increased numbers of animals leaving the park in winter has presented a risk to livestock and human health (Cheville et al. 1998; Baskin 1998). *B. abortus* infection is known to cause abortion, retained placenta, orchitis, epididymitis, and impaired fertility in a wide

range of animal hosts, and viable bacteria have been recovered from uterine discharges associated with birth or abortion, semen, and milk (Ray 1979). Contact with these materials through direct consumption or consumption of contaminated vegetation is considered the most likely vector of transmission among animals (Dobson and Meagher 1996). Management agencies dealing with the disease have committed to the eventual eradication of *B. abortus* from all wildlife in the Greater Yellowstone area (GYA; NPS 1998). Elk are known hosts of *B. abortus*, and attempts to eradicate the disease must address the role of the 120,000 elk in the GYA in the epidemiology of the disease (Cheville et al. 1998).

B. abortus has been considered enzootic in the bison of Yellowstone National Park since shortly before it was first observed in bison in 1917 (Meyer and Meagher 1994; Mohler 1917). Historical surveys for brucellosis in Yellowstone bison yielded sero-prevalence of 63% (Tunnicliff and Marsh 1935), and a disease survey conducted during the winter of 1996-97 found sero-prevalence of ≈60% in adult males (N=344) and ≈50% in adult females (N=337; Peter Gogan pers. comm.). Most elk populations exhibit low levels of sero-prevalence (<6%), though some populations associated with winter feeding programs or sharing common range with infected bison have been shown to have higher sero-prevalence (13-37%; Herriges et al. 1991; McCorquodale and DiGiacomo 1985; Thorne et al. 1978a; Corner and Connell 1958; Tunnicliff and Marsh 1935; Rush 1932). The only confirmed inter-specific transmission of brucellosis in ungulates has occurred in mixed domestic herds, animals in experimental settings, or on winter feedgrounds (Davis et al. 1990; Flagg 1983; Kistner 1982; Thorne et al. 1978b; Corner

and Connell 1958). However, experimental and feedground conditions often have atypically high densities of infected and susceptible animals and might not reflect transmission rates under natural conditions (Boyce 1989; Dobson and Meagher 1996).

The risk of disease transmission increases as the density of infectious animals in the host population and the association between infectious and susceptible animals increases (Anderson and May 1979; Ray 1979). The risk of transmission between species is influenced by ecological and behavioral components which affect the rate of interaction within and among species (Dobson and Meagher 1997; Dobson 1995; Caro and Durant 1995). If transmission of *B. abortus* between bison and elk is a common phenomenon, then elk sharing winter ranges with high densities of bison (thereby increasing the density of infectious and susceptible animals) are likely to have higher risk of exposure to the organism. Overlap in geographic ranges, while necessary for interaction between species, does not necessarily imply the occurrence or intensity of interaction (Smith and Dobson 1994). Ecological separation of sympatric mammalian herbivores has been well documented in African savanna systems even where animals utilize similar areas and habitats (Lamprey 1963: Gwynne and Bell 1968; Leuthold 1978; Jarman 1972; Putnam 1994). Because of the susceptibility of *B. abortus* to environmental mortality factors outside the host (Thorne 1982), animals must not only use the same geographic range, but must come into close contact while the bacterium is still viable for transmission to occur. Previous studies of areas in which bison and elk are sympatric suggest high habitat

overlap, but found little spatial overlap or incidence of co-occurrence (Wydeven and Dahlgren 1985; Telfer and Cairns 1979).

Deep snows in the Madison-Firehole restrict much of the winter range of elk and bison to valley bottoms and areas of geothermal influence presumably to avoid the energetic cost of foraging in deep snow (Craighead et al. 1973; Meagher 1973). Reduction of available range and forage due to severe winter conditions and high densities of over wintering bison and elk (Craighead et al. 1973; Singer 1996; Aune 1981) on the Madison-Firehole winter range suggest the potential for interaction between the two species. Theory suggests that species with similar niche requirements should increase the level of separation as densities increase or resources become scarce (Putnam 1994). Leuthold (1978) found an increase in niche separation among African browsing ungulates during the dry season when forage was limited. Jarman (1972), however, found that spatial and habitat overlap increased in the dry season as species increased use of wetter areas as refuges. Schwartz and Ellis (1981) reported similar results for bison and pronghorn antelope in North American short grass prairie during periods of reduced forage.

The Madison-Firehole is the only system where large numbers of bison and elk are restricted to a common range under natural conditions. I hypothesize that the severity of the weather conditions on the Madison-Firehole winter range restricts bison and elk distribution and increases the degree of inter- species association such that the two populations mimic a single herd with respect to transmission of *B. abortus*. I formulated three predictions, which, if proven, would support this hypothesis. First, that bison and

elk share space during the winter and spring when disease transmission is possible (Cheville et al. 1998). Second, that the degree of association between the two species is correlated to winter conditions. Third, the level of disease prevalence in elk on the Madison-Firehole winter range is higher than would be expected in an elk population that has no contact with infected bison. To address these predictions I collected data on the distributions and temporal and spatial associations of the bison and elk populations in the Madison-Firehole, the potential mechanisms that drive changes in distribution and association, and the prevalence of antibodies to *B. abortus* in the Madison-Firehole elk population.

STUDY AREA

The 26,849 hectare study area was located in the Madison-Firehole region of Yellowstone National Park (Figure 1). The area includes the drainages of the Upper Madison, Gibbon, and Firehole Rivers. The area ranges between 2,250-2,800m in elevation and provides winter range to 500-800 elk and 800-1,100 bison (Eberhardt et al. 1998, Singer 1991). Lodgepole pine (*Pinus contortus*) dominates the forested area with stands of Engleman spruce (*Picea engelmanni*), subalpine fir (*Abies lasiocarpa*), and Douglas fir (*Pseudotsuga mensiesii*) interspersed. More than 50% of the forested area was burned in fires during the summer of 1988. Burned areas are characterized by snags and downed trees, Ross' sedge (*Carex rosii*), elk sedge(*Carex geyeri*), leafy aster (*Aster foliaceus*), and regenerating lodgepole pine (Despain 1990). Wet meadows which occur in the unforested areas along the rivers are characterized by standing water or saturated soils and grasses, sedges (*Carex* spp.), and marsh reedgrass (*Calamagrostis* spp.; Aune 1981). Drier meadow areas are dominated by grasses (*Festuca idahoensis*, *Poa* spp.), and sagebrush (*Artemesia* spp.). The study area contains four major geothermal basins, Norris, Lower, Midway, and Upper Geyser Basins, and many smaller geothermal features in which snow accumulation is retarded or prevented. Thermal effluence from the these

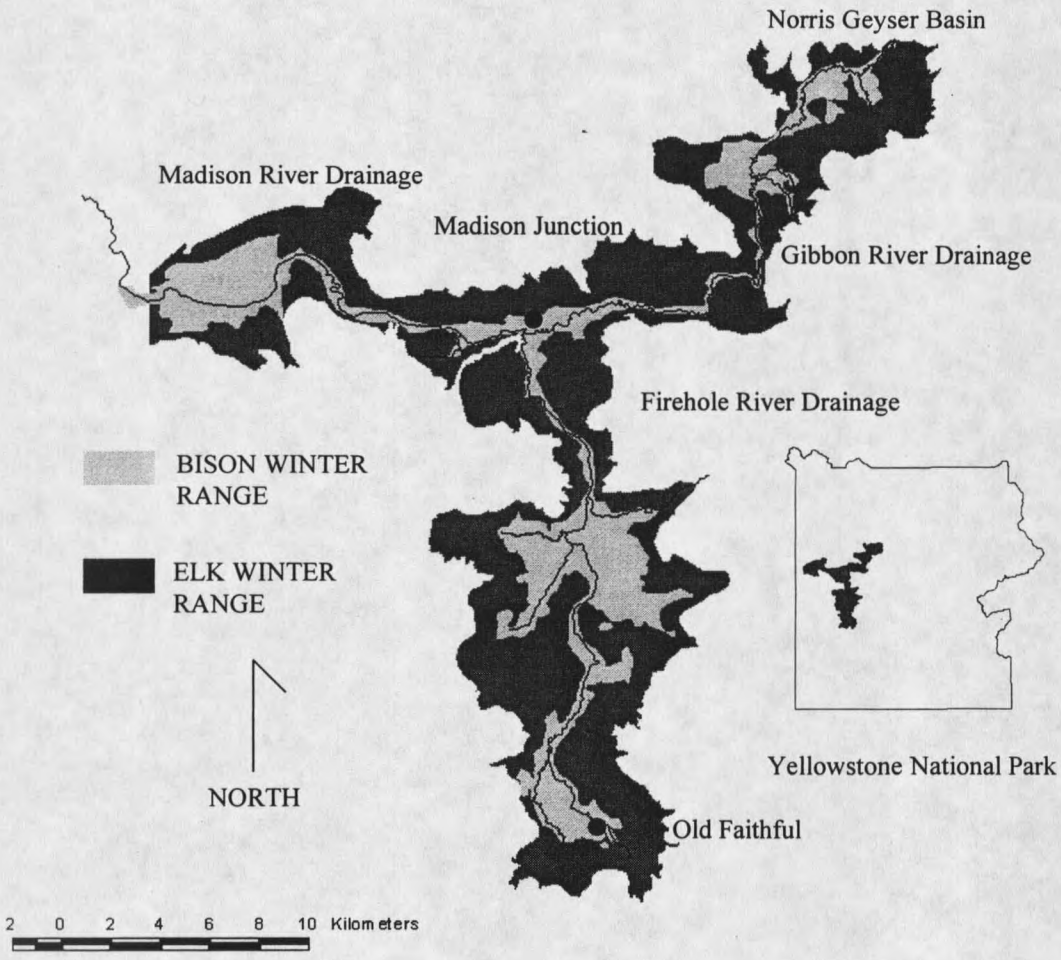


Figure 1. The extent of the bison and elk winter ranges in the Madison-Firehole drainages of YNP. The boundary of the elk range (light area) was verified using elk telemetry locations collected between December-May, 1991-1998. The boundary of the bison range (dark area)was verified using bison group locations collected during ground censuses during January 1997-May 1997 and December 1997-May 1998.

areas keeps the Madison, Gibbon, and Firehole Rivers free-flowing throughout the winter.

Winter conditions in the Madison-Firehole are typically severe. Snow pack begins accumulating in October and averaged 117 days >40 cm and 36 days >70 cm at the Madison Junction ranger station (elevation 2,075m) from 1992-1998. Average start of melt at the Madison Junction ranger station between 1992-1998 was early March. At higher elevations in the study area snow continues to accumulate even after the start of melt in the valleys. The average start of melt at the National Resources Conservation Service Madison Plateau SNOTEL site located at 2,362m was early-mid April from 1992-1998.

METHODS

In order to monitor the numbers and distribution of bison occupying the study area, I delineated the external boundaries of the Madison-Firehole bison winter range based on field observations conducted in the study area from 1991-1996 during an intensive elk research project. I monitored numbers and distribution of bison through tri-monthly ground surveys of the bison winter range during the winters of 1996-97 and 1997-98. I mapped 6 survey routes that covered the 7211 ha area defined as bison winter range: 1 in the Madison River drainage, 2 in the Gibbon River drainage, and 3 in the Firehole River drainage. The field team covered the survey routes over 2-3 days (as weather permitted) at approximately 10 day intervals between December and May. I divided the study area into 72 survey units ranging from 6-716 ha. The location of each bison group seen in each unit was recorded on a laminated USGS 7.5 minute quadrangle map. We recorded the composition of each group (adults and calves) and approximate snow depth at the center of the group. The habitat occupied by each group was recorded as unburned forest, burned forest, wet or dry meadow, geothermal, or other. When groups occupied two habitat categories we recorded the habitat category into which the majority of individuals in the group fell. Any bison observed outside the delineated winter range boundary were also recorded. The locations of all groups observed during

all winter surveys, as well as opportunistic observations of bison from ongoing elk and bison studies in the Madison-Firehole, were used to verify the winter range boundaries.

The external boundaries of the Madison-Firehole elk winter range were delimited based on a study by Craighead et al. (1973), ground based telemetry, and aerial surveys conducted in conjunction with long term elk research in the study area (Eberhardt et al. 1998). To verify the extent of the winter range and determine changes in elk distribution a total of 45 adult cow elk on the Madison-Firehole winter range were fitted with radio collars between 1991-98. Animals were immobilized using a combination of Xylazine and Ketamine administered using a 6cc dart and a modified .22 caliber dart rifle. I drew 30 mL of blood by venipuncture of either the jugular vein or carotid artery and removed one canine tooth for aging via cementum lines. Blood samples were centrifuged to separate serum and whole blood and stored at -15 °C for later serologic testing. Animals were reversed using either Tolazine or Yohimbine administered intravenously.

I monitored the distribution of elk on the winter range by relocating 31 radiocollared adult cow elk between December 1996-May 1997 and 28 between December 1997- May 1998. I located animals using telemetry techniques and only recorded locations in which the study animal and collar could be visually identified. The order and frequency in which animals were sampled was determined using a restricted randomization design (Garrott et al. 1996). The study area was divided into 6 regions. Each of three team members was randomly assigned one region each morning and afternoon and elk in those areas were relocated in a randomly determined order. Once all 6 regions had been sampled, the regions were again assigned random order and the

animals resampled. Opportunistic sightings of collared animals were not used in analysis and groups with multiple collared animals were considered as one location. In addition to the elk telemetry locations collected as a part of this study, five years of telemetry locations collected between the winter of 1991-94 and 1995-96 in conjunction with a long term research program were available and used in the analysis. The sampling methodology used in these years was consistent with that used in 1996-98. I verified the external boundary of the Madison-Firehole elk winter range by plotting the telemetry locations collected between 1991-98 and points from aerial surveys conducted between 1991-97 (Eberhardt et al. 1998).

I used the vector-based computer geographic information system (GIS) ArcView and the raster-based GIS package IDRISI to characterize the topographic and habitat attributes of the bison and elk winter ranges. Slope, aspect, and elevation attributes were derived from a USGS digital elevation model (DEM). Habitat attributes were determined using a digital habitat map derived from Despain (1990). In order to assess the level of interaction between bison and elk I monitored association between the two species at two scales. To determine the level of association at a broad scale I used an index of range overlap based on the proportion of elk telemetry locations that fell within the area delimited as bison winter range. I used GIS package ArcView to determine whether each elk telemetry location fell within the boundary of the bison winter range. The proportion of elk telemetry locations that overlapped the bison winter range was considered the proportion range overlap for each month.

I also monitored levels of association between elk and bison at a finer spatial and temporal scale. When radiocollared elk were located I noted the distance between the instrumented animal and the nearest bison. Instrumented elk that were within 100m of the nearest bison were considered "associated" with bison. Data on association with bison were collected between December-May, 1996-1998, and December-April, 1991-1994 and 1995-1996. To explore possible mechanisms that drive changes in levels of association I collected data on snow condition and habitat use for each telemetry location. When an instrumented elk was located I noted the approximate snow depth where the elk was standing. I recorded the habitat occupied by the instrumented elk. Habitat classifications were the same as those used for bison. In cases where the group associated with the instrumented elk was in a different habitat type or in multiple habitat types, only the habitat type used by the instrumented animal was recorded.

Snow is a major impediment to animal travel and foraging (Formozov 1964). To assess the influence of snow and snow avoidance on range overlap and association I collected data on snow pack density at the Madison Plateau SNOTEL site and snow depth at the Madison Junction ranger station. The National Resources Conservation Service (NRCS) automated SNOTEL site is located on the Madison Plateau along the western boundary of the park at an elevation of 2362m. The site provides daily measurements of the centimeters of water in the in the snow pack (snow water equivalent, SWE) which were downloaded from an NRCS mainframe in Portland, OR. The mean of daily snow water equivalent (Madison Plateau SWE) measurements for each month was used as an index of overall snow pack density and mid elevation snow pack conditions. Snow water

equivalent provides a better measure of winter severity with respect to ungulates than does snow depth because it accounts for the density of the snow pack that animals must break through to travel or forage (Formozov 1964; Farnes 1996). The SNOTEL site, however, does not capture the dynamics of snow pack in the low elevation valley bottoms where a large proportion of the wintering ungulates are found during the late winter and spring. To account for snow conditions in these areas I used an index based on snow depth at the Madison Junction ranger station. The Madison Junction Ranger station is located at the center of the study area at an elevation of 2075m (Figure 1). The mean of daily snow depth measurements at the Madison Junction ranger station for each month (Madison Junction snow depth) was used as a second index of snow conditions. Daily snow depth and new precipitation were recorded by rangers at the Madison Junction, West Yellowstone, and Old Faithful ranger stations. Snow depths for unrecorded days at the Madison Junction station were interpolated based on accumulation or melt at the West Yellowstone and Old Faithful ranger stations. As the station is located in the Madison valley it better reflects spring snow conditions and melt in areas in which elk and bison forage, however, as the index does not incorporate snow density, it does not fully capture the energetic costs of ungulate travel and foraging.

I used linear regression to model the relationship between snow pack and overall range overlap and the degree of fine scale association between elk and bison. These data are a time series and potential autocorrelation could lead to dubious levels of significance and invalidation of the assumptions of standard linear regression (Neter et al. 1996). I assumed independence among years and used a heterogeneous, first order autoregression

model to account for non-independence of observations within years and heterogeneity in variance among months (SAS Institute Inc. 1997). Competing models were selected using Akaike's Information Criteria (AIC; Akaike 1974).

The standard R^2 statistic is based on the assumption the error variance is a constant and that observations are not correlated. Neither of these conditions is satisfied in the autoregressive model I used. The R^2 statistic I present is defined as the proportion of the variance explained by the predictors (SS_{model}/SS_{total}). The total corrected sum of squares and the corrected sum of squares explained by the model were computed using a generalized least squares equation (Sen and Srivastava 1990). The covariance structure used in the sum of squares calculation was the heterogeneous, first order autocorrelation matrix estimated using the procedure PROC MIXED in SAS. Additional statistical analyses were conducted using parametric techniques (ANOVA, correlation analysis) and the computer package SAS.

I used the prevalence of antibodies to *B. abortus* as an index of exposure of elk to the bacteria. Serum samples taken during the instrumentation of adult cow elk between 1996-1998 were analyzed using the standard plate agglutination (SPT), brucella antigen rapid card (BBA), rivanol precipitation (Riv)(USDAa, USDAb), compliment fixation (CFT)(Jones et al. 1963), and buffered acidified plate antigen (BAPA) tests. All serum tests were run at the Veterinary Diagnostic Laboratory in Bozeman, Montana. Criteria for seropositive classification were based on Morton et al. (1973). A positive reaction at any level on two or more tests was considered positive. If only one test was positive a level

of + 1:50 on the SPT, a positive on the BBA, 1:25 Riv, or a 4+ at 1:40 on the CFT was considered positive. No suspect classification was used.

To compare the relationship between the level of disease exposure in elk to contact with bison and ungulate management practices I collected data on sero-prevalence in elk from state agencies in Montana, Wyoming, and Idaho. I collected data on elk populations both in and out of the GYA that did and did not have contact with bison, and that did and did not use winter feedgrounds. Only data from populations in which >30 animals of all sex and age classes had been sampled between 1990-1998 and were tested in accordance with the Morton et al. (1981) protocol were selected for comparison. For comparison of sero-prevalence rates I used 95% Clopper-Peterson confidence intervals. The intervals are based on the Beta distribution and, unlike confidence intervals based on the normal distribution, the lower bounds are constrained to positive values even with low proportions (Casella and Berger 1990).

RESULTS

I verified the boundaries of the bison winter range with group locations from 13 bison ground surveys conducted between 2 January 1997-16 May 1997 and 17 surveys conducted between 6 December 1997-25 May 1998 (Figure 1). A total of 2,890 of 2,961 (98%) group locations recorded were within the area delimited as bison winter range. Small groups, usually lone bulls, were rarely observed outside the winter range on the periphery of the Norris Geyser Basin, Upper Geyser Basin, and in the Firehole Lake area. Bison used areas of the Mary Mountain trail between the Hayden Valley and Firehole drainage, and the Cougar Creek area north of the Madison River. Bison use of these areas is the subject of an ongoing research project, and as these areas have not been used by radiocollared elk between 1991-1998, I did not specifically address them. The elk winter range was verified using 4,526 elk telemetry locations collected between December-April, 1991-1994 and December-May, 1996-98. During that time radiocollared elk were recorded outside the area delimited as elk winter range only 29 times, or <0.5% of all observations.

The bison winter range was confined primarily to the lower elevation, flat meadow communities in the study area (Table 1). The elk winter range covered a

Table 1. Areas (ha) of habitat types and topographic attributes for the areas delimited as elk and bison winter ranges in the Madison-Firehole region of YNP. Percentages reported are percent composition of the respective species' winter range. Areas for habitat types were determined from Despain (1990) and elevation and slope from a USGS DEM using GIS.

	Elk Winter Range		Bison Winter Range	
Attribute	Ha	%	Ha	%
Habitat				
Non-Forest	5120	19	3603	50
Unburned Forest	7895	29	1483	21
Burned Forest	13803	51	2124	29
Elevation				
2000-2099 m	3335	12	1876	26
2100-2199 m	4975	19	1515	21
2200-2299 m	9959	37	3425	48
2300-2399 m	7282	27	395	5
> 2400 m	1299	5	0	0
Slope				
0-5	12100	45	5049	70
5-25	10498	39	1896	26
25-45	2486	10	191	3
> 45	1766	7	75	1
Totals	26850		7211	

much broader range of elevations and slopes and was primarily comprised of burned forest habitat. The Madison-Firehole bison winter range overlapped 7,131 ha of the elk winter range. This area comprised 99% of the bison winter range and 27% of the elk winter range. The bison range is almost entirely contained within the valley bottoms of the Madison-Firehole elk winter range. Ninety-four percent of the overlapped area is between 2000-2075m and 2150-2255m, the valley elevations of the Madison River and upper Gibbon and Firehole Rivers respectively. Of the overlapped area, 4,984 ha (70%) had a slope of between 0-5 degrees. The overlapped area was dominated by non-forested habitat (3,587 ha; 50%). The bison range overlapped 70% of the non- forested (meadow and geothermal) habitat in the elk range.

The number of bison counted in the study area varied between 286 and 1,102 over the winters of 1996-97 and 1997-98. While total numbers remained relatively constant in the winter of 1996-97, the total numbers began low in December 1997 and increased to levels comparable to 1996-97 by March (≈800 animals; Figure 2) as bison moved onto the Madison-Firehole winter range from the Hayden Valley (Bjornlie and Garrott unpublished data). The number of bison counted during surveys was positively correlated to Madison Plateau SWE ($r=0.92$) and Madison Junction snow depth ($r=0.53$) on the first day of the survey. The relationship between bison numbers and Madison Plateau SWE was curvilinear and appeared to reach an asymptote of approximately 900 animals on the study area.

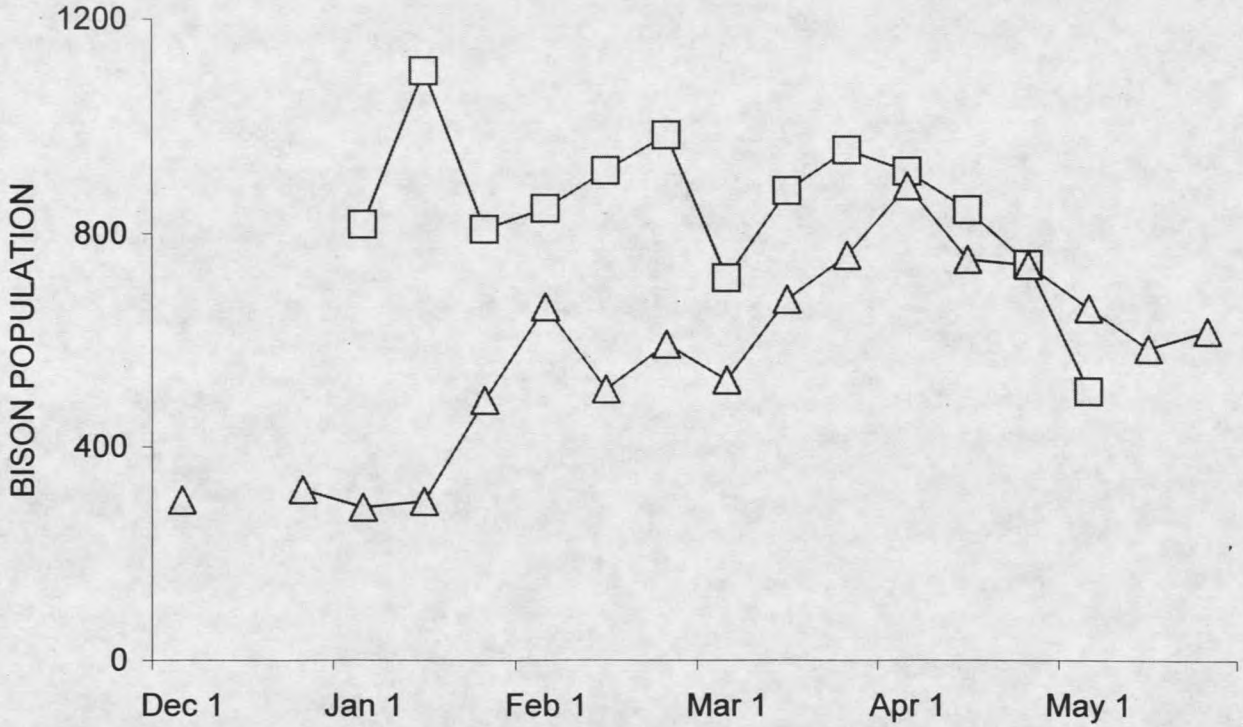


Figure 2. Total bison counted during tri-monthly ground censuses of the Madison-Firehole study area, YNP. The dark line and open squares represent totals for censuses conducted between 2 January 1997 and 16 May 1997. The light line and open triangles represent totals for censuses conducted between 5 December 1997 and 26 May 1998.

Table 2. Mean number of bison counted in the Madison, Gibbon, and Firehole River drainages during ground censuses conducted during the winters of 1996-97 and 1997-98. Three total ground censuses were conducted each month. Only two surveys were conducted in December 1997.

	Madison		Gibbon		Firehole	
Month	1996-97	1997-98	1996-97	1997-98	1996-97	1997-98
December	--	44	--	14	--	251
January	159	80	104	15	646	261
February	78	99	115	26	723	462
March	59	98	87	21	636	528
April	164	145	64	17	251	631
May	--	203	--	17	--	399

Bison were primarily localized in meadow communities. Greater than 60% of bison groups and >70% of individuals were observed in meadow habitat during ground surveys conducted during the winters of 1996-1997 and 1997-1998. Thermal areas were used little (0-7% of groups) in the early winter and spring. Use of thermal habitat increased in January- March (12-14% of groups) of both years and reached a maximum of 30% of observed bison groups in February 1998. Bison numbers in the Firehole River drainage were consistently the highest in all surveys (Table 2). Numbers in the Gibbon River drainage declined throughout the winter of 1996-97 and there were <30 bison during the winter of 1997-8. Utilization of the Madison River drainage was low (<100 animals) during February and March 1997 and from December to March in 1998, but increased as numbers in the Firehole began to decline in April. In both years bison numbers remained high on the Madison-Firehole winter range until May when snow melt began at higher elevations. An average of 654 bison were counted on the winter range during the 8 surveys conducted in 1997 and 1998 between 15 April and 31 May, the peak bison calving period (Meagher 1973).

Of 4,526 independent elk locations collected between December- April, 1991-94 and December - May, 1996-98, 3,132 (69%) fell within the area delimited as bison winter range. The lower bound of a 95% confidence interval on the percentage of points that overlapped the bison winter range (68%) was greater than the percentage of bison winter range that overlapped the elk winter range (27%), suggesting a preference by elk for the overlapped area. The proportion of elk telemetry locations that overlapped the bison range increased from December (mean=0.53, N=5 years) to May (mean=0.76, N=2 years). The difference in the means was moderately significant (ANOVA; $P \leq 0.09$) when autocorrelation (0.55) and heterogeneity of variance were accounted for in the model. Overlap followed a curvilinear trend with increasing snow pack and was positively correlated (r=0.75) to the natural log of mean daily Madison Plateau SWE. Overlap was only weakly correlated to Madison Junction snow depth (r=0.34) and not correlated (r=0.005) to the natural log of Madison Junction snow depth.

Unlike bison, the habitat used by elk varied over the course of the winter. Use of burned forest, which was highest in December, April, and May, declined in January and February during 1997 and 1998. The decrease in burned forest use coincided with an increase in use of unburned forest in both years. Elk were found in wet meadow habitat only 14 and 1% of the time in December of 1996 and 1997 respectively. However, use of these areas increased, and 27% of elk telemetry locations were found in wet meadow habitat between February and May in 1997 and 1998. Use of wet meadow habitat did not change following snow melt in March and April. Elk tended to use thermal habitat more in early winter months (December-February) than late winter and spring (March-May).

Table 3. The percent of monthly elk telemetry locations collected on the Madison-Firehole winter range, YNP, in which collared elk were ≤100m from the nearest bison. Mean and standard deviation (S) are presented for each month.

Month	1991-92	1992-93	1993-94	1995-96	1996-97	1997-98	Mean	S
December		8.06	6.58	9.57	12.16	2.47	7.77	3.61
January	13.51	11.56	4.03	11.81	29.82	13.67	14.18	9.49
February	18.48	12.78	6.63	21.80	40.26	20.41	20.38	12.6
March	8.94	16.33	13.65	22.45	34.22	18.47	21.02	8.05
April	14.81	12.98	15.22	20.00	30.32	20.42	19.79	6.68
May					22.03	15.85		

A total of 778 of 4,415 (18%) of independent elk telemetry locations were within 100m of the nearest bison (data were not recorded for 111 locations). In all years there was an increasing trend in association between elk and bison from December to May (Table 3). While elk utilized wet meadow habitat in only 23% of telemetry locations in the winters of 1996-97 and 1997-98, 48% of occasions in which the radiocollared elk was ≤100m of a bison were in wet meadow habitat. Association between elk and bison occurred in thermal habitat between January-March 1997 and in February and April 1998. These periods, except April 1998, corresponded to increased use of thermal areas by bison and elk. In all other months there were no associated locations in thermal habitat.

Table 4. Results from models of association between elk and bison on the Madison-Firehole winter range, YNP from 1991-94 and 1996-98. I used a first order autoregressive model to account for time series effects and assumed independence among years and heterogeneous variance within years. AIC is computed from Akaike (1974) and models with lower AIC are deemed better. R^2 was calculated using a generalized least squares equation. All factors are significant at $P \leq 0.05$.

Model	Factors	Autocorrelation	AIC	R^2
1	Madison Plateau SWE	0.50	-91.4	0.77
2	Madison Junction Snow Depth	0.77	-103.8	0.59
3	Range Overlap	0.88	-100.3	0.47
4	Madison Plateau SWE + Madison Junction Snow Depth	0.34	-93.4	0.81
5	Madison Plateau SWE + Range Overlap	0.56	-92.2	0.81

Madison Plateau SWE was selected as the most parsimonious model to predict degree of association between elk and bison (Table 4). The relationship was positive and Madison Plateau SWE explained 77% of the total variation in monthly association. Madison Junction snow depth and range overlap were tested as predictors of association but had little predictive power (Figure 3). Including Madison Junction snow depth or range overlap in a model containing Madison Plateau SWE resulted in small gains in explanatory power (partial $R^2 = 0.04$ for both) and larger AIC values. The number of bison wintering on the study area was positively correlated with association ($r=0.92$; Figure 4) but could not be included as a predictor variable as data were only collected for two years.

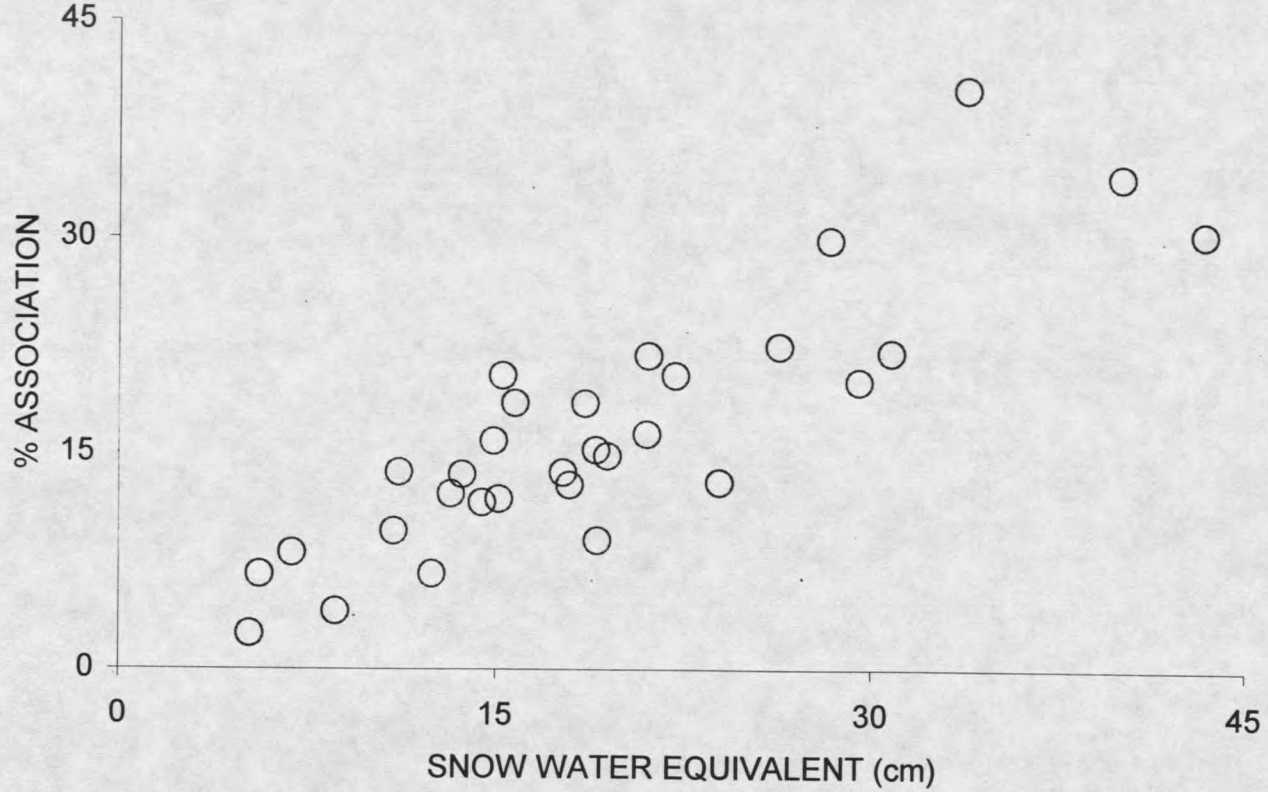


Figure 3. The relationship between the percent of monthly elk telemetry locations in which the collared animal was less than 100m from the nearest bison (association) and the average daily measurement of centimeters of water in the snow pack (snow water equivalent) at the Madison Plateau automated SNOTEL site (elev. 2362) for each month between December and May 1992-1998

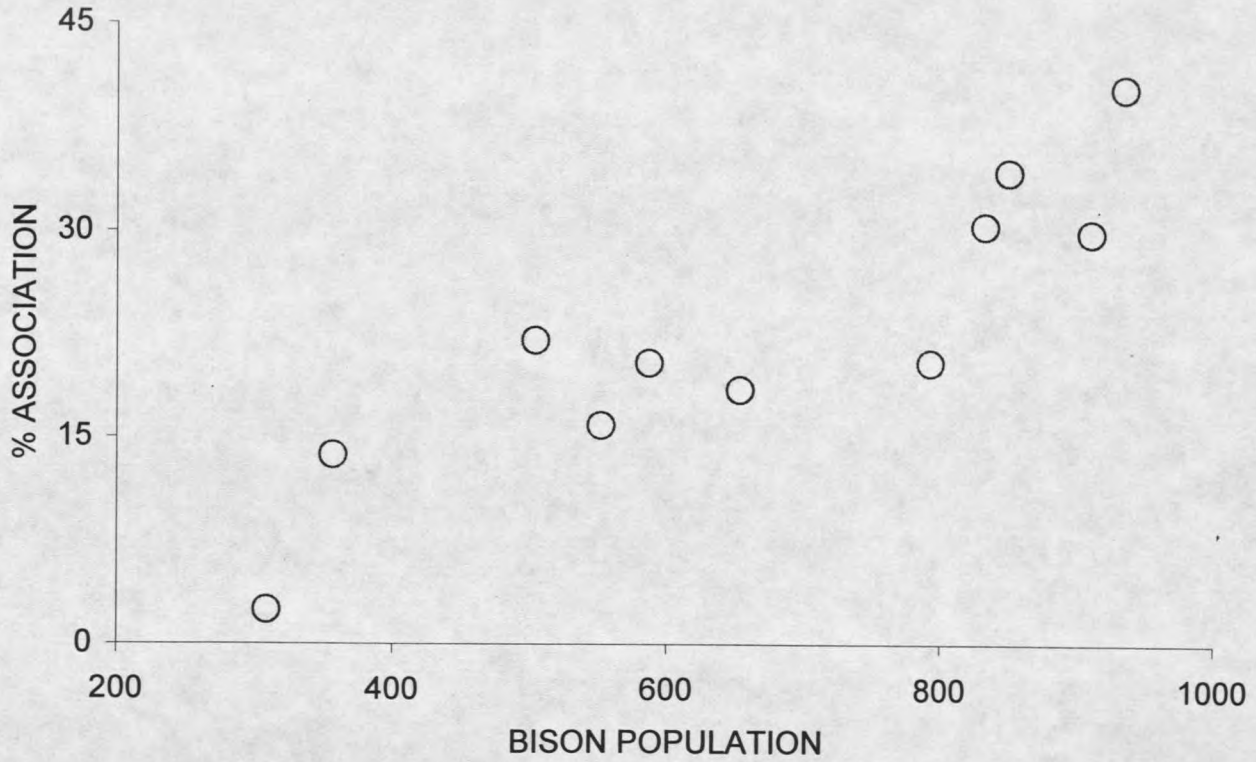


Figure 4. The relationship between the percent of monthly elk telemetry locations in which the collared animal was less than 100m from the nearest bison (association) and the mean monthly bison census total from tri-monthly ground censuses conducted on the Madison Firehole winter range, YNP, between January-May 1997, and December 1997-May 1998. The Pearson product moment correlation is 0.92.

I collected serum samples from a total of 73 adult cow elk ranging in age from 1-17 years between March 1996 and December 1998. Two animals tested positive for antibodies for *B. abortus*. The two animals, age 9 and 10 years, were positive on the BAPA, card, SPT, and CFT tests. The 9 year old animal was also positive on the rivanol precipitation test. Both animals are known to have been in the study area for 4 years prior to testing positive for antibodies for *B. abortus*. A 95% Clopper-Pearson confidence interval estimates the prevalence of exposure to *B. abortus* in the Madison-Firehole elk to be between 0.3-9.5%.

I collected data on prevalence of *B. abortus* antibodies from 18 additional elk populations in Montana, Wyoming, and Idaho (Table 5). Point estimates of prevalence ranged from 0-39%. The prevalence rate in the Madison-Firehole was significantly lower than 5 of the 18 elk populations ($P<0.01$; Fisher exact test). Three of the five populations were from winter feed grounds in Wyoming, and one from a winter feed ground in Idaho, all of which had no contact with bison. The fifth population was from the National Elk Refuge (NER) in Jackson, Wyoming. Elk in the NER utilize winter feed grounds and are in contact with a bison herd that is infected by brucellosis (36% culture positive; Williams et al. 1993). Of the 15 elk populations in which the interval estimate of prevalence overlapped the estimate for the Madison-Firehole, 2 were from winter feed grounds in Wyoming and 11 were from populations in Wyoming and Idaho which were not supplementally fed in the winter and had no contact with bison. Two populations from southwest Montana were not supplementally fed but were assumed to have some contact with Yellowstone bison.

Table 5. Sero-prevalence rates for antibodies to *B. abortus* in 21 elk populations (males and females) in Wyoming, Montana, and Idaho. Clopper-Pearson 95% confidence intervals (Casella and Berger 1990) are presented in parentheses. Populations are characterized by contact with bison and use of winter feedgrounds. All populations are from the Greater Yellowstone area except Ceour D'Alene, ID, and Sierra Madre and Snowy Range, WY. Prevalence rates with an asterix are significantly greater than the Madison-Firehole, YNP ($P<0.01$) based on the Fisher exact test.

State	Location	Year of Study	Citation	Contact with Bison	Use of Feedground	Number Sampled	Seroprevalence p (95% CI)
Wyoming	Madison-Firehole	1996-1998	This study	Y	N	73[1]	0.03 (0.003,0.10)
Montana	SW Montana	1997	Rhyan et al 1997	Y	N	224	0.00
	Gardiner	1997		Possible	N	721	0.01 (0.01,0.02)
	Upper Madison	1997		N	N	389	0.01 (0.00,0.02)
Wyoming	National Elk Refuge	1990,1993, 1995-1997	Bruce Smith pers. comm.	Y	Y	251	0.25 (0.20,0.31)*[2]
Wyoming	Alkali	1990, 1992	Scott Smith pers.	N	Y	230	0.26 (0.20,0.32)*
	Fall Creek	1994-1995	comm.	N	Y	40	0.43 (0.27,0.59)*
	Muddy Creek	1990-1997		N	Y	142	0.39 (0.31,0.48)*
	North Piney	1990-1991		N	Y	82	0.11 (0.05,0.20)
	Upper Green River	1991, 1993		N	Y	52	0.12 (0.04,0.23)
	Clark's Fork	1990-1996		N	N	506	0.02 (0.01,0.03)
	Cody	1990-1996		N	N	674	0.02 (0.01,0.03)
	Gooseberry	1990-1996		N	N	291	0.03 (0.02,0.06)
	South Wind River	1991-1996		N	N	438	0.01 (0.00,0.03)
	West Green River	1991-1996		N	N	114	0.01 (0.00,0.05)
	Wiggin's Fork	1991-1996		N	N	850	0.02 (0.01,0.04)
	Sierra Madre	1990, 1994		N	N	420	0.00 (0.00,0.02)
	Snowy Range	1994		N	N	104	0.00

Table 5. continued.

State	Location	Year of Study	Citation	Contact with Bison	Use of Feedground	Number Sampled	Seroprevalence p (95% CI)
Idaho	Rainey Creek	1998	Dave Hunter pers.	N	Y	33	0.30 (0.16,0.49)*
	Idaho Falls	1992-1993	comm.	N	N	127	0.00
	Coeur d'Alene	1990		N	N	57	0.00

1. Only adult females were sampled in the Madison-Firehole.
2. The prevalence rate for the National Elk Refuge was calculated as the total number of sero-positive animals divided by the total number of animals sampled during the years of 1990, 1993, and 1995-97. The prevalence rate and sample size for individual years (Year, p, N) was: (1990, 0.15, 100), (1993, 0.32, 41), (1995, 0.41, 17), (1996, 0.35, 62), (1997, 0.22, 31).

DISCUSSION

Bison are a specialist herbivore restricted primarily to monocot communities in relatively flat terrain (Meagher 1973, McCullough 1980, Singer and Norland 1994). Elk rely heavily on monocots for much of the year but have the ability to utilize a broad range of browse and varied terrain (McCullough 1980; Singer and Norland 1994). The restricted niche of bison accounts for the fact that 50% of the winter range shared by both bison and elk is non-forested habitat and 70% is on flat terrain. The shared winter range falls primarily in the lower elevations (<7,400 ft) and is concentrated around the three major rivers. Lower elevations typically receive less snow than do higher elevations and provide a refuge from deep snows (Gilbert et al. 1970; Leegee and Hickey 1977). The shared winter range also contains all the major wet meadow communities and the four major geothermal basins (Norris, Lower, Midway, and Upper Geyser Basins) in the elk winter range. The standing water in wet meadow communities slows the accumulation of snow and often results in a less dense snow pack (Van Camp 1978) and the geothermal basins provide large areas of snow free ground throughout the winter (Despain 1990). Thus the shared winter range, while only 27% of the total elk winter range, is primarily comprised of habitat in which the relative severity of the winter is reduced.

Snow is a major impediment to ungulate foraging and travel and animals tend to gravitate to areas of reduced snow pack to minimize energetic costs (Formozov 1964; Gilbert et al. 1970; Van Camp 1978; Sweeny and Sweeny 1984; Farnes 1996). The variation in snow pack in the Madison-Firehole is pronounced due to the wide elevation range from the Madison Plateau to the river valleys and the influence of wet sedge meadows and geothermal activity that retard snow accumulation. The bison numbers in the Madison-Firehole tended to increase with increasing snow pack. While bison are capable of foraging in snow depths of 75-85 cm, foraging in snow exacts a major energetic cost and bison tend to select feeding sites with shallower snow depths and or lower snow density (Van Camp 1978). As snow accumulates in the Hayden Valley, a major bison summer range (Meagher 1973), bison tend to move to the lower elevation Madison-Firehole where snow accumulation is reduced (Meagher 1993, Aune 1981). Bison numbers did not show any temporal trend in the winter of 1996-97, however the snow pack reached record levels early that year and prevented bison from foraging in the higher elevation sites.

Elk tended to spend more time on the lower elevation bison winter range as snow pack increased. The relationship was curvilinear suggesting that snow strongly influenced the movement of elk onto the bison winter range at low levels, but beyond a critical level, when approximately 80% of elk telemetry locations overlapped the bison winter range, additional increases in snow pack had only a moderate effect. Distributional shifts along an elevational gradient to avoid snow have been documented

for elk on winter range in Idaho (Leegee and Hickey 1977) and mule deer in Colorado (Gilbert et al. 1970).

In both 1997 and 1998 bison remained on the Madison-Firehole winter range and elk range overlap was highest during the major pulse of bison calving (15 April - 31 May). *B. abortus* is shed along with birth fluids from infected cow bison (Davis et al. 1990). The high numbers of elk and bison present in the Madison-Firehole during the calving period and 50% sero-prevalence in adult cow bison (Peter Gogan pers. comm.) suggests high potential for the release of bacteria into the environment.

Little is known about the survival and infectivity of *B. abortus* under natural conditions outside the host. It has been suggested that the bacteria may survive outside the host for weeks, but as the minimum infectious dose needed to initiate infection is not known, it is uncertain whether bacterial titers in tissues and contaminated forage remain infectious for that time (Cheville et al. 1998). The rate of transmission depends on susceptible animals contacting contaminated areas during the period of infectiousness which would necessitate close spatial and temporal association. Telfer and Cairns (1979) reported that only 1% of elk were within 1.13 km of bison during a mild winter and 18% during a severe winter in Elk Island National Park, Alberta. The levels of association in the Madison-Firehole were much higher, with an average of 17.6% of all elk telemetry locations ≤100m from the nearest bison during the winters of 1991-98. Association between elk and bison ranged between 12.9-30.3% of elk telemetry locations during April-May, the late gestation and calving period for bison, in 1991-1998.

Given the severe winters in the Madison-Firehole, snow avoidance by both elk and bison decreases the extent of available habitat and increases the potential for contact between the two species. The positive correlation between snow pack and association between elk and bison supports the prediction that snow conditions restrict available foraging area and result in increased association of bison and elk. Greater densities of animals increase the chance of contact between individuals (Anderson and May 1991). As snow pack increases, so does the number of bison wintering in the study area and the level of range overlap between bison and elk. Both factors serve to increase the density of animals and present a biological mechanism by which snow pack could lead to increased association. Despite low snow pack in the valley bottoms as a result of early melt in March and April, persistent snow pack in the higher elevations continues to restrict elk distribution and prevents bison from moving off the winter range. This is reflected in the stronger predictive power (AIC value) of high elevation snow pack (Madison Plateau SWE; elev. 2362m) compared to low elevation snow pack (Madison Junction snow depth; elev. 2075m) in a regression model to predict association.

Ungulates, especially pregnant females, are typically protein deprived following winter (Berger 1991; Robbins 1983). Berger and Cunningham (1994) found that bison, pronghorn antelope, bighorn sheep, and mule deer aggregated in the same areas to feed on protein rich, emergent vegetation in late winter and early spring. Both elk (Pils 1998) and bison (DelGuidice et al. 1994) in the Madison-Firehole undergo severe nutritional deprivation during the winter, and early green up due to snow melt in the valley bottoms may also act to keep elk and bison from dispersing.

Winter snow conditions result in high levels of range overlap and direct association between elk and bison. Large numbers of bison are present on the Madison-Firehole winter range during the third trimester of pregnancy, when brucellosis induced abortion occurs, and during the calving period when bacteria are shed along with birth fluids and tissues (Davis et al. 1990). Given this, it appears that the three components necessary for disease: (1) the disease agent, (2) susceptible hosts, and (3) an environment that supports both the agent and the host (Wobeser 1994); are present in the Madison-Firehole winter range. Despite these conditions, the level of exposure to *B. abortus* in the Madison elk herd, as indexed by prevalence of antibodies, is not significantly higher than that found in 11 elk populations in Montana, Wyoming, and Idaho that have no contact with bison, and 2 elk populations in Montana that have only rare contact with bison. The low sero-prevalence rate in the Madison elk herd suggests that risk of inter-specific transmission from bison to elk in the Madison-Firehole is negligible. Low incidence of inter- specific transmission may be a result of lower levels of active *B. abortus* infection in bison than is suggested by the sero-prevalence rate (Dobson and Meagher 1996), insufficient shedding of *B. abortus* by infected animals, a short interval of viability of *B. abortus* outside the host, niche separation between bison and elk at a scale less than the 100m studied that is sufficient to prevent exposure to an infective dose of *B. abortus*, or some combination of these. The high sero-prevalence rates found in elk associated with winter feed grounds and bison suggests that intra- specific mechanisms may be more important in the transmission of the disease (Cheville et al. 1998).

While the level of sero-prevalence in the elk of the Madison-Firehole and

Yellowstone's northern range is low, the source of infection is potentially important. Emigration of elk from infected southern herds associated with winter feed grounds and contact with infected Yellowstone bison have been proposed as potential sources of infection in the Yellowstone herds (Cheville et al. 1998). Interchange between herd units in the greater Yellowstone area does occur at low levels, including exchange between the National Elk Refuge and Yellowstone's northern range (Craighead et al. 1972). While it is possible that the presence of sero- positive elk in the northern range and Madison-Firehole could be accounted for by dispersal from infected herds, it cannot be confirmed without knowledge of the origins of the sero- positive animals (Cheville et al. 1998). However, both sero-positive cow elk in this study are known to have been in the Madison-Firehole for at least 4 years prior to testing positive.

A National Research Council study found that transmission from free-ranging bison to elk, while never specifically observed, does remain a possibility (Cheville et al. 1998). It is impossible to determine precisely whether the sero-prevalence rate observed in elk on the Madison-Firehole is attributable to inter- or intra- specific mechanisms. However, the finding that the sero-prevalence is not significantly different from that in herds that do not share range with bison supports the conclusion that the high association of elk and bison on the Madison-Firehole winter range does not result in increased risk of disease prevalence in elk.

REFERENCES CITED

Akaike, H. 1974. A new look at the statistical model identification. IEE Transaction on Automatic Control, AC-19. 716-723.

Anderson, R.M. and R.M. May. 1979. Population biology of infectious diseases: part I. Nature 280:361-367.

Aune, K.E. 1981. Impacts of winter recreationists on wildlife in a portion of Yellowstone National Park, Wyoming. M.Sc. Thesis. Montana State University, Bozeman, Montana, USA. 111pp.

Baskin, Y. 1998. Home on the range. Bioscience 48: 245-251.

Berger, J. 1991. Pregnancy, predation constraints, and habitat shifts: experimental and field evidence from wild bighorn sheep. Anim. Beh. 41:61-77.

Berger, J. and C. Cunningham. 1994. Bison: mating and conservation in small populations. Columbia University Press, New York, New York, USA. 330 pp.

Boyce, M.S. 1989. The Jackson elk herd: intensive wildlife management in North America. Cambridge University Press, New York, New York, USA. 306 pp.

Caro, T.M. and S.M. Durant. 1995. The importance of behavioral ecology for conservation biology: examples from Serengeti carnivores. Pages 451-472, in, A.R.E. Sinclair and P. Arcese eds, Serengeti II: Dynamics, management, and conservation of an ecosystem. The University of Chicago Press. Chicago, Illinois, USA.

Casella, G. and R.L. Berger. 1990. Statistical inference. Wadsworth, Inc., Belmont, California, USA. 650pp.

Cheville. N.F., D.R. McCullough and L.R. Paulson. 1998. Brucellosis in the Greater Yellowstone area. National Academy Press, Washington, D.C. USA. 186 pp.

Corner, A.H. and R.H. Connell. 1958. Brucellosis in bison, elk, and moose in Elk Island National Park, Alberta, Canada. Can. J. Comp. Med. 22:9-20.

Craighead, J.J., F.C. Craighead, R.L. Ruff, and B.W. O'Gara. 1973. Home ranges and activity patterns of non-migratory elk of the Madison drainage herd as determined by biotelemetry. Wildl. Monogr. No. 33.

Craighead, J.J., G.A. Atwell and B.W. O'Gara. 1972. Elk migration in and near Yellowstone National Park. Wildl. Monogr. No. 29.

Davis, D.S., J.W. Templeton, T.A. Ficht, J.D. Williams, J.D. Kopek, and L.G. Adams. 1990. Brucella abortus in captive bison. I. Serology, bacteriology, pathogenesis, and transmission to cattle. J. Wildl. Dis. 26:360-371.

DelGuidice, G.D., F.J. Singer, U.S. Seal, and G. Bowser. 1994. Physiological responses of Yellowstone bison to winter nutritional deprivation. J. Wildl. Manage. 58:24-34.

Despain, D. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart, Inc. Publishers, Boulder, Colorado, USA. 239 pp.

Despain, D. 1990. Cover types of Yellowstone National Park. Map. Roberts Rinehart, Inc Publishers. Boulder, Colorado, USA.

Dobson, A. 1995. The ecology and epidemiology of rinderpest virus in Serengeti and Ngorongoro Conservation Area. Pages 485-505, in, A.R.E. Sinclair and P. Arcese eds, Serengeti II: Dynamics, management, and conservation of an ecosystem. The University of Chicago Press. Chicago, Illinois, USA.

Dobson, A. and M. Meagher. 1996. The population dynamics of brucellosis in the Yellowstone National Park. Ecology 77:1026-1036.

Eberhardt L.L., R.A. Garrott, P.J. White, and P.J. Gogan. 1998. Alternative approaches to aerial censusing of elk. J. Wildl. Manage. 60:1046-1052.

Farnes. P.E. 1996. An index of winter severity for elk. Pages 303-306, in F.J. Singer, ed, Effects of grazing by wild ungulates in Yellowstone National Park. National Park Service, Denver, Colorado, USA. 375 pp.

Flagg,D.E. 1983. A case history of a brucellosis outbreak in a brucellosis free state which originated in bison. U.S. Animal Health Assoc. Proc. 87:171-172.

Formozov, A.N. 1964. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Boreal Institute for Northern Studies, Alberta, Canada. 143 pp.

Garrott, R.A., P.J. White, D.B. Vagnoni, and D.M. Heisey. 1996. Purine derivatives in snow-urine as a dietary index for free ranging elk. J. Wildl. Manage. 60:735-743.

Gilbert, P.F., O.C. Walmo and R.B. Gil. 1970. Effect of snow depth on mule deer in Middle Park, CO. J. Wildl. Manage. 34:15-23.

Gwynne, M.D. and R.H.V. Bell. 1968. Selection of grazing components by grazing ungulates in the Serengeti National Park. Nature 220:390-93.

Herriges, J.D., E.T. Thorne, and S.L. Anderson. 1992. Vaccination to control brucellosis in free-ranging elk on western Wyoming feedgrounds. Pages 107-112, in , R.D. Brown, ed, The biology of deer. Springer-Verlag, New York, New York, USA.

Jarman, P.J. 1972. Seasonal distribution of large mammal populations in the unflooded middle Zambezi Valley. J. Appl. Ecol. 9:277-293.

Jones, L.M., J.B. Hendricks, and D.T. Berman. 1963. The standardization and use of the compliment fixation test for the diagnosis of bovine brucellosis with review of literature. Am. J. Vet. Res. 24:1143-1151.

Kistner, T.P. 1982. Diseases and parasites. Pages 187-189 in J.W. Thomas and D.E. Toweill, eds. Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA. 698 pp.

Lamprey, H.F. 1963. Ecological separation of the large mammal species in the Tarangirre Game Reserve, Tanganyika. E. Afr. Wildl. J. 1:63-92.

Laughlin, R.W., W.L. Robinson and E.G. Bohen. 1989. Wildlife ecology and management. MacMillan Publishing, New York, New York, USA. 574 pp.

Leege, T.A. and W.O. Hickey. 1977. Elk-snow-habitat relationships in the Pete King drainage, Idaho. Wildlife Bulletin No. 6. Idaho Dept. of Fish and Game, Boise, Idaho, USA. 24pp.

Leuthold, W. 1978. Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. Oecologia 35:241-52.

McCorquodale, S.M. and R.F. DiGiacomo. 1985. The role of wild North American ungulates in the epidemiology of bovine brucellosis: a review. J. Wildl. Dis. 21:351-357.

McCullough, Y.B. 1980. Niche separation of seven North American ungulates on the National Bison Range, Montana. Ph. D. Dissertation. University of Michigan. Anne Arbor. 226pp.

Meagher, M. 1973. The bison of Yellowstone National Park. National Park Service Scientific Monograph Series No. 1. 161 pp.

Meagher, M. 1993. Winter recreation-induced changes in bison numbers and distribution in Yellowstone National Park. Unpublished Report. Yellowstone National Park Files. 48 pp.

Meagher, M. and M.E. Meyer. 1994. On the origin of brucellosis in bison of Yellowstone National Park: a review. Conservation Biol. 8:645:653.

Meyer, M.E. and M. Meagher. 1994. Brucellosis in free-ranging bison (Bison bison) in Yellowstone, Grand Teton, and Wood Buffalo National parks: a review. J. Wildl. Dis. 31:579-598.

Mohler, J.R. 1917. Abortion disease. Pages 105-106 in Annual reports of the Department of Agriculture. U.S. Government Printing Office, Washington, D.C., USA

Morton, J.K., E.T. Thorne and G.M. Thomas. 1981. Brucellosis in elk III. Serologic evaluation. J. Wildl. Dis. 17:23-31.

National Park Service, U.S. Department of Interior. 1998. Draft environmental impact statement for the interagency bison management plan for the state of Montana andYellowstone National Park. Denver, Colorado, USA. 395 pp.

Neter, J., M.H. Kutner, C.J. Nachtsheim, W. Wasserman. 1996. Applied linear statistical models. Richard D. Irwin Inc., Chicago, Illinois, USA. 1408 pp.

Pils, A.C. 1998. Sampling and analysis methods for snow-urine nutritional assays. M.Sc. Thesis. Montana State University, Bozeman, Montana, USA.

Putnam, R.J. 1994. Community biology. Chapman and Hall. London, England. 178 pp.

Ray, W.C. 1979. Brucellosis (due to *Brucella abortis* and *B. suis*). Pages 99-127 in J.H. Steele, ed. Bacterial, Reckettsial and Mycotic Diseases, Vol 1. CRC Press Inc., Boca Raton, Florida, USA.

Renoux, G. 1957. Brucellosis in wild animals and insects. Arch. Inst. Pasteur. 34:391-404.

Rhyan, J.C., K. Aune, and D.R. Ewalt. 1997. Survey of free-ranging elk from Wyoming and Montana for selected pathogens. J. Wildl. Dis. 33:290-298.

Rhyan, J.C., W.J. Quinn, L.S. Stackhouse. J.J. Henderson, D.R. Ewalt, J.B. Payeur, M. Johnson and M. Meagher. 1994. Aborion caused by Brucella abortus Biovar 1 in a free-ranging bison (Bison bison) from Yellowstone National Park. J. Wildl. Dis. 30:445-446.

Robbins, C.T. 1983. Wildlife feeding and nutrition. Academic Press, New York, New York. USA. 352 pp.

Rush, W.M. 1932. Bang's disease in Yellowstone National Park buffalo and elk herds. J. Mammal. 13:371-372.

SAS Institute Inc. 1997. SAS/STAT Software: changes and enhancements through release 6.12. SAS Institute Inc., Cary, North Carolina, USA. 1167pp.

Schwartz, C.C. and J.E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. J. Appl. Ecol. 18:343-353.

Sen, A. K.and Srivastava, M.S. 1990. Regression analysis: theory, methods, and applications. Springer-Verlag, New York, USA. 347 pp.

Singer, F.J. 1991. The ungulate prey base for wolves in Yellowstone National Park. Pages 323-348, in R.B. Keiter and M.S. Boyce, eds, The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale Univ. Press, New Haven, Connecticut, USA.

Singer, F.J. and J.E. Norland. 1994. Niche relationship within a guild at ungulate species in Yellowstone National Park, Wyoming, following release form artificial controls. Can. J. Zool. 72:1383-1394.

Smith, A.T., and F.S. Dobson. 1994. A technique for evaluation of spatial data using asymmetrical weighted overlap values. Anim. Behav. 48:1285-1292.

Sweeny, J.M. and J.R. Sweeny. 1984. Snow depths influencing winter movements of elk. J. Mammal. 65:524-526.

Telfer, E.S. and A. Cairns. 1979. Bison-wapiti interrelationships in Elk Island National Park, Alberta. Pages 114-121, in M.S. Boyce and L.D. Hayden-Wing, eds, North American elk: ecology, behavior, and management. University of Wyoming, Laramie, Wyoming, USA.

Thorne. E.T. 1982. Bacteria. Pages 54-63, in E.T. Thorne, N. Kingston, W.R. Jolley and R.C. Bergstrom, eds, Diseases of Wildlife in Wyoming. Wyoming Game and Fish Dept. Special Publications Section, Cheyenne, Wyoming, USA.

Thorne, E.T., M. Meagher and R. Hillman. 1991. Brucellosis in free ranging bison: three perspectives. Pages 275-287, in R.B. Keiter and M.S. Boyce, eds, The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale Univ. Press, New Haven, Connecticut, USA.

Thorne, E.T., J.K. Morton and G.M. Thomas. 1978a. Brucellosis in elk I. serologic and bacteriologic survey in Wyoming. J. Wildl. Dis. 14:74-81.

Thorne, E.T., J.K. Morton, F.M. Blunt and H.A. Dawson. 1978b. Brucellosis in elk II. Clinical effects and means of transmission as determined through artificial infections. J. Wildl. Dis. 14:280-291.

Tunnicliff, E.A. and H. March. 1935. Bang's disease in bison and elk in Yellowstone National Park and on the National Bison Range. J. Am. Vet. Med. Assoc. 86:745-752.

Van Camp, J. 1975. Snow conditions and the winter feeding behavior of *Bison bison*in Elk Island National Park. Canadian Wildlife Service Unpubl. Rep. No. CWS(WR)-55-75. 91pp.

Williams, E.S., E.T. Thorne, S.L. Anderson, and J.D. Herriges. 1993. Brucellosis in free-ranging bison (*Bison bison*) from Teton County, Wyoming. J. Wildl. Dis. 29:118-122.

Wobeser, G.A. 1994. Investigation and management of disease in wild animals. Plenum Press, New York, New York, USA. 265 pp.

Wydeven, A.P. and R.B. Dahlgren. 1985. Ungulate habitat interrelationships in Wind Cave National Park. J. Wildl. Manage. 49:805-813.

USDA. (not dated)a. Standard agglutination test procedures for the diagnosis of brucellosis. National Animal Disease Laboratory Diagnostics Reagents Manual 65D. ARS. ANH. National Animal Disease Laboratory, Ames, Iowa, USA.

USDA (not dated)b. Supplemental test procedures for the diagnosis of brucellosis. National Animal Disease Laboratory Diagnostics Reagents Manual 65E. ARS. ANH. National Animal Disease Laboratory, Ames, Iowa, USA.

APPENDIX

Application of the heterogeneous, first order autoregressive model in SAS.

SAS Code

```
proc mixed maxfunc=1000 maxiter=100 ic;
        class year month
        model Y = X1 X2 . . . Xn/ ddfm=sattterth p solution;
        repeated month / subject = year r=1,2,3,4,5,6 type = arh(1);
        lsmeans month;
```

Application in SAS

The PROC MIXED command in SAS allows the generation of mixed models that are not constrained by the assumption that the covariance structure of the residuals is $\sigma^2\mathbf{I}$ (assumption of constant error variance). PROC MIXED allows for the modeling of known covariance structures. The above code generates a regression model [arh(1)] that assumes constant variance structure among years and heterogeneity in variance and time series effects within years. The model assumes that the degree of correlation between classes (months) decreases as the time between classes increases. The covariance structure, **R,** for the model is :

$$\begin{array}{lllll}
\sigma_1^2 & \sigma_1\sigma_2\rho & \sigma_1\sigma_3\rho^2 & \sigma_1\sigma_4\rho^3 \ldots & \sigma_1\sigma_n\rho^{n-1} \\
\sigma_2\sigma_1\rho & \sigma_2^2 & \sigma_2\sigma_3\rho & \sigma_2\sigma_4\rho^2 \ldots & \sigma_2\sigma_n\rho^{n-2} \\
\sigma_3\sigma_1\rho^2 & \sigma_3\sigma_2\rho & \sigma_3^2 & \sigma_3\sigma_4\rho \ldots & \sigma_3\sigma_n\rho^{n-3} \\
\sigma_4\sigma_1\rho^3 & \sigma_4\sigma_2\rho^2 & \sigma_4\sigma_3\rho & \sigma_4^2 \ldots & \sigma_4\sigma_n\rho^{n-4} \\
\ldots & \ldots & \ldots & \ldots \ldots & \ldots \\
\sigma_n\sigma_1\rho^{n-1} & \sigma_2\sigma_n\rho^{n-2} & \sigma_3\sigma_n\rho^{n-3} & \sigma_4\sigma_n\rho^{n-4} \ldots & \sigma_n^2
\end{array}$$

Where : σ_n^2 is the variance for the n^{th} class (month in this case)
ρ is the correlation coefficient among classes (months)

The output generated by the above code includes (1) the covariance parameter estimates σ_n^2 and ρ, (2) information criteria for comparison against models with different covariance structures, and models with the same covariance structure but different fixed effects, (3) parameter estimates for the fixed effects and results of a Type III F test of H_o that $\beta_n = 0$, and (4) a table of predicted values and residuals.

The standard R^2 statistic is not applicable to mixed models because of the constraint that error variance is constant and observations are not correlated. However, an R^2 statistic, defined as the proportion of the variance explained by the predictors (SS_{model}/SS_{total}) can be constructed using a generalized least squares equation (Sen and Srivastava 1990). The equation can be used for any non- standard covariance structure.

Equation for the calculation of R^2

$$R^2 = \frac{SSmodel - SSmean}{SStotal - SSmean} = \frac{\ddot{Y}'\Sigma^{-1}\ddot{Y} - Y'\Sigma^{-1}1(1'\Sigma^{-1}1)^{-1}1'\Sigma^{-1}Y}{Y'\Sigma^{-1}Y - Y'\Sigma^{-1}1(1'\Sigma^{-1}1)^{-1}1'\Sigma^{-1}Y}$$

Where: $\ddot{\mathbf{Y}}$ = the vector of predicted Y values
$\mathbf{Y}$ = the vector of observed Y values
Σ = an nxn block diagonal matrix with structure:

$$\Sigma = \begin{matrix} \Sigma_1 & 0 & 0 & \dots & 0 \\ 0 & \Sigma_2 & 0 & \dots & 0 \\ 0 & 0 & \Sigma_3 & \dots & 0 \\ 0 & 0 & 0 & \dots & \Sigma_n \end{matrix}$$

where Σ_n = the covariance matrix, **R**, for class n.

MONTANA STATE UNIVERSITY - BOZEMAN
3 1762 10421274 9