2004

Landscape-scale factors affecting population dynamics of greater sage -grouse (Centrocercus urophasianus) in north-central Montana 2001--2004

Brendan James Moynahan
The University of Montana

Recommended Citation

Moynahan, Brendan James, "Landscape-scale factors affecting population dynamics of greater sage -grouse (Centrocercus urophasianus) in north-central Montana 2001--2004" (2004). *Graduate Student Theses, Dissertations, & Professional Papers*. 9526.
https://scholarworks.umt.edu/etd/9526

LANDSCAPE-SCALE FACTORS AFFECTING POPULATION DYNAMICS OF GREATER SAGE-GROUSE (*Centrocercus urophasianus*) IN NORTH-CENTRAL MONTANA, 2001-2004

by

Brendan James Moynahan

B.A. Bates College, 1994

M.S. The University of Montana, 1999

Presented in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

The University of Montana

December 2004

Approved by:

Jack Ward Thomas

Jack Ward Thomas, Committee Co-Chair

Mark Lindberg, Committee Co-Chair

Dean, Graduate School

1-19-05

Date

Moynahan, Brendan J. Ph.D., December 2004 Fish and Wildlife Biology

Landscape-Scale Factors Affecting Population Dynamics of Greater Sage-Grouse (*Centrocercus urophasianus*) in north-central Montana, 2001-2004

JWT

Committee Co-Chairs: Dr. Jack Ward Thomas and Dr. Mark S. Lindberg

Populations of Greater Sage-Grouse (*Centrocercus urophasianus*) have declined by 69-99%. Information on population dynamics of these birds at a landscape scale is essential to informed management. I radio-collared 243 female sage grouse, monitored 287 nests and 115 broods, and measured 426 vegetation plots at 4 sites during 2001-2003 in a 3,200 km^2 landscape in north-central Montana, USA. My objective was to examine the relationship between nest success, brood survival, and hen survival rates, habitat conditions, environmental variables, and hen characteristics. I used program MARK to model (1) daily survival rates of nests and broods and (2) seasonal and annual survival of hens.

Nest survival varied with year, grass canopy cover, daily precipitation with a 1-day lag effect, and nesting attempt. The best-approximating model of brood survival included effects of brood age and year, indicating substantial annual variation. Hen survival analyses indicated that survival varies by season within years and by year within seasons, that nesting hens have higher breeding-season survival than non-nesting hens, and that individuals at one site had lower hunting-season survival than hens at other sites. I observed considerable variation in hen survival. Low annual survival in 2003 is a result of the compounded effects of a West Nile virus outbreak in August of that year and a severe winter of 2003-2004.

My findings underscore the importance of large-scale approaches to conservation of sage grouse habitats and to maintenance and recovery of sage grouse populations. Management for hen survival must address hunting pressure and identification and conservation of important wintering areas. Maintaining quality habitat and a high proportion of adult hens will maximize potential for population growth when environmental conditions are favorable.

ACKNOWLEDGMENTS

This research was supported by the Boone and Crockett Wildlife Conservation Program at The University of Montana, National Fish and Wildlife Foundation, U.S. Fish and Wildlife Service, Montana Department of Fish, Wildlife, and Parks, Montana Cooperative Wildlife Research Unit, Bureau of Land Management, Budweiser Conservation Scholarship, Grizzly Riders Fellowship, and Mrs. Margaret Wallace. I am especially thankful to the landowners of south Phillips County, Montana who allowed access to their private lands and who provided support and assistance throughout the study. Logistical support was provided by the staffs of the Charles M. Russell National Wildlife Refuge, The Montana Department of Fish, Wildlife, and Parks, and the Malta Field Office of the Bureau of Land Management. The partnership formed resulted in a product greater in scope and quality than any one could have produced alone.

My co-advisors, Jack Ward Thomas and Mark Lindberg contributed beyond what might be expected. Jack provided expertise on political and historical aspects of wildlife conservation. Mark provided expertise on technical aspects of study design, data collection, analysis, and interpretation. Together they honed my technical and strategic skills and always served as excellent examples of first-rate scientists and men of integrity. I thank Scott Mills, Jay Rotella, and Jeff Marks for serving on my graduate committee and providing guidance that much improved this dissertation and resulting manuscripts.

I thank the field crew members who worked with incredible dedication and integrity through long hours under difficult conditions: Jonas and Dougie LaPointe, Josh Acker, Jessica Brzyski, Shawn Cleveland, Denis Dean, Darek Elverud, Wendy Estes-Zumpf, Lindsay Harmon, Sean Munson, Mischa Neumann, Amy Nicholas, Jeremy Roberts, Max Smith, David Speten, Mandy Walker, and Linette Whitney. I sincerely appreciate the quality work of their efforts, while enduring—day and night—all that the wild prairie had to throw at us, from microbursts to rattlesnakes and from 35 below to 115 above. I am grateful to the numerous volunteers who helped with field work.

I wish to specifically thank Randy Matchett, Dan Pletscher, Joe Ball, Mike Hedrick, Jeff Herbert, Mark Sullivan, Matt DeRosier, JoAnn Dullum, Shawn Bayless, Harold Wentland, and the staffs of the Sand Creek Field Station of the CMR-NWR and of Bowdoin NWR. All these people were teachers and friends.

My wife, October Seastone Moynahan, was tirelessly supportive and helpful through the four years of this project. She provided seasoned advice and guidance through challenging times and encouraged my adventures on the "short forest," though it meant that I would be away from home for many months. Beyond the assistance she gave me on the project itself, she took care of our home and affairs in Missoula without complaint. Her love has made me a better person and, for that, I am eternally indebted to her.

I thank my parents, Elaine and Stephen Moynahan, for always encouraging me to pursue and explore my interests and to follow my heart.

Finally, I dedicate this work to Mischa Neumann, a stand-out member of my 2003 crew. Mischa was killed in an ATV accident on June 9, 2003 while monitoring nests east of the Regina Road and south of Whitcomb Lake. An amazing personality and a solid role-model for other crew members, she was the embodiment of what it means to "work hard, play hard." She had a keen and genuine interest in the natural world and those who shared it with her. Mischa is missed and will be remembered always.

TABLE OF CONTENTS

Abstract ii
Acknowledgments iii
Table of Contents iv
List of Figures vi
List of Tables vii

INTRODUCTION 1
RECENT ADVANCES, NEW OPPORTUNITIES I
THE GREATER SAGE-GROUSE PROBLEM 3
RESEARCH APPROACH 5
RESEARCH CONTRIBUTIONS 6
LITERATURE CITED 7

CHAPTER 1: FACTORS AFFECTING NEST SURVIVAL OF GREATER SAGE-GROUSE IN NORTH-CENTRAL MONTANA 9
ABSTRACT 9
INTRODUCTION 10
STUDY AREA 12
METHODS 13
    Study Site Selection 13
    Locating and Monitoring Nests 15
    Vegetation Sampling 18
    Data Analysis 20
RESULTS 23
    Model Selection 25
DISCUSSION 28
MANAGEMENT IMPLICATIONS 35
LITERATURE CITED 37

CHAPTER 2: FACTORS AFFECTING BROOD SURVIVAL OF GREATER SAGE-GROUSE IN NORTH-CENTRAL MONTANA 56
ABSTRACT 56
INTRODUCTION 57
STUDY AREA 59
METHODS 59
    Data Analysis 61
RESULTS 65
    Model Selection 66
DISCUSSION 67
MANAGEMENT IMPLICATIONS 71
LITERATURE CITED 72

CHAPTER 3: FACTORS AFFECTING SURVIVAL OF FEMALE GREATER SAGE-GROUSE IN NORTH-CENTRAL MONTANA 81
ABSTRACT 81
INTRODUCTION 82
STUDY AREA 83
METHODS 84
    Data Analysis 86
RESULTS 90
    Model Selection 91
DISCUSSION 94
MANAGEMENT IMPLICATIONS 100
LITERATURE CITED 104

CHAPTER 4: RESEARCH SUMMARY AND MANAGEMENT IMPLICATIONS OF RECENT DEMOGRAPHIC INVESTIGATIONS OF GREATER SAGE-GROUSE IN NORTH-CENTRAL MONTANA 120
ABSTRACT 120
INTRODUCTION 121
RESEARCH SUMMARY 122
    Nest Success 122
    Brood Survival 123
    Hen Survival 124
MANAGEMENT IMPLICATIONS 125
    Nest Success 125
    Brood Survival 127
    Hen Survival 127
SUMMARY 131
LITERATURE CITED 131

LIST OF FIGURES

CHAPTER 1:

Figure 1 South Phillips County, Montana study area 43
Figure 2 Daily precipitation in south Phillips County, Montana in 2001-2003 44
Figure 3 Estimates of Daily Survival Rates (DSR) of Greater Sage-Grouse nests in south Phillips County, Montana during 2001-2003 45
Figure 4 Estimates of Greater Sage-Grouse nest success in south Phillips County, Montana during 2001-2003 46

CHAPTER 2:

Figure 1 Estimates of Greater Sage-Grouse brood survival to 30 days in south Phillips County, Montana during 2001-2003 74

Figure 2 Estimates of Daily Survival Rates (DSR) of Greater Sage-Grouse broods to 30 days of age in south Phillips County, Montana during 2001-2003 75

CHAPTER 3:

Figure 1 Greater Sage-Grouse study area in south Phillips County, Montana 110

Figure 2 Monthly survival estimates of Greater Sage-Grouse nesting and non-nesting hens during breeding seasons (May-June) in south Phillips County, Montana during 2001-2004 111

Figure 3 Monthly survival estimates of Greater Sage-Grouse hens during late summer (July-August) in south Phillips County, Montana during 2001-2003 112

Figure 4 Monthly survival estimates of Greater Sage-Grouse hens during hunting seasons (September-October) in south Phillips County, Montana during 2001-2003 113

Figure 5 Monthly survival estimates of Greater Sage-Grouse hens during over-winter months (November-April) in south Phillips County, Montana during 2001-2004 114

Figure 6 Estimates of annual (May to May) survival probabilities of Greater Sage-Grouse hens in south Phillips County, Montana during 2001-2003 115

LIST OF TABLES

CHAPTER 1:

Table 1 Total number, fate, and apparent causes of failure of Greater Sage-Grouse nests found in south Phillips County, Montana during 2001-2003 47

Table 2 Observed nesting and renesting probabilities by age for Greater Sage-Grouse in south Phillips County, Montana during 2001-2003 48

Table 3 Observed habitat and environmental values at south Phillips County, Montana during 2001-2003 49

Table 4 Correlation matrix for measured habitat elements in south Phillips County, Montana, 2001-2003 50

Table 5 Models of Daily Survival Rate (DSR) of Greater Sage-Grouse nests found in south Phillips County, Montana during 2001-2003 51

Table 6 Point estimates and standard errors for the best-approximating model of Daily Survival Rate (DSR) of Greater Sage-Grouse nests found in south Phillips County, Montana during 2001-2003 52

Appendix A Full list of candidate models of Daily Survival Rate (DSR) of Greater Sage-Grouse nests found in south Phillips County, Montana during 2001-2003 53

CHAPTER 2:

Table 1 Models of Daily Survival Rate (DSR) of Greater Sage-Grouse broods monitored in south Phillips County, Montana during 2001-2003 76

Table 2 Point estimates and standard errors for the best-approximating model of Daily Survival Rate (DSR) of Greater Sage-Grouse broods in south Phillips County, Montana during 2001-2003 77

Appendix A Full list of candidate models of Daily Survival Rate (DSR) of Greater Sage-Grouse broods in south Phillips County, Montana during 2001-2003 78

CHAPTER 3:

Table 1	Description of seasonal intervals for survival estimation of Greater Sage-Grouse hens in south Phillips County, Montana, 2001-2004 116
Table 2	Model results for *a priori* models describing survival of Greater Sage-Grouse hens in south Phillips County, Montana, 2001-2004 117
Table 3	Observed habitat and environmental values at south Phillips County, Montana during 2001-2003 118
Table 4	Estimates of annual survival probabilities for Greater Sage-Grouse in south Phillips County, Montana, 2001-2004 119

INTRODUCTION

RECENT ADVANCES, NEW OPPORTUNITIES

The application of new analytical techniques to studies of wildlife populations provides opportunities for understanding how populations function and how they might be best managed. Researchers' abilities to probe the relative dynamism and contributions of vital rates (i.e., probabilities of survival and reproduction) to population growth and how they are affected by extrinsic habitat and environmental factors allow for not only a more thorough and sophisticated understanding of population ecology, but also for designing conservation approaches that are strategic and targeted.

Jones (2001) described trends in wildlife habitat selection research that have led to current approaches. Historically, wildlife studies that attempted to describe relationships between population parameters (e.g., abundance, survival, reproduction) and habitat or environmental conditions relied heavily on correlation (Jones 2001). Recognition of the fact that correlation does not necessarily imply causation led the development of density-dependent models (such as Fretwell's Ideal Free Distribution, Fretwell 1972), which in turn were refined to account for observations that animal density can be a misleading indicator of habitat quality (VanHorne 1983). Source-sink models (Pulliam 1988) were the result, and offered early encouragement to let vital rates – not abundance – define habitat quality. Developments in mark-recapture and modeling techniques through the 1990s (e.g., Lebreton et al. 1992, Hilborn and Mangel 1997, Burnham and Anderson 1998, White and Burnham 1999) have greatly strengthened both the theoretical underpinnings and the practical methodologies of the simultaneous evaluation of demography and habitat.

These developments have effectively harmonized what had been, for some time, a cacophony of approaches, and they have encouraged a shift away from traditional statistical testing and toward information-theoretic and maximum-likelihood approaches. The decline in prominence of statistical significance testing in wildlife research (see Johnson 1999) was welcomed in favor of information-theoretic approaches to model selection. To use the example of the ubiquitous *p*-value, the greatest problem with statistical significance testing was not only that *p*-values are frequently misinterpreted, but that they are predicated on the assumption that the null model is true (when it is invariably known to be false), and then provide the probability of observing more extreme data than were actually observed. The great advance of the maximum-likelihood approach is that it allows for the simultaneous evaluation of multiple models (hypotheses) that begin on equal footing (unless specified otherwise) and it generates a measure of relative support for each model based on the data that were actually observed. The practical application of these approaches has followed nicely. Software packages (including program MARK used here, White and Burnham 1999) allow for efficient construction and evaluation of competing models with varying degrees of complexity and spatial and temporal resolution.

In addition to the technical advances, there has been growing evidence that the assessment of habitat and environmental effects on wildlife populations is most informative when conducted at large scales – the scale of landscapes as opposed to local use areas (e.g., nest or den sites, forage sites, etc.). Indeed, a recent review of nest success studies (Stephens et al. 2003) concluded that such investigations are best conducted at landscape scales and over the course of several years, largely because important effects are difficult to detect at smaller scales. This increase in the scale of consideration has been the trend beginning in the mid-1900s (Jones 2001).

Not only does this shift to information-theoretic approaches and larger geographic scales stand to greatly improve our basic understanding of population ecology, it also meshes exceptionally well with information needs of the applied worlds of conservation and management. With the exception of a few particularly rare species for which the immediate focus is on individuals (e.g., black-footed ferrets, California Condors), most wildlife conservation and management focuses on populations and habitats. Particularly on the public lands of the western United States, on-the-ground management for many wildlife species will take place on landscape-scales – thousands or tens of thousands of hectares – through manipulation of broadly-applied land uses (e.g., livestock grazing). Professionals charged with maintaining or recovering species like Greater Sage-Grouse, for example, will simply not be able to manage for detailed local nest-site characteristics, but may well be able to affect overall understory height and density through innovative grazing systems. They will not be able to simultaneously maximize the quality of all habitat requirements for all vital rates, but may well be able to target management for habitat elements that contribute most to population growth. The opportunities for the marriage of the scales of research and management are unparalleled. Wildlife biologists are in a position to simultaneously make substantive and useful contributions to both basic ecology and applied management.

THE GREATER SAGE-GROUSE PROBLEM

Populations of Greater Sage-Grouse (*Centrocercus urophasianus*, hereafter "sage grouse") have declined by as much as 69-99% from historic to recent times, with much of that decline occurring since the 1980s (USFWS 2004). The geographic extent of sage grouse range in the western U.S. and Canada has been reduced by approximately 50% (Schroeder et al. 1999). The loss and degradation of habitat to expansion of farming and grazing activities are likely the main factors (Connelly and Braun 1997). Other potential factors include changes in fire regimes, predation, over-hunting, weather, disease, and herbicide and insecticide treatments (Connelly and Braun 1997, Braun 1998). The U.S. Fish and Wildlife Service (USFWS) issued a positive 90-day finding in April 2004 in response to a range-wide petition to declare sage grouse as "threatened" or "endangered" under the Endangered Species Act. Such determination would likely have substantial impacts on land management and traditional land-use patterns throughout the range of the sage grouse, particularly on federal lands.

Existing information describes general sage grouse habitat needs across its range and over the period of its noted decline, and almost entirely on a local scale (e.g., nest site or lek locations). Sage grouse literature reviews (e.g., Schroeder et al. 1999) and management guidelines (i.e., Connelly et al. 2000) note that habitat loss and fragmentation – both landscape issues – are a major concern for viability of sage grouse populations. Moreover, despite reports of high levels of geographic and temporal variation in nest survival rates (Schroeder et al. 1999, Connelly et al. 2000), no study has simultaneously assessed a wide range of biotic and abiotic factors suspected to affect population demography at the landscape scale. For these reasons, and because future sage grouse conservation and management will likely apply habitat prescriptions over relatively large areas through manipulation of land-use patterns, it is important to consider factors affecting population dynamics at the landscape scale.

RESEARCH APPROACH

My objective was to investigate the influence of landscape-scale habitat and environmental factors on population dynamics of sage grouse in south Phillips County, Montana. Field work was conducted from March 2001 through June 2004. I chose to work in south Phillips County largely because it represents some of the most expansive and highest-quality sage grouse habitat in Montana and perhaps across the entire range of sage grouse. I used a female-based approach as warranted by the biology of this species (breeding is based on female choice of mates, and hens alone tend to nests and chicks).

With the use of radio-collars, I monitored nest success (n = 258), brood survival (n = 115), and seasonal hen survival (n = 221). I used an information-theoretic approach (Burnham and Anderson 1998) to simultaneously evaluate relative support of multiple models describing relationships between survival and variables of interest. I began by generating candidate models that described competing hypotheses about the three selected vital rates. Each model represented a hypothesis of nest success, brood survival, or hen survival as a function of some combination of biotic and abiotic and environmental sources of variation. I used the program MARK (White and Burnham 1999) to evaluate the relative support for each candidate model given observed data. Program MARK uses generalized linear models with a user-specified link function to generate maximum-likelihood estimates of regression coefficients and their associated sampling variances and covariances. The resulting output yields information on which model terms (e.g., year, site, hen age, grass cover, etc.) and what level of complexity (i.e., how many estimated parameters) are supported by the observed data.

RESEARCH CONTRIBUTIONS

This research indicates that both the absolute values and qualitative relationships of vital rates that contribute to population growth are much more variable than previously believed. The analyses provides quantitative descriptions of complex population processes and documents the effects of a wide range of biotic and abiotic factors, from hen age to winter weather, and from daily spring precipitation to an exotic virus. This dissertation documents not only that the relative importance of survival and reproduction to population growth are not equal, but that the direction and magnitude of that inequality changes on an annual basis. The results provide new understanding of important elements of sage grouse population dynamics and their relationships to population structure, habitat characteristics, and climatic factors. Data-based recommendations for sage grouse management and for future research efforts are provided.

The nest-success analyses demonstrate how estimates of apparent nest success can be considerably biased and describe how precipitation effects nest survival on a daily – not seasonal – basis. Analyses of brood survival indicate that annual environmental conditions are most important and that this vital rate may be least amenable to management. Hen survival analyses indicate substantially more variation than previously believed, describe the major effects of West Nile virus and severe winter weather, and raise the important issue of the potential effects of harvest mortality on population dynamics.

This research builds on the foundations of others to provide detailed, landscape-scale information on sage grouse population ecology and presents implications of that information to wildlife and land management. The analyses make maximum use of the data and generate strong inference. Findings greatly improve our understanding of sage grouse population ecology and will help make efforts to maintain and conserve sage grouse populations more strategic and targeted.

LITERATURE CITED

Burnham, K. P. and D. R. Anderson. 1998. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, NY.

Braun, C. E. 1998. Sage Grouse declines in western North America: what are the problems? Proc. West. Assoc. State Fish and Wildl. Agencies. 78:139-156.

Connelly, J. W. and C. E. Braun. 1997. Long-term changes in Sage Grouse populations in western North America. Wildlife Biology 3:229-234.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse habitats and their populations. Wildlife Society Bulletin 28(4):967-985.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, NJ.

Hilborn and Mangel. 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, New Jersey.

Johnson, D. H. 1999. The insignificance of statistical significance testing. Journal of Wildlife Management 63(3):763-772.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118(2):557-562.

Lebreton, J.D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 61(1):67-118.

Schroeder, M.A, J. R. Young, and C. E. Braun. 1999. Sage Grouse: *Centrocerus urophasianus*. In: Poole A, Gill F, editors. Birds of North America. Philadelphia, PA: The Birds of North America, Inc. p 1-28.

U. S. Fish and Wildlife Service. 2004. 90-day finding for petitions to list the Greater Sage-Grouse as threatened or endangered. 50 CFR 17, 69(77):21484-21494.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: Supplement:120-138.

CHAPTER 1: FACTORS AFFECTING NEST SURVIVAL OF GREATER SAGE-GROUSE IN NORTH-CENTRAL MONTANA

Abstract: Populations of Greater Sage-Grouse (*Centrocercus urophasianus*) have declined by 69-99% from historic levels. Information on population dynamics of these birds at a landscape scale is essential to informed management. I radio-collared 243 female sage grouse, monitored 287 nests, and measured 426 vegetation plots at 4 sites during 2001-2003 in 3,200 km^2 landscape in north-central Montana, USA to examine the relationship between nest success of Sage-Grouse and habitat conditions, environmental variables, and hen characteristics. I used program MARK to model daily survival rates (DSR) of nests. Nest survival varied with year, grass canopy cover, daily precipitation with a 1-day lag effect, and nesting attempt. In all years, DSR increased on the day of a rain event and decreased on the next day. I believe the daily precipitation effect and the 1-day lag effect of precipitation reflect increased hen attentiveness and decreased predator activity on rainy days, followed by decreased hen attentiveness and increased predator activity one day later as both increase forage activity. I observed temporal variation in nest success both within and among years: nest success of early (first 28 days of the nesting season) nests ranged from a low of 0.238 (SE = 0.080) in 2001 to a high of 0.316 (SE = 0.055) in 2003, whereas survival of late (last 28 days of the nesting season) nests ranged from a low of 0.276 (SE = 0.090) in 2001 to a high of 0.418 (SE = 0.055) in 2003. Renests experienced higher survival than first nests. Grass cover was the only important model term that might be managed, but direction and magnitude of the grass effect varied, possibly influenced by the narrow range of grass canopy cover values observed or other complexities associated with habitat changes in 2003. Site, shrub and forb canopy cover, and Robel pole reading were less useful predictors of nest success. I note a marked difference between both values and interpretations of apparent nest success (proportion of all detected nests that hatch at least one egg) and maximum likelihood estimates derived from my modeling process (an information-theoretic extension of the Mayfield method). Apparent nest success here was 0.46, while maximum likelihood estimates that incorporate individual, environmental and habitat covariates are lower. The outputs of this analysis, in concert with extant recommendations, suggest that management of breeding sage grouse should focus on increasing grass cover to increase survival of first nests and contribute to favorable conditions for renesting, which should be less likely if survival of first nests increases.

INTRODUCTION

The long-term decline of Greater Sage-Grouse (*Centrocercus urophasianus*, hereafter "sage grouse") over most of their historic range concerns managers of sagebrush (*Artemisia* spp.) habitats of the western U.S. and Canada (Schroeder et al. 1999). The loss and degradation of habitat to expansion of farming and grazing activities are likely the main factors (Connelly and Braun 1997). Other potential factors include changes in fire regimes, predation, over-hunting, weather, disease, and herbicide and insecticide treatments. The U.S. Fish and Wildlife Service (USFWS) issued a positive 90-day finding in April 2004 in response to a range-wide petition to declare sage grouse as "threatened" or "endangered" under the Endangered Species Act. Such determination would likely have substantial impacts on land management and traditional land-use patterns throughout the range of the sage grouse, particularly on federal lands.

Though there are numerous studies of sage grouse ecology and behavior, there is little information on the influence of landscape-scale habitat and environmental factors on demography in general and nest survival in particular. Most research has focused on leks and bird behavior at leks (Hanna 1936, Wallestad et al. 1975, Gibson et al. 1990, Gibson 1996, Wakkinen et al. 1992), seasonal habitat use (Eng and Schladweiler 1972), and seasonal movements and dispersal (Dunn and Braun 1985; Connelly et al. 1988; Bradbury et al. 1989a, 1989b). Studies of population dynamics have focused largely on reproduction (Peterson 1980; Remington and Braun 1985; Connelly and others 1988; Gibson 1992; Lebreton et al. 1992; Wakkinen and others 1992; Gibson 1996; Sveum et al. 1998a; Sveum et al. 1998b). Studies have examined nest-site characteristics (Patterson 1952; Wallestad and Pyrah 1974; Connelly et al. 1991; Wakkinen et al. 1992;

Gregg et al. 1994), nest-site fidelity (Dunn and Braun 1985; Fischer et al. 1993), and reproductive effort (Connelly et al. 1993; Schroeder 1997). Existing information describes general sage grouse habitat needs across its range and over the period of its noted decline.

As with much other research on avian nest success, most studies of sage grouse nest success have focused on covariates measured at small plots centered on nest sites. Stephens et al. (2003) reviewed the effect of scale on detection of effects of fragmentation on nest success and recommend that such studies be conducted at landscape scales and over several years. Jones (2001) suggested that the next step in the evolution or development of avian habitat selection research must be the incorporation of both habitat and demographic information into landscape-scale conservation planning. Furthermore, sage grouse literature reviews (Schroeder et al. 1999) and management guidelines (Connelly et al. 2002) note that habitat loss and fragmentation – both landscape issues – are a major concern for viability of sage grouse populations. For these reasons, and because future sage grouse conservation and management will likely apply habitat prescriptions over relatively large areas (thousands or tens of thousands of hectares) through manipulation of land-use patterns, it is important to consider factors affecting nest survival at the landscape scale. Moreover, despite reports of high levels of geographic and temporal variation in nest survival rates (Schroeder et al. 1999, Connelly et al. 2000), no study has simultaneously assessed a wide range of biotic and abiotic factors suspected to affect nest success at the landscape scale.

Land uses across central and eastern Montana are spatially divergent, ranging from cropland to various grazing intensities to relatively undisturbed sagebrush-steppe habitats. Avian and mammalian predator assemblages and abundances vary across this heterogeneous landscape, increasing variation in population characteristics. The region is characterized by wet/dry cycles of varying lengths and intensities, which affect sagebrush, grass, and forb growth. Therefore, high levels of spatial and temporal variation produce complex interactions of factors influencing sage grouse vital rates. My objective was to estimate sage grouse nest survival rates in north-central Montana across a study area designed to have landscapes that varied in terms of their habitat and environmental factors.

STUDY AREA

I studied sage grouse on four study sites selected to represent a wide range of habitat conditions (see below). The sites were all within a 3,200-km^2 area in southern Phillips County in north-central Montana (47° 33' N to 48° 01' N, 107° 32' W to 108° 33' W, Fig. 1), bounded by the Missouri River and Fort Peck Lake to the south, the Larb Hills to the east, the Whitcomb Lake area to the north, and the Little Rocky Mountains to the west. Approximately 60% of the study area was in public ownership, managed by the U.S. Bureau of Land Management (BLM, Malta Field Office), the U.S. Fish and Wildlife Service (FWS, Charles M. Russell National Wildlife Refuge [CMR]), and the State of Montana. Remaining lands were predominantly private, and I worked on some 30 private ranches. This area is a mixed-grass prairie with sagebrush flats bordering the southwestern edge of the Prairie Pothole Region (Dinsmore et al. 2002). I selected four study sites within the study area: CMR, Sun Prairie, Little Horse, and Dry Fork (Fig. 1).

The study area represents some of the most expansive, contiguous and intact sagebrush-steppe habitats in Montana with relatively large sage grouse populations.

Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) was the dominant shrub, with lesser amounts of silver sage (*A. cana*), greasewood (*Sarcobatus vermiculatus*), Rocky Mountain juniper (*Juniperus scopulorum*), Gardner saltbush (*Atriplex gardneri*), Yucca (*Yucca glauca*) and snowberry (*Symphoricarpus albus*). Common grasses included western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*), green needlegrass (*Stipa viridula*), and bluebunch wheatgrass (*Agropyron spicatum*). Common forbs included fringed sagewort (*Artemisia frigida*), wild onion (*Allium* spp.), dandelion (*Taraxacum* spp.), American vetch (*Vicia americana*), prairie goldenbean (*Thermopsis rhombifolia*), poverty weed (*Monolepis nutalliana*), scarlet globemallow (*Sphaeralcea coccinia*), and yellow sweetclover (*Melilotis officianalis*). The area is characterized by high annual variation in average daily temperature (-9°C to 22°C) and low mean annual precipitation (32 cm), most of which falls between May and July. Mean elevation is ~800 m. Potential sage grouse nest predators included coyote (*Canis latrans*), badger (*Taxidea taxus*), California gull (*Larus californicus*), American crow (*Corvus brachyrhynchos*), black-billed magpie (*Pica hudsonia*), Common Raven (*Corvus corax*) and bull snake (*Pituophis catenifer*).

METHODS

Study Site Selection

Lek locations were central to the site-selection process because they have been identified as the geographic center of year-round activity for non-migratory populations (Eng and Schladweiler 1972; Wallestad and Pyrah 1974; Wallestad and Schladweiler 1974) and because they serve as the focal point for trapping and marking birds each spring. The four study sites were selected in a three-step mapping process using

Geographic Information System (GIS) layers provided the Montana Department of Fish, Wildlife, and Parks (FWP) to obtain multiple sites that represented a range of habitat conditions and with proximity that made work logistically feasible.

First, I mapped all known active leks. Second, I placed a 5-km-radius buffer around those leks to identify "lek complexes," i.e., groups of leks with overlapping or contiguous buffers. The 5-km distance was chosen based on pre-project expectations that leks are the geographic center of year-round activity and that most individuals attending the lek would confine their use of habitats to areas within 5 km. Third, I overlaid the lek-complex map with a GIS layer of sagebrush coverage generated from satellite imagery and calculated the percent of pixels within a given lek complex that was classified as sagebrush. However, the remote sensing process used to classify pixels as sagebrush or other is most accurate only when actual sagebrush canopy cover exceeds 15-20%. Sagebrush cover of 20% is fairly high, and many areas of lower sagebrush cover are important sage grouse habitat (Schroeder et al. 1999, Connelly et al. 2000). As a result, these percentages of sage-occupied pixels gave a relative ranking of lek complexes based on sagebrush coverage but could not provide accurate estimates of actual sagebrush coverage.

Each complex was considered as a candidate study site and assigned a rank of high, medium, or low sagebrush coverage. Final selection was made based on a desire to have sites represent a range of landscape-scale sagebrush conditions and considerations of logistics and funding. I initially selected 6 sites, with 2 in each of the 3 high, medium, and low sagebrush coverage categories. Ground-truthing eliminated 2 of these sites because some leks were so small as to not provide an opportunity to mark an adequate sample of birds and because some expected sage grouse leks were actually Sharp-tailed grouse (*Tympanuchus phasianellus)* leks. I ultimately chose one low sagebrush site (CMR), two medium sites (Little Horse and Dry Fork), and one high site (Sun Prairie).

Locating and Monitoring Nests

I marked hens with radio transmitters to facilitate location of nests. Hens were trapped primarily by rocket-netting and spotlighting (Giesen et al. 1982) from all-terrain vehicles and on-foot between mid-March and mid-April 2001-2003. Each hen was fitted with a necklace-type radio transmitter (2001-Telemetry Solutions®, 2002-2003-Advanced Telemetry Systems®, model A4080), a numbered metal leg band, and an individually coded plastic band. Each transmitter weighed 22 g (approximately 1% of mean adult hen body mass), had an expected life of 383 days, and could be detected from the ground and air from approximately 2-5 km and 6-10 km, respectively.

At the time of marking, I determined each hen's age class based on inspection of the 9th and 10th primaries and using two age classes: adult ($\geq$2 years old, second or later breeding season) or sub-adult (<1 year old, first breeding season; Eng 1955; Crunden 1963). Physical measurements taken include body mass (kg), head length (mm), and tarsus length (mm). Trapping and handling protocols were approved by The University of Montana Institutional Animal Care and Use Committee. Trapping, marking, and special-use permits were provided by FWP, FWS, and BLM.

Traveling on foot, ATV, or horseback, I regularly recorded locations of marked birds from the end of the trapping season, typically near 15 April, through the end of the nesting season, defined as 10 consecutive search days without location of any new nests. Locations were recorded typically every 4 days (range = 2 to 14 days) using telemetry.

When homing from ATVs, crew members walked in the final 50-300 m to avoid undue disturbance to nesting hens and nest-site vegetation. Occasional aerial searches augmented ground work. Nest locations were marked with inconspicuous natural markers, e.g., a small rock cairn 2-5 m from the nest and recorded with a Global Positioning System (GPS) receiver.

Sage grouse frequently begin incubation before the last egg is laid, and nests were often found with full clutch. Also, candling eggs to estimate incubation stage was not possible (due to egg color and markings), so estimating expected hatching date on the day a nest was first found was problematic. When a nest was found, I recorded the clutch size and estimated the expected hatching date as follows. I used telemetry to locate hens and determine when a hen had begun incubation. I counted clutch size for at least the first 2 visits to determine when a clutch was complete and whether eggs were added since the previous visit. Based on a laying rate of 2 eggs per 3 days (Schroeder et al. 1999), I calculated date of clutch completion and then estimated hatching date by adding 28 days (Schroeder et al. 1999) from clutch completion. For nests that were located after clutch completion, I floated 2 eggs per nest to estimate hatching date (I knew of no floatation curves for sage grouse eggs, so I used the curves generated for Ring-necked pheasant [*Phasianus colchicus*, Westerkov 1950] as a guideline). Because hens began incubation at different stages of laying, I refined my hatch date estimate in many instances based on direct observation of chicks hatching, chicks in the nest cup, chick size and knowledge of date of previous visit when the nest had not hatched.

Subsequent to being found, each nest was typically revisited every 4 days (range 1-14 days) until successful (≥1 egg hatched), destroyed, or abandoned. I recorded the nest as successful when at least one whole shell, egg membrane, or chick was present in the nest bowl. Care was taken to avoid flushing hens off nests on rainy or particularly cold days. Once a hen stopped using a nest site, I checked its contents to determine if it failed, was abandoned, or was successful. This determination was made based on eggshell evidence or observation of chicks to determine nest fate. When a predator was responsible for nest failure (i.e., several or all eggs missing or broken and no female in attendance), I recorded the type of predator believed responsible – mammal (evidenced by crushed eggs, all eggs missing, destruction of the nest cup, scraping, and scat), bird (intact eggshells other than quarter-sized punctures in one side), reptile (one or two missing eggs with no visible predator sign, attributed to bull snakes), or unknown (mixed or no evidence). I assumed that the nest had been abandoned when the clutch was intact, but the eggs were cold and the female was not present. I re-checked suspected abandonments for ≥ 2 visits before recording the nest's fate as abandoned. In such cases, I dated the failure to the first date when the eggs were found cold and unattended.

If the nest had been abandoned between its discovery and the first revisit, I assumed that it was abandoned at discovery due to investigator disturbance; these nests were not included in analyses. Nests abandoned after ≥2 visits had occurred were presumed not to be observer-caused and were included in the analysis. No abandoned nest was ever observed to be subsequently depredated, so I am confident that no nests classified as "depredated" were actually scavenged after abandonment.

I recorded a nest as a first attempt based on intensive telemetry monitoring and visual location of hens typically every 4 days during the nesting season. A nest was classified as a renest when it followed a known failed prior nest attempt. With little data during the pre-incubation laying stage of nest initiation, my inferences are restricted to nest survival after incubation begins. It is possible that some undetected nests failed early in laying and pre-incubation, which would result in mis-classification of some actual renests as first nests.

Vegetation Sampling

I was interested in characterizing the habitat used by marked birds at the landscape scale, i.e., the level of the study site (156 - 234 km^2 [61 – 92 mi^2]). Thus, I selected 110 to 180 vegetation-sampling points to measure on each study site each year using the following steps. First, I overlaid each lek complex with a grid of points spaced at 1-km intervals. All grid-intersection points that fell within the lek-complex boundaries were candidate vegetation plot locations. UTM coordinates of the candidate plot locations were generated from mapping software (Maptech® Terrain Navigator), downloaded to handheld GPS receivers, and used to locate plots in the field. In the absence of pre-project baseline vegetation data, I was unable to determine adequate sample sizes *a priori*. Thus, in 2001, I randomly selected 80% ($n = 540$) of the candidate plots for measurements. Some plots were lost or could not be measured in subsequent years due to cattle trampling, cultivation, or erosion. Because I wanted to track vegetative changes over time, only plots measured in all three years ($n = 426$; 87 to 134 plots at each site) were included in analyses.

Vegetation on each plot was measured in two ways: ocular canopy cover (CC) estimates within a 1-m^2 frame and visual obstruction measurements following Robel et al. (1970). These methods were selected because they provided quick and repeatable measures that could be applied at many plots across the landscape by both researchers and wildlife managers. The CC metric characterized the presence of distinct life forms that are important to sage grouse for different reasons. For example, shrubs and grasses are important nesting-cover components (Connelly et al. 2000), whereas forbs provide nutritious forage for egg-laying hens (Barnett and Crawford 1994). Hens relied on sagebrush for approximately 95% of all nest attempts, with the remainder located under juniper and greasewood. I used the category of "shrub" rather than considering only sagebrush because hens occasionally nested beneath non-sage shrubs and because sagebrush accounted for ~85% of shrubs in vegetation plots. Residual and green grass cover together contributed vertical structure to nest sites, helping to obscure nests and incubating hens from predators. Robel pole readings provided an index of height, density, and visual obstruction of vegetation. CC by life form (grass, shrub, forb, tree, cactus, moss, lichen) was estimated at 1% intervals up to 10% coverage, and then at 5% increments. Observers standardized CC estimates with the same lead researcher among years and several times within years. Both live and dead standing plant matter were included in CC estimates for each plot as contributing to visual obstruction of the nest from predators. Total CC could exceed 100% because vegetation is recorded for all layers present. I included only shrub, grass, forb, and Robel data in candidate models because they were the most likely to influence nest survival. Plots were measured over the course of the reproductive season (nesting and brood-rearing seasons) for application to nest- and brood-survival analyses. Once I had collected all plot-level data, I averaged all measurements for each plot metric to generate a description of mean landscape-level conditions that was used in subsequent analysis. Thus, vegetation data were included in models as mean CC by life form and mean Robel pole reading for each site and year.

Data Analysis

I used an information-theoretic approach (Burnham and Anderson 1998) to simultaneously evaluate relative support of multiple models describing relationships between DSR and variables of interest. I began by generating candidate models that described competing hypotheses about nest survival. Each model represented DSR as a function of some hypothesized combination of biotic and abiotic sources of variation: year (coded as groups in the input file), site (coded as groups in the input file), season date, hen age class (using a dummy variable coded as 0 = sub-adult and 1 = adult), nest attempt (using a dummy variable coded as 0 = first nest and 1 = renest), four habitat metrics (shrub, grass, and forb CC and Robel pole readings), and daily precipitation and minimum daily temperature (obtained from the Western Regional Climate Center, Malta, Montana 35S station number 245340). Depending on how each habitat covariate was included in model structure, it could exhibit site or year specificity or both. In some models, therefore, I incorporated habitat terms as a more specific and more parsimonious construction of site and year effects. Three individual covariates (hen body mass, ratio of head length to mass, and ratio of tarsus length to mass) were independently added to the best-supported environmental models to evaluate whether hen size or condition resulted in improved model fit.

I modeled season data as a logit-linear trend to allow for the possibility of a non-zero slope in the nest survival function over the course of the nesting season. I did so to address several potential sources of variation: (1) actual season date effects as may be related to changes in predator numbers, predator foraging behavior, or alternate prey availability; (2) the tendency for the average age of active nests to be older as the nesting season progresses, though I acknowledge that this relationship is affected by asynchronous nesting and re-nesting; and (3) individual heterogeneity among nests within a set of covariate conditions that would lead to a pattern of increased survival as the season progresses because the nests with poorer survival will tend to be selectively removed from the sample, leaving a higher-survival set of nests remaining (Klett 1982).

I standardized season dates among years by using the earliest location date for any year as the first day of the season and the latest hatching or failure date in any year as last day of the season. I thus defined a 79-day nesting season beginning 22 April and ending 10 July. This season comprised 78 daily intervals for which DSR was estimated. I documented 3 instances of hens initiating a third nest after two previous failures but did not distinguish 3rd nests from 2nd nests in models. Nesting attempt was confounded with season date, so I considered these variables separately. Effect of nest attempt was not considered for 2001 because I observed no renesting attempts in that year.

I used the nest-survival module in program MARK (White and Burnham 1999) to evaluate the relative support for each candidate model given observed data. This module of Program MARK uses generalized linear models (McCullaugh and Nelder 1989) with a user-specified link function to generate maximum-likelihood estimates of regression coefficients and their associated sampling variances and covariances. I used the logit link function for all models. This approach extends earlier survival models (Johnson 1979, Bart and Robson 1982) by permitting direct evaluation of the influence of nest- and hen-specific covariates—including daily covariates like precipitation or ambient temperature—on DSR (Dinsmore et al. 2002). Individual models were evaluated using Akaike's Information Criterion (AIC) and AIC weights (Burnham and Anderson 1998).

Assumptions of the daily nest-survival models described here are: (1) homogeneity of daily survival rates; (2) nest fates are correctly determined; (3) nest discovery and subsequent nest checks do not influence survival; (4) nest fates are independent; (5) all visits to nests are recorded; and (6) nest checks are conducted independently of nest fate (Rotella et al. *In Press).* I could not model the effect of nest age because it could not be accurately determined, yet nest age could have been a source of heterogeneity in my data. I did, however, model a logit-linear trend for season date, which may have accounted for some of the potential age-related heterogeneity (see above). I did not include nests with unknown fates in the analysis. I reduced the potential effect of visits on nest survival by avoiding flushing the hen from the nest once the clutch was complete, scheduling revisits at 4-7 day intervals, and spending as little time at each nest as possible. If present, individual heterogeneity in DSR for different hens may have led to non-independence of nest fates because (1) most hens provided nest-survival data for multiple observation intervals and (2) some hens provided data for multiple nests and multiple years. Program MARK does not allow for the analysis of random effects due to individuals and so possible individual heterogeneity could not be modeled. However, heterogeneity related to age class and nest attempt type (first nest or renest), both of which were known to us, were explicitly modeled. Because I was concerned about possible sources of heterogeneity that could not be modeled, I estimated overdispersion (c-hat; Anderson and Burnham 1994) using the difference in the log-likelihood of the saturated and most general (most parameters) model (deviance) divided by the deviance degrees of freedom (i.e., difference in number of parameters between models). This estimate of c-hat is positively biased, making inference and model-selection conservative, but is the only goodness-of-fit diagnostic reasonably available for these models. After estimating overdispersion, I attempted to address potential associated problems by adding an index of nest age to the global model, based on the assumptions that (1) nest found date was the date of clutch completion and incubation initiation and (2) eggs were layed at a rate of 2 eggs per 3 days (Schroeder et al. 1999). I could thus use observed clutch size as an index of nest age. Potential effects of overdispersion on model selection and estimates of sampling variance (Anderson and Burnham 1994) are considered below.

I summed AICc weights for top models (i.e., ΔAICc values < 4.0) with common terms to assess the relative support each of those terms; higher ∑AICc weights indicate greater support.

I used back-transformed estimates of DSR from the best-approximating model,

$$\mathrm{D\hat{S}R}_i = \frac{1}{1+\exp(-(\hat{\beta}_0+\hat{\beta}_1 X_1,\ldots,\hat{\beta}_i X_j))}$$

, where the $\hat{\beta}_i$ are the estimated regression coefficients from the model and the X_j are the values of the independent variables (e.g., daily precipitation). The incubation period is 25-29 days (Schroeder et al. 1999); I used a standard 28-day incubation period when extrapolating estimates of daily survival to estimates of nest success. These nest-success estimates were the product of all of the daily survival rates for the model over the assumed 28-day incubation period (Johnson 1979). I estimated the variance of nest success using the delta method (Seber 1982).

RESULTS

I located 287 nests and determined the fates of 258 of those nests. Twenty-nine nests were not included in analyses either because I was unable to determine their fate or because abandonment was likely to have been observer-caused. Of the 258 nests included in analyses, 215 were estimated to be first nests, and 43 were known renests (including 3 third attempts). Apparent survival (ratio of successful to total observed nests) was 0.46 (Table 1). Abandonment accounted for 5% of nest fates and 1% failed due to non-viable eggs. The remainder of nest failures had clutches that went missing or were destroyed *in situ*: these were assumed destroyed by predators. Sixty-three percent of nests assumed destroyed by predators were attributed to avian predators, as evidenced by puncture holes in one side of otherwise intact eggs.

Precipitation and temperature varied within each 79-day nesting season. Nesting-season precipitation was highest in 2002 (16.5 cm), followed by 2001 (14.5 cm) and 2003 (12.4 cm). Distribution and amount of individual rain events were also qualitatively distinct: 2001 was characterized by a relatively small number of large rain events; 2002 saw low precipitation events early to mid-season, then larger events late season; 2003 had more numerous and well-distributed small to medium rain events, with a scattering of medium to large events throughout the season (Figure 2). The 2002 season had the coldest minimum daily temperatures, with 19 days at or below 0 °C (5 days in 2001, 7 days in 2003).

I measured 426 vegetation plots in each of the three years. Mean Robel pole reading was 4.97 cm (SE = 0.22) in 2001, 4.60 (SE = 0.22) cm in 2002, and 7.24 cm (SE = 0.39) in 2003. Mean forb CC was 3.34 (SE = 0.27) in 2001, 6.32 (SE = 0.45) in 2002, and 6.25 (SE = 0.65) in 2003. Grass and shrub CC varied little between years (Table 3). There was no evidence of correlation between the grass, forb, and shrub elements (Table 4). Sweet clover, a biennial forb, had potential for substantial growth in 2001 and 2003.

Due to previous years' drought followed by the precipitation regime described above (rain events were few but relatively large), there was very little sweet clover growth in 2001. In contrast, conditions were favorable in 2003 and the mean forb CC and mean Robel metrics reflect sweet clover that year.

Mean clutch size for all nests was 8.25 (SE = 0.11); mean clutch size was 7.62 (SE = 0.24) in 2001, 8.80 (SE = 0.17) in 2002, and 8.55 (SE = 0.15) in 2003. Mean clutch size for first nests (8.49, SE = 0.11) was 1.26 (SE = 0.13) eggs greater than for renests (7.23, SE = 0.06). Mean clutch size for first nests was 8.67 (SE = 0.13) for adults and 8.06 (SE = 0.17) for sub-adults; for renests, mean clutch size was 7.09 (SE = 0.25) for adults and 7.13 (SE = 0.68) for sub-adults.

Mean nesting probability (proportion of individuals across all years that were detected initiating at least one nest [n = 217]) for adults (0.93, SE = 0.0005) was 0.15 (SE = 0.02) greater than for sub-adults (0.78, SE = 0.02), but varied by year (Table 2). Mean renesting probability (proportion of hens across all years detected initiating a second nest after failure of the first nest) was 0.43 (SE = 0.003) for adults and 0.19 (SE = 0.004) for sub-adults, but this also varied by year (Table 2). Mean date on which nests were found was 5 May (SE = 1.2 days) in 2001, 15 May (SE = 1.1 days) and 8 May (SE = 0.8 days) in 2003.

Model Selection

The best-approximating model (AICc weight = 0.220) indicated that DSR of nests varied among years and with annual grass CC, daily precipitation, a 1-day lag effect of precipitation, and nesting attempt (selected models in Table 5, full model set in Appendix A). Support for this model was strong; with 9 estimated parameters, this top model was

2.04 AICc units better than the second-best model with 3 estimated parameters. Summed AICc weights were greatest for precipitation with 1-day lag (0.48), year (0.41), attempt (0.36), grass CC (0.35), and season date trend (0.12).

The relationship between mean annual grass CC was positive in 2001 (though the 95% confidence interval overlapped zero, -0.198 to 0.438) and 2002, but negative in 2003. The effect of daily precipitation was positive ($\hat{\beta}$=7.25, SE = 4.41), but the 95% confidence interval overlapped zero (95% CI: -1.38 to 15.90). The 1-day lag effect of daily precipitation was negative ($\hat{\beta}$= -2.62, SE = 0.738). DSR increases on days with rain and decreases the day after rain (Fig. 3). The effect of nest attempt was positive (β= 0.196, SE = 0.097), indicating that renests experienced higher DSRs than did first nests. There was no support for models that included daily precipitation in the absence of the lag effect term (ΔAICc $\geq$ 6.89). All $\hat{\beta}_i$ and corresponding standard errors for the best-approximating model are reported in Table 6.

Models with incorporating shrub CC performed poorly in general (ΔAICc values ranging from 4.2 – 15.0), though shrub CC varied less between sites than I had expected during the study design and site selection processes (Table 3). I would not expect sage grouse vital rates to be detectably influenced by site-specific shrub coverage within such a narrow range as observed here. There was little to no support for site specificity, Robel values, hen age class, or minimum daily temperature (ΔAICc values ranging from 6.5 – 18.0). Site distinctions and the interaction of site and year were not supported, even when I reduced the number of estimated parameters while maintaining site and year structure by using site- and year-specific habitat information (Robel, shrub, grass, and forb) in lieu of site*year terms (Table 5).

I did not calculate a mean annual nest survival rate because DSRs varied daily within years; i.e., including a mean daily precipitation value would not be realistic. Therefore, I report two nest survival rates for each year: early and late nests using mean grass CC values and observed daily precipitation. Estimates of nest survival for early nests for all years are the product of the first 28 estimated DSRs (nesting season days 1-28). Nest survival estimates for late nests for each year are the products of the last 28 estimated DSRs, starting at the latest nest observation date for that year and including the previous 28 DSRs. In this way, reported nest survival estimates apply to dates for which actual nest observations exist for each year. Because no renests were observed in 2001, the nest survival estimate for late nests includes season days 21-49, where 2002 includes days 51-79, and 2003 includes 50-78. For all years, the estimate for early nests coded the nest attempt term as first nests. I also coded the late nest estimate for 2001 for first nests, again because no renests were observed that year. The late nest estimates for 2002 and 2003 are coded as renests. Nest success rates for early nests were 0.238 (SE = 0.080) in 2001; 0.267 (SE = 0.063) in 2002; and 0.316 (SE = 0.055) in 2003. Nest success rates for late nests were 0.276 (SE = 0.090) in 2001; 0.319 (SE = 0.061) in 2002; and 0.418 (SE = 0.055) in 2003 (Figure 4).

Adding individual physical covariates (mass, head length: mass ratio, tarsus length: mass ratio) singly to the top model did not result in an improvement (all ΔAICc < 2.00). Hen age class, which I thought could have an effect similar to weight, did not improve on the top model (increase of 2.00 ΔAICc units), indicating slightly more support for the hen weight term than the age class term.

If I used the estimate of c-hat (3.24), sampling variances would be inflated by 1.80 ($\sqrt{3.24} = 1.80$). Model selection criteria would favor simpler models. In this case, the best approximating model would be a 3 parameter model that includes the daily and 1 day lag effects of precipitation. The direction and magnitude of these effects are similar to those presented above, but considerable model selection uncertainty (11 models with <2.0 ΔQAICc) masked support for other variables. I suspected that lack of information on nest age may have introduced overdispersion in my data because this variable was shown to be important in similar studies (e.g., Dinsmore et al. 2000). Even with my addition of a parameter indexing nest age based on clutch size and laying rates, c-hat was still 3.05 and the resulting adjustment was not qualitatively different from the adjustment described above. Therefore, it is difficult to discern to what factors the observed overdispersion can be attributed.

DISCUSSION

I simultaneously evaluated the relative support of competing candidate models by using an extension of the Mayfield method (as modified by Johnson 1979). Other studies that have evaluated nest survival in relation to measured habitat characteristics have focused on fine-scale features of nest sites (e.g., Wallestad and Pyrah 1974; Connelly and others 1991; Gregg and others 1994). I built off those findings to consider the influence of habitat, environmental, and individual hen and nest characteristics on nest success at the landscape scale.

All previous published studies of sage grouse nest success report apparent nest success rates (Wallestad and Pyrah 1974, Connelly et al. 1993, Gregg et al. 1994, Schroeder 1997, Aldridge 2003). I demonstrated that apparent nest success can be biased high and may lead to erroneous interpretations of productivity. The apparent nest success rate of 0.46 is markedly higher than any of my seasonal estimates for average habitat and observed precipitation conditions, which range from 0.24 to 0.32 for early nests and 0.32 to 0.42 for late nests. Because this is the first landscape-scale assessment of sage grouse nest success, and no other studies have considered such covariates, the results presented here are unique. My analysis of factors influencing nest success leads to a dramatically different and more detailed understanding of variation within and among years, indeed among days, as affected by environmental, habitat, and individual covariates.

Yearly variation in nest success was likely related to nesting effort, precipitation, and habitat conditions. The estimated effect of precipitation on DSR was positive and the 1-day lag effect was negative, with the relative effect of precipitation being greater than that of the lag effect. As a result, the net effect of precipitation over the course of a season can be either positive or negative, depending upon timing, amount, and number of consecutive days with precipitation.

DSR was influenced both positively and negatively by rain events. I reasoned that hen attendance was high and predator activity was low on days with rain, resulting in an increase in DSR for that day. On the day after a rain event, however, the likely increase in both hen foraging and predator activity would result in decreases in DSR. Most nest failures (94%) were attributed to depredation, and most nest depredations (63%) were attributed to avian predators. I suspected that California gulls were the primary avian predator. Gulls in the study area were associated with Fort Peck Lake, the Missouri River, and stock ponds; however, they were regularly observed away from open water, particularly in the several days immediately after rain when they foraged in large flocks (20-100 individuals) for crickets (*Gryllus* spp.) on clayey sagebrush flats with a sparse grass understory (B. Moynahan, personal observation). Crows, ravens, and magpies were present on the study area, though apparently in low numbers and sparsely distributed. Regardless of the predator species, I suspect that avian depredations are opportunistic – i.e., potential avian predators flying overhead may observe a single hen leaving a nest bush or foraging nearby, land, and search.

Several terms that I thought during the study design phase might be important received virtually no support in my analyses. Models with shrub CC, Robel values, and site specificity performed poorly in general. Possible explanations for the lack of support for these terms include that (1) landscape-scale effects of shrub CC and visual obstruction (Robel values) on nest survival truly did not exist across the range of values observed (Table 3), i.e., there truly were no site differences, (2) my site definition (5 km-radius buffer around active leks) is too small for this large area of relatively intact and contiguous sagebrush habitat, or (3) that my vegetation sampling design failed to capture true site differences at the appropriate scale. I believe that the first explanation is the most plausible. While I detected annual change in vegetation elements over time (particularly for forb CC and Robel values, Table 3) and across sites (particularly grass CC, forb CC, and Robel values), site differences in the mean shrub CC category were small and not as distinct as I had anticipated based on my site selection process using a GIS with the available sagebrush coverage layer (CMR: 9.46 [SE = 1.61], Sun Prairie: 11.25 [SE = 1.14], Little Horse: 8.90 [SE = 1.09], Dry Fork: 10.56 [SE = 1.12]). Further, these observed mean sagebrush CC values are below the known detection threshold of the classification process (approximately 15-20% CC for sagebrush) that was used to select sites and assign a relative ranking, but are capable of supporting populations of sage grouse across extensive areas. I would not expect sage grouse vital rates to be detectably influenced by site-specific shrub coverage within such a narrow range. However, in landscapes where shrub coverage is more variable or fragmented the influence of shrub coverage in general and sagebrush coverage in particular could have a greater effect. The lack of support for the Robel term may be due to nest fate being more influenced by nest site visual obstruction values than landscape values, i.e., selected nest sites may have more or less visual obstruction than mean landscape values.

The effect of grass on nest survival was in the best model but it was not precisely estimated and the direction of the effect was equivocal over the narrow range of grass CC observed. This inconsistency raises the question of other complexities in 2003 that were not adequately captured by the selected habitat metrics. More structural cover existed in 2003 by the coincidence of early season precipitation and the biannualism of sweet clover, but the most dramatic clover growth did not occur until mid- to late-season. The tall, bushy growth form of sweet clover was likely the single factor that contributed most to the 2003 increase in mean Robel pole readings and a high overall forb CC value. Two *a priori* models were constructed to consider the possibility that grass may have been most important in the absence of sweet clover, but that the forb CC or Robel term might better capture the importance of sweet clover in 2003. These models with year-specificity that included the grass term for 2001 and 2002, but a forb (clover) term in 2003 did not perform well (ΔAICc > 6.25). Two exploratory models that replaced the third year grass term in the best approximating model with forb and Robel terms did not improve fit (increases of 0.89 and 1.58 ΔAICc units). The estimated negative effect of grass in 2003 was effectively compensated for by that year having the highest $\hat{\beta}_i$ for the year term, further indicating unspecified annual variation that was not otherwise captured by precipitation, habitat, or nesting attempt terms. Virtually the entire study area was grazed by cattle and has been historically; I suspect that the magnitude and direction of the grass effect would become clearer were there available ungrazed sites of the size described here, or had the range of variation in observed grass CC values been greater.

Nesting attempt received nearly the same support as the grass term, and the effect of nesting attempt was always positive (renests having higher DSRs than first nests). Relatively low proportion of hens nesting followed by low survival of first nests in 2001 was compounded by the fact that severe drought conditions over 4 previous years and minimal precipitation after mid-June resulted in extremely unfavorable conditions for renesting. No renesting attempts were observed that year. By comparison, the relatively low renesting rate in 2003 was driven largely by relatively high survival of first nest attempts. With minimal data during the pre-incubation laying stage, my inferences are restricted to nest survival after incubation begins. Indeed, nest survival during the laying stage could change once a hen begins regular incubation. It is possible that some undetected nests failed early in laying and pre-incubation, which would result in mis-classification of some actual renests as first nests. However, I am certain of the status of all nests classified as renests because that classification was predicated on the failure of a known prior attempt. If the higher estimated survival of renests relative to first nests is due to some inherent characteristic of the nest itself (and not a seasonality effect, for example; see below), the potential inclusion of some misclassified renests as first nests would slightly inflate my estimate of survival of first nests.

The season date trend term was weakly supported. The effects of nesting attempt and season date trend terms are likely confounded, as second nests generally occur later in the season than first nests. Both of these terms may be related to DSR increasing with vegetation growth and thus nesting cover over time, as well as an increase in availability of alternate prey for predators.

I believe my site-selection process used an appropriate approach but that, in hindsight, the 5-km-radius buffer may have been too small because approximately 40% of all nests monitored were located farther than 5 km from the lek at which hens were trapped. Most habitats used by nesting hens that were farther than 5 km from the lek at which they were trapped were captured by vegetation plots centered around adjacent leks that were included in the same lek complex (i.e., in these instances, the nearest lek was not the same as the trapped-at lek), but the sample of nesting hens used a somewhat larger area than was characterized by my vegetation sampling protocol. It is possible that site habitat characterization may have been different had I used a larger radius around leks, though this seems unlikely.

Several previous studies also documented higher nesting probability for adults than for sub-adults (Gregg 1991, Connelly et al. 1993); others have recorded nearly all hens nesting regardless of age class (Schroeder 1997). I observed lowest nesting probability in 2001 when the study area was affected by severe drought and there was very little growth of non-sagebrush food items (i.e., forbs). Nesting probabilities increased markedly in 2002 and 2003 when range conditions improved. This pattern, coupled with the lower mean clutch sizes observed in 2001, supports the notion that better range condition may result in improved condition of pre-laying hens and thus higher nesting probabilities (Barnett and Crawford 1994). Virtually no chicks survived the 2001 breeding season, leaving very few sub-adults in the next spring's breeding population (see Chapter 2). Nesting and renesting effort exhibited by a population is, therefore, influenced by current environmental conditions as well as by the previous year's productivity; high nesting effort in 2002 is attributable both to favorable environmental conditions that year as well as the fact that nearly all hens were adults with correspondingly high nesting and renesting probabilities and clutch sizes.

Reported renesting rates for sage grouse vary widely (Connelly et al. 2000) and likely are greatly affected by weather conditions in at least the three different ways observed here: no renesting in a dry year with little current year's vegetative growth (2001); relatively high renesting effort when habitat conditions were more favorable, but first nest survival rates were moderate (2002); and lower when conditions were favorable and relatively high survival of first nests precluded many hens from renesting (2003). No other studies of sage grouse nesting have documented age-specific differences in renesting probability that I observed (e.g., Connelly et al. 1993, Connelly et al. 2000).

My estimate of overdispersion (deviance/degrees of freedom) is known to be a positively biased estimate of overdispersion because this value is only asymptotically chi-squared distributed, but I know of no other means to quantify the potential effects of heterogeneity and lack of independence in my data (Anderson et al. 1994). Nonetheless, I recognize that this is an imperfect adjustment for model selection criteria and sampling variances and true amount of extra-binomial variation is somewhere between my estimate and none. Indeed, in a recent paper on advanced techniques for modeling nest survival (Dinsmore et al. 2002), overdispersion was not quantified or used to adjust model selection criteria or sampling variances so I do not attempt to resolve this issue here. Additional research on model fit and realistic solutions to the effects of overdispersion (Natarajan and McCulloch 1999) are still needed.

MANAGEMENT IMPLICATIONS

Sage grouse nest success is generally high, though managers should expect considerable annual variation. Managers should work to ensure high annual hen survival by ensuring that (1) harvest levels do not affect the number or age-structure of spring breeding populations and (2) that winter habitats are clearly identified and actively conserved (see Chapter 3). The observed variation in nesting effort, renesting effort, and clutch size demonstrate that management should further encourage identification, conservation, and enhancement of important winter habitat, the availability of which may influence condition of nesting hens and their nesting effort and clutch sizes the following spring.

Researchers and managers should be aware of the problems posed by apparent nest success rates. Such rates are likely to be biased high and cannot offer insights into the factors or mechanisms affecting nest success. Apparent nest success rates are therefore not reliable and may not accurately inform management.

There was strong support for the conclusion that DSR of nests in this study varied with precipitation with 1-day lag, year, attempt, and grass CC at the landscape scale considered here. Though wildlife and land managers have no control over precipitation, they would do well to maintain or enhance herbaceous understory conditions favorable for survival of first nests and that remain intact for later-season renesting attempts. Land uses that reduce contributions of herbaceous vegetation to visual obstruction of sage grouse nests (including grazing) may reduce nest survival at the landscape scale by resulting in increased depredation.

The threat of continued habitat loss and alteration and disturbance to nesting hens due to oil and natural gas development is substantial (USFWS 2004). While existing energy development in north-central Montana is minimal, future development is likely and has already been intense and expansive in the Powder River Basin of Wyoming and southeast Montana. Wholesale loss of habitat due to surface activity, coupled with effective fragmentation due to construction of fences, power lines, and roads and apparent avoidance by sage grouse of such structures (Braun 1998), reduces and degrades available nesting and brood rearing habitat (Connelly et al. 2000). This is underscored by the threat of West Nile virus because nest and chick survival will become relatively more important to annual and long-term population maintenance should increased adult mortality, as first documented for sage grouse in 2003 (Naugle et al. 2004), persist.

Condition of summer and winter habitats will likely vary with intensity of grazing, species of grazer (and relative preference for grass, i.e., cattle, or forbs, i.e., sheep), species composition of the herbaceous community, and annual and seasonal precipitation. Future research should further explore the influence of sagebrush and grass cover on nest success. Selection of study sites with greater variation in those habitat elements and in grazing regimes may be better able to describe the effect of those habitat elements.

LITERATURE CITED

Aldridge, C. L. and R. M. Brigham. 2003. Nesting and reproductive activities of Greater Sage-Grouse in a declining northern fringe population. Condor 103:537-543.

Anderson, D. R., K. P. Burnham, A. B. Franklin, R. J. Gutierrez, E. D. Forsman, R. G. Anthony, G. C. White and T. M. Shenk. 1999. A protocol for conflict resolution in analyzing empirical data related to natural resources controversies. Wildlife Society Bulletin 27:1050-1058.

Anderson, D. R. and K. P. Burnham. 1994. AIC model selection in over-dispersed capture-recapture data. Ecology 75:1780-1793.

Barnett, J.F. and J.A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal of Range Management 47:114-118.

Bart, J. and D. S. Robson. 1982. Estimating survivorship when the subjects are visited periodically. Ecology 63:1078-1090.

Bradbury, J. W., R. M. Gibson, C. E. McCarthy, and S. L. Vehrencamp. 1989a. Dispersion of Displaying Male Sage Grouse II. The Role of Female Dispersion. Behavioral Ecology and Sociobiology 24(1):15-24.

Bradbury, J. W., S. L. Vehrencamp, and R. M. Gibson. 1989b. Dispersion of Displaying Male Sage Grouse I. Patterns of Temporal Variation. Behavioral Ecology and Sociobiology 24(1):1-14.

Braun, C. E. 1998. Sage Grouse declines in western North America: what are the problems? Proc. West. Assoc. State Fish and Wildl. Agencies. 78:139-156.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, NY.

Connelly, J. W., H. W. Browers, and R. J. Gates. 1988. Seasonal Movements of Sage Grouse in Southeastern Idaho USA. Journal of Wildlife Management 52(1):116-122.

Connelly, J. W., R. A. Fischer, A. D. Apa, K. P. Reese, and W. L. Wakkinen. 1993. Renesting by sage grouse in southeastern Idaho. Condor 95(4):1041-1043.

Connelly, J. W., W. L. Wakkinen, A. D. Apa, and K. P. Reese. 1991. Sage Grouse Use of Nest Sites in Southeastern Idaho, USA. Journal of Wildlife Management 55(3):521-524.

Connelly, J. W. and C. E. Braun. 1997. Long-term changes in Sage Grouse populations in western North America. Wildlife Biology 3:229-234.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse habitats and their populations. Wildlife Society Bulletin 28(4):967-985.

Crunden, C. W. 1963. Age and sex of grouse from wings. Journal of Wildlife Management 27:846-849.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83(12):3476-3488.

Dunn, P. O. and C. E. Braun. 1985. Natal Dispersal and Lek Fidelity of Sage Grouse Centrocercus-Urophasianus. Auk 102(3):621-627.

Eng, R. L. 1955. A method for obtaining Sage Grouse age and sex ratios from wings. Journal of Wildlife Management 19:267-272.

Eng, R. L. and P. Schladweiler. 1972. Sage Grouse Winter Movements and Habitat Use in Central Montana. Journal of Wildlife Management 36(1):141-146.

Fischer, R. A., A. D. Apa, W. L. Wakkinen, K. P. Reese, and J. W. Connelly. 1993. Nesting-area fidelity of sage grouse in southeastern Idaho. Condor 95(4):1038-1041.

Gibson, R. M. 1992. Lek Formation in Sage Grouse the Effect of Female Choice On Male Territory Settlement. Animal Behaviour 43(3):443-450.

Gibson, R. M. 1996. Female choice in sage grouse: The roles of attraction and active comparison. Behavioral Ecology and Sociobiology 39(1):55-59.

Gibson, R. M., C. E. Taylor, and D. R. Jefferson. 1990. Lek formation by female choice: a simulation study. Behavioral Ecology 1:36-42.

Giesen, K. M., T. J. Schoenbert, and C. E. Braun. 1982. Methods For Trapping Sage Grouse Centrocercus-Urophasianus in Colorado, USA. Wildlife Society Bulletin 10(3):224-231.

Gregg, M. A., J. A. Crawford, M. S. Drut, A. K. Delong. 1994. Vegetational cover and predation of sage grouse nests in Oregon. Journal of Wildlife Management 58(1):162-166.

Hanna, W.C. 1936. Sage Grouse breeding in California. Condor 38:38.

Hilborn and Mangel. 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, New Jersey.

Johnson, D. H. 1979. Estimating nest success: they Mayfield method and an alternative. Auk 96:651-661.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. The Auk 118(2):557-562.

Klett, A. T. and D. H. Johnson. 1982. Variability in nest survival rates and implications to nesting studies. Auk 99:77-87.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: case studies and recent advances. Ecological Monographs 62:67-118.

McCullagh, P. and J. A. Nelder. 1989. Generalized linear models. Chapman and Hall CRC, Washington, D.C., USA.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2004a. Factors affecting survival of Greater Sage-Grouse broods in north-central Montana. In preparation.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2004b. Factors affecting survival of Greater Sage-Grouse hens in north-central Montana. In preparation.

Natarajan, R. and C. E. McCulloch. 1999. Modeling heterogeneity in nest survival data. Biometrics55:553-559.

Naugle D.E., B.L. Walker, Aldridge, C.L., T.E. Cornish, B.J. Moynahan, M.J. Holloran, K. Brown, G.D. Johnson, E.T. Schmidtman, R.T. Mayer, C.Y. Kato, M.R. Matchett, T.J. Christiansen, W.E. Cook, M.S. Boyce, and E.T. Rinkes. 2004. West Nile virus: An emerging issue in sage-grouse conservation. Ecology Letters 7:704-713.

Patterson, R. L. 1952. The Sage Grouse in Wyoming. Denver, CO: Sage Books, Inc.

Peterson, B. E. 1980. Breeding and nesting ecology of female Sage Grouse in North Park, Colorado. Fort Collins, CO: Colorado State University.

Remington, T. E. and C. E. Braun. 1985. Sage Grouse Centrocercus-Urophasianus Food Selection in Winter North Park Colorado USA. Journal of Wildlife Management 49(4):1055-1061.

Schroeder, M.A. 1997. Unusually high reproductive effort by sage grouse in a fragmented habitat in north-central Washington. Condor 99(4):933-941.

Schroeder, M.A, J. R. Young, and C. E. Braun. 1999. Sage Grouse: *Centrocerus urophasianus*. In: Poole A, Gill F, editors. Birds of North America. Philadelphia, PA: The Birds of North America, Inc. p 1-28.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2003. Effects of habitat fragmentation on avian nest success: a review of the evidence at multiple spatial scales. Biological Conservation 115:101-110.

Sveum, C. M., J. A. Crawford, and W. D. Edge. 1998a. Use and selection of brood-rearing habitat by sage grouse in south central Washington. Great Basin Naturalist 58(4):344-351.

Sveum, C. M., W. D. Edge and J. A. Crawford. 1998b. Use and selection of brood-rearing habitat by Sage Grouse in south-central Washington. Great Basin Naturalist 58:344-351.

U. S. Fish and Wildlife Service. 2004. 90-day finding for petitions to list the Greater Sage-Grouse as threatened or endangered. 50 CFR 17, 69(77):21484-21494.

Wakkinen, W. L., K. P. Reese and J. W. Connelly. 1992. Sage Grouse nest locations in relation to leks. Journal of Wildlife Management 56:381-383.

Wallestad, R., J. G. Peterson JG and R. L. Eng. 1975. Foods of Adult Sage Grouse in Central Montana Usa. Journal of Wildlife Management 39(3):628-630.

Wallestad, R. and D. Pyrah. 1974. Movement and Nesting of Sage Grouse Hens in

Central Montana USA. Journal of Wildlife Management 38(4):630-633.

Wallestad, R. and P. Schladweiler. 1974. Breeding Season Movements and Habitat Selection of Male Sage Grouse. Journal of Wildlife Management 38(4):634-637.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: Supplement:120-138.

Figure 1. South Phillips County, Montana study area. Black circles represent locations of four study sites. CMR = Charles M. Russell National Wildlife Refuge site, DF = Dry Fork site, LH = Little Horse site, and SP = Sun Prairie site.

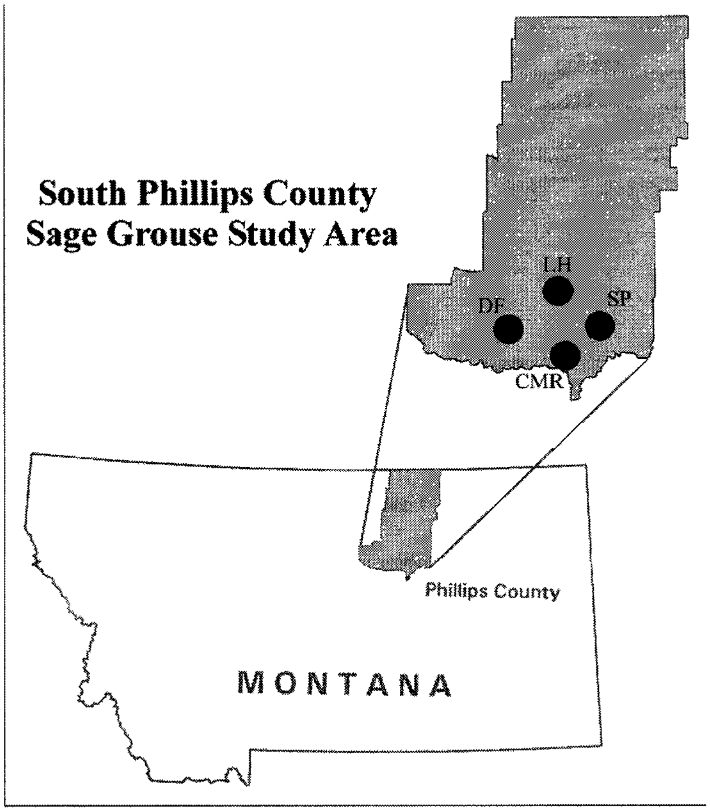

Figure 2. Daily precipitation in south Phillips County, Montana in 2001-2003. Day 1 corresponds to April 22 and day 79 corresponds to July 10. Precipitation recorded in tenths of inches.

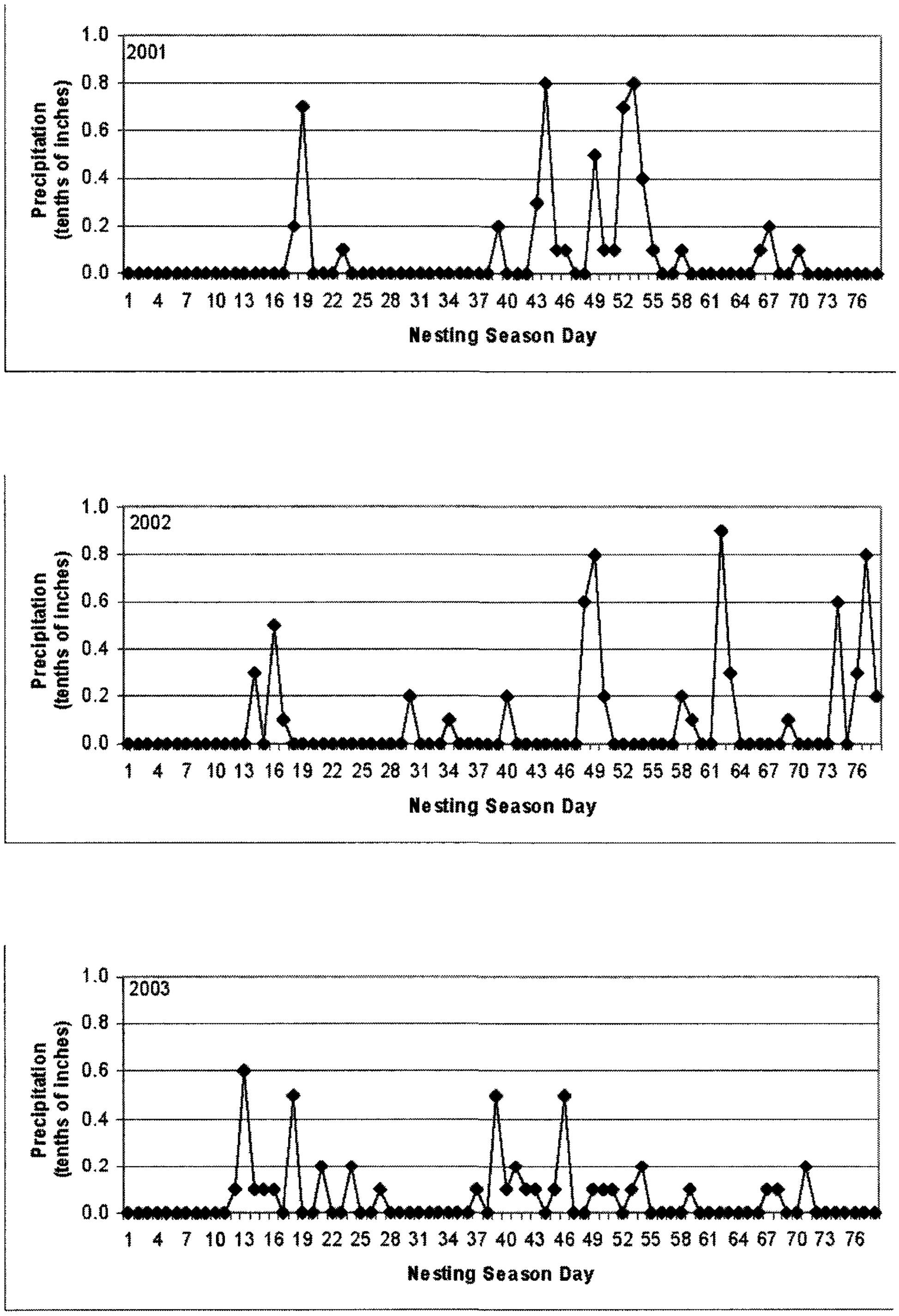

Figure 3. Estimates of Daily Survival Rates (DSR) of Greater Sage-Grouse nests in south Phillips County, Montana during 2001-2003. Day 1 represents April 22 and Day 78 represents July 10. Error bars represent 95% confidence intervals. Upward spikes in DSR represent the effect of daily precipitation and downward spikes represent a 1-day lag effect of precipitation.

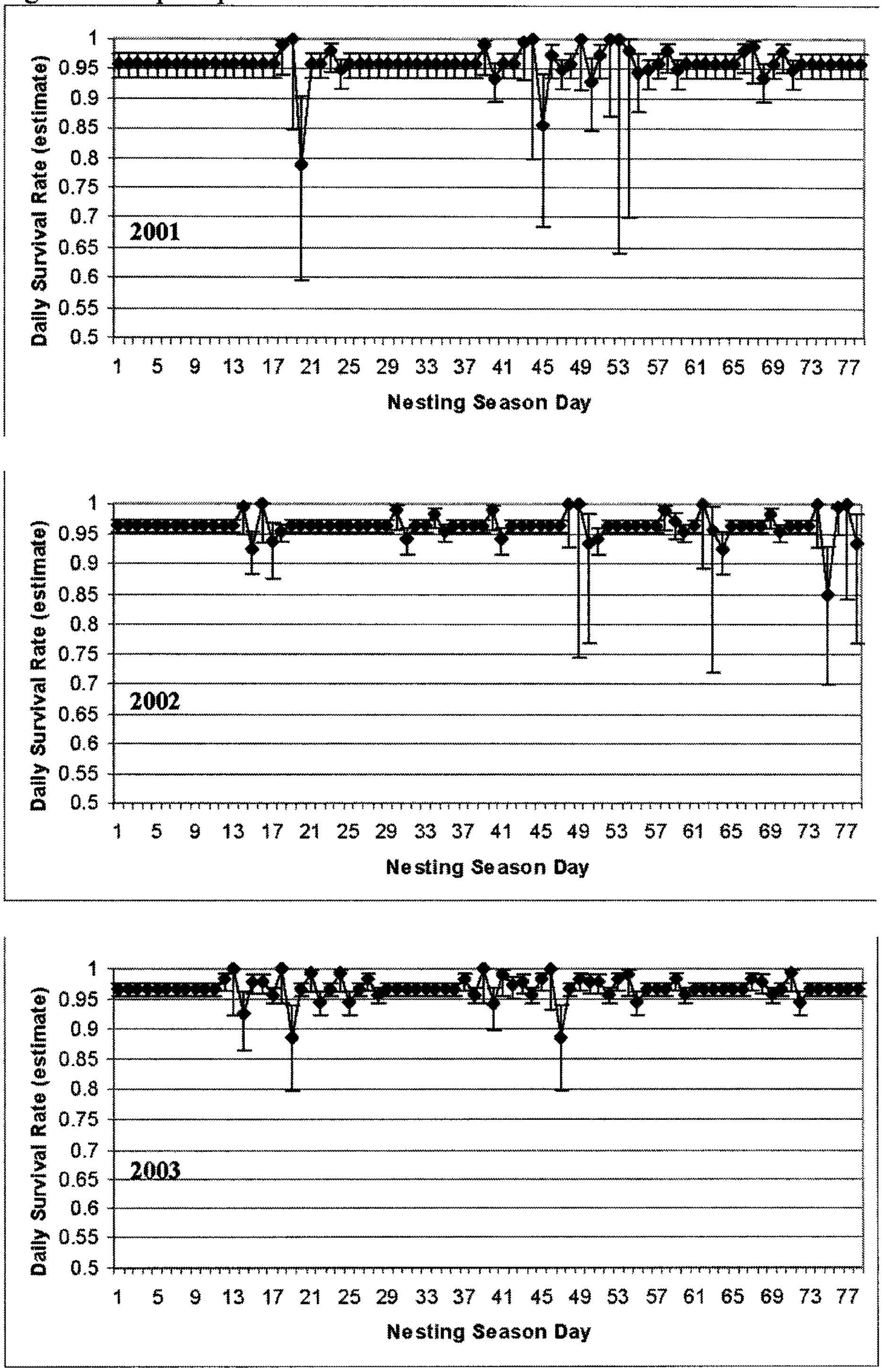

Figure 4. Estimates of Greater Sage-Grouse nest success in south Phillips County, Montana during 2001-2003. Using estimates of DSR from the best-approximating model, early nests are the product of the first 28 DSRs for each nesting season and late nests are the product of the last 28 DSRs of the observed nesting season for each year (up to day 49 in 2001, day 79 in 2002, and day 78 in 2003, where day 1 represents April 22 and day 78 represents July 10). Model inputs included mean annual grass CC, daily precipitation, 1-day lag effect of daily precipitation. Late nests for 2002 and 2003 were coded as renests. Error bars represent standard errors.

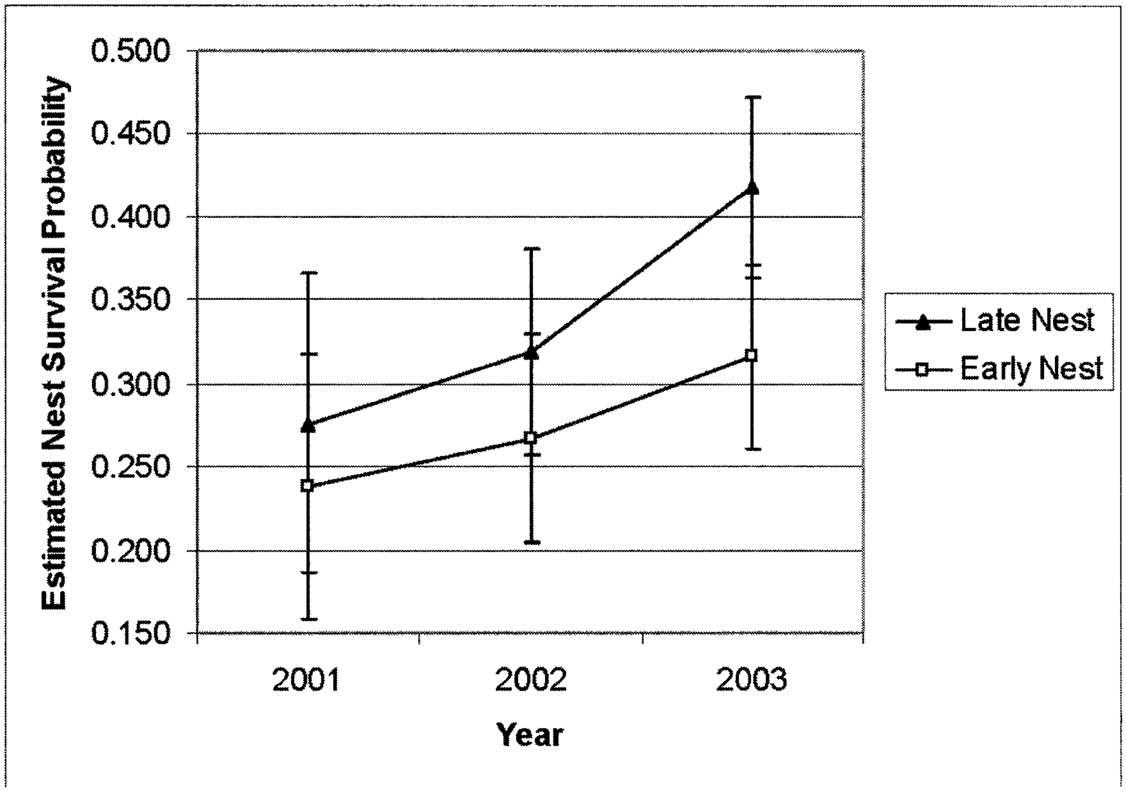

Table 1. Total number, fate, and apparent causes of failure of sage grouse nests found in south Phillips County, Montana during 2001-2003. First nests and renests are designated for adults and sub-adult birds as (# successful / total number).

	Adults		Sub-Adults			Cause of Failure		
	First Nests	Renests	First Nests	Renests	# Failed	Predator	Abandoned	Non-viable
2001	10/22	0/0	2/12	0/0	22	20	2	0
2002	30/66	11/20	3/10	3/3	52	50	2	0
2003	33/68	7/16	18/37	2/4	65	61	3	1
Total	73/156	18/36	23/59	5/7	139	131	7	1

Table 2. Observed nesting probabilities (proportion of individuals across all years that were detected initiating at least one nest) and renesting probabilities (proportion of hens across all years detected initiating a second nest given a failed first nest) (± SE) by age for sage grouse in south Phillips County, Montana during 2001-2003. These probabilities only represent data from hens in the year they were trapped (n = 217).

	Nesting Probability		Renesting Probability	
	Adults	Sub-adults	Adults	Sub-adults
2001	0.80 ± 0.0021	0.63 ± 0.010	0.0 ± 0.0	0.0 ± 0.0
2002	0.97 ± 0.0004	1.00 ± 0.0	0.56 ± 0.007	0.43 ± 0.035
2003	1.00 ± 0.0	0.62 ± 0.005	0.46 ± 0.007	0.21 ± 0.009
All Years	0.93 ± 0.0005	0.78 ± 0.002	0.43 ± 0.003	0.19 ± 0.004

Table 3. Observed habitat and environmental values (mean ± SE) at south Phillips County, Montana during 2001-2003.

Year	2001	2002	2003
Robel[a]	4.97 ± 0.22	4.60 ± 0.22	7.24 ± 0.39
Shrub[b]	11.68 ± 0.65	10.02 ± 0.67	8.75 ± 0.65
Grass[b]	24.27 ± 1.18	22.00 ± 1.02	22.08 ± 1.09
Forb[b]	3.34 ± 0.27	6.32 ± 0.45	6.25 ± 0.65
Precipitation[a]	14.5	16.5	12.4
DMT[c]	7.84 ± 0.53	5.52 ± 0.75	7.14 ± 0.53

[a] centimeters

[b] Percent canopy cover

[c] Daily minimum temperature, °C

Table 4. Correlation matrix for measured habitat elements in south Phillips County, Montana, 2001-2003. Reported values are correleation coefficients (r2) of simple linear regressions for listed element pairings.

Year	Grass:Forb	Grass:Shrub	Shrub:Forb
2001	0.0099	0.0285	0.0117
2002	0.0029	0.0704	0.0375
2002	0.0003	0.0037	0.0353

Table 5. Models of Daily Survival Rate (DSR) of Greater Sage-Grouse nests found in south Phillips County, Montana during 2001-2003. Models are ranked by differences in AIC values.

Model	#Param	ΔAICc	AICc	AICc Weight	Deviance
Year*Grass+Precip+PrecipLag+Attempt	9	0	754.415	0.21814	736.366
Precip+ PrecipLag	3	2.04	756.455	0.07867	750.448
Year*Grass+Attempt	7	2.18	756.593	0.07343	742.562
Year*Grass+Precip+ PrecipLag	8	2.51	756.928	0.06211	740.888
Season T + Precip + PrecipLag	4	2.56	756.97	0.06079	748.959

Table 6. Point estimates and standard errors for the best-approximating model of Daily Survival Rate (DSR) of Greater Sage-Grouse nests found in south Phillips County, Montana during 2001-2003.

				95% Confidence Interval	
Parameter Number	Label	Estimate	Std. Error	Lower	Upper
1	Year 2001	3.1537	0.2658	2.6327	3.6748
2	Year 2002	3.2924	0.1638	2.9714	3.6135
3	Year 2003	3.3694	0.1823	3.0120	3.7267
4	Grass 2001	0.1199	0.1624	-0.1984	0.4383
5	Grass 2002	0.2854	0.1262	0.0380	0.5327
6	Grass 2003	-0.4744	0.2177	-0.9010	-0.0477
7	Daily Precip	7.2568	4.4097	-1.3863	15.8999
8	1-d Lag of Daily Precip	-2.6228	0.7388	-4.0709	-1.1747
9	Nesting Attempt	0.1961	0.0966	0.3853	0.0068

Appendix A. Full list of candidate models of Daily Survival Rate (DSR) of Greater Sage-Grouse nests found in south Phillips County, Montana during 2001-2003. Models are ranked by differences in AIC values.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(Year*Grass+Precip+PLag+Attempt)}	754.4151	0.000	0.218	1.000	9	736.3657
{Phi(Precip+Plag}	756.4548	2.040	0.079	0.361	3	750.4482
{Phi(Year*Grass+Attempt)}	756.5926	2.178	0.073	0.337	7	742.5619
{Phi(Year*Grass+Precip+Plag)}	756.9275	2.512	0.062	0.285	8	740.888
{Phi(Intercept+SeasonTrend+Precip+Plag)}	756.9704	2.555	0.061	0.279	4	748.9594
{Phi(Year*SeasonTrend+Precip+Plag)}	757.0981	2.683	0.057	0.261	8	741.0586
{Phi(Forb as Site +Attempt)}	758.0987	3.684	0.035	0.159	6	746.0756
{Phi(Attempt)}	758.1649	3.750	0.033	0.153	2	754.1616
{Phi(Shrub+Attempt)}	758.6295	4.214	0.027	0.122	3	752.6229
{Phi(Forb+Attempt)}	758.6833	4.268	0.026	0.118	3	752.6767
{Phi(Robel+Attempt)}	758.8854	4.470	0.023	0.107	3	752.8788
{Phi(Robel as Site+Attempt)}	759.1149	4.700	0.021	0.095	6	747.0919
{Phi(TempMin)}	759.5016	5.087	0.017	0.079	2	755.4983
{Phi(Year+Grass+Precip+Plag+Attempt)}	759.5721	5.157	0.017	0.076	7	745.5414
{Phi(Shrub as Site + Attempt)}	759.8978	5.483	0.014	0.065	6	747.8748
{Phi(Year*SeasonTrend)}	760.2709	5.856	0.012	0.054	6	748.2479
{Phi(Year*(Precip+Plag))}	760.3418	5.927	0.011	0.052	5	750.3254
{Phi(.)}	760.3817	5.967	0.011	0.051	1	758.3806
{Phi(Forb as Site)}	760.3986	5.984	0.011	0.050	5	750.3822
{Phi(Year+Grass01,02,Rob03+Precip+Plag+Attempt)}	760.6674	6.252	0.010	0.044	7	746.6367
{Phi(Year*Attempt, not for 2001)}	760.7896	6.375	0.009	0.041	5	750.7732
{Phi(SeasonTrend)}	760.9171	6.502	0.008	0.039	2	756.9138
{Phi(Year+Grass01,02,Forb03+Precip+Plag+Attempt)}	760.9254	6.510	0.008	0.039	7	746.8947
{Phi(Site+Attempt)}	760.9381	6.523	0.008	0.038	5	750.9216
{Phi(Year+Grass+Precip+Plag)}	760.9645	6.549	0.008	0.038	6	748.9415
{Phi(Year+Grass*Attempt)}	760.9765	6.561	0.008	0.038	6	748.9535
{Phi(precip+TempMin)}	761.098	6.683	0.008	0.035	2	757.0948
{Phi(Year*Robel+Precip+Plag+Attempt)}	761.2065	6.791	0.007	0.034	9	743.1572
{Phi(Precip)}	761.309	6.894	0.007	0.032	2	757.3057
{Phi(Year+Attempt)}	761.463	7.048	0.006	0.030	4	753.452
{Phi(Year*SeasonTrend+precip)}	761.9033	7.488	0.005	0.024	7	747.8726
{Phi(Year+Grass01,02,Rob03+Precip+Plag)}	761.9064	7.491	0.005	0.024	6	749.8834
{Phi(Robel as Site)}	761.9156	7.501	0.005	0.024	5	751.8992
{Phi(Year+Grass+Attempt)}	761.9809	7.566	0.005	0.023	5	751.9644

{Phi(AgeClass)}	762.1424	7.727	0.005	0.021	2	758.1391
{Phi(Year+Grass01,02,Forb03+Precip+Plag)}	762.1736	7.759	0.005	0.021	6	750.1506
{Phi(Forb+AgeClass)}	762.262	7.847	0.004	0.020	6	750.239
{Phi(Forb*Attempt)}	762.2684	7.853	0.004	0.020	9	744.219
{Phi(Shrub as Site)}	762.3328	7.918	0.004	0.019	5	752.3164
{Phi(Sage)}	762.3832	7.968	0.004	0.019	2	758.3799
{Phi(Grass as Site+Attempt)}	762.41	7.995	0.004	0.018	6	750.387
{Phi(Site+AgeClass+Attempt)}	762.8334	8.418	0.003	0.015	6	750.8104
{Phi(precip*TempMin)}	762.8401	8.425	0.003	0.015	4	754.8291
{Phi(Year*Forb*Attempt)}	763.0043	8.589	0.003	0.014	8	746.9648
{Phi(Forb*Year+Attempt)}	763.0418	8.627	0.003	0.013	7	749.0112
{Phi(Forb*Year)}	763.3097	8.895	0.003	0.012	7	749.279
{Phi(Site)}	763.3562	8.941	0.003	0.012	4	755.3452
{Phi(Site+Sage)}	763.3562	8.941	0.003	0.012	4	755.3452
{Phi(Year)}	763.3828	8.968	0.002	0.011	3	757.3762
{Phi(Robel*Year+Attempt)}	763.6294	9.214	0.002	0.010	7	749.5987
{Phi(Robel+AgeClass)}	763.634	9.219	0.002	0.010	6	751.611
{Phi(Year*Shrub+Precip+Plag+Attempt)}	763.7827	9.368	0.002	0.009	9	745.7333
{Phi(Year*Robel*Attempt)}	763.8545	9.439	0.002	0.009	8	747.8151
{Phi(Robel*SeasonTrend)}	763.8593	9.444	0.002	0.009	9	745.81
{Phi(Grass as Site)}	764.1057	9.691	0.002	0.008	5	754.0893
{Phi(Robel*Attempt)}	764.1238	9.709	0.002	0.008	9	746.0744
{Phi(Shrub+AgeClass)}	764.1614	9.746	0.002	0.008	6	752.1384
{Phi(Year+SeasonTrend)}	764.1888	9.774	0.002	0.008	4	756.1778
{Phi(Shrub*Attempt)}	764.3777	9.963	0.002	0.007	9	746.3284
{Phi(Year*Precip)}	764.6728	10.258	0.001	0.006	4	756.6618
{Phi(Shrub*Year)}	764.7962	10.381	0.001	0.006	7	750.7655
{Phi(Year+AgeClass)}	765.0368	10.622	0.001	0.005	4	757.0259
{Phi(Site+AgeClass)}	765.1751	10.760	0.001	0.005	5	755.1587
{Phi(Robel*Year)}	765.4169	11.002	0.001	0.004	7	751.3863
{Phi(2001pooled, else Site*Year)}	765.4194	11.004	0.001	0.004	9	747.37
{Phi(Site*Attempt)}	765.7721	11.357	0.001	0.003	8	749.7326
{Phi(Year*Shrub*Attempt)}	765.7792	11.364	0.001	0.003	8	749.7398
{Phi(Year*AgeClass)}	765.9445	11.529	0.001	0.003	6	753.9215
{Phi(Grass+AgeClass)}	766.0324	11.617	0.001	0.003	6	754.0094
{Phi(Forb*SeasonTrend)}	766.1582	11.743	0.001	0.003	9	748.1088
{Phi(Shrub*Year+Attempt)}	766.195	11.780	0.001	0.003	7	752.1643
{Phi(Site*Year+Attempt)}	767.1062	12.691	0.000	0.002	13	741.0062
{Phi(Grass*Attempt)}	767.3126	12.898	0.000	0.002	9	749.2632

{Phi(Grass*Year)}	767.3728	12.958	0.000	0.002	7	753.3421
{Phi(Forb*AgeClass)}	768.0003	13.585	0.000	0.001	9	749.951
{Phi(Shrub*SeasonTrend)}	768.1531	13.738	0.000	0.001	9	750.1037
{Phi(Site*SeasonTrend)}	768.9469	14.532	0.000	0.001	8	752.9075
{Phi(Robel*AgeClass)}	769.1936	14.779	0.000	0.001	9	751.1442
{Phi(Shrub*AgeClass)}	769.4132	14.998	0.000	0.001	9	751.3638
{Phi(Grass*SeasonTrend)}	769.8921	15.477	0.000	0.001	9	751.8428
{Phi(Site*AgeClass)}	770.1747	15.760	0.000	0.000	8	754.1353
{Phi(Site*Year)}	770.6019	16.187	0.000	0.000	12	746.5163
{Phi(Grass*AgeClass)}	771.3117	16.897	0.000	0.000	9	753.2623
{Phi(Site*Year+AgeClass)}	772.3963	17.981	0.000	0.000	13	746.2964
{Phi(Site*(Attempt+AgeClass)}	772.4791	18.064	0.000	0.000	12	748.3935
{Phi(Site*Year*Attempt)}	772.63	18.215	0.000	0.000	20	732.399
{GLOBAL}	794.4172	40.002	0.000	0.000	41	711.4646

CHAPTER 2: FACTORS AFFECTING BROOD SURVIVAL OF GREATER SAGE-GROUSE IN NORTH-CENTRAL MONTANA

Abstract: Populations of Greater Sage-Grouse (*Centrocercus urophasianus*) have declined by 69-99% from historic levels. Information on population dynamics of these birds at a landscape scale is essential to informed management. I radio-collared 243 female sage grouse, monitored 100 broods, and measured 426 vegetation plots at 4 sites during 2001-2003 in 3,200 km^2 landscape in north-central Montana, USA. My objective was to examine the relationship between brood survival and a suite of landscape-scale habitat and environmental conditions. I used program MARK to model daily survival rates (DSR) of broods as influenced by a variety of habitat and environmental explanatory variables. The best-approximating model only included the effects of brood age and year. Considerable model selection uncertainty existed, though all models scoring < 3 ΔAICc units contained the term for year specificity (∑ΔAICc weights = 0.90). There was also support among top-ranked models for a positive effect of brood age (∑ΔAICc weights = 0.44), though 95% confidence intervals overlapped zero. Based on the top model, estimates of 30-day brood survival probabilities were 0.21 in 2001 (SE = 0.12), 0.69 in 2002 (SE = 0.07), and 0.76 in 2003 (SE = 0.06). Shrub canopy cover, receiving modest support among top-ranked models (∑ΔAICc weights = 0.24), was the only parameter that could potentially be managed for, though the 95% confidence intervals of the estimated effect always overlapped zero. My results suggest that unspecified annual variation in brood survival can be large enough to mask finer effects of habitat variables measured at the landscape scale.

INTRODUCTION

The long-term decline of Greater Sage-Grouse (*Centrocercus urophasianus*, hereafter "sage grouse") over most of their historic range concerns managers of sagebrush (*Artemisia* spp.) habitats of the western U.S. and Canada (Schroeder et al. 1999). The loss and degradation of habitat to expansion of farming and grazing activities are likely the main factors (Connelly and Braun 1997). Other potential factors include changes in fire regimes, predation, over-hunting, weather, disease, and herbicide and insecticide treatments. The U.S. Fish and Wildlife Service (USFWS) issued a positive 90-day finding in April 2004 in response to a range-wide petition to declare sage grouse as "threatened" or "endangered" under the Endangered Species Act. Such determination would likely have substantial impacts on land management and traditional land-use patterns throughout the range of the sage grouse, particularly on federal lands.

Brood survival is one component of reproduction that affects population dynamics. Like nest success (see Chapter 1), brood survival is influenced by habitat and environmental conditions, and potentially by factors related to the individual hen and nest. The specific factors affecting brood survival, however, may be different than for nest success, and management strategies for these two phases of the life cycle are likely different. Therefore, studies on brood survival are needed in addition to studies of nest success.

Though there are numerous studies relative to sage grouse ecology and behavior, there is little information on the influence of landscape-scale habitat and environmental factors on demography in general and brood survival in particular. Some studies of sage grouse population dynamics have focused primarily on reproduction (Peterson 1980;

Remington and Braun 1985; Connelly and others 1988; Gibson 1992; Lebreton et al. 1992; Wakkinen and others 1992; Gibson 1996; Sveum et al. 1998a; Sveum et al. 1998b). Precise estimates of chick and brood survival are elusive because chicks' precocial nature and cryptic coloration make accurate chick counts difficult.

Jones (2001) suggested that the next step in the development of avian habitat selection research must incorporate both habitat and demographic information into landscape-scale conservation planning. Despite information on general sage grouse ecology and the well-known geographic and temporal variation in reproductive parameters (Schroeder et al. 1999, Connelly et al. 2000), no studies have simultaneously assessed a wide range of biotic and abiotic factors suspected to affect chick or brood survival at the landscape scale. For these reasons, and because future sage grouse conservation and management will likely apply habitat prescriptions over large areas (thousands or tens of thousands of hectares) through manipulation of land-use patterns, it is important to consider factors affecting brood survival at the landscape scale.

High plant species richness and abundant forbs often characterize brood-rearing areas, though a wide variety of habitats may be used (Dunn and Braun 1986, Klott and Lindzey 1990, Connelly et al. 2000). Early brood rearing often occurs in upland sagebrush habitats near nest sites, though movements of individual broods vary (Connelly 1982). Broods move to more mesic sites during late summer, making use of green draws, wet meadows, and irrigated fields (Connelly and Markham 1983, Connelly et al. 1998, Connelly et al. 2000). Insects and forbs are essential food items for chicks before they shift to a sagebrush diet during their first fall (Peterson 1970, Wallestad et al. 1975, Drut et al. 1994). Survival of chicks and broods is believed to exhibit considerable annual variation, though the factors influencing this variation are less clear (Connelly and Braun 1997).

Land uses across central and eastern Montana are spatially divergent and range from cropland to various grazing intensities to relatively undisturbed sagebrush-steppe habitats. Avian and mammalian predator assemblages and abundances vary across this heterogeneous landscape, increasing variation in population characteristics. The region is characterized by wet/dry cycles of varying lengths and intensities, which affect sagebrush, grass, and forb growth. Therefore, high levels of spatial and temporal variation produce complex interactions of factors influencing sage grouse vital rates both within and among years. My objective was to estimate sage grouse brood survival rates in north-central Montana as influenced by a variety of habitat and environmental factors.

STUDY AREA

I studied sage grouse on a 3,900 km^2 area in southern Phillips County in north-central Montana (47° 33' N—48° 01' N, 107° 32' W—108° 33' W, Fig. 1 in Chapter 1); general characteristics of the study area are described in Chapter 1. I selected four study sites within the study area: CMR, Sun Prairie, Little Horse, and Dry Fork. The study area represents some of the most expansive, contiguous and intact sagebrush-steppe habitats in Montana with relatively large sage grouse populations.

METHODS

Methods for study site selection, location and monitoring of nests, and vegetation sampling are identical to those described in Chapter 1. I marked hens with radio transmitters to facilitate later location of nests. Hens were trapped primarily by rocket-netting and spotlighting (Giesen et al. 1982) from all-terrain vehicles and on-foot between mid-March and mid-April 2001-2003. Each hen was fitted with a necklace-type radio transmitter (2001-Telemetry Solutions®, 2002-2003-Advanced Telemetry Systems®, model A4080), a numbered metal leg band, and with an individually coded plastic band. Each transmitter weighed 22 g, had an expected life of 383 days, and could be detected from the ground and air from approximately 2-5 km and 6-10 km, respectively.

Due to extreme variation in chick counts (see Discussion) and concerns about lack of independence of fates of chicks within a brood, I used the brood as the sampling unit. Broods were visited typically every 4 days (range 1-14 days) by relocating radio-marked hens until the brood reached ≥ 30 days of age or failed. I visually located the hen before approaching to count chicks. Hens often walked, feigned injury, or flew a short distance when approached, and most hens stayed within 50-200m when chicks were present. I searched at and near the hens roost or brooding site to locate and count chicks for the first 10-14 days. Chicks can fly weakly by 10 days of age (Girard 1937, Schroeder 1999), and I began flush counts when chicks were >10 days old. Flush counts were always augmented with visual searching to located chicks that didn't fly, unless the initial flush count equaled the maximum number of chicks in the brood (i.e., number of eggs at full clutch).

When a count of zero chicks was recorded for a brood, I revisited ≥ 3 additional times before recording fate as failed. Failure was determined when no chicks were observed and when one of the following occurred: the hen made a large (>3 km) movement, was observed to flock with other non-brooding hens, or died. When these conditions were met I recorded date of brood failure as the date of the first zero count.

Hen behavior (feigning wing injury, slowly walking from the observer while "clucking," or flushing only a short distance [5-30 m]), sometimes indicated that a brood was present even when no chicks were counted. In these cases, I followed broods for additional visits. When such behavior was observed on the last scheduled brood observation (at 30 days of age), I revisited the brood beyond 30 days to confirm brood fate. The brood was recorded as having survived to day 30 if a non-zero count was obtained on or before the brood was 35 days old. If brood fate could not be determined before age 35 days (e.g., due to difficulty in obtaining a non-zero count, hen and brood moving onto land for which I did not have access permission), only data up to the last non-zero count was used. In applying these steps, I was assured of not introducing unknown fate data into my known fate modeling process.

Data Analysis

I used an information-theoretic approach (Burnham and Anderson 1998) to simultaneously evaluate relative support of multiple models describing relationships between daily survival rate (DSR) of a brood and variables of interest. I began by generating candidate models that described competing hypotheses about brood survival. Each model represented the DSR of the brood as a function of some combination of biotic and abiotic sources of variation: year, site, brood age, season date, age of the brooding hen, nest attempt (first nest or renest), four habitat metrics (shrub, grass, and forb canopy cover [CC] and Robel pole readings), daily precipitation and minimum daily temperature (from a weather station near the center of the study area).

Year and site terms account for variation (e.g., regional weather patterns) not attributable to other specified sources of variation. Average brood size declines in the weeks post hatch (see Schroeder et al. 1999) so I modeled brood age to allow for age-specific variation in survival. I modeled season date as a logit-linear trend and nesting attempt (as a binomial term for first nest or renest) to examine seasonality in DSRs not attributable to brood age. The hen age term (adult [≥ 2 years old] or subadult [1 year old]) accounted for the possibility that hens with more breeding experience might be more successful at raising broods. Daily precipitation and minimum daily temperature might singly or synergistically affect survival by challenging a hen's ability to effectively shelter her brood on wet and/or cold days.

I selected Robel pole readings and shrub, grass, and forb CC for habitat covariates. Robel readings represent the maximum height of complete visual obstruction (Robel et al. 1970), effectively combining vegetation height and density. I used the category of "shrub" rather than only considering sagebrush because sagebrush accounted for ~85% of shrubs in vegetation plots. Residual and green grass cover together contributed visual obstruction structure to brood-rearing sites, helping to obscure chicks and brooding hens from predators. Forbs and insects associated with forbs are essential chick forage (Connelly et al. 2000). Shrub, grass, and forb data were included in the form of mean CC per site per year. Depending on how each habitat covariate was included in model structure, it could exhibit site or year specificity or both. Daily precipitation and temperature data were obtained from the Western Regional Climate Center, Malta, Montana 35S station (station number 245340).

I constructed two *post-hoc* exploratory models to examine whether the year effect might be better described by seasonal precipitation. Though several *a priori* models examined the effect of daily precipitation events, these exploratory models considered cumulative precipitation over several months prior to the nesting and brood-rearing seasons by substituting winter (January through February) and winter-spring (January through May) precipitation for the year term.

I standardized season dates among years by using the earliest hatching date for any year as the first day of the brood season and the latest observation date in any year as last day of the season. I thus defined an 87 day brood season beginning 13 May and ending 7 August. This season comprised 86 daily intervals for which DSR was estimated. Nesting attempt was confounded with season date, so I considered these variables separately. Effect of nest attempt was not considered for 2001 as I observed no renest attempts that year.

I used the nest survival module in program MARK (White and Burnham 1999), a type of known-fate analysis, to generate point estimates of daily survival rates (DSR) and their precision to evaluate relative support for candidate models given observed data. This nest survival module allows for variable visitation schedules. Program MARK uses generalized linear models (McCullaugh and Nelder 1989) with a user-specified link function to generate maximum-likelihood estimates of regression coefficients and their associated sampling variances and covariances. I used the logit link function and binomial error distribution. This approach extends earlier survival models (Johnson 1979, Bart and Robson 1982) by permitting direct evaluation of the influence of hen-specific covariates—including daily covariates like brood age, precipitation, or ambient temperature—on DSR (Dinsmore et al. 2002). Individual models were evaluated using Akaike's Information Criterion (AIC) and AIC weights (Burnham and Anderson 1998).

To assure accurate estimation of DSR, five general assumptions must be met: (1) brood ages are correctly determined (for models including that term), (2) brood fates are known with certainty, (3) investigator activity does not influence brood fate, (4) fates of broods are uncorrelated, and (5) there is no heterogeneity in survival among broods (Dinsmore et al. 2002). Hatching date, and thus brood age, was known to us. For broods whose fate was unknown at 30 days (e.g., broods that moved onto inaccessible private property after several observations), I included data only up to the point for which fate was certain. Broods with unknown fates were not included in the analysis. I reduced the potential effect of my visits on brood survival by scheduling revisits at 4-7 day intervals, and spending as little time searching for chicks as possible. I used the difference in the log-likelihood of the saturated and most general (most parameters) model (deviance) divided by the deviance degrees of freedom (i.e., difference in number of parameters between models) as an estimate of overdispersion (c-hat; Anderson and Burnham 1994). This estimate of c-hat is positively biased, but is the only goodness-of-fit diagnostic reasonably available for these models. Potential effects of overdispersion on model selection and estimates of sampling variance (Anderson and Burnham 1994) were considered.

I used back-transformed estimates of DSR,

$$\hat{\mathrm{DSR}}_{\mathrm{i}} = \frac{1}{1+\exp(-(\hat{\beta}_0 + \hat{\beta}_1 X_1, \ldots, \hat{\beta}_i X_j))}$$

, where the $\hat{\beta}_i$ are the estimated regression coefficients from the model and the X_j are the values of the independent variables (e.g., brood age, daily precipitation). I calculated estimates of brood survival to 30 days as the product of the 30 DSRs beginning on hatch date (Johnson 1979). Sampling variances of brood survival were estimated with the Delta Method (Seber 1982).

RESULTS

I monitored 117 broods. Histories of 2 broods were discarded because the broods were not available for observation after hatch date (both moved onto private land for which I did not have permission to access). I included 115 broods in the analysis (10 in 2001, 46 in 2002, and 59 in 2003). Of all broods, 69% survived to 30 days (or, for those with unknown fate, through the maximum number of days for which they contributed data) and 31% failed. Causes of brood failure could not be determined because chick remains were never found.

Mean hatching date for first nests was 26 May (SE = 1.25 days) in 2001, 4 June (SE = 1.68 days) in 2002, and 28 May (SE = 1.60 days) in 2003. Brood season precipitation was 18.3 cm in 2001 and 2002, and 8.9 cm in 2003.

I measured 426 vegetation plots each year. Mean Robel pole reading was 4.97 cm (SE = 0.22) in 2001, 4.60 (SE = 0.22) cm in 2002, and 7.24 cm (SE = 0.39) in 2003. Mean forb CC was 3.34 (SE = 0.27) in 2001, 6.32 (SE = 0.45) in 2002, and 6.25 (SE = 0.65) in 2003. Grass and shrub CC varied little between years (Chapter 1, Table 3). Sweet clover (*Melilotis officinalis*), a non-native biennial forb, had potential for substantial growth in 2001 and 2003. Due to previous years' drought followed by low precipitation during the growing season, there was very little sweet clover growth in 2001. In contrast, conditions were favorable in 2003 and the mean forb CC and mean Robel metrics reflect sweet clover that year.

Model Selection

I constructed and evaluated 64 candidate models (Appendix A). Twenty-one models had ΔAICc values of <3.0 (see reduced model list, Table 1), indicating substantial model selection uncertainty. All of these models included year specificity. The ∑AICc weight for those models with the year term was 0.90. The effect of brood age, with ∑AICc weight of 0.44, was always positive though the 95% confidence intervals always overlapped zero (for the best-approximating model, $\beta = -0.01$ to 0.08). The highest ranking model included only the year and brood age terms. Several top models included shrub CC, with ∑AICc weight of 0.24. The shrub effect was always positive, though here also the 95% confidence intervals always overlapped zero. All other model terms had weak or virtually no support. All $\hat{\beta}_i$ and corresponding standard errors for the best-approximating model are reported in Table 2.

Using the best-approximating model (Year + Brood Age, 4 estimated parameters), 30-day brood survival was 0.21 (SE = 0.12) in 2001, 0.69 (SE = 0.07) in 2002, and 0.76 (SE = 0.06) in 2003 (Fig. 1). DSR increased with brood age (Fig. 2), though low nest success in 2001 (Chapter 1) resulted in sparse brood data which in turn hampered estimates of precision for that year.

I estimated overdispersion using deviance divided by degrees of freedom for the global model (15 parameters) and assessed the potential effect by applying a c-hat adjustment in program MARK. Although the deviance/df is known to be a positively biased estimate of overdispersion because this value is only asymptotically chi-squared distributed, I know of no other means to quantify the potential effects of heterogeneity and lack-of-independence (Anderson et al. 1994). I also recognize that this is an imperfect adjustment for model selection criteria and sampling variances and true amount of extra-binomial variation is somewhere between my estimate and none. Indeed, in a recent paper on advanced techniques for modeling nest survival (Dinsmore et al. 2002), overdispersion was not quantified or used to adjust model selection criteria or sampling variances. If I used my inflated estimate of c-hat (1.99), sampling variances would be inflated by 1.41 ($\sqrt{1.99} = 1.41$). In my case, the best-approximating model and my interpretation of model results would not change (i.e., variations between years still have the greatest influence, with support for a positive brood age effect), though model selection uncertainty would increase slightly. Additional research on model fit and realistic solutions to the effects of overdispersion (Natarajan and McCulloch 1999) are still needed.

DISCUSSION

No other studies of sage grouse chick or brood survival have simultaneously evaluated the effects of explanatory variables defined by habitat and environment. Several studies have evaluated the effect of micro-transmitters on survival of 1-day old chicks (Burkepile et al. 2002). My study of 115 broods spanned three years that exhibited wide variation in precipitation and vegetative growth.

I observed wide annual variation in brood survival rates, documenting a 3.5-fold increase in brood survival between 2001 and 2003. Reproduction of gallinaceous birds is generally known to vary widely with environmental conditions and I documented both extremes during my study (Johnsgard 1983). Beyond year specificity, however, considerable model selection uncertainty and sparse data in 2001 precluded precise estimation of habitat and environmental effects. The sparse data in 2001 was largely a result of low nest survival and therefore few broods in that year (Chapter 1). There was considerable support for a positive effect of brood age term based on ∑AICc weights.

Two exploratory models that examined whether the year effect might be better described by seasonal precipitation did not markedly improve upon the best-approximating model. Including January-February precipitation (a 4 parameter model) resulted in an improvement of 1.69 ΔAICc units, indicating that winter precipitation may be a more precise descriptor than unspecified annual variation. A plausible explanation would be that annual plant growth (grasses and forbs contributing to brood cover and forage) in the three years of this study was influenced by soil moisture early in the growing season as determined by winter precipitation. Inclusion of January-May precipitation did not improve the top model, resulting in an increase of 3.97 ΔAICc units.

Extreme variation in chick counts and lack of independence of fates of chicks within brood precluded estimation of chick survival. I found that chick counts (by searching for chicks up to 10-12 days of age and flush counts afterwards) were not a reliable indicator of brood size (and thus chick survival). For example, I might count 8 chicks at hatching, 2 on the next visit, and then 0 on several visits before counting 4 chicks with the single hen. These problems were magnified in areas of dense vegetative cover and in 2003 when chick cover over the entire study area was extensive – precisely the conditions that would be expected to result in high chick survival. Despite the fact that broods were sometimes missed (counted 0 chicks) on individual brood visits in 2003, brood survival was highest in this year indicating that probably few, if any, broods were missed entirely and that cover is likely important for survival, but the exact structure of the cover was difficult to measure. I often had low confidence in the accuracy of search counts in the vicinity of the radioed hen location because chicks younger than 10 days old were small, cryptically colored, and often stationary. Effectiveness of flush counts (coupled with searching for un-flushed chicks near the hen location) very likely varied among years, spatially within years, and temporally within individual broods because chicks in thick cover were less likely to fly and less visible when they didn't fly. However, detection probability likely increased with chick age as they became larger and more mobile.

By way of a qualitative evaluation, the number of chicks per brood was, by all accounts, low in 2001, moderate in 2002, and high in 2003. I observed one marked brood with apparently 1 chick surviving to 30 days in 2001. Based on my incomplete counts, average marked-brood size at 30 days was approximately 2-3 individuals in 2002 and 5-6 individuals in 2003. Numerous marked-broods in 2003 consisted of 6-8 chicks even at 40 and 50 days old. These approximations were supported in all years by incidental observations of unmarked broods. This ancillary information underscores the 3.5-fold increase in brood survival and indicates that total chick production in 2003 was many times that of 2001. Moreover, I suspect, based on these reasons, that estimates of chick survival may have supported more habitat variables than my assessment of brood survival.

Model terms that did not receive much support included site, Robel, forb CC, daily precipitation (with or without a 1-day lag effect), daily minimum temperature, hen age, and nesting attempt. If broods selected habitats based on finer resolution than my landscape scale assessment captured, then measurement of habitat characteristics at sites of observed brood use may have been more informative. However, that broods make use of different habitats at different ages (Connelly 2000) complicates measurement of the salient habitat elements. As a result, efforts to collect finer-resolution brood-habitat data should also explicitly model brood age to partition age-driven variation in used habitats.

I conducted pre-fieldwork simulations to determine the number of marked hens that would be required to detect several specified differences in survival. I determined that a minimum of 20 marked hens was necessary to detect a survival difference of 0.10 between sites with reasonable probability. Though I marked large numbers of hens, brood data were reduced through the multiplicative probabilities of hen survival, breeding, nesting, and nest success that must occur before broods exist for monitoring. Future studies that require a marked sample of 20 broods may need to mark many more hens to allow for hen mortality, breeding probability, and nest failures. Intensive studies in single or paired sites of interest might be informative regarding habitat effects considered here. Some sites exhibited marked annual differences in single habitat features. For example, the CMR site showed annual increases in mean annual forb canopy cover from 4.1 cm (SE = 0.8) in 2001 to 8.6 cm in 2002 (SE = 1.5) to 12.1 in 2003 (SE = 2.45).

The dramatic growth of sweet clover on my study area in 2003 was somewhat of an anomaly given its biannual nature and the favorable environmental conditions present that year. Sweet clover was the dominant ground cover across the entire study area in 2003, such that brood selection of particular habitat conditions was not distinguishable in the field. By contrast, the 2001 growing season extended the drought of the previous 5 years and there was little cover or chick forage available. That year, I observed many hens leading their broods 1.5 – 3 km to find relatively mesic habitats within 1-2 days immediately after hatching. Virtually all of these broods failed entirely within the first week post-hatch. Based on observed field conditions, I attribute most brood losses that year to drought stress and drought-mediated predation (via chick physical stress, long movements, and poor forage and structural cover) rather than any inherent baseline level of predation. I believe environmental conditions and associated habitat condition in 2001 (when brood survival was lowest) were poorer than was captured by habitat and environmental metrics. What little vegetation did grow that year quickly desiccated, such that vegetation parameters better represented structural cover than forage availability.

MANAGEMENT IMPLICATIONS

Brood survival can vary dramatically among years. My data indicate that, at the landscape scale and within the context of expansive high-quality habitat, environmental factors likely drive population-level brood survival on an annual basis.

These results do not demonstrate, however, that localized management for high quality brood habitat would be unsuccessful. Nor do they suggest that management for brood habitat in fragmented or degraded habitats would be ineffective. Management of sage grouse habitats for productivity will likely need to take place at multiple scales. While nesting conditions might effectively be managed for by landscape-scale improvements of range condition in general and increase of grass cover in particular (Chapter 1), brood survival might be best managed for at specific sites within and around known nesting areas, though it would still likely exhibit wide variation in conjunction with annual environmental variation. Based on existing recommendations, local management for brood habitat should focus on increasing forbs and grass understory (Connelly et al. 2000).

LITERATURE CITED

Anderson, D. R. and K. P. Burnham. 1994. AIC model selection in over-dispersed capture-recapture data. Ecology 75:1780-1793.

Burkepile, N. A., J. W. Connelly, D. W. Stanley, and K. P. Reese. 2002. Attachment of radio transmitters to one-day-old sage grouse chicks. Wildlife Society Bulletin 30(1):93-96.

Connelly, J. W. 1982. An ecological study of sage grouse in southeastern Idaho. Dissertation, Washington State University, Pullman, WA, USA.

Connelly, J. W. and C. E. Braun. 1997. Long-term changes in Sage Grouse populations in western North America. Wildlife Biology 3:229-234.

Connelly, J. W. and O. D. Markham. 1983. Movements and radionuclide concentrations of sage grouse in southeastern Idaho. Journal of Wildlife Management 47:169-177.

Connelly, J. W., H. W. Bowers, and R. J. Gates. 1988. Seasonal movements of sage grouse in southeastern Idaho. Journal of Wildlife Management 52:116-122.

Connelly, J. W., M. A. Schroeder, A. R. Sands and C. E. Braun. 2000. Guidelines to manage sage grouse habitats and their populations. Wildlife Society Bulletin 28(4):967-985.

Drut, M. S., J. A. Crawford and M. A. Gregg. 1994. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54(2):170-176.

Dunn, P. O. and C. E. Braun. 1986. Summer Habitat Use by Adult Female and Juvenile Sage Grouse Centrocercus urophasianus. Journal of Wildlife Management 50(2):228-235.

Johnsgard, P. A. 1983. Grouse of the World. University of Nebraska Press, Lincoln, NE.

Klott, J. H. and F. G. Lindzey. 1990. Brood Habitats of Sympatric Sage Grouse and Columbian Sharp-Tailed Grouse in Wyoming USA. Journal of Wildlife Management 54(1):84-88.

Peterson, J. G. 1970. The Food Habits and Summer Distribution of Juvenile Sage Grouse in Central Montana. Journal of Wildlife Management 34(1):147-154.

Schroeder, M.A, J. R. Young, and C. E. Braun. 1999. Sage Grouse: *Centrocerus urophasianus*. In: Poole A, Gill F, editors. Birds of North America. Philadelphia, PA: The Birds of North America, Inc. p 1-28.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.

Wallestad, R., J. G. Peterson and R. L. Eng. 1975. Foods of Adult Sage Grouse in Central Montana USA. Journal of Wildlife Management 39(3):628-630.

Westerkov, K. 1950. Methods for determining the age of game bird eggs. Journal of Wildlife Management 14:56-67.

Figure 1. Estimates of Greater Sage-Grouse brood survival to 30 days in south Phillips County, Montana during 2001-2003. Inputs to the best-approximating model (Year + Brood Age). Error bars represent standard errors.

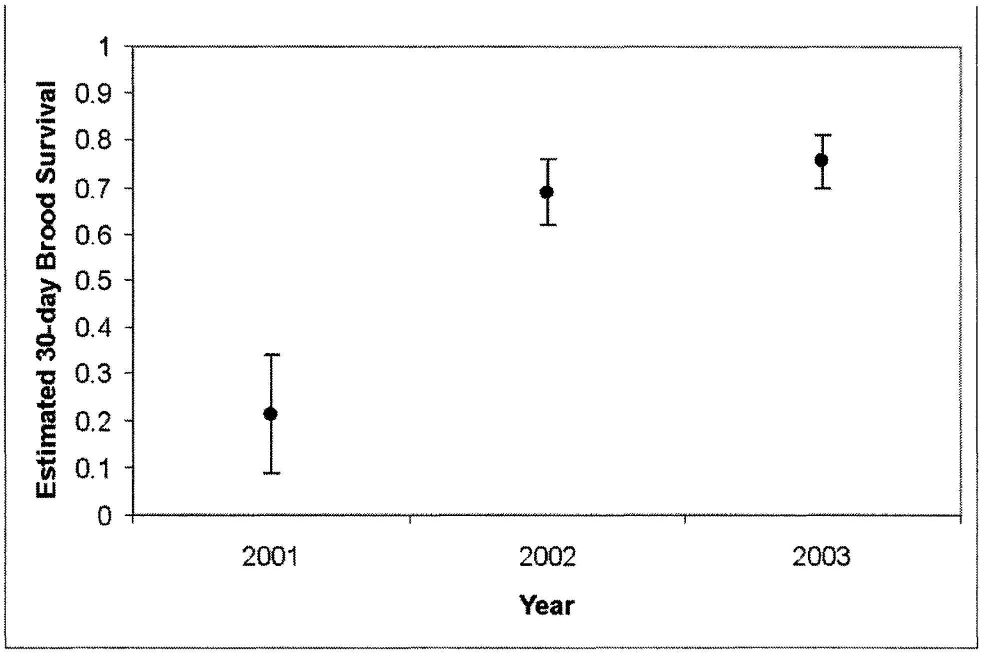

Figure 2. Estimates of Daily Survival Rates (DSR) of Greater Sage-Grouse broods to 30 days of age in south Phillips County, Montana during 2001-2003. Estimates generated from the best-approximating model (Year + Brood Age + Shrub) for days 1 to 30 and using mean shrub canopy cover. Error bars represent 95% confidence intervals.

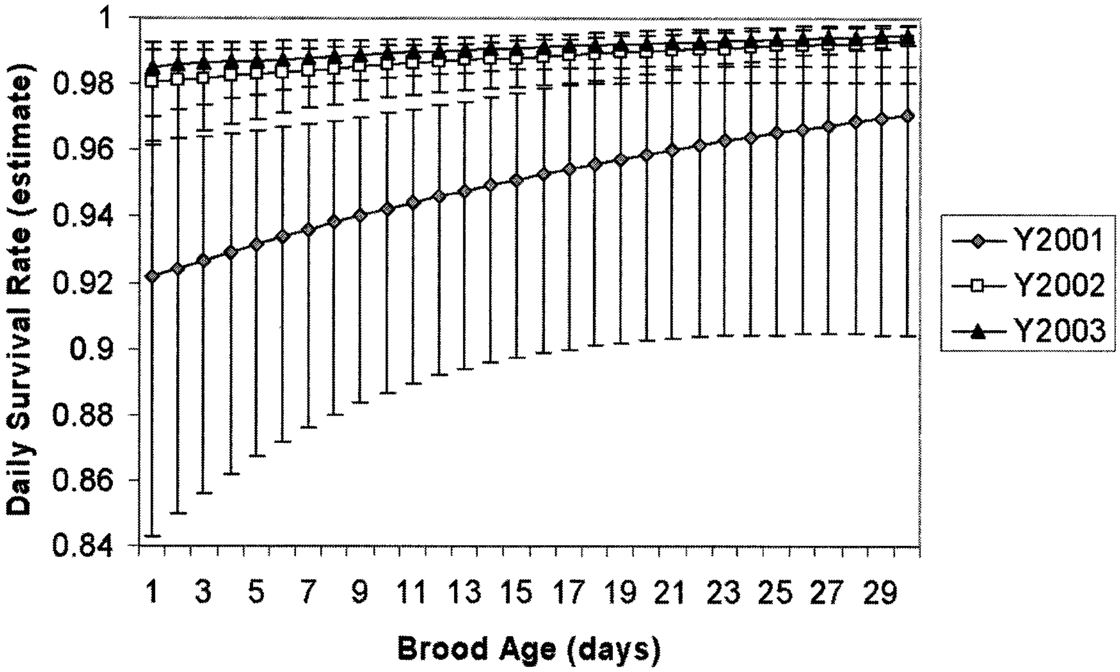

Table 1. Models of Daily Survival Rate (DSR) of Greater Sage-Grouse broods monitored in south Phillips County, Montana during 2001-2003. Only models with ΔAICc scores < 3.0 are shown. Models are ranked by differences in AIC values. Precipitation included as daily precipitation in tenths of inches; Lag is 1-day lag effect of daily precipitation.

Model	ΔAICc	AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
Year + Brood Age	0.000	213.068	0.082	1.000	4	205.052
Year + Brood Age + Shrub	0.190	213.258	0.074	0.910	5	203.233
Year + Brood Age + Grass	0.327	213.395	0.069	0.849	5	203.370
Year + Shrub	0.349	213.417	0.069	0.840	4	205.400
Year + Brood Age + Precip + Lag	0.411	213.479	0.067	0.814	6	201.445
Year	0.434	213.502	0.066	0.805	3	207.492
Year + Min Daily Temp	1.134	214.202	0.046	0.567	4	206.185
Year + Grass + Shrub	1.317	214.385	0.042	0.518	5	204.360
Year + Brood Age + Robel	1.337	214.405	0.042	0.512	5	204.381
Year + Brood Age + Precip	1.397	214.465	0.041	0.497	5	204.441
Year + Brood Age + Hen Age	1.782	214.851	0.034	0.410	5	204.826
Year + Brood Age + Forb	1.863	214.931	0.032	0.394	5	204.906
Year + Precip + Lag	1.895	214.963	0.032	0.388	5	204.938
Year * Grass	1.996	215.064	0.030	0.369	6	203.029
Year + Precip	1.999	215.068	0.030	0.368	4	207.051
Year + Shrub + Forb	2.313	215.381	0.026	0.315	5	205.356
Year + Shrub + Robel	2.316	215.384	0.026	0.314	5	205.359
Year * Hen Age	2.352	215.420	0.025	0.309	4	207.404
Year * Nest Attempt	2.565	215.633	0.023	0.277	5	205.609
Year + Min Daily Temp + Precip	2.636	215.704	0.022	0.268	5	205.679
Year * Season date trend	2.685	215.753	0.021	0.261	5	205.728

Table 2. Point estimates and standard errors for the best-approximating model of Daily Survival Rate (DSR) of Greater Sage-Grouse broods in south Phillips County, Montana during 2001-2003.

Parameter Number	Label	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1	Year 2001	2.4298	0.4116	1.6231	3.2364
2	Year 2002	3.8757	0.3712	3.1482	4.6032
3	Year 2003	4.1584	0.3739	3.4256	4.8912
4	Brood Age	0.0359	0.0236	-0.0104	0.0821

Appendix A. Complete list of candidate models of Daily Survival Rate (DSR) of Greater Sage-Grouse broods in south Phillips County, Montana, during 2001-2003. Models are ranked by differences in AICc values. Precipitation included as daily precipitation in tenths of inches; Lag is 1-day lag effect of daily precipitation.

Model	Delta AICc	AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
Year + Brood Age	0.000	213.068	0.082	1.000	4	205.052
Year + Brood Age + Shrub	0.190	213.258	0.074	0.910	5	203.233
Year + Brood Age + Grass	0.327	213.395	0.069	0.849	5	203.370
Year + Shrub	0.349	213.417	0.069	0.840	4	205.400
Year + Brood Age + Precip + Lag	0.411	213.479	0.067	0.814	6	201.445
Year	0.434	213.502	0.066	0.805	3	207.492
Year + Min Daily Temp	1.134	214.202	0.046	0.567	4	206.185
Year + Grass + Shrub	1.317	214.385	0.042	0.518	5	204.360
Year + Brood Age + Robel	1.337	214.405	0.042	0.512	5	204.381
Year + Brood Age + Precip	1.397	214.465	0.041	0.497	5	204.441
Year + Brood Age + Hen Age	1.782	214.851	0.034	0.410	5	204.826
Year + Brood Age + Forb	1.863	214.931	0.032	0.394	5	204.906
Year + Precip + Lag	1.895	214.963	0.032	0.388	5	204.938
Year * Grass	1.996	215.064	0.030	0.369	6	203.029
Year + Precip	1.999	215.068	0.030	0.368	4	207.051
Year + Shrub + Forb	2.313	215.381	0.026	0.315	5	205.356
Year + Shrub + Robel	2.316	215.384	0.026	0.314	5	205.359
Year * Hen Age	2.352	215.420	0.025	0.309	4	207.404
Year * Nest Attempt	2.565	215.633	0.023	0.277	5	205.609
Year + Min Daily Temp + Precip	2.636	215.704	0.022	0.268	5	205.679
Year * Season date trend	2.685	215.753	0.021	0.261	5	205.728
Brood Age + Grass	3.6542	216.7223	0.01314	0.1609	3	210.712
Year * Robel	3.823	216.8911	0.01208	0.1479	6	204.856
Season date T+Grass	4.3074	217.3755	0.00948	0.1161	3	211.366
Forb	4.6469	217.715	0.008	0.0979	4	209.698
Year*precip	4.8895	217.9576	0.00709	0.0868	6	205.923

Year*Robel+Shrub	5.2041	218.2722	0.00605	0.0741	7	204.226
Grass	5.3955	218.4636	0.0055	0.0673	2	214.459
Year*Forb	5.9261	218.9942	0.00422	0.0517	6	206.959
Season date T+Robel	6.2483	219.3164	0.00359	0.044	3	213.306
Year*Grass*Robel	6.4944	219.5625	0.00318	0.0389	9	201.488
GrassForb	7.1631	220.2312	0.00227	0.0278	4	212.215
BroodAge+Robel	7.1817	220.2498	0.00225	0.0275	3	214.24
BroodAge+Forb	7.3395	220.4076	0.00208	0.0255	3	214.398
Grass as Year	7.4217	220.4898	0.002	0.0245	4	212.473
BroodAge	7.4374	220.5055	0.00198	0.0242	2	216.501
BroodAge+HenAge	7.7598	220.8279	0.00169	0.0207	3	214.818
Season date T+Forb	8.0763	221.1444	0.00144	0.0176	3	215.134
Year*Precip+lag	8.0875	221.1556	0.00143	0.0175	9	203.081
Shrub as Site	8.141	221.2091	0.00139	0.017	5	211.184
Season date T	8.369	221.4371	0.00124	0.0152	2	217.432
BroodAge+Shrub	8.7768	221.8449	0.00101	0.0124	3	215.835
GrassForb+Shrub	8.8318	221.8999	0.00099	0.0121	5	211.875
Year*Forb*Robel	9.0418	222.1099	0.00089	0.0109	9	204.035
Robel	9.1244	222.1925	0.00085	0.0104	2	218.188
Site*Year	9.1726	222.2407	0.00083	0.0102	8	206.181
Precip+lag	9.184	222.2521	0.00083	0.0102	7	208.206
Grass+Shrub	9.2729	222.341	0.00079	0.0097	5	212.316
Season date T+Shrub	9.2739	222.342	0.00079	0.0097	3	216.332
Forb	9.2796	222.3477	0.00079	0.0097	2	218.343
Grass as Site	9.4936	222.5617	0.00071	0.0087	5	212.537
{.}	9.6709	222.739	0.00065	0.008	1	220.737
Precip	9.6904	222.7585	0.00064	0.0078	4	214.742
HenAge	9.8035	222.8716	0.00061	0.0075	2	218.867
Precip+lag single	10.0342	223.1023	0.00054	0.0066	3	217.092
Robel+Shrub	10.6049	223.673	0.00041	0.005	5	213.648
Shrub	10.9682	224.0363	0.00034	0.0042	2	220.031
Forb as Site	11.1855	224.2536	0.0003	0.0037	5	214.229

Attempt	11.6589	224.727	0.00024	0.0029	2	220.722
Site+Shrub	11.9405	225.0086	0.00021	0.0026	5	214.984
Site+BroodAge	12.1982	225.2663	0.00018	0.0022	5	215.242
Site	14.2635	227.3316	0.00007	0.0009	4	219.315
Robel as Site	14.9555	228.0236	0.00005	0.0006	5	217.999
Global	16.6944	229.7625	0.00002	0.0002	15	199.563

CHAPTER 3: FACTORS AFFECTING SURVIVAL OF FEMALE GREATER SAGE-GROUSE IN NORTH-CENTRAL MONTANA

Abstract: Populations of Greater Sage-Grouse (*Centrocercus urophasianus*) have declined by 69-99% from historic levels. Information on population dynamics of these birds at a landscape scale is essential to informed management. I radio-collared 237 female sage grouse and measured 426 vegetation plots at 4 sites during 2001-2003 in 3,200 km^2 landscape in north-central Montana, USA. My objective was to examine the relationship between hen survival and a suite of landscape-scale habitat and environmental conditions. I used program MARK to model monthly survival rates for 11 seasonal intervals as influenced by a variety of habitat and environmental explanatory variables. There was strong support for the best-approximating model (AICc weight = 0.810) that indicated that hen survival varies by season within years and by year within seasons, that nesting hens have higher breeding-season survival than non-nesting hens, and that individuals at one site had lower hunting-season survival than at other sites. Though hen survival has been presumed to be high and vary little relative to other galliforms, I observed considerable variation in hen survival. Process variation was 0.255, with a expected range of annual survival of 0.12 to 1.0. The ratio of process to total variation was 0.999, indicating that observed variation was real and not attributable to sampling variation. I observed a 4-fold difference in maximum and minimum annual survival, ranging from 0.96 for nesting birds in 2001-2002 to 0.24 for non-nesters in 2003-2004. Low annual survival in 2003 is a result of the compounded effects of a West Nile virus outbreak in August of that year and a severe winter of 2003-2004. Increased hen mortality associated with severe winter weather contrasts with prior beliefs that sage grouse populations are typically unaffected by winter weather conditions and underscores the importance of protecting winter sagebrush habitats. My observations raise the possibility that pre-winter mortality of sage grouse hens due to hunting and WNv is additive.

INTRODUCTION

Despite information on sage grouse ecology and the well-known geographic and temporal variation in at least some vital rates (Schroeder et al. 1999), no studies have simultaneously assessed a wide range of biotic and abiotic factors suspected to affect survival of hens at the landscape scale. Studies that have estimated hen survival have concluded that, relative to other galliforms, it is high and fairly resilient to annual and seasonal perturbations (e.g., Connelly et al. 1993, Zablan 2003), though the range of habitat, weather, and management conditions over which that conclusion would hold remains unclear. For these reasons, and because future sage grouse conservation and management will likely apply habitat prescriptions over relatively large areas (thousands or tens of thousands of hectares) through manipulation of land-use patterns, I considered factors affecting survival of hens at the landscape scale, i.e., the level of the study site (156 - 234 km^2 [61 – 92 mi^2]). Further, sage grouse breeding is based in large part on female selection of mates, with few males performing most copulations (Eng 1963, Wiley 1973). As a result, and because nests and chicks are tended to by females alone, adult hen survival is likely much more important to sage grouse populations on an annual basis than is survival of males.

West Nile virus (WNv) was first observed in sage grouse on this and several other study areas in July and August 2003 and was documented as a direct cause of markedly increased late-summer mortality that year (Naugle et al. 2004). A severe winter in 2003-2004 resulted in considerable hen mortality, apparently due to deep snow followed by extremely cold temperatures. These two factors alone suggested that hen survival may not be nearly as high and static as previously thought or observed (Connelly et al. 2000, Zablan et al. 2003).

Land uses across central and eastern Montana are spatially divergent and range from cropland to various grazing intensities to relatively undisturbed sagebrush-steppe habitats. Predator communities and abundances vary across this heterogeneous landscape, increasing variation in population characteristics. The region is characterized, temporally, by wet/dry cycles of varying lengths and intensities, which affect sagebrush, grass, and forb growth. Therefore, high levels of spatial and temporal variation produce complex interactions of factors influencing sage grouse vital rates. My objective was to estimate survival rates of adult female sage grouse in north-central Montana as influenced by landscape-scale habitat and environmental factors.

STUDY AREA

I studied sage grouse on a 3,900 km^2 area in southern Phillips County in north-central Montana (47° 33' N to 48° 01' N, 107° 32' W to 108° 33' W, Fig. 1), bounded by the Missouri River and Fort Peck Lake to the south, the Larb Hills to the east, the Whitcomb Lake area to the north, and the Little Rocky Mountains to the west. Approximately 60% of the study area was in public ownership, managed by the U.S. Bureau of Land Management (BLM, Malta Field Office), the U.S. Fish and Wildlife Service (FWS, Charles M. Russell National Wildlife Refuge [CMR]), and the State of Montana. Remaining lands were predominantly private, and I worked on some 30 private ranches. This area is a mixed-grass prairie with sagebrush flats bordering the southwestern edge of the Prairie Pothole Region (Dinsmore et al. 2002). I selected four study sites within the study area: CMR, Sun Prairie, Little Horse, and Dry Fork (Fig. 1).

The study area represents some of the most expansive, contiguous and intact sagebrush-steppe habitats in Montana with relatively large sage grouse populations. Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) was the dominant shrub, with lesser amounts of silver sage (*A. cana*), greasewood (*Sarcobatus vermiculatus*), Rocky Mountain juniper (*Juniperus scopulorum*), Gardner saltbush (*Atriplex gardneri*), Yucca (*Yucca glauca*) and snowberry (*Symphoricarpus albus*). Common grasses included western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*), green needlegrass (*Stipa viridula*), and bluebunch wheatgrass (*Agropyron spicatum*). Common forbs included fringed sagewort (*Artemisia frigida*), wild onion (*Allium* spp.), dandelion (*Taraxacum* spp.), American vetch (*Vicia americana*), prairie goldenbean (*Thermopsis rhombifolia*), poverty weed (*Monolepis nutalliana*), scarlet globemallow (*Sphaeralcea coccinia*), and yellow sweetclover (*Melilotis officinalis*). The area is characterized by high annual variation in average daily temperature (-9°C to 22°C) and low mean annual precipitation (32 cm), most of which falls between May and July. Mean elevation is ~800 m. Potential sage grouse predators included coyote (*Canis latrans*), Golden Eagle (*Aquila chrysaetos*), Ferruginous Hawk (*Buteo regalis*), Gyrfalcon (*Falco rusticolus*), Northern Goshawks (*Accipiter gentilis*) and other raptors. Red fox (*Vulpes vulpes*) are rare on the study area.

METHODS

Methods for study site selection and vegetation sampling are identical to those described in Chapter 1. Briefly, 4 study sites were selected based on the distribution of lek sites and varying levels of sage brush coverage. I recorded survival of radio-marked birds from April 2001 – July 2004. I trapped hens primarily by rocket-netting and spotlighting (Giesen et al. 1982) from all-terrain vehicles and on-foot between mid-March and mid-April 2001-2003. I determined age class of hens at time of capture as adult (≥2 years old, second or later breeding season) or subadult (<1 year old, first breeding season) based on inspection of 9th and 10th primary feathers (Eng 1955; Crunden 1963). Hens were fitted with a necklace-type radio transmitter (2001-Telemetry Solutions®, 2002-2003-Advanced Telemetry Systems®, model A4080). Transmitters weighed 22 g, had an expected life of approximately 2 years, and could be detected from the ground and air from approximately 2-5 km and 6-10 km, respectively. Transmitters were equipped with a mortality switch which would double signal pulse-rate when the transmitter had not moved for more than 4 hours.

Hens were fitted with a numbered metal leg band with return information (National Band and Tag size 16) and with an individually coded plastic band designed for re-sighting with spotting scopes. Physical measurements included weight (kg), head length (mm) and tarsus length (mm). Trapping and handling protocols were approved by The University of Montana Institutional Animal Care and Use Committee. Trapping, marking, and special use permits were provided by the Montana Department of Fish, Wildlife, and Parks (FWP), the U. S. Fish and Wildlife Service (FWS), and the U. S. Bureau of Land Management (BLM).

Crews of 4-5 began locating each marked bird (traveling by foot or ATV) upon completion of the trapping season, typically near April 15. Because I was also interested in locating nests and monitoring nest and brood fate, I typically confirmed fate of every bird with visual confirmation from April through the end of July. Occasional aerial searches augmented ground work. In general, survival status was determined by ground crews for April-July periods (typically every 4 days), while aerial searches were used for late summer, fall and winter periods.

Data Analysis

I used an information-theoretic approach (Burnham and Anderson 1998) to simultaneously evaluate relative support of multiple models describing relationships between survival and variables of interest. I used the known fate module in program MARK (White and Burnham 1999) to generate point estimates of survival rates and their precision to evaluate relative support for candidate models given observed data. Program MARK uses generalized linear models (McCullaugh and Nelder 1989) with a user-specified link function (logit link used here) to generate maximum likelihood estimates of regression coefficients and their associated sampling variances and covariances. Individual models were evaluated using Akaike's Information Criterion (AIC) and AIC weights (Burnham and Anderson 1998).

I collapsed telemetry data into 12 discrete observation occasions based on biological questions of interest and sampling intensity, resulting in 11 intervals between Spring 2001 and Summer 2004 for which survival probabilities could be estimated (Table 1). I considered 4 breeding intervals (late-April through end of June, 2001-2004), 1 interval in 2001 that spanned late summer 2001 to April 2002; 2 discrete late summer intervals (July-August 2002 and 2003), 2 discrete hunting seasons (September-October 2002 and 2003), and 2 discrete over-winter periods (November-April, 2002-2003 and 2003-2004). Program MARK allows for user-specified variation in interval length; I standardized interval length to a monthly unit by dividing the total number of days in each interval by 30 (Table 1). The resulting outputs were estimates of monthly survival.

I began by generating candidate models that described competing hypotheses about survival. Each model represented hen survival as a function of some combination of biotic and abiotic sources of variation: interval, site, season, spring nesting status (a dummy variable for each year coded as 0 = no nest initiations detected and 1 = at least one nest initiated), hen age class (a dummy variable coded as 0 = subadult and 1 = adult), four habitat metrics (shrub, grass, and forb canopy cover [CC] and Robel pole readings), a late-summer West Nile virus effect (a dummy variable coded as 0 = non-West Nile virus years and 1 = West Nile virus year, i.e., 2003), and snowfall (January-February 2002-2004; recorded at the Western Regional Climate Center, Malta, Montana 35S station, station number 245340).

The interval term accounted for annual and seasonal variation (e.g., regional weather patterns) not attributable to other specified sources of variation. Models structured for seasonality were a more parsimonious interval model, where survival estimates for like seasons were held equal.

I considered two types of site effects. I structured some models with full site specificity to consider inherent differences among all four sites. I also constructed several *a priori* models considering an effect of only the Dry Fork site and only during hunting seasons. My rationale for doing so was based on information reported by hunters who had killed marked birds during the fall hunting seasons. Virtually all reported hunter kills were taken on the Dry Fork site, which is crossed by two well-traveled roads (Highway 191 runs north-south through the western end of the site, and the Dry Fork Road runs east-west through the length of the site). Though hunting pressure for sage grouse in the area is generally thought to be low, I suspected that birds at this site might be more vulnerable to hunting than birds at other sites due to the opportunistic encounters afforded by these two roads, which receive much travel by big game hunters accessing the Missouri Breaks country.

Snow might affect winter survival because as snow depth increases and sagebrush availability is reduced so is thermal cover and the sole winter forage source. I selected Robel pole readings and shrub, grass, and forb CC for habitat covariates. Robel readings represent the maximum height of complete visual obstruction (Robel et al. 1970), effectively combining vegetation height and density. Shrub, grass, and forb data were included in the form of mean CC per site per year. Depending on how each habitat covariate was included in model structure, it could exhibit site, interval, season, or year specificity. In models with no site specificity, I used annual averages across all sites. I used the category of "shrub" rather than only considering sagebrush because sagebrush accounted for ~85% of shrubs in vegetation plots and because sage grouse made occasional use of non-sage shrubs for roosting and thermal cover. Standing residual and green grass cover both contributed visual obstruction, helping to obscure nesting and brooding hens from predators. Though adults rely heavily on sagebrush for food in all seasons, forbs and insects associated with forbs may be included diets, particularly for nesting hens (Barnett and Crawford 1994). When included, forb CC, grass CC, and Robel measurements were considered only in the 4 breeding season intervals; shrub CC was available for inclusion in all intervals. Hens aged as subadult at initial capture graduated to the adult age class at the start of the next spring.

Nesting status was used as an individual covariate to examine whether nesting birds might exhibit different survival probabilities than their non-nesting counterparts during the nesting seasons (late-April through June). No nest initiation data are available for 2004, as hens were not monitored for nesting activity that year. Survival data for 2004 were acquired from aerial telemetry.

In models structured for season effects (where all late summer intervals were held otherwise equal), a dummy variable for WNv was added in summer 2003 to allow for distinction of that known effect during that single interval.

I used the difference in the log-likelihood of the saturated and most general (most parameters) model (deviance) divided by the deviance degrees of freedom (i.e., difference in number of parameters between models) as an estimate of overdispersion (c-hat; Anderson and Burnham 1994). This estimate of c-hat is positively biased, but is the only goodness-of-fit diagnostic reasonably available for these models. Potential effects of overdispersion on model selection and estimates of sampling variance (Anderson and Burnham 1994) were considered.

I used the best-approximating model to generate monthly survival estimates and to estimate sampling variances of those estimates. From these interval-specific survival estimates I generated annual survival from the beginning of one breeding season to the next (i.e., May in year *n* to May in year *n*+1) and used the delta method (Seber 1982) to approximate sampling variances for each annual estimate. After interpretation of the main model set, I conducted a secondary analysis with a slightly reduced data set to determine whether the independent addition of physical individual covariates (weight at trapping, weight:tarsus length ratio, and weight:head length ratio) improved fit of the best-approximating model. The data set was reduced slightly because individual covariates were not available for all individuals included in the full data set (e.g., some individuals escaped before a weight could be recorded).

I used an intercept-only, random effect model with the data structured in yearly intervals (Burnham and White 2002), to estimate process variation ($\hat{\sigma}$, total variance - sampling variance: Burnham et al. 1987: 260, Gould and Nichols 1998) in yearly survival probability and to calculate the ratio of process variation to total variation

RESULTS

I radio-marked 237 individuals (64 in 2001, 88 in 2002, and 85 in 2003). Three hens in 2002 and 2 hens in 2003 had been marked in previous years and were recaptured and fitted with new transmitters. Encounter histories of 16 hens were censored either because they were not located after release or because the first and only location yielded a mortality that could not be assigned to a particular interval. I included 221 hens in the analysis. All intervals had adequate data for known-fate survival estimation. The mean number of individuals contributing data per interval was 77 (SE = 10.0, range = 33 to 134). Causes of mortality generally could not be determined because it was uncommon to find more than a few feathers or bone fragments.

I measured 426 vegetation plots in each of the three years across all 4 sites. Mean Robel pole reading was 4.97 cm (SE = 0.22) in 2001, 4.60 cm (SE = 0.22) in 2002, and 7.24 cm (SE = 0.39) in 2003. Mean forb CC was 3.34 (SE = 0.27) in 2001, 6.32 (SE = 0.45) in 2002, and 6.25 (SE = 0.65) in 2003. Grass and shrub CC varied little between years (Table 3). Sweet clover, a biennial forb, had potential for substantial growth in 2001 and 2003. Due to previous years' drought followed by the precipitation regime described above (rain events were few but relatively large), little sweet clover grew in 2001. In contrast, conditions were favorable in 2003 and the mean forb CC and mean

Robel metrics reflect sweet clover that year.

I confirmed that West Nile virus killed sage grouse on the study area during July and August 2003. Each of 4 recovered carcasses that provided testable samples to evaluate WNv infection were positive, and WNv was determined as the cause of death in each case. December through February snowfall totaled 15.2 cm in 2001-2002, 46.0 cm in 2002-2003, and 121.9 cm in 2003-2004.

I evaluated the relative support of each of 34 models (Table 2). Models including full specificity for each interval included a minimum of 11 estimated (beta) parameters – one for each interval. Estimated overdispersion (c-hat) from the global model (20 parameters) was 2.84. The potential effect of this estimated overdispersion is considered below.

Model Selection

The best-approximating model (AICc weight = 0.810) was a 13-parameter model (Interval + Spring Nesting Status + Dry Fork Site Effect [hunting season]). This was the only model supported by the data, as the second-ranked model had a ΔAICc score of 6.17. The effect of nesting status was positive ($\hat{\beta}$ = 1.86, 95% CI = 1.12 to 2.60), indicating higher survival probabilities for nesting hens. The effect of site on the Dry Fork population for hunting season intervals was negative ($\hat{\beta}$ = -1.64, 95% CI = -2.75 to -0.53), indicating lower hunting season survival at Dry Fork than at other sites.

The addition of the Dry Fork site parameter for hunting season intervals to any model nearly always improved model fit by approximately 6.0 AICc units. The second-ranked model had 12 parameters and was the same as the best-approximating model without the Dry Fork site term (Interval + Spring Nesting).

Monthly survival estimates varied by interval (i.e., by seasons within and between years), by site during hunting seasons, and by whether or not a hen initiated a nest. Estimated monthly survival for nesting hens during breeding seasons (late April, May, and June was 0.991 (SE = 0.006) in 2001, 0.949 (SE = 0.015) in 2002, and 0.976 (SE = 0.008) in 2003. For non-nesting hens during the breeding season, estimated monthly survival was 0.942 (SE = 0.032) in 2001, 0.745 (SE = 0.061) in 2002, 0.862 (SE = 0.040) in 2003 (Fig. 2). No nesting data were collected in 2004 – monthly survival for all hens during the 2004 breeding season was 0.911 (SE = 0.027). Monthly survival estimates for late-summer months (July and August) were 0.973 (SE = 0.010) in 2002 and 0.917 (SE = 0.018) in 2003 (Fig. 3).

Monthly hunting season (September and October) survival estimates for birds at the CMR, Sun Prairie, and Little Horse sites were 0.980 (SE = 0.011) in 2002 and 0.959 (SE = 0.019) in 2003. At Dry Fork, those estimates were 0.904 (SE = 0.046) in 2002 and 0.820 (SE = 0.067) in 2003 (Fig. 4).

Over-winter (November, December, January, February, March, through late April) monthly survival estimates were 0.986 (SE = 0.006) in 2002 and 0.913 (SE = 0.016) in 2003 (Fig. 5). Monthly survival estimates for late-summer, hunting season, and over-winter periods in 2001 were confounded and not independently estimable. The monthly survival estimate for July 2001 through late April 2002 was 0.989 (SE = 0.002). The product of these point estimates for the 12 months from the start of one breeding season to another (May to May) gave estimated annual survival probabilities (Fig. 6, Table 4).

Using an intercept-only, random effect model with data structured in yearly intervals (Burnham and White 2002), I estimated that process variation ($\hat{\sigma}$, total variance - sampling variance: Burnham et al. 1987: 260, Gould and Nichols 1998) in yearly survival probability was 0.255. The ratio of process variation to total variation was 0.999, indicating that virtually all observed variation was process variance and not attributable to sampling variance. Adding two standard deviations ($2\hat{\sigma} = 0.510$) to average annual survival (0.633) indicated an expected range of annual hen survival from 0.123 to 1.00.

There was virtually no support for the inclusion of landscape-level habitat variables. I consider this issue further below. Addition of individual covariates (weight, weight:head length, weight:tarsus length) to the best-approximating model typically resulted in increases of approximately 2.0 AICc units. Therefore, these terms did not improve on the best-approximating model and I did not interpret estimates from models with individual covariates.

If I adjusted model selection criteria for my estimate of overdispersion from the global model (c-hat = 2.84), sampling variances would be inflated by 1.69 ($\sqrt{2.84} = 1.69$). In my case, the best-approximating model and my interpretation of model results would not change, though model selection uncertainty would increase marginally. The best-approximating model (AICc weight = 0.422) was followed by the same second-ranked model (Interval + Nest) which would receive greater support (ΔAICc = 2.82, AICc weight = 0.103). There was still overwhelming support for models including interval and nest status parameters. I recognize that my estimate of c-hat is an imperfect adjustment for model selection criteria and sampling variances and true amount of extra-binomial variation is somewhere between my estimate and none. For that reason, and because using the adjustment did not change my interpretation of results, I consider only the unadjusted model set. Additional research on model fit and realistic solutions to the effects of overdispersion (Natarajan and McCulloch 1999) are still needed.

DISCUSSION

It is notable that I observed little support for the inclusion of habitat terms. This study area represents some of the most intact, contiguous sagebrush-mixed grass prairie in Montana. I believe that the most plausible explanation for the lack of support of landscape-level habitat variables is that habitat for adult and subadult hens in the study area is stable, even between years (Table 3), though conditions may vary considerably at much smaller scales. This would suggest that hen survival is influenced more by predation, hunting, extreme weather, and other non-structural and non-forage factors, including WNv. Acute (e.g., plowing, spraying, burning), chronic (e.g., overgrazing), and cumulative (e.g., fragmentation) impacts to sagebrush habitats certainly affect obligate populations directly and indirectly (e.g., through mediation of change in predator communities).

Ours is the first sage grouse data set that allows for precise survival estimation partitioned seasonally. The considerable seasonal and annual variation I observed in hen survival demonstrates that, over the short term, hen survival is influenced by factors operating on time scales shorter than one year.

The positive effect of nesting on survival probability was opposite my expectations. I expected that nesting hens would be more susceptible to predation during incubation. The nesting effect was most pronounced in 2002, when the estimate for monthly survival during the breeding season for hens that nested at all sites was 0.949 (SE = 0.015) compared with 0.745 (SE = 0.061) for hens that did not nest (Fig. 1). A possible explanation for this difference is that nesting hens are in better physical condition at the start of the nesting season than hens that do not nest. Another explanation would be that sage grouse hens may be more visible and thus more vulnerable when not concealed by sage brush cover during incubation.

I do not have data to support a claim that the strong negative DF site effect during hunting seasons is attributable only to hunting mortality. Other mortalities not known to us at Dry Fork may have been natural, unreported hunter kills, or road kills associated with the 2-lane highway and the well-traveled gravel Dry Fork Road. I received reports from hunters of only 7 birds killed during the 2001-2003 hunting seasons (6 by shotgunners, 1 by a falconer), so I am unable to estimate specific effects and levels of hunting mortality, or hunters' reporting rate of harvested marked birds. However, the anecdotal information is worth considering. Five of those 7 reported birds were taken at the Dry Fork site (1 at CMR and 1 at Sun Prairie). Though I banded more cocks than hens over the entire study area (327 males, 243 females) and also at the Dry Fork site (87 males, 52 females), 4 of those 5 reported kills from Dry Fork were hens, raising the possibility of a hen-biased kill rate.

Connelly et al. (2000b) attributed a greater proportion of hen mortality to hunting than for males, suggesting greater susceptibility of females to hunting. If it exists, a hen-biased kill rate could be due to some hunters intentionally selecting smaller birds (based on the belief that smaller, young-of-the-year birds are more palatable), or due simply to opportunistic encounters with flocks of hens. I observed that hens that had not nested or had failed nesting attempts would often flock together by late summer and that flocks of multiple hens with broods would form (particularly in dryer years) during late summer and early fall. These larger flocks (20-40 or more individuals) may be easier for hunters to locate than smaller male flocks (3-10 individuals). When the strength of support for the DF site effect became apparent, I constructed several exploratory models to examine support for hunting season site effects for other sites (CMR, Sun Prairie, and Little Horse). There were not enough mortality data to generate estimates for those parameters, indicating a lack of support for the same type of site effect during hunting seasons at those sites.

Hunting mortality for many gallinaceous birds is presumed to be compensatory versus additive to winter mortality, though the debate has recently been stirred by evidence of additive hunting mortality in a population of northern bobwhites (*Colinus virginianus*) (Williams et al. 2004) and by suggestions of additive mortality in sage grouse (Connelly et al. 2000b). I can reason how hunting mortality of sage grouse may be additive. I document high survival of hens during mild winters (2001-2002 and 2002-2003), but lower survival during a severe winter (2003-2004). Little natural mortality (attributable to environmental and habitat conditions) during those mild winters may be exceeded by hunting mortality. Though higher mortality during severe winters may well be associated with limited availability of sagebrush forage, I believe that winter mortality observed during 2003-2004 was more a result of severe environmental conditions (deep snow) rendering habitat inaccessible, as opposed to competition-mediated mortality associated with the exhaustion of limited resources. Further, if pre-winter mortality were entirely compensatory, I might have expected to see little winter mortality in 2003-2004 directly following the August 2003 outbreak of WNv (mortality during that period exceeded my estimates of mortality during any of the hunting seasons on any of the study sites).

Due to the breeding system of sage grouse where few males perform the vast majority of copulations and with the hen being the sole caretaker of the nest and brood, additive mortality of males at current levels would not likely unduly influence population-level breeding rates of females. However, even though a recent study (Connelly et al. 2003) found higher rates of population growth for non-hunted versus hunted populations in Idaho, the proportion of mortality directly attributable to hunting is often not estimable. Though I have seasonal (as opposed to annual) resolution in this study, partitioning of total estimated mortality during hunting seasons into hunting mortality and non-hunting mortality is not possible and I cannot conclude that mortality was additive at Dry Fork.

This research demonstrates considerably more seasonal and annual variation in hen survival than previously documented. I identify contributions to this variation by demographic (nesting), seasonal (environmental), and management (hunting season) sources. Indeed, hen survival has been shown elsewhere to be not only high but also to exhibit little variability (Connelly et al. 1993, Zablan 2003), though it is not clear whether populations in those studies experienced as great variation in environmental conditions as observed during the 3 years described here. Annual hen survival has been reported as 0.59 (SE = 0.011) in Colorado (Zablan 2003) and 0.75 in Idaho (Connelly et al. 1994), though those studies employ different analyses from ours and from each other. Zablan et al. (2003) used maximum-likelihood modeling of band-return data in Program MARK and found no support for temperature or precipitation terms for both spring and winter, though they found that their band-return data yielded low power to detect such an effect. Moreover, their analysis focused on annual survival and did not allow assessment of those environmental effects during particular seasons.

Annual survival probability ranged from 0.96 (2001, nesting birds, no hunting season DF site effect) to 0.24 (2003, non-nesting birds, negative hunting season DF site effect; Fig. 6). While annual survival estimates for 2001 are the highest reported, the 2003 estimates are the lowest. I attribute exceptionally low survival in 2003 to two events: a West Nile virus outbreak during July and August 2003 and a particularly hard winter in 2003-2004 that combined heavy snow with extreme cold. I documented a mortality rate in this study of approximately 18% in July and August 2003 (Naugle et al. 2004), compared to an estimated background monthly rate of 1-3% in prior years with no detection of WNv. Only 4 of 20 mortalities recovered during August 2003 provided testable tissue samples and all were positive for WNv. WNv was determined as the cause of death for each individual and further investigation has indicated that WNv infection is likely always fatal for sage grouse (Naugle et al. 2004).

The winter period of 2003-2004 brought heavy snow and extreme cold to the study area and much of Montana's northern plains. The winters of 2001-2002 and 2002-2003 were notably mild, in terms of both precipitation and temperature, but many areas of north-central and north-eastern Montana had near-record snowfall in 2003-2004. My study area had over 1.2 m of snow between December and February, with most (60%) of it falling in a single 2-day storm in late December. This snowfall event covered nearly all sagebrush within and beyond the study area (R. Matchett, pers. comm.), and was followed by two weeks of cold that ranged from daily highs of -3° C (27° F) to lows of -47° C (-52° F). By the time of the first mid-winter telemetry flight on February 4, apparent mortality of adult hens exceeded 30% since November 1. The monthly survival estimate for the period of November 2003 through April 2004 of 0.913 (SE = 0.016) generates an over-winter survival probability of 0.58. In models of a reduced structure that estimated a single parameter for like seasons, the addition of a parameter for an annual snowfall covariate was always supported and negative. My findings of a strong effect of a severe winter in an area of expansive, high-quality habitat are noteworthy. Connelly (2000a) noted that there was no evidence that severe winter weather affects sage grouse populations unless sagebrush cover has been greatly reduced or eliminated (see also Wallestad 1975, Beck 1977).

I also observed extremely high survival in 2001, a year of severe drought that coincided with low nest success and brood survival (see Chapters 1 and 2). My estimates of hen survival indicate that adults are well-suited to endure drought conditions, particularly when followed by mild, open winters as in 2001-2002. I stress, though, the potentially devastating results of the chance of concurrent impacts of various population-level processes. For example, if WNv and winter increases in hen mortality had been experienced in a year with near-zero production, such as 2001, this population would likely have declined by as much as 60-75% in a single year. Conversely, if a year of high hen survival (such as 2001) had been coupled with high nest success and brood survival (such as 2003), the population would have grown dramatically. It remains unclear, however, whether high hen survival observed in 2001 was due to environmental conditions (i.e., mild, dry weather), or was influenced by a life-history trade-off of increased hen survival in years when hens invest little in nesting or rearing broods. That is, if there is a cost to hen survival generated by successful reproduction in a given year, it may not be possible to have high hen survival (e.g., 2001) and high chick production (i.e., 2003) in the same year.

Understanding variation in hen survival is important because it affects abundance and age class composition of the spring breeding population, which in turn can impact productivity with potentially lingering effects. I have observed higher nesting and re-nesting probabilities and larger clutch sizes for adult than yearling hens (Chapter 1). Therefore, habitat and environmental conditions that favor high annual hen survival and thus a large number and proportion of adults in the next spring's breeding population will provide the greatest potential productivity the following year. Further, low annual survival may result in a negative lag effect on productivity for at least two years as abundance and demographic issues compound. For example, low hen survival in one year will result in fewer birds breeding the following spring. Even if chick production and annual survival increases that second year, there would be a greater proportion of yearling breeders in year 3, which will likely exhibit lower nesting and renesting probabilities and clutch sizes.

MANAGEMENT IMPLICATIONS

The finding of markedly increased mortality during a severe winter has clear management implications. The implications of two other findings – site-specific hunting season mortality and the advent of WNv – are less definitive and warrant further evaluation.

Even without any evidence that severe winter weather could affect sage grouse populations, many biologists and researchers have advocated for the protection of winter habitats for years (see especially Connelly et al. 2000a). Variation in topography and height of sagebrush is believed to ensure availability of essential sagebrush forage in different snow conditions and depths (Beck 1977, Hupp and Braun 1989, Schroeder 1999, Connelly 2000a). My observations during the severe winter of 2003-2004 underscore these beliefs, and demonstrate that occasionally, even in areas of expansive, high-quality habitat such as south Phillips County, winters may be so severe as to have clear and substantial population-level impacts.

In areas where winter habitats are destroyed or altered such that sagebrush height is reduced, average or moderate winter weather could approach effectively severe conditions when sagebrush plants are not present or are covered by snow. I suspect that the same winter conditions that would not impact sage grouse populations in high-quality habitats could be effectively severe in degraded habitats. I, therefore, echo other researchers' recommendations that sage grouse managers prioritize the identification and conservation of wintering areas. This will necessitate field work to locate flocks particularly in moderate and severe winters. Further, as I have witnessed quick formation of large flocks (<100 individuals) immediately after snowstorms, winter surveys should be as flexible and responsive to weather changes as possible so that surveys are conducted within several days of substantial snowfalls. This would allow the best opportunity to observe quick movements of relatively large numbers of birds immediately after winter storms. Optimally, a survey would also be conducted within a day or two before an expected winter storm so that movements from non-critical wintering areas could be described and quantified. The best opportunities for such work would come with coordination with on-going studies using radio-marked individuals.

I presented evidence of substantial site-specific increases in mortality during fall months with a hunting season. The possibility of a hen-biased kill rate by hunters, either by selection or by virtue of increased hen encounters, coupled with the possibility of additive mortality, warrants further investigation.

The effects of WNv were pronounced. The increase in late-summer mortality attributable to WNv on this study was less than in other study areas (Wyoming and Alberta, Canada) in the same year (Naugle et al. 2004), though it remains unclear whether that difference is due to variation in habitat quality, spatial configuration of habitat, anthropogenic alteration of the landscape, land use, geographic patterns of spread during the first documented year of impact, or some other factor or combination of factors. In any case, careful consideration of the amount and location of current and proposed surface water is necessary.

My estimates of seasonal and annual hen survival indicate that sage grouse population dynamics are complex but can be described. In addition to long-term and large-scale approaches to habitat conservation and rehabilitation, managers should consider refining activities on an annual basis according to what they know about current year's survival and reproduction. In years when production is poor, managers should do all they can to maximize hen survival over the remainder of the year, particularly during hunting season (e.g., consider substantial harvest restrictions) and winter (through identification and long-term conservation of winter habitats). When spring habitat and environmental conditions are favorable, and with a large proportion of adults in the hen population (provided by high hen survival in previous years), reproduction may carry populations through even dramatic increases in hen mortality (e.g., WNv and/or severe winter weather). However, the decision-space to refine management annual is afforded by effective conservation of quality habitat over the long term. More important, having high-quality breeding and winter habitat in place may well reduce the potential impact of compounded effects of poor production and high WNv and winter mortality all occurring in one year.

Others have noted that vital rates exhibiting the most variation, such as brood survival (Chapter 2) might be the most difficult to affect change in (Pfister 1998). Within the context of analytical elasticity analyses, vital rates with low elasticities tend to have high variance (Pfister 1998), and vital rates with high variation can have larger effects on population growth than rates with high elasticity (Gaillard et al. 1998, Mills et al. 1999). I have documented elsewhere (Chapters 1 and 2) that nest success and brood survival are quite variable and are likely driven by annual environmental variation. By contrast, I have documented in this paper that hen survival can be affected by vulnerability during hunting seasons (at one of four sites and in two of three years), an invading exotic virus (WNv), and by weather. Two of these three factors may be manageable to some extent through manipulation of harvest season lengths or dates and of amount or structure of anthropogenically-generated surface water containment (settling ponds and stock ponds that may provide habitat for *Culex tarsalis*, the mosquito that is a primary vector of WNv). In areas with reduced or degraded winter habitats, even winter survival might be increased with conservation and restoration of expansive sagebrush stands of varied height and density. On the other hand, it may be easier to affect population growth in some areas where nest success or brood survival is limited by non-environmental factors such as predation or poor understory cover.

Several independent lines of evidence suggested the possibility of a hen-biased harvest rate and provide ground for a discussion of additive versus compensatory mortality in sage grouse. However, I reiterate that the evidence is anecdotal and I cannot claim that observed elevated fall mortality at one site corresponding with a hunting season is directly or entirely attributable to hunter harvest. Until the causes of mortality are determined (e.g., harvest, road-kills, predation), one should not conclude that hunter harvest is the cause of increased fall mortality.

Sage grouse have certainly evolved to persist through occasional population-level impacts of severe winters. I observed, however, the dramatic compounded effects of a new stressor (WNv) and a severe winter. Populations may well be ill-equipped to cope with natural perturbations that are coupled both with new threats such as WNv as well as the historic and on-going loss and degradation of sagebrush habitats. And for local populations that are already stressed by chronic and cumulative impacts to habitat, the potential concurrence of acute annual impacts of low production, WNv, and severe winter weather poses a particularly threatening eventuality.

LITERATURE CITED

Anderson, D. R. and K. P. Burnham. 1994. AIC model selection in over-dispersed capture-recapture data. Ecology 75:1780-1793.

Anderson, D. R., K. P. Burnham, A. B. Franklin, R. J. Gutierrez, E. D. Forsman, R. G. Anthony, G. C. White and T. M. Shenk. 1999. A protocol for conflict resolution in analyzing empirical data related to natural resources controversies. Wildlife

Society Bulletin 27:1050-1058.

Barnett, J.F. and J.A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal of Range Management 47:114-118.

Beck, T. D. I. 1977. Sage grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41(1):18-26.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, AND K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, NY.

Burnham, K.P., AND G. C. White. 2002. Evaluation of some random-effects methodology applicable to bird ringing data. Journal of Applied Statistics 29:254-264.

Connelly, J. W. and C. E. Braun. 1997. Long-term changes in Sage Grouse populations in western North America. Wildlife Biology 3:229-234.

Connelly, J. W., M. A. Schroeder, A. R. Sands and C. E. Braun. 2000a. Guidelines to manage sage grouse habitats and their populations. Wildlife Society Bulletin 28(4):967-985.

Connelly, J.W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000b. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227-232.

Connelly, J. W., K. P. Reese, E. O. Garton, and M. L. Commons-Kemner. 2003.

Response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation in Idaho, USA. Wildlife Biology 9(4):255-260.

Crunden, C. W. 1963. Age and sex of grouse from wings. Journal of Wildlife Management 27:846-849.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83(12):3476-3488.

Drut, M. S., J. A. Crawford and M. A. Gregg. 1994. Brood habitat use by sage grouse in Oregon. Great Basin Naturalist 54(2):170-176.

Dunn, P. O. and C. E. Braun. 1986. Summer Habitat Use by Adult Female and Juvenile Sage Grouse Centrocercus urophasianus. Journal of Wildlife Management 50(2):228-235.

Eng, R. L. 1955. A method for obtaining Sage Grouse age and sex ratios from wings. Journal of Wildlife Management 19:267-272.

Eng, R. L. 1963. Observations on the breeding biology of male sage grouse. Journal of Wildlife Management 27(4):841-846.

Gaillard. J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.

Giesen, K. M., T. J. Schoenbert, and C. E. Braun. 1982. Methods For Trapping Sage Grouse Centrocercus-urophasianus in Colorado, USA. Wildlife Society Bulletin 10(3):224-231.

Gould, W. R., AND J. D. Nichols. 1998. Estimation of temporal variability of survival in animal populations. Ecology 79:2531-2538.

Hillborn, and Mangel. 1997. The Ecological Detective: Confronting Models with Data. Princeton University Press, Princeton, New Jersey.

Hupp, J. W. and C. E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. Journal of Wildlife Management 53(3):823-829.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. The Auk 118(2):557-562.

Klott, J. H. and F. G. Lindzey. 1990. Brood Habitats of Sympatric Sage Grouse and Columbian Sharp-Tailed Grouse in Wyoming USA. Journal of Wildlife Management 54(1):84-88.

McCullagh, P. and J. A. Nelder. 1989. Generalized linear models. Chapman and Hall CRC, Washington, D.C., USA.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13(4):815-829.

Moynahan, B. J., M. S. Lindberg, J. J. Rotella, and J. W. Thomas. 2004a. Factors affecting nest survival of Greater Sage-Grouse in north-central Montana. In review.

Moynahan, B. J., M. S. Lindberg, and J. W. Thomas. 2004b. Factors affecting survival of Greater Sage-Grouse broods in north-central Montana. In review.

Naugle D.E., B.L. Walker, Aldridge, C.L., T.E. Cornish, B.J. Moynahan, M.J. Holloran, K. Brown, G.D. Johnson, E.T. Schmidtman, R.T. Mayer, C.Y. Kato, M.R. Matchett, T.J. Christiansen, W.E. Cook, M.S. Boyce, and E.T. Rinkes. 2004. West Nile virus: An emerging issue in sage-grouse conservation. Ecology Letters 7:704-713.

Natarajan, R. and C. E. McCulloch. 1999. Modeling heterogeneity in nest survival data. Biometrics 55:553-559.

Peterson, J. G. 1970. The Food Habits and Summer Distribution of Juvenile Sage Grouse in Central Montana. Journal of Wildlife Management 34(1):147-154.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213-218.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 22:295-297.

Schroeder, M.A, J. R. Young, and C. E. Braun. 1999. Sage Grouse: *Centrocerus urophasianus*. In: Poole A, Gill F, editors. Birds of North America. Philadelphia, PA: The Birds of North America, Inc. p 1-28.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.

U. S. Fish and Wildlife Service. 2004. 90-day finding for petitions to list the Greater Sage-Grouse as threatened or endangered. 50 CFR 17, 69(77):21484-21494.

Wallestad, R., J. G. Peterson and R. L. Eng. 1975. Foods of Adult Sage Grouse in Central Montana USA. Journal of Wildlife Management 39(3):628-630.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: Supplement:120-138.

Williams, C. K., R. S. Lutz, R. D. Applegate. 2004. Winter survival and additive harvest in Northern Bobwhite coveys in Kansas. Journal of Wildlife Management 68(1): 94-100.

Zablan, M. A., C. E. Braun, G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67(1): 144-154.

Figure 1. Greater Sage-Grouse study area in south Phillips County, Montana. Black circles represent locations of four study sites. CMR = Charles M. Russell National Wildlife Refuge, DF = Dry Fork site, LH = Little Horse site, and SP = Sun Prairie.

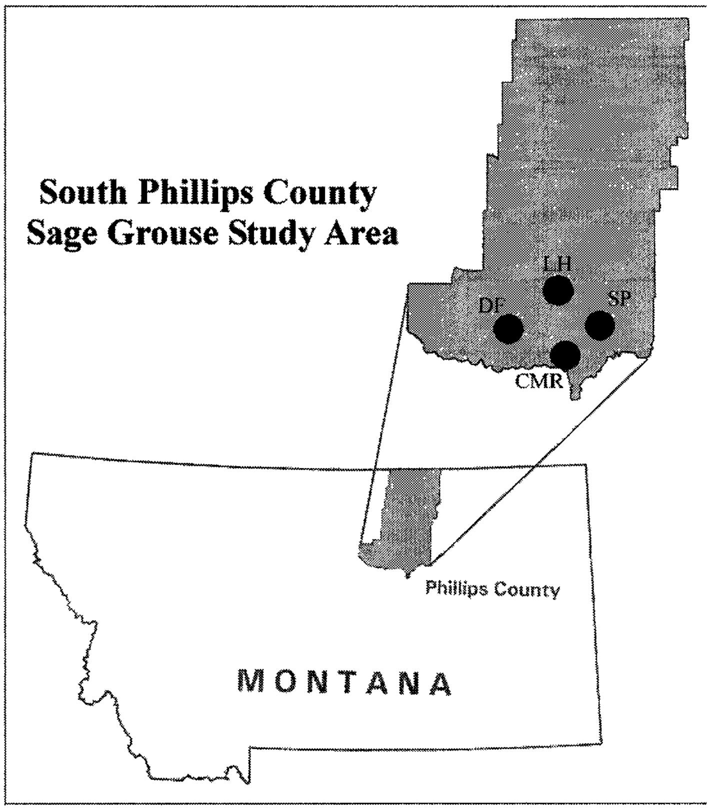

Figure 2. Monthly survival estimates of Greater Sage-Grouse nesting and non-nesting hens during breeding seasons (May-June) in south Phillips County, Montana during 2001-2004. Point estimates generated from the best-approximating model (Interval + Nest Status + Hunting Season Dry Fork Site, AICc Weight = 0.811). Error bars represent standard errors.

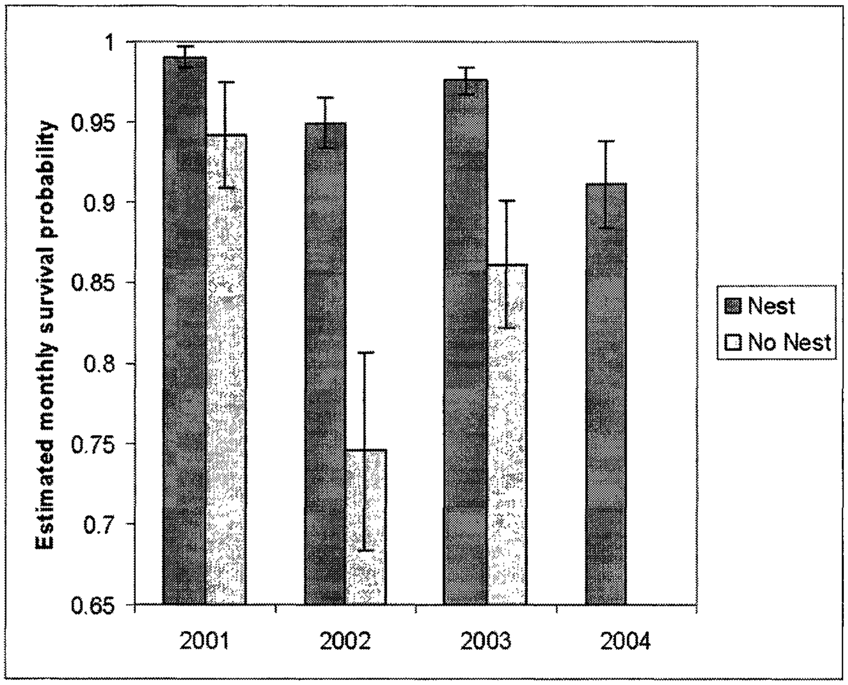

Figure 3. Monthly survival estimates of Greater Sage-Grouse hens during late summer (July-August) in south Phillips County, Montana during 2001-2003. Estimate for 2001 is confounded with hunting season 2001 and with over-winter season 2001-2002. Point estimates generated from the best-approximating model (Interval + Nest Status + Hunting Season Dry Fork Site, AICc Weight = 0.811). Error bars represent standard errors.

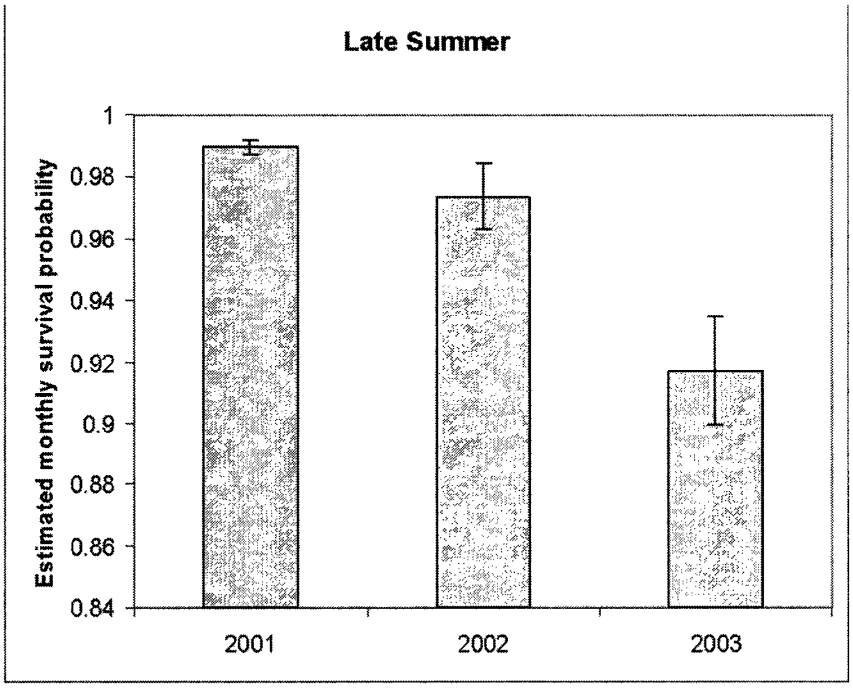

Figure 4. Monthly survival estimates of Greater Sage-Grouse hens during hunting seasons (September-October) in south Phillips County, Montana during 2001-2003. Estimate for 2001 is confounded with hunting season 2001 and with over-winter season 2001-2002. Point estimates generated from the best-approximating model (Interval + Nest Status + Hunting Season Dry Fork Site, AICc Weight = 0.811). Error bars represent standard errors.

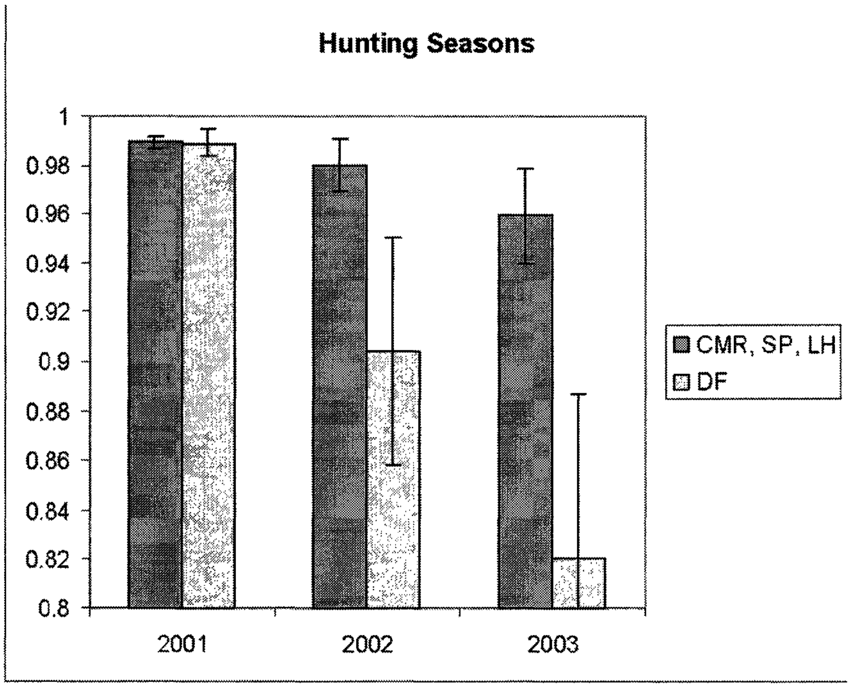

Figure 5. Monthly survival estimates of Greater Sage-Grouse hens during over-winter months (November-April) in south Phillips County, Montana during 2001-2004. Estimate for 2001 is confounded with hunting season 2001 and with over-winter season 2001-2002. Point estimates generated from the best-approximating model (Interval + Nest Status + Hunting Season Dry Fork Site, AICc Weight = 0.811). Error bars represent standard errors.

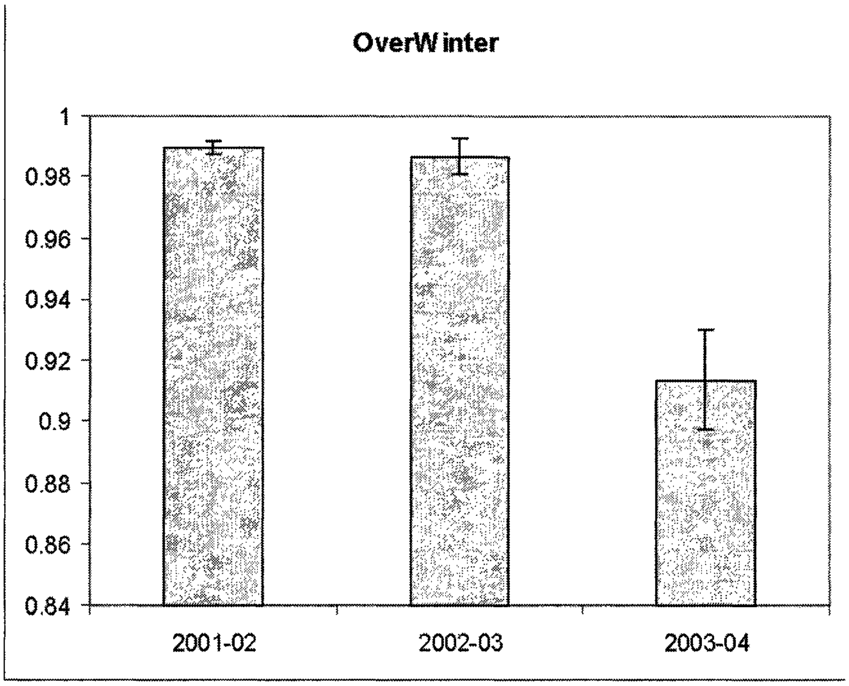

Figure 6. Estimates of annual (May to May) survival probabilities of Greater Sage-Grouse hens in south Phillips County, Montana during 2001-2003. Estimates generated from the best-approximating model (Interval + Nesting Status + Hunting Season Dry Fork Site, AICc Weight = 0.811). The distance between closed and open markers represents the effect of being at the Dry Fork site during the hunting season given >1 nesting attempt that year (circles) or not nesting (triangles). The distance between solid lines represents the effect nesting (closed circle) or not nesting (closed triangle) at either the CMR, Sun Prairie (SP), or Little Horse (LH) sites. The distance between dashed lines represents the effect of nesting (open circle) or not nesting (open triangle) for birds that are at the Dry Fork Site during the hunting season. The distance between solid and dashed lines of like markers represents the Dry Fork hunting season site effect for birds that nest (circles – top two lines) or do not nest (triangles – bottom two lines). Relatively low annual survival of all birds in 2003-2004 represents the cumulative effects of the first documented occurrence of West Nile virus in sage grouse during July and August and increased winter mortality associated with deep snow in December and January. Error bars are standard errors.

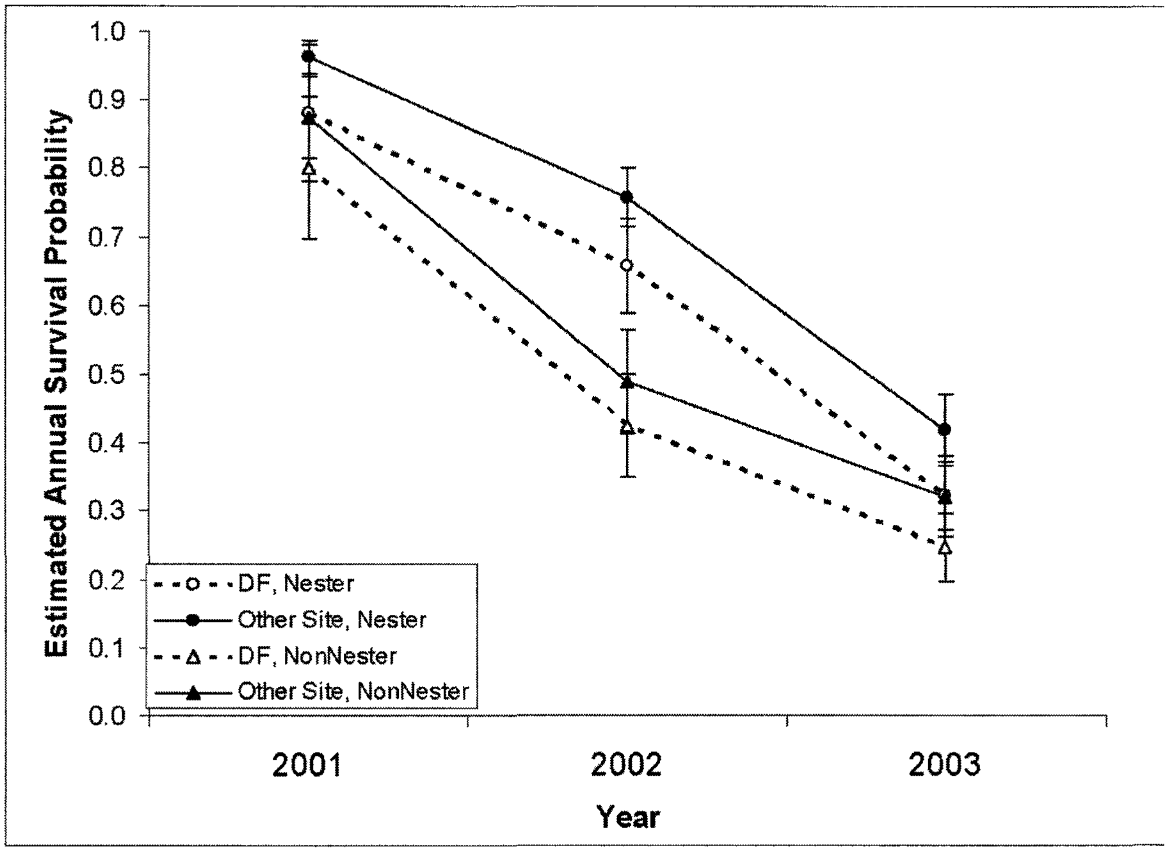

Table 1. Description of seasonal intervals for survival estimation of Greater Sage-Grouse hens in south Phillips County, Montana, 2001-2004. Survival estimates were standardized to monthly periods based on observed number of months per season. Number of birds marked per interval indicates the number of individual radio-marked hens contributing known-fate survival data for the specified interval.

Interval #	Description	No. Months (total days / 30)	Time Frame	# Marked Birds Per Interval
1	Breeding 2001	1.87	Late April – June 2001	56
2	Hunting+Overwinter 2001-2002	10.23	July 2001 - Late April 2002	33
3	Breeding 2002	1.88	Late April – June 2002	112
4	Late summer 2002	2.58	July – August 2002	91
5	Hunting Season 2002	1.73	September – October 2002	83
6	Overwinter 2002-2003	5.60	November 2002 – Late April 2003	69
7	Breeding 2003	2.10	Late April – June 2003	134
8	Late summer 2003	2.47	July – August 2003	105
9	Hunting Season 2003	1.70	September – October 2003	64
10	Overwinter 2003-2004	5.87	November 2003 – Late April 2004	64
11	Breeding 2004	2.40	Late April – June 2004	36

Table 2. Model results for 32 a priori models describing survival of Greater Sage-Grouse hens in south Phillips County, Montana, 2001-2004.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
Interval + Spring (Nesting) + Hunting Season (DF Site)	597.190	0.000	0.810	1.000	13	570.747
Interval + Spring (Nesting)	603.361	6.171	0.037	0.046	12	578.982
Interval + Spring (Nesting, Age Class) + Winter (Age Class)	603.385	6.195	0.037	0.045	13	576.942
Interval + Spring (Nesting) + All Seasons (Age Class)	604.757	7.567	0.018	0.023	13	578.314
Interval + Spring (Nesting, Age Class) + Winter (Age Class, Shrub)	604.789	7.599	0.018	0.022	14	576.277
Interval + Spring (Nesting, Robel)	605.282	8.093	0.014	0.018	13	578.840
Interval + Spring (Nesting, Shrub)	605.290	8.100	0.014	0.017	13	578.847
Interval + Spring (Nesting, Age Class, Robel) + Winter (Age Class)	605.442	8.252	0.013	0.016	14	576.930
Interval + Spring (Nesting, Age Class, Grass) + Winter (Age Class, Shrub)	606.509	9.320	0.008	0.010	15	575.924
Interval + Spring (Nesting, Age Class, Forb) + Winter (Shrub)	606.799	9.609	0.007	0.008	14	578.287
Interval + Spring (Nesting, Age Class, Robel) + Winter (Age Class, Shrub)	606.855	9.665	0.006	0.008	15	576.269
Interval + Spring (Nesting, Robel) + Winter (Shrub)	606.921	9.732	0.006	0.008	14	578.410
Interval + Spring (Nesting, Age Class) + Winter (Age Class, Site)	607.027	9.837	0.006	0.007	16	574.363
Interval + Spring (Nesting, Age Class, Grass, Forb) + Winter (Age Class, Shrub)	608.587	11.397	0.003	0.003	16	575.922
Season + Spring (Nesting) + Hunting Season (DF Site) +Winter (Snow) + 2003 WNv	609.091	11.902	0.002	0.003	8	592.917
Global	611.478	14.289	0.001	0.001	20	570.448
Season + Spring (Nesting, Age Class) + Winter (Age Class, Snow) + 2003 WNv	612.896	15.706	0	0	8	596.722
Season + Spring (Nesting) + Winter (Snow) + 2003 WNv	615.268	18.078	0	0	7	601.133
Season + Spring (Nesting) + Winter (Snow)	619.373	22.183	0	0	6	607.271
Interval + Hunting Season (DF Site)	619.565	22.376	0	0	12	595.186
Interval + Spring (Age Class) + Winter (Age Class) + Hunting Season (DF Site)	620.394	23.204	0	0	13	593.951
Interval + Winter Season (+Snow)	624.073	26.883	0	0	10	603.806
Season + WNv + Winter 03-04 + Hunting Season (DF Site)	625.368	28.178	0	0	7	611.232
Interval	625.742	28.552	0	0	11	603.421
Interval + Spring (Age Class) + Winter (Age Class)	626.573	29.383	0	0	12	602.194
Interval + Spring (Robel)	627.090	29.900	0	0	12	602.711
Interval + Spring (Age Class)	627.550	30.360	0	0	12	603.171
Season + WNv + Winter 03-04	631.551	34.361	0	0	6	619.450
Season + Spring (Nesting)	634.767	37.577	0	0	5	624.694
Season + Winter (Snow)	637.032	39.843	0	0	5	626.960
Season	652.431	55.241	0	0	4	644.383
Age Class	664.117	66.927	0	0	4	656.068
Site	669.579	72.389	0	0	4	661.531
Static	670.222	73.032	0	0	1	668.217

Table 3. Observed habitat and environmental values (mean ± SE) at south Phillips County, Montana during 2001-2003.

Year	2001	2002	2003
Robel[a]	4.97 ± 0.22	4.60 ± 0.22	7.24 ± 0.39
Shrub[b]	11.68 ± 0.65	10.02 ± 0.67	8.75 ± 0.65
Grass[b]	24.27 ± 1.18	22.00 ± 1.02	22.08 ± 1.09
Forb[b]	3.34 ± 0.27	6.32 ± 0.45	6.25 ± 0.65
Snowfall[c]	15.2	46.0	121.9

---

[a] centimeters

[b] Percent canopy cover

[c] centimeters, from December 1 of current year to February 28 of next year

Table 4. Estimates of annual survival probabilities for Greater Sage-Grouse in south Phillips County, Montana, 2001-2004. Estimates are based on the best-approximating model (Interval + Spring [Nesting] + Hunting Season [Dry Fork Site]). Year is from beginning of one breeding season to beginning of next (May to May). Standard errors in parentheses.

	2001-2002	2002-2003	2003-2004
Dry Fork, Nester	0.881 (0.100)	0.658 (0.068)	0.322 (0.058)
Dry Fork, Non-Nester	0.801 (0.104)	0.425 (0.075)	0.247 (0.050)
Other Sites, Nester	0.962 (0.024)	0.757 (0.043)	0.419 (0.051)
Other Sites, Non-Nester	0.875 (0.060)	0.489 (0.075)	0.322 (0.050)

CHAPTER 4: RESEARCH SUMMARY AND MANAGEMENT IMPLICATIONS OF RECENT DEMOGRAPHIC INVESTIGATIONS OF GREATER SAGE-GROUSE IN NORTH-CENTRAL MONTANA

Abstract: Populations of Greater Sage-Grouse (*Centrocercus urophasianus*) have declined by 69-99% from historic levels. Information on population dynamics of these birds at a landscape scale is essential to informed management. I radio-collared 243 female sage grouse, monitored 287 nests and 115 broods, and measured 426 vegetation plots at 4 sites during 2001-2003 in 3,200 km^2 landscape in north-central Montana, USA. My objective was to examine the relationship between nest success, brood survival, and hen survival rates, habitat conditions, environmental variables, and hen characteristics. I used program MARK to model (1) daily survival rates (DSR) of nests and broods and (2) seasonal and annual survival of hens. My findings underscore the importance of large-scale approaches to conservation of sage grouse habitats and to maintenance and recovery of sage grouse populations. Management for hen survival must address hunting pressure and identification and conservation of important wintering areas. Predation in my study area does not appear to impact populations as much as severe winter weather and site-specific fall hunting pressure. Efforts aimed at nest success should focus on the standing residual and green herbaceous understory in sagebrush stands. Highly variable brood survival appears to be affected more by unspecified annual variation than the landscape-scale habitat elements measured here. A focus on hen survival and nest success is supported by the fact that adult hens have been documented here and elsewhere to have higher nesting and renesting probabilities, clutch sizes, and possibly nest success than subadult hens. Therefore, maintaining quality habitat and a high proportion of adult hens will maximize potential for population growth when environmental conditions are favorable.

INTRODUCTION

Populations of Greater Sage-Grouse (*Centrocercus urophasianus*, hereafter "sage grouse") have declined by as much as 69-99% from historic to recent times, with much of that decline occurring since the 1980s (USFWS 2004). The geographic extent of sage grouse range in the western U.S. and Canada has been reduced by approximately 50% (Schroeder et al. 1999). The loss and degradation of habitat to expansion of farming and grazing activities are likely the main factors (Connelly and Braun 1997). Other potential factors include changes in fire regimes, predation, over-hunting, weather, disease, and herbicide and insecticide treatments (Connelly and Braun 1997, Braun 1998). The U.S. Fish and Wildlife Service (USFWS) issued a positive "90-day finding" in April 2004 in response to a range-wide petition to declare sage grouse as "threatened" or "endangered" under the Endangered Species Act. Such determination would likely have significant impacts on land management and traditional land-use patterns throughout the range of the sage grouse, particularly on federal lands.

Existing information describing general sage grouse habitat needs has been conducted across its range and over the period of its noted decline, and almost entirely on a local scale (e.g., nest site or lek locations). Stephens et al. (2003) reviewed the effect of scale on detection of effects of fragmentation on nest success and recommended that such studies be conducted at landscape scales and over several years. Jones (2001) suggested that the next step in the evolution or development of avian habitat selection research must be the incorporation of both habitat and demographic information into landscape-scale conservation planning. Literature reviews (e.g., Schroeder et al. 1999) and management guidelines (i.e., Connelly et al. 2000a) relative to sage grouse note that habitat loss and fragmentation – both landscape issues – are a major concern for viability of sage grouse populations. Moreover, despite reports of high levels of geographic and temporal variation in nest survival rates (Schroeder et al. 1999, Connelly et al. 2000a), no studies have simultaneously assessed a wide range of biotic and abiotic factors suspected to affect nest success at the landscape scale. For these reasons, and because future sage grouse conservation and management will likely apply habitat prescriptions over relatively large areas (thousands or tens of thousands of hectares) through manipulation of land-use patterns, it is important to consider factors affecting nest survival at the landscape scale. My objective was to investigate the influence of landscape-scale habitat and environmental factors on population dynamics.

RESEARCH SUMMARY

I analyzed demographic and habitat data collected in south Phillips County, Montana, from 2001-2004. Included in the analyses were 221 radio-marked hens, 258 nests, and 115 broods, and 426 vegetation plots. I used an information-theoretic approach (Burnham and Anderson 1998) for the simultaneous evaluation of relative support for multiple competing hypotheses. For a detailed description of the study area, data collection and analysis methods, and results, see Chapters 1, 2, and 3 of this dissertation. I present a concise summarization of the findings of those chapters below.

Nest Success

Nest survival varied with year, grass canopy cover, daily precipitation with a 1-day lag effect, and nesting attempt. In all years, daily survival rate (DSR) of nests increased on the day of a rain event and decreased on the next day. I believe the daily precipitation effect and the 1-day lag effect of precipitation reflects increased hen attentiveness and decreased predator activity on rainy days, followed by decreased hen attentiveness and increased predator activity one day later as both increase forage activity. I observed temporal variation in nest success both within and among years: nest success of early (first 28 days of the nesting season) nests ranged from a low of 0.238 (SE = 0.080) in 2001 to a high of 0.316 (SE = 0.055) in 2003, whereas survival of late (last 28 days of the nesting season) nests ranged from a low of 0.276 (SE = 0.090) in 2001 to a high of 0.418 (SE = 0.055) in 2003. Renests experienced higher survival than first nests. Grass cover was the only important model term that might be managed, but direction and magnitude of the grass effect varied, possibly influenced by the narrow range of grass canopy cover values observed or other complexities associated with habitat changes in 2003. Site, shrub and forb canopy cover, and Robel pole reading were less useful predictors of nest success. I note a marked difference between both values and interpretations of apparent nest success (proportion of all detected nests that hatch at least one egg) and maximum likelihood estimates derived from the modeling process (an information-theoretic extension of the Mayfield method). Apparent nest success here was 0.46, while maximum likelihood estimates that incorporate individual, environmental and habitat covariates are lower.

Brood Survival

The best-approximating model included only the effects of brood age and unspecified annual variation. Considerable model selection uncertainty existed, though all models scoring < 3 ΔAICc units contained the term for year specificity (∑ΔAICc weights = 0.90). There was also support among top-ranked models for a positive effect of brood age (∑ΔAICc weights = 0.44), though 95% confidence intervals overlapped zero. Based on the best-approximating model, estimates of 30-day brood survival probabilities were 0.21 in 2001 (SE = 0.12), 0.69 in 2002 (SE = 0.07), and 0.76 in 2003 (SE = 0.06). Shrub canopy cover, receiving modest support among top-ranked models ($\sum\Delta$AICc weights = 0.24), was the only parameter that could potentially be managed for, though the 95% confidence intervals of the estimated effect always overlapped zero. My results suggest that unspecified annual variation in brood survival can be large enough to mask finer effects of habitat variables measured at the landscape scale, and that management of brood habitat may be one requirement that is best addressed locally.

Hen Survival

There was strong support for the best-approximating model (AICc weight = 0.810) that indicated that hen survival varies by season within years and by year within seasons, that nesting hens have higher breeding season survival than non-nesting hens, and that individuals at one site had lower hunting season survival than at other sites. Though hen survival has been found elsewhere to be high and vary little relative to other galliforms (e.g., Zablan 2003), I observed considerable variation in hen survival. I observed a 4-fold difference in maximum and minimum annual survival, ranging from 0.96 for nesting birds in 2001-2002 to 0.24 for non-nesters in 2003-2004. Low annual survival in 2003 is a result of the compounded effects of a West Nile virus outbreak in August of that year and a severe winter of 2003-2004. Increased hen mortality associated with severe winter weather contrasts with a lack of evidence that winter weather can substantially affect sage grouse populations (Connelly 2000a, see also Wallestad 1975, Beck 1977) and underscores the importance of protecting winter sagebrush habitats. My observations raise the possibility that pre-winter mortality of sage grouse hens due to hunting and WNv may be additive.

MANAGEMENT IMPLICATIONS

Nest Success

Sage grouse nest success in this study was generally high, though managers should expect considerable annual variation. Overall hen success can be high in years with favorable nesting conditions combined with a high proportion of adults in the breeding population. It follows that managers should strive to support high annual hen survival by (1) minimizing harvest levels and (2) clearly identify and actively conserve winter habitats. Observed variation in nesting effort, renesting effort, and clutch size (all greater for adults than subadults) underscores the importance of supporting high hen survival. A greater abundance and proportion of adult hens in the next spring's breeding population will maintain maximum potential chick production. Conservation of high-quality winter habitats likely will result in greater hen abundance the following spring. Improved range condition, including winter habitats, may also result in improved spring hen condition and thus increase nesting effort and clutch sizes (Barnett and Crawford 1994).

Researchers and managers should be aware of the problems posed by apparent nest success rates. Such rates are likely to be biased high because they do not account for nests that fail prior to being observed. They cannot offer insights into the factors or mechanisms affecting nest success because the proportional nature of these estimates can not incorporate the important effects of habitat, weather, or individual covariates. In this study, apparent nest success for all years was 0.46 (SE = 0.002). Maximum-likelihood estimates ranged from 0.238 (SE = 0.080) to 0.418 (SE = 0.055), and varied within and among years. Apparent nest success rates are therefore not reliable and may not accurately inform management.

There was strong support for the conclusion that DSR of nests in this study varied with precipitation with 1-day lag, year, attempt, and grass CC at the landscape scale considered here. Though wildlife and land managers have no control over precipitation, they would do well to maintain or enhance herbaceous understory conditions favorable for survival of first nests and that remain intact for later-season renesting attempts. Land uses that reduce contributions of herbaceous vegetation to visual obstruction of sage grouse nests (including grazing) may reduce nest survival at the landscape scale by resulting in increased depredation.

The threat of continued habitat loss and alteration and disturbance to nesting hens due to oil and natural gas development is substantial (USFWS 2004). While existing energy development in north-central Montana is minimal, future development is likely and has already been intense and expansive in the Powder River Basin of Wyoming and southeast Montana. Wholesale loss of habitat due to surface activity, coupled with effective fragmentation due to construction of fences, power lines, and roads and apparent avoidance by sage grouse of such structures (Braun 1998), reduces and degrades available nesting and brood rearing habitat (Connelly et al. 2000a). This is underscored by the threat of West Nile virus because nest and chick survival will become relatively more important to annual and long-term population maintenance should increased adult mortality, as first documented for sage grouse in 2003 (Naugle et al. 2004), persist.

Brood Survival

Brood survival can vary dramatically between years. My results suggest that it may not be efficacious to actively manage for high brood survival at the landscape scale. My data indicate that, at the landscape scale and within the context of expansive high-quality habitat, environmental factors likely drive population-level brood survival on an annual basis.

These results do not demonstrate, however, that localized management for high quality brood habitat would be unsuccessful. Nor do they suggest that management for brood habitat in fragmented or degraded habitats would be ineffective. Management of sage grouse habitats for productivity will likely need to take place at multiple scales. While nesting conditions might effectively be managed for by landscape-scale improvements of range condition in general and increase of grass cover in particular (Chapter 1), brood survival might be best managed for at specific sites within and around known nesting areas, though it would still likely exhibit wide variation in conjunction with annual environmental variation. Based on my observations and existing recommendations (Connelly et al. 2000a), I suggest that local management for brood habitat should focus on increasing forbs and grass understory.

Hen Survival

The finding of markedly increased mortality during a severe winter has clear management implications. The implications of two other findings – site-specific hunting season mortality and the advent of WNv – are less definitive and warrant further evaluation.

Even without any evidence that severe winter weather could affect sage grouse populations, many biologists and researchers have advocated for the protection of winter habitats for some years (see especially Connelly et al. 2000a). Variation in topography and height of sagebrush is believed to ensure availability of essential sagebrush forage in different snow conditions and depths (Beck 1977, Hupp and Braun 1989, Schroeder 1999, Connelly et al. 2000a). My observations during the severe winter of 2003-2004 underscore these beliefs, and demonstrate that occasionally, even in areas of expansive, high-quality habitat such as south Phillips County, winters may be so severe as to have clear and substantial population-level impacts.

In areas where winter habitats are destroyed or altered such that sagebrush height is reduced, average or moderate winter weather could approach effectively severe conditions when sagebrush plants are not present or are covered by snow. I suspect that the same winter conditions that would not impact sage grouse populations in high-quality habitats could be effectively severe in degraded habitats. I, therefore, echo other researchers' recommendations that sage grouse managers prioritize the identification and conservation of wintering areas. This will necessitate field work to locate flocks particularly in moderate and severe winters. Further, as I have witnessed quick formation of large flocks (<100 individuals) immediately after snowstorms, winter surveys should be as flexible and responsive to weather changes as possible so that surveys are conducted within several days of substantial snowfalls. This would allow the best opportunity to observe quick movements of relatively large numbers of birds immediately after winter storms. Optimally, a survey would also be conducted within a day or two before an expected winter storm so that movements from non-critical wintering areas could be described and quantified. The best opportunities for such work would come with coordination with on-going studies using radio-marked individuals.

I presented evidence of substantial site-specific increases in mortality during hunting seasons. The possibility of a hen-biased kill rate by hunters (as observed by Connelly et al. 2000b), either by selection or by virtue of increased hen encounters (as discussed in Chapter 3), coupled with the possibility of additive mortality, warrants careful consideration of sage grouse hunting seasons, their length, and bag limits. I agree with Connelly et al.'s (2003) suggestion that hunting mortality for sage grouse may be additive to natural winter mortality. Additive mortality could reduce spring breeding populations, increase the proportion of subadult hens in the breeding population, reduce or eliminate population growth in good years and exacerbate population decline in bad years. Several possibilities exist for manipulation of current hunting seasons: reduction of season length and/or bag limits, elimination of hunting altogether, instituting a permit-only system, or off-setting the sage grouse and pronghorn seasons (because I suspect that much sage grouse hunting mortality is opportunistic during by hunters also pursuing pronghorn).

The effects of WNv were pronounced. The increase in late-summer mortality attributable to WNv on this study was less than in other study areas (Wyoming and Alberta, Canada) in the same year (Naugle et al. 2004), though it remains unclear whether that difference is due to variation in habitat quality, spatial configuration of habitat, anthropogenic alteration of the landscape, land use, geographic patterns of spread during the first documented year of impact, or some other factor or combination of factors. In any case, careful consideration of the amount and location of current and proposed surface water – as habitat for *Culex tarsalis*, the mosquito that is a primary vector of WNv (Naugle et al. 2004) – would be prudent.

I have documented in this paper that hen survival can be affected by vulnerability during hunting seasons, an invading exotic virus (WNv), and by weather. I suggest that two of these three factors may be manageable to some extent through manipulation of harvest season lengths, dates and bag limits, and of amount or structure of anthropogenically-generated surface water containment (settling ponds and stock ponds). In areas with reduced or degraded winter habitats, even winter survival might be increased with conservation and restoration of expansive sagebrush stands of varied height and density. On the other hand, it may be easier to affect population growth in areas where nest success or brood survival is limited by non-environmental factors such as predation or poor understory cover.

Sage grouse have certainly evolved to persist through occasional population-level impacts of severe winters. I observed, however, the dramatic compounded effects of a new stressor (WNv) and a severe winter. Populations may well be ill-equipped to cope with natural perturbations that are coupled both with new threats such as WNv as well as the historic and on-going loss and degradation of sagebrush habitats. I stress, though, the potentially devastating results of the chance of concurrent impacts of various population-level processes. For example, if, by chance, WNv and winter increases in hen mortality had been experienced in a year with near-zero production, such as 2001, this population would likely have declined by as much as 60-75% in a single year.

SUMMARY

As documented here, hen survival is much more variable than previously known. Elevated mortality can be attributed to WNv, severe winter weather, and possibly to hunting and life-history trade-offs. These mechanisms suggest management efforts target identification and conservation of specific important wintering areas; consideration of surface water distribution, abundance, type, and timing, and careful structuring of hunting seasons.

Such a prioritization scheme demands large-scale conservation and rehabilitation of sagebrush, grass and forb understory elements. Sage grouse populations are capable of substantial growth with favorable habitat and environmental conditions. By maintaining high-quality, expansive habitat through appropriate land use practices and working to retain a high proportion of adult hens, populations will be poised for considerable growth when non-manageable environmental conditions are favorable.

LITERATURE CITED

Barnett, J.F. and J.A. Crawford. 1994. Pre-laying nutrition of sage grouse hens in Oregon. Journal of Range Management 47:114-118.

Beck, T. D. I. 1977. Sage grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management 41(1):18-26.

Braun, C.E. 1998: Sage grouse declines in western North America: what are the problems? Proceedings of the Western Association of State Fish and Wildlife Agencies 78: 139-156.

Braun, C. E. 1998. Sage Grouse declines in western North America: what are the problems? Proc. West. Assoc. State Fish and Wildl. Agencies. 78:139-156.

Burnham, K. P. and D. R. Anderson. 1998. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, NY.

Connelly, J. W. and C. E. Braun. 1997. Long-term changes in Sage Grouse populations in western North America. Wildlife Biology 3:229-234.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000a. Guidelines to manage sage grouse habitats and their populations. Wildlife Society Bulletin 28(4):967-985.

Connelly, J.W., A. D. Apa, R. B. Smith, and K. P. Reese. 2000b. Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. Wildlife Biology 6:227-232.

Connelly, J. W., K. P. Reese, E. O. Garton, and M. L. Commons-Kemner. 2003. Response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation in Idaho, USA. Wildlife Biology 9(4):255-260.

Gaillard. J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.

Hupp, J. W. and C. E. Braun. 1989. Topographic distribution of sage grouse foraging in winter. Journal of Wildlife Management 53(3):823-829.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. The Auk 118(2):557-562.

Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13(4):815-

829.

Naugle D.E., B.L. Walker, Aldridge, C.L., T.E. Cornish, B.J. Moynahan, M.J. Holloran, K. Brown, G.D. Johnson, E.T. Schmidtman, R.T. Mayer, C.Y. Kato, M.R. Matchett, T.J. Christiansen, W.E. Cook, M.S. Boyce, and E.T. Rinkes. 2004. West Nile virus: An emerging issue in sage-grouse conservation. Ecology Letters 7:704-713.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213-218.

Schroeder, M.A, J. R. Young, and C. E. Braun. 1999. Sage Grouse: *Centrocerus urophasianus*. In: Poole A, Gill F, editors. Birds of North America. Philadelphia, PA: The Birds of North America, Inc. p 1-28.

Stephens, S. E., D. N. Koons, J. J. Rotella, and D. W. Willey. 2003. Effects of habitat fragmentation on avian nest success: a review of the evidence at multiple spatial scales. Biological Conservation 115:101-110.

U. S. Fish and Wildlife Service. 2004. 90-day finding for petitions to list the Greater Sage-Grouse as threatened or endangered. 50 CFR 17, 69(77):21484-21494.

Wallestad, R., J. G. Peterson and R. L. Eng. 1975. Foods of Adult Sage Grouse in Central Montana USA. Journal of Wildlife Management 39(3):628-630.

Zablan, M. A., C. E. Braun, G. C. White. 2003. Estimation of greater sage-grouse survival in North Park, Colorado. Journal of Wildlife Management 67(1): 144-154.