AN ABSTRACT OF THE THESIS OF

James L. Rebholz for the degree of Master of Science in Wildlife Science presented on June 12, 2007.

Title: Influence of Habitat Characteristics on Greater Sage-grouse Reproductive Success in the Montana Mountains, Nevada

Abstract approved:____

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Greater sage-grouse (*Centrocercus urophasianus*) populations have declined across their geographic range during the last century. They were once widespread throughout the Intermountain West, but lower annual productivity, likely caused by degradation and loss of suitable habitat, has greatly reduced their distribution and population densities. Habitat used for reproduction has been well described, but relationships between habitat characteristics and reproductive output are less understood. Nesting success and chick survival are both important factors influencing annual productivity of sage-grouse. Several studies have investigated the effects of vegetation characteristics on nest success, but due to the variability of vegetation communities across the range, further work is necessary to clarify results from these studies. The relationships between habitat characteristics and chick survival are not as clearly understood. We initiated a study in the Montana Mountains of northwestern Nevada to describe nesting and early brood-rearing habitat and compare hypotheses describing potential relationships between habitat characteristics and reproductive success.

In 2004 and 2005, we monitored 84 sage-grouse hens during the reproductive period and quantified fine-scale habitat characteristics at nest and brood sites. We quantified the vegetation structure at successful and unsuccessful nests and related individual habitat characteristics to the odds of a nest hatching successfully. Individually marked chicks were monitored for 3 weeks after hatching to measure associations of forb, grass and sagebrush cover, and food availability with chick survival.

Grass cover beneath the nest shrub was the best predictor of nest outcome, and increasing amounts of grass cover improved the likelihood of a nest hatching successfully. Conversely, grass cover at early brood sites was negatively associated with chick survival. Early brood sites with greater forb cover were associated with higher sage-grouse chick survival. There was a weak relationship between sagebrush canopy cover at the nest shrub and hatch success, but sagebrush cover did not appear to have an effect on chick survival in the Montana Mountains.

Finally, we examined the relative importance of maternally-influenced variables for chick survival. Total plasma protein levels (TPP) of pre-laying hens have been linked to reproductive success and may be an indication of early spring habitat quality. We evaluated the association of TPP levels with sage-grouse chick survival, and also tested chick weight and chick sex to determine if they influenced chick survival. Total plasma protein levels were a good indicator of chick survival and may indicate a relationship between early spring forb availability and chick survival. Chick survival did not appear to be related to sex or weight at capture.

These results are similar to earlier studies that described the importance of herbaceous understory for both nest success and early brood-rearing. Management activities focusing on the restoration and maintenance of vegetation communities with intact herbaceous understories will likely improve sage-grouse reproductive success and annual production.

Influence of Habitat Characteristics on Greater Sage-grouse Reproductive Success in the Montana Mountains, Nevada

by
James L. Rebholz

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

James L. Rebholz, Author

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CONTRIBUTION OF AUTHORS

Drs. Douglas Robinson, Michael Pope, and Michael Gregg were involved in the study design, coordination and data collection, and editing of this manuscript.

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Influence of Habitat Characteristics on Greater Sage-grouse Reproductive Success in the Montana Mountains, Nevada

Influence of Habitat Characteristics on Greater Sage-grouse Reproductive Success in the Montana Mountains, Nevada

CHAPTER 1: INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) were once widespread in sagebrush (*Artemisia* spp.) habitats throughout the west (Schroeder et al. 1999). The extent of potential habitat before European settlement was greater than 1,200,000 km^2, but sage-grouse currently occupy only 56% (~668,000 km^2) of their estimated historical range (Schroeder et al. 2004). Loss of suitable habitat is the primary factor contributing to population declines. Livestock overgrazing, conversion of sagebrush habitats to agriculture, altered fire regimes, sagebrush control programs, and invasion by exotic species have all contributed to extensive habitat loss (Dalke et al. 1963, Johnsgard 1983, Klebenow 1985, Crawford et al. 2004), resulting in sage-grouse population declines across the geographic range.

Sagebrush habitats in Nevada have suffered from degradation since the beginning of the 20th century (Robertson and Kennedy 1954), and declines in sage-grouse populations were reported as early as 1937 by Girard and again by Rassmussen and Griner in 1938. Despite a lack of published data on population sizes, downward trends are apparent from declining lek sizes over the last 40 years, and while the proportion of active leks has remained relatively constant during this period, the proportion of larger leks has dwindled (Connelly et al. 2004). Populations have declined at a rate of 2.1% per year between 1974 and 2003 with populations in the 1970s being 1.2 – 3.5 times greater than those in 2003 (Connelly et al. 2004).

Determining the factors that influence population dynamics is critical to our understanding of sage-grouse and their successful management. Sage-grouse have high annual survival and low reproductive rates relative to other grouse species (Connelly and Braun 1997, Schroeder et al. 1999). However, productivity is highly variable and research has suggested that population levels are likely influenced by nest success and chick survival (Crawford and Lutz 1985, Schroeder 1997, Sveum et al. 1998a). To address the downward trends in population numbers, recent research has focused on the reproductive period (March – July) to determine factors affecting reproductive success. Early spring diet and nutritional condition of pre-laying females (Barnett and Crawford 1994, Dunbar et al. 2005, Gregg 2006, Gregg et al. 2006), nest site habitat selection (Gregg et al. 1994, Sveum et al. 1998b, Aldridge and Brigham 2002), and selection of brood-rearing habitats (Sveum et al. 1998a, Aldridge and Brigham 2002, Gregg 2006) all influence reproductive success.

Food availability and quality prior to nest initiation play an important role in reproductive success of female sage-grouse (Beckerton and Middleton 1982, 1983, Barnett and Crawford 1994, Dunbar et al. 2005, Gregg 2006, Gregg et al. 2006). In early spring, sage-grouse hens switch from a diet of sagebrush, which is their primary food source through winter (Schroeder et al. 1999), to a diet of nutritionally-rich forbs to prepare for reproduction (Barnett and Crawford 1994). Hens rely on the improved nutritional quality of early spring forbs to obtain the physiological condition necessary for egg laying. Dunbar et al. (2005) and Gregg et al. (2006) evaluated blood parameters as an indication of nutritional condition and were able to predict the likelihood of renesting by females that lost their first nests and the likelihood of chick survival. The use of nutritional condition as a predictor of reproductive success in sage-grouse populations has not been thoroughly tested in other areas.

Another important factor contributing to sage-grouse population dynamics is nest success rate. With estimates ranging between 15 – 86%, nest success varies greatly across the geographic range of sage-grouse (Schroeder et al. 1999). Variations in nest success may be due to geographic differences in vegetation characteristics, either natural variation among intact vegetation communities or variation among altered habitats with differing land-use histories. Nesting habitat is well described and typically consists of big sagebrush species (*Artemisia* spp.) or other shrubs, and tall residual grass cover (Klebenow 1969, Wakkinen 1990, Gregg et al. 1994, Sveum et al. 1998b, Aldridge and Brigham 2002, Holloran et al. 2005). Nest success appears to be influenced by vertical and horizontal components of vegetation coverage (Gregg et al. 1994, Sveum et al. 1998b, Aldridge and Brigham 2002).

After hatching, other factors are important for chick survival including forbs and insects for food (Klebenow and Gray 1968, Johnson and Boyce 1990, Drut et al. 1994b, Sveum et al. 1998a). Brood-rearing hens appear to select habitat based on the availability of particular forbs (Pyle 1992, Sveum et al. 1998a). Drut et al. (1994b) found that chicks in areas with low sage-grouse production primarily consumed sagebrush, and in areas that produced more offspring, diets were composed mostly of forbs and insects. Captive-reared chicks fed a diet of insects survived ≥10 days while chicks not receiving insects died between 4 – 10 days after hatching (Johnson and Boyce 1990). Habitat structure at early brood sites also likely influences chick survival by providing sufficient cover from predators. Early brood-rearing habitats are typically open stands of sagebrush with understories composed primarily of forbs and grasses (Klebenow 1969, Drut et al. 1994a, Sveum et al. 1998a, Aldridge and Brigham 2002). However, it is not clear how the availability of cover influences chick survival or how much cover is needed to increase chick survival.

In 2004 and 2005, we conducted research in the Montana Mountains of northwestern Nevada to evaluate habitat use and reproductive success of sage-grouse. Despite extensive grazing, mining, and high harvest rates from hunting, the Montana Mountains support one of the highest densities of sage-grouse in Nevada and Oregon, and offspring production appears to be high (Nevada Department of Wildlife, personal communication). Estimates from banding efforts coordinated by Nevada Department of Wildlife (2001 – 2005) and wing returns from hunter harvests suggested sage-grouse populations and production in the Montana Mountains may exceed areas with more restrictive land use policies and hunting, including nearby Sheldon and Hart National Wildlife Refuges. Estimates of annual offspring production have been as high as 3.02 chicks per hen in the fall of 2004 (Nevada Department of Wildlife, unpublished report 2006), which was higher than any other site monitored in Nevada during that year. Based on harvest data from marked birds, sage-grouse population estimates were between 7,264 and 13,625 during the 5 years of the banding study (Nevada Department of Wildlife, unpublished report 2006).

We used data collected during the 2004 and 2005 reproductive seasons to investigate relationships between habitat characteristics and maternal factors determined by the nutritional condition of pre-laying hens, and reproductive success.

Reproductive success was measured by nest initiation rates, nest success, and chick survival. The objectives of this study are to:

1) characterize habitat used by female sage-grouse during the reproductive season, and

2) determine relationships between maternal condition, habitat characteristics and reproductive success including nest success and chick survival.

Chapter 2 describes the habitat selected by female sage-grouse for nesting and compares models describing potential relationships between vegetation structure and nest success. Chapter 3 investigates relationships between habitat characteristics at early brood sites and chick survival, and considers predictive models of chick survival derived from similar research at nearby sites (Sheldon and Hart National Wildlife Refuges) in Nevada and Oregon. Exploratory analysis of variables related to maternal condition and their effects on chick survival are described in the Appendix.

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CHAPTER 2: NEST SITE CHARACTERISTICS AND FACTORS AFFECTING NEST SUCCESS OF GREATER SAGE-GROUSE

ABSTRACT

Nesting success of greater sage-grouse (*Centrocercus urophasianus*) influences annual reproductive success and population dynamics. To describe nesting habitat and measure the effects of vegetation characteristics on nesting outcomes, we sampled 87 sage-grouse nests during 2004 and 2005 in the Montana Mountains of northwestern Nevada. Within a 78.5 m^2 circular plot surrounding each nest, we quantified sagebrush canopy cover and grass cover. We used Akaike's Information Criterion to rank competing models describing potential relationships between vegetation characteristics at and surrounding sage-grouse nests and to determine those characteristics associated with nest success. Nest initiation rate was high (90.0%), and apparent nest success was 40.2%. We used a Mayfield estimation to determine a probability of nest success of 36% (hatching $\geq$1 chick). There was a positive effect on nest success from grass cover within a 3 m^2 area centered on the nest (odds ratio: 1.030, 95% CI: 1.005 – 1.059). We also found weak support for a positive effect of sagebrush cover at the nest on nest success (odds ratio: 1.02, 95% CI: 0.993 – 1.043). Our results are similar to previous findings and confirm the importance of sagebrush cover and herbaceous understory for nesting. We recommend managing sagebrush communities to provide sufficient grass cover and sagebrush cover for successful nesting by greater sage-grouse.

INTRODUCTION

The distribution and population densities of greater sage-grouse (*Centrocercus urophasianus*) have declined since European settlement of western North America in the late 19th and early 20th centuries (Schroeder et al. 1999). Sage-grouse were widespread throughout the Intermountain West, with records that documented their occurrence in 13 states and 3 Canadian provinces (Schroeder et al. 2004). There were ≥1,200,000 km^2 of potential habitat for sage-grouse prior to European settlement, but ≥40% of suitable habitat was lost in the last century (Schroeder et al. 2004). Livestock overgrazing, conversion of sagebrush communities to agriculture, altered fire regimes, sagebrush control programs, and introduction of exotic vegetation (Dalke et al. 1963, Johnsgard 1983, Klebenow 1985, Crawford et al. 2004) have led to rangewide habitat loss and are implicated in most sage-grouse population declines.

Nevada has various sagebrush communities that support sage-grouse, and most have been affected by the same factors degrading sage-grouse habitat across their geographic range. Population declines were reported as early as the 1930s (Girard 1937, Rassmussen and Griner 1938). The mean decline statewide is 50%; however, some local sage-grouse populations have declined as much as 80% (Nevada Wildlife Federation 2002). These declines are thought to be caused by reduced reproductive success (Klebenow 1985). Despite a similar history of habitat loss that impacted populations throughout the rest of the state (Nevada Wildlife Federation 2002), sage-grouse populations in northern Nevada remain relatively stable.

The Montana Mountains in northwestern Nevada support one of the highest densities of sage-grouse in Nevada and reproductive success appears to be high.

Between 2001 and 2005, banding efforts coordinated by Nevada Department of Wildlife and data collected from hunter harvests indicated population densities and reproductive success in this area exceeded neighboring areas with more restrictive land use policies and hunting. Estimates of annual offspring production have been as high as 3.02 chicks per hen (Nevada Division of Wildlife, unpublished report 2006), which was higher than any other site monitored in Nevada during that year. Based on harvest data collected from marked birds in the Montana Mountains, population estimates were between 7,264 and 13,625 during the 5 years of the banding study (Nevada Department of Wildlife, unpublished report 2006).

Several measures of reproductive success have been used to compare sage-grouse populations across their range, and these vary greatly whether measuring clutch size, nesting and renesting rates, nest success, or ratios of chicks per hen (Schroeder et al. 1999). Regardless of the index of reproductive success used, variation may result from differences in habitat availability and quality due to differing land-use histories and practices and natural community variability. The loss of nesting habitat is hypothesized to be a primary factor causing sage-grouse population declines (Crawford et al. 2004), so research has focused on the reproductive period (March – July) to clarify how habitat characteristics influence reproductive success.

Nesting success is one of the primary factors influencing reproductive success and sage-grouse population dynamics (Crawford and Lutz 1985, Gregg et al. 1994). Nest success varies greatly across the geographic range of sage-grouse with estimates between 15 – 86% of nests hatching ≥1 chick (Schroeder et al. 1999). This variability may be due to differences in vegetation structure among areas. Females select nest sites with greater shrub cover than the surrounding habitat (Klebenow 1969, Wakkinen 1990, Sveum et al. 1998, Holloran et al. 2005), and nest success appears to be associated with adequate shrub and grass cover which provide protection from predators but also allows the hens to escape (Delong et al. 1995, Gregg et al. 1994, Holloran et al. 2005).

We investigated factors considered to influence sage-grouse nest success in the Montana Mountains. We examined potential relationships between habitat characteristics and nest outcome at two scales: the nest shrub and the area surrounding the nest site. Results from this study will improve our understanding of an important factor likely influencing sage-grouse population dynamics in the Montana Mountains, and may provide wildlife and land managers with the critical information to maintain suitable habitat for nesting and restore sage-grouse populations across their geographic range.

STUDY SITE

The Montana Mountains, in Humboldt County, are approximately 18 km northwest of Orovada, Nevada (Figure 1). The range is part of the Lone Willow Population Management Unit managed by the Bureau of Land Management in Winnemucca, NV. The core study area encompassed approximately 100,792 hectares ranging from 1200 to 2300 m in elevation. Annual precipitation is 21.9 cm and average temperatures range from a minimum of -8.6°C in January to a maximum of 33.1°C in July in Kings River Valley, immediately west of the Montana Mountains (Western Regional Climate Center, Reno NV). Precipitation is higher across the core

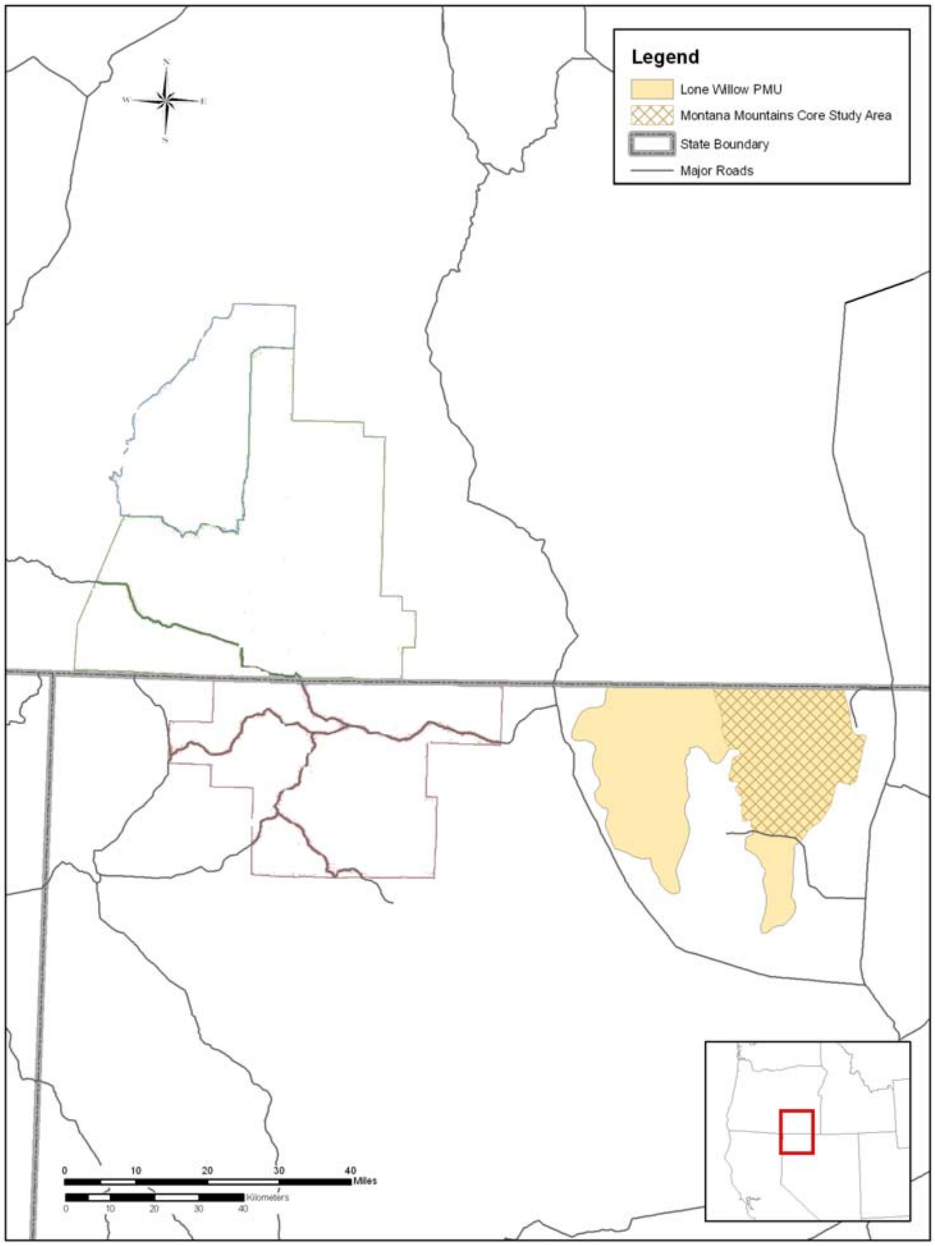

Figure 1. Greater sage-grouse study area in the Montana Mountains, Nevada, 2004-5 and other locations (outlined) in northern Nevada and southeastern Oregon where sage-grouse reproductive ecology has been studied.

study area due to higher elevations, and average minimum and maximum temperatures are cooler.

Vegetation is typical of shrub-steppe habitats in southeast Oregon and northern Nevada. Prominent vegetation includes low sagebrush (*Artemisia arbuscula*), mountain big sagebrush (*A. tridentata vaseyana*), and Wyoming big sagebrush (*A. t. wyomingensis*). Other shrub species, including antelope bitterbrush (*Purshia tridentata*), western snowberry (*Symphoricarpos occidentalis*) and rabbitbrush (*Chrysothamnus* spp.) are dispersed throughout the site. Common forbs include *Agoseris* spp., *Crepis* spp., *Phlox* spp., *Lupinus* spp., and *Astragulus* spp. Grasses include bluegrass (*Poa* spp.), fescue (*Festuca* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), needlegrass (*Stipa* spp.), giant wildrye (*Leymus cinereus*), and bottlebrush squirreltail (*Elymus elymoides*).

The area includes 7 grazing allotments. Licensed grazing included 34,112 Animal Unit Months managed on a rest-rotational system since the 1960s.

METHODS

Data Collection

Female sage-grouse were trapped and radio-marked in March and April, 2004-5, prior to nest initiation. Trapping efforts targeted known leks, and birds were captured opportunistically. Females were captured using a spotlighting technique modified from Giesen et al. (1982). Hens were captured throughout the study site so we assumed our sample of birds was a representative sample of reproductive females in the Montana Mountains. We fitted birds with 21 g necklace-style radio transmitters (Advanced Telemetry Systems, Inc., Isanti, MN) and a numbered aluminum leg band.

Radio-marked hens were monitored throughout the reproductive period (March – July) for nest initiation and outcome. Every 3 – 7 days, we located radio-marked females using a portable receiver and 3-element Yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MN). Once a hen was found nesting, we monitored the nest from >20 m for indications of depredation or hatching. Clutch size was determined opportunistically when a hen was found away from her nest, when a female was inadvertently flushed from her nest, or after hatching. We recorded exact nest locations after abandonment, predation, or hatching with hand-held GPS units (eTrex, Garmin International Inc., Olathe, KS) using Universal Transverse Mercator (UTM) coordinates. We sampled all nests found for radio-marked hens. The sample of nests was distributed throughout the study site and nesting period (April – June). Unsuccessful hens were monitored for renesting attempts through mid-July. All nests were categorized as successful (≥1 egg hatched) or unsuccessful, and after each nest hatched or failed, vegetation characteristics were measured within a circular, 78.5 m^2 plot surrounding each nest. We estimated the percent cover of sagebrush and grass within this area using line-intercept and Daubenmire frame methods (Canfield 1941, Daubenmire 1959). The intercept distance of all shrubs along 2 perpendicular, 10 m transects centered at the nest was used to calculate sagebrush cover, and 10 20x50 cm frames equidistantly spaced along the transects were used to determine the percent grass cover. We categorized total percent sagebrush cover in 2 height categories: short (<40 cm) and tall (≥40 cm). To investigate the influence of vegetation characteristics at the nest and the vegetation surrounding the nest site, we separated the nest area into 2 plots (Gregg 1991). The circular plot immediately surrounding the nest with 1 m radius (~3 m^2) was classified as *1-m*, and the remaining area delineated by the 10 m sample transects (~75.5 m^2) was classified as *10-m*.

Nest initiation rates were calculated from the total number of radio-marked hens available for nesting and the number of females that initiated nests. Apparent nest success was calculated from the number of successful nests (≥1 chick hatched) and the total number of nests laid, including renesting events. Renesting initiation rates were calculated from the birds that remained in the sample after initial nests failed and attempted to renest. Additionally, we calculated a Mayfield estimate for nest survival for sampled nests (Mayfield 1975) by counting known exposure days for nests and using an incubation period of 27 days (median incubation period, Schroeder et al. 1999). Mean clutch size was calculated from successful nests only due to the uncertainty of original clutch size after predation events.

We pooled data from the 2 study years because our primary interest was in variation in vegetation characteristics and annual differences account for part of this variation. We calculated mean values and standard errors for habitat characteristics including grass, sagebrush and total shrub cover, and the proportion of tall sagebrush to total sagebrush.

Data Analysis

We used logistic regression to calculate the change in odds of nest success due to the influence of vegetation characteristics at *1-m* and *10-m* plots. Akaike's Information Criterion, adjusted for small sample size (AIC_c), was used to infer the relative importance of vegetation characteristics based on variables present in top competitive models (Burnham and Anderson, 2002). Models were derived from explanatory variables including total sagebrush canopy cover at *1-m* and *10-m* plots, proportion of tall sagebrush to total sagebrush cover at *1-m* and *10-m* plots, and total grass cover at *1-m* and *10-m* plots (Table 1). We considered vegetation characteristics as vertical or horizontal structure when developing models describing possible relationships.

Table 1. Description of explanatory variables used in the candidate model set to associate greater sage-grouse nest site characteristics with nest outcome, Montana Mountains, NV, 2004-5.

Plot	Variable Type	Code	Description	Units
1-m	Horizontal cover	STOGR	Total grass cover	%
1-m	Horizontal cover	STOTALSAGE	Total sagebrush cover	%
1-m	Vertical structure	SPROPTALLSAGE	Proportion of tall sagebrush (≥40cm) to total sagebrush	%
10-m	Horizontal cover	LTOGR	Total grass cover	%
10-m	Horizontal cover	STOTALSAGE	Total sagebrush cover	%
10-m	Vertical structure	LPROPTALLSAGE	Proportion of tall sagebrush (≥40cm)	%
1-m	Interaction	SPTALLSG*TOTAL	Proportion of tall sagebrush * Total sagebrush	%
10-m	Interaction	LPTALLSG*TOTAL	Proportion of tall sagebrush * Total sagebrush	%

We screened variables for multicollinearity prior to developing the candidate model set and examined a matrix of scatter plots for all explanatory variables to look for possible relationships. If 2 or more variables were correlated (Pearson correlation coefficient: r >0.60), they were not used together in any model. However, we included correlated variables in the model set among different models when we believed one variable was better at describing a hypothesis than its related variable.

We developed a set of 17 *a priori* candidate models, based on a review of previous studies and observations in the field, to represent potential relationships between vegetation characteristics and nest outcome. The models are described by the format:

$$Logit(\pi) = \beta + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 ... + \beta_k x_k$$

where β_1 is the estimate of the effect of explanatory variable x_1 after accounting for variables x_2 through x_k. The response variable, nest outcome, has a Bernoulli distribution, Y~Bernoulli (π), and the mean response is $\mu \{y|x_1,\dots,x_k\} = \pi$. The variance structure is described by $Var\{ y|x_1,\dots,x_k \} = \pi (1 - \pi)$. We calculated ΔAIC_c values between the best fitting model and remaining models in the candidate set and Akaike's weights (w_i) to determine the relative likelihood of each model.

RESULTS

Seventy-six of 84 (90%) radio-marked hens initiated at least one nest. Fifty-two unsuccessful nests and 35 successful nests were sampled. Eight nests were abandoned, likely due to our monitoring activities, and were not sampled. Successful nests hatched as early as 28 April and as late as 21 June. We sampled first, second and third nesting attempts, and most failed nests were likely due to predation or abandonment. The apparent nesting success was 40% (35/87), and of the 76 hens that initiated a nest, 46% were successful (35/76). We estimated the probability of nest success at 36% (Mayfield 1975). Of the 43 birds that failed their first attempt, 37% attempted a second nest (Table 2). Twenty-five percent of the hens in 2004 attempted to renest and 48% attempted renests in 2005. No females attempted a third nest in 2004, but in 2005, 43% of the birds that remained in the sample attempted a third nest. The clutch size for successful nests ranged from 4 – 10 eggs ($\bar{x}$ = 7.3, *n* = 35).

Table 2. Nesting parameters of radio-marked greater sage-grouse hens monitored in the Montana Mountains, NV, 2004-5.

	2004	2005	Total
Nest Initiation	90% (38/42)	90% (38/42)	90% (76/84)
Initial Nest Success	42% (16/38)	29% (11/38)	36% (27/76)
Renest Initiation	25% (5/20)	48% (11/23)	37% (16/43)
Renest Success	60% (3/5)	27% (3/11)	38% (6/16)
2nd Renest Initiation		43% (3/7)	43% (3/7)
2nd Renest Success		67% (2/3)	67% (2/3)

We sampled 22 nests that were repeated efforts by several hens that attempted renest(s) during the same season or nested in both years. These 22 nests were treated as independent due to the complexity of modeling potential dependence between nests from the same hen. To test this assumption, we repeated our analysis using only one nest from each hen and model selection results and parameter estimates for vegetation characteristics were similar to those presented.

Nests were generally laid in areas with 15.6% (SE ± 1.0) mean grass cover, 30.2% (SE ± 1.3) sagebrush cover, and 37.2% (SE ± 1.5) total shrub cover and were typically placed under shrubs (*1-m* plot) with greater canopy and more grass cover than the surrounding general location (*10-m*) (Table 3). Sixty percent of sagebrush cover at *1-m* plots was ≥40 cm. Successful nest sites (*1-m* plot) had more grass cover ($\bar{x}$ = 24.2 ± 4.1) than unsuccessful sites ($\bar{x}$ = 14.8 ± 1.7).

Only 2 variables were highly correlated, proportion of tall sagebrush at *1-m* and *10-m* plots (Pearson correlation coefficient: $r = 0.76$, $p<0.0001$). We did not include these variables together in any model but used them interchangeably in the model set to best describe the biological hypotheses represented by our models.

Table 3. Habitat characteristics of successful and unsuccessful nests in the Montana Mountains, NV, 2004-5.

	Plot	Grass Cover (%) $\bar{x}$ (±SE)	Sagebrush Cover (%)[a] $\bar{x}$ (±SE)	Prop. Tall Sagebrush[b] $\bar{x}$ (±SE)	Shrub Cover (%)[c] $\bar{x}$ (±SE)
All Nests	(n = 87)				
	1-m	18.6 (2.0)	52.9 (2.2)	0.60 (0.04)	61.8 (2.1)
	10-m	14.9 (1.0)	24.5 (1.4)	0.43 (0.04)	31.1 (1.6)
	Total[d]	15.6 (1.0)	30.2 (1.3)	0.50 (0.04)	37.2 (1.5)
Successful Nests	(n = 35)				
	1-m	24.2 (4.1)	54.0 (3.9)	0.61 (0.07)	62.1 (3.5)
	10-m	16.6 (2.0)	23.8 (2.1)	0.48 (0.06)	30.5 (2.5)
	Total	18.1 (1.8)	29.8 (2.0)	0.54 (0.06)	36.8 (2.4)
Unsuccessful Nests	(n = 52)				
	1-m	14.8 (1.7)	52.2 (2.6)	0.59 (0.05)	61.5 (2.6)
	10-m	13.8 (1.1)	25.0 (1.9)	0.40 (0.05)	31.4 (2.1)
	Total	14.0 (1.1)	30.4 (1.8)	0.48 (0.05)	37.4 (1.9)

[a] Sagebrush cover included all *Artemisia* spp.
[b] Proportion of sagebrush ≥40 cm tall to total sagebrush cover.
[c] Total shrub cover included *Artemisia* spp. and other woody shrubs including *Purshia* spp., *Symphoricarpos* spp. and *Chrysothamnus* spp.
[d] Total included *1-m* and *10-m* plots.

We calculated the relative likelihood for each model in our candidate set and ranked models accordingly (Table 4). The best fitting model contained only grass cover at the nest site (*1-m* plot). The relative likelihood for this model was approximately 0.3 (w_i = 0.295). However, the *horizontal cover (1-m)* model, including grass and sagebrush cover at the nest site, was the second best model and very competitive, sharing a similar likelihood (w_i = 0.266). This model was approximately twice as likely as the third competing model which contained grass cover at *1-m* and *10-m* plots (w_i = 0.125). The null model, with no explanatory variables, ranked fourth in our model set and had a likelihood of 0.05 (w_i = 0.051).

Table 4. Candidate model set and AIC_c results comparing hypotheses describing potential relationships between habitat characteristics and greater sage-grouse nest outcomes in the Montana Mountains, NV, 2004-5.

Model	Variables	AIC_c [a]	ΔAIC_c [b]	w_i [c]
Grass cover (*1-m*)	**STOGR**	**115.795**	**0.000**	**0.295**
Horizontal cover (*1-m*)	**STOGR + STOTALSAGE**	**116.002**	**0.207**	**0.266**
Grass cover (*1-m* and *10-m*)	**STOGR + LTOGR**	**117.522**	**1.727**	**0.125**
Null Model	No Explanatory Variables	119.311	3.516	0.051
Vertical and horizontal structure (*1-m*)	STOGR + STOTALSAGE + SPROPTALLSAGE + SPTALLSG*TOTAL	119.334	3.539	0.050
Grass cover (*10-m*)	LTOGR	119.715	3.919	0.042
Horizontal cover (*1-m* and *10-m*)	STOGR + LTOGR + STOTALSAGE + LTOTALSAGE	119.955	4.159	0.037
Vertical structure (*10-m*)	LPROPTALLSAGE	120.246	4.451	0.032
Sagebrush cover (*10-m*)	LTOTALSAGE	121.234	5.439	0.019
Sagebrush cover (*1-m*)	STOTALSAGE	121.246	5.451	0.019
Vertical structure (*1-m*)	SPROPTALLSAGE	121.373	5.578	0.018
Horizontal cover (*10-m*)	LTOGR + LTOTALSAGE	121.861	6.065	0.014
Sagebrush cover (*1-m* and *10-m*)	STOTALSAGE + LTOTALSAGE	123.050	7.255	0.008
Horizontal cover and vertical structure (*1-m*) and horizontal cover (*10-m*)	STOGR +LTOGR + STOTALSAGE + SPROPTALLSAGE + SPTALLSG*TOTAL + LTOTALSAGE	123.203	7.407	0.007
Vertical structure and horizontal cover (*10-m*)	LTOGR + LTOTALSAGE + LPROPTALLSAGE + LPTALLSG*TOTAL	123.344	7.549	0.007
Total cover of tall sagebrush (*1-m*)	STOTALSAGE + SPROPTALLSAGE + SPTALLSG*TOTAL	123.379	7.583	0.007
Vertical structure (*1-m*) and sagebrush cover (*10-m*)	STOTALSAGE + SPROPTALLSAGE + SPTALLSG*TOTAL + LTOTALSAGE	125.267	9.472	0.003

[a] AIC_c is the Akaike Information Criterion values with small sample bias adjustment (Burnham and Anderson 2002).
[b] ΔAIC_c is the difference between a model's AIC_c value and the smallest AIC_c value ($AIC_{c\,i}$ - $AIC_{c\,min}$).
[c] w_i is the Akaike weight describing the relative likelihood of a model.

Grass cover at the nest site (*1-m* plot) was present in the 3 top models. The estimate for the effect of nest site grass cover on the odds of nest success changed slightly between the top 3 models (Table 5). Using the estimate from the *grass cover (1-m)* model, grass cover at the nest site increased the odds of nest success 1.03 times for each percentage increase in the amount of grass cover (95% CI: 1.005 – 1.059). Sagebrush cover at the nest site and grass cover surrounding the nest (*10-m* plot) were also present in the top models. Grass cover surrounding the nest and sagebrush cover at the nest site both had a slight positive effect on nest success (odds ratio: 1.016, 95% CI: 0.968 – 1.068 and 1.017, 95% CI: 0.993 – 1.043).

Table 5. Relative likelihoods of top three models, odds ratios, and 95% confidence intervals for total grass cover at *1-m* from the top three models, Montana Mountains, NV, 2004-5.

Model	w_i [a]	β [b]	Odds ratio (e^{β}) [c]	95% CI for odds ratio
Grass cover – nest site	0.295	0.0295	1.030	1.005 – 1.059
Horizontal cover – nest site	0.266	0.0366	1.037	1.010 – 1.069
Grass cover – nest site and nest location	0.125	0.0267	1.027	1.002 – 1.057

[a] w_i is the Akaike weight describing the relative likelihood of a model (Burnham and Anderson 2002).
[b] Parameter estimate.
[c] Odds ratio = the factor by which the odds of a nest hatching successfully changes for every 1-unit increase in grass cover.

DISCUSSION

Grass cover at the nesting shrub likely protects nests from predation by providing scent and visual barriers (Gregg et al. 1994). In the Montana Mountains, greater sage-grouse nest areas (*1-m* and *10-m* plots) had the minimum recommended amount of grass cover for managing breeding habitats (Connelly et al. 2000). We found nests with higher percent grass cover had an increased likelihood of hatching successfully. Our data show an increase of 10 to 20% in grass cover at the nest (*1-m*) increased the odds of success by 34.3%. Our results are similar to those found by Gregg (1991) in Oregon, where grass cover at nests was greater for successful than unsuccessful nests. In other study areas, the height of the grass cover at nest sites also affected the likelihood of nest success (Gregg et al. 1994, DeLong et al. 1994, Sveum et al. 1998). However, we did not include grass height because there may be some temporal variation in grass height from the time of nest initiation and incubation to vegetation sampling. Hausleitner et al. (2005) found a significant change in both grass height and cover from nest initiation to nest cessation but doubted whether these changes were biologically significant. To avoid this potentially confounding effect, we assumed total grass cover changed less from nest outcome to sampling date, and therefore, may be a more reliable measure of the potential effect of grass cover than tall grass cover, particularly later in the season when drier conditions limit grass growth. Nevertheless, our results are consistent with results from earlier research demonstrating the importance of grass at the nest (Gregg 1991, Gregg et al. 1994, DeLong et al. 1995, Sveum et al. 1998).

The amount of sagebrush cover surrounding nests in the Montana Mountains appears to be higher than cover reported in most other study areas and slightly exceeds levels recommended for management of breeding habitats (15 – 25%, Connelly et al. 2000). Sagebrush canopy at the nest appeared to have a positive effect on nesting success, but the confidence intervals overlapped 1 so the effect of this variable may be overstated. The importance of sagebrush canopy cover for nest success in other studies has been variable. A positive effect of sagebrush canopy cover at the nest was reported from Oregon (Gregg 1991, Gregg et al. 1994, DeLong et al. 1995), whereas no significant effect of canopy cover and height of nesting shrub was reported in Washington or Canada (Sveum et al. 1998, Aldridge and Brigham 2002). Given our results of only a weak relationship between sagebrush cover and nesting success, and the mixed results from previous studies, it appears that sagebrush cover may not have a strong and consistent influence on sage-grouse nesting success. Nevertheless, most sage-grouse nests are under sagebrush species (Klebenow 1969, Connelly et al. 1991, Gregg et al. 1994, Sveum et al. 1998, Schroeder et al. 1999), so sagebrush is important for nesting sage-grouse, but the degree to which sagebrush cover at nest sites influences nesting success varies. The availability of suitable shrubs for nests is not likely a limiting factor for nest success in the Montana Mountains.

There was only weak evidence suggesting grass cover surrounding the nest had a positive effect on nest success in the Montana Mountains. Our results were similar to those reported for sage-grouse nests in Oregon where grass cover surrounding the nest was not different between successful and unsuccessful nests (Gregg 1991). However, a study in Canada found grass cover surrounding the nest was a good predictor of nest outcome, where unsuccessful nests had greater amounts of grass cover than successful nests (Aldridge and Brigham 2002). But comparison is difficult because grass cover in the Montana Mountains was less than half that reported for nesting areas and random locations in Canada. The weak relationship between nest success and grass cover surrounding the nest and the inconsistent results from other areas indicate that vegetation characteristics surrounding the nest may not be a good predictor of nest outcome across the geographic range of sage-grouse. Females appear to select nests based on vegetation characteristics at a fine scale – the nest shrub and associated herbaceous understory (Gregg 1991).

Nest initiation in the Montana Mountains was high compared to other studies (Schroeder et al. 1999). The nest success rates (proportion of females that attempted to nest and nested successfully) in the Montana Mountains were comparable to values for other sage-grouse populations (Schroeder et al. 1999), but renesting rates in the Montana Mountains were high, particularly during 2005. Approximately half of the hens that failed a first nest attempted another nest in 2005, and almost half of the females that failed their first 2 attempts initiated a third nest. There are few reports of second renesting attempts for sage-grouse (Sveum 1995, Schroeder 1997), but the lack of information on this occurrence may be related to reduced monitoring effort of radio-marked hens after loss of their second nest. Also misclassifying nests as initial nests when they may be renests may be more common than reported. The presence of ovulated follicles in some birds (Dalke et al. 1963) prior to 'first' attempts indicates that misclassifications are not unusual.

Several factors influence renesting rates including: seasonal timing of nest initiation, the number of days incubating a first nest, and indirectly, early spring habitat characteristics (Schroeder 1997, Gregg et al. 2006). Maternal physiological condition may also play an important role in renesting. Hens consume a diet of protein-rich forbs available in early spring to prepare for reproduction (Barnett and Crawford 1994), and this forb consumption has been related to productivity. Total plasma protein levels may provide an index of dietary protein uptake prior to nest initiation and may be a good measure of reproductive condition. Plasma protein levels of pre-laying hens have been linked to reproductive success (Dunbar et al. 2005, Gregg et al. 2006). Gregg et al. (2006) used radio-marked hens in the Montana Mountains to test the relationship between plasma protein levels and renesting. Hens in the Montana Mountains exhibited high plasma protein levels which may explain high renesting rates and ultimately indicate higher quality habitat for reproduction. Plasma protein levels for hens in the Montana Mountains were also a good indicator of chick survival (see APPENDIX).

MANAGEMENT IMPLICATIONS

Management strategies aimed at increasing nesting success of greater sage-grouse should focus primarily on increasing grass cover but also on maintaining shrub communities. Similar to other sage-grouse studies (Gregg 1991, Gregg et al. 1994, DeLong et al. 1994, Sveum et al. 1998), we found that nesting success increased as grass cover at the nest increased. Sagebrush cover also had a positive influence on nesting success even though the relationship was not conclusive. Proposed management guidelines for proportions of sagebrush cover near nests should be conservative until further studies clarify this relationship. Most nests are placed under sagebrush, so the sagebrush component of nesting habitat is important, but it appears management of grass cover for nest success should take precedent.

Our analyses compared vegetation characteristics measured at a fine scale, but successful management of sage-grouse populations must occur at multiple scales and must be able to effect nesting habitat characteristics at a landscape level. Minimally, nesting habitat must have suitable shrubs and sufficient herbaceous understory to provide protection for sage-grouse nests. But more research is needed to relate fine-scale site features to landscape-level characteristics so land managers can apply broad-scale management strategies.

To manage habitat for improved nesting success, management strategies should limit potential disturbances that reduce grass cover or excessively reduce sagebrush cover. Overgrazing, fire, and invasion by exotic grasses that can influence the frequency of fire and thereby reduce shrub cover, can all reduce grass and sagebrush cover. With increased grazing intensity, livestock seek out grasses beneath shrubs after foraging on the grasses in the interspaces between shrubs (France 2005). Excessive livestock grazing could thereby reduce grass cover at nesting shrubs and increase the likelihood of predation. Limiting the impacts of livestock grazing by reducing excessive use of reproductive habitat during nesting and maintaining diverse mosaic of habitat types across the landscape, could insure sufficient sage-grouse habitat will persist in the event of disturbances.

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CHAPTER 3: INFLUENCE OF HABITAT CHARACTERISTICS AT EARLY BROOD SITES ON SURVIVAL OF GREATER SAGE-GROUSE CHICKS

ABSTRACT

Low chick survival is a primary factor contributing to greater sage-grouse (*Centrocercus urophasianus*) population declines across their geographic range, but little is known about this aspect of their reproductive ecology. In 2004 and 2005, we radio-tagged 115 sage-grouse chicks from a highly productive population in the Montana Mountains of northwestern Nevada to examine relationships between habitat characteristics and survival of newly hatched chicks to 18 days post-capture. We quantified grass, forb and sagebrush cover, and insect availability at early brood locations. Akaike's Information Criterion was used to compared the relative importance of hypotheses describing relationships between vertical and horizontal vegetation cover as well as food availability, and we examined the effects of habitat characteristics using weighted parameter estimates. Chick survival to 18 days after radio-marking was 0.437 (SE ± 0.048). We found chick survival increased by 13% for each percent unit increase of forb cover, whereas survival decreased by 15% for each percent unit increase in grass cover at early brood sites. Our results are similar to previous research describing the importance of forbs during early brood-rearing. We recommend management activities aimed at maintaining or increasing greater sage-grouse populations focus on maintaining or restoring forb communities.

INTRODUCTION

Populations of greater sage-grouse (*Centrocercus urophasianus*) have declined greatly in the last several decades. Some populations across the geographic range have declined as much as 80% since the 1950s (Braun 1998). Long-term monitoring programs indicated the loss of habitat for reproduction was responsible for sage-grouse population declines. Habitat degradation and loss is likely affecting mortality of juveniles, resulting in reduced annual offspring production and recruitment (Crawford and Lutz 1985). Understanding the relationships between offspring survival and habitat characteristics will provide the information necessary to successfully manage the species and assist in restoration of declining populations.

Most juvenile mortality occurs in the first days after hatching (Schroeder et al. 1999, Aldridge 2005, Gregg 2006, Gregg et al. 2007). Predation is likely the most direct effect influencing chick survival (Gregg et al. 2007), but the indirect factors contributing to mortality are not completely known. During early brood-rearing, vegetation cover and food availability can influence chick survival and productivity. Due to the difficulty of monitoring chicks during this period, previous research focused on habitat use patterns of brood-rearing hens and food availability and selection (Drut et al. 1994a,b, Sveum et al. 1998, Aldridge and Brigham 2002). While this research established the importance of food and cover for brood survival, it did not directly link individual chick survival with habitat characteristics. Key forbs and insects for chicks were described from samples collected at early brood sites, crop samples of juvenile chicks, and study of captive birds (Johnson and Boyce 1990, Pyle 1992, Drut et al. 1994b, Gregg 2006). Drut et al. (1994b) found chicks in areas producing low numbers of sage-grouse consumed primarily sagebrush, and in areas producing more offspring, chick diets included >75% insects and forbs. Captive-reared chicks fed a diet of insects survived ≥10 days whereas chicks not receiving insects died within 4 – 10 days (Johnson and Boyce 1990).

The habitat structure at early brood sites may influence the risk of predation and predator detection (Aldridge 2005). Early brood locations are typically open stands of sagebrush with additional cover from grasses and forbs (Drut et al. 1994a, Sveum et al. 1998, Aldridge and Brigham 2002). But the relationships between these characteristics and individual chick survival are not well understood. By monitoring individually marked chicks during the first weeks after hatching, recent research found relationships between vegetation structure and food availability with chick survival (Aldridge 2005, Gregg 2006).

We investigated relationships between habitat characteristics and chick survival in the Montana Mountains of northwestern Nevada. Banding efforts and hunter harvest data suggested the Montana Mountains support one of the highest densities of sage-grouse in Nevada and Oregon (Nevada Division of Wildlife, unpublished report 2006). By monitoring survival of individually radio-tagged chicks, we collected data on the habitat characteristics at early brood locations. This data was used to evaluate relationships between chick survival, vegetation structure and food availability.

STUDY SITE

The Montana Mountains, in Humboldt County, are approximately 18km northwest of Orovada, Nevada. The range is part of the Lone Willow Population Management Unit managed by the Bureau of Land Management in Winnemucca, NV. The core study area encompassed approximately 100,792 hectares ranging from 1200 to 2300 m in elevation. Annual precipitation is 21.9 cm and average temperatures range from a minimum of -8.6°C in January to a maximum of 33.1°C in July in Kings River Valley, immediately west of the Montana Mountains (Western Regional Climate Center, Reno NV). Precipitation is higher across the core study area due to higher elevations, and average minimum and maximum temperatures are cooler.

Vegetation is typical of shrub-steppe habitats in southeast Oregon and northern Nevada. Prominent vegetation includes low sagebrush (*Artemisia arbuscula*), mountain big sagebrush (*A. tridentata vaseyana*), and Wyoming big sagebrush (*A. t. wyomingensis*). Other shrub species, including antelope bitterbrush (*Purshia tridentata*), western snowberry (*Symphoricarpos occidentalis*) and rabbitbrush (*Chrysothamnus* spp.), are dispersed throughout the site. Common forbs include *Agoseris* spp., *Crepis* spp., *Phlox* spp., *Lupinus* spp. and *Astragulus* spp. Grasses include bluegrass (*Poa* spp.), fescue (*Festuca* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), needlegrass (*Stipa* spp.), giant wildrye (*Leymus cinereus*), and bottlebrush squirreltail (*Elymus elymoides*).

The area included 7 grazing allotments. Licensed grazing includes 34,112 Animal Unit Months managed on a rest-rotational system since the 1960s.

METHODS

Data Collection

Female sage-grouse were trapped and radio-marked in March and April of 2004-5, prior to nest initiation. Trapping efforts focused on known leks throughout the study site, and birds were captured opportunistically. Females were captured using a spotlighting technique modified from Giesen et al. (1982). We weighed and fitted birds with a 21 g necklace-style radio transmitter (Advanced Telemetry Systems, Inc., Isanti, MN) and numbered aluminum leg band. Radio-marked females were located every 3 – 7 days using a portable receiver and 3-element Yagi antenna (Advanced Telemetry Systems, Inc., Isanti, MN) to monitor nesting activity. Once a hen was determined to be nesting, the nest was monitored for hatching. Beginning 26 days after the last observation date prior to nest initiation, nests were monitored daily to determine hatch date.

To quantify habitat characteristics and chick survival, we captured broods and radio-marked chicks 1 – 4 days after hatching. Chicks were captured by hand in the early morning after flushing the brood hen. Chicks were radio-marked by surgically implanting 0.8 g radio transmitters (Holohil Systems Ltd, Ontario, Canada) subcutaneously at the base of the neck, between the scapulars (Gregg et al. 2007). To increase the sample size of brood-rearing hens with radio-marked chicks, entire broods were not radio-marked. Radio-marked chicks were selected by pulling one chick at a time from a bag until all that would be radio-marked had transmitters attached. We radio-tracked broods daily for 18 days after marking or until all radio-marked chicks were missing or known dead. Hens with radio-marked chicks were located remotely from approximately 20 m and visually identified when possible. The approximate center of brood locations was recorded in UTM coordinates. Locations were flagged for subsequent habitat sampling.

We sampled all brood locations, including the nest and pre-capture locations, through 18 days after chick captures to determine total forb, grass and sagebrush cover, and insect availability. Sites were sampled ≤14 days after the brood location was recorded. Sampling was conducted along 2 perpendicular 10 m transects intersecting at the estimated center of each brood location. We used the intercept distance of all shrubs along each transect to determine sagebrush canopy cover (Canfield 1941). Shrubs were categorized as tall (≥40 cm) or short (<40 cm), and identified to subspecies for sagebrush and species for other shrubs. We estimated the percent cover of forbs and grasses in 10 plots spaced equidistantly along the 2 transects (5 plots per transect) using a 20x50 cm Daubenmire frame (Daubenmire 1959).

Terrestrial arthropods were sampled with pitfall traps within 14 days of identifying a brood location. Five, 0.47 l plastic cups were buried flush to the ground at each brood location. We spaced cups equidistantly every 2 m along one transect line (Morrill 1975). Traps were filled with non-toxic glycerin glycol solution and covered with a plywood lid approximately 5 cm off the ground to minimize non-target insects and rodents. After 6 days, we collected the traps and froze the contents from each site in zip-loc bags. These samples were counted to determine the abundance of insect taxa previously identified as important dietary components for sage-grouse chicks including *Coleoptera*, *Orthoptera*, and *Lepidoptera* (Drut et al. 1994b, Gregg 2006).

We considered a brood successful if ≥1 chick was alive at end of the 18 day monitoring period. Brood success was calculated by dividing the number of successful broods by the number of monitored broods determined by flush counts at the end of the monitoring period.

Data Analysis

We pooled data from the 2 study years because our primary interest was in the variation of habitat characteristics and annual differences account for part of this variation, and chick survival rates were similar between years. We calculated Kaplan-Meier estimates for survival (Kaplan and Meier 1958) to 18 days post-capture, and used Cox regression (Cox 1972) to model relationships between chick survival and habitat variables. Although survival estimates are not biased, to account for intrabrood dependence (e.g., chicks from the same brood) (Flint et al. 1995), standard errors were adjusted by bootstrapping 500 replicates (Efron and Tibshirani 1993, Flint et al. 1995). Estimated coefficients for the hazard function for individual chicks, using a partial likelihood function, followed (Allison 1995):

$$h_i(t) = \lambda_0(t)\exp(\beta_1 x_{i1} + \ldots + \beta_k x_{ik})$$

where β is the regression coefficient, x is the covariate and λ_0 is the baseline hazard function, which is unspecified, for individual i at time t. To adjust the standard errors for each parameter estimate to account for intrabrood dependence, we used a robust sandwich estimate for the covariance matrix using *brood* as the distinct pattern (Lin and Wei 1989, SAS Institute 2003). Time of death was the day an individual was found dead, disappeared without prior indications of radio-failure, or the radio was recovered with signs of predation (feathers, scat, bent / chewed antenna or transmitter) (Gregg et al. 2007). Chick survival data was right censored if chicks were alive on the 18th day post-capture or for unknown fates including probable radio failures, adoption, transmitter pull-out or loss, and possible surgery-related mortality. For data that included tied events, the *EXACT* method was used to estimate the partial likelihood, which assumes there is a true but unknown order of events which are tied due to imprecise measurement of time (Allison 1995, SAS Institute 2003).

Akaike's Information Criterion, adjusted for small sample size (AIC_c), was used to infer the relative importance of habitat characteristics based on variables present in top competitive models (Burnham and Anderson, 2002). We calculated Akaike's weights (w_i) to determine the relative likelihood of each model, and calculated ΔAIC_c values between the best fitting model and the remaining models in the candidate set. To account for model uncertainty, model-weighted parameter estimates were calculated and unconditional standard errors were used to determine hazard ratios (e^{β}) and 95% unconditional confidence intervals for the effect of each variable on the daily hazard of death for individual chicks.

We screened variables for multicollinearity prior to developing the candidate model set and examined a matrix of scatter plots for all explanatory variables to assess possible relationships. If 2 or more variables were correlated (Pearson correlation coefficient: r >0.60), they were not used in the same model. Models were derived from explanatory variables that included total sagebrush cover, proportion of short sagebrush to total sagebrush cover, total forb and grass cover, and the total availability of 3 insect orders (Table 6). Because all habitat variables were time-dependent, we calculated the cumulative mean values of each variable for each exposure day. We assumed the effects of habitat variables on chick survival changed at a constant rate, so only evaluated linear relationships (Gregg 2006). For incomplete data, we used the

Table 6. Descriptions and units of explanatory variables collected at daily brood locations and non-habitat variables used in candidate models describing relationships between habitat characteristics and greater sage-grouse chick survival to 18 days post-capture in the Montana Mountains, NV, 2004-5.

Type	Variable	Description	Units
Food	Insects	Number of insects collected in pitfall traps from 3 orders: Lepidoptera, Coleoptera and Orthoptera	Number
	Total forb cover	Estimated forb cover	Percent
Cover	Total forb cover	Estimated forb cover	Percent
	Total grass cover	Estimated grass cover	Percent
	Total sagebrush cover	Sagebrush coverage estimated by line-intercept method	Percent
	Proportion of short sagebrush cover (<40 cm)	Proportion of short sagebrush to total sagebrush	Percent
	Sagebrush Interaction	Interaction between total sagebrush cover and proportion of sagebrush <40cm	
Non-Habitat*	Chick age	Age of chicks at capture	Days
	Movement	Daily movement between brood locations	Meters
	Hatch Date	Date of nest hatch	Number of days after April 1

* Included in all models

last calculated cumulative mean value to fill in missing intervals (Allison 1995). We developed a set of 9 *a priori* candidate models based on results from previous studies to represent hypotheses that described potential relationships between habitat characteristics and chick survival to 18 days post-capture (Table 7).

Because most chick mortality occurs within the first several days after hatching (Gregg et al. 2007), we included the age of chicks at capture in all models to account for potential bias from capturing older broods. Previous research found that daily brood movement and hatch date were important predictors of survival (Gregg 2006). To account for the importance of these variables, we included movement and hatch date in all models.

Table 7. *A priori* candidate model set comparing hypotheses describing relationships between habitat characteristics and greater sage-grouse chick survival to 18 days post-capture in the Montana Mountains, NV, 2004-5.

Model	Variables [a]
Vegetation Cover	Forbs + Grass + Sagebrush + Prop. short sagebrush + Age + Mvmt + Hday
Vegetation Cover (with sagebrush interaction)	Forbs + Grass + Sagebrush + Prop. short sagebrush + Sagebrush interaction + Age + Mvmt + Hday
Vertical Vegetation Cover	Prop. short sagebrush + Age + Mvmt + Hday
Horizontal Vegetation Cover	Forbs + Grass + Sagebrush + Age + Mvmt + Hday
Food	Insects+ Forbs + Age + Mvmt + Hday
Vegetation Cover and Food	Insects + Forbs + Grass + Sagebrush + Prop. short sagebrush + Age + Mvmt + Hday
Vegetation Cover and Food (with sagebrush interaction)	Insects + Forbs + Grass + Sagebrush + Prop. short sagebrush + Sagebrush interaction + Age + Mvmt + Hday
Food and Vertical Vegetation Cover	Insects + Forbs + Prop. short sagebrush + Age + Mvmt + Hday
Food and Horizontal Vegetation Cover (with sagebrush interaction)	Insects + Forbs + Grass + Sagebrush + Age + Mvmt + Hday
No Habitat	Age + Mvmt + Hday

[a] Forb = forb cover, Grass = grass cover, Sagebrush = sagebrush cover, Prop. short sagebrush = proportion of sagebrush <40 cm to total sagebrush cover, Age = chick age at capture, Mvmt = daily movement, Hday = hatch day.

RESULTS

We captured 21 broods between 8 May and 21 June, 2004-5 and radio-marked 115 chicks. Exposure days were continuous throughout the reproductive period. We assumed our sample of birds was a representative sample of chicks and reproductive hens in the Montana Mountains because brood locations were distributed throughout the study site.

Mean brood size at hatching was 7.1 (SE ± 0.27), excluding chicks found dead at the nest. Brood age at capture was between 1 and 4 days ($\bar{x}$ = 1.6 ± 0.18), and we radio-marked 2 – 8 chicks from each brood ($\bar{x}$ = 5.5 ± 0.36). A total of 1151 exposure days were used for survival analysis, and the survival rate for radio-marked chicks to 18 days post-capture was 0.437 (SE ± 0.048) (Figure 2).

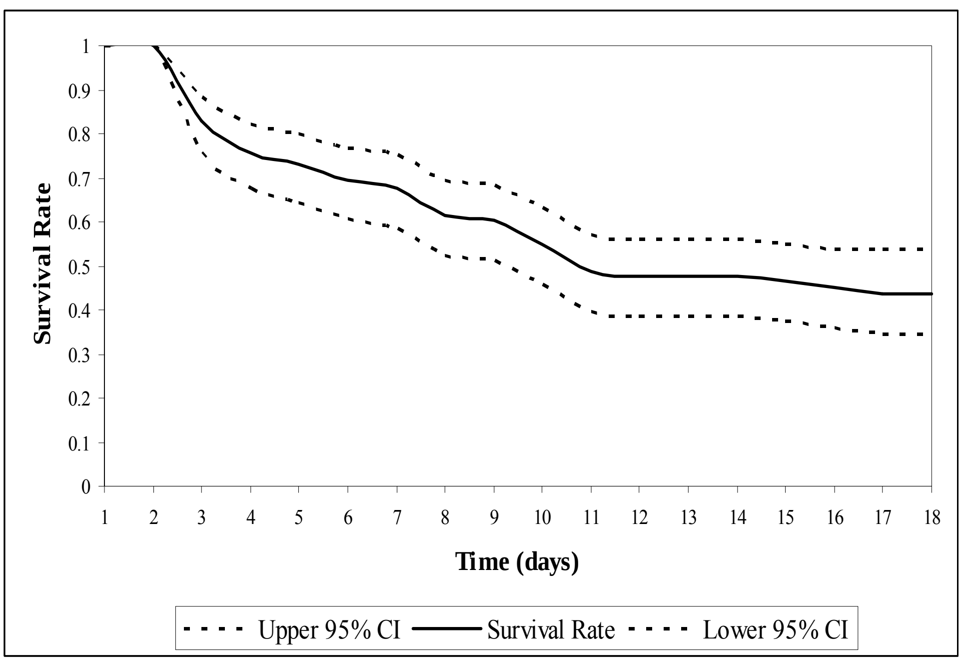


Figure 2. Survival rate and 95% confidence intervals for 115 radio-marked greater sage-grouse chicks to 18 days post-capture in the Montana Mountains, NV, 2004-5.

Outcomes were classified as dead (n = 35, 30.4%), missing (n = 26, 22.6%), radio failure (n = 28, 24.3%) or pull-outs (n = 5, 4.3%), potential surgery-related mortality (n = 1, 0.9%), adoption (n = 1, 0.9%), or survival to 18 days post-capture (n = 19, 16.5%).

Early brood sites had 15.6% (SE ± 0.6) mean forb cover, 13.7% (SE ± 0.5) grass cover and 22.9% (SE ± 0.6) sagebrush canopy cover (Table 8). Sixty-four percent of the sagebrush cover at brood sites was short (<40 cm). Mean total insect abundance for the 3 orders was higher at successful brood locations than unsuccessful locations. Mean forb cover was also higher at successful brood locations but grass cover was lower. Young broods (≤1 week) used habitat that had a higher proportion of short sagebrush (68%) than two or three week-old broods (61% and 60%). Fifteen of 21 radio-marked broods had at least one chick surviving to the end of the 18 day monitoring period (71.4%).

The best model was the *vegetation cover and food* model which included forb, grass, and sagebrush cover, proportion of short sagebrush, and insects (Table 9). The relative likelihood for this model was only 0.29 (w_i = 0.292), and the next best model, *food and horizontal vegetation cover* was competitive, sharing a similar likelihood (w_i = 0.276). There were 5 competing models within 3 AIC_c units of the top model. Forb, grass and sagebrush cover are present in the top 6 models representing the 99.9% confidence model set.

Table 8. Habitat characteristics for early brood sites (including nest), successful and unsuccessful brood sites, and first, second and third week brood sites for greater sage-grouse chicks in the Montana Mountains, NV, 2004-5.

Variable	All Brood Locations (Including Nest)		Successful Broods[a]		Unsuccessful Broods[a]		1st Week[b]		2nd Week[b]		3rd Week[b]	
	$\bar{x}$ (±SE)	*n*	$\bar{x}$ (±SE)	*n*	$\bar{x}$ (±SE)	*n*	$\bar{x}$ (±SE)	*n*	$\bar{x}$ (±SE)	*n*	$\bar{x}$ (±SE)	*n*
Forb Cover (%)	15.6	354	15.8	296	14.4	58	15.2	172	15.6	118	16.6	64
	(0.6)		(0.6)		(1.4)		(0.7)		(1.0)		(1.4)	
Grass Cover (%)	13.7	353	13.4	295	15.1	58	13.3	171	13.5	118	15.0	64
	(0.5)		(0.5)		(1.5)		(0.7)		(0.8)		(1.3)	
Sagebrush Cover (%)	22.9	354	22.8	296	23.4	58	22.8	172	22.7	118	23.4	64
	(0.6)		(0.7)		(1.8)		(0.9)		(1.1)		(1.7)	
Prop. Short Sagebrush	64.3	354	64.9	296	61.2	58	68.0	172	61.3	118	59.6	64
	(1.9)		(2.1)		(4.2)		(2.6)		(3.4)		(4.7)	
Shrub Cover (%)	26.5	354	26.1	296	28.6	58	25.6	172	26.9	118	28.2	64
	(0.7)		(0.7)		(2.2)		(1.1)		(1.2)		(1.6)	
Lepidoptera	4.4	283	4.7	235	2.9	48	3.5	157	5.3	96	6.5	30
	(0.4)		(0.4)		(0.3)		(0.4)		(0.7)		(1.6)	
Coleoptera	13.2	283	13.5	235	11.4	48	12.4	157	14.3	96	13.6	30
	(0.7)		(0.7)		(1.2)		(0.9)		(1.1)		(2.0)	
Orthoptera	3.5	283	3.6	235	2.8	48	2.8	157	4.0	96	5.3	30
	(0.2)		(0.3)		(0.6)		(0.3)		(0.5)		(0.6)	
Total Insect	21.0	283	21.8	235	17.1	48	18.6	157	23.6	96	25.4	30
	(0.9)		(1.0)		(1.6)		(1.1)		(1.6)		(2.4)	

[a] Successful broods had ≥1 chick alive at end of 18 day post-capture monitoring period.
[b] First, 2nd and 3rd week after hatching.

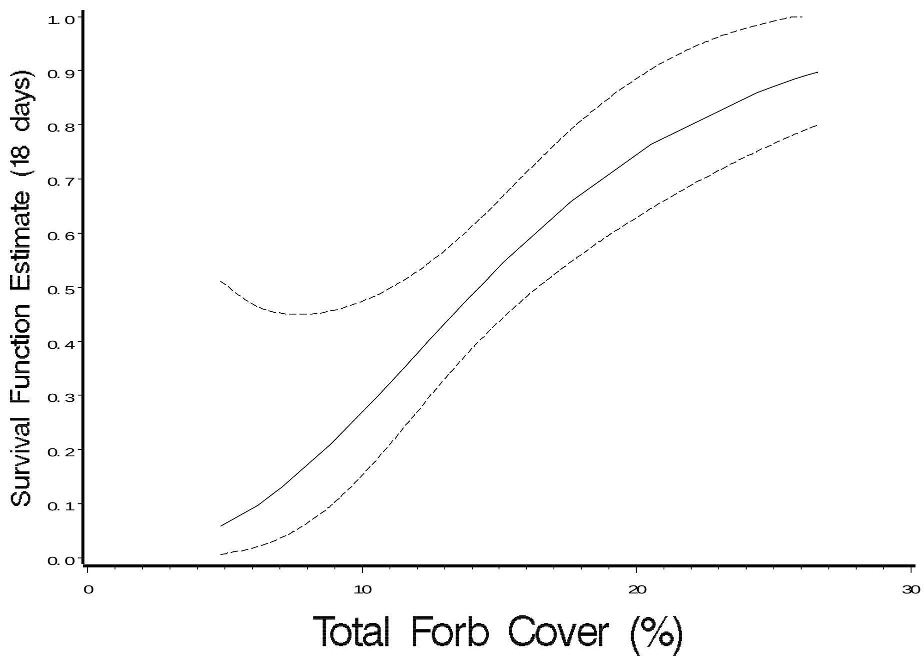
Table 9. Model selection results, AIC_c, ΔAIC_c and w_i, comparing hypotheses describing associations between habitat characteristics and greater sage-grouse chick survival to 18 days post-capture in the Montana Mountains, NV, 2004-5.

Model	AIC_c [a]	ΔAIC_c [b]	w_i [c]
Vegetation Cover and Food	**344.873**	**0.000**	**0.292**
Food and Horizontal Vegetation Cover	**344.988**	**0.115**	**0.276**
Vegetation Cover	**345.920**	**1.046**	**0.173**
Vegetation Cover and Food (and interaction)	**346.822**	**1.949**	**0.110**
Horizontal Vegetation Cover	**347.458**	**2.585**	**0.080**
Vegetation Cover (and interaction)	**347.804**	**2.930**	**0.067**
Food	356.372	11.498	0.001
Food and Vertical Vegetation Cover	358.332	13.459	0.000
No Habitat	361.018	16.145	0.000
Vertical Vegetation Cover	362.713	17.839	0.000

[a] AIC_c is the Akaike Information Criterion values with small sample bias adjustment (Burnham and Anderson 2002).
[b] ΔAIC_c is the difference between a model's AIC_c value and the smallest AIC_c value ($AIC_{c\,i}$ - $AIC_{c\,min}$).
[c] w_i is the Akaike weight describing the relative likelihood of a model.

The top model set shows strong evidence for the relative importance of forb, grass and sagebrush cover as predictors of chick survival. Chick survival increased as total forb cover at brood sites increased (hazard ratio: 0.869, 95% CI: 0.787 – 0.959) (Figure 3A), but decreased with increasing grass cover (hazard ratio: 1.154, 95% CI: 1.040 – 1.281) (Figure 3B). We found no evidence supporting an effect of sagebrush cover on chick survival (hazard ratio: 0.988, 95% CI: 0.890 – 1.096). We calculated hazard ratios and 95% confidence intervals for each habitat characteristic used in our model set (Table 10).

A.



B.

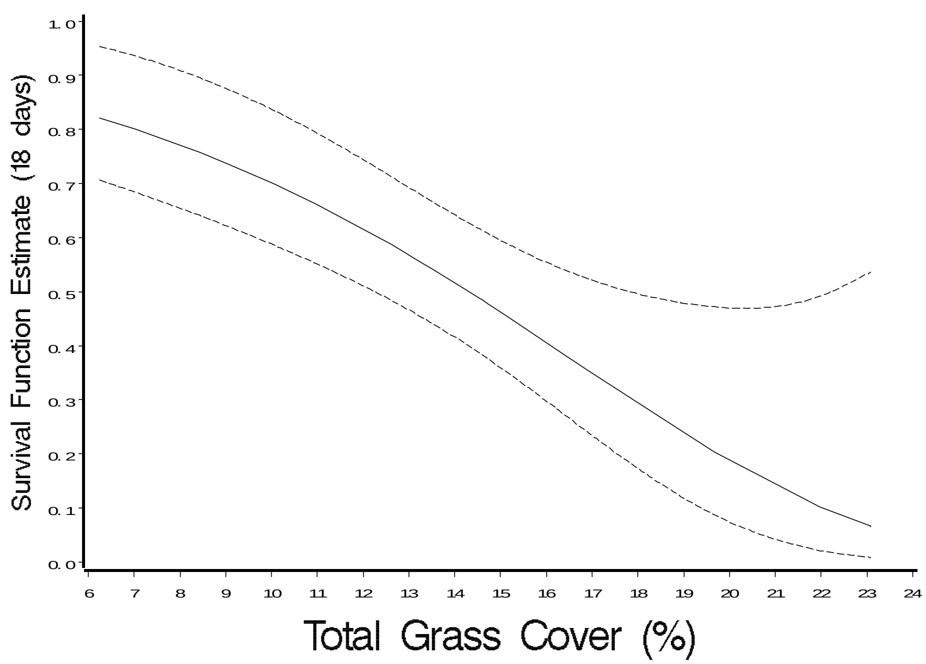


Figure 3. Survival function estimates and 95% confidence intervals for the effects of (A) total forb cover and (B) total grass cover with all other variables at mean values, for 115 radio-marked greater sage-grouse chicks at 18 days post-capture in the Montana Mountains, NV, 2004-5.

Table 10. Estimates of hazard ratios and 95% confidence limits for all habitat variables used in candidate model set, Montana Mountains, NV, 2004-5.

Parameter	Hazard Ratio [a]	95% CI for hazard ratio
Total Forb Cover	0.869	0.787 – 0.959
Total Grass Cover	1.154	1.040 – 1.281
Total Sagebrush Cover	0.988	0.890 – 1.096
Total Insect Abundance	1.044	0.971 – 1.122
Proportion of Short Sagebrush	1.014	0.972 – 1.057
Sagebrush Interaction	1.041	0.737 – 1.469

[a] Hazard ratio = the effect of a 1-unit change in the independent variable on the hazard of death.

DISCUSSION

The survival rate for sage-grouse chicks in the Montana Mountains during 2004 and 2005 was similar to neighboring sites in Nevada and Oregon (Gregg 2006). However, sage-grouse chicks in Canada had slightly higher survival with approximately half of the radio-marked chicks surviving to 20 days (Aldridge 2005). Chick survival may be influenced by several factors including predator population levels, climatic factors, and food and cover availability. Chick survival was similar for the 2 years of our study, but other results show annual differences in survival with rates ranging from 13 – 65% to 4 weeks after hatching (Gregg 2006). This variation was linked to insect availability, but more research is necessary to test for other potential factors responsible for temporal and spatial variations in chick survival.

Higher forb cover at brood sites in the Montana Mountains was associated with higher chick survival. Forbs are a source of food for young chicks (Pyle 1992, Drut et al. 1994b), but can also provide cover to hide chicks from predators or act as host species for certain insects. Other research in Oregon and Washington demonstrated broods used areas with greater forb cover more than expected based on availability

(Drut et al. 1994a, Sveum et al. 1998), and concluded that 12 – 14% forb cover may be a minimum amount necessary for brood-rearing habitat (Drut et al. 1994a). Forb cover at early brood sites in the Montana Mountains was typically higher than these guidelines. The importance of forb cover was also reported for other sites (Aldridge 2005, Gregg 2006). Aldridge (2005) reported a weak effect of forb abundance on chick survival. The lack of forb abundance in brood-rearing areas reported from other studies may be due to uniformly low forb availability and may bias the differences in survival. Forb cover at brood sites in the Montana Mountains was almost 2 times as high as reported in Canada (Aldridge 2005).

Our results indicated chick survival was greatest in areas with less grass cover, which contrasts Aldridge (2005), who found chick survival actually increased with increasing grass cover. However brood-rearing habitat described in his study had almost 2 times as much grass cover as brood locations in the Montana Mountains. It has been hypothesized that there is a trade-off between using sites which offer enough protection from predators (e.g., dense grass sites) and the need to forage in open sites with increased food availability (Aldridge 2005). We found birds generally were not foraging in areas with dense grass cover. Most other findings demonstrate a relationship between the height of grass and survival but not necessarily all grass cover. Both Aldridge (2005) and Gregg (2006) reported an increase in chick mortality with increasing proportions of tall grass. We did not include grass height in our analysis because of potential measurement errors; however, our results for grass cover do not substantiate these earlier results for total grass cover. Forbs in the Montana Mountains may act as the primary source of herbaceous cover providing concealment for young chicks, and these areas also provide greater foraging opportunities compared to the availability of forbs in areas of greater grass cover.

In the Montana Mountains, we did not find a relationship between insect availability at brood sites and chick survival as previously reported for other study sites. Insects have been shown to be an important component of the diet for sage-grouse chicks during the first weeks of life (Johnson and Boyce 1990, Drut et al. 1994a,b, Gregg 2006), but it has been difficult to relate insect abundance at brood sites and chick survival. However, Gregg (2006) found the abundance of *Lepidoptera* at early brood sites were associated with sage-grouse chick survival. We used total abundance of 3 insect orders thought to be important for chicks and considered this as one index for insect abundance. Ants, which are known to be a food item, were not included because they were abundant at all brood sites. Mean values for insects demonstrated trends towards increasing numbers of insects at successful brood locations, including *Lepidoptera*. Brood survival is frequently used by managers as a metric for reproductive success. We did not analyze brood survival, but our data from successful and unsuccessful brood sites support earlier work demonstrating the importance of insects at early brood sites. Pitfall traps are one of the most common methods for sampling the abundance of ground-surface insect species (Ward et al. 2001), but the abundance of insects at brood locations may not reflect the richness of insects available to sage-grouse chicks. Chicks may forage for insects on the leaves of small forbs, and it is unlikely that the trappability of those taxa is the same as ground-dwelling insects. Nevertheless, we believe our use of pitfalls traps captured the relative abundance of insects at brood locations in the Montana Mountains, but further research is necessary to determine whether this method is the most effective at describing insect availability or richness for sage-grouse chicks.

Our research enhanced the understanding of sage-grouse reproductive ecology by associating patterns in chick survival with habitat characteristics. Previous work in Nevada and Oregon demonstrated the importance of forbs and insects, and we clarified the relationship between forbs and chick survival. Forbs and insects may provide the baseline requirements for chick survival, and their availability may influence chick recruitment into fall populations. In years where *Lepidoptera* abundance was high, sage-grouse chick survival was also high (Gregg 2006). It is possible that sharp increases or declines in annual sage-grouse production may be related to irruptive boom or bust patterns of *Lepidoptera* abundance. Forb availability and other insect orders may provide the nominal food and cover necessary for annual reproduction during years when *Lepidoptera* are scarce.

MANAGEMENT IMPLICATIONS

In the Montana Mountains, forb cover showed the strongest association with chick survival to 3 weeks after hatching. Key forbs consumed by chicks were identified by several authors (Klebenow and Gray 1968, Pyle 1992, Drut et al. 1994b) and represent a list of critical foods necessary for successful sage-grouse reproduction. Management activities should focus on maintaining areas supporting these key forb groups but also aim to increase their availability across the landscape. Species-rich forb communities may also support abundant insect communities, but further work on the relationships between plant and arthropod communities is needed. Forbs, including taxa not previously recognized as food items for sage-grouse, may also contribute to the vegetation structure necessary for cover and protection from predators. Management strategies which protect forb- and insect-rich communities will be necessary for successful management of early brood-rearing habitat.

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CHAPTER 4: CONCLUSION

Greater sage-grouse have relatively high annual survival and low reproductive rates compared to other grouse species (Connelly and Braun 1997, Schroeder et al. 1999) which makes their populations particularly vulnerable to alterations in reproductive habitat. Highly variable productivity appears to be influenced by nest success and chick survival (Crawford and Lutz 1985, Schroeder 1997). To address population declines, considerable research has focused on the reproductive period (March – July) to determine factors influencing reproductive success. Nesting habitat and early brood-rearing habitat has been well described in many areas across the range, but relationships between chick survival and habitat characteristics have only recently been explored. We conducted a study in the Montana Mountains of northern Nevada, which supports a healthy and abundant sage-grouse population, to investigate relationships between habitat characteristics and reproductive success.

Sage-grouse are considered a sagebrush obligate species because they rely heavily on sagebrush communities for nesting and early brood-rearing as well as food (Schroeder et al. 1999), but our study highlighted the importance of herbaceous understory vegetation. Nest success and chick survival were strongly affected by grass cover and forb abundance. We found nest success was associated with greater amounts of grass cover at the nest site, but sagebrush canopy cover at the nest had a weak relationship with nest outcome. In contrast, increased grass cover at early brood sites was associated with higher mortality rates for chicks. These associations may be related to predator detection and avoidance. The effect of grass cover at nest sites is likely the result of increased protection from predators. Sage-grouse on nests need lateral and overhead concealment for protection from predators (Gregg et al. 1994). However, adult hens are capable of fast flight to avoid predators in the event their nest is detected. Conversely, young sage-grouse chicks are only capable of weak flight by 10 days after hatching. Without the ability to fly, dense grass cover at early brood locations may be increasing the likelihood of predation due to reduced ability to detect and avoid predators.

We also found a positive association between forb cover at early brood sites and chick survival. Forbs have been identified as an important component of the diet of sage-grouse chicks (Drut et al. 1994), but may also serve as cover from predators. Furthermore, diverse forb communities may support a rich assemblage of insect taxa, another significant component of a sage-grouse chick diets.

Sage-grouse are a landscape species, and they require large continuous patches of sagebrush habitat for reproduction. However, most studies have focused on habitat characteristics measured at a fine scale. Our results are similar to other research demonstrating the importance of herbaceous understory for reproductive success, but further research is necessary to relate these finding to a landscape scale. Livestock grazing and fire are likely the primary influences on understory vegetation in sagebrush habitats. Excessive grazing can reduce herbaceous vegetation including grasses and forbs (Bork et al. 1998), and widespread livestock grazing affects sage-grouse habitats across their geographic range (Braun 1998). By determining the effects these disturbances have on fine-scale habitat characteristics necessary for sage-grouse reproduction, managers can affect sage-grouse habitats at a landscape level by using management techniques like grazing and fire.

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APPENDIX: MATERNAL FACTORS INFLUENCING GREATER SAGE-GROUSE CHICK SURVIVAL

INTRODUCTION

Early spring forb availability has been shown to affect the nutritional condition of greater sage-grouse (*Centrocercus urophasianus*) hens (Barnett and Crawford 1994), and there appears to be a relationship between pre-laying hen nutrition and reproductive success (Dunbar et al. 2005, Gregg 2006, Gregg et al. 2006). In early spring, female sage-grouse switch from a diet that was dominated by sagebrush species (*Artemisia* spp.) over winter and begin consuming nutritionally-rich forbs as an exogenous protein source, which is necessary for reproduction (Remington and Braun 1988, Barnett and Crawford 1994). The availability of early spring forbs appears to provide the nutritional boost necessary for reproduction due to the increased protein generally found in forb diets. Recently, female nutrition has been directly linked to increased reproductive output and annual recruitment, and blood chemistry values from pre-laying hens have been used to predict the likelihood of renesting and chick survival (Beckerton and Middleton 1982, Dunbar et al. 2005, Gregg 2006, Gregg et al. 2006). As an index of dietary protein (Amand 1986), total plasma protein levels (TPP) are not affected by capture and may reflect the nutritional condition of a hen based on early spring forb availability (Dunbar et al. 2005).

Maternal condition has also been shown to be associated with chick weight at hatch, and larger chicks may have an increased chance of survival. Ruffed grouse hens eating a diet high in protein tended to produce larger chicks with improved survival (Beckerton and Middleton 1982). Gregg (2006) found that greater chick weight at capture was associated with higher survival and hypothesized that larger chicks may have increased fitness.

While sage-grouse exhibit differential mortality rates between older males and females (Swenson 1986), no studies have found sex as a good indicator of chick survival during the first weeks after hatching.

We conducted an exploratory analysis comparing the relative importance of total plasma protein levels of pre-laying hens, chick sex, and chick weight on the survival to 18 days post-capture of individually marked sage-grouse chicks in the Montana Mountains of northwestern Nevada.

METHODS

Data Collection

Female sage-grouse were trapped and radio-marked in March and April of 2004-5, prior to nest initiation. Trapping efforts targeted known leks throughout the site and birds were captured opportunistically. We captured females using a spotlighting technique modified from Giesen et al. (1982). To quantify nutritional condition of individual birds (Dunbar et al. 2005), we collected a 1 ml blood sample by venipuncture of the brachial vein, and then the sample was stored in a Microtainer®EDTA (Becton, Dickinson and Company, Franklin Lakes, NJ) tube to determine plasma protein values. Samples were kept cold while in the field each night and then refrigerated until shipment to the Veterinary Diagnostic Laboratory at Oregon State University, Corvallis, Oregon. We measured total plasma protein levels by refractometry.

We captured broods and radio-marked chicks 1 – 4 days after hatching. Chicks were captured by hand in the early morning after flushing the brood hen. Chicks were weighed and radio-marked by surgically implanting 0.8 g radio transmitters (Holohil Systems Ltd, Ontario, Canada) subcutaneously at the base of the neck, between the scapulars (Gregg et al. 2007). Secondary feathers were removed and stored in alcohol for DNA screening to determine sex (Zoogen Incorporated, Davis, CA). To increase the sample size of brood-rearing hens with radio-marked chicks, entire broods were not radio-marked. We radio-tracked broods daily for 18 days after marking to determine chick survival, or until all radio-marked chicks were missing or known dead.

Data Analysis

We screened variables for multicollinearity prior to analysis to look for possible relationships (Pearson correlation coefficient: r >0.60). We used Cox regression (Cox 1972) to model relationships between chick survival and maternal variables. The relative importance of each variable was tested using Akaike's Information Criterion, adjusted for small sample size (AIC_c) and Akaike's weights (w_i) from a candidate model set including all possible models using the following parameters: chick weight at capture, chick sex and total plasma protein level of the hen (Burnham and Anderson 2002). Because previous research has shown most chick mortality occurs within the first several days after hatching (Gregg et al. 2007), we included the age of chicks at capture in all models to account for potential bias from capturing older broods. We calculated model-weighted parameter estimates and used unconditional standard errors to calculate hazard ratios (e^{β}) and 95% unconditional confidence intervals for the effect of each variable on the daily hazard of death for individual chicks.

RESULTS

We used data collected from 17 broods captured throughout the study area and reproductive period. We monitored 88 chicks for survival for which we had total plasma protein values for the hen, and sex and weight of each chick. This sample consisted of 828 exposure days. We tested the effect of chick weight corrected and uncorrected for age at capture and found no difference in the estimates. None of our variables showed multicollinearity.

Hen total plasma protein levels before nest initiation had the strongest relative effect on chick survival; chick survival increased with increasing levels of hen plasma protein (w_i = 1.000, hazard ratio = 0.582, 95% CI: 0.413 – 0.821) (Table 11, Figure 4). We found no effect of chick weight at capture or chick sex.

Table 11. Relative weights, hazard ratios and 95% confidence limits for three variables tested for potential effects on greater sage-grouse chick survival to 18 days post-capture in the Montana Mountains, NV, 2004-5.

Parameter	w_i [a]	Hazard ratio [b]	95% CI for hazard ratio
Plasma Protein	0.99985	0.582	0.413 – 0.821
Chick Weight at Capture	0.40564	0.938	0.774 – 1.136
Chick Sex	0.27150	1.060	0.594 – 1.890

[a] w_i is the Akaike weight describing the relative likelihood of a model (Burnham and Anderson 2002).
[b] Hazard ratio = the effect of a 1-unit change in the independent variable on the hazard of death.

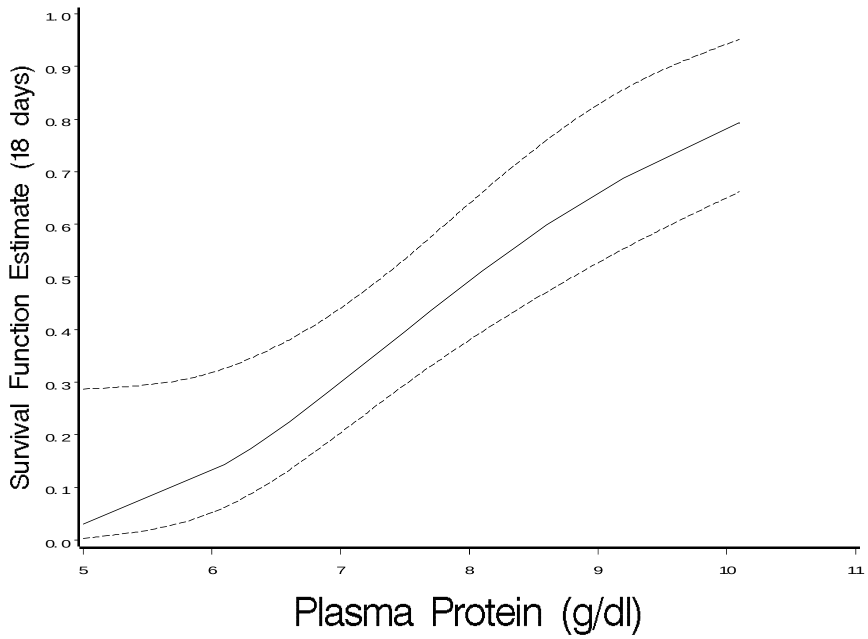

Figure 4. Survival function estimate and 95% confidence interval for 88 radio-marked greater sage-grouse chicks at 18 days post-capture for the effect of total plasma protein levels of the pre-laying hen in the Montana Mountains, NV, 2004-5.

DISCUSSION

Our results are similar to earlier findings demonstrating indirect relationships between early spring habitat, maternal condition and reproductive success. We found total plasma protein levels were positively associated with chick survival, but did not detect an effect of chick weight on survival as previously reported (Beckerton and Middleton 1982, Gregg 2006). However there are other mechanisms by which total plasma protein levels may influence chick survival including immune responses and blood clotting (Dunbar et al. 2005). Spring forb availability in the Montana Mountains may influence reproductive success by an indirect relationship between maternal nutrition obtained during early spring and chick survival, but the mechanism(s) is unclear. More research is needed to determine the direct relationships between hen nutrition and chick survival. Research investigating the relationships between hen nutrition, chick nutrition and chick survival may elucidate these mechanisms.

We did not find survival was affected by chick sex. While there is differential mortality in adult birds, this variation is primarily due to the increased risk of predation on males strutting on leks. There is no evidence supporting a difference in survival rates between the sexes in juvenile birds.

MANAGEMENT IMPLICATIONS

We recommend management strategies that promote or restore vegetation communities which support an abundance of early spring forbs. Forbs including desert parsley (*Lomatium* spp.), hawksbeard (*Crepis* spp.), phlox (*Phlox longifolia*), mountain dandelion (*Agoseris* spp.), and everlasting (*Antennaria* spp.) have been identified as important components in the diets of pre-laying hens (Barnett and Crawford 1994, Gregg 2006). Management activities should focus on maintaining areas supporting these key forb groups, but also aim to increase their availability across the landscape. These communities are critical for the reproductive success of sage-grouse because an abundance of certain forbs appears to be related to improved nutritional condition and increased reproductive success. Active management, such as seeding a small group of forbs selected by pre-laying hens may be necessary to restore or improve early spring habitat, but increased forb availability will likely increase annual production of female sage-grouse.

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