AN ABSTRACT OF THE DISSERTATION OF

Michael A. Gregg for the degree of Doctor of Philosophy in Wildlife Science presented on May 2, 2006.

Title: Greater Sage-Grouse Reproductive Ecology: Linkages Among Habitat Resources, Maternal Nutrition, and Chick Survival

Abstract approved:

Redacted for privacy

Greater sage-grouse (Centrocercus urophasianus) populations declined range wide during the past 50 years. Grouse populations were 2-3 times larger than the current population as recently as the early 1970's. In addition to habitat loss and fragmentation, declines were attributed habitat degradation that caused reduced productivity. Because chick survival remains the most poorly understood aspect of sage-grouse reproductive ecology and may be the single most important limiting factor for sage-grouse population growth, the purpose of my research was to obtain a better understanding of sage-grouse habitat relationships and, ultimately, the habitat factors that influence survival and recruitment of sage-grouse chicks. Because sage-grouse do not rely entirely on stored nutrients for reproduction, I hypothesized that successful sage-grouse reproduction was 1) indirectly related to habitat resources through maternal nutrition and 2) directly related to resources (i.e., food and cover) available to chicks during brood-rearing. Therefore, I collected data on diet, nutrition (protein, calcium, and phosphorus), and habitat use of pre-incubating females, and habitat use, survival, and timing and causes of mortality of chicks to 28-days post-hatch. I then
constructed and simultaneously evaluated several biological hypotheses expressed as regression models to investigate direct and indirect linkages between habitat resources and chick survival. My results identified linkages among availability and consumption of high-nutrient forbs, maternal nutrition, and chick survival. I also found that chick survival was related to availability of insects at brood sites. Specifically, my results indicated hens that forb consumption by hens during March and April was positively associated with likelihood of brood production and, when coupled with high Lepidoptera availability during brood-rearing, produced the most chicks. Hence, my research underscored the importance of both maternal and chick nutrition for sage-grouse chick survival. To increase chick survival, I recommend that habitat management for sage-grouse emphasize (1) forb availability during March and April to increase the nutritional status of hens and (2) insect availability, particularly Lepidoptera, during early brood-rearing to increase chick nutrition. Additionally, increased maternal nutrition may increase likelihood of renest initiation and indirectly result in greater chick recruitment.

by
Michael A. Gregg

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APPROVED:

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Major Professor, representing Wildlife Science

Redacted for privacy

Head of the Department of Fisheries and Wildlife

Redacted for privacy

Dean of the Graduate School

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

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Michael A. Gregg, Author
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I wish to express my love and appreciation to my wife, Jenny Barnett. The 6 ½ years that I spent pursuing my doctorate, Jenny has made many sacrifices on both a personal and professional level. For that, I will always be indebted. With Jenny’s background in sage-grouse ecology, she played an integral role in my research as well, particularly Chapter 3 of which she is my one of my coauthors. She was always good at keeping me on track and my eye on the goal. My beautiful daughter Kristen, came into this world 6 weeks into my doctorate program and has never had a daddy that was not “working on the Ph.D.”, but she seemed to understand what it was all about. Hopefully, I have not tainted her for life in her pursuit of higher education in the years to come.

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CONTRIBUTION OF AUTHORS

Michael Gregg was the lead scientist in all phases of the research and was involved with study design, data collection, and writing of each chapter in this dissertation. Dr. John Crawford was involved with study design and manuscript editing. Jenny Barnett was involved with development of protocols, coordination of field work, data collection, and manuscript editing for Chapter 3. Dr. Mike Dunbar was involved with the development of the radio attachment method used to mark individual sage-grouse chicks (Appendix A), collection and interpretation of blood data, and manuscript editing for Chapter 4. Dr. Michael Pope was involved with data collection in the Montana Mountains, Nevada for Chapter 4 and manuscript editing.
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<td>proportion of chicks alive at 28 days post-hatch</td>
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<td>21.</td>
<td>Model selection results for 8 a priori models used to explore the effect of</td>
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<td>22.</td>
<td>Model averaged parameter estimates, robust standard errors, and standardized</td>
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<td>23.</td>
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<td>variables in sensitivity analysis</td>
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CHAPTER 1: INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) populations have declined range-wide during the past 50 years (Crawford and Lutz 1985, Drut 1994, Connelly and Braun 1997, Connelly et al. 2004). As recently as the early 1970's, sage-grouse populations were 2-3 times greater than current populations (Connelly et al. 2004). Declines in sage-grouse abundance were attributed to loss and fragmentation of habitat due to sagebrush (*Artemisia* spp.) control programs, urban development, and agriculture (Dalke et al. 1963, Drut 1994, Braun 1998), and habitat deterioration due to historical overgrazing (Klebenow 1972, Miller and Eddleman 2000), introduction of exotic plants, and alteration of natural fire regimes (Kauffman 1990, Crawford et al. 2004). As a result, greater sage-grouse were recently evaluated for protection under the U.S. Endangered Species Act. Although sage-grouse were not listed as threatened or endangered at that time (U.S. Fish and Wildlife Service 2005), the heightened interest in sage-grouse created a greater emphasis for understanding habitat relationships and management of sagebrush ecosystems.

Sage-grouse are sagebrush obligates; the importance of sagebrush as a source of food and cover has been well established (Patterson 1952, Wallestad and Pyrah 1974, Braun et al. 1977). Although previous authors identified herbaceous vegetation as a component of sage-grouse habitat (Patterson 1952, Klebenow and Gray 1968, Savage 1969, Peterson 1970, Pyrah 1971, Autenrieth 1981), only recently has the critical nature of the herbaceous understory for successful reproduction been documented (Barnett and Crawford 1994; Drut et al. 1994a, 1994b; DeLong et al. 1995; Gregg et al. 1994; Coggins 1998; Sveum et al. 1998a, 1998b; Aldridge and Brigham 2002,
Holloran et al. 2005). Barnett and Crawford (1994) identified the significance of certain forbs in the diet of pre-laying hens. Their results suggested that nutritional status of hens and, ultimately, productivity were increased when forbs were consumed during the pre-laying period. Research revealed relationships between the amount of residual grass and shrub cover at nests sites and nest success (Gregg et al. 1994, Hanf et al. 1994, DeLong et al. 1995, Sveum et al. 1998b, Holloran et al. 2005) and documented the importance of forbs and insects in the diet of sage-grouse chicks (Johnson and Boyce 1990, Pyle 1992, Drut et al. 1994b).

Habitat relationships identified by these studies were used to develop recommendations and management actions targeted to improve sage-grouse reproductive success (Connelly et al. 2000, Crawford et al. 2004). However, other than nesting, knowledge of sage-grouse habitat relationships was primarily based on habitat selection (Barnett and Crawford 1994, Drut et al. 1994a, Sveum et al. 1998a, Aldridge and Brigham 2002), which may not provide a direct causal link between availability of habitat resources and sage-grouse productivity (Morrison 2001). An understanding of habitat linkages that directly affect reproduction is a prerequisite for development and implementation of habitat management strategies that will increase productivity and, ultimately, sage-grouse populations.

Chick survival remains the most poorly understood aspect of sage-grouse reproductive ecology (Crawford et al. 2004) and may be the single most important limiting factor that affects sage-grouse population growth (Aldridge and Brigham 2001, Connelly et al. 2004, Crawford et al. 2004). Chick survival likely is linked to habitat quality through a complex set of factors that include maternal nutrition (Moss
et al. 1975, Moss and Watson 1984, Brittas 1988, Barnett and Crawford 1994) and availability of food (forbs and insects) and cover (vertical and horizontal) during brood-rearing (Drut et al. 1994a, 1994b). Maternal nutrition influenced reproductive success of captive female ruffed grouse (*Bonasa umbellus*); hens that obtained adequate nutrition in spring diets contributed more nutrients to eggs and produced larger, more viable chicks compared with hens on a less nutritious diet (Beckerton and Middleton 1982). Availability of insects also may be especially important because sage-grouse chicks < 3 weeks old require insects in their diet for survival and development (Johnson and Boyce 1990).

Little information is available on direct linkages between chick survival and habitat components because most sage-grouse chick mortality occurs during the first 2 weeks of life, when chicks are flightless, and monitoring daily survival of individual young chicks was deemed impossible. Only recently has telemetry been used to monitor survival of individual chicks (Burkepile et al. 2002) and identify vegetative factors related to survival during brood-rearing (Aldridge 2005). No previous research investigated linkages among maternal nutrition, insect availability, and sage-grouse chick survival. Therefore, the purpose of my study was to advance our understanding of sage-grouse habitat relationships and, ultimately, the factors that influence survival and recruitment of sage-grouse chicks.

**HYPOTHESIS AND OBJECTIVES**

An understanding of animal/habitat relationships is the most basic and fundamental attribute of wildlife management. Successful reproduction (i.e., recruitment of young) and maintenance of populations are ultimately a reflection of habitat quality. Because
sage-grouse do not rely entirely on stored nutrients for reproduction (Thomas and Popko 1981; Thomas 1982, 1986; Remington and Braun 1988), I hypothesized that successful sage-grouse reproduction was 1) indirectly related to habitat resources through maternal nutrition and 2) directly related to resources (i.e., food and cover) available to chicks during brood-rearing (Figure 1). To test my hypothesis, my research objectives were to:

1) Determine the relationship between diet composition, nutrient content of foods consumed, and maternal nutrition of pre-incubating female sage-grouse.

2) Determine the effect of maternal nutrition on sage-grouse reproductive success.

3) Determine the relationship between chick survival and habitat resources available to chicks during brood-rearing.

RESEARCH APPROACH AND THESIS ORGANIZATION

My first objective is addressed in chapter 3, where I investigate the relationship between availability and consumption of high and low nutrient (i.e., crude protein, calcium, and phosphorus) foods and maternal nutrition of pre-incubating female sage-grouse. My second objective is addressed in chapter 4, where I investigate the relationship between maternal nutrition and reproduction (i.e., renesting) using total plasma protein levels as an index of dietary protein. I evaluated renest initiation because sage-grouse renesting rates are highly variable (Schroeder 1997, Aldridge and Brigham 2001, Connelly et al. 1993, Hanf et al. 1994) and renesting requires additional egg production beyond the first clutch, which may be directly related to protein resources available to hens. In addition, renesting can contribute significantly to recruitment of young (Schroeder 1997; J. A. Crawford, Oregon State University,
unpublished data). I also address my second objective in chapter 5, where I investigate the relationships among total plasma protein, chick weight, and chick survival. I use total plasma protein values of females as an index of maternal nutrition for analyses in chapters 4 and 5 because total plasma protein has been shown to fluctuate relative to dietary protein intake (Leveille et al. 1960, Leveille and Sauberlich 1961), and has been used as an indicator of body condition (de le Court et al. 1995, Dawson and Bortolotti 1997, Schoech and Bowman 2003) and a measure of protein available for breeding (Herbert et al. 2002, Schoech and Bowman 2003, Dunbar et al. 2005) in birds. In addition to total plasma protein, I include chick weight in chapter 5 because hens with good maternal nutrition produce larger chicks (Beckerton and Middleton 1982) and larger chicks have greater survival (Beckerton and Middleton 1982, Riley et al. 1998). My third objective is addressed in chapter 5, where I investigate the relationship between habitat resources (food and cover) available during brood-rearing and chick survival. Finally, I discuss the implications of the totality of my results relative to management of sage-grouse habitat in chapter 6.
Figure 1. Hypothesized conceptual model of linkages between habitat resources and sage-grouse reproductive success. Chick survival is related to availability of forbs during March and April through maternal nutrition and habitat components (food and cover) during brood-rearing.
LITERATURE CITED


CONNELLY, J. W., R. A. FISCHER, A. D. APA, K. P. REESE, and W. L. WAKKINEN.


CHAPTER 2: STUDY AREA DESCRIPTION

My study area was located within the northern Great Basin in southcentral Oregon and northwestern Nevada (Figure 2). Topography was characterized by flat sagebrush plains interrupted by mountains, rolling hills, table lands, ridges, and draws. Elevations ranged from 1200 to 2450 meters and annual average precipitation and average minimum and maximum temperatures ranged from 29 to 33 cm and \(-22^\circ\) and \(38^\circ\) C, respectively (Western Regional Climate Center 2005). Summers were typically hot and dry, but cold fronts and snow were possible at any time of year. Winter months were cold and wet with most precipitation falling between December and March.

Primary shrub species included Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), low sagebrush (*A. arbuscula*), and antelope bitter-brush (*Purshia tridentata*). Stands of western juniper (*Juniperus occidentalis*), curl-leaf mountain-mahogany (*Cercocarpus ledifolius*), and aspen (*Populus tremuloides*) were interspersed throughout the area. Grasses consisted largely of bluegrass (*Poa spp.*), bluebunch wheatgrass (*Pseudoroegneria spicata*), needlegrass (*Stipa spp.*), fescue (*Festuca spp.*), giant wildrye (*Leymus cinereus*), and bottlebrush squirreltail (*Elymus elymoides*). Common annual and perennial forbs included mountain-dandelion (*Agoseris spp.*), everlasting (*Antennaria spp.*), milk-vetch (*Astragalus spp.*), hawksbeard (*Crepis spp.*), buckwheat (*Eriogonum spp.*), lupine (*Lupinus spp.*), and phlox (*Phlox spp.*). Gregg (1991) described 9 cover types characteristic of the northern Great Basin (Table 1).

Common mammalian predators of sage-grouse included coyotes (*Canus latrans*),
Table 1. Description of cover types at Hart Mountain National Antelope Refuge, Sheldon National Wildlife Refuge, Beatys Butte, and Montana Mountains, southcentral Oregon and northwestern Nevada (from Gregg 1991).

<table>
<thead>
<tr>
<th>COVER TYPE</th>
<th>COVER TYPE DESCRIPTION</th>
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<tr>
<td>Mountain big sagebrush</td>
<td>Found at higher elevations (1800 to 2300 m) on ridges and mountain shoulders. Primary plant species are mountain big sagebrush (<em>Artemisia tridentata vaseyana</em>) and Idaho fescue (<em>Festuca idahoensis</em>) or rough fescue (<em>F. scabrella</em>).</td>
</tr>
<tr>
<td>Wyoming big sagebrush</td>
<td>Occurs on rolling uplands and lake basin terraces with slopes &lt;30%. Primary plant species include Wyoming big sagebrush (<em>A. t. wyomingensis</em>), bottlebrush squirreltail (<em>Elymus elymoides</em>), and Thurber's needlegrass (<em>Stipa thurberiana</em>). May also be associated with spiny hopsage (<em>Atriplex spinosa</em>).</td>
</tr>
<tr>
<td>Low Sagebrush</td>
<td>Found on alluvial fans and table lands usually of &lt;30% slope. Primary plant species consist of low sagebrush (<em>A. arbuscula</em>) and bluebunch wheatgrass (<em>Pseudoroegneria spicata</em>), bluegrass (<em>Poa spp.</em>). Idaho fescue may be found in low sagebrush stands at higher elevations. May also be associated with spiny hopsage.</td>
</tr>
<tr>
<td>Mountain shrub</td>
<td>Common at elevations between 1800 and 2300 m. Principal plant species are mountain big sagebrush, antelope bitterbrush (<em>Purshia tridentata</em>) and Idaho fescue. May also be associated with western snowberry (<em>Symphoricarpos occidentalis</em>).</td>
</tr>
<tr>
<td>Basin big sagebrush</td>
<td>Occurs on low terraces associated with drainage sites and lake basins. Primary plant species include basin big sagebrush (<em>A. t. tridentata</em>) and giant wild rye (<em>Leymus cinereus</em>).</td>
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Table 1. (Continued).

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<th>Environment</th>
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<tr>
<td>Lakebed</td>
<td>Found on depressions covered with water during spring. Primary plant species include silver sagebrush (<em>A. cana</em>), spikerush (<em>Eleocharis</em> spp.), and baltic rush (<em>Juncus balticus</em>).</td>
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<tr>
<td>Meadow</td>
<td>Associated with springs and creeks that have poorly drained soils and subsurface water in summer. Principal vegetation includes bluegrass, wheatgrass, and sedge (<em>Carex</em> spp.).</td>
</tr>
<tr>
<td>Grassland</td>
<td>Typically areas disturbed by fire. Characteristic of areas without sagebrush. Primary plant species include cheatgrass (<em>Bromus tectorum</em>), giant wild rye, bottlebrush squirreltail, bluegrass, and needlegrass.</td>
</tr>
<tr>
<td>Juniper/Aspen/Mahogany</td>
<td>Associated with low ridges or footslopes. Principal plant types are western juniper (<em>Juniperus occidentalis</em>), mountain mahogany (<em>Cercocarpus lepisfolius</em>), or aspen (<em>Populus tremuloides</em>). May be found interspersed with big or low sagebrush.</td>
</tr>
</tbody>
</table>

Bobcats (*Felis rufus*), and weasels (*Mustela* spp.). Common avian predators included red-tailed hawks (*Buteo jamaicensis*), rough-legged hawks (*B. lagopus*), northern harriers (*Circus cyaneus*), golden eagles (*Aquila chrysaetos*), and ravens (*Corvus corax*). Less common but possible important predators of sage-grouse chicks included Swainson’s hawks (*B. swainsoni*) and ferruginous hawks (*B. regalis*). Potential reptilian predators of chicks included western rattlesnakes (*Crotalus viridis*) and gopher snakes (*Pituophis catenifer*).

**STUDY SITES**

Within this area of the northern Great Basin in Oregon and Nevada, my research
Figure 2. Location of study sites in southcentral Oregon and northwestern Nevada used for greater sage-grouse research during 1999-2004. Data were collected at the Montana Mountain study site only during 2004.
was conducted at 4 study sites (Figure 2). Data were collected at Hart Mountain National Antelope Refuge and Sheldon National Wildlife Refuge during 1999-2003, Beatys Butte during 2000-2003, and the Montana Mountains during 2004. These four sites were selected as replicates because they had similar habitats and were representative of shrub-steppe in the northern Great Basin. Additionally, previous research documented sage-grouse movement between Hart Mountain and Beatys Butte (Gregg 1991), and between Sheldon and Beatys Butte (Davis 2002).

**Hart Mountain National Antelope Refuge**

Hart Mountain National Antelope Refuge, located in southcentral Oregon, was administered by the U.S. Fish and Wildlife Service and encompassed 114,375 hectares. Research on sage-grouse habitat use during the reproductive period (March-July) was initiated at Hart Mountain during 1988 and continued through 2003 (Gregg 1991, Barnett 1992, Drut 1992, Pyle 1992, DeLong 1993, Coggins 1998, Byrne 2002). Because sage-grouse were not hunted on the Refuge, estimated productivity from wings was not available. However, annual lek counts on the refuge indicated a positive trend in sage-grouse populations since 1996 (U.S. Fish and Wildlife Service, unpublished data). Domestic livestock grazing averaged 12,000 Animal Unit Months (AUM) annually through 1990 and was eliminated on the refuge in December 1990 (U.S. Fish and Wildlife Service 1994). Subsequently, prescribed fire has been the primary habitat management tool used to manage upland and riparian habitats on the refuge (U.S. Fish and Wildlife Service 1994). Approximately 8,872 hectares have been prescribed burned and 3,220 hectares have burned in wildfires since 1991 (A. Goheen, U.S. Fish and Wildlife Service, personal communication).
Beatys Butte was located in southcentral Oregon within the Beatys Butte grazing allotment administered by the Bureau of Land Management (BLM). The study site encompassed 110,682 hectares in the eastern half of the grazing allotment (Figure 2). Sage-grouse productivity, determined from wings collected during the fall hunting season, averaged 2.07 chicks per hen between 2000-2004 (Oregon Department of Fish and Wildlife, unpublished data). Annual lek counts in the Lakeview District BLM, which included the Beatys Butte study site, indicated a positive trend in sage-grouse populations since 1996 (Hagen 2005). Domestic livestock grazing was divided into 2 pastures and averaged 26,121 AUMs from 1983 to 1989 and 14,000 AUMs since 1989 (Bureau of Land Management 1994). Each pasture was grazed during alternate years. In the north pasture, approximately 6,000 hectares were prescribed burned during 1999 and a wildfire burned an additional 14,400 hectares during 2000 (T. Forbes, Bureau of Land Management, personal communication).

Sheldon National Wildlife Refuge

Sheldon National Wildlife Refuge (NWR), located in the northwestern corner of Nevada, was administered by the U.S. Fish and Wildlife Service and encompassed 232,294 ha (Figure 2). The study site was located in the northwest portion of the refuge and encompassed 102,610 hectares. Sage-grouse productivity, estimated from wings collected during the fall hunting season, averaged 1.99 chicks/hen between 2000-2004 (Nevada Division of Wildlife, unpublished data). Annual lek counts on the refuge indicated a positive trend in sage-grouse populations since 1996 (U.S. Fish and Wildlife Service, unpublished data). Domestic livestock grazing averaged 16,317
AUMs annually from 1980 to 1989, was reduced to 1,564 AUMs annually from 1990-1993, and was eliminated from the refuge in 1994. Since 1994, prescribed fire has been the primary tool used to manage upland and riparian habitats on the refuge (A. Goheen, U.S. Fish and Wildlife Service, personal communication). Approximately 8,861 hectares have been prescribed burned and 21,156 hectares burned in wildfires on the refuge since 1994 (A. Goheen, U.S. Fish and Wildlife Service, personal communication).

**Montana Mountains**

The Montana Mountains, located in northwestern Nevada, were primarily public lands administered by the BLM and encompassed 100,792 hectares (Figure 2). The Montana Mountains were included in the Lone Willow sage-grouse population management unit (PMU) and supported one of several sub-populations of sage-grouse in the PMU (Nevada Division of Wildlife 2004). Sage-grouse productivity, estimated from wings collected during the fall hunting season, averaged 2.31 chicks/hen between 2000-2004 (Nevada Division of Wildlife, unpublished data). Annual lek count data were not available to assess spring population trends (Nevada Division of Wildlife 2004). However, the late summer sage-grouse population was estimated >7300 birds between 2000 and 2004 (E. Partee, Nevada Division of Wildlife, unpublished report). Domestic livestock grazing on the study site averaged 34,112 AUMs and was managed on a rest-rotational system since the 1960s.

**LITERATURE CITED**


CHAPTER 3: TEMPORAL VARIATION IN DIET AND NUTRITION OF PRE-INCUBATING GREATER SAGE-GROUSE RELATIVE TO FOOD AVAILABILITY AND AGE OF HEN

ABSTRACT

Poor productivity of greater sage-grouse (*Centrocercus urophasianus*) may result from inadequate nutrition of hens during the breeding season. Because grouse depend primarily on exogenous nutrients for egg production, detailed information on diet and nutrition relative to availability and nutrient content of foods consumed during spring is critical for management of sage-grouse habitat. I investigated temporal variation in diet composition and nutrient content (crude protein, calcium, and phosphorus) of foods consumed relative to food supply and age of hen. I collected 86 pre-incubating female greater sage-grouse at foraging areas during early (18-31 March) and late (1-12 April) pre-incubation periods in 2002 and 2003. Hens consumed 22 food types including low and big sagebrush, 15 different forbs, 2 insect taxa, sagebrush galls, moss, and a trace amount of unidentified grasses. Forbs were found in 89% of the crops and composed 30.1% aggregate dry mass (ADM) of the diet. Forbs were high in crude protein, calcium, and phosphorus compared to low sagebrush, which had the lowest nutrient content of all foods consumed by hens. Percent ADM of forbs in crops of adult females was greater during the late compared with the early collection period during 2002 and greater during 2003 compared with 2002. Aggregate dry mass of forbs did not differ between collection periods during 2003, but species composition of forbs in the diet did differ. Variation in ADM and species composition of forbs in the diet coincided with variation in forb availability. Adult females consumed more
forbs and less low sagebrush compared with yearlings during both collection periods in 2003. Consumption of forbs was positively associated with productivity; adults reportedly had higher reproductive success during 2003 than in 2002 and were more successful than yearlings during 2003. My results suggest that consumption of forbs during spring may increase nutritional status of pre-incubating females and, in turn, positively affect sage-grouse reproductive success.

INTRODUCTION

Populations of greater sage-grouse have declined substantially during the past 50 years (Connelly et al. 2004). Reduced reproductive success has been implicated in these population declines (Crawford and Lutz 1985, Connelly and Braun 1997, Connelly et al. 2004) and may, in part, be related to nutrition of hens during the breeding season (Barnett and Crawford 1994, Dunbar et al. 2005, Chapter 4). Grouse do not rely entirely on endogenous nutrient reserves for reproduction (Thomas and Popko 1981, Thomas 1986); they also depend on exogenous sources of nutrients, particularly for egg formation (Thomas 1982, Beckerton and Middleton 1982, Moss and Watson 1984). Naylor and Bendell (1989) found that spruce grouse (Falcipennis canadensis) hens with the greatest dietary intake of nutrients laid the largest clutches and suggested that clutch size may be proximately limited by food supply. Hence, nutrient content and availability of foods during breeding (March and April) could affect sage-grouse productivity. Therefore, detailed information on diet and nutrition relative to availability and nutrient content of foods consumed by female sage-grouse before reproduction may be important for management of sage-grouse habitat. Other than Barnett and Crawford (1994), no research has been conducted on diet and
nutrition of pre-incubating female sage-grouse.

Protein, calcium, and phosphorus are critical nutrients for successful reproduction in Galliformes (Carey 1996, Klasing 1998). Egg production was reduced for captive ring-necked pheasants (*Phasianus colchicus*) on diets deficient in protein (Breitenbach et al. 1963) and calcium (Greeley 1962, Chambers et al. 1966, Hinkson et al. 1970), and captive bobwhite quail (*Colinus virginianus*) and chickens on diets low in phosphorous (Crowley et al. 1963, Harms et al. 1965, Cain 1982). Lower egg weights (Menge et al. 1979), smaller clutch sizes (Beckerton and Middleton 1982, Aboul-Ela et al. 1992), and reduced chick viability (Hanssen et al. 1982) have been reported for other captive Galliformes on protein deficient diets. Protein and phosphorus may be the most limiting nutrients for grouse reproduction (Moss 1972, Thomas 1982).

Numerous researchers have suggested that grouse select foods high in nutrient content (Gardarsson and Moss 1969, Moss 1972, King and Bendell 1982, Remington and Braun 1985, Naylor and Bendell 1989). Female greater sage-grouse alter their diet during spring and select foods high in crude protein, calcium, and phosphorus (Barnett and Crawford 1994). However, measures of food selection do not indicate if consumption of preferred foods increases with availability (Morrison 2001). Information on how food supply affects consumption of preferred food items by sage-grouse is lacking. In addition, adult female sage-grouse typically are more proficient at all reproductive parameters (i.e., nest initiation, nest success, renesting rates, clutch size, and brood success) than yearlings (Wallestad and Pyrah 1974, Peterson 1980, Connelly et al. 1993, Aldridge and Brigham 2001, Chapter 4), which may be related to variation in maternal nutrition because of differences in foraging patterns between age
classes (Wunderle 1991). However, differences in diet composition between adult and yearling female sage-grouse are not well understood. Barnett and Crawford (1994) found that forbs contributed substantially to the diet of pre-laying sage-grouse, but they did not evaluate differences in diet composition between age classes. Consequently, my objective was to determine the temporal variation in diet composition and nutrient content of foods consumed by pre-incubating sage-grouse hens in relation to food availability and age of hen.

STUDY AREAS

I conducted my study within the Great Basin in southeastern Oregon and northwestern Nevada, USA. This region of the Great Basin, bordered by the Warner mountains to the west, was characteristic of shrub-steppe ecosystems. Topography consisted of sagebrush plains broken up by mountains, rolling hills, and table lands. Elevation of this area ranged from 1200 to 2450 meters. Annual average precipitation and average minimum and maximum temperatures ranged from 29 to 33 cm and −22° and 38° C, respectively (Western Regional Climate Center 2005). Dominant sagebrush communities included low (Artemisia arbuscula), Wyoming (A. tridentata wyomingensis) and mountain big sagebrush (A. t. vaseyana). Basin big sagebrush (A. t. tridentata) was present in areas of deeper soils in drainage bottoms. Other common shrubs and trees included bitter-brush (Purshia tridentata), rabbitbrush (Chrysothamnus spp.), aspen (Populus tremuloides), western juniper (Juniper occidentalis), and curl-leaf mountain-mahogany (Cercocarpus ledifolius).

Within the study area, my research was conducted on 3 sites: Sheldon National Wildlife Refuge (NWR) located in Nevada, and Hart Mountain National Antelope
Refuge (NAR) and Beatys Butte located in Oregon. Sheldon NWR and Hart Mountain NAR were administered by the U. S. Fish and Wildlife Service, encompassed 232,294 and 114,375 ha, respectively. Beatys Butte was administered by the Bureau of Land Management and encompassed 110,682 ha. These areas were >40 km apart and were selected because they were representative of the northern Great Basin, were accessible during spring, and considerable long-term data on sage-grouse habitat use and productivity were available from previous research (Barnett and Crawford 1994, Byrne 2002, Coggins 1998, Davis 2002, Drut et al. 1994, Gregg et al. 1994).

Low sagebrush communities associated with lek sites and nesting areas were primary foraging areas used by pre-incubating hens (Barnett and Crawford 1994, M. A. Gregg, U.S. Fish and Wildlife Service, unpublished data). Grasses in low sagebrush consisted largely of bluegrass (Poa spp.) and bluebunch wheatgrass (Pseudoroegneria spicata). Common annual and perennial forbs included mountain dandelion (Agoseris spp.), balsamroot (Balsamorhiza spp.), blue-eyed Mary (Collinsia pavaflora), buckwheat (Eriogonum spp.), buttercup (Ranunculus spp.), clover (Trifolium spp.), desert parsley (Lomatium spp.), hawksbeard (Crepis spp.), milk-vetch (Astragalus spp.), everlasting (Antennaria spp.), and phlox (Phlox spp.).

METHODS

At each study site, I collected pre-incubating female greater sage-grouse with shotgun within known foraging areas during 20 March-12 April and 18 March-10 April in 2002 and 2003, respectively. Hen collections were grouped into 2, 12-day periods (early and late) each year. I selected these 2 periods because peak breeding of
hens occurs at the end of March in this region of the Great Basin, they represent the pre- and post-breeding periods before initiation of incubation, and there was little evidence of large variations in nesting chronology (J. A. Crawford, Oregon State University, unpublished data). I identified foraging areas from past (Gregg 1991, Barnett 1992, Coggins 1998, Byrne 2002, Davis 2002) and concurrent (M. A. Gregg, U.S. Fish and Wildlife Service, unpublished data) radio-telemetry studies of female sage-grouse. To increase the likelihood of obtaining hens with full crops, I collected during the evening or shortly after dusk (1700 to 2130 hours) with the aid of bird dogs or spotlights. Collection sites were flagged and recorded as Universal Transverse Mercator coordinates to facilitate plot location for later vegetation sampling. I determined age (adult or yearling) of collected hens from molt patterns of primaries (Crunden 1963) and removed ovaries, crop, and ventriculus. I weighed ovaries to the nearest 0.01 g and identified plant species in crops. Crop and ventriculus contents were placed in separate plastic bags and frozen. Hen collection protocol was approved by the Oregon State University Laboratory Animal Resource Center (Animal Care and Use permit Number 2702) and conducted under state scientific collection permits from Oregon (permit number 015-03) and Nevada (permit number 22139).

I determined species composition of hen diets in 2 ways. First, frequency of occurrence was determined by dividing the number of crops in which each food item was found by total number of crops examined. This method provided information about frequencies of foods consumed by the overall sample population of hens. Second, crop contents were sorted by species, dried at 50°C to constant weight, and
weighed to the nearest 0.001 g. I determined percent aggregate dry mass (ADM) of each food item identified in the crop of each hen and averaged across hens (Swanson et al. 1974). This method eliminated potential bias caused by unequal weights among each hen’s crop contents (Swanson et al. 1974).

I estimated availability of forbs within foraging areas during each collection period. Hen collection sites and locations where hens were flushed while feeding but not collected were used as vegetation sampling sites. I defined a sampling site as a circle with a 10-m radius centered at a hen’s first observed location (Barnett and Crawford 1994). I estimated cover and frequency of each key taxon (genus or species) in 10 random plots within the sampling site. Canopy cover was estimated to the nearest percent in 20x50-cm frames (Daubenmire 1959). Forbs with <1% cover were recorded as 0.5%. Frequency of forbs was recorded in 3 (10x10 cm, 40x50 cm, and 80x50 cm) nested frames (Hironaka 1985).

I collected samples of primary plant species (shrubs and forbs) consumed by grouse immediately after cover and frequency data were collected. Primary plant species were food items with >15% frequency of occurrence in crops. Plant samples were dried at 50°C to constant weight. For each year, I randomly combined individual samples of primary plant species into 10-g composite samples for nutrient analyses. The number of composite samples for each food type was dependent on total dry mass of plant material collected each year. Large samples were difficult to obtain for some forbs; therefore, the number of composite samples varied by species and year of collection.

I determined nutrient content (crude protein, calcium, and phosphorous) of all
primary plants consumed by pre-incubating females. Crop and ventriculus contents of each hen were analyzed separately for crude protein content. Nutrient analyses of plant samples, crop contents, and ventriculus contents followed methods described by Barnett and Crawford (1994) and were conducted by the Wildlife Habitat Laboratory, Washington State University, Pullman, USA. I estimated crude protein content of the diet (i.e., index for dietary protein) for each hen by averaging crude protein values of crop and ventriculus contents.

**Data Analysis**

I used General Linear Mixed (GLM) models (PROC MIXED, SAS Version 8.2, 2001) to investigate temporal variation (collection periods and years) in ADM of food types (low sagebrush and forbs), crude protein content of the diet, and ovary weight of pre-incubating adult and yearling females. I also used GLM models to investigate temporal variation in availability and nutrient content (crude protein, calcium, and phosphorous) of food types at foraging areas. Low sagebrush was not included in the availability analysis because it was characteristic of foraging areas and readily available across study sites and years. I included study site as a random effect in my analyses to account for possible differences in diet and nutrition of pre-incubating females across the study area. By design, inclusion of study site as a random effect allowed for inference to the entire study area and not specifically to the individual sites. I considered a 2-way interaction for collection period and year in my analyses. When evaluation of residual and box plots indicated unequal variances for error terms, I partitioned the variances associated with the main effects in my model using the REPEATED statement and the Kenward-Rogers option for degrees of freedom (SAS
Institute 2001, version 8.2).

RESULTS

I analyzed crops of 86 pre-incubating female sage-grouse and 75 (51 adults and 24 yearlings) contained food. Thirty-one (9 during early and 22 during late collection periods) and 44 (20 during early and 24 during late collection periods) hens were collected during 2002 and 2003, respectively. I sampled vegetation and collected plants at 110 locations (37 during early and 73 during late collection periods; 48 sites in 2002 and 62 sites in 2003).

Diet Composition of Hens

Hens consumed 22 different food types, including low and big sagebrush, 15 different forbs, 2 insect taxa, sagebrush galls, moss, and a trace amount of unidentified grasses (Table 2). Low sagebrush was found in 97% (73/75) of crops and accounted for 65.7 ± 3.8% (X ± SE) ADM of the diet (Table 2). Forbs occurred in 89% of crops and comprised 30.1 ± 3.6% ADM of the diet (22.4 ± 5.5% in 2002 and 35.6 ± 4.5% in 2003, Table 2). Forbs consumed with >15% frequency included everlasting (A. dimorpha), hawksbeard, desert-parsley, mountain dandelion, sagebrush buttercup (R. glaberrimus), long-leaf phlox (P. longifolia), big-head clover (T. macrocephalum), and obscure milk-vetch (A. obscurus) and comprised 81.7 ± 3.8% ADM of the forb diet and 29.0 ± 3.5% ADM of the total diet (Table 2). As a group, these forbs were consistently consumed by hens across collection periods and years, except during the early period in 2002 when only 4 forbs were consumed in small amounts and sagebrush comprised 97.7 ± 1.3% ADM of the diet (Table 3). However, ADM of individual forb species consumed was variable across years and age class of hens
Table 2. Frequency of occurrence (%) and aggregate percent dry mass (ADM) of foods consumed by pre-incubating greater sage-grouse (*n* = 75) collected during March and April, 2002-2003, Oregon and Nevada, USA.

<table>
<thead>
<tr>
<th>Food</th>
<th>Frequency of Occurrence</th>
<th>ADM</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sagebrush</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low sagebrush (<em>Artemisia arbuscula</em>)</td>
<td>97</td>
<td>65.7</td>
<td>3.8</td>
</tr>
<tr>
<td>Big sagebrush (<em>A. tridentata</em>)</td>
<td>7</td>
<td>2.0</td>
<td>1.3</td>
</tr>
<tr>
<td>Total sagebrush</td>
<td>99</td>
<td>67.8</td>
<td>3.7</td>
</tr>
<tr>
<td><strong>Forbs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Everlasting (<em>Antennaria dimorpha</em>)</td>
<td>60</td>
<td>11.3</td>
<td>2.6</td>
</tr>
<tr>
<td>Hawksbeard (<em>Crepis spp.</em>)</td>
<td>47</td>
<td>6.1</td>
<td>1.7</td>
</tr>
<tr>
<td>Desert-parsley (<em>Lomatium spp.</em>)</td>
<td>52</td>
<td>3.9</td>
<td>1.2</td>
</tr>
<tr>
<td>Mountain dandelion (<em>Agoseris spp.</em>)</td>
<td>57</td>
<td>2.9</td>
<td>1.1</td>
</tr>
<tr>
<td>Sagebrush buttercup (<em>Ranunculus glaberrimus</em>)</td>
<td>41</td>
<td>1.9</td>
<td>0.5</td>
</tr>
<tr>
<td>Long-leaf phlox (<em>Phlox longifolia</em>)</td>
<td>19</td>
<td>1.7</td>
<td>1.2</td>
</tr>
<tr>
<td>Big-head clover (<em>Trifolium macrocephalum</em>)</td>
<td>16</td>
<td>0.8</td>
<td>0.5</td>
</tr>
<tr>
<td>Obscure milk-vetch (<em>Astragalus obscurus</em>)</td>
<td>27</td>
<td>0.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Pursh’s milk-vetch (<em>A. purshii</em>)</td>
<td>13</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Buckwheat (<em>Eriogonum spp.</em>)</td>
<td>7</td>
<td>0.4</td>
<td>0.3</td>
</tr>
<tr>
<td>Larkspur (<em>Delphinium nuttallianum</em>)</td>
<td>4</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Rockcress (<em>Arabis spp.</em>)</td>
<td>9</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Blue-eyed Mary (<em>Collinsia parviflora</em>)</td>
<td>3</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Yarrow (<em>Achillea millifolium</em>)</td>
<td>1</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Balsamroot (<em>Balsamorhiza spp.</em>)</td>
<td>1</td>
<td>&lt;0.1</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>Unknown forb</td>
<td>15</td>
<td>0.3</td>
<td>0.2</td>
</tr>
<tr>
<td>Total forb</td>
<td>89</td>
<td>30.1</td>
<td>3.6</td>
</tr>
</tbody>
</table>
Table 2. (Continued).

<table>
<thead>
<tr>
<th>Other</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Moss</td>
<td>13</td>
<td>1.4</td>
</tr>
<tr>
<td>Dead grass</td>
<td>76</td>
<td>0.3</td>
</tr>
<tr>
<td>Sagebrush galls</td>
<td>21</td>
<td>0.3</td>
</tr>
<tr>
<td>Insects*</td>
<td>3</td>
<td>&lt;0.1</td>
</tr>
</tbody>
</table>

*Ants and caterpillars.

(Table 3).

**Nutrient Content and Availability of Food**

Low sagebrush had the lowest crude protein, calcium, and phosphorus content of all food plants analyzed during both years and everlasting had the lowest crude protein and phosphorous content of all primary forbs (Table 4). Mean crude protein ($F_{(1,156)} = 62.01, P < 0.0001$) and calcium ($F_{(1,160)} = 5.8, P < 0.02$) content of low sagebrush and primary forbs were greater during 2002 compared with 2003 (Figure 3). Temporal variation in phosphorus content was dependent on food category ($F_{(1,99.6)} = 3.61, P = 0.06$); phosphorus content was greater for low sagebrush ($F_{(1,27)} = 15.93, P = 0.0005$) during 2002 compared with 2003 but did not differ ($F_{(1,131)} = 1.16, P = 0.283$) between years for forbs (Figure 3).

I found no interaction between collection period and year for availability (frequency and cover) of primary food forbs ($F_{(1,104)} = 1.55, P > 0.216$). Therefore, I pooled frequency and cover data across years to test for variation in primary forb availability between collection periods. Frequency and cover of primary forbs, as a group, were greater during the late compared with the early collection period ($F_{(1,104)}$...
Table 3. Aggregate percent dry mass (mean ± SE) of primary plant species a consumed by adult and yearling pre-incubating greater sage-grouse collected during early (18-31 March) and late (1-12 April) collection periods in Oregon and Nevada, USA, 2002-2003.

<table>
<thead>
<tr>
<th>Food</th>
<th>2002 Adults</th>
<th>2003 Adults</th>
<th>2003 Yearlings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early (n = 9)</td>
<td>Late (n = 17)</td>
<td>early (n = 11)</td>
</tr>
<tr>
<td>Low sagebrush</td>
<td>97.7 ± 1.3</td>
<td>64.3 ± 8.4</td>
<td>50.2 ± 11.3</td>
</tr>
<tr>
<td>Forbs</td>
<td>2.0 ± 1.3</td>
<td>25.9 ± 7.8</td>
<td>42.7 ± 10.4</td>
</tr>
<tr>
<td>Everlasting</td>
<td>0</td>
<td>6.7 ± 4.0</td>
<td>31.5 ± 10.6</td>
</tr>
<tr>
<td>Hawksbeard</td>
<td>0</td>
<td>3.0 ± 1.4</td>
<td>2.7 ± 1.2</td>
</tr>
<tr>
<td>Desert-parsley</td>
<td>1.8 ± 1.1</td>
<td>6.3 ± 4.7</td>
<td>3.3 ± 1.6</td>
</tr>
<tr>
<td>Mountain dandelion</td>
<td>0.02 ± 0.02</td>
<td>5.4 ± 3.9</td>
<td>1.1 ± 0.3</td>
</tr>
<tr>
<td>Sagebrush buttercup</td>
<td>0.2 ± 0.2</td>
<td>1.4 ± 0.9</td>
<td>2.8 ± 1.9</td>
</tr>
<tr>
<td>Long-leaf phlox</td>
<td>0.01 ± 0.01</td>
<td>0.1 ± 0.1</td>
<td>0.9 ± 0.7</td>
</tr>
<tr>
<td>Big-head clover</td>
<td>0</td>
<td>2.5 ± 2.0</td>
<td>0.3 ± 0.2</td>
</tr>
<tr>
<td>Obscure milk-vetch</td>
<td>0</td>
<td>0.5 ± 0.2</td>
<td>0.07 ± 0.1</td>
</tr>
</tbody>
</table>

a Primary plant species were food items with >15% frequency of occurrence in crops determined by dividing the number of crops in which each food item was found by total number of crops examined.
Primary plant species were food items with >15% frequency of occurrence in crops determined by dividing the number of crops in which each food item was found by total number of crops examined.

Only 14 samples of sagebrush were analyzed for calcium and phosphorus during 2002.

Only 6 samples of long-leaf phlox were analyzed for calcium and phosphorus during 2002.

---

Table 4. Nutrient content (mean ± SE) of primary plant species* consumed by pre-incubating greater sage-grouse. Plant samples were collected at foraging areas during March and April, 2002-2003, Oregon and Nevada, USA.

<table>
<thead>
<tr>
<th>Food</th>
<th>No. of samples</th>
<th>Crude protein (%)</th>
<th>Calcium (%)</th>
<th>Phosphorus (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low sagebrush</td>
<td>15</td>
<td>15</td>
<td>16.2±0.5</td>
<td>12.0±0.1</td>
</tr>
<tr>
<td>Forbs</td>
<td>60</td>
<td>76</td>
<td>28.4±0.6</td>
<td>24.5±0.6</td>
</tr>
<tr>
<td>Everlasting</td>
<td>3</td>
<td>9</td>
<td>18.7±1.6</td>
<td>16.6±0.5</td>
</tr>
<tr>
<td>Hawksbeard</td>
<td>13</td>
<td>13</td>
<td>30.9±0.6</td>
<td>25.7±0.7</td>
</tr>
<tr>
<td>Desert-parsley</td>
<td>14</td>
<td>15</td>
<td>27.4±1.1</td>
<td>26.0±0.9</td>
</tr>
<tr>
<td>Mountain dandelion</td>
<td>7</td>
<td>10</td>
<td>29.4±1.0</td>
<td>25.7±0.8</td>
</tr>
<tr>
<td>Sagebrush buttercup</td>
<td>8</td>
<td>15</td>
<td>23.0±0.6</td>
<td>20.8±0.6</td>
</tr>
<tr>
<td>Long-leaf phlox</td>
<td>7⁵</td>
<td>9</td>
<td>28.8±1.5</td>
<td>26.7±1.0</td>
</tr>
<tr>
<td>Big-head Clover</td>
<td>6</td>
<td>3</td>
<td>35.2±2.1</td>
<td>40.2±0.1</td>
</tr>
<tr>
<td>Obscure milk-vetch</td>
<td>2</td>
<td>2</td>
<td>29.6±0.5</td>
<td>30.5±1.0</td>
</tr>
</tbody>
</table>

* Primary plant species were food items with >15% frequency of occurrence in crops determined by dividing the number of crops in which each food item was found by total number of crops examined.

⁵ Only 6 samples of long-leaf phlox were analyzed for calcium and phosphorus during 2002.
Figure 3. Annual variation in nutrient content of forbs (F) and low sagebrush (LS) samples collected at female greater sage-grouse foraging areas during March and April, 2002-2003, Oregon and Nevada, USA. Asterisks denote significant differences between years ($P \leq 0.10$).

$F_{(1,104)} = 10.29$, $P \leq 0.002$) and in 2003 compared with 2002 ($F_{(1,104)} \geq 722$, $P \leq 0.008$, Table 5). However, frequency and cover differences between collection periods and years varied for individual forb species (Table 5).

**Temporal Variation in Diet and Nutrition**

*Annual variation*

Only 5 yearling females were collected in 2002, all during the late period. Hence, my analyses of AMD, crude protein intake, and ovary weights between years were restricted to adult females. Adult females had greater ($F_{(1,34.3)} = 15.21$, $P = 0.0004$) ADM of primary forbs in their diet during 2003 (42.0 ± 6.0%) compared with 2002.
Table 5. Availability (% frequency and % cover) of primary forbs\(^a\) consumed by pre-incubating greater sage-grouse at foraging areas during early (18-31 March) and late (1-12 April) collection periods in southeastern Oregon and northwestern Nevada, USA, 2002-2003.

<table>
<thead>
<tr>
<th>Food</th>
<th>2002 Early (n = 11)</th>
<th>2002 Late (n = 37)</th>
<th>2003 Early (n = 26)</th>
<th>2003 Late (n = 36)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Frequency</td>
<td>Cover</td>
<td>Frequency</td>
<td>Cover</td>
</tr>
<tr>
<td>Forbs</td>
<td>6.9 ± 1.1(^b)</td>
<td>0.7 ± 0.2</td>
<td>13.5 ± 1.6</td>
<td>2.3 ± 0.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>13.0 ± 1.3</td>
<td>2.6 ± 0.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>17.3 ± 1.4</td>
<td>3.4 ± 0.6</td>
</tr>
<tr>
<td>Everlasting</td>
<td>1.2 ± 0.3</td>
<td>0.1 ± 0.03</td>
<td>0.9 ± 0.2</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.1 ± 0.4</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.8 ± 0.4</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td>Hawksbeard</td>
<td>0</td>
<td>0</td>
<td>1.6 ± 0.4</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.6 ± 0.2</td>
<td>0.02 ± 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.1 ± 0.4</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td>Desert-parsley</td>
<td>2.0 ± 0.7</td>
<td>0.2 ± 0.2</td>
<td>2.7 ± 0.5</td>
<td>0.9 ± 0.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3.9 ± 0.8</td>
<td>1.3 ± 0.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4.2 ± 0.6</td>
<td>1.7 ± 0.5</td>
</tr>
<tr>
<td>Mountain dandelion</td>
<td>0.4 ± 0.3</td>
<td>0.02 ± 0.02</td>
<td>2.2 ± 0.4</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.8 ± 0.4</td>
<td>0.1 ± 0.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.1 ± 0.4</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td>Sagebrush buttercup</td>
<td>1.1 ± 0.5</td>
<td>0.2 ± 0.05</td>
<td>1.9 ± 0.4</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.6 ± 0.4</td>
<td>0.1 ± 0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.0 ± 0.4</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td>Long-leaf phlox</td>
<td>2.1 ± 0.6</td>
<td>0.2 ± 0.1</td>
<td>1.7 ± 0.3</td>
<td>0.1 ± 0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.4 ± 0.4</td>
<td>0.2 ± 0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2.6 ± 0.4</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td>Big-head Clover</td>
<td>0</td>
<td>0</td>
<td>1.4 ± 0.5</td>
<td>0.6 ± 0.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.2 ± 0.1</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.4 ± 0.5</td>
<td>0.3 ± 0.1</td>
</tr>
<tr>
<td>Obscure milk-vetch</td>
<td>0</td>
<td>0</td>
<td>0.6 ± 0.2</td>
<td>0.1 ± 0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.9 ± 0.3</td>
<td>0.1 ± 0.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.2 ± 0.3</td>
<td>0.2 ± 0.05</td>
</tr>
</tbody>
</table>

\(^a\) Primary forbs were species with >15% frequency of occurrence in crops determined by dividing the number of crops in which each food item was found by total number of crops examined.

\(^b\) Mean ± SE.
Figure 4. Annual variation in (A) aggregate dry mass (ADM) and (B) availability (frequency and cover) of primary food types consumed by pre-incubating female greater sage-grouse during March and April in Oregon and Nevada, USA, 2002-2003. Primary foods were species with >15% frequency of occurrence in crops determined by dividing the number of crops in which each food item was found by total number of crops examined. Availability data were obtained from 110 plots sampled within foraging areas and consumption data were obtained from crops of 75 collected females. Asterisks denote significant differences between years ($P \leq 0.10$).

(17.6 ± 5.5%, Figure 4A), concordant with decreased ADM of low sagebrush ($F_{(1,33.1)} = 15.91, P = 0.0003$, Figure 4A) and greater availability of primary forbs during 2003 (Figure 4B). Crude protein content of the diet was greater ($F_{(1,40.7)} = 7.52, P = 0.009$) during 2002 (20.2 ± 1.1%) compared with 2003 (16.8 ± 0.5%). Ovary weight of adults was greater ($F_{(1,10.6)} = 12.33, P = 0.005$) during 2003 (8.9 ± 2.0g) compared with 2002 (1.7 ± 0.3g) for the early collection period, but there were no differences ($F_{(1,27)} = 0.11, P = 0.739$) in ovary weight between years (17.7 ± 2.7g and 19.2 ± 2.5g during 2002 and 2003, respectively) for the late collection period.

Seasonal variation -

Among adults, I found interaction between collection period and year for ADM of primary forbs ($F_{(1,51)} = 6.65, P = 0.01$). Therefore, I conducted analyses by year for
variation in diet and nutrition between collection periods. During 2002, aggregate percent dry mass of primary forbs in crops of adult females was greater \( F_{(1,17,9)} = 9.68, P = 0.006 \) during the late compared with the early collection period (Table 3). Greater consumption of forbs during the late collection period in 2002 coincided with decreased ADM of low sagebrush \( F_{(1,17,8)} = 16.57, P = 0.0007, \text{Table } 3 \), greater availability of primary forbs (Table 5), and higher \( F_{(1,21,3)} = 12.62, P = 0.002 \) crude protein content of the diet (early: \(16.7 \pm 1.6\% \) and late: \(22.1 \pm 1.2\% \)).

During 2003, no differences in ADM of primary forbs \( F_{(1,41,7)} = 0.61, P = 0.440 \) or low sagebrush \( F_{(1,41,7)} = 0.51, P = 0.481 \) were detected between collection periods for adult or yearling females (Table 3). Crude protein content of the diet did not differ \( F_{(1,44)} = 0.25, P = 0.623 \) between collection periods for either adult (15.1 ± 0.4% vs. 18.1 ± 0.7%) or yearling females (15.1 ± 1.1% vs. 16.0 ± 0.4%). Ovary weights of adult (8.9 ± 2.0g vs. 19.2 ± 2.5g) and yearling (7.0 ± 2.6g vs. 15.1 ± 3.4g) females were greater \( F_{(1,16,3,4,7)} \geq 3.69, P \leq 0.073 \) during the late compared with the early collection period. However, ADM of primary forbs was higher \( F_{(1,34,7)} = 3.22, P = 0.082 \) and low sagebrush was lower \( F_{(1,35)} = 6.29, P = 0.017 \) in crops of adult compared with yearling females in the early and late collection periods (Table 3, Figure 5A). Crude protein content of the diet did not differ \( F_{(1,11,7)} = 0.00, P = 0.959 \) between age-classes (15.1 ± 0.4% and 15.1 ± 1.1% for adult and yearlings, respectively) during the early collection period, but was greater \( F_{(1,21)} = 6.38, P = 0.020 \) for adults (18.1 ± 0.7%) than yearling (16.0 ± 0.4%) females during the late collection period (Figure 5B). No differences \( F_{(1,39,1)} = 1.28, P = 0.266 \) in ovary weights were detected between adult and yearling females for either collection period.
DISCUSSION

I found that forbs contributed substantially to the diet of pre-incubating greater sage-grouse. A relatively small group of forbs was consistently consumed across collection periods and years and included hawksbeard, desert parsley, mountain dandelion, everlasting, sagebrush buttercup, long-leaf phlox, obscure milk-vetch, and big-head clover. Except for sagebrush buttercup, these forbs were among the highest selected food items of pre-laying female sage-grouse identified by Barnett and Crawford (1994) in Oregon. Although sagebrush was the primary food consumed by sage-grouse during winter (Wallestad et al. 1975), the shift in diet composition I observed during March and April was consistent with results of Barnett and Crawford (1994) for sage-grouse and seasonal dietary patterns of other grouse species (Gardarsson and Moss 1969, Naylor and Bendell 1989, Brittas 1988).

Consumption of forbs, which were higher in nutrients (crude protein, calcium, and

---

**Figure 5.** Aggregate percent dry mass (ADM) (A) and crude protein content (B) of forbs (F) and low sagebrush (LS) in crops of adult and yearling pre-incubating female greater sage-grouse, Oregon and Nevada, USA, 2003. Asterisks denote significant differences between collection periods ($P \leq 0.10$).
phosphorus) than low sagebrush, increased from late March to early April during 2002 and was greater during 2003 compared to 2002. Although amount of forbs consumed by female sage-grouse did not change during 2003, the species composition of forbs in the diet differed between collection periods. My results indicate that temporal variation in diet composition (ADM of forbs and forb species composition) of pre-incubating female sage-grouse coincided with greater forb availability during the late collection periods and in 2003. There is little information about the relationship between consumption of high nutrient foods and food supply. Naylor and Bendell (1989) reported female spruce grouse that consumed the most preferred foods had the greatest dietary intake of crude protein, calcium, and phosphorus, and the rate of intake was correlated with the availability of preferred foods on spring territories.

I surmise that increased consumption of forbs by pre-incubating females during spring was directly related to nutrient requirements for reproduction. Dietary intake of crude protein, calcium, and phosphorus was enhanced by consumption of forbs during both years of my study because forbs consistently had higher nutrient content than sagebrush. Sage-grouse productivity on my study area was greater during 2003 compared with 2002 (Gregg et al. 2002, 2003) and coincided with the year of greatest forb availability and consumption by hens. Barnett and Crawford (1994) reported that annual differences in sage-grouse reproductive success positively corresponded with increased consumption of forbs by pre-laying hens. Similarly, sage-grouse renesting rates (Chapter 4) and chick survival (Dunbar et al. 2005) was related to total plasma protein values, an index of dietary protein (Amand 1986). Hence, higher nutritional status and productivity of sage-grouse may be related to increased availability and
consumption of forbs by hens during spring. However, the relationship between maternal nutrition and reproductive success is difficult to ascertain in free-ranging sage-grouse populations because other factors can influence success of reproduction irrespective of maternal nutrition (Drut et al. 1994, Gregg et al. 1994, Sveum et al. 1998, Chapter 4).

My results suggest that nutrient content, as well as availability, of food types consumed by sage-grouse varied temporally. Crude protein content of hen crop contents was lower during 2003 than 2002, irrespective of greater ADM of forbs in crops during 2003, likely because of lower crude protein content of both low sagebrush and forbs. Nutrient content of forage can be directly or indirectly affected by environmental factors including weather, soil, plant competition, and grazing (Laycock and Price 1970). Although grouse increase food intake in preparation for egg production (Savory 1975, Williams et al. 1980, Delahay and Moss 1996), reproductive success may depend more on food quality than quantity (Moss 1969). Sagebrush leaves contain volatile chemicals that reduce palatability and digestibility (Rosentreter 2005). These chemicals (e.g., monoterpenes) have anti-bacterial properties that may reduce symbiotic bacteria in the caeca of sage-grouse (Remington and Braun 1985) and chemical concentrations in sagebrush leaves are highest during spring (Cedarleaf et al. 1983). Although nutrient content of forbs decreased, greater forb availability during 2003 provided more forage of higher quality (i.e., palatable and digestible) than sagebrush and likely enhanced maternal nutrition of hens. However, nutritional requirements for sage-grouse reproduction are not well understood.
Reduced availability and consumption of forbs during 2002 may have been related to late winter snow that covered my study area during the early collection period, which perhaps delayed forb growth. In contrast, my study area was snow free during the early collection period in 2003, forb phenology was advanced, and availability and consumption of forbs was greater than I observed in 2002. Variation in availability and consumption of forbs between years was also related to ovary weight of my hens. Follicle development was advanced for hens collected during the early period in 2003 compared with 2002 and may have been related to greater nutrition because of increased consumption of forbs during 2003 (Thomas 1986, Carey 1996).

My results suggest that diet composition of pre-incubating females was dependent on hen age. Adult females consumed more forbs and less low sagebrush compared with yearlings during both collection periods in 2003. Age-related differences in foraging proficiency have been documented in many species of birds (Wunderle 1991), but little research has been conducted on grouse. Food habits of adult and yearling spruce grouse (Naylor and Bendell 1989) and blue grouse (Dendragapus obscurus, King and Bendell 1982) in Canada were similar during spring. Differences in diet composition during my study may have been related to differences in breeding chronology between adult and yearling sage-grouse. Yearling females typically attend leks and nest later in the spring than adults (Chapter 4), which could also influence dietary patterns. However, yearling sage-grouse had lower nest and renest initiation, nest and renest success, and brood survival compared with adults on my study area during 2003 (M. A. Gregg, U.S. Fish and Wildlife Service, unpublished data). Greater consumption of forbs by adults could partially explain differences in reproductive
success between age classes. Other factors that may cause differences in productivity between adult and yearling sage-grouse include social constraints, breeding experience, reproductive effort, and differential survival rates between age-classes (Hannon 1982, Martin 1985, Forslund and Pärt 1995). I caution that my dietary analysis between age-classes was limited to a single year. Nevertheless, my results warrant further research to elucidate relationships among diet composition, nutrition, age of hens, and reproductive success.

Previous researchers reported that sagebrush comprised between 89 and 100% of sage-grouse diets during March and April (Patterson 1952, Rogers 1964, Wallestad et al. 1975). I also found sagebrush to be an important component of the diet during spring, but forbs averaged 30% ADM of the diet and provided the greatest nutritional contribution of all food types. Differences in diet composition between sexes were not evaluated in these earlier sage-grouse diet studies. Hence, my results were not directly comparable, particularly when differences in spring diet composition between sexes have been reported for blue grouse (King and Bendell 1982) and rock ptarmigan (Lagopus mutus, Gardarsson and Moss 1969).

MANAGEMENT IMPLICATIONS

My findings suggest that habitat management for sage-grouse that includes restoration of forbs within degraded sagebrush stands will improve reproductive success. Restoration techniques that may increase forb abundance in sagebrush stands by manipulating sagebrush cover include prescribed fire, mechanical treatment (e.g., brush-beating), and chemical application (Pyle 1996, Connelly et al. 2001, Wrobleski and Kauffman 2003, Crawford et al. 2004). The goal should be to reduce sagebrush
density to create a plant community with a sagebrush overstory and a diversity of forbs in the understory. Selection of the appropriate restoration technique is site-specific, and I recommend that habitat restoration activities follow guidelines published in Connelly et al. (2000). Not all areas require active restoration to increase forb abundance. In some cases, adjustment of timing and intensity of grazing or elimination of detrimental activities (e.g., off-road vehicle use) may be all that is necessary to increase forb availability during spring. Before restoration projects are initiated, we recommend that the project area is surveyed to determine site potential including the presence of exotic plants to evaluate the likelihood of achieving project objectives.

Seeding may be required to reestablish forbs important for pre-incubating females in some areas. I found a small group of early-season forbs that accounted for most of the high nutrient food consumed by hens. Habitat restoration projects within the northern Great Basin that require seeding should include hawksbeard, desert-parsley, mountain dandelion, sagebrush buttercup, long-leaf phlox, big-head clover, everlasting, and obscure milk-vetch to increase nutrient intake by breeding females. In addition to active restoration, research outside of the Great Basin should be conducted to identify other forb species that provide high nutrient foods during the pre-incubating period. Until more information is available, I recommend forbs from the Chichorieae (dandelion) tribe within the family Compositae, and members of the families Umbelliferae and Leguminosae for restoration projects that require seeding outside the northern Great Basin.

To provide further insight on the influence of nutrition on sage-grouse reproductive
success, I suggest that future research focus on (1) relationships between spring diet composition and nutritional status of hens, (2) seasonal and annual variation in nutrient content of foods, (3) nutritional status of hens and reproductive output, and (4) differences in diet composition between adult and yearling females.

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LITERATURE CITED


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TOTAL PLASMA PROTEIN AND RENESTING BY GREATER SAGE-GROUSE

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ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) population declines have been attributed to reduced productivity. Although renesting by sage-grouse may contribute significantly to annual productivity during some years, little information is available on this aspect of sage-grouse reproductive ecology. We investigated the relationship between total plasma protein, age of hen, time of first nest initiation, and time of first nest loss on occurrence of renesting. We captured, assigned age, extracted blood, and radio-marked pre-laying, female sage-grouse on 4 study areas during 1999-2004. We monitored radio-marked females from mid-April through June to identify period of nest initiation (early, mid, or late), nest loss (early or late), and renesting activity. We only considered hens that were available to renest (*n* = 143) for analysis, and we censored those that nested successfully or died during their first nest attempt. Depredation and abandonment accounted for 85% (122/143) and 15% (21/143) of the unsuccessful first nests, respectively. The proportion of hens renesting was 34% (48/143) across all study areas and years. Akaike's Information Criterion model selection indicated that occurrence of renesting varied by age, nest initiation period, nest loss period, and total plasma protein. The best model had low predictive power for any given hen (*r*^2^ = 0.296), but validation of the best model indicated that our predictor variables were important for distinguishing renesting status and likely explained substantial temporal and spatial variation in renesting rates. A greater proportion of adults than yearlings renested, and hens that nested early in the nesting
season and lost nests early during incubation were the most likely to renest. Hens that renested had greater total plasma protein levels than non-renesting hens independent of age, nest initiation period, and nest loss period. Because sage-grouse depend on exogenous sources of protein for reproduction, land management practices that promote high quality, pre-laying hen habitat could increase dietary protein intake and sage-grouse renesting rates.

INTRODUCTION

Greater sage-grouse populations have declined across their range since the 1950s, and declines have been linked to several factors, particularly reduced productivity (Crawford and Lutz 1985, Connelly and Braun 1997, Connelly et al. 2004). Considerable research has been conducted on factors that influence sage-grouse reproductive success including pre-laying hen condition (Barnett and Crawford 1994), nest success (Wallestad and Pyrah 1974, Connelly et al. 1991, Gregg et al. 1994, Sveum et al. 1998a), and brood survival (Johnson and Boyce 1990, Drut et al. 1994a, Sveum et al. 1998b, Aldridge and Brigham 2001). Few investigations have focused on factors that influence renesting (Connelly et al. 1993, Schroeder 1997), although considerable variation in sage-grouse renesting rates has been reported from radio telemetry studies. Renesting rates for sage-grouse have varied from 87% in Washington (Schroeder 1997), 36% in Alberta (Aldridge and Brigham 2001), 15% in Idaho (Connelly et al. 1993), and 6% in Oregon (Hanf et al. 1994). Understanding factors that influence renesting rates is important for sage-grouse management because renesting can contribute significantly to annual recruitment of young during some years (Schroeder 1997; J. A. Crawford, Oregon State University, unpublished data),
yet little information is available to account for the wide variation in sage-grouse renesting rates.

Protein may be important for renesting because it is one of the major nutrients in eggs (Carey 1996) and may be a greater limiting factor than energy for egg production in grouse (Moss 1972, Thomas and Popko 1981, Thomas 1982). Protein resources available for reproduction originate from the diet, whether from direct (exogenous) or stored (endogenous) sources (Beckerton and Middleton 1982, Carey 1996). Tetraonids generally do not rely entirely on stored protein reserves for reproduction (Thomas and Popko 1981; Thomas 1982, 1986; Remington and Braun 1988). Protein required for egg production by grouse mostly comes directly from the diet during spring (Moss 1977, Naylor and Bendell 1989, Delahay and Moss 1996). During periods when energy demands are high (e.g., reproduction), grouse depend on continuous feeding, large food intake, high forage digestibility, and high food passage rates (Savory 1975, Thomas and Popko 1981, Thomas 1982, Beckerton and Middleton 1983). Therefore, intake of protein during spring may affect the ability of female sage-grouse to renest. Other factors, including hen age (Sopuck and Zwickel 1983, Bergerud 1988), date of first nesting attempt (Grand and Flint 1996), and timing of nest loss (Seubert 1952, Gates 1962) have influenced renesting occurrence in other birds and could affect renesting by sage-grouse irrespective of protein intake. However, these relationships are poorly understood; other than Schroeder (1997) and Connelly et al. (1993), no research has been conducted to identify factors that influence renesting propensity by sage-grouse.

Plasma proteins are the most readily obtainable measure of available protein in the
body of birds (Amand 1986). Total plasma protein has been used as an indicator of body condition (de le Court et al. 1995, Dawson and Bortolotti 1997, Schoech and Bowman 2003) and protein available for breeding (Herbert et al. 2002, Schoech and Bowman 2003, Dunbar et al. 2005) in birds. Plasma protein values of chickens also fluctuated relative to dietary protein intake (Leveille et al. 1960, Leveille and Sauberlich 1961). We hypothesized that total plasma protein may be a good indicator of sage-grouse renesting likelihood because dietary protein can limit egg production (Breitenbach et al. 1963) and influence clutch size of galliformes (Beckerton and Middleton 1982, Aboul-Ela et al. 1992). Our objectives were to: (1) examine the relationship among total plasma protein, hen age, date of nest initiation, and age of nest at loss on renesting by greater sage-grouse and (2) to develop a predictive model of renesting likelihood to provide inference on temporal and spatial variability of sage-grouse renesting rates.

STUDY AREA

We conducted our study at 4 sites within the Great Basin in northwestern Nevada and southeastern Oregon, USA. Sheldon National Wildlife Refuge, Nevada and Hart Mountain National Antelope Refuge, Oregon were administered by the U. S. Fish and Wildlife Service and encompassed 232,294 and 114,375 ha, respectively. Montana Mountains, Nevada and Beatys Butte, Oregon were administered by the Bureau of Land Management and encompassed 170,000 and 110,682 ha, respectively. Elevation ranged from 1,200 to 2,450 m. Annual average precipitation and average minimum and maximum temperatures ranged from 29 to 33 cm and -22° and 38° C, respectively (Western Regional Climate Center 2005).

**METHODS**

We captured female sage-grouse on or near leks by spotlight (Giesen et al. 1982) during March and April 1999-2004 (Byrne 2002, Davis 2002). We fitted hens with a necklace mounted 20-g radio transmitter (Advanced Telemetry Systems, Isanti, MN, USA), and we determined age from molt patterns of primaries (Crunden 1963). Blood (1.0 ml) was extracted from the brachial vein with a 22-gauge needle and collected into Microtainer® EDTA tubes (Becton Dickinson and Company, Franklin Lakes, NJ, USA). Total plasma protein was measured by refractometer at the Veterinary Diagnostic Laboratory, College of Veterinary Medicine, Oregon State University, Corvallis, USA. Blood collection protocol was approved by the Oregon State
University Institutional Animal Care and Use Committee (Animal Care and Use Proposal Number 2656).

Beginning in mid-April, we obtained remote telemetry locations by triangulation, and we used them to monitor radio-marked hens until they dispersed from leks. Subsequently, we obtained visual locations by approaching radio-marked hens with hand-held antennas to ascertain nesting chronology. We visually confirmed incubation of hens on nests, and we recorded nest locations as Universal Transverse Mercator coordinates to facilitate location of nest sites after incubation was terminated. We did not intentionally flush hens from nests, and after incubation was confirmed, we monitored nesting hens ≥100 m from the nest site to avoid disturbance. When incubation ceased, we determined nest fate by condition of nest and eggs, and we used visual observations to confirm hens with broods. We classified nests as unsuccessful if all eggs failed to hatch because of predation or abandonment. We monitored hens with unsuccessful nests to determine renesting activities. Our goal was to monitor radio-marked hens once every 3 days to determine exact dates of nest initiation and nest loss, but distribution and movements of hens precluded frequent monitoring for all birds. Therefore, we used monitoring data from radio-marked females to classify nest initiation dates and nest age at loss for first nests into broad periods.

Data Analysis

We used logistic regression (PROC GENMOD, SAS Institute 2001, version 8.2) to examine patterns in renesting occurrence with respect to date of first nest initiation, age of first nest at loss, hen age, and total plasma protein levels. We only used hens
that were available to renest in our analysis. We censored hens that nested successfully or died during their first nesting attempt. Because nests were very difficult to locate at the initiation of egg laying, we defined nest initiation as the start of incubation. Nests lost during egg laying were not detected, consequently we considered renests only for hens that initiated incubation of first nests. We assumed that hens captured with brood patches had initiated incubation prior to capture, and we censored them. We used the date incubation was confirmed and the last visual location that hens were not incubating to classify nest initiation dates for first nests into 3 periods (NIP): early (11-23 April), mid (24 April-3 May), and late (4-14 May). We divided the age of first nest at loss into 2 periods of incubation (IP): early (0-14 days) and late (15-28 days) based on the last known date hens were incubating and the date we found nests depredated or abandoned. We divided hen age (AGE) into adult (entering at least their second breeding season) or yearling (entering their first breeding season). We investigated multicollinearity by examining a correlation matrix (PROC CORR, SAS Institute 2001) and tolerances (PROC REG, SAS Institute 2001) of all predictor variables (Allison 1999).

We developed 9 a priori candidate models to explain renesting occurrence by sage-grouse based on our knowledge of reproductive ecology from previous sage-grouse research (Barnett and Crawford 1994, Gregg et al. 1994, DeLong et al. 1995, Coggins 1998, Byrne 2002, Davis 2002) and observations during data collection for my study. We treated AGE (yearling = 0, adult = 1) and IP (early = 1, late = 0) as dummy variables. We treated NIP (early = 1, mid = 2, and late = 3) and total plasma protein (TPP) as quantitative variables because model fit did not improve when the linearity
constraint was relaxed (Allison 1999). The global model included TPP, NIP, IP, and AGE and interactions for TPP with AGE, NIP, and IP. We used deviance ($\hat{\chi}^2 = \text{goodness-of-fit } \chi^2/\text{df}$) to determine if the structure of the global model was appropriate for the data (Burnham and Anderson 2002). We used Akaike's Information Criterion adjusted for small samples sizes ($\text{AIC}_c$) and Akaike weights ($w_i$) to choose the best approximating model from the group of candidate models given the data (Burnham and Anderson 2002). We ranked models based on lowest $\text{AIC}_c$ values and calculated differences between the best-fitted model and all other models. We calculated Akaike weights from $\Delta\text{AIC}_c$ values to provide estimates of a model's probability given other candidate models. We used Akaike weights to generate weighted parameter estimates and unconditional standard errors for all 4 predictor variables (Burnham and Anderson 2002). Model averaged parameter estimates were not conditional on a single model and included model selection uncertainty into the final parameter estimates and standard errors. We calculated odds ratios and 95% confidence intervals (CI) from unconditional parameter estimates to evaluate the potential effect each variable had on the probability of renesting by sage-grouse (Allison 1999). We calculated maximum rescaled generalized $r^2$ values to estimate the precision of each model (Allison 1999).

To evaluate robustness of the predictor variables relative to considerable temporal and spatial variation in renesting rates, we did not included year and study area as covariates in candidate models. Data from 1999-2004 collected at all study areas were combined and used for model building. Without year and area variables in candidate models, temporal and spatial uncertainty of renesting were not included in the parameter estimates. We validated the best-fitted model, using model averaged
parameter estimates, with independent data not used for model building. We obtained independent data by randomly removing hens \((n = 16)\) from the original data set before we conducted initial analysis. Because all predictor variables could potentially vary among years and study areas, model validation with independent data provided an assessment of how well the model performed without explicitly incorporating temporal and spatial variation in renesting rates. Because model selection results were dependent on the group of hens removed from the data set for validation, we conducted 100 iterations of our analysis. Data sets (model building and validation) for each iteration were created by simple random sampling without replacement (SAS Institute 2001). We averaged results from the iterations to estimate final \(\Delta AIC_c\) scores, maximum rescaled generalized \(r^2\) values, weighted parameter estimates, and predicted probabilities of renesting.

**RESULTS**

We monitored 143 radio-marked females with unsuccessful initial nests for renesting activity (Table 6). The earliest estimated start of incubation for first nests was 11 April and the latest was 14 May. Capture dates for hens ranged from 16 March to 27 April for all years, but 89% \((127/143)\) were captured before 11 April. Depredation and abandonment accounted for 85% \((122/143)\) and 15% \((21/143)\) of the unsuccessful first nests, respectively. Overall, 34% \((48/143)\) of the hens renested (Table 6). We found no evidence of multicollinearity among predictor variables; \(r\) values and tolerances ranged from -0.09 to 0.16 and 0.96 to 0.99, respectively. The structure of our global model was appropriate for the data \((\hat{c} = 1.09)\). The best-fitted model included TPP, NIP, IP, and AGE (Table 7). All other models were \(>2 AIC_c\).
Table 6. Number of radio-marked female sage-grouse monitored for renesting activity and percent hens renesting at 4 study areas in Oregon (Hart Mountain and Beatys Butte) and Nevada (Sheldon and Montana Mountains), USA, 1999-2004.

<table>
<thead>
<tr>
<th>Year</th>
<th>Hart Mt.</th>
<th>Beatys Butte</th>
<th>Sheldon</th>
<th>Montana Mts.</th>
<th>All areas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>%</td>
<td>n</td>
<td>%</td>
<td>n</td>
</tr>
<tr>
<td>1999</td>
<td>7</td>
<td>4</td>
<td>4</td>
<td>11</td>
<td>64</td>
</tr>
<tr>
<td>2000</td>
<td>3</td>
<td>5</td>
<td>2</td>
<td>10</td>
<td>30</td>
</tr>
<tr>
<td>2001</td>
<td>4</td>
<td>7</td>
<td>5</td>
<td>16</td>
<td>37</td>
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<tr>
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<td>16</td>
<td>9</td>
<td>21</td>
<td>46</td>
<td>39</td>
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<td>2003</td>
<td>17</td>
<td>15</td>
<td>12</td>
<td>44</td>
<td>20</td>
</tr>
<tr>
<td>2004</td>
<td></td>
<td>16</td>
<td></td>
<td></td>
<td>16</td>
</tr>
<tr>
<td>All years</td>
<td>47</td>
<td>19</td>
<td>36</td>
<td>39</td>
<td>44</td>
</tr>
</tbody>
</table>

* Percent hens that renested by study and year.

units from the best model, indicating that all 4 variables were important predictors of renesting occurrence by greater sage-grouse (Table 7).

Mean TPP (g/dl) was greater for renesting ($\bar{x} = 6.4, SE = 0.18, n = 48$) than non-renesting ($\bar{x} = 6.0, SE = 0.11, n = 95$) hens and was independent of AGE, NIP, or IP (Table 7, Figure 6). Each 0.1 g/dl increase in TPP was associated with a 1.55% increase in the predicted odds of renesting (Table 8). Hens that renested typically initiated first nests early in the nesting season and lost nests early during incubation (Table 9). The predicted odds of renesting decreased 1.93 times for each increase in nest initiation period (i.e., early to mid and mid to late) and was 8.53 times greater
Table 7. Mean Akaike's Information Criteria ($\Delta$AIC$_C$) values and maximum rescaled generalized $r^2$ for candidate models used to examine patterns in renesting occurrence of radio-marked female greater sage-grouse ($n = 143$) in Oregon and Nevada, USA, 1999-2004. Variation in renesting was considered with respect to age (adults and yearlings), nest initiation period for first nest (nip; early = 11-23 April, mid = 24 April-3 May, and late = 4-14 May), nest loss period for first nests (ip; early = 0-14 days incubation and late = 15-28 days incubation), and total plasma protein (tpp). Total plasma protein was measured from blood samples collected at time of capture during March and April. Mean values for statistics ($\Delta$AIC$_C$, $w_i$, and $r^2$) were determined from 100 iterations of model selection using 127 hens selected with simple random sampling without replacement.

<table>
<thead>
<tr>
<th>Model</th>
<th>$\Delta$AIC$_C$</th>
<th>SE</th>
<th>$w_i$</th>
<th>SE</th>
<th>$r^2$</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>age + nip + ip + tpp</td>
<td>0.012</td>
<td>0.007</td>
<td>0.562</td>
<td>0.010</td>
<td>0.296</td>
<td>0.003</td>
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<tr>
<td>age + nip + ip</td>
<td>2.272</td>
<td>0.136</td>
<td>0.204</td>
<td>0.010</td>
<td>0.257</td>
<td>0.003</td>
</tr>
<tr>
<td>nip + ip + tpp</td>
<td>3.279</td>
<td>0.135</td>
<td>0.127</td>
<td>0.007</td>
<td>0.248</td>
<td>0.003</td>
</tr>
<tr>
<td>age + nip + ip + tpp + tpp<em>age + tpp</em>nip + tpp*ip</td>
<td>4.991</td>
<td>0.079</td>
<td>0.050</td>
<td>0.002</td>
<td>0.311</td>
<td>0.003</td>
</tr>
<tr>
<td>nip + ip</td>
<td>5.049</td>
<td>0.171</td>
<td>0.056</td>
<td>0.004</td>
<td>0.213</td>
<td>0.003</td>
</tr>
<tr>
<td>age + tpp</td>
<td>18.819</td>
<td>0.300</td>
<td>0.000</td>
<td>0.000</td>
<td>0.078</td>
<td>0.002</td>
</tr>
<tr>
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<td>0.313</td>
<td>0.000</td>
<td>0.000</td>
<td>0.041</td>
<td>0.001</td>
</tr>
<tr>
<td>tpp</td>
<td>20.757</td>
<td>0.304</td>
<td>0.000</td>
<td>0.000</td>
<td>0.036</td>
<td>0.001</td>
</tr>
<tr>
<td>intercept only (null model)</td>
<td>22.043</td>
<td>0.307</td>
<td>0.000</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Akaike weight.
when initial nests were depredated during the first 2 weeks of incubation compared to the last 2 weeks of incubation (Table 8). Adult and yearling hens that initiated and lost first nests during early nest initiation and incubation periods contributed 52% (25/48) of all renests (Figure 7).

A greater proportion of adults than yearlings renested (Table 9). The predicted odds of adult hens renesting were 2.41 times that of yearling females (Table 8). The greatest contribution to renesting (33%, 16/48) was by adult females that initiated first nests in the early nest period and lost nests early during incubation (Figure 7). Mean TPP was similar for adults ($\bar{x} = 6.1$, SE = 0.13, $n = 75$) and yearlings ($\bar{x} = 6.2$, SE = 0.13, $n = 68$), but more adults (59%, 44/75) initiated first nests during the early nest period than yearlings (47%, 32/68).

Table 8. Mean model averaged parameter estimates, unconditional standard errors, odds ratios, and 95% confidence intervals for predictor variables from models used to examine patterns in renesting occurrence of radio-marked female greater sage-grouse ($n = 143$) in Oregon and Nevada, USA, 1999-2004. Predictor variables included age (adults and yearlings), nest initiation period for first nest (early = 11-23 April, mid = 24 April-3 May, and late = 4-14 May), nest loss period for first nests (early = 0-14 days incubation and late = 15-28 days incubation), and total plasma protein. Total plasma protein was measured from blood samples collected at time of capture during March and April. Mean values for statistics were determined from 100 iterations of model selection using 127 hens selected with simple random sampling without replacement.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>Odds ratio</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age</td>
<td>0.866</td>
<td>0.642</td>
<td>2.41</td>
<td>1.15 to 3.67</td>
</tr>
<tr>
<td>Nest initiation period</td>
<td>-0.648</td>
<td>0.479</td>
<td>1.93</td>
<td>0.99 to 2.87</td>
</tr>
<tr>
<td>Nest loss period</td>
<td>2.123</td>
<td>0.694</td>
<td>8.53</td>
<td>7.17 to 9.89</td>
</tr>
<tr>
<td>Total plasma protein</td>
<td>0.434</td>
<td>0.269</td>
<td>1.55</td>
<td>1.02 to 2.08</td>
</tr>
</tbody>
</table>
Table 9. Number of renesting and non-renesting radio-marked female sage-grouse (n = 143) by age, nest initiation period for first nests (early = 11-23 April, mid = 24 April-3 May, and late = 4-14 May), and nest loss period for first nests (early = 0-14 days incubation and late = 15-28 days incubation) in Oregon and Nevada, USA, 1999-2004.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hens</th>
<th>Renesting</th>
<th>Non-renesting</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>n</td>
<td>%</td>
</tr>
<tr>
<td>Age</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>75</td>
<td>31</td>
<td>41</td>
</tr>
<tr>
<td>Yearling</td>
<td>68</td>
<td>17</td>
<td>25</td>
</tr>
<tr>
<td>Nest initiation period</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>76</td>
<td>29</td>
<td>38</td>
</tr>
<tr>
<td>Mid</td>
<td>48</td>
<td>16</td>
<td>33</td>
</tr>
<tr>
<td>Late</td>
<td>19</td>
<td>3</td>
<td>16</td>
</tr>
<tr>
<td>Nest loss period</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>88</td>
<td>41</td>
<td>47</td>
</tr>
<tr>
<td>Late</td>
<td>55</td>
<td>7</td>
<td>13</td>
</tr>
</tbody>
</table>

The proportion of hens renesting varied considerably among years and study areas (Table 6). Validation of the best model indicated that our predictor variables were important for distinguishing renesting status and likely explained substantial temporal and spatial variation in renesting rates. Predicted probabilities of renesting were 0.65 (95% CI: 0.63 to 0.67) for hens that renested and 0.44 (95% CI: 0.42 to 0.46) for hens that did not renest. However, the best model had low predictive power for any given hen (Table 7). Predicted probability for renesting ranged from 0.18 to 0.88 and 0.26 to 0.67 for renesting and nonrenesting hens, respectively.
Figure 6. Mean total plasma protein values by age (Ad = adult, Yr = yearling), nest initiation period (early = 11-23 April, mid = 24 April-3 May, and late = 4-14 May), and nest loss period (early = 0-14 days incubation and late = 15-28 days incubation) for renesting ($n = 48$) and non-renesting ($n = 95$) radio-marked female greater sage-grouse in Oregon and Nevada, USA, 1999-2004.
**DISCUSSION**

Total plasma protein levels were greater for renesting compared to non-renesting hens, irrespective of age or when incubation of first nests was initiated or terminated. Little research has evaluated relationships between protein levels from blood samples and reproduction in Tetraonids. Dunbar et al. (2005) reported that total plasma protein levels of pre-laying, female greater sage-grouse were related to chick survival. In
addition, Herbert et al. (2002) reported that plasma-amino acid concentrations were correlated with productivity of herring gulls (Larus argentatus,) and Schoech and Bowman (2003) indicated that total plasma protein levels of Florida scrub-jays (Aphelocoma coerulescens) were linked to timing of reproduction.

Greater total plasma protein levels of renesting sage-grouse hens during our study may have been related to increased dietary protein intake. Female grouse typically shift to protein-rich foods during spring (Moss 1972, Williams et al. 1980, Thomas and Popko 1981, Brittas 1988, Naylor and Bendell 1989, Barnett and Crawford 1994). Although no data are available on required levels of exogenous protein necessary for egg formation by sage-grouse, Naylor and Bendell (1989) estimated that spring diets of spruce grouse (Falcipennis canadensis) provided 60% of the protein required for clutch formation. In Oregon, consumption of forbs increased protein content of diets of pre-laying female greater sage-grouse, and increased forb consumption coincided with increased sage-grouse productivity (Barnett and Crawford 1994). We suggest that increased consumption of forbs by sage-grouse during spring immediately prior to reproduction provided the necessary exogenous source of protein for reproduction. Although renesting by sage-grouse during our study varied because of other factors, we surmise that inadequate protein for egg production may have accounted for some variation in renesting rates. Reduced forb availability during spring could have limited dietary protein intake and egg production, and it could have influenced the ability of sage-grouse to renest. However, the extent that protein availability limited sage-grouse renesting is unknown.

The extent that total plasma protein serves as an index to dietary protein intake by
sage-grouse is unknown. Total plasma protein values may be influenced by factors other than diet, particularly hormones that are secreted as hens approach laying. During follicle development, estrogen is secreted and protein is mobilized from the liver (Lofts and Murton 1973), which may cause new protein material to appear and cause some existing plasma proteins to increase or decrease (Vanstone et al. 1955, Schjeide et al. 1963). Martin et al. (1981) reported that total plasma protein levels of eastern wild turkeys (Meleagris gallopavo silvestris) gradually increased during spring, and they speculated that the increase was in response to higher estrogen levels. However, Dawson and Bortolotti (1997) reported that total plasma protein values of pre-laying American kestrels (Falco sparverius) increased with capture date during spring, and they suggested that the increase was a function of nutritional condition and not a response to hormonal secretion. Herbert et al. (2002) reported that plasma-amino acid concentrations of herring gulls increased in response to greater dietary protein intake. In addition, Sturkie (1954:34) reported that normal estrogen levels of laying and non-laying chicken hens did not have an appreciable effect on total plasma protein values. Massive doses of estrogen were required before significant increases in total plasma protein were detected (Sturkie 1951). Total plasma protein levels of pre-laying female sage-grouse also tended to increase during spring (M. A. Gregg, U.S. Fish and Wildlife Service, unpublished data). We speculate this increase was, in part, from increased protein intake associated with greater forb consumption. However, elevated estrogen levels could also have affected total plasma protein, and additional research will be required to further elucidate relationships between hormone secretion, dietary protein, and total plasma protein levels of greater sage-grouse.
Renesting occurrence declined for hens that initiated first nests later in the nesting season or lost nests late during incubation. Schroeder (1997) reported that the number of days between start of incubation and loss of first nests tended to be greater for non-renesting sage-grouse hens in Washington. In contrast, Sopuck and Zwickel (1983) reported that renesting by adult blue grouse (*Dendragapus obscurus*) was independent of nest age at time of loss. Connelly et al. (1993) suggested that renesting attempts by sage-grouse could be restricted by quality and quantity of brood-rearing habitat. Sage-grouse live in xeric environments, and survival of chicks is dependent on availability of insects and succulent vegetation (Johnson and Boyce 1990; Drut et al. 1994a,b). Optimum conditions for brood-rearing exist for a relatively short period of time during late spring and early summer; consequently, late renesting hens could experience high rates of brood loss (Connelly et al. 1993). The costs of late renesting may outweigh any benefits and ultimately reduce long-term fitness. The relationship we observed between renesting and date of first nest attempt also could have been influenced by hens that lost first nests during laying or early stages of incubation. We were unlikely to find nests during egg laying, and it was possible that some nests were lost very early in incubation and were not located.

Adult hens were more likely to renest than yearlings during our study. No difference in renesting rates for adult and yearling sage-grouse were found in Idaho (Connelly et al. 1993) or Washington (Schroeder 1997), but differences in monitoring techniques, sample sizes, and timing of nest loss may have accounted for disparities between our results and these studies. However, Bergerud (1988) indicated that adult sage-grouse hens typically renested more often than yearlings. Adult blue grouse also
exhibited higher renesting rates than yearlings (Sopuck and Zwickel 1983). Adult hens may have renested more readily than yearlings during our study because they nested earlier in the nesting season. Schroeder (1997) also reported that adult sage-grouse nested earlier than yearlings in Washington. However, we found differences in renesting rates between adults and yearlings were independent of nest initiation period for first nests. This suggested that additional factors were responsible for different renesting rates between age classes. Nutrient reserves may have accounted for differences in renesting rates of adult and yearling blue grouse (Sopuck and Zwickel 1983), but we found no differences in mean total plasma protein for adult and yearling sage-grouse hens prior to initiation of first nests. Other factors that could explain differences in renesting rates between adults and yearlings include social and physiological constraints and breeding experience (Zwickel 1977, Hannon et al. 1979, 1982, Martin 1995).

We found considerable spatial and temporal variation in renesting rates during our study. Model validation indicated that total plasma protein, date of first nest attempt, age of nest at termination, and hen age were important variables for distinguishing between renesting and non-renesting sage-grouse. Variation in any one of these variables could affect renesting likelihood and, at least partially, account for the wide range of renesting rates reported for sage-grouse. The precision of our best model was relatively low, which was not surprising given that we measured total plasma protein 4 to 6 weeks before renesting and classified nest initiation dates and age of nest at loss into broad categories. In addition, precision of our model was likely reduced by other factors that we did not evaluate and could have influenced sage-grouse renesting
likelihood, including intrinsic variation among hens. However, the precision of our model was comparable to other studies that used total plasma protein to predict reproductive success of greater sage-grouse (Dunbar et al. 2005).

MANAGEMENT IMPLICATIONS

Habitat management for sage-grouse that includes restoration of early-season forbs within degraded sagebrush stands would improve the nutritional status of hens and the potential for renesting. Important sage-grouse food forbs that should be considered for habitat restoration projects include members of Compositae, Umbelliferac, and Leguminosae families (Barnett and Crawford 1994, M. A. Gregg, U.S. Fish and Wildlife Service, unpublished data).

Total plasma protein may be useful for evaluating reproductive potential of sage-grouse. In addition to our results, Dunbar et al. (2005) suggested that blood parameters were useful for assessing condition of greater sage-grouse and were related to reproductive success (e.g., chick survival). Additional research is required before land managers can incorporate physiological parameters into sage-grouse monitoring or conservation plans. We recommend that future research focus on the extent that sage-grouse rely on exogenous sources of protein for reproduction and relationships between total plasma protein, dietary protein, diet composition, and forage availability. Ultimately, total plasma protein may be an effective nutritional index to monitor sage-grouse habitat condition and the health and reproductive potential of sage-grouse populations.

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LITERATURE CITED


population ecology of northern grouse. University of Minnesota Press, Minneapolis, USA.


the Interior, Bureau of Land Management, Prineville District Office, Series P-
SG-01.

in the gonadal cycles of adult and yearling blue grouse. Canadian Journal of
Zoology 57:1283-1289.

blue grouse: evidence for socially induced delayed breeding in yearlings. Auk
99:687-694.

concentrations as an indicator of protein availability to breeding herring gulls

JOHNSON, G. D., and M. S. BOYCE. 1990. Feeding trials with insects in the diet of sage

protein, fat and cholesterol on plasma cholesterol and serum protein
components of the growing chick. Archives of Biochemistry and Biophysics
86:67-70.

serum protein components and cholesterol in the growing chick. Journal of
Nutrition 74:500-504.

New York, USA.

MARTIN, K. 1995. Patterns and mechanisms for age-dependent reproduction and

protein, and cholesterol in female eastern wild turkey. Journal of Wildlife
Management 45:798-802.

MOSS, R. 1972. Food selection by red grouse (Lagopus lagopus scoticus (Lath.)) in


CHAPTER 5: EFFECT OF HABITAT RESOURCES ON SURVIVAL OF GREATER SAGE-GROUSE CHICKS

ABSTRACT

Greater sage-grouse (*Centrocercus urophasianus*) chick survival is an important, but poorly understood, component of sage-grouse population dynamics. I estimated survival of 506 radio-marked chicks from 94 broods to 28-days post-hatch on 3 sites from 2000-2003 to examine relationships between survival and habitat resources. Covariates included hatch date, initial brood size, chick weight at hatching, brood movements, total plasma protein values of breeding females, and 9 habitat variables (food and cover) measured at brood sites. Overall, chick survival was 0.393 (SE = 0.024). Chick deaths were attributed to predation (81%, n = 251), exposure (11%, n = 35), unknown (4%, n = 14), and transmitter effects (3%, n = 8). Akaike’s Information Criterion model selection indicated that survival of chicks was related to total plasma protein values of breeding females and abundance of Lepidoptera at brood locations. I found strong evidence that high total plasma protein coupled with high Lepidoptera abundance was related to increased chick survival, which suggests that food resources available to hens before nest initiation and chicks shortly after hatching influenced chick survival. Factors affecting chick survival were also apparently related to age of female; survival of chicks accompanied by adult females increased with chick weight at hatch, advancing hatch date, and decreased brood movement, while survival of chicks accompanied by yearling females decreased with initial brood size and short sagebrush cover. I recommend that habitat management for sage-grouse focus on
enhancing forb abundance during March and April (i.e., pre-incubation) and
Lepidoptera abundance during May and June (i.e., early brood-rearing) to provide
adequate nutrition for breeding females and for chicks during early growth and
development, respectively.

INTRODUCTION

Greater sage-grouse (*Centrocercus urophasianus*) populations have substantially
deprecated range-wide since the 1950s (Connelly and Braun 1997, Connelly et al. 2004).
Several factors have been implicated in population declines of sage-grouse, including
reduced juvenile survival because of poor habitat quality (Crawford and Lutz 1985,
Connelly and Braun 1997). Chick survival may be the single factor most limiting
sage-grouse population growth (Aldridge and Brigham 2001, Connelly et al. 2004,
Crawford et al. 2004), yet it is one of the most poorly understood aspects of sage-
grouse reproductive ecology (Crawford et al. 2004). Considerable research has been
conducted on use and selection of brood-rearing habitat by monitoring radio-marked
sage-grouse hens with broods (Wallestad 1971, Drut et al. 1994a, Sveum et al. 1998,
Aldridge and Brigham 2002). Habitat relationships identified from these studies have
been used to develop guidelines and management recommendations targeted to
improve sage-grouse chick survival (Connelly et al. 2000, Crawford et al. 2004).
However, habitat selection by hens with broods may not provide a direct link between
habitat resources and chick survival (Morrison 2001). An understanding of the
mechanisms that directly influence daily survival rates of chicks is a prerequisite for
development and implementation of habitat management strategies that affect chick
survival and, ultimately, sage-grouse populations.
There are several habitat factors that could influence sage-grouse chick survival, including food availability (Southwood and Cross 1969, Hill 1985, Park et al. 2001) and habitat structure (e.g., cover and height of vegetation) in brood-rearing habitat. Forb and insect abundance could affect chick survival because they are the primary foods of sage-grouse chicks (Klebenow and Gray 1968, Peterson 1970, Pyle 1993) and critical sources of nutrients necessary for maintenance, growth, and development (Johnson and Boyce 1990, Drut et al. 1994b). Insect abundance may be particularly critical because research on captive sage-grouse chicks revealed that they require insects for growth and survival (Johnson and Boyce 1990). The insect taxa consumed by chicks may be equally important for chick growth and survival because of differences among taxa in nutritional quality (Borg and Toft 2000). Habitat structure may also be important for chick survival because chick mortality due to predation and exposure may be related to availability of vertical and horizontal cover provided by shrubs, grasses, and forbs (Wallestad 1971, Sveum et al. 1998, Aldridge 2005).

Availability of forbs during spring, before nest initiation, also could affect sage-grouse chick survival. Breeding female sage-grouse rely on exogenous sources of nutrients for reproduction (Remington and Braun 1988), obtained from consumption of high-nutrient foods (i.e., forbs) during March and April (Barnett and Crawford 1994, Chapter 3). Protein may be one of the most limiting nutrients in grouse diets (Moss 1972), yet is critical for reproduction in birds (Carey 1996). Research on captive female ruffed grouse (Bonasa umbellus) indicated that hens on high-protein diets during spring allocated more protein to eggs and produced larger, more viable chicks compared with hens on lower protein diets (Beckerton and Middleton 1982).
Hence, protein intake by breeding females (Moss et al. 1975, Moss and Watson 1984, Brittas 1988) and chick weight at hatch (Beckerton and Middleton 1982) may be directly related to the quantity and quality of spring forage. Other maternal variables that may be indirectly affect habitat resources available to chicks during brood-rearing include brood size (Guyn and Clark 1999, Pietz et al. 2003), brood movement (Green 1984), and hatch date (Traylor and Alisauskas 2006).

Only recently have researchers monitored survival of individually marked sage-grouse chicks (Burkepile et al. 2002, Aldridge 2005, Appendix A) and investigated direct relationships between vegetative cover at brood locations and chick survival (Aldridge 2005). Linkages between insect abundance at brood locations, forb availability during spring, and chick survival have not been investigated and remain unknown. The critical period for survival of sage-grouse chicks is the first few weeks after hatching (Appendix A). Therefore, my objective was to determine key habitat factors linked to chick survival by investigating relationships between direct and indirect measures of habitat resources and survival of individually marked sage-grouse chicks to 28-days post-hatch.

STUDY AREA

I conducted my study at 3 sites within the Great Basin in northwestern Nevada and southeastern Oregon, USA. Sheldon National Wildlife Refuge (SNWR), Nevada and Hart Mountain National Antelope Refuge (HMNAR), Oregon were administered by the U. S. Fish and Wildlife Service and encompassed 232,294 ha and 114,375 ha, respectively. Beatys Butte, Oregon was administered by the Bureau of Land Management and encompassed 110,682 ha. These areas were >40 km apart and were
selected because they were representative of the northern Great Basin, were accessible
during spring, and considerable long-term data on sage-grouse habitat use and
productivity were available from previous research (Gregg 1991, Barnett 1992, Drut
domestic livestock was eliminated from SNWR during 1994 and from HMNAR
during 1990. Since 1989, Domestic livestock grazing on Beatys Butte averaged
26,121 AUMs from 1983 to 1989 and 14,000 AUMS (Bureau of Land Management
1994).

All 3 sites were characteristic of shrub-steppe and consisted of flat sagebrush plains
interrupted by rolling hills, ridges, draws, and upland meadows. Elevation ranged
from 1,200 to 2,450 m across areas and annual average precipitation and average
minimum and maximum temperatures ranged from 29 to 33 cm and -22° and 38° C,
respectively (Western Regional Climate Center 2005). Primary shrub species included
Wyoming big sagebrush (Artemisia tridentata wyomingensis), mountain big sagebrush
(A. t. vaseyana), low sagebrush (A. arbuscula), bitter-brush (Purshia tridentata),
western snowberry (Symphoricarpos occidentalis), and green rabbitbrush
(Chrysothamnus viscidifolius). Grasses consisted largely of bluegrass (Poa spp.),
bluebunch wheatgrass (Pseudoroegneria spicata), needlegrass (Stipa spp.), fescue
(Festuca spp.), basin wildrye (Leymus cinereus), and bottlebrush squirreltail (Elymus
elymoides). Common annual and perennial forbs included desert parsley (Lomatium
spp.), mountain-dandelion (Agoseris spp.), milk-vetch (Astragalus spp.), hawksbeard
(Crepis spp.), everlasting (Antennaria spp.), aster (Aster spp.), buckwheat (Eriogonum
spp.), lupine (Lupinus spp.), and phlox (Phlox spp.).
METHODS

Data Collection

I captured female sage-grouse with spotlights and nets (Giesen et al. 1982) during March and April 2000-2003, determined age (Crunden 1963), and fitted each with a 20-g necklace-mounted radio transmitter (Advanced Telemetry Systems, Isanti, MN). I extracted approximately 1.0 ml of blood from the brachial vein and measured total plasma protein (Chapter 4). I monitored radio-marked hens during spring to locate nest (including renest) sites (Chapter 4). For hens with successful nests, I estimated hatch date, determined clutch size, and captured chicks (Appendix A). I weighed chicks to the nearest 0.1g, recorded age (days), and implanted radio transmitters (model BD2-A, Holohil Systems Ltd., Carp, Ontario, Canada) subcutaneously anterior of the scapulars (Appendix A). Age of chicks at capture was estimated based on nest monitoring data and evaluation of morphological characteristics of chicks (i.e., presence of an egg tooth, feather development). I monitored radio-marked chicks daily for 28 days post-hatch to estimate survival and determine causes of mortality (Appendix A). I found no evidence that chicks with implanted transmitters were less likely to survive than unmarked chicks (Appendix B). Grouse capture, blood collection, and transmitter attachment procedures were approved by the Oregon State University Institutional Animal Care and Use Committee (Animal Care and Use Proposal Number 2656).

I estimated relative abundance of forbs, grasses, and shrubs along 2 perpendicular 10-meter transects intersecting at the center of each daily radio-marked brood location.
The center of the plot was identified by a Universal Transverse Mercator coordinate obtained during brood monitoring. I used the line-intercept method (Canfield 1941) to estimate canopy cover of sagebrush along each transect. I measured height of intercepted shrubs from the ground to the top of the shrub canopy and classified them as short (<20 cm) or tall (≥20 cm). I visually estimated percent key food forb (Table 10), total forb, short grass (<18 cm), and total grass cover in five 20 x 50-cm plots spaced equidistantly along each transect (Daubenmire 1959). Grass cover included residual and new growth, and grass height excluded flowering stalks. I sampled ground-dwelling insects in 5 pitfall traps placed equidistantly along one randomly selected transect (Morrill 1975). Traps were buried flush to the ground, filled with a nontoxic glycerin glycol solution, covered to exclude rodents and other debris, and left set for 6 days. I sorted insect samples by common insect taxa found in chick diets (i.e., Coleoptera, Hymenoptera, Lepidoptera, Orthoptera) and counted them to estimate relative abundance at each brood location. I identified juvenile sage-grouse foods from past and present research conducted in Oregon (Pyle 1992, Drut et al. 1994b, M. Gregg, U.S. Fish and Wildlife Service, unpublished data), Idaho (Klebenow and Gray 1968), and Montana (Peterson 1970).

**Data Analysis**

I estimated Kaplan-Meier (KM) survival rates (Kaplan and Meier 1958) and Cox regression models (Cox 1972) with PROC PHREG (SAS Institute 2001, version 8.02) to examine relationships between covariates and failure times to 28-days post-hatch for individually radio-marked chicks (P. Allison, University of Pennsylvania, personal communication). I evaluated other analytical approaches (i.e., PROGRAM MARK),

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forbs</strong></td>
<td><strong>Species/Genera</strong></td>
</tr>
<tr>
<td>Desert-parsley</td>
<td><em>Lomatium</em> spp.</td>
</tr>
<tr>
<td>Hawksbeard</td>
<td><em>Crepis</em> spp.</td>
</tr>
<tr>
<td>Mountain dandelion</td>
<td><em>Agoseris/Micoseris</em> spp.</td>
</tr>
<tr>
<td>Milk-vetch</td>
<td><em>Astragalus</em> spp.</td>
</tr>
<tr>
<td>Broomrape</td>
<td><em>Orbanche</em> spp.</td>
</tr>
<tr>
<td>Clover</td>
<td><em>Trifolium</em> spp.</td>
</tr>
<tr>
<td>Microsteris</td>
<td><em>Phlox gracilis</em></td>
</tr>
<tr>
<td>Fleabane</td>
<td><em>Erigeron</em> spp.</td>
</tr>
<tr>
<td>Common dandelion</td>
<td><em>Taraxacum officinale</em></td>
</tr>
<tr>
<td>Yellow salsify</td>
<td><em>Tragopogon dubius</em></td>
</tr>
<tr>
<td>Yarrow</td>
<td><em>Achillea millifolium</em></td>
</tr>
<tr>
<td>Aster</td>
<td><em>Aster</em> spp.</td>
</tr>
<tr>
<td>Monkey flower</td>
<td><em>Mimulus</em> spp.</td>
</tr>
<tr>
<td>Ground smoke</td>
<td><em>Gayophytum</em> spp.</td>
</tr>
<tr>
<td>Everlasting</td>
<td><em>Antennaria</em> spp.</td>
</tr>
<tr>
<td><strong>Insects</strong></td>
<td><strong>Order</strong></td>
</tr>
<tr>
<td>Ants</td>
<td>Hymenoptera</td>
</tr>
<tr>
<td>Beetles</td>
<td>Coleoptera</td>
</tr>
<tr>
<td>Butterfly/moth larva</td>
<td>Lepidoptera</td>
</tr>
<tr>
<td>Grasshoppers</td>
<td>Orthoptera</td>
</tr>
</tbody>
</table>
but they were not recommended for my data (G. White, Colorado State University, personal communication). Time of chick death was considered the day a chick was discovered dead (Appendix A). If a daily chick location was not obtained and the exact day of chick death was unknown, I used the midpoint between the last known day the chick was alive and the day it was discovered dead. I right censored chicks alive at 28-days post-hatch and chicks with unknown fate (e.g., radio failure, transmitter loss, and chick adoption) on the last date they were known to be present with the radio-marked hen (Appendix A). I conducted a sensitivity analysis to assure that censorship was random and independent of the fate of radio-marked chicks (Allison 1995). I defined the day of marking as time = 0 for all chicks and included age (days) of chicks at capture in all of my regression models. I treated individually radio-marked chicks as independent sampling units, but accounted for intrabrood correlations in my regression analyses using the COVSANDWICH option in SAS statistical software (SAS Version 8.02, 2001; P. Allison, University of Pennsylvania, personal communication). I used a bootstrap resampling method (Efron and Tibshirani 1993, Flint et al. 1995) with 500 replicates to adjust standard errors for 28-day KM chick survival estimates.

I developed a set of 30 candidate models to identify relationships among direct and indirect measures of habitat resources and chick survival (Table 11), based on observations during my study (Chapters 3 and 4) and knowledge from previous research (Johnson and Boyce 1990, Barnett and Crawford 1994, Drut et al. 1996a,b, Aldridge 2005, Dunbar et al. 2005). Each candidate model represented a biological hypothesis of the influence of food (insects and forbs), cover (forb, grass, and shrub),
Table 11. Description of candidate models used to identify relationships between direct (food and cover at brood locations) and indirect (hen nutrition and maternal variables) measures of habitat resources and survival of greater sage-grouse chicks at 3 sites in Oregon and Nevada, USA, 2000-2003.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Model structure</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Global model: food, cover, nutrition, and maternal effects with food × nutrition and cover × maternal interaction.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(L \times W) + \beta_{13}(F \times B) + \beta_{14}(SG \times B) + \beta_{15}(F \times M) + \beta_{16}(SG \times M)$</td>
</tr>
<tr>
<td>2. Food, cover, nutrition, and maternal effects with food × nutrition and reduced cover × maternal interaction.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(L \times W) + \beta_{13}(F \times B) + \beta_{14}(SG \times B) + \beta_{15}(F \times M) + \beta_{16}(SG \times M)$</td>
</tr>
<tr>
<td>3. Food, cover, nutrition, and maternal effects with reduced food × nutrition and reduced cover × maternal interaction.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(L \times W) + \beta_{13}(F \times B) + \beta_{14}(SG \times B) + \beta_{15}(F \times M) + \beta_{16}(SG \times M)$</td>
</tr>
<tr>
<td>4. Food, cover, nutrition, and maternal effects with food × nutrition interaction.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(L \times W)$</td>
</tr>
<tr>
<td>5. Food, cover, nutrition, and maternal effects with reduced food × nutrition interaction.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P)$</td>
</tr>
<tr>
<td>6. Food, cover, nutrition, and maternal effects with cover × maternal interaction.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(F \times B) + \beta_{12}(L \times W) + \beta_{13}(SG \times B) + \beta_{14}(SG \times M) + \beta_{15}(F \times M) + \beta_{16}(SG \times M)$</td>
</tr>
<tr>
<td>7. Food, cover, nutrition, and maternal effects with reduced cover × maternal interaction.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(F \times B) + \beta_{12}(L \times W) + \beta_{13}(SG \times B) + \beta_{14}(SG \times M) + \beta_{15}(F \times M) + \beta_{16}(SG \times M)$</td>
</tr>
<tr>
<td>8. Food, cover, nutrition, and maternal effects.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M)$</td>
</tr>
<tr>
<td>9. Food, cover, and maternal effects with cover × maternal interaction.</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(D) + \beta_7(B) + \beta_8(M) + \beta_9(F \times B) + \beta_{10}(SG \times B) + \beta_{11}(F \times M) + \beta_{12}(SG \times M)$</td>
</tr>
<tr>
<td>Table 11. (Continued).</td>
<td>10. Food, cover, and maternal effects with reduced cover × maternal interaction.</td>
</tr>
<tr>
<td></td>
<td>11. Food, cover, and maternal effects.</td>
</tr>
<tr>
<td></td>
<td>12. Food, nutrition, and maternal effects with food × nutrition interaction.</td>
</tr>
<tr>
<td></td>
<td>13. Food, nutrition, and maternal effects with reduced food × nutrition interaction.</td>
</tr>
<tr>
<td></td>
<td>14. Food, nutrition, and maternal effects.</td>
</tr>
<tr>
<td></td>
<td>15. Food, nutrition, and cover effects with food × nutrition interaction.</td>
</tr>
<tr>
<td></td>
<td>16. Food, nutrition, and cover effects with reduced food × nutrition interaction.</td>
</tr>
<tr>
<td></td>
<td>17. Food, nutrition, and cover effects.</td>
</tr>
<tr>
<td></td>
<td>18. Nutrition, cover, and maternal effects with cover × maternal interaction.</td>
</tr>
<tr>
<td></td>
<td>19. Nutrition, cover, and maternal effects with reduced cover × maternal interaction.</td>
</tr>
<tr>
<td></td>
<td>20. Nutrition, cover, and maternal effects.</td>
</tr>
<tr>
<td></td>
<td>21. Cover and maternal effects with cover × maternal interaction.</td>
</tr>
<tr>
<td></td>
<td>22. Cover and maternal effects with reduced cover × maternal interaction.</td>
</tr>
</tbody>
</table>
Table 11. (Continued).

| 23. Cover and maternal effects. | \( \beta_0 + \beta_1(A) + \beta_2(F) + \beta_3(SG) + \beta_4(SS) + \beta_5(D) + \beta_6(B) + \beta_7(M) \) |
| 24. Food and nutrition effects with food \( \times \) nutrition interaction. | \( \beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(P) + \beta_4(W) + \beta_5(L \times P) + \beta_6(L \times W) \) |
| 25. Food and nutrition effects with reduced food \( \times \) nutrition interaction. | \( \beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(P) + \beta_4(W) + \beta_5(L \times P) \) |
| 26. Food and nutrition effects. | \( \beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(P) + \beta_4(W) \) |
| 27. Nutrition and maternal effects. | \( \beta_0 + \beta_1(A) + \beta_2(P) + \beta_3(W) + \beta_4(D) + \beta_5(B) + \beta_6(M) \) |
| 28. Nutrition and cover effects. | \( \beta_0 + \beta_1(A) + \beta_2(P) + \beta_3(W) + \beta_4(F) + \beta_5(SG) + \beta_6(SS) \) |
| 29. Food and cover effects. | \( \beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) \) |
| 30. Food and maternal effects. | \( \beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(D) + \beta_4(B) + \beta_5(M) \) |

\( ^a \)Reduced food \( \times \) nutrition interaction included L \( \times \) P and reduced cover \( \times \) maternal interaction included F \( \times \) B and SG \( \times \) B.

\( ^b \)Direct habitat measures used in a priori model set included Lepidoptera abundance (L), total forb cover (F), short grass cover (SG), and short sagebrush cover (SS). Indirect habitat measures included total plasma protein of females (P), chick weight at hatch (W), hatch date (D), initial brood size (B), and daily brood movement (M). All models included chick age at capture (A). See Tables 12 and 13 for complete descriptions of covariates.

hen nutrition (total plasma protein, chick weight), and other maternal variables (hatch date, brood movement, and brood size) on chick survival. Candidate models also included plausible food \( \times \) hen nutrition and cover \( \times \) maternal interactions. Because factors that affect chick survival could potentially differ between age classes of hens (Peterson 1980, Chapter 3), I conducted separate survival analyses for each female age class (adult and yearling) using a common set of candidate models. I used Akaike's Information Criterion adjusted for small sample sizes (AIC\(_c\)) and Akaike weights (\( w_i \))
to choose the best approximating model for my data (Burnham and Anderson 2002). I ranked models based on lowest AICc values and calculated differences between the best-fitted model and all other models. Akaike weights were calculated from ΔAICc values to provide estimates of a model’s probability given other candidate models. I used model averaged parameter estimates (β) and robust standard errors (i.e., adjusted for lack of independence among chicks in the same brood) to calculate hazard ratios (eβ), 95% confidence limits (CL), and standardized parameter estimates (|β|/SE (β)) to evaluate the effect of covariates on the daily hazard of an individual chick’s death (Allison 1995).

Chick survival to 28 days post-hatch varied among years (Appendix A). To determine if interannual variation was associated with covariates in my candidate models, I conducted a post hoc analysis of models that included year as a covariate. Candidate models for this analysis included the best approximating model from my first analysis and additional models that replaced important covariates with year.

Direct habitat variables—

Direct habitat variables included food (insect and forbs) and cover (forb, grass, and sagebrush) measured at brood locations (Table 12). I estimated vertical cover of grass and sagebrush by calculating the proportion of horizontal grass and sagebrush cover that consisted of short grass (<18 cm) and short sagebrush (<20 cm). I developed a reduced set of food and cover covariates in 2 ways. First, I screened variables for multicollinearity by examining a correlation matrix of all my covariates. Second, I used AICc values and Σwi to select food and cover variables potentially important for chick survival with a set of models that included all 4 insect orders and cover.
Table 12. Description of habitat variables measured at brood locations and used in candidate models of greater sage-grouse chick survival to 28-days post-hatch at 3 sites in Oregon and Nevada, USA, 2000-2003.

<table>
<thead>
<tr>
<th>Type</th>
<th>code</th>
<th>Variable</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Food</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td></td>
<td>Coleoptera</td>
<td>Number of beetles collected in pitfall traps.</td>
<td>number</td>
</tr>
<tr>
<td>H</td>
<td></td>
<td>Hymenoptera</td>
<td>Number of ants collected in pitfall traps.</td>
<td>number</td>
</tr>
<tr>
<td>O</td>
<td></td>
<td>Orthoptera</td>
<td>Number of grasshoppers and crickets in pitfall.</td>
<td>number</td>
</tr>
<tr>
<td>L</td>
<td></td>
<td>Lepidoptera</td>
<td>Number of butterfly and moth larva/adults in pitfall traps.</td>
<td>number</td>
</tr>
<tr>
<td>KF</td>
<td></td>
<td>Key forb cover</td>
<td>Visually estimated cover of all key food forbs.</td>
<td>%</td>
</tr>
<tr>
<td><strong>Cover</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td></td>
<td>Total forb cover</td>
<td>Visually estimated cover of all forbs.</td>
<td>%</td>
</tr>
<tr>
<td>TG</td>
<td></td>
<td>Total grass cover</td>
<td>Visually estimated cover of grasses.</td>
<td>%</td>
</tr>
<tr>
<td>SG</td>
<td></td>
<td>Short grass cover</td>
<td>Proportion of total grass cover &lt;18 cm tall.</td>
<td>%</td>
</tr>
<tr>
<td>SB</td>
<td></td>
<td>Sagebrush canopy cover</td>
<td>Canopy cover of sagebrush measured by line-intercept.</td>
<td>%</td>
</tr>
<tr>
<td>SS</td>
<td></td>
<td>Short sagebrush canopy cover</td>
<td>Proportion of total sagebrush cover &lt;20 cm tall.</td>
<td>%</td>
</tr>
</tbody>
</table>

* Juvenile sage-grouse foods were identified from research conducted in Oregon (Pyle 1993, Drut et al. 1994b, M. Gregg, U.S. Fish and Wildlife Service, unpublished data), Idaho (Klebenow and Gray 1968), and Montana (Peterson 1970) and are presented in Table 10.
variables. All habitat covariates were time-dependent (i.e., cumulative means) and I
assumed a linear relationship with chick survival in my analyses. I carried forward
cumulative means for chicks with uneven intervals (i.e., missing locations) to fill data
gaps (Allison 1995).

*Indirect habitat variables*—

Indirect habitat variables included hen nutrition (total plasma protein and chick
weight) and other maternal variables (hatch date, initial brood size, daily brood
movement) measured by monitoring radio-marked female sage-grouse and chicks
(Table 13). Total plasma protein measures available protein for reproduction (Amand
1986) and can be used as an index of hen nutrition (Dunbar et al. 2005, Chapter 4).
Therefore, total plasma protein, coupled with chick weight, was used as an indirect
measure of forb availability during March and April. Daily movement of chicks was
determined by measuring the distance between daily radio-marked brood locations. I
estimated daily movement for chicks with missing locations by averaging the distance
between the location immediately before and after the missing point. Initial brood size
was the number of chicks that left the nest and did not include unhatched eggs or dead
chicks found in nests. Daily movement was time-dependent (i.e., cumulative mean)
and the remaining variables were fixed. I evaluated linear relationships for all
variables, which assumed their effect on survival changed at a constant rate.

**RESULTS**

I monitored 506 radio-marked chicks from 94 broods (333 chicks accompanied by
wit 61 adult females and 173 chicks accompanied by 33 yearling hens) for 6480 chick
exposure days (Table 14). Hatch dates ranged from 10 May to 22 June for all years.
Table 13. Description of hen nutrition and maternal variables (i.e., indirect habitat measures) used in candidate models of greater sage-grouse chick survival to 28-days post-hatch at 3 sites in Oregon and Nevada, USA, 2000-2003.

<table>
<thead>
<tr>
<th>Type</th>
<th>Code</th>
<th>Variable</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hen nutrition</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>Chick weight</td>
<td>Weight of chicks at capture measured to the nearest 0.1 g, adjusted for age.</td>
<td>grams</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>Total plasma protein</td>
<td>Measured from blood samples of females collected at time of capture during late March and early April, adjusted for capture date. Used as an index of dietary protein.</td>
<td>g/dl</td>
<td></td>
</tr>
<tr>
<td>Maternal</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>Hatch date</td>
<td>Date chicks departed nest site; estimated from nest monitoring data and morphological characteristics of chicks.</td>
<td>Julian date</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>Initial brood size</td>
<td>The number of chicks that left the nest. Does not include unhatched eggs or dead chicks in nest.</td>
<td>number</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>Daily brood movement</td>
<td>Cumulative mean of the daily distance moved by hens with radio-marked chicks.</td>
<td>hectometer</td>
<td></td>
</tr>
</tbody>
</table>
Initial brood size averaged $7.1 \pm 0.1$ (SE) and $6.1 \pm 0.4$ chicks for first nests and renests, respectively. Age of chicks at capture averaged 1.5 days and ranged from 1 to 5 days. I used 370 radio-marked chicks from 69 broods (231 chicks accompanied by 41 adult females and 139 chicks accompanied by 28 yearling females) in regression analyses because of missing total plasma protein values ($n = 110$ chicks) and habitat variables ($n = 26$ chicks) for some individuals. Results of sensitivity analysis indicated that chick censoring was random and independent of chick fate (Appendix C).

Analysis for multicollinearity among my variables revealed a relationship between chick weight and chick age ($r = 0.69$, $P < 0.0001$), and total plasma protein and hen capture date ($r = 0.33$, $P < 0.0001$). To correct for chick age and capture date effects, I regressed chick weight against chick age and total plasma protein against capture date and added the residuals to mean chick weights and mean total plasma protein values of

<table>
<thead>
<tr>
<th>Year</th>
<th>Hart Mountain Brood</th>
<th>Chick</th>
<th>Beatys Butte Brood</th>
<th>Chick</th>
<th>Sheldon Brood</th>
<th>Chick</th>
<th>Total Brood</th>
<th>Chick</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>7</td>
<td>22</td>
<td>1</td>
<td>3</td>
<td>8</td>
<td>37</td>
<td>16</td>
<td>62</td>
</tr>
<tr>
<td>2001</td>
<td>10</td>
<td>51</td>
<td>7</td>
<td>37</td>
<td>6</td>
<td>33</td>
<td>23</td>
<td>121</td>
</tr>
<tr>
<td>2002</td>
<td>9</td>
<td>52</td>
<td>12</td>
<td>63</td>
<td>8</td>
<td>50</td>
<td>29</td>
<td>165</td>
</tr>
<tr>
<td>2003</td>
<td>5</td>
<td>28</td>
<td>5</td>
<td>35</td>
<td>16</td>
<td>95</td>
<td>26</td>
<td>158</td>
</tr>
<tr>
<td>Total</td>
<td>31</td>
<td>153</td>
<td>25</td>
<td>138</td>
<td>38</td>
<td>215</td>
<td>94</td>
<td>506</td>
</tr>
</tbody>
</table>
all chicks and hens, respectively. Chick weights adjusted for age averaged 30.4 ± 0.1 g and total plasma protein adjusted for capture date averaged 5.79 ± 0.14 g/dl. I also found a relationship (r = 0.53, P < 0.0001) between key food forb cover and total forb cover. Because forbs may provide cover as well as food for chicks, I used total forb cover and did not give key food forb cover further consideration. I found that Lepidoptera abundance (Σw = 0.99), and short grass cover (Σw = 0.82), total forb cover (Σw = 0.61), and short sagebrush cover (Σw = 0.58) were the best predictors of chick survival and consequently were used to represent food and cover covariates in my survival analyses.

**Factors Affecting Chick Survival**

*Adult females—*

The best approximating model (w = 0.576) for survival of chicks with adult females included effects for food, hen nutrition, cover, maternal variables, and interaction between food and hen nutrition (Table 15). The second best model (w = 0.224, ΔAIC = 1.893) was identical to the best model, but had an additional food × hen nutrition interaction variable (Table 15). My third best model was the same as the best model but also included cover × maternal interactions; the AIC score increased to 3.511 units (w = 0.099). All other models received little support and were >5.0 AIC units from the best model. Predictive power was low for all adult models (r² = 0.254 to 0.256 for competitive models, Table 15).

I found strong evidence that the interaction between total plasma protein of breeding females and Lepidoptera abundance at brood locations (standard β = 2.81, e^β = 0.94, CL: 0.90 to 0.98) was related to chick survival. Chick survival was greatest
Table 15. Ranking and maximum rescaled generalized $r^2$ of hypothesized *a priori* models for habitat resource effects on 28-day survival estimates of 231 greater sage-grouse chicks with adult females at 3 sites in Oregon and Nevada, USA, 2000-2003. Models were ranked with Akaike’s Information Criteria for small sample sizes ($AIC_c$).

<table>
<thead>
<tr>
<th>No.</th>
<th>Model structure</th>
<th>$K^c$</th>
<th>$\Delta AIC_c$</th>
<th>$w^d$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P)$</td>
<td>12</td>
<td>0.000</td>
<td>0.576</td>
<td>0.254</td>
</tr>
<tr>
<td>4</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(D) + \beta_7(P) + \beta_8(W) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(L \times W)$</td>
<td>13</td>
<td>1.893</td>
<td>0.224</td>
<td>0.256</td>
</tr>
<tr>
<td>3</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(F \times B) + \beta_{13}(SG \times B)$</td>
<td>14</td>
<td>3.511</td>
<td>0.099</td>
<td>0.255</td>
</tr>
<tr>
<td>2</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(L \times W) + \beta_{13}(F \times B) + \beta_{14}(SG \times B)$</td>
<td>15</td>
<td>5.430</td>
<td>0.038</td>
<td>0.256</td>
</tr>
<tr>
<td>1</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(L \times W) + \beta_{13}(F \times B) + \beta_{14}(SG \times B) + \beta_{15}(F \times M) + \beta_{16}(SG \times M)$</td>
<td>17</td>
<td>5.790</td>
<td>0.032</td>
<td>0.264</td>
</tr>
<tr>
<td>11</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P)$</td>
<td>9</td>
<td>7.546</td>
<td>0.013</td>
<td>0.213</td>
</tr>
</tbody>
</table>

---

*a* Number corresponds to those in Table 11. The top 6 of 30 candidate models shown.

*b* Covariates included chick age (A), Lepidoptera (L), total plasma protein of females (P), chick weight (W), total forb cover (F), short grass cover (SG), short sagebrush cover (SS), hatch date (D), initial brood size (B), and daily brood movements (M). See Tables 12 and 13 for complete description of covariates.

*c* Number of estimable parameters.

*d* Akaike weights.
when high values for total plasma protein in hens corresponded with high abundance of Lepidoptera at brood sites (Figure 8). There was also strong evidence that chick survival increased with age-adjusted chick weight at capture (standard $\beta = 2.31$, $e^\beta = 0.89$, CL: 0.80 to 0.99, Figure 9). I found strong evidence that chick survival increased with advancing hatch date (standard $\beta = 4.88$, $e^\beta = 0.95$, CL: 0.93 to 0.97) and decreased with brood movement (standard $\beta = 2.43$, $e^\beta = 1.16$, CL: 1.04 to 1.29, Figure 10), but no evidence that chick survival was affected by initial brood size

Figure 8. Estimated survivor function for 231 radio-marked chicks with adult females at 28-days post-hatch for interactive effect between female total plasma protein (TPP) during March-April and Lepidoptera abundance at brood locations on 3 sites in Oregon and Nevada, USA, 2000-2003. Other variables in the model were held at their mean value.
Figure 9. Estimated survivor function for 231 radio-marked greater sage-grouse chicks with adult females at 28-days post-hatch for effects of age-adjusted chick weight at 3 sites in Oregon and Nevada, USA, 2000-2003. Other variables in the model were held at their mean value. Dashed lines are 95% confidence intervals.

(standard $\beta = 0.45$, $e^\beta = 1.07$, CL: 0.76 to 1.39). I found moderate evidence that chick survival increased with short grass cover (standard $\beta = 1.40$, $e^\beta = 0.17$, CL: 2.30 to 2.64), but no evidence that chick survival was affected by total forb cover (standard $\beta =$ 0.58, $e^\beta = 1.03$, CL: 0.93 to 1.12) or short sagebrush cover (standard $\beta = 0.84$, $e^\beta = 1.87$, CL: 0.42 to 3.33).

**Yearling females**–

The best approximating model ($w_i = 0.291$) for survival of chicks with yearling females included cover, maternal factors, and the interaction between cover and maternal factors (Table 16). My second best model ($w_i = 0.190$, $\Delta$AIC$_C = 0.855$) was
Figure 10. Estimated survivor function for 231 radio-marked greater sage-grouse chicks with adult females at 28-days post-hatch for effects of cumulative mean daily movements (A) and hatch date (B) at 3 study areas in Oregon and Nevada, USA, 2000-2003. Dashed lines are 95% confidence intervals.
Table 16. Ranking and maximum rescaled generalized $r^2$ of hypothesized a priori models for resource effects on 28-day survival estimates of 139 greater sage-grouse chicks with yearling females at 3 sites in Oregon and Nevada, USA, 2000-2003. Models were ranked with Akaike’s Information Criteria for small sample sizes ($\text{AIC}_c$).

<table>
<thead>
<tr>
<th>No.</th>
<th>Model structure b</th>
<th>$K^c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$w_i^d$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>20</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(F) + \beta_3(SG) + \beta_4(SS) + \beta_5(D) + \beta_6(B) + \beta_7(M) + \beta_8(F \times B) + \beta_9(SG \times B)$</td>
<td>10</td>
<td>0.000</td>
<td>0.291</td>
<td>0.325</td>
</tr>
<tr>
<td>1</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M)$</td>
<td>17</td>
<td>0.855</td>
<td>0.190</td>
<td>0.375</td>
</tr>
<tr>
<td></td>
<td>$+ \beta_{11}(L \times P) + \beta_{12}(L \times W) + \beta_{13}(F \times B) + \beta_{14}(SG \times B) + \beta_{15}(F \times M) + \beta_{16}(SG \times M)$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(P) + \beta_7(W) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P) + \beta_{12}(F \times B) + \beta_{13}(SG \times B)$</td>
<td>14</td>
<td>1.895</td>
<td>0.113</td>
<td>0.349</td>
</tr>
<tr>
<td>10</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(F) + \beta_4(SG) + \beta_5(SS) + \beta_6(D) + \beta_7(B) + \beta_8(M) + \beta_9(F \times B) + \beta_{10}(SG \times B)$</td>
<td>11</td>
<td>1.922</td>
<td>0.111</td>
<td>0.325</td>
</tr>
<tr>
<td>22</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(F) + \beta_3(SG) + \beta_4(SS) + \beta_5(D) + \beta_6(B) + \beta_7(M) + \beta_8(F \times B) + \beta_9(SG \times B) + \beta_{10}(F \times M) + \beta_{11}(SG \times M)$</td>
<td>12</td>
<td>2.357</td>
<td>0.089</td>
<td>0.335</td>
</tr>
<tr>
<td>29</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(F) + \beta_3(SG) + \beta_4(SS) + \beta_5(D) + \beta_6(W) + \beta_7(D) + \beta_8(B) + \beta_9(M) + \beta_{10}(F \times B) + \beta_{11}(SG \times B)$</td>
<td>12</td>
<td>3.398</td>
<td>0.056</td>
<td>0.335</td>
</tr>
</tbody>
</table>

a Number corresponds to those in Table 11. The top 6 of 30 candidate models shown.
bCovariates included chick age (A), Lepidoptera (L), total plasma protein of females (P), chick weight (W), total forb cover (F), short grass cover (SG), short sagebrush cover (SS), hatch date (D), initial brood size (B), and daily brood movements (M). See Tables 12 and 13 for complete description of covariates.
cNumber of estimable parameters.
dAkaike weights.
the global model and included all food, nutrition, maternal, and cover variables, plus all food × nutrition and cover × maternal interactions (Table 16). My third best model ($w_i = 0.113, \Delta AIC_C = 1.895$) was similar to the second best model, but included fewer interaction terms. The fourth best model ($w_i = 0.111, \Delta AIC_C = 1.923$) was similar to the best model, but included food variables (Table 16). All other models received little support and were >2.0 AIC_C units from my best model. Predictive power was low for all yearling models ($r^2 = 0.325$ to $0.375$ for competitive models), but was greater than predictive power of all adult models (Table 16).

![Figure 11. Estimated survivor function for 139 radio-marked greater sage-grouse chicks with yearling females at 28-days post-hatch for interactive effect between female total plasma protein (TPP) during March-April and Lepidoptera abundance at brood locations on 3 sites in Oregon and Nevada, USA, 2000-2003. Other variables in the model were held at their mean value.](image-url)
Similar to chicks with adult females, my analysis indicated that survival of chicks with yearling females was related to the interaction between total plasma protein of breeding females and Lepidoptera abundance at brood locations (standard $\beta = 2.57$, $e^\beta = 1.12$, CL: 1.03 to 1.21, Figure 11). I found strong evidence that survival of chicks with yearling hens decreased with initial brood size (standard $\beta = 3.70$, $e^\beta = 13.39$, CL: 12.02 to 14.77), but the disparity decreased as total forb cover (standard $\beta = 6.05$, $e^\beta = 0.82$, CL: 0.76 to 0.89) and short grass cover increased (standard $\beta = 1.87$, $e^\beta = 0.22$, CL: -1.38 to 1.82, Figure 12). I also found strong evidence that chick survival decreased as short sagebrush cover increased (standard $\beta = 3.10$, $e^\beta = 9.09$, CL: 7.69 to 10.48). I found no evidence that chick survival was effected by hatch date (standard $\beta = 0.93$, $e^\beta = 0.97$, CL: 0.91 to 1.03) or chick weight at capture (standard $\beta = 0.44$, $e^\beta = 97$, CL: 0.84 to 1.10).

**Temporal Variation in Chick Survival and Proximate Mortality Factors**

At the end of the 28-day monitoring period, 70 chicks were alive and 308 were dead. Chick deaths were attributed to predation (81%, $n = 251$), exposure (11%, $n = 35$), unknown (4%, $n = 14$), and transmitter effects (3%, $n = 8$). For estimates of chick survival, I right censored chicks with transmitter-caused deaths or at time of radio failure ($n = 88$), transmitter loss ($n = 31$), or adoption ($n = 9$). Survival of chicks at 28-days post-hatch was $0.393 \pm 0.024$ and averaged higher for chicks accompanied by adult females ($\hat{S} = 0.405$, $SE = 0.053$, 95% CL: 0.292 to 0.500, $n = 333$) compared to chicks accompanied by yearling females ($\hat{S} = 0.296$, $SE= 0.084$, 95% CL: 0.211 to 0.542, $n = 173$), but was not statistically different because of the large variation in survival within each age class.
Figure 12. Estimated survivor function for 139 radio-marked greater sage-grouse chicks with yearling females at 28 days post-hatch for interactive effect between initial brood size and total forb cover (A) and short grass cover (B) at brood locations on 3 sites in Oregon and Nevada, USA, 2000-2003. Other variables in the model were held at their mean value.
Table 17. Model rankings and maximum rescaled $r^2$ values for post hoc analysis of temporal variation in 28-day survival estimates of 231 greater sage-grouse chicks accompanied by adult females at 3 sites in Oregon and Nevada, USA, 2000-2003. Models were ranked with Akaike's Information Criteria for small sample sizes ($AIC_c$).

<table>
<thead>
<tr>
<th>Model description</th>
<th>Model structure*</th>
<th>K</th>
<th>$\Delta AIC_c$</th>
<th>$w_i^b$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Best model from adult analysis: Food, nutrition, cover, maternal with reduced food $\times$ nutrition interaction</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(P) + \beta_4(W) + \beta_5(F) + \beta_6(SG) + \beta_7(SS) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P)$</td>
<td>12</td>
<td>0.000</td>
<td>0.487</td>
<td>0.254</td>
</tr>
<tr>
<td>Best model with cover variables replaced with year covariate</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(P) + \beta_4(W) + \beta_5(YEAR) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(L \times P)$</td>
<td>10</td>
<td>1.172</td>
<td>0.271</td>
<td>0.252</td>
</tr>
<tr>
<td>Best model with food $\times$ nutrition interaction replaced with year covariate</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(L) + \beta_3(P) + \beta_4(W) + \beta_5(F) + \beta_6(SG) + \beta_7(SS) + \beta_8(D) + \beta_9(B) + \beta_{10}(M) + \beta_{11}(YEAR)$</td>
<td>12</td>
<td>1.625</td>
<td>0.216</td>
<td>0.265</td>
</tr>
<tr>
<td>Best model with food $\times$ nutrition interaction replaced with year covariate</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(YEAR) + \beta_3(W) + \beta_4(F) + \beta_5(SG) + \beta_7(SS) + \beta_8(D) + \beta_9(B) + \beta_{10}(M)$</td>
<td>10</td>
<td>5.951</td>
<td>0.025</td>
<td>0.242</td>
</tr>
<tr>
<td>YEAR only</td>
<td>$\beta_0 + \beta_1(A) + \beta_2(YEAR)$</td>
<td>3</td>
<td>22.381</td>
<td>0.000</td>
<td>0.142</td>
</tr>
</tbody>
</table>

*Covariates included chick age (A), Lepidoptera (L), total plasma protein of females (P), chick weight (W), total forb cover (F), short grass cover (SG), short sagebrush cover (SS), hatch date (D), initial brood size (B), and daily brood movements (M). See Tables 12 and 13 for complete description of covariates.

*b Akaike weights.
Results of my post hoc analysis revealed that interannual variation in total plasma protein of females in March-April and Lepidoptera abundance at brood locations accounted for some of the interannual variation in survival estimates for chicks accompanied by adult females (Table 17). Replacement of Lepidoptera, total plasma protein, and Lepidoptera × total plasma protein covariates with year did not improve model fit (Table 17), and total plasma protein and Lepidoptera abundance corresponded with estimated chick survival among years (Table 18). Small sample sizes precluded similar comparisons for chicks accompanied by yearling females.

Table 18. Total plasma protein (g/dl) of females, abundance of Lepidoptera at brood locations, and 28-day survival estimates of radio-marked greater sage-grouse chicks with adult females at 3 sites in Oregon and Nevada, USA, 2000-2003.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total plasma protein</th>
<th>Lepidoptera abundance</th>
<th>Chick survival</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x</td>
<td>SE</td>
<td>n</td>
</tr>
<tr>
<td>2000</td>
<td>5.8</td>
<td>0.9</td>
<td>5</td>
</tr>
<tr>
<td>2001</td>
<td>5.2</td>
<td>0.2</td>
<td>20</td>
</tr>
<tr>
<td>2002</td>
<td>6.5</td>
<td>0.2</td>
<td>15</td>
</tr>
<tr>
<td>2003</td>
<td>6.4</td>
<td>0.2</td>
<td>22</td>
</tr>
</tbody>
</table>

DISCUSSION

Chick survival during my study was related to both total plasma protein levels of breeding females and Lepidoptera abundance at brood locations, which suggests that food resources available to hens before nest initiation and chicks shortly after hatching influenced chick survival. Because I did not measure maternal and chick nutrition
directly, I do not know the extent that each contributed to chick survival. I surmise
that both were important because direct linkages between hen nutrition and
reproduction (Beckerton and Middleton 1982) and consumption of insects and chick
survival (Johnson and Boyce 1990, Park et al. 2001) have been previously identified in
captive grouse. Although previous researchers have suggested that total plasma
protein (Dunbar et al. 2005) and insect availability (Drut et al. 1994a, b) were related
to sage-grouse chick survival, no other research on free-ranging sage-grouse
populations demonstrated direct linkages between these parameters and chick survival.

I found that chick survival increased as hatch weight of chicks increased, which
provided additional evidence that quantity and quality of spring forage were important
for chick survival. Captive female grouse on high protein diets produced larger, more
viable chicks than females on low protein diets (Beckerton and Middleton 1982,
Hanssen et al. 1982). Presumably, larger chicks at hatch had larger protein reserves,
which enhanced survival (Beckerton and Middleton 1982). In addition, larger chicks
are more homothermic (Visser and Ricklefs 1995) and may be less susceptible to
hypothermia (Koskimies 1962 from Potts 1986), more efficient at foraging (Anderson
and Alisauskas 2001), and better able to evade predators (Potts 1986). Research has
documented female sage-grouse that consumed more forbs before incubation had a
greater protein intake (Barnett and Crawford 1994, Chapter 3). Hence, I suggest that
availability of forbs during March and April could influence survival and recruitment
of chicks because greater protein intake by hens may produce larger chicks with
higher survival. Hatch weight also has been linked to survival in wild red grouse
(Lagopus lagopus, Hudson et al. 1994) and ring-necked pheasants (Phasianus
colchicus) chicks (Riley et al. 1998).

Predation was the predominant cause of chick deaths and the primary proximate reason for interannual variation in chick survival during my study. High predation rates were also reported by other researchers who monitored individually marked sage-grouse chicks (Aldridge 2005, N. Burkepile, Yakima Nation, personal communication) and chicks of other Galliforms (Riley et al. 1998, Hubbard et al. 1999, Larson et al. 2001). Although predation was the proximate mortality factor, my post hoc analysis suggests that chick survival may have been ultimately related to interannual variation in habitat resources, particularly Lepidoptera abundance. However, the predictive power of my models was low because we did not measure all factors that potentially affect chick survival. For example, predator abundance was not measured during my study and artificially high predator densities, introduction of exotic predators, or changes in abundance of alternate prey could affect chick survival irrespective of habitat quality (Schroeder and Baydack 2001). Nevertheless, my results suggest that habitat management that improves the quality of brood-rearing habitats may reduce predation and increase survival of sage-grouse chicks.

Food availability may have indirectly influenced predation by altering daily movements and home range size of broods. Forbs not only provide food for chicks, but may be host plants for Lepidoptera larvae consumed by sage-grouse chicks (Miller and Hammond 2003). I found an inverse relationship between brood movement and chick survival; broods with the greatest cumulative mean daily movements tended to have less total forb cover at brood locations ($r = -0.24, P = 0.0001$). Greater movement of chicks in search of food could have increased exposure of chicks to
predators and resulted in reduced survival because of increased predation (Potts 1986). Drut et al. (1996b) reported that home range size of sage-grouse broods in Oregon was inversely related to availability of food and suggested broods with larger home ranges had lower survival. Similarly, survival of ring-necked pheasant and partridge (Perdix perdix and Alectoris rufa) chicks in Europe was linked to daily brood movement, which was related to insect availability (Green 1984, Hill 1985, Rands 1986).

My results revealed that chick survival decreased as tall grass cover increased. A similar relationship was reported for radio-marked sage-grouse chicks in Alberta, Canada (Aldridge 2005) and Idaho (N. A. Burkepile, personal communication). Aldridge (2005) suggested that tall grass may inhibit the ability of hens to detect and evade predators. I classified grass $\geq 18$ cm as tall, but Aldridge (2005) reported that grass height did not become a factor in chick survival until it reached 35-40 cm.

The factors that affected chick survival during my study were apparently related to age of female. Initial brood size and short sagebrush cover were inversely related to survival of chicks with yearling females, but were unrelated to survival of chicks with adult females. In contrast, chick survival increased with hatch date and chick weight for adult females, but was unrelated to survival of chicks with yearling females. Differences in the factors related to chick survival between adult and yearling females may have been caused by disparities in breeding ability (Moss et al. 1981, Forslund and Pärt 1995, Mauck et al. 2004). For example, brood size may have been related to survival of chicks accompanied by yearling females because they were less experienced (Weibe and Martin 1998). Hatch date was likely related to survival of chicks with adult females because they initiate nests earlier in the spring compared to
yearling females, likely to provide the opportunity to renest if the first nest is unsuccessful (Chapter 4). Survival was lower for chicks hatched from early compared to late season nests during my study (M. A. Gregg, unpublished data), possibly because greater variation in temperature and precipitation early in the season affected availability of insects and forbs.

Although we did not find statistically significant differences in survival of chicks with adult vs. yearling females, adult female sage-grouse reportedly had greater success for many other reproductive parameters (i.e., nest initiation, nest success, renesting rates, clutch size, and brood success) compared to yearling females (Wallestad and Pyrah 1974, Peterson 1980, Connelly et al. 1993, Aldridge and Brigham 2001, Chapter 4). Age-dependent reproduction has been documented in grouse (Martin 1995, Wiebe and Martin 1998), but has not been explicitly evaluated in sage-grouse. However, knowledge of age-dependent reproduction has relevance for conservation and management of sage-grouse populations and warrants further investigation (Martin 1985).

MANAGEMENT IMPLICATIONS

Habitat management that increases abundance of forbs during March and April and Lepidoptera larva during May and June should result in increased survival of sage-grouse chicks. Forbs consumed by female sage-grouse and recommended for habitat restoration projects to increase nutrient intake before nest initiation include hawksbeard, mountain dandelion, sagebrush buttercup (*Ranunculus glaberrimus*), long-leaf phlox (*P. longifolia*), big-head clover (*Trifolium macrocephalum*), obscure milk-vetch (*A. obscurus*), and desert-parsley (Barnett and Crawford 1994, Chapter 3).
All of these forbs (except long-leaf phlox and sagebrush buttercup) in addition to yarrow (*Achillea millifolium*), microsteris (*P. gracilis*), common dandelion (*Taraxacum officinale*), and yellow salsify (*Tragopogon dubius*) were preferred food forbs of sage-grouse chicks (Klebenow and Gray 1968, Peterson 1970, Pyle 1992, Drut et al. 1994b) and may be associated with Lepidoptera (Miller and Hammond 2003) and other insects (Johnson et al. 2004) consumed by chicks. Therefore, I recommend that land management practices focus on the maintenance and restoration of this small group of critical forbs to provide adequate nutrition for hens and chicks, in association with shrubs and grasses to provide chicks with necessary cover for protection from predation and exposure.

ACKNOWLEDGMENTS

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LITERATURE CITED


CANFIELD, R. H. 1941. Application of the line interception method in sampling of


DAVIS, D. M. 2002. Breeding season habitat use and response to management activities by greater sage-grouse on Sheldon National Wildlife Refuge,
Nevada. Thesis, Oregon State University, Corvallis, USA.


MORRISON, M. L. 2001. A proposed research emphasis to overcome the limits of


THE "GENERATION GAP" BETWEEN RECENT SAGE-GROUSE RESEARCH AND INTEGRATION OF NEW KNOWLEDGE FOR MANAGEMENT OF SAGE-GROUSE HABITAT

Michael A. Gregg and John A. Crawford
CHAPTER 6: THE "GENERATION GAP" BETWEEN RECENT SAGE-GROUSE RESEARCH AND INTEGRATION OF NEW KNOWLEDGE FOR MANAGEMENT OF SAGE-GROUSE HABITAT

INTRODUCTION

Greater sage-grouse (Centrocercus urophasianus) were recently evaluated for protection under the Endangered Species Act because populations declined significantly range-wide during the past 50 years (Crawford and Lutz 1985, Connelly and Braun 1997, Connelly et al. 2004). Sage-grouse population declines were attributed to loss and fragmentation of sagebrush (Artemisia spp.) habitats (Dalke et al. 1963, Braun 1998) and habitat deterioration that caused reduced sage-grouse productivity (Connelly and Braun 1997). Although sage-grouse were not listed as threatened or endangered (U.S. Fish and Wildlife Service 2005), the heightened interest in sage-grouse resulted in a greater emphasis on understanding habitat needs and management of sagebrush habitats. Sage-grouse conservation plans have been initiated or completed in all 11 states with extant sage-grouse populations (Connelly et al. 2004).

Because of the close relationship between sage-grouse and sagebrush, protection of sagebrush habitats has been the primary focus for management of sage-grouse populations (Patterson 1952, Braun et al. 1977, Autenrieth et al. 1982). Management recommendations in the first sage-grouse management guidelines (Braun et al. 1977) focused entirely on protection of sagebrush habitats. Previous authors have identified herbaceous vegetation as an important component of sage-grouse habitat (Klebenow and Gray 1968, Peterson 1970, Pyrah 1971, Autenrieth 1981). However, only recently
was the critical nature of the herbaceous understory for successful reproduction documented (Barnett and Crawford 1994; Drut et al. 1994a, 1994b; DeLong et al. 1995; Gregg et al. 1994; Coggins 1998; Sveum et al. 1998a, 1998b; Aldridge and Brigham 2002). Improvement of sage-grouse reproductive success by restoration of understory vegetation may well be the key to recovery of many populations (Dobkin 1995, Connelly and Braun 1997). Although state (Hemker 1997, Stinson et al. 2004) and federal (Bureau of Land Management 2000) sage-grouse conservation plans identified restoration of herbaceous vegetation as a conservation measure, the focus on sagebrush for management of sage-grouse habitat has changed little since publication of the original management guidelines (Braun et al. 1977). We suggest there is a "generation gap" between recent sage-grouse research and the application of new knowledge in management of sage-grouse habitat. The purpose of this paper is to present a hierarchical view of sage-grouse habitat relationships, identify causes for the "generation gap", and propose solutions to integrate current knowledge of sage-grouse habitat requirements into effective management strategies.

ARE SAGE-GROUSE SAGEBRUSH OBLIGATES?

Sage-grouse are classified as sagebrush obligates because of their dependence on sagebrush habitats for survival and reproduction; the link between sage-grouse and sagebrush has been well documented (Braun et al. 1976, Roberson 1986). Sagebrush provides the primary source of food and cover for sage-grouse during winter (Patterson 1952, Wallemstad et al. 1975, Roberson 1986) and may be the only vegetative component necessary to describe winter habitat at multiple scales (Beck 1977, Hupp and Braun 1989, Homer et al. 1993). Nests typically are located under

THE ROLE OF HERBACEOUS VEGETATION

There are three distinct phases during reproduction when forbs and grasses are essential components of sage-grouse habitat: pre-laying, nesting, and brood-rearing. The pre-laying period encompasses approximately the five-week period that immediately precedes incubation (Barnett and Crawford 1994). Dietary protein is important during this period for egg production and chick survival (Beckerton and Middleton 1982, Carey 1996) because grouse generally do not have high endogenous protein reserves to use for reproduction (Carey 1996). In Oregon and Nevada, forbs were an important food for female sage-grouse during spring because they contributed more crude protein to the diet than sagebrush (Barnett and Crawford 1994, M. A. Gregg, unpublished data 2004). Consumption of high protein foods during the pre-laying period prepares the hen physiologically for reproduction (Barnett and Crawford 1994). Sage-grouse nest initiation (Barnett and Crawford 1994) and renesting (M. A. Gregg, unpublished data 2004) rates may be enhanced when hens consume more forbs before incubation.
Herbaceous vegetation in sagebrush stands, particularly tall (>18 cm) residual native bunchgrass, provides a critical component of sage-grouse nesting habitat (Gregg et al. 1994, DeLong et al. 1995, Sveum et al. 1998b). Tall herbaceous vegetation surrounding sage-grouse nests increased the likelihood of nest success (Gregg et al. 1994, Sveum et al. 1998b). Sage-grouse nests located in areas with inadequate tall herbaceous cover were predisposed to high rates of nest predation by ravens (Corvus corax), coyotes (Canis latrans), and other mammals (Gregg 1991, Gregg et al. 1994, DeLong 1993, Sveum et al. 1998b). Tall, dense herbaceous cover may provide scent, visual, and physical barriers between nesting hens and predators (DeLong 1993, Gregg et al. 1994). Although tall herbaceous cover typically is composed of native bunchgrass, other types of herbaceous vegetation (e.g., forbs) can provide the necessary cover to conceal sage-grouse nests (Sveum et al. 1998b, Aldridge and Brigham 2002). Exotic grass species such as cheatgrass (Bromus tectorum) and medusahead (Taeniatherum asperum) do not provide adequate cover for nesting hens.

Insects and forbs are critical dietary components of juvenile sage-grouse and influence growth and survival (Johnson and Boyce 1990; Drut 1994a, 1994b). Insects are consumed almost exclusively during the first few days after hatching; forbs become a common dietary component thereafter (Klebenow and Gray 1968, M A. Gregg unpublished data 2004). Chicks deprived insects exhibit reduced growth rates and low survival (Johnson and Boyce 1990). In Oregon, sage-grouse productivity was enhanced when forbs and insects were the primary dietary components (Drut et al. 1994b). In areas where forb availability was low, chicks transitioned to a sagebrush
diet at a younger age (6 weeks) and exhibited reduced survival (Drut et al. 1994b). Lower survivability was attributed to reduced nutrient intake (Drut 1992). Low forb availability could have indirectly reduced survival by increasing home range size for hens with broods, which increased exposure of chicks to predation, accident, and other mortality factors (Drut 1992).

HIERARCHICAL VIEW OF SAGE-GROUSE HABITAT

Sage-grouse habitat relationships are far more complex than the obligatory sage-grouse/sagebrush relationship implies because grouse select habitat factors at different scales. The habitat selection process presented by Johnson (1980) provides the framework to understand the hierarchical nature of sage-grouse habitat selection. Johnson (1980) presented four levels of selection that identified multiple spatial scales of habitat selection. First order selection represented selection of the geographical range of a species. Second order selection identified home ranges of individuals or groups within the geographical range. Third order selection described use of habitat types within home ranges. Finally, fourth order selection delineated the important habitat components within each habitat type. The complexity of sage-grouse habitat relationships increases as the scale of selection decreases (i.e., first order to fourth order selection). For example, the geographical distribution (first order selection) of sage-grouse is inherently related to the distribution of sagebrush (Johnsgard, 1983). The presence of sagebrush is the primary habitat factor that determines the occurrence of sage-grouse at the geographic or landscape scale. Landscapes that are not predominately covered with sagebrush will not provide all habitat components needed to support a self-sustaining population of sage-grouse. At the other extreme, use of a
habitat within a home range (third order selection) may depend on habitat components other than sagebrush, particularly during the reproductive phases. Hens with broods typically use areas where forbs are abundant (Klebenow 1969, Drut et al. 1994a, Apa 1998, Sveum et al. 1998a) and alter habitat use in response to changes in forb availability (Klebenow 1969, Peterson 1970, Wallestad 1971, Dunn and Braun 1986, Drut 1992, Drut et al. 1994a). Availability of forbs differs depending on cover type, moisture, and elevation. When dessication reduces forb availability in sagebrush uplands, hens with broods move to areas with greater forb abundance, including bottoms and grassland cover types (Peterson 1970, Wallestad 1971), and meadows and lakebeds (Drut 1992) which typically have little or no sagebrush cover. Hence, sage-grouse may at times select areas without sagebrush cover.

At the fourth order level (habitat components within habitat types), sage-grouse are dependent on understory vegetation and the associated insects for successful reproduction. At this level of selection, herbaceous plants fulfill a key role throughout the reproductive period and ultimately determine sage-grouse reproductive success. Sage-grouse could be viewed as “forb” or “insect” obligates at this scale (both temporal and spatial) of habitat use because consumption of forbs and insects by chicks is required for survival. Thus, the answer to the question “are sage-grouse sagebrush obligates?” ultimately depends on the scale or level of habitat use and the life-history trait under consideration.

THE “GENERATION GAP”

Management procedures for sage-grouse habitat have not changed substantially since publication of the 1977 guidelines (Braun et al. 1977) despite increased
knowledge of sage-grouse habitat relationships from recent research. Conservation measures have been identified for most key sage-grouse habitat components, but management activities have typically focused on mapping and protection of sagebrush stands, not restoration of understory vegetation. We suggest that the herbaceous component of sage-grouse habitat is not integrated into sage-grouse management activities because of differences in the spatial scale at which sage-grouse habitat research has been conducted and conservation measures applied.

Sage-grouse are a landscape species because they require large (thousands of hectares), continuous patches of sagebrush habitat for reproduction and survival. Some sage-grouse populations are migratory and move considerable distances among nesting, brood-rearing, and wintering areas (Connelly et al. 2000). Movements greater than 78 miles (125 km) between seasonal-use areas and annual home ranges of 1,727 square miles (2,764 km²) have been reported (Leonard et al. 2000). Movements within seasonal ranges can also be substantial. Movements greater than 25 miles (40 km) for hens with chicks less than three weeks old have been documented (M. A. Gregg, unpublished data 2004). Therefore, management of sage-grouse habitat must occur at the landscape scale (first or second order), but research that identified key habitat components required for reproduction (i.e., herbaceous vegetation) has largely been conducted at a much smaller spatial scale (third and fourth order levels). Methods are available to quantify distribution of sagebrush at large scales (Wisdom et al. 2000, Comer et al. 2002), but not to evaluate composition of understory vegetation (Knick et al. 1997, Wisdom et al. 2000). The importance of herbaceous vegetation as a component of sage-grouse habitat has been recognized (Connelly et al. 2000, 2004;
Crawford et al. 2004; Hockett 2002, Wambolt et al. 2002), but this knowledge has not been used to quantify and qualify sage-grouse habitat at the scale necessary for effective restoration and management of sage-grouse habitat.

Because of limitations for large-scale evaluations of herbaceous understory, the focus has remained on the extent and density of sagebrush as the primary habitat factor that controls sage-grouse populations. Sagebrush has been the single habitat component used to quantify sage-grouse habitat at the landscape scale (Patterson 1952, Johnsgard 1983, Beck et al. 2003, Schroeder et al. 2004). These landscape habitat maps based on presence of sagebrush are useful for identifying potential sage-grouse habitat and estimating historic and present distribution of sage-grouse, but they would perform poorly as predictors of sage-grouse population persistence, densities, or trends. Estimating the extent of sage-grouse habitat over large geographic areas based solely on the presence of sagebrush is deceptive and provides a false sense of security because composition of understory vegetation is largely unknown (Knick et al. 2003). Assessment of sage-grouse habitat must include all critical habitat components (e.g., sagebrush overstory and herbaceous understory). Sage-grouse populations cannot persist in large, homogenous stands of a single cover type because of their reliance on the herbaceous understory during reproduction and their seasonal use of areas dominated by different types of sagebrush and other vegetation (Crawford et al. 2004). Sage-grouse habitats quantified solely on the presence of sagebrush would likely overestimate potential habitat and include areas devoid of sage-grouse.

Before European settlement, management of sage-grouse habitat based on presence of sagebrush would likely have been sufficient. A diverse herbaceous understory,
composed of native forbs and grasses, is thought to have been characteristic of most undisturbed sagebrush communities (Miller and Eddleman 2000). However, there has been a notable reduction in herbaceous vegetation throughout a large portion of sagebrush-dominated communities since European settlement (Young 1979, Miller and Eddleman 2000, Miller et al. 1994). The reduction of herbaceous understory plants has been attributed to changes in species composition of woody plants, displacement by exotic annuals, and alteration of soil characteristics because of historically unregulated livestock grazing, altered fire regimes, and introduction of non-native plants (Young 1979, Miller et al. 1994, Gruell 1996, Miller and Eddleman 2000). Current conditions in sagebrush stands range from areas containing adequate native herbaceous plants, areas dominated by exotic annuals, or areas with a near complete lack of understory vegetation. Those areas with altered or depleted understories support few or no sage-grouse.

BRIDGING THE "GENERATION GAP"

For effective management and restoration of sage-grouse habitat, we believe that it is imperative to bridge this "generation gap" between our current state of knowledge of sage-grouse habitat relationships and management of sage-grouse habitat. However, there are no simple solutions that will integrate all key habitat components into a successful management strategy for sage-grouse habitat. There have been recent attempts to incorporate understory composition, in addition to distribution of sagebrush, into landscape models of sage-grouse habitat in the interior Columbia Basin (Hemstrom et al. 2002; Wisdom et al. 2002a, 2002b) and regional assessments of sage-grouse habitat in the sagebrush ecosystem (Wisdom et al. 2003). These
landscape models used differences between historic and current levels of livestock grazing, and the departure of disturbance regimes and composition, structure, and patterns of vegetation from historic conditions as an index of herbaceous understory composition (Hemstrom et al. 2002, Wisdom et al. 2002b). They provided insight on the restoration potential of a sagebrush habitat (Hemstrom et al. 2002) and effects of habitat restoration on sage-grouse populations (Wisdom et al. 2002a), and performed well at differentiating areas where grouse were present or extirpated (Wisdom et al. 2002b). Procedures for regional assessments of sage-grouse habitat provided methods to estimate and map habitats that may be at-risk of degradation from invasion of exotic annual grasses and encroachment of juniper (Wisdom et al. 2003). Delineation of at-risk habitats enhances our ability to manage sage-grouse habitats at landscape scales by identifying potential areas in need of restoration.

These recent landscape models and habitat assessment procedures provide an appropriate starting point for management and restoration of sage-grouse habitat and are a step in the right direction for bridging the “generation gap”. However, the applicability of these models is limited because they do not adequately quantify composition of understory vegetation (Wisdom et al. 2003). Potential habitat is based on dominant overstory plants and does not reflect composition of understory vegetation and, therefore, does not enhance our ability to predict persistence, densities, or trends of sage-grouse populations. An accurate estimate of extant sagebrush communities that are in optimum or tolerable condition for sage-grouse is currently unavailable (Crawford et al. 2004). Technological advances have increased our ability to quantify landscape patterns and change (Wisdom et al. 2003, Crawford et al. 2004),
but the inability to quantify composition of understory vegetation at large scales limits our ability to manage and restore sagebrush habitat and affect sage-grouse populations. Current methods employed to quantify understory vegetation in sage-grouse habitat are not practical for use at large scales. A new technique to estimate cover in sagebrush communities using ultra-light aircraft has been developed (Seefeldt and Booth 2005) and may have potential to quantify understory vegetation at much larger scales than current methods. Continued development of techniques to quantify sage-grouse habitat at the landscape scale will be essential to fully evaluate habitat condition, determine status of sage-grouse populations, and prioritize areas in need of restoration.

We suggest three additional areas of research to integrate current knowledge of sage-grouse habitat relationships with management of sage-grouse habitat. First, we must identify the appropriate spatial scales for management of sage-grouse habitat. The need to manage sage-grouse at the landscape scale has been recognized (Connelly et al. 2000, Wisdom et al. 2003, Crawford et al. 2004), but sage-grouse management units are often arbitrarily identified based on agency, political, or geographic boundaries. The appropriate spatial scale for habitat management to affect sage-grouse populations is unknown. Management of landscapes between 250,000 and 2.5 million hectares has been recommended because improvement of only a portion of year-around habitat may be offset by degradation of habitat used at other times (Crawford et al. 2004). However, these landscape recommendations were not supported by any quantified information on structure of sage-grouse populations. Although migratory and non-migratory sage-grouse populations have been identified
(Connelly et al. 2000), we know very little about the spatial structure of sage-grouse populations. Sage-grouse populations could exist as one continuous population, a metapopulation, a set of isolated populations, or some combination (Wisdom et al. 2002b). Understanding what constitutes a population of sage-grouse would help determine the spatial scale at which habitat management must occur to affect populations. The appropriate scale may differ from population to population across the range of the species. An understanding of the spatial structure of sage-grouse populations is a fundamental question that must be addressed to successfully manage habitat or evaluate management actions and is a critical step for "bridging the gap" between sage-grouse research and management of sage-grouse habitat.

Secondly, research is needed to identify landscape characteristics that influence sage-grouse habitat use, productivity, and survival. Sage-grouse research conducted at fine scales was instrumental for understanding sage-grouse habitat relationships and identification of key habitat components. However, these studies were not designed to identify optimum cover values for key habitat components at the landscape scale. Cover and juxtaposition of sagebrush and herbaceous vegetation are highly variable across the landscape (Miller and Eddleman 2000). For example, landscape patterns of sagebrush can range from large, homogenous communities to heterogenous stands that are mosaics of sagebrush patches interspersed with areas of no sagebrush cover. Because selection for habitat components by sage-grouse likely occurs at the fourth order level (Drut et al. 1994a, Gregg et al. 1994, Sveum et al. 1998a, Aldridge and Brigham 2002), vegetative characteristics measured at fine scales (e.g., nest sites, brood sites) could be similar irrespective of the variation in cover and juxtaposition of
sagebrush and other habitat components at the landscape scale. However, the
variation in landscape patterns of sagebrush communities could be important for sage-grouse habitat use, reproduction, and survival, but these relationships have not been investigated. Fuhlendorf et al. (2002) found that response of lesser prairie chickens (*Tympanuchus pallidicinctus*) to landscape characteristics was scale-dependent, which supported the importance of multi-scale analyses of habitat use. Understanding the influence of the variation in cover and juxtaposition of habitat components at the landscape scale on sage-grouse populations would link our understanding of fine-scale habitat relationships with landscape management of sage-grouse habitat.

Finally, we need to identify direct relationships between pervasive land management practices and key sage-grouse habitat components identified from fine-scale research. The principal land-use practice in sagebrush habitats that influence herbaceous understory vegetation includes livestock grazing (cattle and feral horses), prescribed fire, and restoration activities following wildfire (Rowland and Wisdom 2002). Identification of direct relationships between these practices and key sage-grouse habitat components would facilitate large-scale management of sage-grouse habitat. For example, livestock grazing is a widespread land use that affects fine-scale sage-grouse habitat components virtually throughout the range of the species (Braun 1998). Livestock grazing is also the principal land use practice that land managers can control by manipulating timing and intensity of use. Hence, understanding the effect of livestock grazing on key sage-grouse habitat components could help bridge the gap between current knowledge of sage-grouse habitat relationships and management of sage-grouse habitat. There is indirect evidence that domestic livestock grazing
influences (both positively and negatively) sage-grouse habitat, but direct effects of livestock on sage-grouse habitat and reproduction are largely unknown (Connelly and Braun 1997, Beck and Mitchell 2000, Hockett 2002, Crawford et al. 2004). Research on effects of grazing, including timing and intensity of use, on critical sage-grouse habitat components and reproduction could potentially lead to management actions that could be applied to sage-grouse habitat at the landscape scale. However, we caution that adjustments of current grazing practices alone may not result in range-wide increases in sage-grouse populations. Sagebrush habitats dominated by woody plants, exotic grasses, or with significant soil loss will remain in poor condition for long periods because many have crossed thresholds and are in irreversible steady states (Laycock 1991) without active restoration.

CONCLUSIONS

Sagebrush is a critical component of sage-grouse habitat. Removal of sagebrush has been found to negatively impact sage-grouse populations as areas devoid of sagebrush do not support sage-grouse (Patterson 1952, Braun et al. 1977, Call and Maser 1985). Loss and fragmentation of sagebrush habitats have been implicated in the reduced distribution and abundance of sage-grouse populations range-wide (Dalke et al. 1963, Braun 1998). However, sage-grouse habitat relationships are complex, and sagebrush is only one of several critical habitat components necessary for reproduction and survival (Connelly et al. 2000, Crawford et al. 2004). A deficiency in any one habitat variable could lead to impaired productivity or reduced survival and depressed sage-grouse populations. Management of sage-grouse habitat must include all critical habitat components, and management will be most effective at the
landscape scale.

The characterization of the sage-grouse/sagebrush relationship as “obligate” has perpetuated an overly simplistic view of sage-grouse habitat relationships. Management of sage-grouse habitat is considerably more complicated than previously recognized. First-order habitat models based on overstory vegetation should be used only for identification of potential sage-grouse habitat and estimating potential distribution of sage-grouse. Landscape models that incorporate all habitat components will be required before land managers can prioritize areas for restoration, predict population persistence, densities, and trends, and fully implement habitat conservation measures that benefit sage-grouse populations. Development, validation, and applicability of these models will be greatly enhanced with a better understanding of sage-grouse population structure; landscape characteristics that influence sage-grouse habitat use, productivity, and survival; and the effects of land use practices on key sage-grouse habitat components. A multi-disciplinary approach that includes wildlife biologists and range and landscape ecologists will be required to solve these complex problems before effective management strategies can be implemented to benefit sage-grouse habitat and ultimately enhance sage-grouse populations.

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LITERATURE CITED


BUREAU OF LAND MANAGEMENT. 2000. Greater sage-grouse and sagebrush-steppe
ecosystems management guidelines. Oregon: Bureau of Land Management, Portland, USA.


HEMKER, T. P. 1997. Idaho sage grouse management plan. Idaho Department of Fish and Game, Boise, USA.
HEMSTROM, M. A., M. J. WISDOM, W. J. HANN, M. A. ROWLAND, B. C. WALES, and
R. A. GRAVENMIER. 2002. Sagebrush-steppe vegetation dynamics and
restoration potential in the interior Columbia Basin. Conservation Biology
16:1243-1255.


HOMER, C. G., T. C. EDWARDS, JR., R. D. RAMSEY, and K. P. PRICE. 1993. Use of
remote sensing methods in modeling sage grouse winter habitat. Journal of
Wildlife Management 51:78-84.


JOHNSGARD, P. A. 1983. Grouse of the world. Lincoln: University of Nebraska Press,
USA.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for

JOHNSON, G. D., and M. S. BOYCE. 1990. Feeding trials with insects in the diet of sage


KNICK, S. T., D. S. DOBKin, J. T. ROTENBURRY, M. A. SCHROEDER, W. M. VANDER
HAEGEN, and C. VAN RIPER III. 2003. Teetering on the edge or too late?
Conservation and research issues for avifauna of sagebrush habitats. Condor
105:611-634.

of Landstat thematic mapper imagery in a semi-arid rangeland by
nonparametric discriminant analysis. Photogrammetric Engineering and

LAYCOCK, W. A. 1991. Stable states and thresholds of range condition on North
American rangelands - A viewpoint. Journal of Range Management 44:427-
433.


recovery plan for greater sage-grouse. Washington Department of Fish and Wildlife, Olympia, USA.


CHAPTER 7: SUMMARY

BACKGROUND

The decline in distribution and abundance of sage-grouse has been attributed to reduced productivity because of loss, fragmentation, and degradation of habitat (Connelly and Braun 1997, Crawford et al. 2004, Connelly et al. 2004). In Oregon, decline in sage-grouse abundance was recognized in the early-1980's (Crawford and Lutz 1985) and research was initiated on sage-grouse habitat relationships during the reproductive period in 1987 by the Game Bird Research Program at Oregon State University and was continued through 2000 (Gregg 1991, Barnett 1992, Drut 1992, Pyle 1992, DeLong 1993, Coggins 1998, Byrne 2002, Davis 2002). Results of this long-term research identified individual linkages between habitat resources and sage-grouse reproductive success (Barnett and Crawford 1994, DeLong et al. 1995, Drut et al. 1994a, b, Gregg et al. 1994). Maternal nutrition and quality of brood-rearing habitat (food and cover) were both suggested to be important for chick survival, but habitat factors that directly affected survival of chicks remained poorly understood. This information is critical for development and implementation of habitat management strategies that can increase sage-grouse productivity (Crawford et al. 2004). Therefore, the purpose of my dissertation research was to advance our understanding of sage-grouse habitat relationships by investigating direct linkages between habitat resources and chick survival and, ultimately, to identify key habitat factors that through management, can be manipulated to increase survival and recruitment of sage-grouse chicks.
SUMMARY OF RESULTS

My results revealed two principal habitat factors related to chick survival: availability of forbs during March and April and insects abundance (i.e., Lepidoptera) during May and June. I identified a relationship between availability and consumption of high nutrient (i.e., protein, calcium, and phosphorus) forbs by breeding females during March and April (Chapter 3). Forb consumption (i.e., nutrient intake) by breeding females increased with forb availability, which likely enhanced maternal nutrition. I also found relationships between maternal nutrition (i.e., total plasma protein), and renesting (Chapter 4) and survival of chicks to 28-days post-hatch (Chapter 5). Hence, my results not only revealed that availability of forbs during March and April was likely related to chick survival, but increased the likelihood of renesting and the potential for chick recruitment. I found that availability of insects (i.e., Lepidoptera) at brood locations was related to chick survival, which revealed that chick nutrition was also an important factor for survival of sage-grouse chicks (Chapter 5). Interestingly, I found an interactive effect between maternal and chick nutrition (Chapter 5). Breeding females with the highest total plasma protein levels coupled with high Lepidoptera availability at brood locations resulted in the greatest chick survival. Because I did not measure nutrition directly, I was unable to determine the extent that spring forb and insect availability affected chick survival. However, the totality of my results suggested food resources available to hens before nest initiation and chicks shortly after hatch were key habitat factors related to chick survival.

I found evidence of age-related differences in foraging proficiency for breeding
females (Chapter 3). My results suggested that adult females consumed more forbs, less low sagebrush, and had a greater crude protein intake compared with yearling females. My results also revealed that factors influencing chick survival were apparently related to age of female (Chapter 5). I found that initial brood size and short sagebrush cover were inversely related to survival of chicks with yearling females, but were unrelated to survival of chicks with adult females. In contrast, chick survival increased with hatch date and chick weight for adult females, but was unrelated to survival of chicks with yearling females. The implications of these differences between adult and yearling females were unknown; I did not detect differences in survival rates between chicks accompanied with adult compared to those accompanied by yearling females. However, variation in diet composition and factors related to chick survival between adult and yearling females could be caused by disparities in breeding ability (Moss et al. 1981, Forslund and Pärt 1995, Mauck et al. 2004). Adult female sage-grouse reportedly had greater success for many reproductive parameters including nest initiation, nest success, renesting rates, clutch size, and brood success compared to yearling females (Wallestad and Pyrah 1974, Peterson 1980, Connelly et al. 1993, Aldridge and Brigham 2001, Chapter 4).

CONCLUSIONS

I believe a greater emphasis should be placed on sage-grouse nutrition and its role in sage-grouse reproductive success. Results of my research underscore the importance of nutrition for chick survival and have important implications for management of sage-grouse habitats. Habitat management should focus on forb availability during March and April and insect abundance during late spring to
increase nutritional status of hens and chicks, in association with adequate cover of sagebrush and grasses. In addition, knowledge of age-dependent reproduction has relevance for conservation and management of sage-grouse populations (Martin 1985). Age-related differences in foraging proficiency (Wunderle 1991) and breeding ability (Forslund and Pärt 1995, Weibe and Martin 1998, Mauck et al. 2004), but has not been explicitly evaluated for sage-grouse and warrants further investigation.

Sage-grouse reproductive ecology is complex and, as my results have demonstrated, sagebrush is only one of several critical habitat components necessary for reproduction and survival. Management of sage-grouse habitats must include all critical habitat components and in Chapter 6, I discussed key issues, particularly the role of scale, that has affected our ability to effectively manage sage-grouse populations. Sage-grouse are a landscape species and require large continuous patches of sagebrush habitat for reproduction and survival. Home ranges as large as 2,764 km² have been reported (Leonard et al. 2000). Hence, sage-grouse habitat management will be most effective at the landscape scale. The key to restoration of depressed sage-grouse populations is the application and integration of my findings, and findings of other researchers, into effective management strategies at a scale that will affect sage-grouse populations.

LITERATURE CITED


WIEBE, K. L., and K. MARTIN. 1998. Age-specific patterns of reproduction in white-
tailed and willow ptarmigan *Lagopus leucurus* and *L. lagopus*. Ibis 140:14-24.

CHAPTER 8: BIBLIOGRAPHY


BARNETT, J. K., and J. A. CRAWFORD. 1994. Pre-lying nutrition of sage grouse hens


HEMKER, T. P. 1997. Idaho sage grouse management plan. Idaho Department of Fish and Game, Boise, USA.

HEMSTROM, M. A., M. J. WISDOM, W. J. HANN, M. A. ROWLAND, B. C. WALES, and


JOHNSON, G. D., and M. S. BOYCE. 1990. Feeding trials with insects in the diet of sage


protein and energy on reproductive performance on turkey hens. Poultry Science 58:419-426.


NAYLOR, B. J., and J. F. BENDELL. 1989. Clutch size and egg size of spruce grouse in relation to spring diet, food supply, and endogenous reserves. Canadian


of sage grouse during winter. Condor 90:15-19.


APPENDICES
USE OF IMPLANTED RADIOTRANSMITTERS TO ESTIMATE SURVIVAL
OF GREATER SAGE-GROUSE CHICKS

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APPENDIX A: USE OF IMPLANTED RADIOTRANSMITTERS TO ESTIMATE SURVIVAL OF GREATER SAGE-GROUSE CHICKS

ABSTRACT

Reduced chick survival has been implicated in declines of greater sage-grouse (Centrocercus urophasianus) populations. Because monitoring survival of unmarked sage-grouse chicks is difficult, radiotelemetry may be an effective technique to estimate survival rates, identify causes of mortality, and collect ecological data. Subcutaneous implants have been used to attach radiotransmitters to hatchlings of several species of birds with precocial young. Previous researchers that used subcutaneous implants in free-ranging populations removed chicks from the capture location and implanted transmitters at an alternate site. Because logistics precluded removing newly hatched greater sage-grouse chicks from the field, we evaluated a method for implanting transmitters at capture locations. We captured 288 chicks from 52 broods and monitored 286 radio-marked chicks daily to 28-days post-hatch during May and June 2001-2002. Two (<1%) chicks died during surgery and were not radio-marked. Inflammation or infection from implants was not revealed from necropsies of 22 radio-marked chicks and was not implicated in death of any chicks. Most (98%, 207/212) radio-marked chick mortality occurred ≤21-days post-hatch and predation (82%, 174/212) was the primary cause of death. Fate of 16 (6%, 16/275) chicks was unknown because their transmitters potentially were lost. Overall, chick survival at 28-days post-hatch was 0.220 (SE = 0.028). We found that mortalities related to the implant procedure and transmitter loss were similar to rates reported by previous researchers who implanted transmitters in chicks at an alternate location.
Subcutaneous implants may be a useful method for attaching transmitters to newly hatched sage-grouse chicks.

INTRODUCTION

Limited information is available concerning survival and mortality factors of greater sage-grouse (*Centrocercus urophasianus*) chicks. Because poor chick survival may be related to sage-grouse population declines (Crawford and Lutz 1985, Connelly and Braun 1997), information on factors that influence survival is critical for management. This information has been difficult to obtain because most sage-grouse chick mortality typically occurs within 6 weeks after hatching (Drut 1992), when monitoring survival of unmarked chicks is difficult. Previous researchers identified habitat characteristics that may be important for sage-grouse chick survival by monitoring radio-marked hens with broods (Wallstad 1971, Drut et al. 1994, Sveum et al. 1998), but were unable to provide direct linkages between habitat parameters and chick survival rates. Research that establishes these linkages will be necessary before specific management guidelines for sage-grouse brood-rearing habitat can be developed.

The development of miniaturized radiotransmitters affords the use of telemetry to estimate survival rates, identify causes of mortality, and collect ecological data for hatchlings of precocial species. Attachment techniques for miniature transmitters include backpacks (Speake et al. 1985), prong and suture (Mauser and Jarvis 1991, Davis et al. 1999), glue (Bowman et al. 2002, Spears et al. 2002), suture (Larson et al. 2001, Burkepile et al. 2002), and subcutaneous implants (Ewing et al. 1994, Korschgen et al. 1996b). The subcutaneous implant technique was one of the first
methods developed to mark hatchlings of precocial birds (Korschgen et al. 1996b) and was originally designed for use in waterfowl (Krementz and Pendleton 1991, Korschgen et al. 1996a). More recently, subcutaneous implants have been used to radio-mark hatchlings of gallinaceous species including ring-necked pheasants (Phasianus colchicus, Riley et al. 1998), wild turkeys (Meleagris gallopavo, Hubbard et al. 1999), and ruffed grouse (Bonasa umbellus, Larson et al. 2001).

Burkepile et al. (2002) evaluated a suture method to externally attach transmitters to greater sage-grouse chicks, but no other method of radio attachment for sage-grouse hatchlings has been examined. We evaluated subcutaneous implants for attaching transmitters to newly hatched sage-grouse chicks. Previous researchers who used subcutaneous implants in free-ranging populations of gallinaceous species relocated chicks to alternate sites (e.g., vehicle, research facility) to implant transmitters and returned radio-marked chicks to the brood after surgery (Riley et al. 1998, Hubbard et al. 1999, Larson et al. 2001). Because logistics precluded removal of sage-grouse chicks from the field to implant transmitters, our objectives were to develop field methods for implanting transmitters and document effects of the procedure on survival. We also identified cause of death and estimated survival of radio-marked chicks to 28-days post-hatch.

STUDY AREA

We conducted our study at 3 areas during 2001 and 2002 in the northern Great Basin of southeastern Oregon and northwestern Nevada, USA. The Beatys Butte Allotment (BBA), located in Oregon, was administered by the Bureau of Land Management and encompassed 220,301 ha. Hart Mountain National Antelope
Refuge, located in Oregon, and Sheldon National Wildlife Refuge, located in Nevada, were administered by the U. S. Fish and Wildlife Service and encompassed 114,375 and 232,294 ha, respectively. Our study areas were characteristic of shrub-steppe habitats and consisted of flat sagebrush (Artemisia spp.) plains interrupted by mountains, table lands, ridges, and draws. Elevation ranged from 1,200 to 2,450 m. Annual mean precipitation and minimum and maximum temperatures ranged from 29 to 33 cm and -1.5°C and 14.3°C, respectively (Western Regional Climate Center 2005).

Primary plant communities used by sage-grouse broods included low sagebrush (A. arbuscula), Wyoming big sagebrush (A. tridentata wyomingensis), mountain big sagebrush (A. t. vaseyana), and Antelope bitter-brush (Purshia tridentata). Mammalian and avian predators of chicks (Schroeder and Baydack 2001) common to the study areas included coyotes (Canus latrans), bobcats (Felis rufus), weasels (Mustela spp.), red-tailed hawks (Buteo jamaicensis), rough-legged hawks (B. lagopus), northern harriers (Circus cyaneus), golden eagles (Aquila chrysaetos), and common ravens (Corvus corax). Less common but possible important predators of sage-grouse chicks included Swainson’s hawks (B. swainsoni) and ferruginous hawks (B. regalis). Potential reptilian predators of chicks included western rattlesnakes (Crotalus viridis) and gopher snakes (Pituophis catenifer).

METHODS

We captured and fitted female sage-grouse with 20-g necklace mounted radiotransmitters (Advanced Telemetry Systems, Isanti, Minn., USA) during March and April 2001-2002 (Gregg et al. 2006). We used protocols described by Gregg et al.
(2006) to locate nest sites and monitor nesting hens. We estimated the nest initiation date for each hen from telemetry data and predicted the hatch date based on an incubation period of 26 days (Schroeder 1997). We monitored nesting hens daily near predicted hatch dates and when monitoring indicated that incubation had ceased, we inspected nest sites to determine nest fate and classified nests as successful if ≥1 egg hatched.

We flushed radio-marked hens with broods and captured as many chicks by hand that could be visually located. Capture was postponed during periods of precipitation or freezing temperatures to reduce potential for hypothermia, but chicks were typically captured 24 to 36 hours after hatching. Chicks were captured at all times of day during 2001, but to reduce capture time and minimize brood disturbance we attempted most captures just after sunrise during 2002. Chicks were weighed to the nearest 0.1 g and transmitters were subcutaneously implanted anterior of the scapulars. We used 2 different-sized implantable transmitters (model BD2-A, Holohil Systems Ltd., Carp, Ont., Canada) with a normal battery life of 28 days (range 21-35). The large transmitter was 17 mm × 8 mm × 5 mm and weighed 1.1 g. The small transmitter was 14 mm × 6 mm × 4 mm and the weight was reduced to 0.85 g by decreasing battery size and the transmitter’s plastic coating. All transmitters had 23-cm stranded steel wire antennas with black nylon coating.

We conducted surgeries at capture locations (Figure 13). We moistened the implant area and disinfected surgical tools and transmitters with chlorhexidine
Figure 13. Transmitters were implanted in greater sage-grouse chicks at capture locations while one individual held the chick and a second person trained in the method implanted the transmitter (left) and a 1-day-old greater sage-grouse chick after completion of the implant procedure (right).

diacetate (Nolvasan solution, Wyeth, Madison, N.J, USA) before the procedure, but we did not anesthetize chicks (American Ornithologists’ Union 1988). The skin was lifted with forceps below the nape of the neck and a 5-mm incision perpendicular with the vertebrae was made with 11.4 cm surgical scissors. We inserted the scissors into the incision and slowly opened them to create a pocket approximately 25-mm deep.
The transmitter antenna was threaded through a 22-gauge hypodermic needle (Monoject, The Kendall co., Mainsfield, Mass., USA) with the hub removed. We lifted the skin above the pocket with forceps and inserted the needle into the incision until it exited at the posterior end of the pocket. We removed the needle and antenna through the posterior hole and placed the transmitter under the skin posterior to the incision by lifting the skin at the incision and gently pulling on the antenna. We closed the incision parallel to the midline with a single suture of polyglycolic absorbable material (4-0 Dexon II, United States Surgical, Norwalk, Conn., USA) and
one drop of surgical glue (Nexaband S/C, Closure Medical Corp, Raleigh, N.C., USA). This procedure was approved by the Oregon State University Laboratory Animal Resource Center (Animal Care and Use Protocol Number 2656). We released chicks from a brood together after all transmitters were implanted.

We monitored radio-marked chicks daily for 28-days following capture to estimate survival and determine causes of mortality. Radio-marked chicks found within a 30-m radius around the female were assumed alive. Females and broods were not intentionally flushed to avoid disturbance. We used ground and aerial telemetry to locate radio-marked chicks separated from brood hens. We recovered chick remains and transmitters and classified chick deaths into predation, exposure, and unknown based on necropsy results and evidence found at recovery sites. Dead intact chicks were necropsied by a local veterinarian or staff at the Washington Animal Disease Diagnostic Laboratory, Washington State University, Pullman. We identified predation as cause of death when transmitters were found with bite marks or in scat, or when recovered chick remains indicated predation. We also assigned predation as cause of death when radio-marked chicks disappeared with no evidence of radio failure and we assumed that a predator destroyed the chick and transmitter. We classified deaths as exposure when intact dead chicks were found in the vicinity of capture sites <1 day after marking, after brood hens were depredated, or in conjunction with freezing temperatures and precipitation. We classified cause of death as unknown when intact chicks were recovered, other mortality factors were excluded, and necropsy results did not provide a definitive diagnosis.

We estimated survival probabilities of radio-marked chicks with the Kaplan-Meier
product limit estimator (Kaplan and Meier 1958). The day of marking was defined as
time = 0 for all chicks, regardless of capture date. We used log-rank tests to identify
differences in survival functions between chicks with small and large transmitters
(Allison 1995, Larson et al. 2001). We right censored radio-marked chicks with
unknown fate on the last date known alive. We radio-marked multiple chicks from a
single brood and may have violated the assumption of independent observations for
the Kaplan-Meier survival probabilities. Our estimates of survival were unbiased but,
standard errors may have been underestimated (Pollock et al. 1989, Flint et al. 1995).
Therefore, we used a bootstrap resampling method (Efron and Tibshirani 1993, Flint
et al. 1995) with 500 replicates to estimate standard errors from the Kaplan-Meier
procedure for each survival estimate. We used SAS statistical software (PROC
LIFETEST, SAS Institute 2001, version 8.2) for all survival analyses. We applied an
alpha of 0.05 for all tests.

RESULTS

We captured 288 chicks from 52 broods between 18 May-12 June, 2001 and 10
May-16 June, 2002 (Table 19). The number of captured chicks/brood ranged from 1
to 9. Mean weight of chicks was 29.5 g (SE = 0.2) and transmitters averaged 3.6%
(SE = 0.03) of chick body weights. Two (<1%) chicks died during surgery and were
not radio-marked. We implanted large transmitters in 228 chicks. We only used small
transmitters during 2002 and implanted them in 58 chicks. Mean age of chicks with
large (1.3 ± 0.1 days) and small (1.4 ± 0.1 days) implanted transmitters was similar.
The surgical procedure was typically completed in 3–5 minutes per chick. The time
required to complete the entire procedure (capture and marking) was reduced
Table 19. Number of greater sage-grouse broods captured and chicks radio-marked at 3 study areas in Oregon and Nevada, USA, 2001-2002. All chicks were equipped with implanted radiotransmitters.

<table>
<thead>
<tr>
<th>Year</th>
<th>Hart Mountain</th>
<th>Beatys Butte</th>
<th>Sheldon</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Broods</td>
<td>Chicks</td>
<td>Broods</td>
</tr>
<tr>
<td>2001</td>
<td>10</td>
<td>51</td>
<td>7</td>
</tr>
<tr>
<td>2002</td>
<td>9</td>
<td>53</td>
<td>12</td>
</tr>
<tr>
<td>Total</td>
<td>19</td>
<td>104</td>
<td>19</td>
</tr>
</tbody>
</table>

approximately 50% (≤90 minutes and ≤45 minutes per brood during 2001 and 2002, respectively) by restricting the capture period to early morning. No hens abandoned broods as a result of our activities and they often remained nearby while we handled chicks. Six radio-marked chicks from 5 broods were adopted by unmarked hens 5 to 22 days post-hatch.

Nearly all chick deaths (98%, 207/212) occurred ≤21 days post-hatch. Predation was the primary cause of death during both years and accounted for 82% (174/212) of all mortality. Chick predation was attributed to mammalian (n = 88), avian (n = 20), and reptilian (n = 4) predators. Predator identification was not possible for 36% (62/174) of depredated chicks because of insufficient evidence. Exposure was the second leading cause of mortality for radio-marked chicks and accounted for 12% (25/212) of chick deaths. Death of 11 chicks was associated with cold wet weather shortly after capture, 1 chick was found dead 6 days after capture with the transmitter antenna tangled in a shrub, 1 chick drowned, and 1 chick died after its brood hen was depredated. The remaining 11 chicks died <1 day after capture and were found dead.
at or near capture sites. Cause of death was unknown for 6% (13/212) of our radio-marked chicks, which were recovered 2- to 15-days post-hatch. Necropsy results from one of these chicks revealed that the dorsal thoracic cavity may have been inadvertently entered during surgery and may have resulted in pulmonary hemorrhage that could have caused death. However, necropsy results were not definitive and this chick survived to 15-days post-hatch and had excellent muscling, full crop, and ventricular and intestinal contents at time of death. Necropsies of an additional 21 chicks failed to provide a definitive diagnosis, but no inflammation or infection from implants was detected.

Overall, survival at 28 days post-hatch for 2001-2002 was 0.220 (SE = 0.028). At the end of the monitoring period, 26 chicks were alive and 212 were dead. We censored 48 chicks because we were unable to determine fate. Brood mixing resulted in loss of radio contact of 3 chicks and monitoring data indicated that 29 transmitters failed and 16 large transmitters potentially fell off. Radio failure was identified by changes in signal characteristics or irregular performance immediately preceding disappearance of chicks. Potentially lost transmitters were found undamaged in the vicinity of radio-marked broods and no additional evidence was present to confirm death. Dried skin was attached to most of these transmitters, which also indicated that they could have sloughed off surviving chicks. If these 16 chicks were treated as dead, the 28-day survival rate was reduced to 0.171 (SE = 0.024). We found no evidence that small transmitters were lost. Survival did not differ between study areas for small or large transmitters during 2002 (log-rank test, \( \chi^2_1 \leq 3.538, P \geq 0.170 \)). Therefore, we pooled data from all areas to test for effects of transmitter size on
survival. We found no difference in survival between chicks with large and small transmitters at 28-days post-hatch regardless if chicks with sloughed transmitters were censored or treated as dead (log-rank test, $\chi^2 \leq 0.154, P \geq 0.694$; Figure 14). Most radio failure (90%, 26/29) and transmitter loss (87%, 14/16) occurred ≥12 days after capture.

Figure 14. Comparison of survival rates to 28-days post-hatch for greater sage-grouse chicks with small (0.85 g, $n = 58$) and large (1.1 g, $n = 107$) subcutaneously implanted transmitters, Oregon and Nevada, USA, 2002. Survival for chicks with small transmitters was 0.205 (SE = 0.055) and large transmitters was 0.220 (SE = 0.043). Standard errors were corrected for lack of independence among chicks.

DISCUSSION

Although death of chicks directly related to implant surgeries was low during our study (<1%), other researchers who used the technique and implanted transmitters at
an alternate location reported no mortality during the surgical procedure (Korschgen et al. 1996b, Hubbard et al. 1999, Larson et al. 2001). Death of 1 chick was likely related to the experience of the individual conducting the surgery and the other chick apparently died because of stress associated with capture and surgery. We found that implanting transmitters in the field did not result in inflammation or infection of the implant site and apparently was not a contributing factor to chick mortality during our study. Ewing et al. (1994) reported no signs of infection in captive ring-necked pheasant chicks with implanted transmitters. Similarly, Korschgen et al. (1996b) reported that subcutaneous implants in canvasback (Aythya valisineria) ducklings caused only minor inflammation that did not contribute to any duckling deaths.

Subcutaneous implanted transmitters may have indirectly influenced chick survival to some extent. We recovered 11 (4%) dead chicks <1 day after marking in the vicinity of capture locations that apparently died from exposure. Similarly, Hubbard et al. (1999) reported that 9 (8%) wild turkey pouls with implanted transmitters failed to leave the point of release and died from exposure. Bowman et al. (2002) indicated that subcutaneously implanted transmitters in captive turkey pouls had a short-term (2 to 4 hours) negative effect on mobility. Impaired mobility could have increased the risk of exposure and other mortality factors because newly marked chicks lost contact with their brood hen. We noted that a few radio-marked sage-grouse chicks were unstable and had difficulty walking immediately after release, but they typically were mobile within a few minutes. Mauser and Jarvis (1991) reported that lack of mobility was related to transmitter size for captive ducklings with externally attached radios. Of the 11 chicks that I recovered at capture sites, 10 had large transmitters. However,
we also documented several cases of entire and partial brood loss within 24 hours after hatching for unmarked broods during both years of our study and we observed similar proportions of marked and unmarked chicks during flush counts at 28-days post-hatch (M. Gregg, U. S. Fish and Wildlife Service, unpublished data). Hence, the indirect effect of implants on chick survival during our study was difficult to ascertain, but appeared to be low.

Our survival estimate for sage-grouse chicks with implanted transmitters ($\hat{S} = 0.220$) was low compared to survival reported for sage-grouse chicks with external transmitters ($\hat{S} = 0.432$) in Alberta, Canada (Aldridge 2005). Survival differences between studies could have been related to radio attachment technique, but a direct comparison of survival between implanted and external radioed sage-grouse chicks is not available. Larson et al. (2001) reported that survival for ruffed grouse chicks was lower for chicks with implanted transmitters compared to chicks with radios sutured to the back. They indicated that differences in survival were most likely related to loss of implanted transmitters, but greater mortality of chicks with implants was not ruled out. Results from Larson et al. (2001) were not directly comparable with our study because they monitored marked chicks from near hatching to fall dispersal and compared survival between the 2 techniques at approximately 85 days post-marking. Survival rates apparently were similar for chicks with implanted and sutured transmitters 28-days after chicks were marked (Larson 1998, Larson et al. 2001). In addition, Kenow et al. (2003) suggested that the response of chicks to comparable transmitters and attachment techniques may be species-specific.

We found no difference in survival probabilities between small and large
transmitters, which was consistent with results reported by Burkepile et al. (2002) for radio-marked sage-grouse chicks in Idaho. However, our results suggested that transmitter size was related to retention rates. During our study, fate of 16 chicks marked with large transmitters was not known because radios were recovered without evidence of death. Large transmitters tended to fit tightly under the skin and we speculated that necrosis of the tissue on top of the radio resulted in scabs that were lost with transmitters, which was supported by radios recovered undamaged with dead skin attached. Extrusion of implanted transmitters caused by necrosis of the skin above the implant has been reported for captive turkey pouls (Bowman et al. 2002) and ring-necked pheasant chicks (Ewing et al. 1994), but the necrosis apparently did not influence survival. Small transmitters were loose under the skin, which likely reduced necrosis of skin over the radio. In addition, small transmitters were easier to implant and required less time to implant than large transmitters. Kenow et al. (2003) also reported greater retention rates for small (0.76g) compared to large (1.5g) implanted transmitters in common loon (Gavia immer) chicks. Overall, loss of implanted transmitters during our study was comparable to loss of transmitters implanted in captive ring-necked pheasant chicks (Ewing et al. 1994) and transmitters sutured on free-ranging sage-grouse chicks (Burkpile et al. 2002).

Larson et al. (2001) reported a preference for the suture method for attaching transmitters to ruffed grouse chicks because external suturing required less time, equipment, and expertise compared to the implant technique. In addition, wetting of chicks was not required and there was less chance for trauma (Larson et al. 2001). The suture method has been used to attach transmitters to sage-grouse chicks in
Alberta (Aldridge 2005), Colorado (T. Thompson, University of Idaho, personal communication), and Idaho (Burkpile et al. 2002) apparently with good success. Sutured transmitters on sage-grouse chicks were less intrusive, easily attached, and easily replaced (Burkpile et al. 2002, T. Thompson, University of Idaho, personal communication), but the use of subcutaneous implants does not preclude radio replacement for long-term monitoring of chicks (Korschgen et al. 1996a, Kenow et al. 2003). Bowman et al. (2002) recommended glued transmitters over implants for estimating short-term survival (<29 days) of wild turkey poults. Glued transmitters were preferred because the simple application procedure required little training and poults with glued transmitters did not exhibit any impaired mobility that could potentially compromise survival (Bowman et al. 2002). However, glued transmitters have not been evaluated for sage-grouse chicks. Krementz and Pendleton (1991) reported that implanted transmitters provided more accurate information on duckling mortality factors than external transmitters. Because we only used implanted transmitters during our study, we were unable to make this comparison for sage-grouse.

**MANAGEMENT IMPLICATIONS**

Subcutaneous implanted transmitters may be a useful method for estimating survival of sage-grouse chicks. However, the surgical procedure necessary to implant transmitters requires training from individuals that are proficient with the method. Before the technique is used, we recommend practicing on dead chicks or domestic chicken chicks to become skilled with the surgical procedures. We found that once the method was mastered, transmitters could be easily implanted in <5 minutes. We
recommend that the smallest available transmitter that meets study objectives be used with the implant technique. Our results suggested that smaller transmitters would increase retention rates and reduce chick handling time. Small transmitters were easier to implant, less intrusive, and may reduce any potential bias in survival estimates. However, implanted transmitters may not provide advantages compared with externally attached radios to warrant the greater training and expertise required to properly apply the technique. A direct comparison between implanted and external methods would be useful to determine the most appropriate technique to radio-mark sage-grouse chicks.

We also recommend additional research that compares survival of marked and unmarked sage-grouse chicks in free-ranging populations to identify potential bias in survival estimates from telemetry techniques. Previous researchers have reported reduced or similar survival rates for marked compared to unmarked chicks of other bird species with precocial young using implanted (Korschgen et al. 1996b, Hubbard 1997, Kenow et al. 2003) and external radios (Mauser and Jarvis 1991, Pietz et al. 2003). However, no research has been conducted that compares survival of marked and unmarked free-ranging sage-grouse chicks, and the effects of transmitters on survival are unknown.

ACKNOWLEDGMENTS

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LITERATURE CITED


APPENDIX B: EFFECT OF SUBCUTANEOUS IMPLANTED TRANSMITTERS ON SURVIVAL OF GREATER SAGE-GROUSE CHICKS

ABSTRACT

The use of radio telemetry to monitor survival of greater sage-grouse (Centrocercus urophasianus) chicks has increased in recent years, yet little information is available on the potential bias of survival estimates from radio-marked chicks. Violation of the assumption of no transmitter effect could lead to erroneous results and misdirected management. I evaluated effects of subcutaneously implanted transmitters on survival of sage-grouse chicks. I located and flushed radio-marked hens with broods, captured a portion of the brood, and implanted transmitters in the chicks at 3 study areas during 2001-2002. Of a possible 149 chicks from 21 broods, I surgically implanted transmitters in 108 and left 41 chicks unmarked. I monitored broods daily for 28 days after capture to determine fate of radio-marked chicks. At the end of the monitoring period, I flushed broods with bird dogs and counted all chicks. Unmarked chicks of the brood that were not counted were assumed dead. I used logistic regression and Akaike’s Information Criterion to examine relationships between chick survival and implants, individuals conducting surgery, study areas, and years. Results indicated that survival varied considerably among study areas and years, but the proportion of implanted (21%) and unmarked (23%) chicks alive at 28-days post-hatch did not differ. I found no evidence that implanted transmitters or individuals conducting surgery reduced the likelihood of sage-grouse chicks surviving to 28-days post-hatch and concluded that survival estimates of radio-marked chicks were not substantially biased.
INTRODUCTION

Since the development of miniature radiotransmitters, radio telemetry has become an increasingly common technique used to estimate survival rates and identify factors related to survival of precocial hatchlings (Korschgen et al. 1996, Riley et al. 1998, Larson et al. 2001, Pietz et al. 2003, Aldridge 2005) including greater sage-grouse (Burkepile et al. 2002, Aldridge 2005, Gregg et al. 2006a). Researchers who have used telemetry to monitor chick survival assumed that capture and transmitters effects did not significantly bias survival estimates. Violation of this assumption could lead to erroneous results and misdirected management. Nevertheless, capture and transmitter effects on survival of precocial chicks have not been fully evaluated.

The subcutaneous implant technique is one of several methods (Mauser and Jarvis 1991, Bowman et al. 2002, Burkepile et al. 2002) used to attach transmitters to precocial chicks and has been used in waterfowl (Krementz and Pendleton 1991, Korschgen et al. 1996) and Galliformes (Riley et al. 1998, Hubbard et al. 1999), and was recently adapted for use in Greater sage-grouse (Gregg et al. 2006a). Research has been conducted to evaluate the effect of implanted transmitters on survival of captive Galliformes (Ewing et al. 1994, Hubbard et al. 1998, Bowman et al. 2002) and waterfowl (Mauser and Jarvis 1991, Bakken et al. 1996, Zenitsky 1993), but rarely has the assumption been addressed in free-ranging populations (Hubbard 1997, Kenow et al. 2003). Hence, relatively little information is available on the potential bias of survival estimates from hatchlings with implanted transmitters in wild populations. In addition, Kenow et al. (2003) suggested that the response of chicks to comparable transmitter and attachment techniques may differ among species and recommended
species-specific assessments; no research specific to sage-grouse has been conducted. Therefore, my objective was to evaluate the effect of subcutaneously implanted transmitters on survival of newly-hatched chicks in free-ranging sage-grouse populations in the northern Great Basin.

STUDY AREA

I conducted my study on 3 areas: Sheldon National Wildlife Refuge (NWR) located in northwestern Nevada, and Hart Mountain National Antelope Refuge (NAR) and the Beatys Butte Allotment in southeastern Oregon. Sheldon NWR and Hart Mountain NAR were administered by the U. S. Fish and Wildlife Service and encompassed 232,294 and 87,253 ha, respectively. The Beatys Butte Allotment was administered by the Bureau of Land Management and consisted of 220,301 ha. These areas were characteristic of shrub-steppe and consisted of flat sagebrush (*Artemisia* spp.) plains interrupted by rolling hills, ridges, and draws. Elevations ranged from 1200 to 2450 meters. Annual mean precipitation and minimum and maximum temperatures ranged from 29 to 33 cm and -1.5°C and 14.3°C, respectively (Western Regional Climate Center 2005). Primary shrub species included Wyoming big sagebrush (*A. tridentata wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), low sagebrush (*A. arbuscula*), and antelope bitter-brush (*Purshia tridentata*). Stands of western juniper (*Juniper occidentalis*), curl-leaf mountain-mahogany (*Cercocarpus ledifolius*), and aspen (*Populus tremuloides*) were found on all areas but were more prevalent on Sheldon NWR and Hart Mountain NAR. Grasses consisted largely of bluegrass (*Poa* spp.), bluebunch wheatgrass (*Pseudoroegneria spicata*), needlegrass (*Stipa* spp.), fescue (*Festuca* spp.), giant wildrye (*Leymus cinereus*), and bottlebrush...

**METHODS**

I captured female sage-grouse with spotlights and nets (Giesen et al. 1982) during March-April 2001-2002 and fitted them with 20-g necklace-mounted radio transmitters (Advanced Telemetry Systems, Isanti, MN). I monitored radio-marked hens beginning in mid-April to locate successful nests (Gregg et al. 2006a, 2006b) and determined initial brood size by counting hatched eggs and detached shell membranes. I located and flushed radio-marked hens with broods and captured by hand all chicks that could be visually located, but I only captured a portion of the brood. Chicks were captured ≤24 hours after leaving the nest; hens were not brooding chicks at time of capture. Therefore, I assumed that the initial brood size at hatch was equal to brood size at capture, chicks not captured were alive, and the probability of capture was equal for all chicks within a brood. I radio-marked chicks throughout the hatching period (mid-May through mid-June) during both years.

I implanted transmitters (model BD2-A, Holohil Systems Ltd., Carp, Ontario, Canada) subcutaneously anterior of the scapulars (Gregg et al. 2006a) and released all radio-marked chicks from a brood together after transmitters were implanted. I monitored broods daily for 28 days after capture to determine fate of radio-marked chicks (Gregg et al. 2006a). Broods were not intentionally flushed, but survival of marked and unmarked chicks was verified when broods were unintentionally flushed
during monitoring. At the end of the monitoring period, I flushed broods and counted marked and unmarked chicks. I assumed that unmarked chicks of the brood that were not flushed were dead. Because of potential differences in detection probabilities for marked and unmarked chicks, I used a bird dog to flush broods. I determined the presence of radio-marked chicks with telemetry before and after flushing the brood. In no case did radio-marked chicks remain in the vicinity after the brood had been flushed. Therefore, I assumed that all unmarked chicks that were alive and with the brood were counted.

I used logistic regression (PROC GENMOD; SAS Institute 2001, version 8.2) to examine patterns in proportion of chicks alive at 28 days post-hatch relative to chicks with and without implanted transmitters, individuals conducting surgeries, study areas, and years. My dependent variable distinguished between chicks that were alive (1) and dead (0). The independent variable MARK distinguished between marked and unmarked chicks and CREW identified the 4 different individuals that implanted transmitters during my study. I included STUDYAREA and YEAR as independent variables because telemetry data indicated substantial temporal and spatial variation in chick survival. In addition to my main effects, I included 2-way interactions for MARK×CREW to determine if implant effects were dependent on the individual conducting the surgery and STUDYAREA×YEAR to account for variation in chick survival among study areas and years.

provide efficient parameter estimates and improved standard errors when observations in clusters may not be independent (Allison 1999). I used Akaike’s Information Criterion adjusted for small samples sizes (AICc) to choose the best approximating model from a group of 8 a priori candidate models (Burnham and Anderson 2002). Initially, I measured deviance ($\hat{c} = \text{goodness-of-fit } \chi^2/\text{df}$) of my global model (main effects and 2-way interactions) to determine if the model structure was appropriate for the data (Burnham and Anderson 2002). I ranked models based on lowest AICc values and calculated differences between the best-fitted model and all other models. Akaike weights ($w_i$) were calculated from $\Delta$AICc values to provide estimates of a model’s probability given other candidate models. Akaike weights were used to calculate model averaged parameter estimates and unconditional standard errors for my independent variables (Burnham and Anderson 2002). Model averaged parameter estimates were not conditional on a single model and included model selection uncertainty into the final parameter estimates and standard errors. I used standardized parameter estimates ($|\beta|/\text{SE (\beta)}$) that were calculated from weighted parameter estimates and unconditional standard errors to evaluate the potential effect each variable had on the proportion of chicks alive at 28 days post-hatch (Allison 1999).

RESULTS

I monitored 21 broods and 149 chicks (Table 20). All broods had marked and unmarked chicks. The average brood size and number of marked chicks per brood was 7.1 and 5.1 chicks, respectively. I counted 33 (22%) chicks from 9 (43%) broods during flush counts at 28-days post-hatch. Brood integrity was high; 5 (3%) radio-marked chicks from 4 (19%) broods were adopted by other hens and 2 of these chicks
were alive at 28-days post-hatch. The structure of my global model fit the data
($\chi^2_{90}/df = 0.889$) and the scale parameter was set at 1. Of the 8 candidate models I
evaluated, the best-fitted model received 71.4% of the Akaike weight and contained
the variables STUDYAREA, YEAR, and STUDYAREA×YEAR, which indicated that
the proportion of chicks alive 28-days post-hatch was highly variable among study
areas and years (Table 20 and 21). The second best model received 24.9% of the
Akaike weight and was identical to the best-fitted model but included the covariate
MARK (Table 21). The inclusion of MARK reduced model fit and the AICC score
increased by 2.11 (Table 21). The second model was not considered a competing
model because the proportion of marked (21%, 23/108) and unmarked (24%, 10/41)
chicks alive at 28-days post-hatch was similar and the similarity was consistent across
study areas and years (Table 20). The final 6 models received the remaining 3.6% of
the Akaike weight and were > 5.97 AICC units from the best-fitted model, which
indicated that survival of marked chicks was not dependent on individuals conducting
surgeries (Table 21). The STUDYAREA×YEAR covariate had the greatest effect on
model fit because when it was excluded from the best-fitted model the AICC score
increased by 27.09 units (Table 21). My results were further supported by the
standardized parameter estimates for STUDYAREA×YEAR, which was the highest of
all variables (Table 22). The standardized parameter estimates for MARK, CREW,
and MARK×CREW were among the lowest, which provided additional evidence that
capture and transmitter effects on survival were negligible (Table 22).

**DISCUSSION**

I found no evidence of differential survival to 28 days among sage-grouse chicks
Table 20. Number of greater sage-grouse broods and chicks monitored for survival and proportion (%) of chicks alive at 28 days post-hatch at 3 study areas in Oregon and Nevada, USA, 2001-2002. All marked chicks were equipped with implanted radiotransmitters.

<table>
<thead>
<tr>
<th>Year</th>
<th>Hart Mountain Chicks</th>
<th>Beatys Butte Chicks</th>
<th>Sheldon Chicks</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Broods</td>
<td>Marked</td>
<td>Unmarked</td>
</tr>
<tr>
<td>2001</td>
<td>4</td>
<td>17 (35)</td>
<td>11 (36)</td>
</tr>
<tr>
<td>2002</td>
<td>3</td>
<td>16 (0)</td>
<td>6 (0)</td>
</tr>
<tr>
<td>Total</td>
<td>7</td>
<td>33 (18)</td>
<td>17 (23)</td>
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</tbody>
</table>
Table 21. Model selection results for 8 *a priori* models used to explore the effect of implanted transmitters on survival of greater sage-grouse chicks at 3 study areas in Oregon and Nevada, USA, 2001-2002.

<table>
<thead>
<tr>
<th>Model</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Studyarea+year+studyarea×year</td>
<td>134.99</td>
<td>0.00</td>
<td>0.71</td>
</tr>
<tr>
<td>Mark+studyarea+year+studyarea×year</td>
<td>137.10</td>
<td>2.11</td>
<td>0.25</td>
</tr>
<tr>
<td>Mark+crew+studyarea+year+mark×crew+studyarea×year</td>
<td>140.97</td>
<td>5.98</td>
<td>0.04</td>
</tr>
<tr>
<td>Mark+crew+studyarea+year+mark×crew</td>
<td>150.08</td>
<td>15.09</td>
<td>0.00</td>
</tr>
<tr>
<td>Mark+crew+mark×crew</td>
<td>154.03</td>
<td>19.04</td>
<td>0.00</td>
</tr>
<tr>
<td>Mark</td>
<td>161.49</td>
<td>26.50</td>
<td>0.00</td>
</tr>
<tr>
<td>Studyarea+year</td>
<td>162.09</td>
<td>27.09</td>
<td>0.00</td>
</tr>
<tr>
<td>Mark+studyarea+year</td>
<td>164.05</td>
<td>29.05</td>
<td>0.00</td>
</tr>
</tbody>
</table>

*a* MARK distinguished between marked and unmarked chicks, CREW identified the 4 different individuals that implanted transmitters.

Table 22. Model averaged parameter estimates ($\beta$), robust standard errors (SE), and standardized parameter estimates (Standardized $\beta$) for variables used to explore the effect of implanted transmitters on survival of greater sage-grouse chicks at 3 study areas in Oregon and Nevada, USA, 2001-2002.

<table>
<thead>
<tr>
<th>Variable</th>
<th>$\beta$</th>
<th>SE</th>
<th>Standardized $\beta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>MARK</td>
<td>-0.804</td>
<td>0.628</td>
<td>1.280</td>
</tr>
<tr>
<td>CREW</td>
<td>-0.294</td>
<td>0.604</td>
<td>0.487</td>
</tr>
<tr>
<td>MARK×CREW</td>
<td>-0.074</td>
<td>0.633</td>
<td>0.117</td>
</tr>
<tr>
<td>STUDYAREA</td>
<td>-5.736</td>
<td>1.602</td>
<td>3.580</td>
</tr>
<tr>
<td>YEAR</td>
<td>-6.635</td>
<td>1.717</td>
<td>3.864</td>
</tr>
<tr>
<td>STUDYAREA×YEAR</td>
<td>3.992</td>
<td>0.959</td>
<td>4.162</td>
</tr>
</tbody>
</table>

*a* MARK distinguished between marked and unmarked chicks, CREW identified the 4 different individuals that implanted transmitters.
with implanted transmitters and unmarked chicks, which supported the assumption that survival estimates derived from radio-marked sage-grouse chicks were relatively unbiased. My results also failed to reveal observer bias; implant effects on survival were not dependent upon the individual conducting the surgery. Hence, subcutaneous implants may be a viable method for attaching transmitter to greater sage-grouse chicks and could facilitate studies investigating survival and habitat use of chicks (Gregg et al. 2006a). No other research has compared survival between implanted and unmarked sage-grouse chicks, but my conclusions were supported by research on free-ranging wild turkeys (Meleagris gallopavo, Hubbard 1997) and common loons (Gavia immer, Kenow et al. 2003), which revealed no difference in survival between implanted and unmarked hatchlings. Similarly, Aldridge (2005) concluded that external transmitters on sage-grouse chicks had a minimal effect on survival by comparing survival estimates generated from brood flush counts and radio-marked chicks.

Although I did not detect a difference between survival of marked and unmarked chicks, my results did not exclude the possibility that survival was compromised to some extent. Capture, handling, and marking hatchlings likely has a negative effect on survival (Pietz et al. 2003). Captive studies of ring-necked pheasant chicks (Phasianus colchicus, Ewing et al. 1994) and wild turkey poults (Hubbard et al. 1998, Bowman et al. 2002) revealed a slight short-term reduction in growth and mobility of hatchlings with implanted transmitters compared with unmarked hatchlings, but no discernable long-term effect on survival was found. Reduced mobility could indirectly influence survival of chicks in free-ranging populations by predisposing
them to predation or other mortality factors. Most of my radio-marked chicks showed no signs of mobility problems and dispersed into nearby vegetation immediately after release. However, I noted that a few marked chicks initially had difficulty walking and were unstable, but typically they were mobile within a few minutes following release. My results suggested that the infrequent impaired mobility I observed during my study did not significantly compromise survival of sage-grouse chicks. However, potential for the predisposition of radio-marked chicks to predation or other mortality factors cannot be completely eliminated.

My results could have been biased if brood disturbance during capture or the presence of marked chicks in a brood had a negative effect on brood survival. I did not have an adequate random sample of unmarked broods during my study to make a direct comparison with marked brood survival. However, of the 21 broods with radio-marked chicks that I monitored, 43% had ≥1 chick alive at 28-days post-hatch, which was similar to survival of unmarked sage-grouse broods monitored on my study areas before (1989-2000) my research (M. A. Gregg, U.S. Fish and Wildlife Service, unpublished data). Additionally, survival of unmarked sage-grouse broods in Alberta, Canada (Aldridge and Brigham 2001) and Oregon (Hanf et al. 1994) was similar to marked broods during my study. Likewise, similar brood survival rates were reported for externally marked and unmarked waterfowl broods (Pietz et al. 2003, Mawhinney and Diamond 1999).

I assumed that ingress and egress of unmarked chicks from marked broods was similar. However, my results would have been biased if ingress and egress of unmarked chicks differed. I believe this was not a significant factor during my study.
because I documented little movement of radio-marked chicks between broods. In addition, I seldom encountered hens with unmarked broods in the vicinity of marked broods during my daily monitoring. I also did not observe size discrepancies between marked and unmarked chicks during flush counts, which would have indicated that unmarked chicks joined marked broods. Nevertheless, the possibility remained that survival of unmarked chicks was underestimated and my results were biased.

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LITERATURE CITED


APPENDIX C: SENSITIVITY ANALYSIS FOR CENSORING

INTRODUCTION

Censoring individuals from survival analysis for any reason could lead to seriously biased parameter estimates and study results if censoring is informative. Informative censoring refers to cases where hazards are systematically higher or lower than uncensored observations (Allison 1995). However, random censoring, which is out of investigator control, occurs when individuals censored are not related to an event and do not appreciably bias parameter estimates (Allison 1995). Hence, my objective was to determine if censoring chicks because of transmitter failure, transmitter loss, or egress (adoption) of radio-marked chicks from a brood was informative or random.

METHODS

I tested 2 conflicting hypotheses: 1) Censored individuals were at greater risk of having an event and 2) Censored individuals had a lower risk of having an event. For censoring to be random, both of these hypotheses are false. To test these hypotheses, I conducted 2 analyses using the radio-marked chick data set that I analyzed in Chapter 5. In the first analysis, I assumed that all censored individuals survived to the end of monitoring period (28-days) and in the second analysis I assumed that all censored individuals died immediately after censoring. I estimated Cox regression models (Cox 1972) with PROC PHREG (SAS Institute 2001, version 8.2) to examine relationships between 6 covariates and failure times to 28-days post-hatch for individually radio-marked chicks. The covariates I considered in my analyses included hatch date, chick age, chick weight, brood size, total plasma protein, and hen age. I did not consider
habitat variables because they were all time-dependent, and habitat data were not available for all censored chicks to 28 days post-hatch. I compared parameter estimates, standard errors, hazard ratios, and Wald chi-square statistic of each covariate between analyses.

RESULTS AND DISCUSSION

My analyses included 370 radio-marked chicks from 69 broods that included individuals censored because of suspected radio failure ($n = 72$), transmitter loss ($n = 35$), and adoption ($n = 9$). I found little variation in parameter estimates, hazard ratios, or Wald chi-square statistic for any covariate between analyses. Although I was unable to compare my entire set of variables, my results indicated that censoring individuals in my data set was likely random (Table 23). Hence, censoring of individuals in my data set likely did not bias parameter estimates and results of my study.

Table 23. Parameter estimates ($\beta$), hazard ratios ($e^\beta$), and Wald Chi-Square statistics for variables in sensitivity analysis for censoring radio-marked sage-grouse chicks because of failed transmitters ($n = 72$), lost transmitters ($n = 35$), or adoption ($n = 9$).

<table>
<thead>
<tr>
<th>Variables</th>
<th>Censored alive analysis</th>
<th>Censored dead analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\beta$</td>
<td>$e^\beta$</td>
</tr>
<tr>
<td>Hatch date</td>
<td>-0.035</td>
<td>0.965</td>
</tr>
<tr>
<td>Brood size</td>
<td>0.095</td>
<td>1.099</td>
</tr>
<tr>
<td>Total plasma protein</td>
<td>-0.106</td>
<td>0.900</td>
</tr>
<tr>
<td>Chick weight</td>
<td>-0.017</td>
<td>0.983</td>
</tr>
<tr>
<td>Chick age</td>
<td>-0.356</td>
<td>0.700</td>
</tr>
<tr>
<td>Hen age</td>
<td>-0.165</td>
<td>0.848</td>
</tr>
</tbody>
</table>

*aCensored individuals were assumed to have survived to 28 days post-hatch and assumed to have died immediately after censoring in separate analyses.
LITERATURE CITED

