

REPRODUCTION AND HABITAT USE
BY SAGE GROUSE (*Centrocercus urophasianus*)
IN A NORTHERN FRINGE POPULATION

A thesis

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ABSTRACT

Sage Grouse (*Centrocercus urophasianus*) are the largest of all North American grouse and depend on sagebrush (*Artemisia spp.*) for food and protective cover. In Canada, Sage Grouse are at the northern edge of the species' range, occurring only in southeastern Alberta and southwestern Saskatchewan. The Canadian population has declined by 66 to 92% over the last 30 years. I used radiotelemetry to monitor Sage Grouse survival and measure productivity in southeastern Alberta, and assess habitat use at nesting and brood rearing locations. Annual male survival was low (31%), and female survival may also be low (spring to fall; 56.5%) if overwinter mortalities are considered. All females (n = 22) attempted to nest. Nest success (46.2%) and breeding success (54.5%) were within the range found for more southerly populations (15 to 86% and 15 to 70%, respectively). Sage Grouse selected nest areas based on stands that had greater amounts of tall sagebrush cover at a scale between 7.5 and 15 m in radius. Nests were under the densest sagebrush present. Clutch size (7.8 eggs/nest) was within the normal range for Sage Grouse (6.6 to 9.1), but at the high end of the spectrum. Fledging success was comparable to that reported in other studies; however, chick survival to ≥ 50 days of age (18%), was less than half of the required 35% survival for a stable or only slightly declining population. Brood rearing sites were selected based on greater amounts of taller sagebrush cover, but not forb content. High quality mesic areas containing 20 to 40% cover of lush forbs that chicks eat were limiting in southern Alberta (only 12% cover available), despite spring precipitation, which was above average in both years of my study. I developed a population model based on these estimated parameters. The model predicts that by 2018, the Sage Grouse population in Alberta will fall to below 100

birds and the Canadian population to ≤ 190 birds, which may not be sufficient to sustain a viable population.

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TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS	iv
TABLE OF CONTENTS	viii
LIST OF TABLES	xi
LIST OF FIGURES	xii
GENERAL INTRODUCTION.....	1
CHAPTER 1. STATUS OF SAGE GROUSE IN CANADA	3
INTRODUCTION	4
DISTRIBUTION.....	8
PROTECTION.....	9
<i>Federal.....</i>	<i>9</i>
<i>British Columbia.....</i>	<i>9</i>
<i>Saskatchewan.....</i>	<i>10</i>
<i>Alberta.....</i>	<i>10</i>
POPULATION SIZE AND TRENDS	11
<i>Between Year Trends</i>	<i>12</i>
<i>Seasonal Lek Attendance.....</i>	<i>17</i>
HABITAT	20
<i>Leks.....</i>	<i>20</i>
<i>Nesting Areas</i>	<i>20</i>
<i>Brood Rearing.....</i>	<i>21</i>
<i>Wintering Habitat</i>	<i>22</i>

GENERAL BIOLOGY.....	23
<i>Lek Behaviour</i>	23
<i>Nesting</i>	24
<i>Non-breeding Season</i>	25
<i>Diet</i>	26
<i>Survival</i>	28
LIMITING FACTORS	28
<i>Agricultural Practices</i>	29
<i>Human Disturbance</i>	30
<i>Predation</i>	30
<i>Oil and Gas Exploration</i>	31
<i>Roadways and Traffic</i>	32
<i>Climate</i>	32
SPECIAL SIGNIFICANCE OF THE SPECIES	33
EVALUATION.....	34
CHAPTER 2. NESTING AND REPRODUCTIVE ACTIVITIES	35
INTRODUCTION	36
METHODS AND MATERIALS	38
RESULTS	41
<i>Initiation of Incubation</i>	42
<i>Clutch Size</i>	42
<i>Nesting Attempts</i>	43
<i>Nest Success</i>	43
<i>Renesting Likelihood</i>	45
<i>Breeding Success</i>	46
<i>Fledging Success</i>	46
<i>Chick Survival</i>	46
DISCUSSION	47

CHAPTER 3. NESTING AND BROOD HABITAT USE	58
INTRODUCTION	59
METHODS AND MATERIALS	61
RESULTS	65
<i>Nests</i>	68
<i>Nesting Habitat Characteristics by Nest Fate</i>	69
<i>Nest Habitat</i>	71
<i>Brood Habitat</i>	75
<i>Line Transects</i>	77
DISCUSSION	79
 CHAPTER 4. MODELING POPULATION TRENDS	 87
 LITERATURE CITED	 98

LIST OF TABLES

Table 3.1. Spearman rank correlations for vegetation variables measured at all Sage Grouse nest, brood, and random locations combined	67
Table 3.2. Vegetation characteristics at successful and unsuccessful nests	70
Table 3.3. Discriminant Functions Analysis of vegetation characteristics at successful and unsuccessful nests	72
Table 3.4. Vegetation characteristics at nests and random locations.....	73
Table 3.5. Vegetation characteristics at brood use and random locations	76
Table 3.6. Sagebrush characteristics at use locations (nest and brood) and random locations along line transects	78
Table 4.1. Parameters used in population model	91

LIST OF FIGURES

Figure 1.1. Current and known historic distribution of Sage Grouse. (Adapted from Johnsgard 1983)	5
Figure 1.2. Range of Sage Grouse in Canada	6
Figure 1.3. Population trends for Sage Grouse in Alberta and Saskatchewan from 1968 to 1999.....	13
Figure 1.4. Estimated Sage Grouse population in Alberta from 1968 to 1969.....	16
Figure 1.5. Predicted lek attendance for male and female Sage Grouse (adapted from Jenni and Hartzler 1978).....	18
Figure 1.6. Weekly attendance by male Sage Grouse on leks in Alberta from 1996 to 1999.....	19
Figure 2.1. Clutch size for first nests and renesting attempts by Sage Grouse in southeastern Alberta in 1998-99	43
Figure 2.2. Kaplan-Meier product limit estimate for nest survival in relation to date after initiation, for Sage Grouse nests in southern Alberta in 1998 and 1999	44
Figure 2.3. Timing of nest failure for 14 unsuccessful Sage Grouse nests in southeastern Alberta in 1998-99	45
Figure 4.1. Maximum Sage Grouse lek counts in Alberta shown as a function of spring (April - June) precipitation (mm) for each year	90
Figure 4.2. Actual Sage Grouse population size in Alberta based on lek counts for 1968 through 1999 shown with the predicted population superimposed	92
Figure 4.3. Actual Sage Grouse population in Alberta based on lek counts for 1968 through 1999 and predicted population from 2000 to 2030	93

GENERAL INTRODUCTION

Sage Grouse (*Centrocercus urophasianus*) are strongly associated with sagebrush (*Artemisia spp.*) habitat within the prairie ecozone. Population declines have been reported throughout North America and range from 33 to 80% (Connelly and Braun 1997, Braun 1998). Declines have been most severe at the northern fringe of the species' range, where the Canadian population has declined by at least 80% from historical levels (Aldridge 1998).

The long-term decline in Sage Grouse populations across their range was originally due to the loss of 2.5 million ha of sagebrush steppe habitat since the early 1900s (Patterson 1952, Eng and Schladweiler 1972, Braun 1995). Historically, Sage Grouse occupied approximately 100,000 km² within Alberta and Saskatchewan, but today occupy only about 6,000 km² (Aldridge 1998). With a reduction in range of approximately 90% within the two provinces, this is the most severe range contraction throughout the species' range.

Many factors may be contributing to the Canadian Sage Grouse population decline, including 1) reduced reproductive success, and 2) reduced survival of post-fledged young and/or adults. Habitat degradation, fragmentation, disturbance, predation pressure, reduced nest success, and climatic change all influence reproduction and survival.

The overall objective of my study was to collect data on the population dynamics and ecology of Sage Grouse in Canada; specifically the Alberta population, in an attempt to identify, from a proximate perspective, why the Canadian Sage Grouse population is declining. In 1998 and 1999 I performed spring lek counts to monitor population trends

and estimated survival of adults through the use of radiotelemetry. I followed females to their nesting sites and monitored measures of reproductive effort and reproductive success. Females that successfully hatched their chicks were followed so that I could estimate chick survival, and thus, overall recruitment. I used these data to assess the status of the Alberta and Canadian populations, and used the various population parameters to predict future population trends and compare measures of productivity to other stable and declining populations in the United States.

I measured vegetation characteristic at nest locations, and in habitats used for brood rearing. By assessing habitat use by Sage Grouse, I was able to assess selection, and compare the quality of available habitat to that used by other populations. This allowed me to make inferences about how habitat quality might affect survival and productivity, and thus, population trends.

I have chosen to structure my thesis as series of individual Chapters, each of which is written as a manuscript that will be submitted to a peer reviewed scientific journal. Thus, there is some repetition of data and results between individual Chapters. The first Chapter, (Status of Sage Grouse in Canada), is written for submission to the Canadian Field Naturalist. Thus, sections within this Chapter are arranged based on the format for a species status and distribution manuscript for that journal. Chapter Two, Nesting and Reproductive Activities, and Three, Nesting and Brood Habitat Use, are each written in a style for publication in an ornithology journal. The final Chapter, Modeling Population Trends, ties together all the population parameters that I measured, and explains the population model that I have developed to predict the Alberta/Canadian Sage Grouse population.

CHAPTER 1. STATUS OF SAGE GROUSE IN CANADA

INTRODUCTION

Sage Grouse (*Centrocercus urophasianus*) are strongly associated with sagebrush (*Artemisia spp.*) habitats throughout the Great Plains and Intermountain West. Historically, they occurred in British Columbia, Alberta, Saskatchewan and at least 16 U.S. states, but they have been extirpated from British Columbia and five states (Braun 1998, Schroeder et al. 1999) (Fig. 1.1). The long-term decline seen in Sage Grouse populations across their range was originally due to the direct loss of the sagebrush steppe associated with grassland habitats. This habitat has been reduced by more than 50% (2.5 million ha) since the early 1900s (Patterson 1952, Eng and Schladweiler 1972, Braun 1995) (Fig. 1.1). Of the two subspecies of Sage Grouse, the eastern race (*C. u. urophasianus*) is found at the northern edge of its range in extreme southeastern Alberta and southwestern Saskatchewan (Fig. 1.1).

Both Alberta and Saskatchewan still support Sage Grouse populations (Fig. 1.2), yet springtime lek counts indicate the Canadian population has decreased by approximately 80% since the mid 1980s, and was between 549 to 813 individuals in 1997 (Aldridge 1998). As a consequence of the decline, Alberta closed the Sage Grouse hunting season in 1996 for the first time since 1967 (Aldridge 1998). Sage Grouse have not been hunted in Saskatchewan since 1938 (Kerwin 1971).

In 1997, the Committee on the Status of Endangered Wildlife In Canada (COSEWIC) listed Sage Grouse as a Threatened species. This listing was upgraded to Endangered in 1998, reflecting the imminent threat of extinction of Sage Grouse in Canada (Hyslop 1998).



Figure 1.1. Current and known historic distribution of Sage Grouse. 'E' represents the eastern subspecies (*C. u urophasianus*) and 'W' represents the western subspecies (*C. u. phaios*). The current distribution is not continuous and is more fragmented than indicated. (Adapted from Johnsgard 1983).

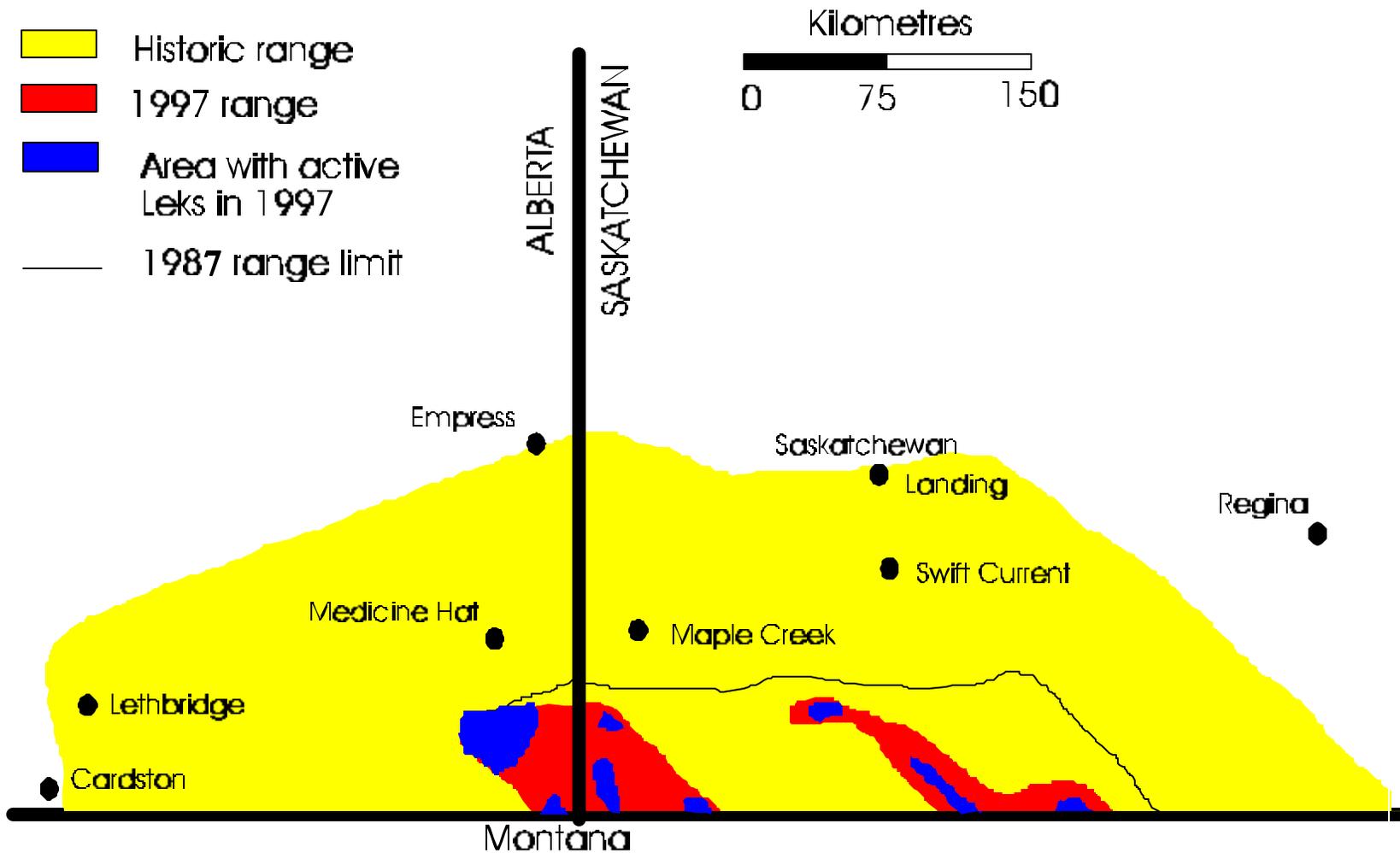


Figure 1.2. Range of Sage Grouse in Canada. Historical range is based on anecdotal sightings of birds prior to the 1960s. The present (1997) range is based on the locations of known active leks in 1997. The 1987 range limits are shown to illustrate the range contraction. (Map produced by W. C. Harris).

Sage Grouse are found almost exclusively within the North American range of sagebrush (*Artemisia spp.*), and are associated with sagebrush habitats throughout the year (Patterson 1952, Eng and Schladweiler 1972, Wallestad 1975, Braun et al. 1977, Crawford and Lutz 1985, Swenson et al. 1987, Braun 1995). This is also the case in Canada, where Sage Grouse are found within the range of sagebrush in the semi-arid mixed-grass prairie. Silver sage (*A. cana*) is the main species of sagebrush on the Canadian prairies and is most frequently associated with grasses such as june grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), speargrass (*Stipa comata*), and western wheatgrass (*Agropyron smithii*). Pasture sage (*Artemisia frigida*) is the main forb (Aldridge 1998). Mean annual precipitation within the Alberta range is about 332 mm, and mean temperatures for July and January average 19.5 and -11.7°C, respectively (Onefour Research Station, Environment Canada).

Although Sage Grouse have a close association with sagebrush habitats, specific habitat requirements vary throughout the year. Areas used by Sage Grouse must contain suitable habitat which satisfies requirements for strutting grounds (leks), nesting areas, feeding and loafing sites, brood rearing sites, and wintering areas (Klebenow 1969, Eng and Schladweiler 1972, Wallestad and Pyrah 1974, Beck 1977).

The purpose of this Chapter is to evaluate the status of the Sage Grouse in Canada, discussing the species distribution, biology, habitat requirements, and potential factors that might be affecting the population. I will also discuss long term and present population trends, addressing the population decline, range contraction, and relevant research.

DISTRIBUTION

Sage Grouse have been extirpated from at least five U. S. states and British Columbia (Braun 1998, Schroeder et al. 1999) (Fig. 1.1). Throughout their range, Sage Grouse have declined by 45-80% since the 1950s (Braun 1998). The long-term decline was originally due to the direct loss of sagebrush steppe associated with grassland habitats (Patterson 1952; Eng and Schladweiler 1972; Braun 1995, 1998; Schroeder et al. 1999). Sage Grouse presently inhabit about 50% of the area they once occupied in Oregon (Crawford and Lutz 1985) and Colorado (Braun 1995) at the turn of the century. Range contractions of similar magnitude have occurred elsewhere in the species' range (Patterson 1952, Eng and Schladweiler 1972, Wallestad 1975, Braun et al. 1977, Crawford and Lutz 1985, Swenson et al. 1987, Braun 1995). The current distribution of Sage Grouse is fragmented (Patterson 1952, Eng and Schladweiler 1972, Hupp and Braun 1991, Braun 1995) (Fig. 1.1).

The eastern subspecies (*C. u. urophasianus*) is at the northern edge of its range in extreme southeastern Alberta and southwestern Saskatchewan (Fig. 1.1). Historically, Sage Grouse occupied approximately 100,000 km² within the two prairie provinces, but today, occupy only about 6,000 km² (Fig. 1.2). The range contraction within Canada is primarily attributed to habitat loss.

The western subspecies (*C. u. phaios*) occurs in smaller numbers from eastern Washington to southeastern Oregon (Fig. 1.1). Historically, this subspecies extended into the southern Okanagan and Similkameen valleys of British Columbia, but was considered extirpated by 1918 (Cannings et al. 1987).

A smaller-bodied Sage Grouse that is behaviourally, morphologically and genetically different from the larger bodied birds, has been proposed as a distinct species; the Gunnison Sage Grouse (*C. minimus*; Kahn et al. 1999, Oyler-McCance et al. 1999, Schroeder et al. 1999). These birds are found from southwestern Colorado into southeastern Utah, and were likely geographically isolated in the Pleistocene (C. E. Braun, pers. commun.).

PROTECTION

Federal

Sage Grouse were hunted in Saskatchewan (prior to 1938) and in Alberta (prior to 1996), but are no longer hunted in Canada. There is some indication that Sage Grouse populations can be hunted with minimal effects on population numbers (Braun 1984, Braun and Beck 1985), however, hunting small populations in fragmented areas may have significant implications.

After initially being listed as Threatened by COSEWIC in 1997, Sage Grouse (prairie population) were upgraded to Endangered status in 1998 (Hyslop 1998). However, until the new Federal Species At Risk Act (SARA) is passed, the species is afforded little Federal protection. Thus, at this time, protection of Sage Grouse is limited to that afforded by Provincial regulations.

British Columbia

Sage Grouse have not been observed in British Columbia since the 1960s (Cannings et al. 1987), and the population is considered Extirpated (Hyslop 1998).

Saskatchewan

In Saskatchewan, Sage Grouse were listed as a Threatened species in 1987, based on a declining population and a reduction in range. In 1999, they were upgraded to Endangered. Now that Sage Grouse are on the Provincial Endangered species list, their habitat is protected under The Wildlife Habitat Protection Act, which means that lands containing Sage Grouse habitat can not be sold or have their native vegetation cultivated.

In 1994, Saskatchewan implemented restrictions that limited development and disturbance at Sage Grouse lek sites. The Saskatchewan Wildlife Act was amended in 1997 to list and protect wild species at risk. With the 1999 Saskatchewan classification of Endangered, Sage Grouse are now protected under the Saskatchewan Wildlife Act. These regulations provide protection of Sage Grouse, their nests, and leks sites. No developments within 500 m of leks are permitted and no construction activities within 1000 m of leks are allowed between 15 March to 15 May.

Alberta

In 1991, Sage Grouse in Alberta were given a “Yellow” listing, meaning they were considered a species of concern due to their naturally low populations, their limited distribution, and the limited available habitat (Anonymous 1991). They were subsequently added to the “Blue” list of species that may be at risk in 1996 (Anonymous 1996). This designation was assigned due to the species’ limited distribution, declining population numbers, and specific habitat requirements. Despite this, Sage Grouse are still considered a game bird in Alberta. The Alberta Endangered Species Conservation Committee has recommended Sage Grouse be listed as Endangered under the Alberta

Wildlife Regulations (K. J. Lungle, pers. commun.). By virtue of being a non-hunted species, they are afforded limited protection. Once they are listed provincially as an Endangered species, more rigid protection will be available to protect against the capture, killing or harming of individuals or their nests.

Sage Grouse habitat is not currently protected within the Province of Alberta, although there is the potential to enforce and protect habitat under other provincial legislation. Listing Sage Grouse as a provincially Endangered species will put the Endangered Species Conservation Committee in charge of the species' recovery. It will also afford significantly higher enforcement penalties and provide greater opportunity to protect Sage Grouse and their habitat.

Alberta Environmental Protection has developed recommendations and land use guidelines, which propose to limit activities surrounding Sage Grouse leks throughout the year. From 16 June to 29 February, seismic activities, surveying, and monitoring would all be prohibited within 100 m of leks, and from 1 March to 15 June, these activities would be prohibited within 500 m. Permanent developments would be prohibited within 1000 m of leks, regardless of the time of year. However, these recommendations can not currently be legally enforced and are only guidelines.

POPULATION SIZE AND TRENDS

The most cost effective and time efficient method to estimate Sage Grouse population size is through lek counts. Lek counts involve counting the number of male Sage Grouse displaying on a strutting ground (lek) during the spring mating season. The maximum number of males observed at each lek is then used as an index of population

status (Beck and Braun 1980, Emmons and Braun 1984). Lek counts are used to make population estimates and as indicators of population trends for many lekking species, including all Sage Grouse populations, even though there is no direct evidence of a relationship between attendance of males at leks and population size.

Between Year Trends

Sage Grouse lek counts within Alberta and Saskatchewan have been performed independently, and for this reason, I discuss population trends separately (Fig.1.3). In Alberta, surveys have been performed on average, every two years since 1968, although gaps as long as five years have occurred (Fig. 1.3). During 1968/69, and in the early 1980s, Sage Grouse numbers peaked, and approached 600 males counted on about 20 leks, with an average of greater than 25 males/lek (Fig. 1.3). In Saskatchewan, the first surveys were performed in 1987 and 1988. They resulted in counts of nearly 600 males on about 30 active leks, with an average of about 20 males/lek (Fig. 1.3). Since surveys began, there has been a general decline in population numbers. In 1997, there were only 8 and 10 active leks, supporting 122 and 61 males in Alberta and Saskatchewan, respectively (Fig. 1.3).

The most intensive lek counts have been conducted over the last two years in both provinces. Maximum lek counts in Alberta resulted in a total count of 147 males on 8 active leks in 1998, and 140 males on 8 leks in 1999 (Fig. 1.3). A similar trend occurred in Saskatchewan, where a maximum of 144 males were counted on 12 active leks in 1998 and 131 males on 10 leks in 1999 (W. C. Harris, pers. commun.) (Fig. 1.3). I estimate the

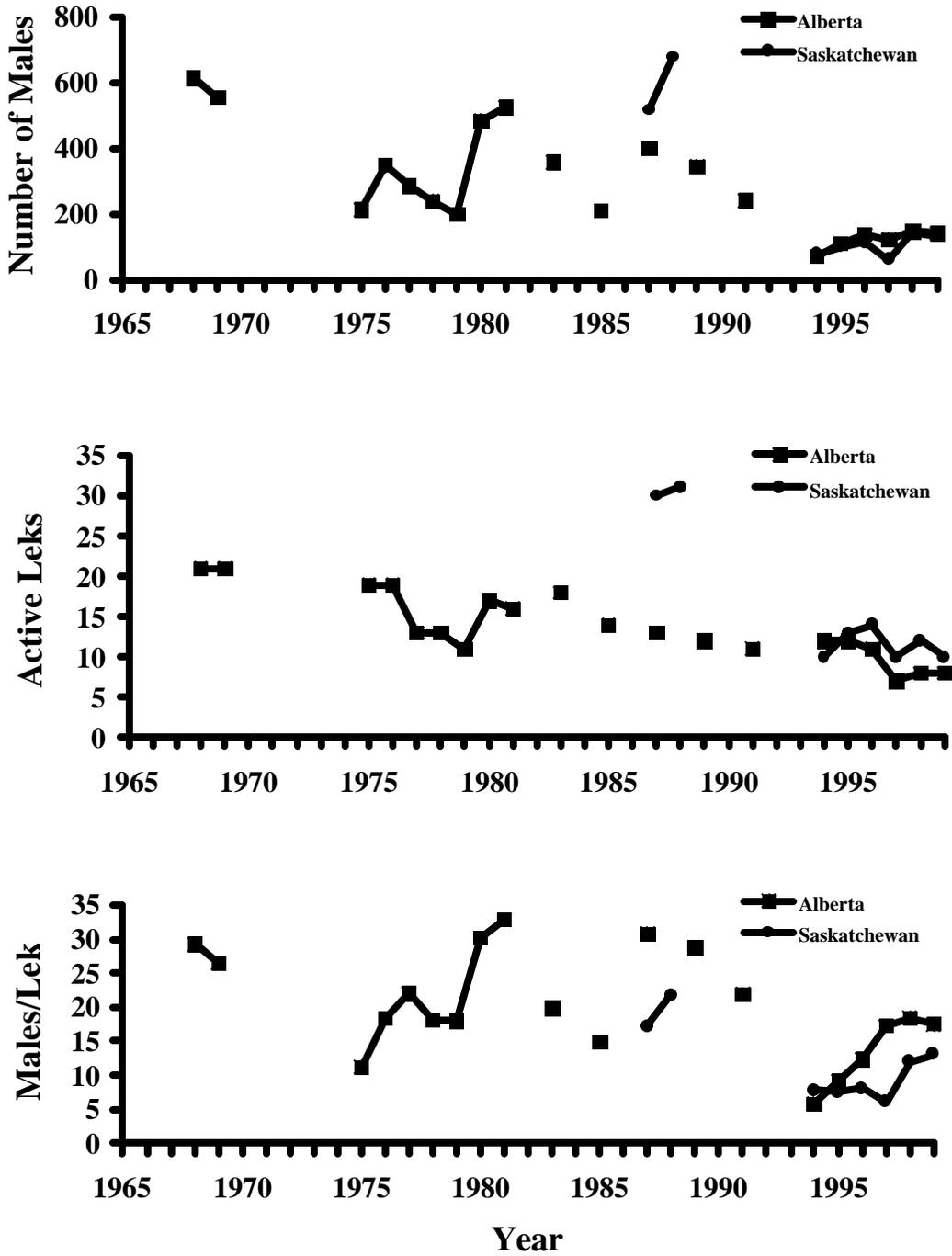


Figure 1.3. Population trends for Sage Grouse in Alberta and Saskatchewan from 1968 to 1999 shown as the number of males, number of males per lek, and number of active leks. Years when sampling efforts consisted of less than eight leks surveyed are not included. Lines are shown to illustrate trends between years with consecutive lek counts.

1999 Canadian spring population was between 813 and 1204 individuals. These estimates are based on spring lek counts of males, and the low estimate assumes a spring sex ratio of two females for every male; whereas the high estimate assumes the same sex ratio, but also takes into account the potential that only 90% of all leks are located and that only 75% of males attend leks at any given time.

In 1987, counts were performed in both provinces, and a total of 915 males (400 in Alberta, 515 in Saskatchewan) was counted at 34 active leks (Fig. 1.3). This gives an estimated 1987 spring population of between 2745 and 4067 individuals. Based on 1999 estimates, the population has declined by as much as 80% since 1987. However, the 1987 total likely does not represent historic population levels, considering that Alberta counts in 1968 and 1981 in Alberta totaled 613 and 524 males respectively, and counts were also greater in Saskatchewan in 1988 (677 males). If these numbers are used to estimate a historic (\approx 1968) spring Sage Grouse population for the Canadian prairies (only covering the current range), the population would have been between 3870 and 5733 individuals. This represents a potential decline of 86% over the last 3 decades, which may be underestimated, considering the historic range of Sage Grouse was likely much greater (Fig. 1.2). Search efforts have been much greater over the last six years in both provinces, and likely resulted in higher count totals for the surveyed leks. Thus, the population decline may be even greater than lek counts indicate.

While it is evident the Canadian Sage Grouse population has declined, the exact rate of decline is difficult to ascertain, due to inconsistent sampling efforts (Madsen 1995b; Aldridge 1997, 1998). It is also difficult to determine whether in some years, leks that apparently contained no birds, were simply not checked, or could not be located and

surveyed (Aldridge 1998). The assessment of trends is further complicated by the fact that Sage Grouse populations appear to cycle every 7 to 10 years (Fig. 1.3) (Patterson 1952, Rich 1985, Aldridge 1998, Braun 1998, Hyslop 1998). Regardless of the decline, it has been suggested that a minimum population of 500 (Franklin 1980, Lande 1988) and possibly even 5000 (Braun 1995, Anonymous 1997) individuals may be required to maintain sufficient genetic diversity to sustain a viable population. This number may be even higher for Sage Grouse, considering that only 10-15% of males actually breed in any given year (Anonymous 1997; C. E. Braun, pers. commun.; Chapter 4).

Using long-term lek count data for Alberta (Aldridge 1998, Alberta Environmental Protection Natural Resource Service), I estimated the population for each year from 1968 to 1999 (Fig. 1.4) using the assumptions previously discussed. In the late 1960s, the Alberta population was between 1839 and 2724 birds. At its lowest levels in 1994, I estimate the population was between 210 and 311 individuals. In 1999, the population consisted of between 420 and 622 individuals. Thus, the Alberta population has declined from 1968 to 1999 by between 66 and 92%. This decline could be even greater, considering that as little as 5 years ago, Sage Grouse were known to exist outside of their current range, but these areas were not surveyed in past lek counts.

Similar declines are seen in terms of lek abandonment in both Alberta and Saskatchewan. There were at least 21 active leks in Alberta in the late 1960s, and 31 active leks in 1988 in Saskatchewan (Fig. 1.3); 62 and 67% of leks have been abandoned in each province, respectively. The mean number of males per lek has also decreased in both provinces. Alberta averaged 29.2 males per lek in 1968, while Saskatchewan

averaged 21.8 in 1988. By 1994, these numbers had decreased by 80% in Alberta and 64% in Saskatchewan to 5.8 and 7.8 males per lek, respectively.

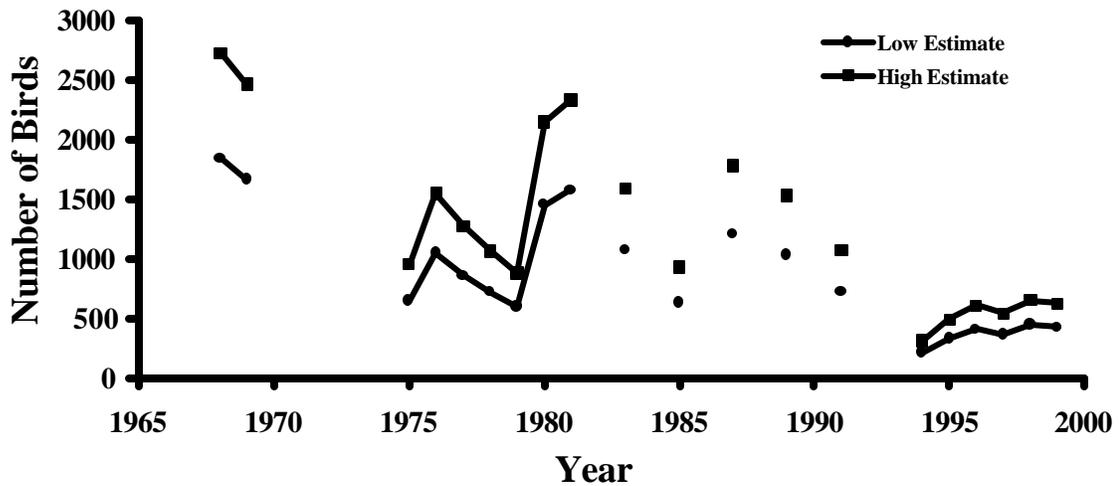


Figure 1.4. Estimated Sage Grouse population in Alberta from 1968 to 1969. Low estimates are based on a spring sex ratio of two females for every male. High estimates assume the same sex ratio; that only 90% of all leks are located; and that only 75% of males attend leks at any given time. Years when sampling efforts consisted of less than eight surveyed leks are not included. Lines are shown to illustrate trends between years with consecutive lek counts.

Despite the overall decrease in population numbers, counts of males have remained relatively stable over the last six years in both provinces (Figs. 1.3, 1.4). During this period, 1995 was the last year that Sage Grouse were hunted in Alberta, even though the season was short (1 week long) and the estimated harvest, based on hunter surveys, was below 10% (K. J. Lungle, pers. commun.). However, over the last six years, more rigorous lek counts have been performed each year in both provinces, and a concerted effort has been made to locate all leks (Aldridge 1998; W. C. Harris, pers. commun.). This increased effort may mask a continuing population decline.

Even though counts of males on leks over the last six years have remained relatively stable, the number of active leks in Canada decreased from 22 in 1994 to 18 in 1999 (Fig. 1.3). Over the same time period, the mean number of males counted per lek has more than doubled from 6.7 males/lek in 1994 to 15.1 in 1999 (Fig. 1.3). It is common for smaller subsidiary or satellite leks to be abandoned during population lows (Dalke et al. 1963), but the attendance at main lek complexes has increased over this time period. This suggests that changes in habitat quality or fragmentation have been occurring, making smaller leks less desirable and forcing birds to move to leks in more suitable habitat.

Seasonal Lek Attendance

Adult males begin returning to leks once they are clear of snow. This typically occurs in mid-March in Alberta (C. L. Aldridge unpubl. data). Yearling males do not attend leks until after the peak of breeding activities. Breeding occurs over a one to two week period, as indicated by the peak in female attendance at leks; late March - early April in California (Bradbury et al. 1989), mid-April in Colorado (Petersen 1980), early April in Idaho (Autenrieth 1981), mid- to late April in Montana (Wallestad 1975, Jenni and Hartzler 1978), late April in Washington (Schroeder 1997) and in early April in Alberta (Chapter 2). This peak typically occurs two to three weeks after peak hen attendance/breeding at leks (Jenni and Hartzler 1978) (Fig. 1.5). This figure is based on attendance of Sage Grouse at leks from three different studies (Dalke et al. 1963, Eng 1963, Jenni and Hartzler 1978). Attendance is shown as the percent of the seasonal maximum attendance for both males and females. All three studies found that only about

50% of male Sage Grouse attend leks prior to the peak in female attendance (breeding) (Fig. 1.5). Radiotelemetry studies indicate that yearling males do not attend leks until two to three weeks after the peak of female attendance (Jenni and Hartzler 1978, Emmons and Braun 1984).

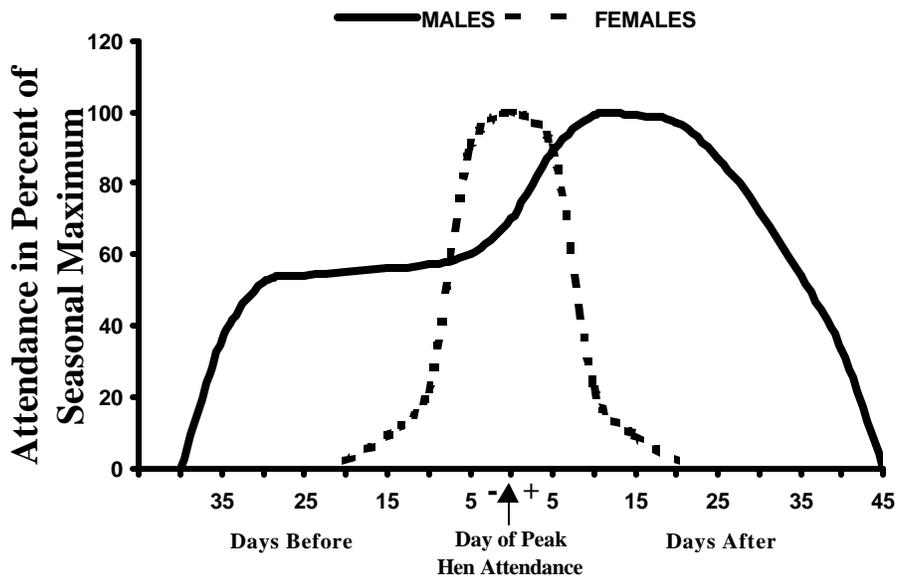


Figure 1.5. Predicted lek attendance for male and female Sage Grouse (adapted from Jenni and Hartzler 1978). In Canada, peak female attendance usually occurs in the first week of April.

The attendance of male Sage Grouse at leks in Alberta within each breeding season varied slightly from 1996 to 1999 (Fig. 1.6). Lek counts were divided into 4 seven-day periods, spanning the three 10-day periods recommended by Jenni and Hartzler (1978) and Beck and Braun (1980). The third week of counts occurred during the last week of April, when the peak in male attendance at leks should occur (Aldridge 1998) due to the arrival of yearling males (Dalke et al. 1963, Eng 1963, Jenni and

Hartzler 1978). I obtained a maximum count for each lek during each of the four-week periods and used a two-way ANOVA to evaluate Week*Year interaction ($F_{9, 100} = 0.02, P > 0.10$), Week ($F_{3, 100} = 0.11, P > 0.10$), and Year effects ($F_{3, 100} = 1.24, P > 0.10$). The lack of significant differences in the attendance of males at leks over each year as a function of week suggests that yearling Sage Grouse are under represented in the Canadian population, and that low recruitment may be contributing to the population decline.

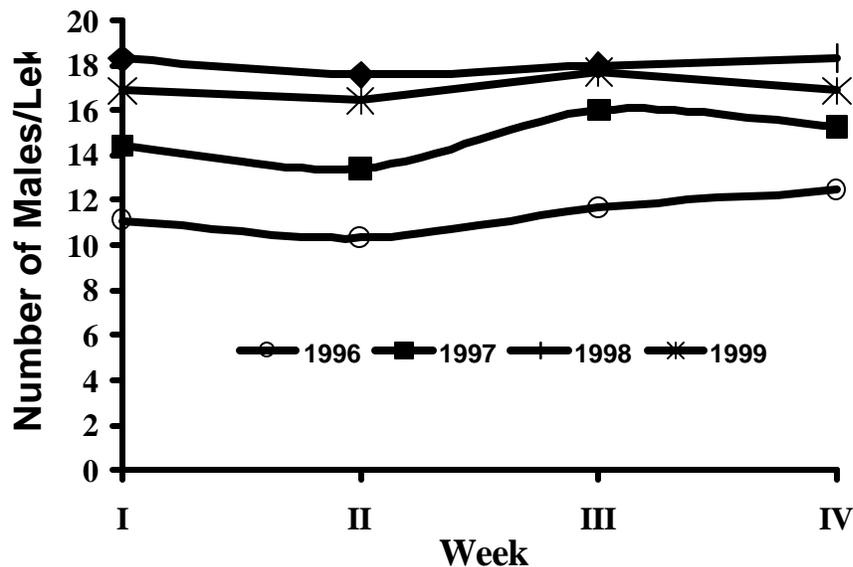


Figure 1.6. Weekly attendance by male Sage Grouse on leks in Alberta from 1996 to 1999. Week III represents the time when peak male attendance historically occurred in Alberta and Saskatchewan.

HABITAT

Leks

Leks (strutting grounds) are sites where displaying males congregate and are highly visible to females. They range in size from 0.04 to 4 ha and are traditional, with some known to remain active for upwards of 100 years (Dalke et al. 1963). Leks are typically in flat, open areas, such as dried mud flats or valley bottoms (Scott 1944, Patterson 1952, Dalke et al. 1963, Peterson 1970). They are often slightly lower than surrounding areas, and frequently located near standing water in Alberta (Aldridge 1998; C. L. Aldridge, pers. observ.). Patterson (1952) reported that some leks were located on slight knolls and ridges. Leks themselves are in areas with little vegetation but are typically surrounded by sagebrush flats that are important as feeding and roosting sites (Scott 1944, Patterson 1952, Peterson 1970, Clark and Dube 1984). Spring daytime roosting sites of males have 20-50% sagebrush canopy cover and consist of plants that are < 30 cm tall (Wallestad and Schladweiler 1974, Wallestad 1975).

Nesting Areas

Nesting habitat is largely associated with sagebrush flats surrounding strutting grounds. Martin (1970) found that 80% of all nests were within 3.2 km of leks, and similarly, Wallestad and Pyrah (1974) found that 68% of all nests occurred within 2.5 km of a lek. Despite the apparent association of nests with leks, Wakkinen et al. (1992) found that nest distribution with respect to leks was random, even though 92% of nests in their southeastern Idaho study area occurred within 3 km of a lek. Nests are almost exclusively placed under sagebrush plants (Patterson 1952, Klebenow 1969, Wallestad

and Pyrah 1974, Braun et al. 1977, Gates 1985) although in some areas Sage Grouse nest under other shrub species which provide dense canopy cover (Connelly et al. 1991, Sveum et al. 1998b). Connelly et al. (1991) found that yearling females placed their nests under sagebrush more often than adults (95% vs. 79%). Sagebrush used for nesting has a dense canopy cover (20-50%) and taller plants are preferred, ranging from 17 to 79 cm in height (Patterson 1952, Klebenow 1969, Wallestad and Pyrah 1974, Schroeder et al. 1999).

Brood Rearing

Broods tend to shift from sagebrush uplands early in the brood rearing period, to more mesic sites later in the summer (Patterson 1952, Dunn and Braun 1986b). In early summer, broods concentrate in areas with sparse sagebrush that are more open and moist, due to the presence of important foods such as succulent forbs (Patterson 1952, Klebenow 1969, Wallestad 1971, Drut et al. 1994a). This shift is usually a result of the desiccation of forbs in sagebrush uplands later in the summer (Dunn and Braun 1986b), and reflects the importance of forbs in the diet of juveniles (Martin 1970, Peterson 1970, Klott and Lindzey 1990, Fischer et al. 1993, Drut et al. 1994b, Pyle and Crawford 1996, Sveum et al. 1998a). Females and broods searching for forbs move further into moist areas (wetlands and wet meadows), away from sagebrush flats, and are often found near open water (Patterson 1952, Klebenow 1969, Wallestad 1971, Autenrieth 1981, Drut et al. 1994a). Habitat shifts occur when chicks are approximately seven weeks of age as broods move to more mesic sites with lush forbs (Martin 1970, Drut et al. 1994b, Sveum

et al. 1998a). This shift coincides with dietary changes (Martin 1970, Peterson 1970, Drut et al. 1994a).

Birds return to areas with dense sagebrush in late summer and fall before moving to wintering grounds (Patterson 1952, Wallestad 1971, Drut et al. 1994b, Dunn and Braun 1986a). Dunn and Braun (1986b) found that females and juveniles selected habitat that was more homogeneous in terms of shrub size and density, and had the greatest horizontal and vertical vegetational cover.

Wintering Habitat

During winter, sagebrush is extremely important as it makes up nearly 100% of the diet of Sage Grouse, and provides cover during inclement weather (Patterson 1952; Wallestad 1975; Johnsgard 1973, 1983; Remington and Braun 1985). In winter, birds are usually found at lower elevations such as drainage basins (Patterson 1952, Hupp and Braun 1989b), where sagebrush is tall enough to remain above the snow (Eng and Schladweiler 1972, Johnsgard 1973). Southwest-facing slopes with a gradient of less than 5% are important wintering areas, as they are wind-swept and relatively snow free, leaving sagebrush exposed (Eng and Schladweiler 1972, Beck 1977). Eng and Schladweiler (1972) found that 82% of all Sage Grouse winter locations were in sagebrush stands with > 20% canopy cover, although sagebrush cover in winter habitat ranges from 6 to 43% (Schroeder et al. 1999).

GENERAL BIOLOGY

Sage Grouse are the largest of all North American grouse (Johnsgard 1973, Beck and Braun 1978). This species exhibits extreme sexual dimorphism, with females averaging 48 to 58 cm in length and males 65 to 75 cm in length, and weighing about 1100 and 2400 g, respectively (Nelson and Martin 1953, Johnsgard 1973, 1983). Body mass fluctuates throughout the year, with the largest gain taking place from January to March (Beck and Braun 1978). Maximum mass is attained during the breeding season (April to May) (Patterson 1952, Beck and Braun 1978, Hupp and Braun 1991). Beck and Braun (1978) suggest that overwinter mass gain is necessary to meet the energy demands of breeding, rather than for overwinter survival. Breeding mass for adult male Sage Grouse in Alberta averages 3122 g (n = 48, C. L. Aldridge, unpubl. data). This is heavier than most southern populations (3190 g in Colorado, Beck and Braun 1978; 2450 g in Eastern Idaho, Dalke et al. 1963; 2900 g in central Montana, Eng 1963; 2700 g in Wyoming, Patterson 1952). The greater mass of Sage Grouse at the northern edge of the species' range may be an adaptation to the more extreme weather conditions.

Lek Behaviour

Males begin returning to leks in late winter. They establish territories on leks and display as soon as the snow begins to disappear. Older males arrive first, and obtain the most central territories (Patterson 1952). After the period of peak female attendance, yearling males begin to visit leks (Fig. 1.5). If a yearling male manages to obtain a territory, he is usually displaced to the lek periphery. Each female attends a lek for a

period of 2 to 3 days and mates only once (Gibson and Bradbury 1986), typically with one of the dominant males (Gibson 1996).

Males attend and display at leks at both dusk and dawn, but activity peaks during the hour surrounding sunrise (Patterson 1952, Johnsgard 1983). The male display is used both to attract females and defend a territory from other males (Patterson 1952, Johnsgard 1983). The display itself consists of a series of “struts,” in which the male fans his tail feathers, inflates his esophageal air sacs and puffs out his white chest feathers while displaying his olive green-yellow gular sacs. Males lift their drawn wings and produce a brushing sound, and finish with a characteristic “plopping” sound that is produced as air is released from the esophageal sacs (Patterson 1952, Johnsgard 1983). Displays are most intense when females are present (C. L. Aldridge, pers. observ.). Both males and females tend to return to the same strutting ground each year (Dalke et al. 1963, Eng 1963, Emmons and Braun 1984, Berry and Eng 1985, Fischer et al. 1993), and > 50% of yearlings return to the strutting ground at which they were conceived (Dunn and Braun 1985). Inter-lek movements by adult males during the breeding season are uncommon (Dalke et al. 1963, Wallestad and Schladweiler 1974). Juvenile males and females sometimes move between leks (Emmons and Braun 1984).

Nesting

After mating, females move to nesting areas, which are typically close to the previous years’ nest sites (Patterson 1952, Fischer et al. 1993, C. L. Aldridge, unpubl. data). Egg laying is initiated within a few days of mating (Patterson 1952) and approximately 1.3 days elapse between the laying of successive eggs (Patterson 1952,

Schroeder et al. 1999). Incubation lasts about 27 days (range 25 to 29; Schroeder et al. 1999, Chapter 2). Average clutch size is 7 to 9 eggs (Schroeder et al. 1999), and in Alberta, peak hatching occurs in the first week of June (Chapter 2, Clewes 1968). Wallestad and Pyrah (1974) found that nesting success of adult females was greater than yearlings (77% vs. 44%). In Idaho, Connelly et al. (1993) found that 78% of all adult females and only 55% of yearlings initiated a nest, yet 52% of both age groups produced a clutch. Schroeder (1997) found that 100% of females attempted to nest with no age-related effects on nest success.

In Alberta, mean brood size from 1967 to 1976 decreased from 4.4 to 3 chicks per female (both n = 20; Windberg 1976). In 1985, brood size was 3.4 (n = 29; Banasch 1985). Crawford and Lutz (1985) reported similar trends in Oregon, with brood sizes decreasing from 4.5 chicks per female in the late 1950s, to 3.3 in the early 1980s. They also reported the percentage of adults with broods declined from a maximum of 55% to only 9% over the same time period. Limited brood surveys conducted in Alberta in 1995 suggested that only 21% of females (n = 19) had broods, with an average of 1.5 chicks per brood (n = 4; Madsen 1995a). Unfortunately, it is difficult to compare productivity between these studies due to differences in sampling techniques.

Non-breeding Season

In late summer and fall, Sage Grouse gather in sexually segregated flocks, although some flocks contain females and immature males (Eng and Schladweiler 1972, Beck 1977). Movements to wintering grounds begin at this time (September to November) and may last until December (Connelly et al. 1988). Distances moved from

breeding to wintering ranges averaged 7.9 to 11.6 km for Sage Grouse in northern Colorado (Beck 1977), 28 to 30 km in Colorado (Schoenberg 1982), and 11.3 km for adults in southeastern Idaho (Connelly et al. 1988). However, one-way migrations of 80 km are not uncommon (Patterson 1952, Dalke et al. 1963, Connelly et al. 1988) and distances of 160 km have been reported (Patterson 1952). Movements of juveniles in Colorado are sporadic and tend to follow corridors of sagebrush (Dunn and Braun 1986a). Similarly, fall movements by adults in Idaho were found to be slow and meandering (Connelly et al. 1988). The longest reported migration movements are usually of birds moving to lower elevations (see Patterson 1952, Connelly et al. 1988).

In Montana, Sage Grouse populations are considered non-migratory, with minimal movements occurring between winter and summer ranges due to the overlap of habitats (Eng and Schladweiler 1972). Wintering grounds in southeastern Idaho also overlap with spring and summer ranges (Connelly et al. 1988). Sage Grouse in Canada are also considered to be non-migratory, as winter ranges overlap with spring and summer ranges (Aldridge 1998; C. L. Aldridge, unpubl. data). Beck (1977) found that wintering areas composed only 7% of the sagebrush habitat, suggesting that winter habitat may be the most limited resource (Patterson 1952, Eng and Schladweiler 1972, Beck 1977, Remington and Braun 1985).

Diet

Sage Grouse lack a muscular gizzard necessary for grinding seeds or other hard materials (Patterson 1952, Remington and Braun 1985). Consequently, their diet is limited to soft vegetation such as sagebrush leaves and lush forbs and insects. Sagebrush

constitutes 62% of the overall diet (Wallestad et al. 1975) and makes up 100% of the diet in winter (Patterson 1952).

All Sage Grouse include some lush forbs in their summer diet, but forbs appear to be particularly important to pre-laying females (20 to 50% of diet) (Barnett and Crawford 1994). Forbs are also important to juveniles, making up 75% of the diet of Sage Grouse < 12 weeks of age (Peterson 1970). The majority of forbs consumed are leaves and flower buds of common dandelion (*Taraxacum officinale*), common salsify (*Tragopogon dubius*), and prickly lettuce (*Lactuca serriola*) (Klebenow and Gray 1968, Peterson 1970, Wallestad et al. 1975). In Canada, vegetation consumed by Sage Grouse includes sweet clover (*Melilotus spp.*) alfalfa (*Medicago sativa*), pasture sage (*A. frigida*), common salsify, and silver sagebrush (Kerwin 1971).

Insects are also an important component of the diet of juveniles (Patterson 1952, Klebenow and Gray 1968, Peterson 1970, Johnson and Boyce 1990, Drut et al. 1994b). Grasshoppers (Orthoptera), beetles (Coleoptera), and ants (Formicidae) have all been found in the diets of juveniles, as well as adults (Patterson 1952, Kerwin 1971, Wallestad et al. 1975). In feeding trials with captive chicks, Johnson and Boyce (1990) found that increasing amounts of insects in the diet increased both growth and survival. In the wild, insects may make up as much as 60% of the diet of chicks less than one week old (Peterson 1970). A decrease in the consumption of insect matter and changes in plant food sources occur in broods at about 7 weeks of age, which has been linked to a shift in habitat use (Martin 1970, Petersen 1970, Drut et al. 1994a, 1994b). At 12 weeks of age, insects only make up 5% of the diet (Peterson 1970). Sage Grouse generally obtain

enough moisture from the food they eat, but in dry years they have been observed drinking from standing water (Patterson 1952; C. L. Aldridge, pers. observ.).

Survival

Annual adult survival has been estimated at 30 to 75% with males having lower survival rates than females (June 1963, Johnsgard 1973, Braun and Beck 1985, Schroeder et al. 1999). Adult males often have lower survival rates than do yearlings (Braun and Beck 1985, Schroeder et al. 1999), likely due to the costs incurred during courtship (Braun and Beck 1985). Dalke et al. (1963) observed a female that had been banded seven years earlier. Juvenile mortality may be high, with large numbers succumbing to disease and predation (Patterson 1952). Major predators include hawks, falcons (*Falco spp.* and *Accipiter spp.*), eagles, coyotes (*Canis latrans*), and red fox (*Vulpes vulpes*) (Schroeder et al. 1999). Ground squirrels (*Spermophilus spp.*), striped skunks (*Mephitis mephitis*), Black-billed Magpies (*Pica pica*), Common Ravens (*Corvus corax*), American Crows (*Corvus brachyrhynchos*) and coyotes prey upon eggs and chicks (Patterson 1952, Schroeder et al. 1999). Both the red fox and raccoon (*Procyon lotor*) have increased in numbers on the Canadian prairies and may also be important nest predators (Aldridge 1998; W. C. Harris, pers. commun.). Crawford and Lutz (1985) found that survival rates of adults in Oregon were similar from 1941 to 1983, even though the population declined.

LIMITING FACTORS

Although many different factors may have contributed to a reduction in Sage Grouse numbers throughout the species' range, most deal with loss of suitable habitat

(Patterson 1952, Eng and Schladweiler 1972, Braun 1995, Braun 1998, Schroeder et al. 1999) and the degradation and fragmentation of remaining habitat (Schroeder 1997, Braun 1998, Schroeder et al. 1999). These alterations due to human encroachment and development as well as changes in climate and predator communities all may affect survival and productivity. A number of more localized disturbances, such as industrial development, have also contributed to the loss of suitable habitat. These potential limiting factors are addressed below.

Agricultural Practices

The demand for productive agricultural land in the 20th century resulted in massive sagebrush eradication programs. This decreased the range of sagebrush and, thus, potential Sage Grouse habitat by an estimated two and a half million ha from 1952 to 1977 (Braun et al. 1977). Cultivation of sagebrush-grasslands has directly resulted in the desertion of at least one lek in Alberta (Dube 1993), and possibly a second (C. L. Aldridge, pers. observ.). Ploughing in Montana reduced Sage Grouse habitat by 16%, including 30% of the wintering range, and the population declined by 73% (Swenson et al. 1987). In addition, birds moving to forage in crop fields can be killed or injured by machines and other farm equipment (Patterson 1952; C. L. Aldridge, pers. observ.). Insecticides and herbicides are potentially lethal to Sage Grouse (Blus et al. 1989), although their use on Canadian rangelands is limited.

Overgrazing has long been suggested as one of the main reasons for declining Sage Grouse numbers (Dalke et al. 1963, Johnsgard 1973, 1983). The declines indicated by lek counts in Alberta since 1968 correspond with an increase in number of livestock

grazing in the southeastern part of the Province (Windberg 1975). The removal of cover by cattle can impact Sage Grouse populations either by reducing habitat suitability, or by increasing the exposure of birds to predators or extreme weather. Grazing may simply decrease the carrying capacity of Sage Grouse habitat (Windberg 1976), especially in years with below average annual precipitation.

Human Disturbance

The unique spring mating rituals of Sage Grouse attract naturalists, researchers, and interested members of the public each year. Nature photographers set up blinds at leks each spring, in an attempt to photograph male Sage Grouse in full breeding display. However, if birds are disturbed at leks, individuals will not return until the next day (C. L. Aldridge, pers. observ.). Continual disturbance at leks could result in abandonment of that site, and may ultimately have detrimental effects on breeding success and survival of the population.

Predation

The predator community on the Canadian prairies has undergone drastic changes in the last 150 years. With the loss of the Plains Grizzly Bear (*Ursus horribilis*) and the Plains Wolf (*Canis lupis*), the coyote is now the top predator. The swift fox (*Vulpes velox*) was extirpated from Canada, although a small population now exists after an extensive reintroduction effort. Raccoons, striped skunks, and red fox, have all increased on the prairies, especially in last half century (see Survival section). Richardson's ground squirrels are potential nest predators of Sage Grouse. While Common Ravens do not

coexist with Sage Grouse in Canada, American Crows and Black-billed magpies are common on the prairies and may be nest predators. These changes in the predator community, combined with alterations in habitat structure and/or species composition, may have resulted in increased predation pressure.

Oil and Gas Exploration

Oil and gas exploration and extraction within the Canadian range of Sage Grouse is a key component of the economies of both Alberta and Saskatchewan. The removal of vegetation for well sites, access roads, pipelines, and associated facilities can reduce and fragment suitable habitat. Human and mechanical activities at well sites may disrupt breeding and nesting activities. Even if sites are reclaimed, birds often fail to return to use these areas as leks, as has been the case for at least one site in Alberta (C. L. Aldridge, pers. observ.). A total of six traditional strutting grounds in Alberta have been disturbed by oil and gas activities in the past, four of which are no longer active (Dube 1993; Aldridge 1998; C. L. Aldridge, pers. observ.).

The construction of power lines to well sites and pump jacks and compressor stations provide perching sites for raptors, likely increasing the risk of predation. Power lines and roads tend to fragment habitat, providing corridors for predators such as coyotes, and making habitat less suitable to Sage Grouse. Sage Grouse have also been killed flying into power lines (Borell 1939; Patterson 1952; C. L. Aldridge, pers. observ.).

Roadways and Traffic

Heavily used roads and highways result in Sage Grouse mortalities (Patterson 1952). Sage Grouse travel on the ground to and from leks and foraging sites, and many individuals are killed by vehicles (Patterson 1952). Some leks are located on frequently traveled roads (Patterson 1952), which can have obvious detrimental effects. In addition, roadways may render leks more visible to humans, which could lead to abandonment if breeding activities are continually disturbed.

Climate

Although Sage Grouse are fairly robust birds, harsh climatic conditions at the northern edge of the species' range may affect populations. Short summers and particularly harsh winters likely reduce the ability of individuals to find enough food in winter months and decrease lipid reserves necessary for reproduction (Back et al. 1987, Hupp and Braun 1989a) and possibly lower overwinter survival (Back et al. 1987).

There is a positive relationship between spring precipitation and Sage Grouse productivity (Gill 1966, Chapter 4). Years with below average spring moisture result in less vegetation growth, potentially reducing Sage Grouse nest success and limiting the availability of lush vegetation that is an important summer dietary component for Sage Grouse, especially chicks. During the 1980s, spring precipitation was considerably lower than the long-term average (Fig. 4.2; Onefour Research Station, Environment Canada). This likely contributed to decreased productivity and survival (Chapters 3, 4).

The effects of other limiting factors may be compounded during drought conditions. For example, consistent cattle stocking rates during the drought of the 1980s

may have resulted in a substantial loss of vegetative cover, perhaps lowering nest success, increasing predation, and possibly lowering overwinter survival (K. J. Lungle, pers. commun.). Impacts may have been particularly severe in more moist habitats, which supply important herbaceous growth during nesting and brood rearing. The attraction of cattle to these areas was probably increased during drought conditions, which may have decreased brood survival.

SPECIAL SIGNIFICANCE OF THE SPECIES

When Sage Grouse were hunted in Canada, they were hunted as a trophy species, rather than for food. Sage Grouse have no current commercial value other their value to the eco-tourism industry, and as an indicator of the health of the prairie ecosystem. With the increasing number of species in peril on the Canadian prairies, interest and concern about Sage Grouse continues to increase. The concern stems from the need to understand the reasons for the continued population decline, and to understand threats that are related to the real and imminent extirpation of Sage Grouse and other species of concern native to the prairie ecosystem.

In part, public interest in Sage Grouse stems from the mating rituals that birds perform each spring at strutting grounds, which are a unique sight on the prairies. With the decline in population numbers, there is an ever-increasing interest by naturalists, biologists, and the general public to observe these displays. Sage Grouse are particularly sensitive to disturbances, and thus, may be a good indicator of the general health of the prairie ecosystem. The Canadian population may offer scientists an opportunity to understand strategies that have enabled species to exist at the fringe of their range.

EVALUATION

Connelly and Braun (1997) reported that range-wide decreases from prior to 1985 to after 1995 averaged 33% (range 17 to 47%). Braun (1998) suggested that overall breeding populations have declined by 45 to 80% since the early 1950s. The decline may have been the most drastic in Canada over the last 30 years; lek counts indicate a decline of between 66 and 92% in Alberta since 1968. The species now occurs in less than 10% of its historic prairie range within Canada. As a result of declining population numbers, the species' limited distribution, and specific habitat requirements, COSEWIC listed Sage Grouse as an Endangered species in 1998 (Hyslop 1998).

Oil and gas activities continue to threaten remaining habitats, and pose many different hazards. Activities in important breeding, nesting, and brood rearing areas, or the alteration of key wintering habitat may have profound negative effects on the population. Combined with recent changes in the predator community, and the loss of suitable nesting and escape cover related to cattle grazing and recent drought on the prairies, changes in land management practices may be needed for the continued existence of these birds in the Canada.

CHAPTER 2. NESTING AND REPRODUCTIVE ACTIVITIES

INTRODUCTION

Sage Grouse (*Centrocercus urophasianus*) across their range have experienced declines ranging from 45 to 80% since the 1950s (Braun 1998) with the majority of the decrease in population size occurring since 1980. The historical declines are attributed to human induced reduction in sagebrush (*Artemisia spp.*) habitats (Patterson 1952, Eng and Schladweiler 1972, Braun 1995, Braun 1998, Schroeder et al. 1999). However, many other factors have altered and fragmented current habitat and may also have contributed to recent population declines. These include the construction of roads, highways, fences and power lines, domestic livestock grazing, and a variety of natural changes [reviewed by Braun (1998) and Schroeder et al. (1999)]. Although these changes affect all aspects of Sage Grouse life history, variation in productivity has been proposed as the most important factor regulating all grouse populations (Bergerud 1988). In some populations, survival has remained relatively constant, while productivity has declined; as for Sage Grouse in Oregon (Crawford and Lutz 1985). Thus, the majority of research on grouse has focused on the relationship between measures of productivity and population dynamics (Bergerud 1988, Schroeder 1997, Schroeder et al. 1999). More recently, there have been attempts to relate productivity to measures of habitat quality (Schroeder 1997; Sveum et al. 1998a, 1998b; Schroeder et al. 1999).

Productivity is often considered in terms of reproductive effort and reproductive success. For the purpose of this study, I define reproductive effort to include nesting effort or attempt(s) and clutch size, whereas reproductive success includes breeding success, nest success, and fledging success (see definition below). However, productivity measures should go one step further and include data on the number of young produced

during the breeding season that survive to age of independence and reproductive maturity (recruitment; Gill 1990). Thus, I consider productivity to include reproductive effort, reproductive success, and recruitment.

Most research on Sage Grouse has shown that population declines are related to reduced nest success (Schroeder 1997, Braun 1998, Schroeder et al. 1999). Stable populations tend to have high nesting success (35–86%) (Dalke et al. 1963; Schroeder et al. 1999; J. W. Connelly, pers. commun.). However, the same factors that affect nesting success, may also affect chick survival and juvenile overwinter survival (recruitment). Little research has been conducted to address issues such as chick survival, primarily due to the difficulties in estimating brood size, and technological limitations making it difficult to affix radio transmitters to juvenile birds.

Sage Grouse are associated with big sagebrush (*A. tridentata* spp.) throughout most of their range; however, the dominant species in Canada is silver sagebrush (*A. cana*) (Aldridge 1998). Silver sagebrush is not as tall or as dense as big sagebrush and, thus, does not provide the same extent of cover for nesting or to escape from predators. Nesting success is higher in areas containing big sagebrush (Wallestad and Pyrah 1974, Connelly et al. 1991, Gregg et al. 1994, Young et al. 1994, DeLong et al. 1995, Schroeder et al. 1999). As a result, the apparently lower quality habitat at the northern fringe of the species range in Canada may limit the population, which might be expected to fluctuate to a greater extent than core populations.

Sage Grouse in Canada have declined to less than 20% of the numbers recorded in the late 1960s in Alberta and the mid 1980s in both Alberta and Saskatchewan (Aldridge 1998, Chapter 1). It has been suggested the decline is related to poor survival

and/or poor productivity; specifically low nesting success. There has been no recent research on Sage Grouse in Canada to address either survival or productivity. I estimated the 1999 Canadian spring population to be 813-1204 individuals (Chapter 1). An average of 15 males were counted on 18 active leks spread over approximately 10,000 km² in Canada (Chapter 1; Aldridge 1998; W. C. Harris, Pers. Commun.). This represents a density of less than one bird/km² in potential habitat in Canada. Density estimates for Sage Grouse in other areas are as high as 15 birds/km² (Patterson 1952, Wallestad 1975, Schroeder et al. 1999). The purpose of this Chapter is to compare the timing of reproductive activities and measures of productivity for a declining Sage Grouse population in apparently sub-optimal habitat at the periphery of the species range, with measures of productivity for other declining (Colorado, Idaho, and Montana) and drastically reduced (Washington) populations. Assuming adult survival is comparable to other populations, I hypothesize the decline observed in the Canadian Sage Grouse population is related to reduced reproductive effort, reduced reproductive success, or a combination of both.

METHODS AND MATERIALS

I monitored the reproductive activities of Sage Grouse within a 4,000 km² area of southeastern Alberta (49° 35' N, 110° 50' W). Silver sagebrush is the dominant shrub and pasture sage (*A. frigida*) the dominant forb. Grasses include speargrass (*Stipa comata*), june grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*) (Aldridge 1998).

I captured females at seven different mating grounds (leks) using walk-in traps (Schroeder and Braun 1991) and with a long handled hoop net and handheld spotlights (Giesen et al. 1982) from March through May 1998 and 1999. Several other females were captured by nightlighting flocks of broodless females in summer. Sex and age [(yearlings < 2 years old) and (adults \geq 2 years old)] of all captured individuals were assigned based on the shape and length of the outermost primaries of each bird (Eng 1955, Crunden 1963, Braun 2000). Captured females were fitted with a 14 g necklace style radio transmitter (RI-2B transmitters; Holohil System Ltd.; Carp, Ontario).

Females were located every second day using a 3-element Yagi antenna and portable receiver (TR2 scanning receiver, Telonics Inc., Mesa, Arizona; Merlin 12 receiver, Custom Electronics of Urbana, Inc., Urbana, Illinois). Standard telemetry techniques were used to determine location of females. Signals were triangulated until birds could be observed from approximately 30 m away. These locations were recorded in Universal Transverse Mercator Coordinates using a hand held 12 Channel Global Positioning System (Garmin 12 XL and GPS II Plus units; Garmin International Inc., Olathe, KS). When signals disappeared, I searched the entire study area from a fixed-winged aircraft.

Measures of reproductive success were calculated in a manner similar to Schroeder (1997). Clutch size was estimated by counting the number of egg shells following either successful hatch or after destruction of the nest. In all cases, egg shells were counted within 3 days of hatch or nest destruction. I estimated the date of nest initiation as the midpoint between the last observation in which the female did not display localized movements and the first direct observation of the hen on a nest. Nest success

was defined as the percentage of nests that hatched ≥ 1 egg. Date of nest success or nest failure was estimated as the midpoint between the last observation of the female on the nest and the first observation in which she was off the nest. Breeding success was defined as the percent of females that hatched ≥ 1 egg during a single breeding season (first or renest). Fledging success was the percent of females that raised at least one chick to independence (assumed ≥ 50 days of age for comparison with other studies; Schroeder 1997). This parameter can be calculated relative to either the number of females that made nesting attempts (Schroeder 1997), or compared to only those females that successfully hatch at least one egg (successful breeders). The latter differentiates between nest success and survival of the brood. I calculated fledging success relative to successful breeders only, because females that are unsuccessful nesters inherently cannot successfully fledge young. However, I also calculated fledging success for all females that attempted to nest, to allow for comparison with other studies. Lastly, I estimated chick survival as the percent of young that lived ≥ 50 days.

Due to a limited sample size of nesting females in 1998 and nesting yearlings throughout the study, I was limited in my analyses of year and age effects. I tested for age related differences in reproduction and timing of reproductive activities, and also for differences in clutch size, nest success, and timing of reproductive events, as they related to first and renesting attempts. Analyses were conducted using one-way Analysis of Variance for clutch size and timing of reproductive events, and a Chi-square test was used to analyse nesting success, fledging success, and breeding success. I conducted all analyses using an α value of 0.05. My productivity measures were then compared with estimates from other populations.

RESULTS

I captured thirty-seven female Sage Grouse on leks and fitted them with radio transmitters; 2 adults and 3 yearlings in 1998; 22 adults and 10 yearlings in 1999. Three additional adult females were captured in summer 1998 and 1 in summer 1999. Two females captured in summer of 1998 were eaten by a predator before the 1999-breeding season and the female captured in summer 1999 had a brood, but was depredate two weeks after capture.

I collected reproductive data for 20 different individual females; 3 females in 1998; 19 females in 1999, 2 of which I collected data in both years. Of a total of 41 radio-marked females, 5 radios apparently malfunctioned and 4 females died prior to the breeding season. I could not relocate 12 of the remaining 32 females during the breeding season; 4 were found dead with damaged transmitters in late spring or early summer and were likely died before nesting; 1 was captured with chicks after nesting; 1 was recaptured on 23 July 1999 with a brood patch but no brood. The fate of 6 females is unknown.

The mean date of capture for 36 females caught during the breeding season was 8 April \pm 1.9 days (SE), while the mean date of maximum attendance of females (breeding) at 7 leks in 1999 was 5 April \pm 0.91 days. This suggests the peak in breeding occurred during the first week of April (1998 data were not used to calculate maximum attendance dates due to limited counts at leks prior to 11 April; one lek in 1999 was not used in the analyses due to limited observations early in the breeding season).

Initiation of Incubation

The mean initiation date of incubation for 25 nests was 10 May (range 22 April to 18 June). Initiation dates were based on restricted movements of females, or the observation of a female under the same shrub on consecutive relocations. Age (adult vs. yearling; $F_{1,23} = 0.004$, $P = 0.95$) did not explain a significant amount of variation in the dates of incubation initiation. Age, however, did explain a significant amount of the variation ($F_{1,18} = 7.34$, $P = 0.01$) for first nesting attempts only. Average date of first nest incubation for adult females (1 May, range 23 April to 10 May) was earlier than that for yearlings (10 May, range 5 to 14 May). Incubation of first nests began approximately 35 days earlier than renesting attempts ($F_{1,23} = 113.45$, $P < 0.001$).

Incubation lengths ranged from 23 to 29 days ($O = 27 \pm 0.6$ days (SE), $n = 10$) and was similar for both first nests and renesting attempts ($F_{1,8} = 0.97$, $P = 0.35$). Hatch date for successful nests ($O = 5$ June ± 4.59 days, $n = 12$) was significantly earlier (33 days) for first nests ($O = 28$ May ± 1.58 days, $n = 9$) than for renesting attempts ($O = 30$ June ± 5.36 days, $n = 3$; $F_{1,10} = 68.97$, $P < 0.001$).

Clutch Size

Clutch size for 28 nests ranged from 4 to 11 eggs. Nest success was independent of clutch size ($O = 7.8 \pm 0.36$, $F_{1,26} = 0.46$, $P = 0.50$), therefore I pooled successful ($O = 8.0 \pm 0.53$, $n=12$) and unsuccessful nests ($O = 7.6 \pm 0.48$, $n = 16$) for analyses. First nests ($O = 8.2 \pm 0.24$ eggs, $n = 23$) had larger clutches than renesting attempts ($O = 5.6 \pm 0.70$ eggs; $n = 5$, Fig. 2.1, $F_{1,26} = 12.38$, $P < 0.002$). Egg viability (% of all eggs laid in successful nests that hatched at least one egg) was 92% (96 of 104 eggs).

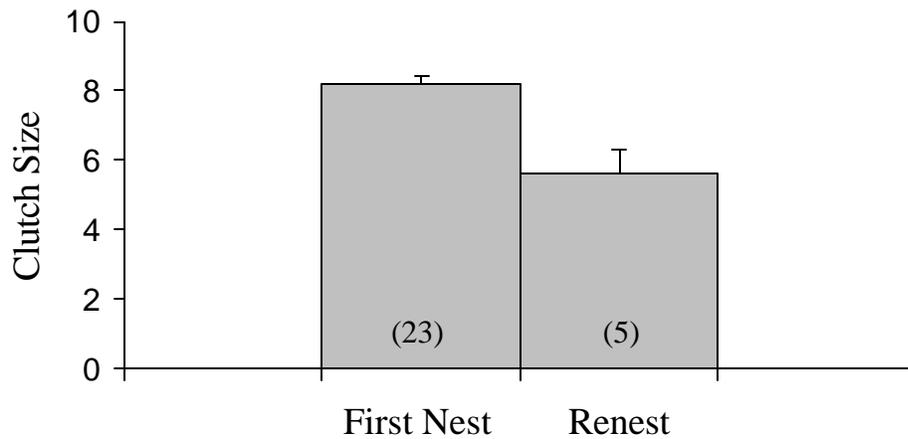


Figure 2.1. Clutch size for first nests and renesting attempts by Sage Grouse in southeastern Alberta in 1998-99. Values are shown as means \pm one standard error. Number of nests is indicated in brackets.

Nesting Attempts

I based my estimate of annual nesting effort on data from 22 females. In all cases, females displayed localized movements within an area and a nest was eventually located after a successful hatch or a predation event. Nesting effort was 100%, with all females attempting to nest.

Nest Success

Overall nest success (percent of all nests that hatched \geq 1 egg) was estimated at 46.2% for 26 nests (1/3 nests in 1998, 11/ 23 nests in 1999). This is actual nest success. I did not use a Mayfield estimator as all females that were tracked attempted to nest (Mayfield 1975). Nest success was independent of nest order (first nest attempt or renest; $X^2_1 = 0.26, P = 0.61$) and female age ($X^2_1 = 0.46, P = 0.50$) although adults (11/22, 50%)

were more successful than yearlings (1/4, 25%). The majority of nest failures occurred in mid-incubation (Fig. 2.2). As a result, I grouped nest failure into four

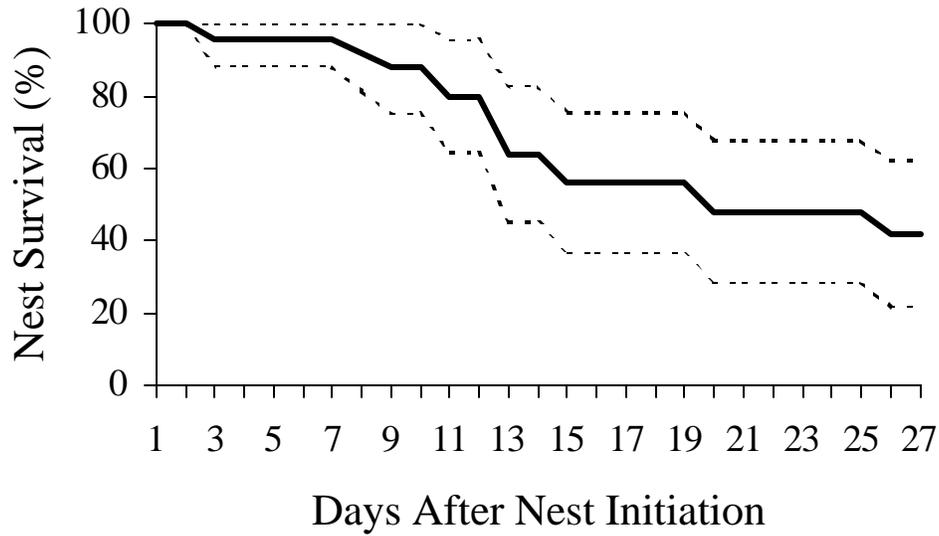


Figure 2.2. Kaplan-Meier product limit estimate for nest survival in relation to date after initiation, for Sage Grouse nests in southern Alberta in 1998 and 1999. The 95% confidence limits are shown by the dashed lines.

separate 7-day stages of incubation (Fig. 2.3). The majority of nest failures occurred between day 8 and 21 of incubation (86%, 12/14 failures). If number of nests entering each time period is considered, the percentage of nests that were destroyed within each stage of incubation was also highest during the second and third weeks of incubation (Fig. 2.3).

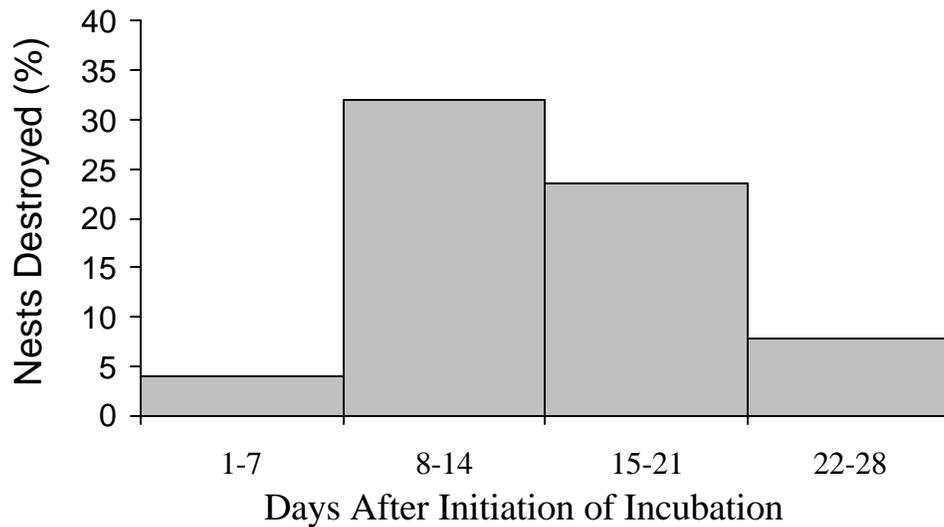


Figure 2.3. Timing of nest failure for 14 unsuccessful Sage Grouse nests in southeastern Alberta in 1998-99. Percentage of nest failures within each of the four categories is calculated based on the number of nests entering that period (including successful nests).

Renesting Likelihood

Only 4 of 13 (30.8%) females that were unsuccessful in their first nest attempts in 1999 renested (4 of 10 adults and 0 of 3 yearlings). Despite the fact that no yearlings attempted to renest, there was no statistically significant age effect on renesting likelihood ($X^2_1 = 1.20, P = 0.27$). In 1998, one adult female was captured at a lek late in the breeding season (22 May) with a well developed brood patch. I assumed she had failed in her first nesting attempt. She did initiate a second nest that year, but was unsuccessful.

Breeding Success

Breeding success was estimated to be 54.5% for 22 females monitored throughout a single breeding season. Breeding success was independent of age ($X^2_1 = 0.78$, $P = 0.38$; adults = 61%, $n = 18$; yearlings = 25%, $n = 4$) although adults appeared to be more successful at hatching at least one egg than yearlings.

Fledging Success

I estimated fledging success to be 22.7% for females that attempted to nest. This was independent of age ($X^2_1 = 0.91$, $P = 0.34$; adults = 27.8%, $n = 18$; yearlings = 0%, $n = 4$). Fledging success calculated for successful breeders was 41.7% ($n = 12$ females). This was independent of age ($X^2_1 = 0.33$, $P = 0.56$; adults = 41.7%, $n = 11$; yearlings = 0%, $n = 1$). Using both methods, fledging success was statistically independent of age, despite the fact that no yearlings successfully fledged chicks. However, these differences are based on only four yearlings.

Chick Survival

Due to the difficulty in locating all chicks when a brooding female was flushed, I estimated chick survival to 50 days of age as a range (minimum and maximum). Chick survival ranged from 13.6 to 22.7% for 88 chicks, with no yearling females successfully rearing chicks to fledge (≥ 50 days of age).

DISCUSSION

Initiation of incubation ranges from late March to mid-May across the species' range (Dalke et al. 1963, Schroeder 1997). Mean nest initiation date was 10 May in my study; 3 May for first nesting attempts. Thus, nesting activities occur later in Canada, even when compared to Sage Grouse with only a slightly more southern latitude in Washington; mean date of incubation initiation in Washington was 22 April (Schroeder 1997). Sage Grouse are at the northern extent of their range in Canada and longer winters may reduce the length of the breeding season and result in later nesting events compared to the rest of their range. Combined with the shorter growing season and the different species of sagebrush, habitat and conditions might always be less suitable in Canada compared to the rest of the species' range.

It is possible that trapping Sage Grouse affects nesting efforts and timing of nesting activities. However, only three individuals trapped in 1998 were relocated in 1999, which did not allow me to test for such effects. Schroeder (1997) found that newly captured female Sage Grouse in Washington nested, on average, one day later than those captured the previous year.

Mean date of hatch in my study was 28 May for first nesting attempts, and 30 June for renests. Kerwin (1971) estimated the mean hatch date for Sage Grouse in Saskatchewan to be in the first or second week of June, which is comparable with my data. The mean date of breeding activities (peak attendance of females at leks) for Sage Grouse ranges from late March to late April (Schroeder et al. 1999, see Chapter 1, Population Trends), and is typically later at more northern latitudes and higher elevations (Petersen 1980). Kerwin (1971) for Saskatchewan and Clewes (1968) for Alberta both

found the peak in breeding occurred at the end of April. The peak in breeding activities in my study occurred in the first week of April, earlier than estimates for Sage Grouse in Canada. These previous studies may have missed the peak in breeding activities or females may have attempted to renest more often, increasing female attendance at leks later in the breeding season.

Incubation length typically ranges from 25 to 29 days (Patterson 1952, Schroeder 1997, Schroeder et al. 1999) but some estimates are as low as 20-24 days (Schroeder et al. 1999). In my study, mean incubation length was 27 days (range 23-29). Incubation was estimated to be 23 days for 2 females; however, both individuals could not be located for several days prior to being observed on the nest, and thus, the incubation time for both is likely underestimated.

Mean clutch size in my study was 7.8, which is high compared to most other studies in North America (typically between 6.6 and 8.2) (Patterson 1952, Wallestad and Pyrah 1974, Petersen 1980, Connelly et al. 1993, Gregg et al. 1994, Schroeder et al. 1999). This was also likely an underestimate, as one female that only had 4 eggs in her nest when it was destroyed, had 6 eggs in her nest 10 days earlier when accidentally flushed (I assumed a clutch of 6 eggs for this female). Similar inferences about clutch sizes being underestimated have also been reported by Schroeder (1997) and it is possible that Richardson's ground squirrels (*Spermophilus richardsonii*), American Crows (*Corvus brachyrhynchos*), or Black-billed Magpies (*Pica pica*) removed eggs during incubation, or removed shells after nest failure or hatch. Schroeder (1997) found that Sage Grouse in Washington had unusually high clutch sizes ($O = 9.1 \pm 1.30$, $n = 55$). Clutch size may be correlated with nutrition (Lack 1968). Schroeder suggested that

nutrition is likely a direct reflection of habitat quality, but a relationship between clutch size and nutrition has yet to be illustrated for any grouse species (Schroeder 1997). Considering that egg production and laying begin in northern grouse populations (where clutch size tends to be larger) prior to the time of new plant growth, spring growth and nutrition should have little effect on clutch size (Bergerud 1988), especially in highly fragmented habitats, as was the case in Schroeder's (1997) study area.

It has been suggested that clutch size for grouse is negatively correlated with annual survival of breeding-age individuals (Bergerud 1988). Bergerud further suggested that grouse with annual survival rates of $\geq 50\%$ had low clutch sizes (5-8 eggs), and grouse with survival rates $\leq 45\%$ had large clutches (9-13 eggs). He based his hypothesis on a Sage Grouse population with a 40% survival rate for breeding age individuals and a clutch size of about 8. Schroeder (1997) found survival to be high (55 to 75%) and clutch sizes large ($O = 9.1$) and concluded that the Washington Sage Grouse population did not fit Bergerud's hypothesis. Survival of females in my study was below 56.5% if potential fall and winter mortality is considered (Chapter 4, Table 4.1). Thus, with a relatively high clutch size of 7.8 eggs per nest (8.0 for successful nests) and higher survival rates than in Bergerud's (1988) synthesis (40%), my data support Schroeder's contention that Sage Grouse clutch size is not negatively correlated with survival. However, my data for survival by breeding age males (31%) and females ($\leq 56.5\%$) are both lower than typically reported for Sage Grouse (males 38-60%, females 55-75%) (Schroeder et al. 1999), yet clutch size was at the high end of the range for Sage Grouse (6.6-9.1) (Schroeder et al. 1999). Bergerud (1988) suggested that clutch size should also decrease with increasing risk of predation. Schroeder (1997) reported high levels of nest predation

in his study (nest success was low at 36.7%) and, thus, clutch size should have been lower rather than increased, due to the high risk of predation.

Clutch size in some populations of Sage Grouse is age-specific, with adults having larger clutches (Wallestad and Pyrah 1974, Petersen 1980), although Schroeder (1997) found no differences. My sample sizes do not permit a test of whether adults produced larger clutches than yearlings. Capture rates for Sage Grouse indicate that yearlings are under represented in the population (3 to 1 adult to yearling ratio; Chapters 1, 4). Assuming that adults produce larger clutches than yearlings, the large proportion of adults in this population may have influenced mean clutch size in my study.

Previous research using telemetry has shown that in any year, 20 to 32% of females do not nest (Wallestad and Pyrah 1974, Connelly et al. 1993, Gregg et al. 1994, Schroeder et al. 1999). However, my results are consistent with Schroeder's (1997) findings for Washington, which indicate that all females make nesting attempts. Based on follicular development, 98% of 338 females in Idaho (Dalke et al. 1963) and 91% of 395 females in Colorado (Braun 1979) ovulated, suggesting that nearly all females mated and attempted to nest. It is likely that previous telemetry studies have underestimated nesting attempts. Reproductive activities may also be influenced by intrinsic factors such as density dependence and local survival rates (Bergerud 1988). High densities could conceivably result in competition by females for nest sites, to the point of precluding some females from nesting. In low density populations (e.g., Washington and Canada), competition for nest sites may not exist and, thus, all females attempt to nest.

Two studies have shown that Sage Grouse select nest sites independently of lek location (Bradbury et al. 1989, Wakkinen et al. 1992). However, while nest locations

may be random with respect to lek locations (Wakkinen et al. 1992), the average distance that females nest from the lek where they were captured ranges from 4.0 km in Colorado (Petersen 1980) to 7.8 km in Washington (Schroeder et al. 1999), with the majority of nests occurring within 3.2 km of a lek (80% within 3.2 km, Martin 1970; 92% within 3.0 km, Wakkinen et al. 1992; and 68% within 2.5 km, Wallestad and Pyrah 1974). In areas where habitat is more fragmented and of poor quality, nest success and survival would be expected to decline. However, habitat quality could indirectly affect reproductive efforts, including both nesting and reneating likelihood. Poor quality habitat could force females to search over larger areas for suitable nesting sites. It has been suggested that nest-lek distances may be inversely correlated with habitat quality (Autenrieth 1981). The largest known mean nest-lek distance of 7.8 km was found in a highly fragmented habitat in north-central Washington (Schroeder et al. 1999).

Average nest to lek distance in my study was 4.7 km (\pm 0.66 km; range 0.42-15.45 km) with only 40.7% of 27 nests occurring within 3.2 km of the lek. This suggests that suitable nesting habitat within the Canadian range may be limiting, and females are moving considerable distances to locate suitable habitat. The costs associated with extended search efforts and increased movements to locate suitable nest sites could result in reduced reproductive effort and/or success. This did not appear to be the case in Washington as all females attempted to nest; however, it may have affected nesting success, which was low (36.7%) (Schroeder 1997). Although Sage Grouse in my study moved greater distances to locate suitable nest sites, all females attempted to nest, had relatively large clutches, and were fairly successful nesters, when compared to other populations.

Based on the population estimates from my study, I conclude that reproductive effort is not the cause of the decline of the Canadian Sage Grouse population. All females attempted to nest and clutch size was within the expected range.

In a recent review, Schroeder et al. (1999) showed that Sage Grouse nest success ranges from 15-86% throughout North America. In nine of fourteen studies for which there are productivity data, nest success was between 30 and 60%. Nest success in my study (46.2%) is within this range. However, spring precipitation (April - June) was above average in both years of my study (1998 = 152.5 mm, 1999 = 159.5 mm, 1965-1999 0 = 133.5 mm; Onefour Research Station, Environment Canada). Gill (1966) found a weak positive correlation between nest success and spring precipitation, suggesting the increase in spring moisture likely resulted in above average nest success in my study.

The probability of renesting by radio-marked Sage Grouse in my study was 30.8%. Renesting varies from 5 to 87% for other populations (Schroeder et al. 1999). Schroeder (1997) suggested that estimates of renesting and nest success would be negatively correlated with a researcher's ability to find all nests, as successful nests are easier to locate. If nests that have been destroyed prior to incubation are not located, nest success and renesting attempts will be underestimated. It is possible that I missed some first nesting attempts, underestimating nesting effort. However, most females that were tracked after their capture, displayed localized movements and, in all cases, a nest was subsequently found.

The mean capture date of females on leks was 8 April. Most females returned to the lek for approximately 3 days after capture (C. L. Aldridge, pers. observ.) and, thus, 11 April is a reasonable date to assume that females began searching for suitable nest sites.

Patterson (1952) suggested that egg laying begins a few days after females move from leks to nesting areas. Thus, I estimate that the mean date of egg laying for initial nests based on lek attendance would be 16 April. With a mean clutch size of 8.2 for first nests, and 1.3 days between the laying of successive eggs (Patterson 1952), egg laying should last approximately 11 days. Combined with mean incubation time of 27 days, egg laying and incubation would last approximately 38 days for first nests. Thus, based on peak attendance of females at leks, mean hatch date for first nests should have occurred on approximately 24 May. Mean hatch date for first nesting attempts was 28 May, only four days after that predicted by female movements. This strongly supports my contention that I did not miss any first nesting attempts. However, the estimated 38 days from breeding to hatching of clutches is probably minimal.

Bergerud and Gratson (1988) hypothesized that renesting in grouse should be negatively correlated with female life expectancy; similar to Bergerud's (1988) hypothesis that clutch size was negatively correlated with life expectancy. It is conceivable that nesting likelihood is also negatively correlated with survival. Sage Grouse are relatively long lived compared to other grouse (Patterson 1952, Bergerud 1988, Bergerud and Gratson 1998) and, if the hypothesis is true, should exhibit low renesting rates. However, survival of females in my study was less than 56.5%, which is low compared to female survival estimates in other populations (range 55-75%; Schroeder et al. 1999). Therefore, given the low survival probability, renesting rates of Sage Grouse in Canada should be high, yet I found only 30.8% of females attempted to renest. These data do not support the hypothesis that renesting is negatively correlated with life expectancies of breeding-age females (Bergerud and Gratson 1988). Schroeder

(1997) found that Sage Grouse in Washington also do not fit the reneesting hypothesis, with high reneesting rates (87%) and high annual female survival (55-75%).

Survival estimates in this population may be underestimated due to the biases associated with radiotelemetry studies. However, survivorship for other populations was also ascertained using radiotelemetry and thus, my estimates should be comparable.

I expected that nests have an overall greater likelihood of hatching the longer they survived, because vegetation structure should increase, better concealing nests from predators. This effect should be enhanced over the course of this study due to the moist springs of 1998 and 1999. This was the case, with nest failure greatest during the second week of incubation and declining over the third and fourth weeks of incubation (Figs. 2.2, 2.3).

Breeding success has been reported to range from 15-70% (Schroeder et al. 1999). In my study, breeding success (54.5%) was higher than reported in 6 of 8 previous studies (see Schroeder et al. 1999). This implies that breeding success is not limiting the Canadian population. However, similar to nest success, breeding success may have been elevated over the course of my study due to higher than average spring precipitation.

Overall, nest success and breeding success for Sage Grouse in Alberta were comparable to other populations. Fledging success estimated from those females that were successful breeders was 41.7%, indicating that less than half of all broods had at least one chick survive to the fall. However, when compared to Schroeder's (1997) estimate of fledging success calculated from all nesting attempts (49.5%), fledging success in my study was lower (27.7%), despite high nesting success. Female Sage

Grouse tend to flock together with other females when they loose their broods (C. L. Aldridge, pers observ., C. E. Braun, Pers. Commun.). Thus, I am confident that brood survival was not underestimated. This suggests that low overall brood survival could be causing decreased reproductive success for Sage Grouse in Canada.

Brood counts are often used to estimate chick survival for grouse. However, it is often difficult to locate all chicks associated with a brood, and a direct relationship between brood flush counts and actual brood size has yet to be shown. Brood size for Sage Grouse declines during the summer by as much as 68.4% (Schroeder et al. 1999), which may reflect the characteristic low survival rates for juveniles. However, Schroeder (1997) estimated chick survival in Washington at 33.4% and June (1963) reported that 38% of Sage Grouse chicks in Wyoming survived to the autumn. Both populations showed slight decreases over the course when the studies were performed (June 1963; M. A. Schroeder, pers. commun.). This suggests that chick survival of at least 35% may be required to sustain a Sage Grouse population, assuming reasonable levels of reproductive effort and reproductive success. Even though reproductive effort, and, for the most part, reproductive success (fledging success was low) for Sage Grouse in Canada is comparable to other studies, chick survival to 50 days of age (14-23%) was less than half of the estimated 35% survival required for stable populations.

Spring precipitation was above average over the course of my study. While spring precipitation has been linked to increased nest success (Gill 1966), Peterson (1970) also found that wet years resulted in greater forb production and increased brood success in Montana. My estimates of chick survival could also be elevated due to increased spring precipitation.

With brood counts indicating that chick survival was extremely low, I expected low recruitment rates. Several long-term studies that involve capturing Sage Grouse have shown that between 44% (n = 440; Dalke et al. 1963) and 46% (n = 1371; Braun and Beck 1985) of captured birds are yearlings. Over the two years of my study, I captured 96 different Sage Grouse and only 25% were yearlings. This suggests that overall recruitment is low for the Canadian population (Figs. 1.5, 1.6).

From 1996 to 1999 the Canadian Sage Grouse population has remained relatively stable, at low numbers, despite apparently low chick survival. However, over the course of my study (1998-99), nest success and breeding success were likely inflated due to increased spring precipitation (Fig. 4.1) (June 1963, Gill 1966), possibly masking the effects of low chick survival. The ultimate test of these predictions will be evaluated by assessing population status in 2000.

I conclude that reproductive effort (clutch size, nesting effort) does not appear to be related to Sage Grouse population declines in Canada. Reproductive success in this study, including nesting success, breeding success, and fledging success, was comparable to other populations, however, these measures of productivity may have been elevated throughout my study due to above average spring precipitation. Overall, productivity appears to be limited by low chick survival (14-23% compared to 35% in other populations). Food availability and quality may influence chick survival (Pyle and Crawford 1996) as well as clutch size (Lack 1968) and nest success. Habitat quality may also affect productivity (Sveum et al. 1998a) and may be directly related to food availability and quality for chicks (Chapter 3). Sage Grouse in Canada exist at some of the lowest known densities (< 1 bird/km²; Chapter 1). The carrying capacity of the

population may be limited due to decreased productivity and possibly poor chick survival, as a result of limited availability of mesic habitats with higher forb availability (Chapter 3). Over the course of this study, estimates of reproductive effort, nest success, and breeding success suggest that suitable habitat may be limiting for Sage Grouse in Canada. These results are based on two years of data, with most data from 1999. In both of these years, spring precipitation was above the 35-year average, which may have increased habitat quality and elevated my measures of productivity compared to average productivity over the last 20 years. Even though this may have been the case, chick survival was still extremely low, and availability and/or quality of food resources for chicks, may affect chick survival and/or increase the chance of chick predation (Chapter 3). Overwinter mortality of juvenile Sage Grouse, which was not measured in this study, may add to the already low estimates of recruitment.

CHAPTER 3. NESTING AND BROOD HABITAT USE

INTRODUCTION

The distribution of Sage Grouse throughout North America has been reduced by at least 50% since the early 1900s. Populations have been extirpated from five of 16 states and one of three provinces (Braun 1998). Population declines averaged 33% from 1985 to 1995 (Connelly and Braun 1997) and declines from 45 to 80% have occurred since the 1950s (Braun 1998). The most severe declines have occurred at the northern fringe of the species' range, where the Alberta population has decreased by 66 to 92% since 1968 (Chapter 1). The historical range within Alberta and Saskatchewan has been reduced by approximately 90% (Figure 1.2, Chapter 1).

Long term data on Sage Grouse population trends in Oregon suggest that a 60% decline in numbers is related to changes in productivity (Crawford and Lutz 1985). Changes in productivity can be attributed to changes in reproductive effort (nesting effort and clutch size), reproductive success (nest success, breeding success, fledging success, chick survival), and/or post fledging mortality (Chapter 2). Many studies of declining Sage Grouse populations have investigated reproductive effort and measures of reproductive success. Population declines appear to be linked to nest success and/or measures of brood survival (Crawford and Lutz 1985, Schroeder et al. 1999). Unsuitable nesting and brood rearing habitat may contribute to decreases in productivity by reducing nest success and/or chick survival (Crawford and Lutz 1985, Sveum et al. 1998a).

Sage Grouse tend to place their nests under sagebrush (*Artemisia spp.*, > 90% of 154 nests in Wyoming, Patterson 1952; 91% of 87 nests in Idaho, Klebenow 1969; 79% of 83 nests in Idaho, Connelly et al. 1991; 71% of 93 nests in Washington, Sveum et al. 1998b). Greater canopy cover of shrubs (primarily sagebrush) is preferred (Patterson

1952, Klebenow 1969, Wallestad and Pyrah 1974, Schroeder et al. 1999), particularly shrubs of medium height (40-80 cm; Gregg et al. 1994, Sveum et al. 1998b). Nests with greater overall shrub cover are more successful (Wallestad and Pyrah 1974, Connelly et al. 1991, Sveum et al. 1998b). Tall grass cover is also selected in areas immediately surrounding nest sites and is positively correlated with nest success (Gregg et al. 1994, Sveum et al. 1998b). Some nests are placed under shrubs other than sagebrush (Patterson 1952, Klebenow 1969, Connelly et al. 1991, Gregg et al. 1994) and it may be that females select nest sites based on suitable cover, not by shrub species. Klebenow (1969) suggested that females might be reacting to the uneven distribution of preferred cover within the available habitat.

Grouse may or may not select for sagebrush at brood rearing locations (Sveum et al. 1998a) but forb cover is greater at brood use sites than at random sites, particularly cover of forbs used as food (Klebenow and Gray 1968, Peterson 1970, Schoenberg 1982, Drut et al. 1994a, Sveum et al. 1998a). Brood habitat tends to shift from sagebrush uplands early in the brood rearing period, to more mesic sites later in the summer (Patterson 1952, Peterson 1970, Autenrieth 1981, Dunn and Braun 1986b). This shift is usually a result of the desiccation of forbs in sagebrush uplands and an increase in forb growth at more mesic sites later in the summer (Dunn and Braun 1986b). The initial selection for sagebrush at brood rearing sites may be linked to a female's choice of nest sites, as sagebrush is a relatively minor component of the diet of nesting females and juveniles ≤ 10 weeks of age (Patterson 1952, Klebenow and Gray 1968, Peterson 1970).

Few studies have assessed whether habitat selection by Sage Grouse is based on a minimum patch size of certain vegetation characteristics. Dunn and Braun (1986b)

measured horizontal cover 5 and 10 m from the center of summer use sites. They found that the extent of horizontal cover at 5 m, but not 10 m, contributed to statistically differentiating between summer use versus random sites. Data from telemetry studies indicate that Sage Grouse select for certain vegetation characteristics at nest sites and brood sites (Patterson 1952, Peterson 1970, Wallestad and Pyrah 1974, Schoenberg 1982, Dunn and Braun 1986b, Drut et al. 1994a, Gregg et al. 1994, Sveum et al. 1998a, Sveum et al. 1998b). However, no attempt has been made to address the scale at which selection is taking place. Nest success and brood survival should be related to the scale at which a female selects habitat patches, which implies that females select nest and brood rearing locations based on vegetation characteristics of a certain patch size.

The purpose of this study was to ascertain if Sage Grouse are selecting nest locations and brood locations based on vegetation characteristics, and if there are certain scales at which they are selecting habitat. I tested the null hypotheses that there were no differences in vegetation characteristics between successful and unsuccessful nests, and that there were no differences between nest locations and random sites, or brood locations and random sites. I also tested the null hypothesis that Sage Grouse were not selecting nesting or brood rearing locations based on a patch size of 7.5 and/or 15 m radius surrounding nests and brood sites.

METHODS AND MATERIALS

I monitored the habitat selection of Sage Grouse within a 4,000 km² area of southeastern Alberta (49° 35' N, 110° 50' W). Silver sagebrush (*A. cana*) is the dominant shrub and pasture sage (*A. frigida*) the dominant forb (Madsen 1995a, Aldridge

1998). Common grasses include speargrass (*Stipa comata*), june grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*) and western wheatgrass (*Agropyron smithii*).

I captured females at 6 of 8 known active mating grounds (leks) from March through May 1998 and 1999 using walk-in traps (Schroeder and Braun 1991) or with a long handled hoop net and handheld spotlight (Giesen et al. 1982). Several females were captured by nightlighting flocks of broodless females during summer. Sex and age [(yearlings < 2 years old) and (adults \geq 2 years old)] of all captured individuals were assigned based on the shape and length of the outermost primaries (Eng 1955, Crunden 1963, Braun 2000). Captured females were fitted with a 14 g necklace style radio transmitter (RI-2B transmitters; Holohil System Ltd. Carp, Ontario).

I used a 3-element Yagi antenna and portable receiver (TR2 scanning receiver, Telonics Inc., Mesa, Arizona; Merlin 12 receiver, Custom Electronics of Urbana, Inc., Urbana, Illinois) to locate females every other day during the nesting period (Musil et al. 1994, Schroeder 1997). Locations were recorded in Universal Transverse Mercator Coordinates using a hand held 12 Channel Global Positioning System (Garmin 12 XL and GPS II Plus units; Garmin International Inc., Olathe, Kansas). When signals disappeared, I searched the study area from a fixed-winged aircraft.

When approaching a nest, signals were triangulated until the marked bird could be observed from approximately 30 m to minimize disturbance (after Schroeder 1997). Nest site characteristics were measured similar to Klebenow (1969), Wallestad and Pyrah (1974), Musil et al. (1994) and Commons (1997). At each nest site, I estimated the percent sagebrush canopy cover, as well as the percent cover of grasses, palatable (to

Sage Grouse) forbs, non-palatable forbs, other shrubs, and bare ground/dead materials within a 1 m² quadrat using a protocol similar to Daubenmire's (1959) method. The mean maximum heights of the vegetation types were also calculated for each plot using three measurements for each vegetation class. To identify the scale at which habitat characteristics might be selected, I took measurements at the nest itself as well as at 8 additional dependent non-random 1 m² plots. The additional plots were placed 7.5 and 15 m away from the nest site in each of the four ordinal directions. I used a similar method to Canfield's (1941) line intercept method to estimate the canopy cover of live sagebrush along the four 15 m transects radiating from the nest site in each ordinal direction. I estimated the density of sagebrush by counting the number of plants within 0.5 m of the transect (Commons 1997). The mean height of sagebrush along these transects was also estimated. Measurements were recorded separately for the first and second half (7.5 m each) of the transect.

Measurements of habitat characteristics were also taken at a dependent random site using the same protocol for plots and line transects. I chose the random location by walking 100 to 500 m (distance randomly chosen) in a random direction from the nest site (dependent random plots). The closest sagebrush plant to the random location was used as the "random" nest site, since the majority of nests are under sagebrush (Patterson 1952, Klebenow 1969, Connelly et al. 1991, Sveum et al. 1998b). The dependent non-random plots represented non-nest site characteristics within the same sagebrush "stand", and the dependent random plots represented non-nest site characteristics from different stands.

I considered a nest successful if the amniotic membranes of one or more egg shells in the nest were detached (Schroeder 1997). A nest was considered unsuccessful if eggs were broken, or the membranes of egg shells remained intact. Vegetation characteristics were measured at nest and random locations immediately following a successful hatch, or after a predation event.

Broods were located regularly using telemetry; typically I attempted to get within 100 m of females and their broods once per week. These locations were used for habitat analyses. I tried not to flush females and their broods at an early age (≤ 3 weeks of age). Older broods were intentionally flushed once per week to estimate chick survival. Brood “use” locations were recorded in Universal Transverse Mercator Coordinates (UTMs), and I returned the following day to measure vegetation characteristics. I performed the same vegetation measurements at brood use locations and corresponding dependent random locations that I performed for nests.

Most vegetation variables had non-normal distributions and the means of some variables were somewhat correlated with the variances, therefore, I log transformed all variables. However, for reporting purposes, I present means and standard errors of the un-transformed data.

I used forward stepwise Discriminant Functions Analysis (DFA) to determine if a linear function of one or more variables discriminated between successful and unsuccessful nest locations. I also used DFA to determine if early and late brood rearing periods could be differentiated based on vegetation characteristics. I used a multivariate paired T-test (T^2 ; Morrison 1990) to test for differences between vegetation characteristics at use (nests and broods) and random locations. I chose a paired design to

account for individual micro-site differences, and because my random locations were dependent on use site locations. I chose a multivariate test which allowed me to investigate potential interactions between variables and identify overall differences between habitat at use and random locations. When the overall model was significant, I used a post-hoc limits test of confidence intervals to test for differences between nests or brood locations and random locations. If the 95% confidence interval difference for the tested variable did not include zero, the variable was considered to make a significant contribution to the model.

All analyses were conducted at four different scales. First, a test was completed using only the 1 m² plot at the use “site” (nest or brood) to differentiate between vegetation characteristics at use sites alone (successful vs. unsuccessful nests and nest or brood use sites versus random sites). I analysed vegetation characteristics for nesting/brood rearing “areas” by averaging the measurements from all nine plots for each use and random location. I analysed vegetation characteristics at two intermediate scales by averaging measurements from the four plots at the 7.5 m radius and the four plots at the 15 m radius (successful vs. unsuccessful nests and nest/brood versus random). For all analyses, results were considered significant when alpha was < 0.05. Where necessary, I applied a Bonferroni correction (Sokal and Rolf 1995).

RESULTS

I captured and fitted 7 females (4 adults and 3 yearlings) with transmitters in 1998 and 34 females (23 adults and 11 yearlings) in 1999. Due to predation events, difficulties with two transmitters, the unknown fate of some females, and the fact that some females

were captured after the breeding season, data were collected for 22 females over individual breeding seasons.

I had eleven habitat variables (Table 3.1) from plot measurements available to enter into all models. I chose to enter only cover types into each model, as some variables were highly correlated with height ($R > 0.70$, using a correlation matrix for all use and random habitat measurements combined), indicating these variables measured similar habitat characteristics (Table 3.1). Cover and height measurements for shrubs ($R = 0.928$) and unpalatable forbs ($R = 0.810$) were correlated and measured the same characteristics (Table 3.1). While the correlation between cover and height for other vegetation measurements was not as strong ($R < 0.70$), each cover type was somewhat correlated with height measurements of the same class ($P \leq 0.01$, Table 3.1). Therefore, I chose to enter only selected cover types and not vegetation heights into my models. Bare ground was highly correlated with grass cover only ($R > 0.70$, Table 3.1) and was inversely correlated to the sum of all cover types, thus, it was not entered into any models. Unpalatable forbs represented a small percentage of cover at all habitat sites (use and random combined; $O = 1.1 \pm 0.06$) and this variable was not included in any models. Thus, the variables that I entered into all models were sagebrush cover, shrub cover, palatable forb cover, and grass cover. I did not incorporate line transect data into models, as they were measured at different scales. Measurements of both sagebrush density and line intercept of sagebrush along transects were both highly correlated with sagebrush cover estimates from plots ($R = 0.811$, Table 3.1) and thus reflected biologically similar characteristics. I analysed transect data individually using univariate statistics to compare sagebrush characteristics.

Table 3.1. Spearman rank correlations for vegetation variables measured at all Sage Grouse nest, brood, and random locations combined. Data for plot variables were averaged for all nine plots, and data for line transects were averaged for all four 15 m transects. Using a Bonferroni Correction, $\alpha = 0.003$.

	R	t-value	<i>P</i> value
PLOT VARIABLES n=240			
Sagebrush Cover * Height	0.597	11.49	≤ 0.0001
Shrub Cover * Height	0.928	38.40	≤ 0.0001
Unpalatable Forb Cover * Height	0.810	21.30	≤ 0.0001
Palatable Forb Cover * Height	0.539	9.88	≤ 0.0001
Grass Cover * Height	0.209	3.30	≤ 0.001
PLOT VARIABLES and DEAD/BARE			
Bare/Dead * Sagebrush Cover	-0.070	-1.08	0.28
Bare/Dead * Shrub Cover	-0.144	-2.24	0.03
Bare/Dead * Unpalatable Forb Height	-0.141	-2.19	0.03
Bare/Dead * Palatable Forb Cover	-0.307	-4.98	≤ 0.0001
Bare/Dead * Grass Cover	-0.792	-19.98	≤ 0.0001
SAGEBRUSH PLOTS and LINE TRANSECTS			
Sagebrush Cover * Line Intercept - Cover	0.906	32.94	≤ 0.0001
Sagebrush Cover * Line Transect Height	0.472	8.24	≤ 0.0001
Sagebrush Cover * Line Transect Density	0.811	21.37	≤ 0.0001
Sagebrush Height * Line Transect Height	0.742	17.04	≤ 0.0001

Nests

In 1998, three nests of radio-marked birds were located and two additional nests of unmarked females were found. In 1999, I located 24 nests used by radio-marked birds, for a total of 29 nests. Due to the small number of nests located in 1998, I did not statistically test for between year differences in vegetation characteristics. Yearlings made four nests, adults made 23 nests, and two nests were of by unmarked females of unknown age.

Vegetation characteristics were measured at all 29 nest locations (14 successful and 15 unsuccessful nests) and 29 dependent random locations. Nest success in my study (percent of all nests that hatched ≥ 1 egg including renesting attempts) was 46.2% for 26 nests; 1/3 nests in 1998, 11/23 nests in 1999 (Chapter 2). Three nests were not included in this nest success estimate due to difficulties with one transmitter, and the biases inherent in locating successful versus unsuccessful nests of unmarked birds.

Twenty-six of 29 (89.6%) nests were located under silver sagebrush (*A. cana*). One of the three nests not under sagebrush was under snowberry (*Symphoricarpos albus*), one was in tall grass along an irrigation dike (although there were some dead shrubs present of an unidentified non-native *Artemisia* species), and the other nest was under an uprooted tumbleweed (*Salsola kali*) plant in a wheat stubble field. Two of 26 nests under sagebrush had $\leq 15\%$ cover of sagebrush, but greater than 50% canopy cover of other shrubs (snowberry and rose, *Rosa spp.*).

Nesting Habitat Characteristics by Nest Fate

I incorporated grass height into the DFA model to test for differences between successful and unsuccessful nests only. Grass cover was only weakly correlated with grass height ($R \leq 0.209$, Table 3.1) and in two artificial nest predation experiments in the study area, grass height was shown to be an important variable predicting nest fate (Seida 1998, Watters 1999). At nest “sites” (1 m² plot over nest), successful nests had greater sagebrush cover, shrub cover, and forb cover but lower grass cover. Vegetation variables in all five-cover types were taller at successful nests (Table 3.2). Sagebrush cover was the dominant cover type both at successful ($32.9\% \pm 7.05$) and unsuccessful nests ($31.0\% \pm 4.58$; Table 3.2). However, the DFA contrasting successful nests and unsuccessful nests was not statistically significant ($F_{4, 24} = 2.69$, $P > 0.068$).

Overall (all 9 plots combined), successful nesting areas could be statistically differentiated from the areas surrounding unsuccessful nests, as they had taller grass but less grass cover ($F_{2, 26} = 6.17$, $P < 0.006$; Table 3.2). The DFA allowed for correct classification 75.9% of the time (Table 3.3). Successful nests were at the positive end of the discriminant function axis and unsuccessful nests at the negative end for all scales tested (1, 7.5, 15, m and over all 9 plots). Grass cover [Wilks' $\lambda = 0.937$, $P < 0.004$, Standardized Canonical Coefficient (SCC) = -1.039] contributed the most to the discriminant function. Grass height (Wilks' $\lambda = 0.830$, $P = 0.023$, SCC = 0.845) was also significant in the model (Table 3.3). Thus, at successful nests, there was less grass cover, but taller grass (Table 3.2). The squared Mahalanobis distance (a measure of the distance between two centroids on a linear axis) between successful and unsuccessful nest locations (1.90) was significant ($F_{2, 26} = 6.17$, $P < 0.0064$).

Table 3.2. Vegetation characteristics at successful and unsuccessful nests. Values are shown as means \pm one standard error. Variables with a (*) were entered into the Discriminant Functions Analysis. Means with a (*) contributed significantly to discriminating between successful (n=14) and unsuccessful (n=15) nests for that scale ($P < 0.05$, Table 3.3).

Variables	Nest Site		7.5 m Plots		15 m Plots		All 9 Plots	
	Successful	Unsuccessful	Successful	Unsuccessful	Successful	Unsuccessful	Successful	Unsuccessful
COVER (%)								
Sagebrush Cover*	32.9 (7.05)	31.0 (4.58)	7.9 (1.57)	7.3 (1.7)	8.5 (2.50)	6.3 (1.43)	10.9 (2.03)	9.5 (1.57)
Shrub Cover*	8.9 (4.89)	6.0 (5.65)	2.2 (1.5)	4.3 (3.46)	1.4 (0.69)	1.9 (1.04)	2.6 (1.16)	3.4 (2.6)
Unpalatable Forb Cover	0.7 (0.49)	0.0	0.4 (0.20)	1.4 (0.49)	0.4 (0.28)	0.8 (0.26)	0.4 (0.24)	1.0 (0.30)
Palatable Forb Cover*	10.4 (2.06)	6.0 (0.72)	13.9 (2.75)	7.0 (1.03)	10.3 (2.11)	8.7 (1.20)	11.9 (2.09)	7.6 (0.84)
Grass Cover*	26.8 (5.61)	36.7 (5.47)	33.2* (5.80)	49.7* (3.78)	36.2* (5.32)	51.3* (4.51)	33.8* (5.36)	48.9* (3.60)
Dead/Bare Ground	20.4 (6.08)	20.3 (6.01)	42.4 (6.51)	30.3 (4.46)	43.3 (6.89)	31.1 (4.47)	40.4 (6.47)	29.5 (3.93)
HEIGHT (cm)								
Sagebrush Height	42.0 (6.69)	40.7 (4.04)	18.6 (2.98)	22.9 (3.88)	20.2 (4.31)	26.4 (4.48)	24.4 (4.31)	28.5 (3.43)
Shrub Height	12.1 (5.73)	5.4 (3.89)	5.9 (2.41)	10.5 (4.28)	6.1 (2.91)	12.2 (5.72)	15.2 (4.46)	16.1 (5.90)
Unpalatable Forb Height	0.9 (0.63)	0.0	0.6 (0.33)	4.3 (1.16)	0.4 (0.27)	3.8 (1.13)	1.1 (0.52)	4.9 (1.1)
Palatable Forb Height	20.1 (3.85)	11.2 (1.88)	17.4* (2.91)	10.1* (1.73)	17.0 (2.75)	10.7 (1.22)	18.5 (2.45)	10.8 (1.24)
Grass Height*	37.0 (6.53)	25.3 (2.83)	29.9* (3.61)	24.8* (2.60)	32.8* (3.98)	23.0* (2.26)	31.6* (4.06)	24.4* (2.25)

The DFA at the 7.5 m scale (4 plots at 7.5 m) was significant ($F_{2, 26} = 3.77$, $P < 0.023$) and correctly classified nest fate 72.4% of the time (Table 3.3). Grass cover, which was greater at unsuccessful nesting areas at 7.5 m, contributed the most to the discriminant function (Wilks' $\lambda = 0.908$, $P < 0.009$, $SCC = -0.926$). Palatable forb cover (Wilks' $\lambda = 0.740$, $P < 0.077$, $SCC = 0.494$) and grass height (Wilks' $\lambda = 0.725$, $P < 0.260$, $SCC = 0.430$) made smaller but significant contributions to the discriminant function and were both greater at 7.5 m surrounding successful nests. The squared Mahalanobis distance between successful and unsuccessful nest locations (1.81) was significant ($F_{2, 26} = 3.77$, $P < 0.0232$; Table 3.3).

At the 15 m scale (4 plots at 15 m), successful nest locations also had less grass cover but significantly taller grass (Table 3.2). The DFA was significant ($F_{2, 26} = 8.056$, $P < 0.005$) and allowed for correct classification of nest locations 82.8% of the time. Grass cover again contributed the most to the discriminant function (Wilks' $\lambda = 0.861$, $P < 0.003$, $SCC = -0.979$). Grass height also significantly contributed to the model (Wilks' $\lambda = 0.862$, $P \leq 0.003$, $SCC = 0.980$). The squared Mahalanobis distance between the groups (2.48) was significant ($F_{2, 26} = 8.05$, $P < 0.005$; Table 3.3).

Nest Habitat

Nests could be significantly differentiated from random sites by vegetation characteristics ($T^2 = 18.35$, $P \leq 0.001$; Table 3.4). A limits test on the 95% confidence intervals indicated that sagebrush cover was the only variable that contributed to the difference between nests (1 m plot) and random sites. Sagebrush cover was the greatest

Table 3.3. Discriminant Functions Analysis of vegetation characteristics at successful and unsuccessful nests. Values are shown as means \pm one standard error. Sagebrush cover, shrub cover, palatable forb cover, grass cover, and grass height were the only variables entered into the model. The models for the 7.5 m, 15 m, and all 9 plot scales were all significant ($P < 0.05$). Variables that contributed significantly to discriminating between successful ($n = 14$) and unsuccessful ($n = 15$) nests for that scale are shown below ($P < 0.05$). The larger the Wilks' λ , the greater the variable contributed to the discriminant function. SCC = Standardized Canonical Coefficient.

Over all Model	All 9 Plots				15 m Plots				7.5 m Plots			
Wilks' λ	0.678				0.617				0.688			
F	6.17				8.056				3.772			
P	0.0064				0.0016				0.023			
% Correct Classification	75.9				82.8				72.4			
Variables	Wilks' λ	P -level	R2	SCC	Wilks' λ	P -level	R2	SCC	Wilks' λ	P -level	R2	SCC
Grass Cover	0.937	0.004	0.204	- 1.039	0.861	0.003	0.223	- 0.979	0.908	0.009	0.094	- 0.926
Palatable Forb Cover	/	/	/	/	/	/	/	/	0.740	0.182	0.077	0.494
Grass Height	0.830	0.023	0.204	0.845	0.862	0.003	0.230	0.980	0.725	0.260	0.123	0.430

Table 3.4. Vegetation characteristics at nests and random locations. Values are shown as means \pm one standard error. Variables with a (*) were entered into the model. Means with a (*) contributed significantly to differentiating between nest locations and random locations for that scale. (n = 29 for nests and random locations at all scales).

Variables	Nest Site		7.5 m Plots		15 m Plots		All 9 Plots	
	Nest	Random	Nest	Random	Nest	Random	Nest	Random
COVER (%)								
Sagebrush Cover*	31.9*	15.7*	7.6*	3.6*	7.3	4.9	10.2	5.5
	(4.07)	(2.44)	(1.14)	(0.86)	(1.41)	(1.04)	(1.26)	(0.77)
Shrub Cover*	7.4	1.7	3.3	1.1	1.67	1.4	3.1	1.3
	(3.70)	(1.39)	(1.91)	(0.41)	(0.62)	(0.41)	(1.43)	(0.36)
Unpalatable Forb Cover	0.3	0.2	0.9	1.1	0.6	1.2	0.7	1.1
	(0.24)	(0.2)	(0.28)	(0.25)	(0.19)	(0.35)	(0.20)	(0.26)
Palatable Forb Cover*	8.1	8.4	10.3	10.6	9.4	11.9	9.7	10.9
	(1.12)	(1.03)	(1.55)	(1.53)	(1.18)	(1.58)	(1.15)	(1.39)
Grass Cover*	31.9	41.7	41.7	41.7	44.0	42.9	41.6	42.2
	(3.96)	(4.83)	(3.70)	(4.04)	(3.70)	(3.38)	(3.44)	(3.6)
Dead/Bare Ground	20.34	32.2	36.1	41.9	37.0	37.7	34.8	39.0
	(4.20)	(4.01)	(4.00)	(4.17)	(4.14)	(3.21)	(3.80)	(3.64)
HEIGHT (cm)								
Sagebrush Height	41.3	27.5	20.8	14.4	23.4	16.3	26.5	22.2
	(3.78)	(3.38)	(2.46)	(2.10)	(3.11)	(2.19)	(2.56)	(1.77)
Shrub Height	8.6	2.2	8.3	5.7	9.3	10.0	15.7	10.9
	(3.42)	(1.35)	(2.50)	(2.89)	(3.27)	(3.75)	(3.67)	(3.53)
Unpalatable Forb Height	0.4	0.1	2.5	2.3	2.2	1.7	3.0	2.4
	(0.31)	(0.07)	(0.70)	(0.56)	(0.67)	(0.43)	(0.71)	(0.47)
Palatable Forb Height	15.5	11.2	13.6	12.5	13.8	13.6	14.5	12.9
	(2.22)	(1.24)	(1.78)	(1.11)	(1.56)	(1.15)	(1.51)	(10.7)
Grass Height	30.9	28.5	27.2	25.7	27.7	27.0	27.9	26.6
	(3.58)	(1.97)	(2.21)	(1.92)	(2.39)	(1.84)	(2.34)	(1.80)

cover type at nest sites ($31.9\% \pm 4.07$) where it was more than double that of random sites ($15.7\% \pm 2.44$; Table 3.4). Shrub cover was also greater at nest sites, although not significantly so. None of the vegetation height measurements was entered into the model due to correlations with cover. Sagebrush height and grass height were both greater at nests than random sites; however, not significantly ($P \geq 0.01$; univariate paired t-test using a Bonferroni correction factor). Within nesting areas, nests were placed under tall sagebrush plants, which averaged $41.3 \text{ cm} \pm 3.78$ in height (Table 3.4).

Nesting areas could be significantly differentiated from dependent random locations at the 7.5 m scale ($T^2 = 32.2, P \leq 0.001$). Sagebrush cover was the only variable that contributed significantly to the model and was greater at nest locations ($7.6\% \pm 1.14$ vs. $3.6\% \pm 0.86$). A univariate paired t-test indicated that none of the height measurements at the 7.5 m scale differed between nest and random locations ($P \geq 0.01$, using a Bonferroni correction factor), even though sagebrush and other shrubs were taller at the 7.5 m scale at nest locations.

Nest locations could not be differentiated from random locations at the 15 m scale ($T^2 = 5.64, = 1.26, P \geq 0.05$), or over the entire nesting area (all 9 Plots; $T^2 = 17.52, = 3.91, P \geq 0.05$). None of the five height variables at nest locations at the 15 m scale alone or over all 9 plots combined differed from random locations ($P \geq 0.01$, using a Bonferroni correction factor).

I combined sagebrush and other shrub cover to determine if nest locations could be differentiated from random locations on this basis. Overall shrub cover did allow significant differentiation of nests from random locations at the nest site ($T^2_{4, 25} = 20.12, P$

≤ 0.01), at the 7.5 m scale ($T^2_{4, 25} = 17.62, P \leq 0.01$), and for all nine plots combined, ($T^2_{4, 25} = 18.81, P \leq 0.01$), but not at the 15 m scale alone ($T^2_{4, 25} = 4.94, P \geq 0.05$).

Brood Habitat

I gathered data on habitat use by 15 different radio-marked females and their broods. Vegetation characteristics were measured at 91 brood locations (63 for broods < 7 weeks of age and 28 for broods 7 to 12 weeks of age) and 91 corresponding dependent random locations. I entered sagebrush cover, shrub cover, forb cover, and grass cover into a forward stepwise DFA, but could not discriminate between early (< 7 weeks of age) and late brood (7 to 12 weeks of age) locations ($P \geq 0.05$). Thus, I combined early and late brood rearing locations to test for overall habitat selection (use vs. random locations).

Brood use “sites” (one plot centered on the location where the marked female and her brood were located) could be differentiated from random sites ($T^2_{4, 87} = 155.07, P \leq 0.001$; Table 3.5). Brood rearing areas could also be significantly differentiated from random locations overall (all 9 m plots; $T^2_{4, 87} = 72.06, P \leq 0.001$), and at both the 7.5 m ($T^2_{4, 87} = 21.48, P \leq 0.001$) and 15 m scales ($T^2_{4, 87} = 28.79, P \leq 0.001$; Table 3.5). A limits test indicated that sagebrush cover was the only variable entered into the model that allowed for differentiation at all levels. Palatable forb cover was low at brood use locations, ranging from 10.9 to 12.9% at the different scales (Table 3.5). Likewise, none of the vegetation heights was entered into the model due to correlations with cover measurements. However, the heights of all vegetation types at brood sites and brood rearing areas (7.5 m scale, 15 m scale, and overall) were greater than at random

Table 3.5. Vegetation characteristics at brood use and random locations. Values are shown as means \pm one standard error. Variables with a (*) were entered into the model. Means with a (*) contributed significantly to differentiating between brood locations and random locations for that scale.

	Brood Site		7.5 m Plots		15 m Plots		All 9 Plots	
	Brood	Random	Brood	Random	Brood	Random	Brood	Random
COVER (%)								
Sagebrush Cover*	20.9*	2.9*	7.1*	4.7*	7.3*	4.6*	8.7*	4.5*
	(1.63)	(0.54)	(0.68)	(0.50)	(0.69)	(5.52)	(0.65)	(0.47)
Shrub Cover*	1.2	1.7	1.6	1.9	2.0	2.1	1.7	2.0
	(0.39)	(0.92)	(0.34)	(0.53)	(0.53)	(0.62)	(0.36)	(0.57)
Unpalatable Forb Cover	0.9	1.4	1.1	1.4	1.1	1.3	1.1	1.3
	(0.23)	(0.36)	(0.20)	(0.25)	(0.19)	(0.21)	(0.15)	(0.21)
Palatable Forb Cover*	10.9	11.5	12.8	11.5	12.9	10.7	12.6	11.2
	(1.20)	(1.52)	(1.21)	(1.23)	(1.07)	(1.06)	(1.10)	(1.14)
Grass Cover*	34.2	36.9	36.0	33.8	35.2	36.6	35.4	35.4
	(2.05)	(2.52)	(1.71)	(1.84)	(1.75)	(1.98)	(1.61)	(1.89)
Dead/Bare Ground	32.0	45.5	41.5	46.7	41.6	44.7	40.5	45.7
	(2.07)	(2.72)	(1.73)	(2.14)	(1.76)	(2.07)	(1.65)	(2.06)
HEIGHT (cm)								
Sagebrush Height	32.0	7.6	22.9	16.0	21.9	15.5	27.6	17.8
	(2.36)	(1.2)	(1.61)	(1.52)	(1.48)	(1.34)	(1.61)	(1.30)
Shrub Height	2.5	2.2	6.7	5.3	7.0	6.4	8.8	6.9
	(0.83)	(0.89)	(1.22)	(11.78)	(1.29)	(1.34)	(1.35)	(1.29)
Unpalatable Forb Height	1.4	1.2	2.9	2.2	2.3	2.0	4.1	2.8
	(0.50)	(0.51)	(0.42)	(0.35)	(0.39)	(0.32)	(0.57)	(0.40)
Palatable Forb Height	21.7	15.3	20.7	17.5	20.4	17.5	20.8	17.8
	(1.46)	(1.37)	(1.16)	(1.13)	(1.07)	(1.18)	(1.05)	(1.11)
Grass Height	45.3	36.6	41.5	39.1	43.1	39.7	42.5	39.5
	(1.86)	(2.01)	(1.36)	(1.72)	(1.33)	(1.50)	(1.30)	(1.53)

sites/locations (Table 3.5). Only the height of sagebrush and palatable forbs were significantly greater at brood use sites/locations for all scales ($P \leq 0.01$, using a Bonferroni correction factor). Grass was significantly taller only at the brood site level ($P \leq 0.01$). Grass height at brood locations was similar at all scales, ranging from 41.5 to 45.3 cm, and was taller than grass height at nest locations (range 27.2-30.9; Table 3.4).

Line Transects

I used the line intercept method (Canfield 1941) to estimate sagebrush canopy cover and line transects to estimate sagebrush vegetation characteristics (height and density). Since sagebrush was the only variable that differentiated between use and random locations, I compared line intercept and line transect data to assess which characteristics of sagebrush were selected for by Sage Grouse (Table 3.6).

At nesting locations, sagebrush cover was greater over the entire 15 m radius surrounding nest sites, when compared to random locations. Cover was also greater at nesting areas than random locations at 0 to 7.5 m from the nest and between 7.5 and 15 m from the nest. However, the estimate of sagebrush cover at nest locations using the line intercept method (all 15 m; $4.5\% \pm 0.65$) was significantly less than that using all nine plots ($10.9\% \pm 1.26$; $t_{28} = 8.93$, $P \leq 0.001$; Table 3.4).

Sagebrush density over the entire 15 m radius was greater surrounding nest sites, than random sites ($P \leq 0.017$, using a Bonferroni correction factor), however, when separated into the two scales, density was only greater ≤ 7.5 m from nest sites ($P \leq 0.017$) and not from 7.5 to 15 m ($P \geq 0.017$). Sagebrush height along line transects was not significantly different between nest and random locations at all scales ($P \geq 0.017$,

Table 3.6. Sagebrush characteristics at use locations (nest and brood) and random locations along line transects. Values are shown as means \pm one standard error. Means with a (*) were significantly different between use locations and random locations for that scale using a univariate paired t-test. A Bonferroni Correction was used ($\alpha = 0.017$).

Variables	≤ 7.5 m		7.5 m to 15 m		All 15 m of Transect	
	Use	Random	Use	Random	Use	Random
NESTS (n = 29)						
Sagebrush Cover (%)	5.6*	2.9*	3.5*	1.8*	4.5*	2.4*
Line Intercept	(0.75)	(0.52)	(0.64)	(0.51)	(0.65)	(0.48)
Sagebrush Height (cm)	26.4	19.9	22.1	17.1	24.4	18.5
	(2.50)	(1.59)	(2.54)	(1.31)	(2.45)	(1.29)
Sagebrush Density (# Plants/m ²)	2.1*	1.5*	1.7	1.4	1.9*	1.4*
	(0.28)	(0.36)	(0.24)	(0.30)	(0.25)	(0.32)
BROODS (n = 91)						
Sagebrush Cover (%)	5.8*	2.4*	4.3*	2.7*	5.0*	2.5*
Line Intercept	(0.47)	(0.30)	(0.42)	(0.36)	(0.42)	(0.31)
Sagebrush Height (cm)	26.0*	19.0*	24.2*	17.6*	25.6*	19.6*
	(1.60)	(1.57)	(1.42)	(1.30)	(1.45)	(12.7)
Sagebrush Density (# Plants/m ²)	1.9*	1.2*	1.8*	1.2*	1.8*	1.2*
	(0.19)	(0.16)	(0.17)	(0.14)	(0.17)	(0.14)

Table 3.6). Sagebrush height ($24.4 \text{ cm} \pm 2.45$ for the entire nesting area along transects) was not significantly different from estimates using all 9 plots ($26.5 \text{ cm} \pm 2.56$; $t_{28} = 2.03$, $P \geq 0.05$).

Using line transect data, brood use areas had taller sagebrush with more canopy cover and a greater density of sagebrush than random locations at all three scales (≤ 7.5 m from brood sites, 7.5 to 15 m from sites, and over all 15 m; $P \leq 0.017$; Table 3.6). However, as was the case at nest locations, values for sagebrush cover at brood locations (all 15 m intercept; $5.0\% \pm 0.42$; Table 3.6) were significantly less than values estimated using plots ($8.7\% \pm 0.65$; $t_{90} = 12.94$, $P \leq 0.001$; Table 3.5). Sagebrush height estimated at brood locations from line transects ($25.6 \text{ cm} \pm 1.45$; Table 3.6) was similar to height estimated from plots ($27.6 \text{ cm} \pm 1.61$; $t_{90} = 1.81$, $P \geq 0.05$; Table 3.5).

DISCUSSION

Although Sveum et al. (1998b) found no difference in the probability of success for nests under sagebrush compared to nests under other plants, Connelly et al. (1991) found that nests under non-sagebrush plants were less successful ($P \leq 0.025$). In the Connelly et al. (1991) study, 21% of nests (18/84) were under species other than live sagebrush, even though sagebrush comprised $\geq 16\%$ of the available canopy cover in the area. This suggests that Sage Grouse may be selecting nest sites based on suitable amounts of shrub and herbaceous cover regardless of the vegetation species that provides it (Connelly et al. 1991, Sveum et al. 1998b).

The majority of the nests I found (89.6%, 26 of 29) were under sagebrush, even though it comprised $\leq 11\%$ of the canopy cover at nest locations and $\leq 6\%$ of the canopy

cover available in the area (Table 3.4). Thus, there is less available sagebrush habitat in Canada than in other areas. This is likely due to the species of sagebrush present. *Artemisia cana* is the only shrubby species of tall sagebrush available to Sage Grouse in Canada. It is smaller and does not provide as much cover as big sagebrush (*A. tridentata* spp.) found throughout most of the core range of Sage Grouse. Despite these differences, nest success in my study (46.2%) was comparable to other areas (30 to 60%; Schroeder et al. 1999).

Successful nests could not be differentiated from unsuccessful nests by the vegetation characteristics of the nest site itself. In Alberta, Seida (1998) found that artificial Sage Grouse nests were more likely to be successful if they had taller grass and more forb cover at the nest site. In a similar experiment, Watters (2000) found that successful nests had taller forbs and grass, but less grass cover and shorter sagebrush surrounding the nest. These results are similar to those of both natural (Gregg et al. 1994, Sveum et al. 1998a) and artificial nests (DeLong et al. 1995) at other locations. This highlights the importance of greater cover of medium height sagebrush and tall grasses. Watters (2000) found that successful nests had less grass cover, similar to my results for natural nests, which contrasts with other studies. This difference is not easily explained, but may be related to grazing. Perhaps more importantly, grass height was vital to nest success in both instances. Nests located in areas that are intensely grazed will intuitively have shorter grasses, resulting in decreased nest success. However, continual grazing may cause the grasses to tiller (fill out and add stems) and increase the grass cover at unsuccessful nests.

Most nests are found under sagebrush (Patterson 1952, Klebenow 1969, Connelly et al. 1991, Gregg et al. 1994, Sveum et al. 1998b), with selection for taller plants that generally provide greater amounts of cover (Wallestad and Pyrah 1974, Musil et al. 1994). I found that females selected nest locations that had a greater amount of sagebrush cover compared to available cover at the nest site itself, and up to 7.5 m from nests. However, sagebrush characteristics were not selected for at the 15 m scale. Sage Grouse are selecting nesting areas based on sagebrush stands that are at least 7.5 m, but not 15 m in radius, which provide greater amounts of cover ($7.6\% \pm 1.14$).

Sage Grouse selected nest areas that had a greater density of sagebrush within 7.5 m of nest sites. There was no difference in sagebrush density from 7.5 to 15 m from nest sites. Within the stands selected, females placed their nests under taller sagebrush ($O = 41.3 \text{ cm} \pm 3.78$) that provide greater canopy cover ($O = 31.9\% \pm 4.07$). Sveum et al. (1998b) found that Sage Grouse nested in locations based on vegetative characteristics at both the nest-area and nest-site levels, similar to my study. However, they did not test for vegetation differences at different distances from nest sites and were unable to compare vegetation characteristics between nest sites and nest areas because of differences in measurements scales. To my knowledge, my study is the first to show that Sage Grouse select nesting areas based on habitat characteristics of a certain patch size and that nest sites are selected for within those patches.

When sagebrush and other shrub cover were combined in my analysis, total shrub cover at nest sites was greater than random locations. Nest areas had greater total shrub cover at the 7.5 m scale but there was no difference 15 m from nest sites. Shrub height was highly correlated with shrub cover, and sagebrush height was weakly correlated with

sagebrush cover. Thus, a female's selection of nest habitat appears to be based on structure; shrubs that are taller and provide more cover in an area at least 7.5 m in radius but less than 15 m in radius are selected for as nesting areas. The tallest shrubs providing the greatest cover within those stands are typically used for nest sites. Other studies have shown that Sage Grouse tend not to place nests under the tallest available sagebrush (Klebenow 1969, Gregg et al. 1994, Sveum et al. 1998b). This is because tall shrubs are often associated with reduced lateral cover, due to a depleted understory (Klebenow 1969). Since the canopy of *A. cana* is not as dense as *A. tridentata* spp., the understory may not be as sheltered and, thus, is not as depleted. If Sage Grouse in Canada select the tallest sagebrush available, compared to available habitat, the understory is still suitable. Other shrubs may also provide suitable concealment of nests, but sagebrush is by far the most common shrub in the area.

For both nest and brood locations, the line intercept method resulted in significantly lower estimates of sagebrush canopy cover than estimates generated from plots. While these two methods resulted in different estimates, they were highly correlated ($R = 0.906$; Table 3.1), indicating that both techniques accurately reflect relative sagebrush cover. However, in absolute terms, one or both of the measures are not precise. Regardless of the method used, my estimates of sagebrush canopy cover (plots 10.9%; line intercept 4.5%) are below the 20 to 50% recommended as suitable nesting habitat (Patterson 1952, Klebenow 1969, Wallestad and Pyrah 1974, Braun et al. 1977, Schroeder et al. 1999). Despite the low amount of cover provided by sagebrush in southeastern Alberta, differences in the amount of cover were great enough that birds were able to select for areas and sites with greater sagebrush cover to nest.

Broods remained in areas with denser, taller sagebrush, which was comparable to sagebrush characteristic of nest locations. Greater sagebrush cover differentiated brood use from random locations at all measured scales. In contrast, Klebenow (1969) found that brood rearing habitat in Idaho had a lower density of sagebrush than was available. Dunn and Braun (1986b) also showed that hens with broods selected areas with less sagebrush. My data are the first to suggest that brood rearing locations had greater sagebrush cover than was available at random locations.

While brood sites and brood rearing areas had more sagebrush than random locations, Sage Grouse appear to be selecting brood rearing locations on a larger scale than that at which nesting areas were selected for (areas of radius greater than 15 m). Dunn and Braun (1986b) found that summer habitat use locations for broods and unsuccessful females had taller sagebrush compared to random locations, but there was no difference in sagebrush height surrounding the use site itself. They also found that use locations compared to random locations had greater horizontal cover at 5 m from use sites, but not at 10 m, suggesting that scaled habitat selection may be occurring. Other than horizontal cover, Dunn and Braun (1986) did not measure vegetation characteristics > 5 m from use sites.

Grass cover at brood use locations ($35.4\% \pm 1.61$) was similar to nesting areas ($41.6\% \pm 3.44$), however, grass was taller at brood locations ($42.5 \text{ cm} \pm 1.30$ vs. $27.9 \text{ cm} \pm 2.34$). This could simply be due to increased growth later in the season. Sveum et al. (1998a) found that broods selected areas with more protective cover and tall ($\geq 18 \text{ cm}$) grass cover and vertical vegetation cover. Grass cover available to broods in my study averaged $39.5 \text{ cm} (\pm 1.53)$ in height, reflecting the exceptional grass growth over the

course of my study. I conclude that suitable protective cover was not limited during 1998-99.

I did not observe a shift in habitat used by broods, which typically occurs due to changing dietary requirements of chicks (Martin 1970, Peterson 1970, Johnson and Boyce 1990, Drut et al. 1994a, 1994b). Early brood rearing locations tend to be in sagebrush uplands, but as temperature increases and moisture disappears, forbs become desiccated, and broods shift to more mesic sites that have increased availability of forbs (Peterson 1970, Dunn and Braun 1986b, Sveum et al. 1998a). Sveum et al. (1998a) suggested that broods remained in areas with more sagebrush during early brood rearing for the added escape cover it provides. Broods may remain in sagebrush uplands during years when above average precipitation results in increased forb availability (Dunn and Braun 1986b). Spring precipitation was above average in both years of my study (Chapters 2, 4), resulting in increased vegetation growth. Thus, broods likely had increased food resources available to them in sagebrush habitat, allowing them to remain in sagebrush uplands. In dry years, broods should have to move from sagebrush uplands to more mesic sites. However, mesic wetland type habitats are generally limited and may not be available for broods in dry years. Thus, brood survival may be even lower during times of drought.

Forb cover in brood use areas averaged 12.6% for early and late brood rearing periods combined. Schoenberg (1982) found that young broods in Colorado used areas with relatively low forb cover (6.9%) and quickly moved to wet meadows where forbs comprised 41.3% of the cover. Peterson (1970) also found that forb cover was important, accounting for 33% of the available cover at brood use sites. Forb cover in Oregon was

estimated at 10-14% for early brood rearing locations and 19-27% for late brood rearing locations (Drut et al. 1994a). Drut et al. (1994a) suggested that 12-14% forb cover might represent the minimum cover needed for brood habitat.

Increased forb cover in years with above average spring precipitation (Peterson 1970) may allow for greater movements and distribution of broods (Dunn and Braun 1986b). In years when precipitation is average or below average, forb cover may be below that required to provide suitable brood habitat. The lack of a shift in brood habitat between early and late-brood rearing in my study, suggests that differences in the availability of forbs did not exist, at least in wet years. However, the limited cover provide by forbs at brood locations despite high spring precipitation suggests that key brood habitat in moist wetlands and drainages may be limiting in southeastern Alberta, even in moist years.

Nesting success (46.2%) was within the range reported for studies in other areas. Five of 12 (41.7%) females that were successful nesters raised at least one chick to fledging (50 days of age; Schroeder 1997). However, the percentage of chicks that survived from hatch to fledge (50 days of age) was only between 14 and 23% (Chapter 2), which is extremely low, given that estimates of between 33 and 38% have been found in slightly declining populations (June 1963, Schroeder 1997). Despite low chick survival estimates, grass cover and height likely contributed to suitable escape cover throughout the study area. However, the lack of cover from sagebrush may ultimately make the available escape cover unacceptably low.

Virtually all research on brood habitat use has found that areas with forbs are selected and that a shift to more mesic sites occurs after broods reach six weeks of age.

Sage Grouse broods in my study did not select use sites based on forb availability and no shift in habitat use occurred. Mesic areas with nutrient rich forbs may be limiting and forbs as a food resource may be even more limiting during drier years. Lack of suitable moist drainages for broods to forage in may also be a factor contributing to low chick survival and poor recruitment (Chapters 1 and 2).

Management strategies for Sage Grouse should consider the identification and protection of sagebrush stands that are at least 7.5 m in radius and preferably 15 m. These stands should also have a suitable understory of tall grasses and forbs to enhance nest concealment. In Canada, sagebrush is also an important component of brood rearing habitat. My results suggest that managing for suitable nesting areas will also provide suitable brood rearing sites for Sage Grouse, at least in some years. Even though spring precipitation was higher than normal over the course of this study, important mesic areas, such as wet meadows that provide high quality succulent forbs of $\geq 12\%$ cover, may be lacking within the Canadian range of Sage Grouse. This decreased availability of food resources for chicks may be related to reduced chick survival and overall low recruitment. Additional mesic areas with higher forb availability should be identified and protected to increase chick survival. Management strategies should focus on enhancing the number and quality of mesic sites where increased forb growth can occur. Considerations should be given to managing grazing within mesic habitats to decrease the effects that cattle may have on reducing the amount of succulent forbs necessary for chick survival.

CHAPTER 4. MODELING POPULATION TRENDS

In Chapter 1, I discussed historical Sage Grouse population trends in Canada. I gathered data on population parameters (Chapters 2 and 3), which allowed me to develop a model to predict future population trends. The parameters that I measured may be influenced by intrinsic factors such as density dependence or genetic heterogeneity, and also extrinsic factors such as climate. In this Chapter, I will assess some of these influences on previous population trends and integrate the parameters that I measured into the model to predict future population trends.

The Alberta Sage Grouse population declined by 66-92% from historical levels, to an estimated 210 and 311 individuals in 1994 (Chapter 1). Lek counts in both Alberta and Saskatchewan show the Canadian population has remained relatively stable but at low numbers since that time (Fig. 1.3). The reason(s) for the sharp decline from the population maintained in the early to mid-1980s is/are not clearly understood, but might be related to changes in habitat quality and recruitment (Chapters 2, 3). The population appears to have stabilized from 1996 to 1999, although this may simply be a consequence of intensified lek count efforts in both provinces over that time (Aldridge 1998; W. C. Harris, pers. commun.). Although Sage Grouse were not heavily hunted in Alberta in the early 1990s (K. J. Lungle pers. commun.), they have not been hunted at all since 1996. It is therefore also possible that removal of hunting pressure in Alberta has allowed the declining population to stabilize.

Although a number of factors may have resulted in the relatively stable population over the last six years, I believe it is most likely due to increased spring precipitation. Sage Grouse productivity appears to be positively correlated with increasing spring (April to June) precipitation (June 1963, Gill 1966, Chapter 2). Years with below

average spring moisture result in less vegetation growth, likely reducing Sage Grouse nest success, as well as limiting the availability of lush vegetation important as food for chicks (Martin 1970; Peterson 1970; Johnson and Boyce 1990; Klott and Lindzey 1990; Drut et al. 1994a, 1994b; Pyle and Crawford 1996; Sveum et al. 1998a). Spring precipitation from 1994 to 1999 in southeastern Alberta was above average (Fig. 4.1) and, thus, it is likely that Sage Grouse productivity was relatively high. When the population was declining in the late 1980s, the prairies experienced some of the driest springs over the previous 30 years (Fig. 4.1). Population data for Alberta suggest a correlation between spring precipitation and the number of males counted on leks the following year, although the trend is not statistically significant ($P \geq 0.05$). The lack of continuous lek count data decreased the statistical power to detect a significant trend. If my hypothesis is true, I predict that when spring precipitation is below average, productivity will be adversely affected and the population will decline.

Little is understood about the survival and life history requirements of Sage Grouse chicks, due to the difficulty of finding them. Only 24 of 96 Sage Grouse captured in 1998 and 1999 were yearlings (Chapter 1), suggesting that recruitment over the course of my study was about 25%. Other long-term research on stable Sage Grouse populations has found that approximately 50% of captured birds are yearlings (Dalke et al. 1963, Eng 1963, Jenni and Hartzler 1978, Chapter 1). This suggests that recruitment is low in Canada, possibly due to low chick survival and/or high overwinter mortality.

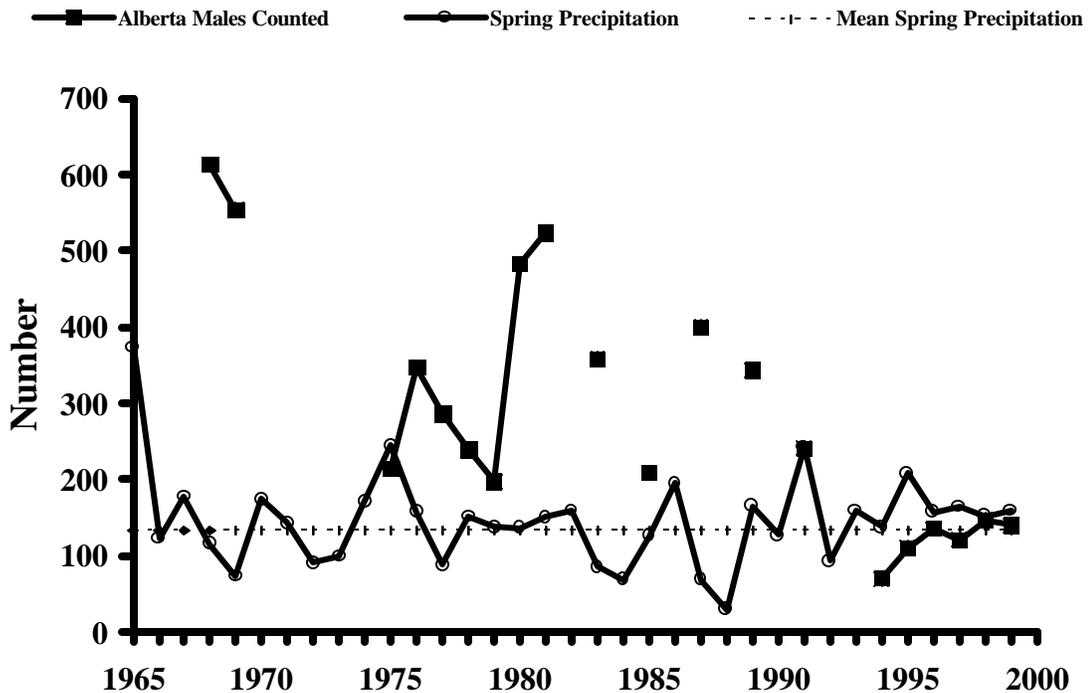


Figure 4.1. Maximum Sage Grouse lek counts in Alberta shown as a function of spring (April - June) precipitation (mm) for each year. The mean spring precipitation since 1928 is shown for reference. Years when sampling efforts consisted of less than eight surveyed leks are not included.

Using the survival rates and measures of productivity that I calculated from my results (Table 4.1), I developed a population model to predict the future Alberta/Canadian Sage Grouse population. The model incorporates estimated survival rates from radio-marked males and females, clutch size, egg viability, breeding success (includes nesting success, and re-nesting attempts), and chick survival (Table 4.1). Annual female survival is likely not as high if overwinter mortalities are considered. However, survival estimates for this population are also likely slightly underestimated due to the biases associated with radiotelemetry studies (Chapter 2). I also assumed that juvenile overwinter survival is 100%, which is unlikely. Female survival in Alberta (56.5% from March to August)

was within the expected range. To simplify the model, I did not incorporate any stochastic measures. Thus, all parameters are fixed and do not vary between years when the model is simulated, even though these will likely change from year to year. For any given year (N_t), the subsequent year's population can be predicted as follows: $N_{t+1} = \text{♀}N_{t+1} + \text{♂}N_{t+1}$.

Where: $\text{♂}N_{t+1} = (N_{t\text{♂}} \times \text{♂}A_{\text{surv}}) + ((N_{t\text{recruit}})/2)$ and

$$\text{♀}N_{t+1} = (N_{t\text{♀}} \times \text{♀}B_{\text{surv}} \times \text{♀}W_{\text{surv}}) + ((N_{t\text{recruit}})/2) \text{ and}$$

$$N_{t\text{recruit}} = N_{t\text{♀}} \times \text{♀}B_{\text{surv}} \times \text{♀}W_{\text{surv}} \times Cl_{\text{Size}} \times Htc \times Br_{\text{Succ}} \times ChFl_{\text{surv}} \times ChW_{\text{surv}}$$

See Table 4.1 below for an explanation of model parameters. $N_{t\text{recruit}}$ is annual recruitment.

Table 4.1. Parameters used in population model. Overwinter survival of females and chicks was not measured and was set at 100%. Based on 1999 lek count data, low spring population estimates of 140 males and 280 females and high estimates of 207 males and 415 females were used as starting population numbers for the model.

Population Parameter	Variable	Measure
Annual Male Survival	$\text{♂}A_{\text{surv}}$	31.0%
Female Survival (breeding season to fall)	$\text{♀}B_{\text{surv}}$	56.5%
Female Overwinter Survival (assumed)	$\text{♀}W_{\text{surv}}$	100%
Clutch Size	Cl_{Size}	7.75 eggs/nest
Egg Viability	Htc	92%
Breeding Success	Br_{Succ}	54.5%
Chick Survival to Fledge (50 days)	$ChFl_{\text{surv}}$	18%
Chick Overwinter Survival (assumed)	ChW_{surv}	100%

To test whether the model reflects the actual population trend over the past 30 years in Alberta, I ran the model using the 1968 population estimate as the starting point. I let the model run from 1968 to 1999 and compared predicted population numbers from the model to the actual population estimate based on lek counts for each year (Fig. 4.2). The actual population estimates fluctuate consistently around the model generated population numbers. This suggests that the population parameters that I measured in 1998 and 1999 are generally representative of the population over the last 30 years.

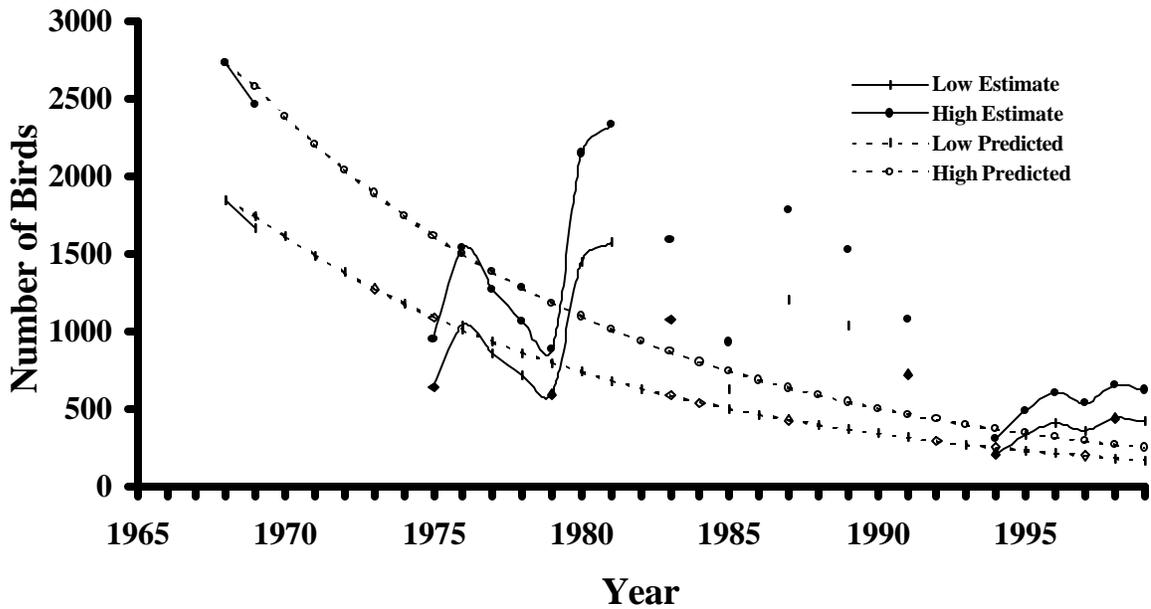


Figure 4.2. Actual Sage Grouse population size in Alberta based on lek counts for 1968 through 1999 shown with the predicted population superimposed. Predicted population size is based on survival and productivity data measured in 1998 and 1999. The model starting point is based on the population in 1968. Years when sampling efforts consisted of less than eight leks surveyed are not included. Lines are drawn to illustrate trends between years with consecutive lek counts, and to show the predicted population trend.

I iterated the population model 31 years into the future, from 2000 to 2030, to examine future Sage Grouse population status for Alberta (Fig. 4.3). I used both high and low population estimates in 1999 as starting points. From these data, I predict the Alberta spring population will decrease from between 420 and 622 individuals in 1999 to between 397 and 589 individuals in 2000. This means that lek counts should decrease from 140 males in 1999 to approximately 132 males in 2000. This model can also be applied to the entire Canadian population by combining Alberta lek counts with the most recent lek counts in Saskatchewan.

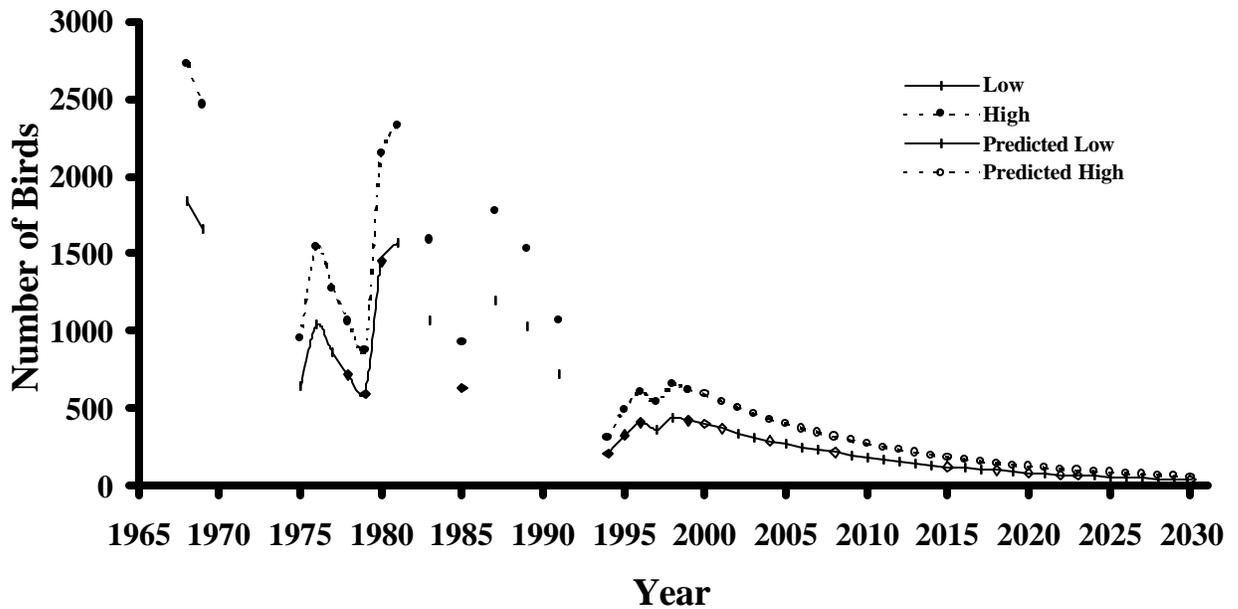


Figure 4.3. Actual Sage Grouse population in Alberta based on lek counts for 1968 through 1999 and predicted population from 2000 to 2030. Years when sampling efforts consisted of less than eight leks surveyed are not included. Lines are shown to illustrate trends for years with consecutive lek counts, and to show the predicted population trend.

The model predicts that the Alberta population will fall below 300 individuals by 2004 (Fig. 4.3). Similarly, the Canadian population will fall below 300 individuals in 2013. By 2018 the Alberta population will decline to less than 100 individuals and the Canadian population will be below 190 individuals. Based on 1999 productivity and survival estimates, yearlings should represent approximately 49% of the 2000 spring population. However, only 25% of the birds captured over the course of my study were yearlings (Chapter 1). A lack of attendance by yearling male Sage Grouse at leks also suggests that yearlings are under represented in the population (Figure 1.6). To improve the predictive capabilities of my model, some parameters need to be refined, including both adult and chick survival rates. If juvenile overwinter mortality is considered and all other parameters remain constant, to have a yearling to adult ratio close to 25%, juvenile overwinter survival would be approximately 40%. There currently are no data available on juvenile overwinter survival. However, given that adult mortality is high, 40% juvenile overwinter survival may be a reasonable estimate. If I reiterate the model using 40% overwinter juvenile survival, the Alberta population will decline to zero in 2017, and the Canadian population will approach zero in 2019.

It has been suggested that Sage Grouse populations cycle (Patterson 1952, Rich 1985, Aldridge 1998, Braun 1998, Hyslop 1998), although these cycles tend to be irregular, if they do exist (Braun 1998). Both the Alberta and Saskatchewan populations appear to cycle (Fig. 1.3), however, inconsistencies in lek counts (Madsen 1995b, Aldridge 1998) and the irregularity with which counts were performed, make it difficult to accurately characterize these cycles.

Even though the cause(s) for the population decline in Canada are not definitively known, I suggest it is likely the problem is related to poor chick survival and low recruitment. However, reduced adult survival may confound the problem. It is possible that a lack of genetic diversity due to such low population numbers could be adversely affecting the population. It has been suggested (Franklin 1980, Lande 1988, Braun 1995), that to maintain genetic diversity, individual populations should consist of at least 500, and maybe even 5000 individuals. However, Sage Grouse have persisted in Alberta for over 30 years with a population that was likely below 5000 individuals. These estimates assume that random mating is occurring and that all individuals in the population obtain mating opportunities. However, with a lek mating system, Sage Grouse mating is not random. While most, if not all females breed, as few as 10% of males in the population will obtain successful mating attempts (Anonymous 1997; C. E. Braun, pers. commun.). This would mean that as few as 14 males would obtain mating opportunities each year in Alberta (based on 140 males counted on leks in 1999).

At any given lek, one dominant male typically performs about 75% of the matings at that lek, and one to three other males will obtain the majority of the other 25% of the matings (Simon 1940, Scott 1944, Wiley 1973, Gibson 1996). Thus, with eight active leks remaining in Alberta, approximately 24 males likely obtain all of the successful mating opportunities. Assuming that 100% of all estimated 280 females mated, the effective population size [$N_e \approx 4(\sigma \times \text{♀}) / (\sigma + \text{♀})$] (Ewens et al. 1987) for Alberta would be 88 Sage Grouse. Similarly, based on 18 active leks and an estimated 542 females in 1999, the effective population size for the Canadian population would be approximately 196 individuals. Braun (1995) suggested that populations with less than 500 breeding

individuals in Colorado were at risk of extirpation. The Canadian population is far below these suggested minimum levels and genetic diversity may be confounding the problem.

Bouzat et al. (1998) found that a population of Greater Prairie-chickens (*Tympanuchus cupido*) in Illinois experienced a decrease in genetic diversity due to recent geographic isolation. This decrease in genetic diversity was associated with a reduction in population fitness, through reduced hatching and fertility rates. This population was below 50 individuals, compared to larger populations with greater than 4,000 individuals that have not experienced decreases in genetic diversity or reductions in population fitness.

With the Alberta Sage Grouse population estimated at between 420 and 622 individuals, and the Canadian population at between 873 and 1293 individuals, the potential exists for a reduction in population fitness due to decreased genetic diversity. Sage Grouse populations appear to cycle every 7-10 years (Fig. 4.2) (Patterson 1952, Rich 1985, Aldridge 1998, Braun 1998, Hyslop 1998). Due to these cycles, populations at low numbers may be more susceptible to extinction events, and genetic bottlenecks could easily occur. Egg hatching success for Sage Grouse over the course of my study was relatively high (92%, Table 4.1; Chapter 2), and suggests that genetic diversity may not presently be a problem in the Canadian Sage Grouse population. However, low genetic diversity may potentially affect population fitness in other ways, such as reducing chick survival, or make the population particularly sensitive to stochastic events. Even without considering these potential negative effects related to low genetic diversity, my model predicts the population will approach zero over the next 20 to 30 years.

Without adequate habitat management, I predict that the Canadian Sage Grouse population will continue to decline. The cause of the decline is likely linked to poor chick survival. While survival estimates are slightly lower compared to other populations, all other measures of productivity are comparable to similar populations and do not appear to be linked to the population decline at this time. Habitat use by broods indicates that variations in forb availability do not exist, that overall availability of forbs is low. There appears to be a lack of moist wetland type habitats that provide succulent food resources for Sage Grouse chicks, despite above average spring moisture in 1998 and 1999. Competition with cattle for already limited resources may compound the problem, especially in dry years, when abundance of forbs may be even more limiting.

The Alberta and Saskatchewan populations may not be distinct, but movements between southern populations in Montana are unlikely due to the lack of contiguous habitat. Thus, given the lek mating system of Sage Grouse and the presently low Canadian population numbers, a lack of genetic variability may confound the problem.

Management practices need to focus on the fact that given normal reproductive effort and success by Sage Grouse in Canada, small fluctuations in chick survival can have profound implications on population size. Efforts should be made to maintain, or preferably, enhance suitable breeding and nesting habitat, while attempting to enhance brood rearing habitat through the protection and creation of mesic habitats with high forb availability.

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