DO SAGE-GROUSE HAVE A FUTURE IN CANADA? POPULATION DYNAMICS AND MANAGEMENT SUGGESTIONS

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Abstract: Sage-Grouse (*Centrocercus urophasianus*) populations have declined by 45 to 80% throughout their North American range. The species currently exists at the northern fringe of their range, on the mixed grass prairie of southeastern Alberta and southwestern Saskatchewan. The population decline in Canada has been the most severe, with declines ranging from 66 to 92% over the last 30 years. There has been relatively little research in Canada to address the population decline. I used radio telemetry to monitor Sage-Grouse survival and measure productivity in southeastern Alberta in 1998 and 1999. Survival of both females and males was low. Reproductive effort was high, with all females attempting to nest and clutch size within the expected range. Nest success was also within the normal range, and 55% of all females were successful breeders. Chick survival was only 18%; less than half of that required for stable and slightly declining populations. I used these data to develop a preliminary population model to predict the long-term viability of Sage-Grouse in Canada. My model predicts that by 2018, the Canadian Sage-Grouse population will decline to fewer than 190 birds, which may not be sufficient to maintain a viable population. I quantified habitat characteristics to understand how habitat variables might influence these parameters, and thus, the population decline. Sage-Grouse selected nest areas based on sagebrush stands that provided greater amounts of tall cover, specifically sagebrush, with nests located under the tallest and densest sagebrush within these stands. Brood rearing sites were also selected for based on sagebrush characteristics, but not based on forb availability, as has been demonstrated for other populations. High quality mesic areas containing lush forbs important in the diet of chicks are limiting in southern Alberta. Management practices need to focus on the fact that small fluctuations in chick survival can have profound implications on population trends. 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.

INTRODUCTION

In this manuscript, I review some of the recent literature dealing with understanding the reasons for the decline of Sage-Grouse (*Centrocercus* spp.) populations throughout North America. I provide an overview of currently submitted publications dealing with my recent research to address population declines in Canada, and then bring together data from these studies to develop a population model. I discuss the inherent parameters, and use the model to make predictions about the viability of Sage-Grouse in Canada.

Sage-Grouse (*Centrocercus urophasianus*) across their range have experienced declines ranging from 45 to 80% since the 1950s (Braun 1998) with declines averaging 33% from 1985 to1995 (Connelly and Braun 1997). The historical declines are attributed to human induced reductions in sagebrush (*Artemisia* spp.) habitats, with the sagebrush steppe ecosystem being reduced by 2.5 million ha since the early 1900s (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 domestic livestock grazing, construction of roads, highways, fences and power lines, 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, most 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).

Research has shown that Sage-Grouse population declines are related to reduced nest success (Schroeder 1997, Braun 1998, Schroeder et al. 1999), with stable populations having high nest success (35-86%) (Dalke et al. 1963, Schroeder et al. 1999). However, the same factors that affect nest 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 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* sspp.) throughout most of their range; however, the dominant species in Canada is silver sagebrush (*A. cana*) (Aldridge 2000). 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 escape from predators. Nest success is higher in areas containing big sagebrush (Wallestad and Pyrah 1974, Connelly et al. 1991, Gregg et al. 1994, DeLong et al. 1995). As a result, the apparently lower quality habitat at the northern fringe of the species range in Canada may limit the population, which might cause larger fluctuations in productivity than in core populations.

Greater Sage-Grouse (*C. urophasianus*; here after referred to as Sage-Grouse) in Canada have declined by 66-92% from historical numbers recorded over the same area in the late 1960s in Alberta and the mid 1980s in both Alberta and Saskatchewan (Aldridge 2000). The 1999 spring population for Alberta is estimated at 420-622 individuals, and the Canada population at 813-1204 individuals (Aldridge 2000). With the current rate of decline, the population will reach non-viable levels, increasing the threat of extinction in Canada.

I compiled productivity (Aldridge and Brigham 2000b) and survival data (Aldridge 2000) for Sage-Grouse from southern Alberta in 1998 and 1999 to develop a preliminary population model to predict future population trends (Aldridge 2000). Below, I discuss the parameters inherent in this model, and discuss some of the key intrinsic factors (i.e. density dependence and genetic heterogeneity) and extrinsic factors (i.e. climate) that may be regulating this population. From the model, I predict the long-term probability of extinction of Sage-Grouse in Canada. I discuss some potential management options that might elevate some of the most limiting parameters in the model, and potentially reverse the population decline.

THE MODEL

Population estimates were determined for historical lek counts performed on the Alberta Sage-Grouse population (Aldridge 2000). These estimates are based on spring counts of males at leks, and the low estimate assumes a spring sex ratio of two females for every male (Schroeder et al. 1999, Aldridge 2000); 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 (Aldridge and Brigham 2000a).

The parameters incorporated into this model include estimated survival rates from radio-marked males and females (Aldridge 2000), clutch size, egg viability, breeding success (includes nesting success, and renesting attempts), and chick survival (Aldridge and Brigham 2000b; Table 1). The female survival estimate is only from spring to fall, and annual survival may not be as high if overwinter mortalities are considered. In addition, survival estimates for this population are also likely slightly underestimated due to the biases associated with radiotelemetry studies (Aldridge 2000). Since there are no data for juvenile overwinter survival in this population, I have assumed that it is 100%, which is unlikely, but conservative. To simplify the model, I have not incorporated 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:

$$N_{t+1} = EN_{t+1} + \Gamma N_{t+1}.$$

Where: $\Gamma N_{t+1} = (N_{t\Gamma} \times \Gamma_{surv}) + ((N_{t\ recruit})/2)$ and

$$EN_{t+1} = (N_{tE} \times EB_{surv} \times E\,W_{surv}) + ((N_{t\ recruit})/2) \text{ and}$$

$$N_{t\ recruit} = N_{tE} \times EB_{surv} \times EW_{surv} \times Cl_{size} \times Htc \times Br_{succ} \times ChFl_{surv} \times ChW_{surv}$$

See Table 1 for an explanation of model parameters. $N_{t\ recruit}$ is annual recruitment.

Table 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	ΓA_{surv}	31.0%
Female Survival (breeding season to fall)	EB_{surv}	56.5%
Female Overwinter Survival (assumed)	EW_{surv}	100%
Clutch Size	Cl_{size}	7.75 eggs/nest
Egg Viability	Htc	92%
Breeding Success (successful nest: 1st or 2nd)	Br_{succ}	54.5%
Chick Survival to Fledge (50 days)	$ChFl_{surv}$	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 high and low population estimates as the starting point (Fig. 1) (see Aldridge and Brigham 2000a for a detailed description of how population estimates are derived). I let the model run from 1968 to 1999. Assuming that the measured population parameters represent the mean for each of those parameters over the course of the population decline (≈ 30 years), predicted population numbers from the model should closely follow the actual population estimate based on lek counts for each year (Fig. 1). Actual population estimates fluctuate consistently around the model generated population numbers, suggesting that the population parameters that I measured in 1998 and 1999 are generally representative of the population over the last 30 years.

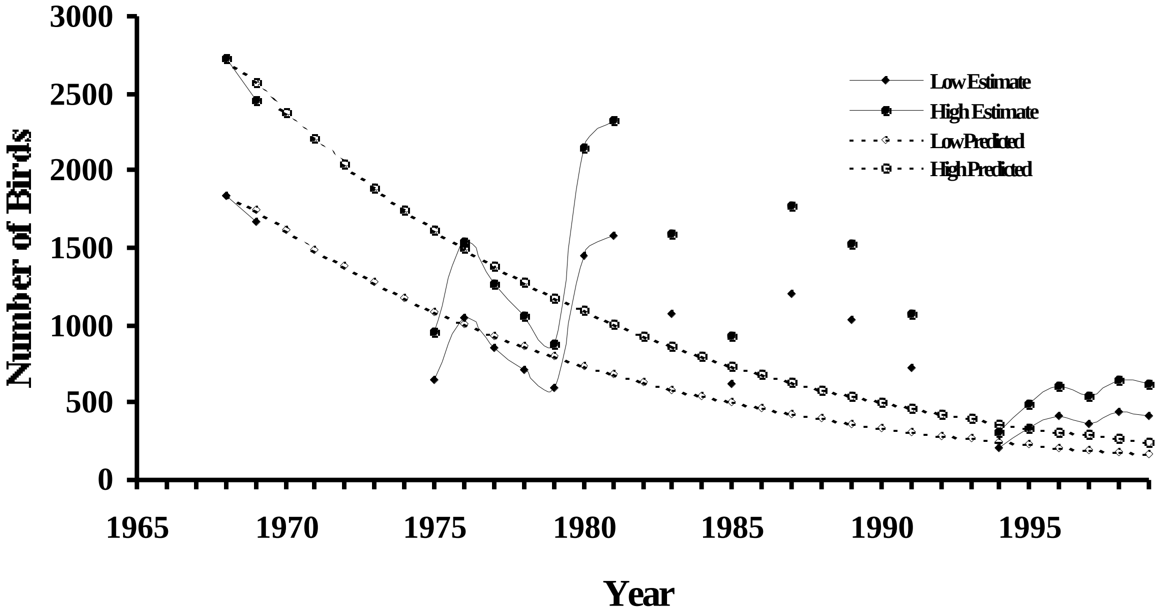

Figure 1. Actual Sage-Grouse population size in Alberta based on lek counts for 1968 through 1999 shown with the predicted population superimposed. Predicted population size is based on survival and productivity data measured in 1998 and 1999. Years when sampling efforts consisted of less than eight leks surveyed are not included. This model starting point is based on the population size in 1968. 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. 2). 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. Thus, lek counts should decrease from 140 males in 1999 to approximately 132 males in 2000. I have chosen to just show Alberta data here, for ease of interpretation. However, this model can also be applied to the entire Canadian population by combining 1999 lek counts form both Alberta and Saskatchewan.

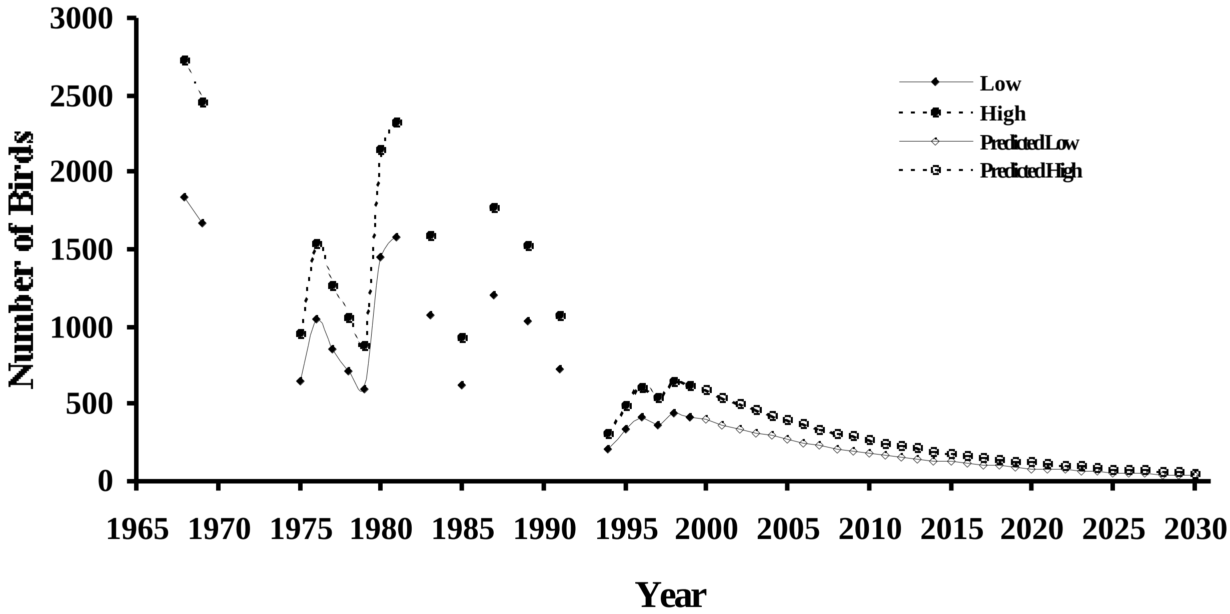

Figure 2. Actual Sage-Grouse population in Alberta based on lek counts for 1968 through 1999 and predicted population from 2000 to 2030. Years when sampling efforts consisted of less than eight leks surveyed are not included. Lines are shown to illustrate trends for years with consecutive lek counts, and to show the predicted population trend.

The model predicts that the Alberta population will fall below 300 individuals by 2004 (Fig. 2). 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 this research were yearlings (Aldridge and Brigham 2000b). 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, juvenile overwinter survival would have to be as low as 40% to obtain a yearling to adult ratio close to 25%. 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, both the Alberta and Canadian populations will be extirpated in less than 20 years.

Even though the cause(s) for the population decline in Canada are not definitively known, I suggest the most likely bottleneck is poor chick survival and low recruitment (see Aldridge and Brigham 2000a). Only 24 of 96 Sage-Grouse captured in 1998 and 1999 in Alberta were yearlings (Aldridge 2000), suggesting that recruitment is low, about 25%. Several long-term studies based on capture data show that about 45% [(44%, *n* = 440, Dalke et al. 1963) (45%, *n* = 3680, Braun and Beck 1985) (46%, *n* = 506, Wallestad 1975) (48%, *n* = 1317, Beck and Braun 1978)] of birds captured on or around leks in the breeding season are yearlings. This suggests that recruitment is low in Canada, possibly due to low chick survival and/or high overwinter mortality (Aldridge 2000).

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 that to maintain genetic diversity, individual populations should consist of at least 500, and maybe even 5000 individuals(Franklin 1980, Lande 1988, Braun 1995). 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 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, Aldridge 2000).

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 [$N_e \approx 4(\Gamma \times E)/(\Gamma + E)$] (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. However, Sage-Grouse have persisted in Alberta with a population likely below 5000 individuals for over 30 years.

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.

Given the current population estimates, 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. 1) (Patterson 1952, Rich 1985, Aldridge 1998, Braun 1998). Populations in the low part of the cycle may be more susceptible to extinction events, and genetic bottlenecks could easily occur. Egg hatching success for Sage-Grouse in Alberta is relatively high (92%), 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. Sage-Grouse populations in Alberta and Saskatchewan may not be distinct, but a genetic bottleneck may already be in place, as there is relatively little contiguous habitat between southern populations in Montana, making movements between populations unlikely. 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.

The cause of the population decline appears to be linked to reduced recruitment as a result of poor chick survival (Aldridge and Brigham 2000b). Mesic habitats that provide protective cover and lush forbs and insects as food resources for chicks are limiting in southern Alberta and this likely related to low chick survival rates (Aldridge and Brigham 2000c). Thus, without suitable habitat management, I predict that the Canadian Sage-Grouse population will continue to decline.

Sage-Grouse productivity appears to be positively correlated with increasing spring (April to June) precipitation (June 1963, Gill 1966, Aldridge 2000). Aldridge (2000) found a correlation between productivity and spring precipitation in Alberta, although the trend is not statistically significant ($P \geq 0.05$). 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, Pyle and Crawford 1996, Sveum et al. 1998a). Spring precipitation from 1994 to 1999 in southeastern Alberta was above average and, thus, it is has been suggested that Sage-Grouse productivity was above the long-term average. Thus, when spring precipitation is below average, productivity will be adversely affected, further reducing recruitment.

Management practices need to focus on the fact that given normal reproductive effort and reproductive success by Sage-Grouse in Canada, small fluctuations in chick survival can have profound implications on recruitment, and, the population trends. Important mesic habitats are limiting, and competition with cattle for already limited resources may compound the problem, especially in dry years, when abundance of forbs may be even more limiting. 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 and insect abundance.

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