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NESTING AND REPRODUCTIVE ACTIVITIES OF GREATER SAGE-GROUSE IN A DECLINING NORTHERN FRINGE POPULATION

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Abstract. In Canada, Greater Sage-Grouse (*Centrocercus urophasianus*) are at the northern edge of their range, occurring only in southeastern Alberta and southwestern Saskatchewan. The population in Canada has declined by 66% to 92% over the last 30 years. We used radio-telemetry to follow 20 female Greater Sage-Grouse and monitor productivity in southeastern Alberta, and to assess habitat use at nesting and brood-rearing locations. All females attempted to nest. Mean clutch size (7.8 eggs per nest) was at the high end of the normal range for sage-grouse (typically 6.6–8.2). Nest success (46%) and breeding success (55%) were within the range found for more southerly populations (15% to 86% and 15% to 70%, respectively). Thirty-six percent of unsuccessful females attempted to renest. Fledging success was slightly lower than reported in other studies. Thus, reproductive effort does not appear to be related to the population decline. However, chick survival to ≥50 days of age (mean = 18%) was only about half of that estimated (35%) for a stable or slightly declining population, suggesting that chick survival may be the most important factor reducing overall reproductive success and contributing to the decline of Greater Sage-Grouse in Canada.

Key words: *Canada,* Centrocercus urophasianus, *Greater Sage-Grouse, nesting, reproductive effort, reproductive success.*

Actividades de Anidación y Reproducción de *Centrocercus urophasianus* en una Población del Extremo Norte en Declive

Resumen. En Canadá, *Centrocercus urophasianus* está en el extremo norte de su distribución, encontrándose sólo en el sureste de Alberta y el suroeste de Saskatchewan. La población de Canadá ha disminuido entre el 66% y 92% durante los últimos 30 años. Utilizamos radio-telemetría para seguir a 20 hembras de *C. urophasianus* y monitorear su productividad en el sureste de Alberta y para evaluar el uso de hábitat en sitios de anidación y de cría de los pichones. Todas las hembras intentaron anidar. El tamaño promedio de la nidada (7.8 huevos por nido) estuvo en el extremo superior del rango normal de *C. urophasianus* (típicamente 6.6–8.2). El éxito de anidación (46%) y de reproducción (55%) estuvieron dentro de los rangos encontrados en poblaciones de más al sur (15% a 86% y 15% a 70%, respectivamente). El treinta y seis por ciento de las hembras que no tuvieron éxito intentaron volver a anidar. El éxito en la crianza de polluelos hasta la etapa de volantones fue ligeramente menor que el reportado en otros estudios. Por lo tanto, el esfuerzo reproductivo no parece estar relacionado con el declive poblacional. Sin embargo, la supervivencia de los polluelos hasta 50 días de edad o más (promedio = 18%) fue sólo aproximadamente la mitad de lo que se ha estimado para una población estable o en ligero declive (35%), lo que sugiere que la supervivencia de los pichones podría ser el factor más importante reduciendo el éxito reproductivo en general y contribuyendo al declive de *C. urophasianus* en Canadá.

INTRODUCTION

Sage-grouse (*Centrocercus* spp.) across their range have experienced declines ranging from 45% to 80% since the 1950s (Braun 1998), with declines from 1985 to 1995 averaging 33% (Connelly and Braun 1997). Historical declines are attributed to human-induced reduction in sagebrush (*Artemisia* spp.) habitats, with 2.5 million ha of the sagebrush steppe ecosystem destroyed since the early 1900s (Braun 1998, Schroeder et al. 1999). Many other factors have altered or fragmented current habitat and may also have contributed to recent population declines. These include domestic livestock graz-

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ing, fire, construction of roads, highways, fences and power lines, and a variety of natural changes (Braun 1998, Schroeder et al. 1999).

Most research on sage-grouse has shown that population declines are related to reduced nesting success (Schroeder 1997, Braun 1998, Schroeder et al. 1999). Nesting success ranges from 15–86%, with stable populations generally having higher nesting success (Dalke et al. 1963, Schroeder et al. 1999). Little research has been conducted to address aspects of overall reproductive success such as chick survival, primarily due to difficulties in estimating brood size, and technological limitations in affixing radio-transmitters to juvenile birds.

Sage-grouse are associated with big sagebrush (*A. tridentata*) throughout most of their range, and nest success is higher in areas containing big sagebrush (Wallestad and Pyrah 1974, Connelly et al. 1991, DeLong et al. 1995). Silver sagebrush (*A. cana*) is the dominant species in Canada (Aldridge 2000), but does not provide the same extent of cover for nesting or escape from predators. As a result, the Greater Sage-Grouse (*C. urophasianus*) population in southern Alberta provides an excellent opportunity to examine productivity where big sagebrush is absent.

Greater Sage-Grouse have declined by 66–92% (for the currently occupied range only) over the last 30 years in both Alberta and Saskatchewan (Aldridge 2000). Aldridge (2000) estimated the 1999 spring population in Canada to be 813–1204 individuals. Previous research suggests the Alberta population is nonmigratory (CLA, unpubl. data). Thus, the population decline is likely related to decreases in survival or productivity, but the significance of each is unknown.

We compared timing of reproductive activities and measures of productivity for a declining Greater Sage-Grouse population in southern Alberta, with measures of productivity for other declining (Colorado, Idaho, Montana) and drastically reduced but stable (Washington) sage-grouse populations. We hypothesized that the decline observed in the Greater Sage-Grouse population in Canada was related to reduced reproductive effort, reduced reproductive success, or a combination of both.

METHODS

STUDY AREA

The study area consisted of a 4000-km^2 area in the mixed-grass prairie of southeastern Alberta (49°24′N, 110°42′W, ca. 900 m elevation). The area, although essentially flat, is interrupted by vast draws that lead to small creeks. Silver sagebrush is the dominant shrub and pasture sage (*A. frigida*) the dominant forb. Grasses include needle-and-thread grass (*Stipa comata*), June grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*) (Aldridge 2000).

FIELD TECHNIQUES

We counted the maximum number of male and female Greater Sage-Grouse attending all active leks, on at least four different occasions during the breeding season (Beck and Braun 1980). The maximum number of males counted at each lek was used to estimate population size, and the date of maximum hen attendance at each lek was used to estimate the peak time of breeding activities (Beck and Braun 1980, Emmons and Braun 1984). We captured females at five 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 spotlights (Giesen et al. 1982). Trapping effort was consistent throughout the breeding season (March through May). In addition, several females were captured by nightlighting flocks of broodless females in summer. Sex and age (yearlings $<$2 years old or adults $\geq$2 years old) of all captured individuals was determined based on shape and length of the outermost primaries of each bird (Eng 1955, Crunden 1963). Captured females were fitted with a 14-g necklace-style radio-transmitter (RI-2B transmitters, Holohil Systems Ltd., Carp, Ontario, Canada).

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). When we approached a potential nesting female, we triangulated signals until the marked bird could be observed from approximately 30 m (to minimize disturbance, Schroeder 1997). After a female was observed on two consecutive relocations under the same shrub, signals were triangulated from at least 50 m away until the female moved from the nest. These locations were recorded in Universal Transverse Mercator coordinates using a handheld 12-channel Global Positioning System (Garmin 12 XL and GPS II Plus, Garmin International Inc., Olathe, Kansas). When signals disappeared, we searched the study area from a fixed-wing aircraft.

Measures of productivity were calculated following Schroeder (1997). Clutch size was estimated by counting the number of eggshells following either hatching or destruction of the nest. Eggshells were always counted within 3 days of hatch or nest destruction. We estimated the date of nest initiation as the midpoint between the last day the female made non-localized movements prior to nesting, and the first direct observation of the female on a nest. Nest success was defined as the percentage of nests that hatched ≥1 egg. Date of nest success or failure was estimated as the midpoint between the last observation of the female on the nest and the first observation of the female off the nest. Breeding success was defined as the percentage of females that hatched ≥1 egg during a single breeding season (first or renest). Fledging success was the percentage of females that raised at least one chick to independence (≥50 days, Schroeder 1997). This parameter can be calculated relative to either the number of females that made nesting attempts (Schroeder 1997), or for only those females that hatched at least one egg (successful breeders). The latter differentiates between breeding success and survival of the brood. We calculated fledging success relative to successful breeders only, because unsuccessful nesters cannot fledge young. However, we also calculated fledging success for all females that attempted to nest, to allow for comparison with other studies. We estimated chick survival as the percentage of young that lived ≥50 days.

STATISTICAL ANALYSES

Due to a limited sample size of nesting females in 1998, and the limited number of renesting attempts and nesting yearlings throughout the study, our analyses of year and age effects were limited. We 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 ANOVA to test for differences in clutch size and timing of reproductive events, and a Chi-square test was used to test for differences in nesting success, fledging success, and breeding success, between age groups and nest order. We used the Kaplan-Meier product limit procedure to investigate nest survival over the course of incubation (Pollock et al. 1989). Sample sizes varied between analyses due to the difficulty in obtaining measurements for all parameters for each individual. We did not conduct statistical tests when the sample size was less than five. We used an α-value of 0.05 for all analyses. Values reported are means ± SE.

RESULTS

We captured 37 female Greater Sage-Grouse at five leks and fitted them with radio-transmitters (two adults and three yearlings in 1998, 22 adults and 10 yearlings in 1999). Three additional adult females were captured in summer 1998 and one in summer 1999. Two females captured in summer 1998 were killed by predators before the 1999 breeding season; the female captured in summer 1999 had a brood, but was killed by a predator two weeks after capture.

We collected data on reproductive success for 20 females; 3 in 1998 and 19 in 1999 (two birds were followed in both years). Of 41 radio-marked females, 5 carried radios that apparently malfunctioned and 4 females died prior to the breeding season. We could not relocate 12 of the remaining 32 females during the breeding season; of these 12, four were found dead with damaged transmitters in late spring or early summer and likely died before nesting, one was captured with chicks after nesting, and one was recaptured on 23 July 1999 with a brood patch but no brood. The fate of the other six birds is unknown.

The mean date of capture for 36 females caught during the breeding season was 8 April ± 1.9 days, while the mean date of maximum attendance of females (based on lek counts) at seven of eight active leks in 1999 was 5 April ± 0.9 days (1998 data were not used to calculate maximum attendance dates due to limited counts at leks prior to 11 April). One lek was not used in the analyses due to limited observations early in the 1999 breeding season. This suggests the peak in breeding occurred during the first week of April.

TIMING OF REPRODUCTION

The mean initiation date of incubation for 20 first nests (3 May, range 27 April to 9 May) was 35 days earlier than the mean date of five renesting attempts (7 June, range 29 May to 16 June). The average onset of first-nest incubation for adult females (1 May, range 23 April to 10 May, $n = 17$) was earlier than for yearlings (10 May, range 5 to 14 May, $n = 3$).

Incubation lengths ranged from 23 to 29 days (mean = 27 ± 0.6 days, $n = 10$) and was similar for both first nests ($n = 7$) and renesting attempts ($n = 3$). Hatch date for successful nests (mean = 5 June ± 4.6 days, $n = 12$) was 33 days earlier for first nests (mean = 28 May ± 1.6 days, $n = 9$) than for renesting attempts (mean = 30 June ± 5.4 days, $n = 3$).

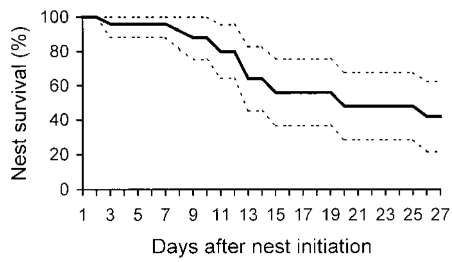

FIGURE 1. Kaplan-Meier product limit estimate for nest survival in relation to date after initiation, for Greater Sage-Grouse nests in southern Alberta in 1998 and 1999. The 95% confidence limits are shown by the dashed lines.

REPRODUCTIVE EFFORT

Clutch size for successful (mean = 8.2 ± 0.6, $n = 11$) and unsuccessful (mean = 7.9 ± 0.5, $n = 12$) first nesting attempts was independent of nest success ($F_{1,21} = 0.12$, $P > 0.7$). Therefore, we pooled successful and unsuccessful first nests for analyses. For all 28 nests together (first and renests), clutch size ranged from 4 to 11 eggs. First nests (mean = 8.0 ± 0.4 eggs, $n = 23$) had larger clutches than renesting attempts (mean = 5.6 ± 0.7 eggs, $n = 5$, $F_{1,26} = 8.4$, $P < 0.01$). Egg viability (percentage of all eggs laid in successful nests that hatched) was 92% (96 of 104 eggs).

We based our estimate of annual nesting effort on data from 20 females (2 followed in both years). In all cases, females displayed localized movements within an area and a nest was eventually located after hatching or predation.

In 1998, one adult female was captured at a lek late in the breeding season (22 May) with a well-developed brood patch. We assumed she had failed in her first nesting attempt, and considered her subsequent unsuccessful nesting attempt as a renesting effort. Even with this bird, only 5 of 14 (36%) females that were unsuccessful in their first nest attempts renested (5 of 11 adults and 0 of 3 yearlings).

REPRODUCTIVE SUCCESS

Actual nest success (percent of all nests that hatched ≥1 egg) was 46% for 26 nests (1 of 3 in 1998, 11 of 23 in 1999). We did not use a Mayfield estimator (Mayfield 1975) as all females that were tracked attempted to nest. Nest success was similar for first (9 of 12, 43%) and renesting (3 of 5, 60%) attempts ($\chi^2_1 = 0.3$, $P > 0.6$). Adults (11 of 22, 50%) appeared more likely to have successful nests than yearlings (1 of 4, 25%). The majority of nest failures occurred in mid-incubation (Fig. 1).

Breeding success was 54% for 22 females monitored throughout a breeding season. Adult females were more successful (11 of 18, 61%) than yearlings (1 of 4, 25%). We estimated fledging success to be 23%; five females produced chicks that survived to 50 days of age (5 of 18 adults, 0 of 4 yearlings). Fledging success calculated for successful breeders was 42% (5 of 11 adults, 0 of 1 yearling).

Due to the difficulty in locating all chicks when a brooding female was flushed, it is possible that we underestimated fledging success. Thus, we calculated a range of chick survival to 50 days (minimum and maximum). The minimum was the number of chicks counted 50 days after hatch. If a greater number of chicks was observed with the female 43–50 days post hatch, we considered that we might have missed those chicks on day 50, and calculated a maximum value for chick survival. Thus, chick survival was 14% to 23% for 88 chicks, with no yearling females successfully rearing chicks to fledge.

DISCUSSION

In summary, we conclude that lack of reproductive effort is not the principal cause for the Canadian Greater Sage-Grouse population decline. However, low fledging success due to low chick survival apparently resulted in poor reproductive success and reduced recruitment, and this is likely a major contributor to the decline.

Although two studies have shown that sage-grouse select nest sites independently of lek location (Bradbury et al. 1989, Wakkinen et al. 1992), the majority of nests occur within 3.2 km of the lek of capture (80% within 3.2 km, Martin

1970; 55% within 3.0 km, Wakkinen et al. 1992; and 68% within 2.5 km, Wallestad and Pyrah 1974). While average distance from nest to lek of capture in our study (4.7 ± 0.7 km; range 0.4–15.5 km) was within the range for other reported studies (average 4.0 km to 7.8 km, Schroeder et al. 1999), only 41% of 27 nests occurred within 3.2 km of the lek. Autenrieth (1981) suggested that lek-to-nest distances may be inversely correlated with habitat quality. Thus, suitable nesting habitat in Canada may be limited close to leks.

All females we tracked made nesting attempts, similar to birds in Washington (Schroeder 1997). 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. Schroeder (1997) suggested that previous telemetry studies indicating that 20–32% of females do not nest each year underestimated nesting attempts. However, competition by females for nest sites in high-density populations could preclude some females from nesting. Thus, in low-density populations (e.g., Washington and Canada), competition for nests sites is less likely, and all females make nesting attempts.

Mean clutch size for first nesting attempts (8.2) was higher than other studies (typically between 6.6 and 8.2; Patterson 1952, Wallestad and Pyrah 1974, Schroeder et al. 1999). Because yearlings are under-represented in the population (3:1 adult to yearling ratio, Aldridge 2000), our mean clutch size may be inflated because adult clutch size tends to be 0.02–2.1 eggs larger than for yearlings (Schroeder et al. 1999). Schroeder (1997) found that Greater Sage-Grouse in Washington also laid large clutches (mean = 9.1 ± 1.3, n = 55) and suggested that clutch size may be correlated with nutrition. However, given that egg production and laying began in our population prior to new plant growth, clutch size is not likely affected by the flush of spring growth (Bergerud 1988).

Incubation occurred later in Canada (3 May) compared to Washington (mean initiation date 22 April, Schroeder 1997) but earlier than in Montana (14 May, Wallestad 1975). Greater Sage-Grouse in Washington also have higher renesting rates (87%, Schroeder 1997), compared to our study (36%) and in other populations (5% to 41%, Schroeder et al. 1999).

Spring precipitation has been linked to increased nest success (Gill 1966). Peterson (1970) found that wet years in Montana resulted in greater forb production and increased brood success. Spring precipitation (April–June) was >19 mm above the 35-year average in both years of our study (Onefour Research Station, Environment Canada), implying above-average nest success. Even though spring precipitation was elevated, mesic sites that provide important food resources for chicks (Peterson 1970, Sveum et al. 1998) were not common (≤12% of available habitat, Aldridge 2000). Thus, we predict lower nest success in dry years, resulting in even fewer broods produced each year, and chick survival will likely decrease below our current estimate (mean = 18%).

Brood size declines during the summer by as much as 68% (Schroeder et al. 1999), reflecting the characteristically low survival rates of juveniles. Schroeder (1997) estimated chick survival in Washington to be 33%, while June (1963) reported that 38% of chicks in Wyoming survived to the autumn. Both populations declined slightly over the period of the studies (June 1963; M. A. Schroeder, pers. comm.). The level of chick survival (14–23%) we found is only about half of that required to sustain a population, assuming reasonable levels of reproductive effort and reproductive success. Fledging success calculated from all nesting attempts (28%) was also about half of that found in Schroeder's 1997 study (50%), despite high nesting success. Again, we are confident that we did not underestimate this parameter because females that lost their broods flocked together (CLA, pers. obs.; C. E. Braun, pers. comm.).

Our brood counts indicated that chick survival was extremely low, leading us to expect that recruitment rates would be low. Long-term studies based on capture data show that about 45% of birds captured on or around leks in the breeding season are yearlings (Dalke et al. 1963, Wallestad 1975, Beck and Braun 1978, Braun and Beck 1985). Over the two years of our study, consistent trapping throughout the breeding season resulted in the capture of 96 individuals; only 25% were yearlings (Aldridge 2000). Therefore we conclude that recruitment is low for Greater Sage-Grouse in Canada.

In summary, Greater Sage-Grouse in our study displayed high reproductive effort (nesting effort, clutch size, and egg viability). Reproductive success (including nesting success and breeding success) was comparable to other populations, although likely elevated due to above-average spring precipitation. Overall, productivity appears to be limited by low chick survival (mean = 18% compared to 35% in other populations) resulting in reduced recruitment. 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. 1998) and may be directly related to food availability and quality for chicks. Greater Sage-Grouse in Canada exist at some of the lowest known densities (<1 bird km^{-2}, Aldridge 2000) of any population. Chick survival may be limited by the availability of mesic habitats with higher forb availability, resulting in population changes (Aldridge 2000). Overwinter mortality of juvenile Greater Sage-Grouse, which was not measured in this study, may contribute to the low rates of recruitment.

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