

UNUSUALLY HIGH REPRODUCTIVE EFFORT BY SAGE GROUSE IN A FRAGMENTED HABITAT IN NORTH-CENTRAL WASHINGTON¹

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Abstract. Productivity of Sage Grouse (*Centrocercus urophasianus*) was studied in north-central Washington during 1992–1996. Nest timing and success, clutch size, probability of nesting and renesting, and variation associated with age and year were examined for 84 females monitored with the aid of radio telemetry. Although date of nest initiation varied annually, yearling females (hatched in previous year) consistently nested later than adults; mean date of initiation of incubation was 22 April overall. The average nest contained 9.1 eggs and was incubated for 27 days. Clutch size was smaller for renests than for first nests; clutch size also varied annually. Although the overall rate of nest success was only 36.7%, all females apparently nested at least once, and at least 87.0% of females renested following predation of their first nests. As a result of renesting, annual breeding success was estimated as 61.3%. Percent of all females that produced a brood at least 50 days old was 49.5%; at least 33.4% of 515 chicks survived \geq 50 days following hatch. Although the rates of nesting and renesting appear to have been under-estimated in other studied populations, Sage Grouse in north-central Washington display more reproductive effort overall; they lay more eggs and are more likely to nest and renest.

Key words: *Centrocercus urophasianus*, clutch size, life history, nesting, productivity, renesting, Sage Grouse.

INTRODUCTION

Population dynamics of Tetraoninae has long been an area of interest for behavioral ecologists and wildlife biologists. Although intrinsic factors such as territoriality (Hannon 1988) and extrinsic factors such as predation pressure (Angelstam 1988) may ultimately influence population regulation, variation in productivity appears to be the most significant proximal factor influencing population size (Bergerud 1988). Consequently, a large body of research has focused on relationships between productivity and variables such as habitat quality, predation pressure, and demography (review in Bergerud 1988).

There are several aspects to productivity in Tetraoninae including the probability of nesting, clutch size, nest success (percent of all nests that hatch \geq 1 egg), the probability of renesting following destruction or abandonment of the first nest, breeding success (percent of all females that produce a brood), and fledging success (percent of all females that produce a brood to the age of independence). Two characteristics of

Sage Grouse (*Centrocercus urophasianus*) productivity that are particularly notable are the relatively low probability of nesting and the low likelihood that females will renest in the event that their first nest is unsuccessful (Connelly et al. 1993). The low reproductive effort reported for Sage Grouse (probability of nesting 55% for yearlings and 78% for adults, Connelly et al. 1993) is extremely unusual for grouse (Bergerud 1988). Furthermore, most research indicates that renesting by Sage Grouse is unusual (Connelly et al. 1993, Hanf et al. 1994).

Previous research on Sage Grouse productivity often has been difficult because of large movements by female Sage Grouse, the relative inaccessibility of their nest sites, and the infrequent presence of females at their nest sites during the egg laying period. Consequently, research may have been adversely influenced by the difficulty in locating nests prior to their destruction by predators (Connelly et al. 1993).

Research on Sage Grouse in north-central Washington was initiated because of declining populations and related management concerns (Washington Dept. Fish and Wildlife 1995). Although previous research failed to illustrate differences in productivity that could be attributed to differences between subspecies or popula-

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tions, the Western Sage Grouse (*C. u. phaios*) in north-central Washington offered a unique opportunity for comparison with Sage Grouse in other areas. North-central Washington is dominated by winter wheat, planted crested wheatgrass (*Agropyron cristatum*), and fragmented areas of tall big sagebrush (*Artemisia tridentata*), whereas other study areas have been typically dominated by relatively unfragmented short big sagebrush habitats. In addition, the density of roads in north-central Washington is substantially higher than in other Sage Grouse study areas, thus making the daily monitoring of nesting females possible.

The purpose of this paper is to examine nest timing and success, nesting and renesting likelihood, clutch size, breeding and fledging success, and variation associated with age and year in a population of Western Sage Grouse in north-central Washington and to compare their productivity with Sage Grouse productivity in other regions.

METHODS

Sage Grouse were studied on a 3,000 km² area centered near Mansfield, Washington (47°50'N, 119°40'W). The area is a mix of dryland wheat and shrub steppe habitat dominated by big sagebrush, threetip sagebrush (*Artemisia tripartita*), bluebunch wheatgrass (*Agropyron spicatum*), crested wheatgrass, and bluegrass (*Poa* spp.). Sage Grouse were trapped on seven different display sites (leks) with the aid of walk-in traps (Schroeder and Braun 1991) during March and April, 1992–1996. Sex and age were determined for all captured birds (Beck et al. 1975); all females were fitted with battery-powered radio transmitters attached to poncho-like collars (Amstrup 1980) or necklaces.

Females were located with a portable receiver and 4-element Yagi antenna at least once every three days to collect data on the timing of incubation, nest failure, and nest success. Most females were located either visually or with triangulation techniques designed to determine whether the female was on her nest. Variation in intensity of transmitter signals also was used as an indication of female behavior; radio transmitters emitted a constant signal when a female was on her nest and a variable signal when she was walking or flying. Fixed-wing aircraft were used to locate lost birds. "Visual" observations of females on nests consisted of triangulation

from a distance of about 30 m from the nest site; this minimized disturbance of females and usually allowed nest sites to be located following hatch or failure. Clutch size was estimated by counting egg shells following a successful hatch or the destruction of the nest within 5 days of the female's departure from the nest site.

Nest success was calculated as the percent of all nests that hatched ≥ 1 egg. Breeding success was estimated as the percent of females that hatched ≥ 1 chick during the breeding season (regardless of whether the chick was produced from a first nest or renest). Fledging success was estimated as the percent of females that produced a brood ≥ 50 days old. Chick survival was estimated as the percent of hatched chicks that lived ≥ 50 days. Date of first day of nest incubation and date of nest failure were estimated as the midpoints between consecutive observations. For example, if a female was on her nest on 14 April and off her nest on 16 April following nest failure, the date of nest failure was considered 15 April. Nesting and renesting likelihood were estimated with different types of information including the direct observation of nests, localized movements by females (non-nesting movements by Sage Grouse were often extremely large and erratic), dates of lek visits, and appearance of females with broods.

Analyses of nest success, breeding success, and renesting likelihood were conducted with logistic regressions (Proc CATMOD, SAS Institute 1988). Examinations of clutch size and date of nest initiation were conducted with general linear models (Proc GLM). Because of difficulty in obtaining complete measurements for all parameters for all females, sample sizes were not consistent between analyses. Results were considered significant at $\alpha \leq 0.05$.

RESULTS

Eighty-nine female Sage Grouse were captured on leks and fitted with radio transmitters: 20 adults and 2 yearlings in 1992; 12 adults and 4 yearlings in 1993; 12 adults and 9 yearlings in 1994; 9 adults and 12 yearlings in 1995, and 8 adults and 1 yearling in 1996. Nest data were obtained for 84 radio-marked females; this sample did not include 3 females that died prior to the nesting season and 2 females that disappeared (damaged radio transmitter and/or undetected movement).

INITIATION OF INCUBATION

Average date of initiation of nest incubation for all nests was 22 April (range 1 April–26 May) for 182 nesting attempts (Fig. 1). Age ($F_{1,167} = 8.4$, $P < 0.01$) and year ($F_{4,167} = 10.2$, $P < 0.01$) were both significant factors explaining variation in incubation date (general linear model with nest order [first nests or renests] also included as a class variable, $F_{1,167} = 779.6$, $P < 0.01$). Interactions between age and year ($F_{4,167} = 3.3$, $P = 0.01$) and year and nest order ($F_{4,167} = 4.9$, $P < 0.01$) also were significant.

Initiation of incubation was latest in 1993 and yearlings tended to nest later than adults in most years for both first nests and renests (Fig. 1). The annual variation in initiation of incubation was supported with evidence from 32 adult females monitored during consecutive years. Date of incubation initiation was 10.8 days later in 1993 than in 1992 ($n = 5$), 11.7 days earlier in 1994 than in 1993 ($n = 3$), 0.5 days earlier in 1995 than in 1994 ($n = 11$), and 7.5 days later in 1996 than in 1995 ($n = 13$). Age-specific variation in initiation of incubation was supported with evidence from 14 females monitored as both yearlings and adults. Females nested 9.4 days earlier as adults than they did as yearlings, after control for annual variation in date of nest initiation.

The possibility that trapping efforts affected dates of nest incubation also was examined. Date of nest incubation was compared for females captured in previous years and adult females captured during the year of interest. Capture history was not significantly related to date of nest incubation in a general linear model with year included as a class variable ($F_{1,176} = 1.61$, $P = 0.21$); 34 newly captured females tended to nest an average of 1 day later than 46 previously captured females.

CLUTCH SIZE

Clutch size was extremely variable, 6 to 12 eggs for 88 nests. Examination of clutch size in a general linear model with age, year, nest order, and nest success as independent variables indicated that clutch size varied with nest success ($F_{1,80} = 3.75$, $P = 0.06$); clutch size tended to be smaller for unsuccessful nests ($\bar{x} = 8.52 \pm 1.35$ eggs, $n = 33$) than for successful nests ($\bar{x} = 9.11 \pm 1.30$ eggs, $n = 55$). This difference was likely related to the methodologies associated with estimation of clutch size; egg shells may have been more likely to have been removed from unsuccessful

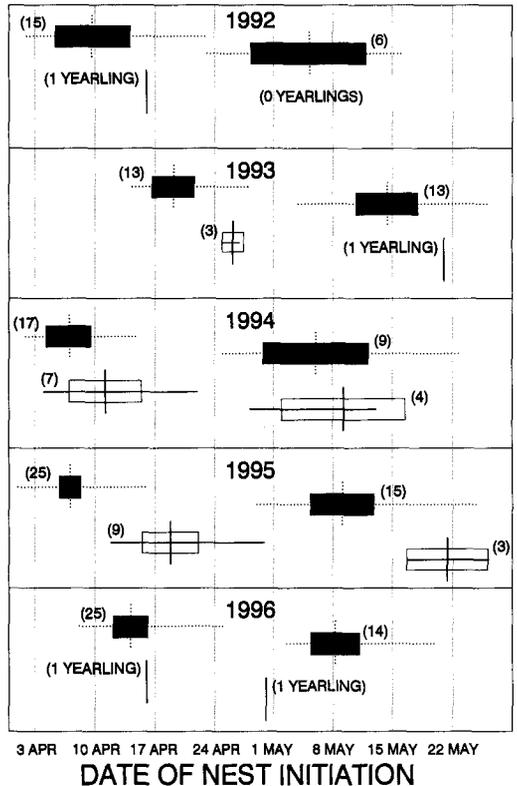


FIGURE 1. Date of Sage Grouse nest initiation for 116 first nests and 66 renests in north-central Washington, 1992–1996. The means are represented by vertical lines, the ranges by horizontal lines, and the 95% confidence intervals by solid rectangles for adults and open rectangles for yearlings; sample sizes are in parentheses.

nests. Consequently, all further analyses of clutch size were done on successful nests only. Variation in clutch size was strongly related to nest order ($F_{1,48} = 10.1$, $P < 0.01$) and year ($F_{4,48} = 5.7$, $P < 0.01$) (Fig. 2); age was not a significant factor ($F_{1,48} = 0.8$, $P = 0.37$). Mean clutch size was larger for first nests ($\bar{x} = 9.50 \pm 1.25$ eggs, $n = 32$) than renests ($\bar{x} = 8.57 \pm 1.17$ eggs, $n = 23$) and relatively large in 1995 ($\bar{x} = 10.23 \pm 0.80$ eggs, $n = 13$).

The embryo viability (% of all eggs laid in successful nests that hatched) was 95.7% (493 of 515 eggs); 2 eggs that disappeared for unknown reasons were excluded from the analysis. Most unhatched eggs appeared to be infertile; these included a complete clutch that was incubated for 76 days before being destroyed by a predator. Five of 10 eggs in one clutch did not

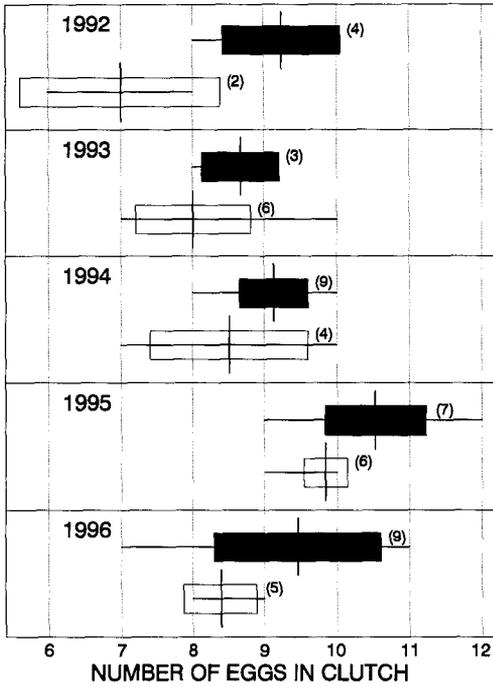


FIGURE 2. Number of eggs in Sage Grouse nests in north-central Washington, 1992–1996. The means are represented by vertical lines, the ranges by horizontal lines, and the 95% confidence intervals by solid rectangles for first nests and open rectangles for re-nests; sample sizes are in parentheses.

hatch because they rolled out of the nest during incubation (the nest was located on a slope of about 35°).

NESTING LIKELIHOOD

Annual nesting efforts were not confirmed for 6.7% of 105 adult and 8.3% of 24 yearling female Sage Grouse. Essentially all females were assumed to have nested because of the following information. All females displayed localized movements around their actual or apparent nest sites, despite the fact that nine females were not observed on nests. Twenty-four females were observed visiting leks after the actual or apparent failure of their first nests, including three females that were not observed on nests. Three radio-marked females were observed with broods that were not observed on nests. Probable re-nests were found for 12 females that had not been observed with first nests, despite the observation of all females in “localized” areas around their likely first nests.

NEST SUCCESS

The mean duration of incubation was 26.8 days (range 25–28 days) for 66 successful Sage Grouse nests. The rate of nest failure was estimated as 39.2% during the first half of the incubation period and 34.0% during the second half of the incubation period (Fig. 3). Overall nest success was estimated as 36.7% for 188 nests. Nest success did not appear to be related to female age ($\chi^2_1 = 0.0, P = 0.92$), nest order ($\chi^2_1 = 0.1, P = 0.70$), year ($\chi^2_4 = 2.3, P = 0.68$), or date of incubation ($\chi^2_1 = 0.0, P = 0.90$) when examined in a logistic regression.

RENESTING LIKELIHOOD

Renesting information was obtained for 69 females. Four females captured late in April 1994 were excluded from the analysis because they already had developed full brood patches indicating that they had already nested. Variation in renesting probability was not significantly related to age ($\chi^2_1 = 0.2, P = 0.64$) in a logistic regression; the probability of renesting was 87.9% ($n = 58$) for adult females and 81.8% ($n = 11$) for yearling females. In addition, variation in renesting probability was not significantly related to the number of days between initiation of incubation and failure of their first nest ($\chi^2_1 = 1.3, P = 0.26$) or the date of failure of their first nest ($\chi^2_1 = 3.6, P = 0.06$) in a logistic re-

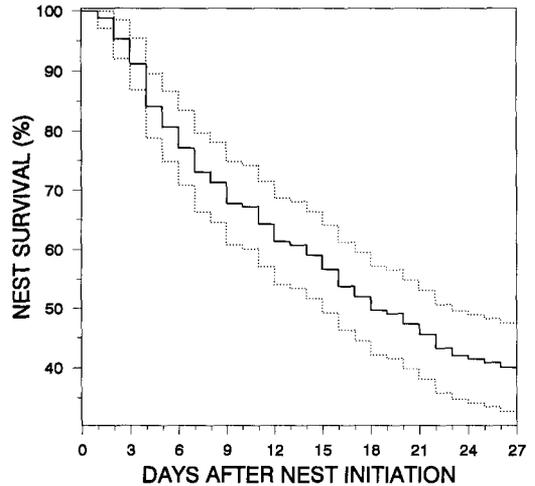


FIGURE 3. Kaplan-Meier product limit estimate of nest survival in relation to the date of initiation of incubation for Sage Grouse in north-central Washington, 1992–1996. The 95% confidence interval is bounded by dotted lines.

gression. The average date of failure of the first nest tended to be later, and the average number of days between initiation of incubation and failure of the first nest tended to be greater for birds that did not renest than for birds that renested.

Overall, 87.0% of 69 females renested, including 2 females that renested twice. Renesting females initiated incubation of their second nests an average of 20.7 ± 4.3 days ($n = 60$) after the estimated date of failure of their first nest (Fig. 4). Although it was not clear if females bred prior to laying their renest clutch, 24 females were observed on leks soon after the failure of their first nest. In contrast, the four shortest intervals between date of failure and initiation of incubation for the subsequent nest were observed in situations where the previous nest failed prior to the initiation of incubation (during egg laying); it is possible that the female began laying eggs in a new nest bowl in these situations, without breeding again.

BREEDING SUCCESS

Breeding success was estimated as 61.3% for 111 females that were monitored throughout the breeding season. Renesting accounted for 38.2% of the overall breeding success. Neither age ($\chi^2_1 = 0.2$, $P = 0.63$) nor year ($\chi^2_4 = 4.2$, $P = 0.38$) were significantly related to breeding success in a logistic regression.

FLEDGING SUCCESS

Overall fledging success was 49.5% for 99 females monitored throughout the breeding season. Fledging success did not appear to be related to female age ($\chi^2_1 = 0.7$, $P = 0.40$) or year ($\chi^2_4 = 4.8$, $P = 0.31$) when examined in a logistic regression. The overall estimate of chick survival was 33.4% for 515 chicks monitored between date of hatch and at least 50 days after hatch.

DISCUSSION

The results of this study document numerous similarities and differences between Sage Grouse in north-central Washington and Sage Grouse studied in other regions. In north-central Washington the mean date for initiation of incubation was 12 April for first nests and 9 May for reneests. The typical estimated dates for initiation of incubation in other regions ranged between late March and mid-May (Girard 1937, Rasmussen and Griner 1938, Dalke et al. 1963);

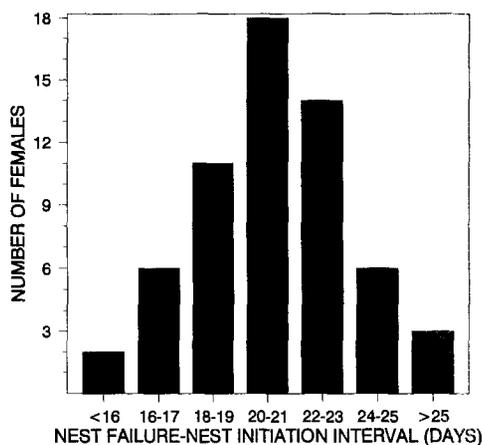


FIGURE 4. Number of days between failure of first nests and date of nest initiation for reneests for Sage Grouse in north-central Washington, 1992–1996.

the earliest dates were from southern Washington (Hofmann 1991, Sveum 1995).

The annual variation in date of nest initiation observed in this study of almost 2 weeks was similar to that recorded in other studies (Batterson and Morse 1948, Young 1994). The variation in nest initiation appeared to be related to annual variation in weather; cold, snowy winters and/or cold, wet springs appeared to result in later dates of nest initiation.

Adults nested earlier than yearlings in north-central Washington by an average of about 9 days. This observation was similar to results from Oregon (Batterson and Morse 1948), Idaho (Schlatterer 1960), and Colorado (Peterson 1980). The difference in date for initiation of incubation may be attributable to differences in the timing of nest site selection by adults and yearlings. Bradbury et al. (1989) noted that females in California typically selected nest sites prior to visiting leks; yearlings arrived on nesting areas about 10 days later than adults.

The estimated length of incubation of 25–28 days in my study was comparable to other studies (Patterson 1952, Pyrah 1963, Wallestad 1975), whereas the mean clutch size of 9.1 was larger than recorded for other Sage Grouse studies in North America; range of means of 6.6 to 8.2 (Wallestad and Pyrah 1974, Sveum 1995). These differences in clutch size occurred despite the difficulty in estimating clutch size precisely. Because eggs were counted following hatch in this study, some of the counts of egg shells were

likely low. For example, although only 5 clutches were examined during incubation, 2 of 48 eggs were lost prior to hatch. It is possible that some animals such as ground squirrels (*Spermophilus* spp.) and chipmunks (*Eutamias* spp.) removed individual eggs and/or egg shells (unpubl. data).

Despite predictions of age-specific differences in clutch size (Wallestad and Pyrah 1974, Petersen 1980), no differences were observed in this study. However, the differences in clutch size that were related to the effects of year and nest order were substantial (Fig. 2). Variation in clutch size due to nest order was similar to observations of Patterson (1952) that later clutches are smaller than earlier clutches. Annual variation in clutch size also was observed in southern Washington for a 2-year period (Sveum 1995). The annual variation in north-central Washington occurred despite the presence of more yearling females in the years with the largest clutches.

It is possible that the annual variation in clutch size may be related in some way to fluctuations in populations of Sage Grouse. For example, variable clutch sizes may directly result in variable populations (Bergerud 1988). It also is possible that clutch sizes may be indirectly correlated with another factor that is related to the fluctuating populations, such as habitat. For example, larger clutch sizes may be a reflection of improved habitat and consequently improved nutrition (Lack 1968). However, despite the observations of annual variation in clutch size in Willow Ptarmigan *Lagopus lagopus* (Bergerud 1970, Myrberget 1988), Rock Ptarmigan *L. mutus* (Weeden and Theberge 1972), Ruffed Grouse *Bonasa umbellus* (Maxson 1974), and White-tailed Ptarmigan *L. leucurus* (Braun et al. 1993), direct relationships between nutrition and clutch size have been difficult to document (Barnett and Crawford 1994). Bergerud (1988) suggested that clutch size for grouse was negatively correlated with annual survival of breeding-aged birds; his observations for Sage Grouse were based on an estimated survival rate of about 40% and a clutch size of about 8. The average clutch size of 9.1 in this study and the estimated female survival rate of 55 to 75% (Zablan 1993, Connelly et al. 1994) would indicate that Sage Grouse do not fit Bergerud's (1988) hypothesized relationship.

Essentially all females in this study attempted

to nest. These results dramatically contrast with results from other telemetry-based research indicating that 20 to 32% of females (usually higher for yearlings) did not attempt to nest (Wallestad and Pyrah 1974, Connelly et al. 1993). Research on follicular development of collected birds indicated that at least 91% of females in Colorado (Braun 1979) and 98% of females in Idaho (Dalke et al. 1963) bred during their previous breeding season. The results on follicular development and the results on nesting attempts from this study indicate that nesting attempts are probably under-represented in the literature.

It is difficult, if not impossible, to find all nests prior to their destruction by predators. With an average clutch size of 9.1 eggs in this study, there may have been an interval of at least 11 days between the day the first egg was laid and the date when incubation was initiated (Patterson 1952). Consequently, a typical nest would be susceptible to predators for about 38 days; 11 days of egg laying plus 27 days of incubation. Because females may spend about 1 hr on nests when they are laying eggs (Griner 1939), most nests are unlikely to be discovered by researchers prior to initiation of incubation. Hence, 29% of the predation period would be relatively unmonitored.

Twenty-one females were found on nests prior to initiation of incubation in this study; seven of these nests were destroyed by predators prior to initiation of incubation. Why was the observed rate of nesting so high, given the likely predation of nests prior to discovery? Previous research has indicated that Sage Grouse may begin laying eggs in a second nest immediately following the destruction of their first nest during the egg-laying period, without attempting to breed a second time (Batterson and Morse 1948, Patterson 1952). This type of behavior could explain some of the relatively late nest initiation dates for "first" nests (Fig. 1) and some of the shorter intervals between date of nest failure and date of initiation of incubation for the subsequent nest (Fig. 4).

Although the actual rate of nesting in other studies can not be determined, the impact of inaccurate nesting rates should be considered on subsequent analyses such as nest success rates and likelihood of renesting. For example, estimates of nest success are likely to be negatively correlated with the researcher's ability to find all nests; successful nests are clearly easier to doc-

ument. Perhaps as a consequence of the methodological problems, nest success varies widely from 18 to 86% (Trueblood 1954, Gregg 1991). The rate of 37% nest success recorded in this study is on the low end of the spectrum.

Estimates of renesting rates are determined with information on both rates of nest discovery and estimates of nest failure for first nests. The low rate of nest discovery in some studies may indicate that some observed "first" nests may actually be re-nests. Unfortunately, the lack of published information on timing of nest initiation and observed lek visitation by females makes interpretation of previous studies difficult. Nevertheless, the frequent presence of > 15 ovulated follicles in females in Idaho (Dalke et al. 1963) and the secondary peak of female attendance at leks in Montana (Eng 1963) indicate that renesting efforts in other regions are probably under-estimated.

The 87% rate of renesting in north-central Washington was dramatically higher than the 5 to 41% rates recorded in other areas (Peterson 1980, Young 1994, Sveum 1995). Two females also were observed renesting twice (also observed in southern Washington, Sveum 1995). These regional differences are substantial, even if potential biases in rates of nest discovery between different studies are considered.

Because of frequent renesting, the observed rate of breeding success in north-central Washington was 61%; renesting contributed 38% to the overall annual productivity of Sage Grouse. As a consequence of renesting, the rate of breeding success was relatively high when compared to the range of rates of 15 to 70% recorded in other areas (Wallestad and Pyrah 1974, Gregg 1991). The significance of renesting also has been documented for Blue Grouse *Dendragapus obscurus* (Zwickel and Lance 1965), White-tailed Ptarmigan (Giesen and Braun 1979), and Willow Ptarmigan (Parker 1981).

Bergerud and Gratson (1988) suggested that rate of renesting for grouse is negatively correlated with annual survival rate of breeding-age females. This prediction appears contradicted by this study: the high rate of renesting appears to occur despite a relatively high estimated female survival rate.

Survival of juveniles during the first 50 days of life was estimated at about 33%. Because of the difficulty of finding all chicks around brood females, it is possible that this was an under-es-

timated of survival. It was difficult to compare survival of juveniles in this study with research in other regions; data were rarely collected and/or analyzed with comparable methods. Nevertheless, Wallestad (1975) estimated an annual survival rate of 15% for juveniles. Seasonal declines in brood size ranged between 18% and 68% (Bean 1941, Rothenmaier 1979); a comparable analysis in this study resulted in an estimated decline of 61%.

In general, Sage Grouse in north-central Washington display more reproductive effort than Sage Grouse in other regions; they lay more eggs and are more likely to nest and re-nest. In addition, detectable differences between adults and yearlings in north-central Washington are relatively minor when compared with age-specific differences in other regions. Because of the difficulties in comparing different studies, it is unclear whether the higher reproductive effort by Sage Grouse in north-central Washington ultimately results in increased productivity.

It is possible that environmental conditions in north-central Washington provide Sage Grouse with a larger "window-of-opportunity" for reproduction. Observations from other regions have indicated that Sage Grouse may move large distances between breeding areas and summer areas because of desiccation of forbs on their breeding areas (Dalke et al. 1960, Connelly et al. 1988); desiccation of vegetation does not appear to be a factor in north-central Washington. Other regions also tend to have relatively unfragmented habitats, especially when compared with north-central Washington. However, it is not clear how habitat fragmentation would influence reproductive effort.

Another possible explanation for the differences in reproductive effort of Sage Grouse between north-central Washington and other regions is that the Western Sage Grouse is considered a distinct subspecies. Although the observed differences in this study could add support to the taxonomic differentiation, the support is weak without further illustration of the potential effects of environmental variation on nest productivity. In addition, reproductive effort of Sage Grouse in north-central Washington differed from reproductive effort of Sage Grouse in Oregon and south-central Washington, despite the fact that they are considered the same subspecies.

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