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Fidelity of greater sage-grouse *Centrocercus urophasianus* to breeding areas in a fragmented landscape

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In this paper, we report on breeding site fidelity for a small, localized population of greater sage-grouse *Centrocercus urophasianus* inhabiting a highly altered and fragmented landscape in north-central Washington, USA. One hundred sixteen greater sage-grouse were captured, fitted with radio transmitters and monitored during 1992-1998. Of 19 males captured as adults and nine captured as yearlings, one and four, respectively, were observed visiting two different leks. Of 78 females, 24 were observed visiting at least two leks, and eight visited at least three leks. Although the incidence of multiple lek visitation was similar to what has been reported for other regions, the average of 10.2 km distance between neighbouring leks was substantially further in north-central Washington. Average distance between a female's first nest and her renest was higher for yearlings (6.3 km) than for adults (2.0 km). Successful females moved an average of 1.6 km and unsuccessful females moved 5.2 km to nest in subsequent years. Most distances between consecutive nests were < 3.0 km, but some females, including adults, moved > 20 km. These data suggest that fidelity of greater sage-grouse to nesting areas in north-central Washington is substantially lower than has been found for other populations. Although the relationship between behaviour of greater sage-grouse and regional habitat fragmentation is a possible explanation for these observations, we were not able to detect a correlation between fidelity and local habitat availability.

Key words: Centrocercus urophasianus, fidelity, greater sage-grouse, landscape fragmentation, lek visitation, nesting success, Washington

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Many birds exhibit fidelity to their first breeding area in successive years; even when individuals change areas they rarely move further than a few territories (Greenwood 1980, Greenwood & Harvey 1982). Fidelity to a breeding area offers potential advantages including maintenance of an established territory, reduction in costs of dispersal and increased knowledge of an area and its predators and competitors (Bergerud & Gratson 1988). However, as habitats become altered and/or fragmented, birds with high philopatric tendencies may continue to occupy unsuitable areas (Rolstad & Wegge 1987, Knick & Rotenberry 2000).

Fidelity to a particular breeding site has been observed for many grouse species (Choate 1963, Rusch & Keith 1971, Jamieson & Zwickel 1983, Schroeder 1985, Wegge & Larsen 1987, Schieck & Hannon 1989). Among the prairie grouse in North America (greater prairie-chicken *Tympanuchus cupido*, lesser prairie-chicken *Tympanuchus pallidicinctus*, sharp-tailed grouse *Tympanuchus phasianellus*, greater sage-grouse and

Gunnison sage-grouse *Centrocercus minimus*), fidelity of males to traditional display sites (leks) is especially strong; once established on a lek males tend to remain faithful to that site for life (Hamerstrom & Hamerstrom 1949, Campbell 1972, Moyles & Boag 1981, Emmons & Braun 1984, Schroeder & Braun 1992). However, fidelity by female prairie grouse to leks and nesting areas is less clearly understood (Dunn & Braun 1985, Svedarsky 1988, Young 1994).

The greater sage-grouse is a large, sexually dimorphic grouse restricted to sagebrush *Artemisia* spp. dominated rangelands in western North America. Populations have declined throughout much of its range in recent decades primarily due to habitat loss, fragmentation and degradation (Connelly & Braun 1997, Braun 1998). Although sage-grouse tend to display fidelity to their breeding sites (Berry & Eng 1985, Dunn & Braun 1985, Fischer, Apa, Wakkinen, Reese & Connelly 1993), much of our understanding of their breeding biology is based on studies of populations in relatively large tracts of contiguous rangeland. As greater sage-grouse, like other grouse species, face increased loss and fragmentation of habitat, it is important to understand if, and how, aspects of breeding behaviour may differ in the altered landscapes. Here we report on breeding site fidelity for a small, localized population of greater sage-grouse inhabiting a highly altered and fragmented landscape in north-central Washington, USA.

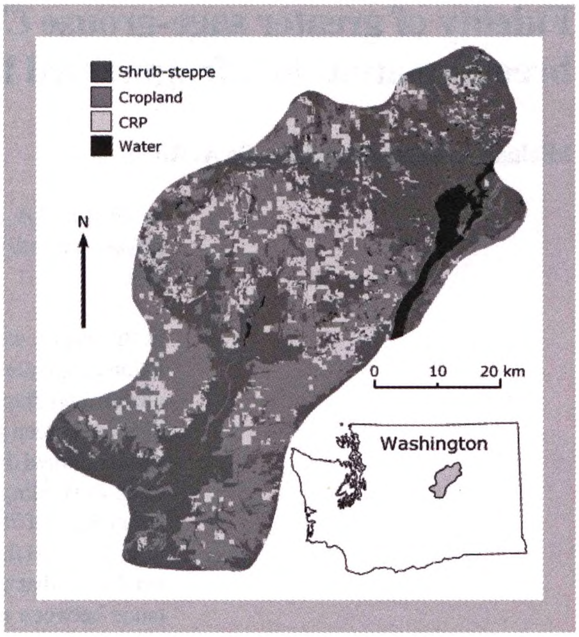

Figure 1. Distribution of general habitat types in north-central Washington within the occupied greater sage-grouse range.

Methods

Greater sage-grouse were studied in an isolated population on a 3,529 km^2 area centered near Mansfield, in north-central Washington (47°50'N, 119°40'W; Schroeder, Hays, Livingston, Stream, Jacobson & Pierce 2000). This population is separated from larger, more contiguous populations by approximately 400 km. Annual lek surveys have been used to monitor greater sage-grouse in this area since the 1960s with increased effort put into monitoring all known leks and finding 'new' sites beginning in the early 1970s. Based on survey data, sage-grouse have declined by about 60% in north-central Washington from 1960 to 1999 (Schroeder et al. 2000); the 2002 population was estimated to be about 640 (Schroeder 2002).

The habitat in our study area was dominated by a fragmented mix of dryland wheat (35%), shrub-steppe (44%) and lands enrolled in the federal Conservation Reserve Program (CRP, 17%; Fig. 1). Shrub-steppe was dominated by big sagebrush *Artemisia tridentata*, three-tip sagebrush *Artemisia tripartita*, bluebunch wheatgrass *Agropyron spicatum* and bluegrass *Poa* spp. These native rangelands were commonly grazed by domestic livestock. The CRP habitat was dominated by non-native planted grasses, predominantly crested wheatgrass *Agropyron cristatum*. Although the area was extremely fragmented, most conversion of shrub-steppe habitat to cropland occurred prior to the 1940s. During this study, the habitat distribution and composition remained relatively constant.

Greater sage-grouse were trapped on seven leks with the aid of walk-in traps (Schroeder & Braun 1991) in March and April 1992-1996. Trapping was typically conducted on designated leks for 1-4 days in a given year. Captured birds were identified by age and sex (Beck, Gill & Braun 1975) and fitted with 13-14 g battery-powered radio transmitters attached to necklaces (Holohil Systems, 112 John Cavanagh Road, Toronto, Ontario K0A 1L0, Canada), or in a few cases, poncho-like collars (Amstrup 1980). The transmitters produced 50-70 electronic pulses per minute and had a typical lifespan of between two and three years.

A portable receiver (Advanced Telemetry Systems, 470 First Ave. N., Box 398, Isanti, Minnesota 55040, USA) and a handheld 4-element Yagi antenna were used to locate radio-marked birds at least once every three days throughout the breeding season. Females were either visually observed on nests or the nest site was estimated by triangulation from a distance of approximately 20-30 m. Variation in the intensity of transmitter signals was used as an indication of behaviour as radio transmitters emitted a constant signal when individuals were sedentary and a variable signal when birds were moving. Fixed-wing aircraft were usually used two times per year to find 'lost' birds, generally after seasonal periods of migration in April and December. Universal Transverse Mercator (UTM) locations were recorded to the nearest meter with the aid of a Global Position System (Magellan, 960 Overland Court, San Dimas, California, 91773, USA).

Analysis of distances between consecutive nests was conducted with general linear models (Proc GLM, SAS Institute 1990). Independent variables included age, year, habitat availability within 3 km of the previous nest and the success of the previous nest (except in the case of first nest-renest distances where all first nests were unsuccessful by definition). Nests were considered successful if ≥ 1 egg hatched. Renests were defined as nests initiated following failure of a female's initial nesting attempt in a single breeding season. Consecutive nests represented the chronological history of a female's nesting attempts through > 1 breeding season. Habitat availability was determined with 1993 satellite images of the study area (Jacobson & Snyder 2000, Schroeder et al. 2000; see Fig. 1) and included the proportion of potential nesting habitat (combination of CRP and shrub-steppe) within 3 km of the nest site. This distance was chosen as most females moved ≤ 3 km between nests. Analysis of nesting success in relation to distance of movement was conducted using logistic regression (Proc CATMOD, SAS Institute 1990). All results were considered significant at $\alpha \leq 0.05$.

Results

Lek visitation

Of the 116 greater sage-grouse captured on leks and fitted with radio transmitters during 1992-1996, 22 females and six males, 16 females and nine males, 21 females and five males, 21 females and seven males, and eight females and one male were caught in the respective years. Lek visitation data included observations of 28 males and 78 females that were seen on leks following their capture.

A total of 207 visits to leks was observed for 22 males (including three males captured as yearlings) following capture. All but one visit was to the same lek where captured or first observed as an adult (95.5% of males and 99.5% of visits), including visits by four adult males monitored for > 1 year. Yearlings were more likely to be recorded on > 1 lek site within a year than adults ($\chi^2 = 7.52$, df = 1, $P < 0.01$), and four of nine yearlings (44.4%) were seen on > 1 lek (35.9% of 39 observed visits) during their first breeding season. One of these transient males became established on a 'new' lek in its second year and was seen there on eight occasions.

There was no evidence of age-specific variation in the proportion of females observed visiting > 1 lek site ($\chi^2 = 0.27$, df = 1, $P = 0.92$). When age categories were combined, 30.8% of 78 females were observed on ≥ 2 different leks. Four females (6.3% of 63 individuals with ≥ 3 observations on leks) were recorded visiting ≥ 3 leks. Although the likelihood of seeing a female on > 1 lek site increased with the number of observations, this proportion seemed to level off at 40-50% for individuals with ≥ 5 sightings (Fig. 2).

The rate of visitation to ≥ 2 leks by females tended to increase with the number of years monitored. Of 40 females, 13 (32.5%) were observed on a 'new' lek on their first recorded visit to a lek in the year following their capture. For example, one female was seen three times on the lek where she was captured in 1992 and three times on a different site in 1993. In contrast, within a breeding season, only three of 18 (16.7%) females were observed on a 'new' lek during their first observed visit prior to renesting.

Annual variation in lek visitation did not appear to be related to the possible disturbance associated with capture. Only four of 78 (5.1%) females and two of 28 (7.1%) males were observed attending a 'new' lek on the visit following capture. The average distance between visited leks was 10.6 km (SD = 3.8 km) for five of nine males observed on more than one lek. This was similar to the average of 10.2 km distance between neigh-

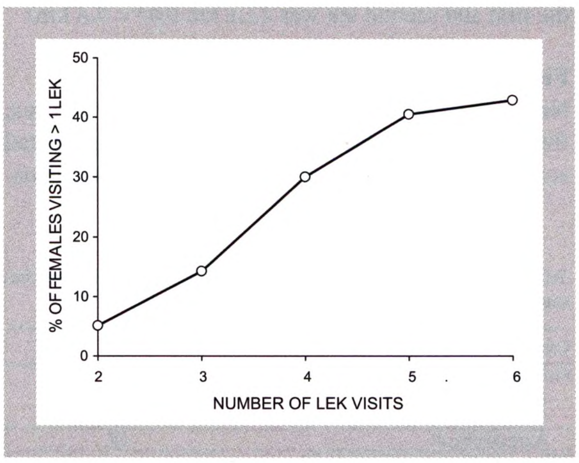

Figure 2. Percent of female greater sage-grouse visiting > 1 lek in relation to the number of times they were observed on leks in north-central Washington during 1992-1998.

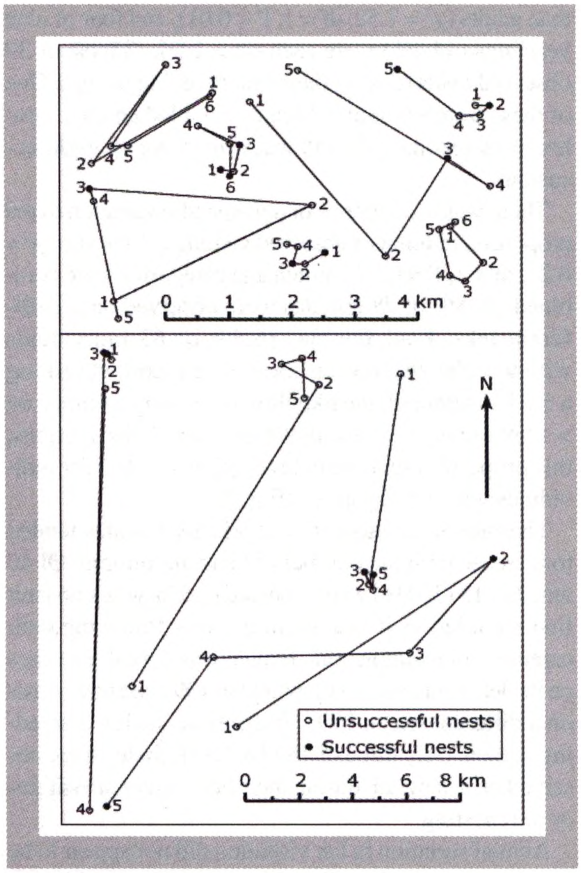

Figure 3. Examples of nest distributions for female greater sage-grouse with ≥ 5 nests located in north-central Washington during 1992-1998. The nests are numbered in order of observed occurrence.

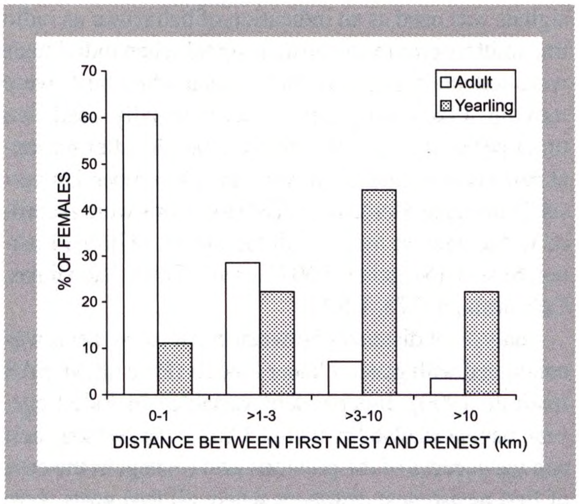

Figure 4. Distribution of distances between 65 pairs of first nests and renests for adult (N = 56) and yearling (N = 9) greater sage-grouse in north-central Washington during 1992-1998.

bouring leks (SD = 3.7 km, N = 12). In contrast, 14 of 24 females (58.3%) that visited a second lek, visited a lek that was not the closest; the average distance between the first and second lek was 13.1 km (SD = 7.4 km).

Fidelity to nest sites

Nest data were obtained for 82 radio-marked females; five additional females that died prior to being located at a nest and one that disappeared (damaged radio transmitter and/or undetected movement) were excluded from the analysis. Many females had more than one nest (within and between years) and a total of 204 nests was found (25 in 1992, 30 in 1993, 37 in 1994, 55 in 1995, 42 in 1996, 14 in 1997 and one in 1998). Individuals were found nesting up to six times and were monitored for up to four breeding seasons (Fig. 3). The availability of nesting habitat within 3 km of each nest site varied dramatically throughout the study area, i.e. 16.4-97.4%, with an average of 65.7% (SD = 17.5%).

Average distance between a female's first nest in a breeding season and her renest was 2.6 km (Table 1). Although the variation in distance between the first nests and renests was considerable (0.0-26.6 km), 81.5% were < 3 km. Age explained some of the variation in first nest-renest distance (F = 7.71, df = 1, P = 0.01; Fig. 4), whereas variation in year (F = 0.78, df = 5, P = 0.57) and local habitat availability (F = 0.07, df = 1, P = 0.80) were not significant factors. For six females observed renesting as both yearlings and adults, all moved further between nests as yearlings than they did as

Table 1. Distances between first nests and renests following failure of the first nest and between nests in consecutive years for female greater sage-grouse in north-central Washington during 1992-1998.

Category	N	Median (km)	Range (km)	$\bar{x} \pm$ SD (km)
First nest - renest distance				
Adults	56	0.8	0.0-26.6	2.0 ± 4.2
Yearlings	9	3.6	0.4-14.3	6.3 ± 4.9
Ages combined	65	0.9	0.0-26.6	2.6 ± 4.5
Distance between nests in consecutive years				
Previous year's nest was successful	35	0.7	0.1-18.9	1.6 ± 3.2
Previous year's nest was unsuccessful	22	1.3	0.2-32.9	5.2 ± 9.9
Nests combined regardless of success	57	0.8	0.1-32.9	3.0 ± 6.8

adults (average of 7.2 vs 2.1 km). However, the greatest distances between first nests and renests (17.4 and 26.6 km) were observed for adult birds.

The average distance between a female's nest sites in consecutive years was 3.0 km, 84.2% of the distances were < 3 km, and the longest distance was 32.9 km (see Table 1). Variation in distance between a female's nests in consecutive years was not explained by year (F = 0.94, df = 5, P = 0.46), age (F = 1.46, df = 1, P = 0.23) or habitat (F = 1.30, df = 1, P = 0.26), but was influenced by success in the previous year (F = 4.01, df = 1, P = 0.05). The distance between a female's nest in one year and her nest the following year tended to be greater when the first year's nest was unsuccessful (see Table 1, Fig. 5). One female moved 32.9 km between her first year's nest and her second year's nest, and then moved 32.4 km to her third year's nest, in the vicinity of her original nesting area. Another female made a similar return trip of about 19 km.

We found no evidence that movement by females following nest failure (within and between years) increased the probability of success of their subsequent nesting attempt ($\chi^2 = 0.36$ in logistic regression, df = 1, P = 0.55). Successful females moved an average of 3.8 km (median = 0.9 km, SD = 7.5 km, N = 35) from their previous nest while unsuccessful females moved an average of 2.9 km (median = 1.3 km, SD = 5.4 km, N = 52).

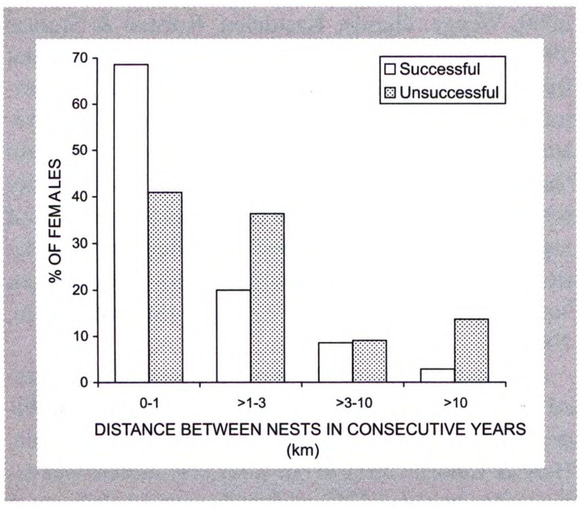

Figure 5. Distribution of distances between 57 pairs of nests in consecutive years for successful (N = 35) and unsuccessful (N = 22) greater sage-grouse in north-central Washington during 1992-1998.

Discussion

Lek visitation

Similar to other grouse species, adult male greater sage-grouse in Washington exhibit high fidelity to lek sites as only one adult male was observed to visit more than a single lek. Additionally, we observed four of nine yearling males visiting more than one lek before establishing a breeding territory, which is similar to results reported in studies of sharp-tailed grouse (Moyles & Boag 1981), greater prairie-chicken (Schroeder & Braun 1992), capercaillie *Tetrao urogallus* (Wegge & Larsen 1987) and black grouse *Tetrao tetrix* (Willebrand 1988). Although other studies of greater sage-grouse have documented males visiting different lek sites, in many cases the age class of the birds was not determined and methodologies were not comparable. When we pooled our age class data, the proportion of males we observed at more than one lek (17.9% of 28 males) was within the range of what has been reported for radio-marked males in other regions (7% in Montana (Wallestad & Schladweiler 1974), 19% in Colorado (Dunn & Braun 1985) and 47% in Oregon (Hanf, Schmidt & Groshens 1994)). Although the rate of inter-lek movements we observed was similar to what has been found in other studies, lek sites in north-central Washington are substantially further apart (10.2 km) than what has generally been reported. For instance, the inter-lek distance averaged 4.1 km in Montana (Wallestad 1975), 1.2 km in Colorado (Braun & Beck 1976) and 4.0 km in Oregon (Hanf et al. 1994). An intensive banding study in Idaho found 33% of males visiting more than one lek, but the inter-lek distance was only 1.1 km (Dalke, Pyrah, Stanton, Crawford & Schlatterer 1963).

The proportion of females that visited at least two different lek sites in north-central Washington (31%) was comparable to what has been reported for radio-marked birds in other regions (28% in Montana (Wallestad 1975) and 11% in Colorado (Dunn & Braun 1985)). Of the banded females in Idaho, 38% were observed visiting more than one lek (Dalke et al. 1963). The pattern of lek visitation by females in Washington indicated that females typically visited the same lek within a single nesting cycle, with occasional visits to 'new' leks prior to renesting. Females were more likely to be observed visiting a 'new' lek in years following their capture. As with males, the average distance between leks visited by females was large (13 km), especially when compared with the typical distance between neighbouring leks in other regions. It is not clear whether the visitation to different leks by females is due to annual changes in home range or variation in their selection of either males or leks (Gibson, Bradbury & Vehrencamp 1991). It is also likely that birds radio marked in previous years were monitored earlier and longer during subsequent breeding seasons. For example, some females may visit leks while in transit from their wintering areas to their breeding areas (Bradbury, Gibson, McCarthy & Vehrencamp 1989).

Fidelity to nest sites

Grouse, in general, display fidelity to nesting areas. For example, consecutive nests are on average separated by < 0.1-0.8 km for greater prairie-chickens (Toepfer & Eng 1988, Svedarsky 1988, Schroeder & Braun 1993), 0.4 km for sharp-tailed grouse (Meints 1991), 0.2 km for blue grouse *Dendragapus obscurus* (Sopuck & Zwickel 1983) and 0.2 km for black grouse (Wegge 1984). There is no record of a grouse (especially an adult) moving as far as 32 km between consecutive years' nests or 27 km between a first nest and a renest, as was observed for greater sage-grouse in our study. Svedarsky (1988) documented one greater prairie-chicken moving 5.6 km between her first nest and a renest, and Zwickel (1992) documented one blue grouse moving 2.0 km between nests in consecutive years.

The longest previously recorded distance between consecutive nests was 2.6 km for 22 greater sage-grouse in Idaho (Fischer et al. 1993). In our study, 19.7% of 122 recorded distances between consecutive nests exceeded 2.6 km. Fischer et al. (1993) also recorded an average distance of 0.7 km between nests in consecutive years (N = 22 females), whereas the average in Washington was 2.8 km between nests in consecutive years and 3.0 km between first nests and renests. Even if the longest distances (> 10 km) were not included in the Washington sample, the average distance between nests in consecutive years was 1.2 km, and the average first nest-renest distance was 1.6 km. Renesting in most populations of greater sage-grouse is relatively infrequent, and there is limited information on distances between first nests and renests (Connelly, Fischer, Apa, Reese & Wakkinen 1993). However, females in north-central Washington have an unusually high (87%) rate of renesting (Schroeder 1997).

Distances between first nests and renests in north-central Washington were significantly longer for yearlings than for adults. This relationship appeared to be consistent with a strategy by yearling females to establish a nesting area. Age was not a significant explanation for differences in movements between years. This was similar for greater sage-grouse in Idaho (Fischer et al. 1993).

Females moved further in subsequent years to nest when their previous year's nest was unsuccessful. Fischer et al. (1993) observed a similar trend (P = 0.35) for greater sage-grouse in Idaho. In other grouse, such as white-tailed ptarmigan (Braun, Martin & Robb 1993) and willow ptarmigan (Hannon, Eason & Martin 1998), females were likely to change territories in years following the death of their mates and/or predation of their nests. Movement to a new territory resulted in the females being paired with older males, possibly improving their opportunities for success in subsequent years (Martin 1985). However, there was no evidence in our study that movement between nest sites increased the subsequent nesting success.

Habitat considerations

Although fidelity to a breeding area may be generally advantageous (Bergerud & Gratson 1988), as the habitat is altered, the benefits of fidelity may decrease. This may explain, in part, why the movements of greater sage-grouse in north-central Washington are large relative to other areas, and why some birds move exceptional distances. The alteration and fragmentation of the habitat in our study area is dramatic; only 44% of the area remains in native shrub-steppe, and much of this habitat consists of small patches (Schroeder et al. 2000). The habitat fragments are often situated along roadsides, fences, field edges, rocky outcrops and coulees. Because of extensive fragmentation and small patch size, females may have to move relatively long distances to find alternate or new nest sites.

There is substantial research illustrating a relationship between habitat fragmentation, grouse occupancy (Åberg, Jansson, Swenson & Angelstam 1995, Saari, Åberg & Swenson 1998, Segelbacher & Storch 2002) and populations dynamics (Åberg, Swenson & Andrén 2000, Wegge, Gjerde, Kastdalen, Rolstad & Storaas 1990). Nevertheless, the relationship between habitat fragmentation and greater sage-grouse in north-central Washington is not clear. The lack of a definitive relationship may be due, in part, to the interaction between fragment size and habitat quality. The highest quality nesting habitats (based on the cover and composition of native grasses, forbs and shrubs) were often found in relatively small fragments, whereas many of the larger, 'intact' habitats were in poor condition (Schroeder et al. 2000).

Although nest predation is often higher in fragmented landscapes (Andrén, Angelstam, Lindström & Widén 1985, Andrén & Angelstam 1988, Kurki, Nikula, Helle & Lindén 1997), in our study nest success was estimated to be about 37%, well within the 15-86% range for estimates of nest success in other areas (Schroeder et al. 1999). Additionally, greater sage-grouse in north-central Washington have larger clutch sizes and a greater propensity to nest and renest than elsewhere in their distribution area (Schroeder 1997).

Habitat fragmentation in north-central Washington has not been shown to be associated with lower sage-grouse productivity. However, the large inter-lek distances and declining population (Schroeder et al. 2000) suggest that habitat fragmentation, loss and degradation may be impacting the population. We estimated an average inter-lek distance of 6.9 km (SD = 2.4 km) for 30 leks monitored between 1960 and 1999 within our study area boundary. During 1992-1998, the inter-lek distance for the 12 remaining leks had increased to 10.2 km. This observation was concurrent with a substantial population decline (Schroeder et al. 2000) suggesting that habitat fragmentation and condition may eventually result in extirpation of this population. Additional research may be necessary to understand the interactions between habitat fragmentation and quality and their effects on sage-grouse behaviour and population dynamics.

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