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Source: Wildlife Biology, 9(4) : 335-340

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2003.022

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Connelly, J.W., Reese, K.P., Garton, E.O. & Commons-Kemner, M.L. 2003: Response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation in Idaho, USA. - Wildl. Biol. 9: 335-340.

We investigated the response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation. From 1995 through 2002 we monitored breeding populations in areas closed to hunting, open to limited hunting (1-bird daily bag limit; 7-day season), and open to moderate hunting (2-bird daily bag limit; 23-day season). We used three approaches to assess the effects of hunting on sage-grouse populations. Results were consistent regardless of the method used and indicated that overall, areas closed to hunting had greater rates of increase for breeding populations than areas open to hunting ($P = 0.018$). Limited or moderate rates of exploitation apparently slowed population recovery for sage-grouse. These effects may have been more pronounced for grouse occupying relatively xeric habitats close to human population centers or highly fragmented habitats. Our results suggest that hunting seasons for sage-grouse should generally be conservative and reflect both sage-grouse population trend and quality of habitat occupied by the population.

Key words: Centrocercus urophasianus, exploitation, greater sage-grouse, hunting, Idaho, lek counts, population

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Throughout much of the sagebrush-dominated rangeland of western North America, greater sage-grouse *Centrocercus urophasianus* populations were heavily exploited by commercial and sport hunting in the late 1800s and early 1900s (Patterson 1952, Autenrieth 1981). Because of concerns about sage-grouse populations (Hornaday 1916, Girard 1937), many states prohibited harvest by the 1930s (Patterson 1952, Autenrieth 1981). By the 1950s, populations had recovered in numerous areas and limited hunting seasons were again instituted in most portions of the species' range (Patterson 1952, Autenrieth 1981). In response to declining sage-grouse populations during the 1980s and 1990s, sage-grouse hunting has generally become more conservative (Wambolt, Harp, Welch, Shaw, Connelly, Reese, Braun, Klebenow, McArthur, Thompson, Torrell & Tanaka 2002).

During the 1980s and 1990s, the sage-grouse hunting season in Idaho allowed a daily bag limit of three grouse, a possession limit of six and a season length of 30 days. Following a drought and widespread population declines, sage-grouse seasons in Idaho were reduced in 1996, with new regulations taking effect in 1997.

Braun & Beck (1985) and Zablan, Braun & White (2003) reported on band return rates and population trends for hunted sage-grouse populations, and Connelly, Apa, Smith & Reese (2000a) documented differences in vulnerability to harvest by gender. However, little empirical evidence is available to evaluate the response of sage-grouse populations to different levels of exploitation. We used lek attendance data to assess the response of sage-grouse breeding populations to changes in exploitation rates. These data were analyzed to test the general hypothesis that changes in breeding populations would not differ among areas closed to hunting, open to limited hunting, and open to moderate hunting.

Methods

Study area

All areas were dominated by sagebrush *Artemisia* spp. with bunchgrass understories. We classified our study sites as lowland or mountain valley areas. Leks within the lowland area generally occurred in habitats dominated by Wyoming big sagebrush *A. tridentata wyomingensis* with an understory of bluebunch wheatgrass *Agropyron spicatum* and a variety of forb species. Many of these habitats were affected by wildfires during the 1990s. Throughout the fall hunting season, birds associated with these leks were located relatively close (i.e. ≤1.5 hours driving time) to major cities and towns along the Snake River Plain of southern Idaho. Leks within the mountain valley area generally occurred in habitats dominated by Wyoming big sagebrush, mountain big sagebrush *A. t. vaseyana* and low sagebrush *A. arbuscula* with an understory of bluebunch wheatgrass and a variety of forb species. During the fall hunting season, birds associated with these leks were located relatively far (i.e. > 1.5 hours driving time) from major cities and towns. Mountain valley leks occurred in habitats with greater annual precipitation than habitats within the lowland areas, and thus grouse breeding in mountain valleys tended to use more productive habitats than grouse occupying lowland areas (Autenrieth 1981).

Data collection and analysis

To assess the impacts of exploitation from 1996 through 2001, some areas were closed to hunting, other areas were restricted to a limited 7-day season with a 1-bird bag limit (2-bird possession), and some areas had a moderate 23-day season with a 2-bird limit (4-bird possession). Many sage-grouse populations are migratory (Connelly, Browers & Gates 1988, Connelly, Schroeder, Sands & Braun 2000c), thus we established closed areas to minimize the chance that grouse from areas closed to hunting would move to areas open to hunting.

Population changes were documented by counting male sage-grouse on leks throughout south-central and southeastern Idaho. Natural resource agency personnel and other trained observers counted leks using standard techniques (Jenni & Hartzler 1978, Emmons & Braun 1984) along established lek routes (groups of leks with grouse from the same breeding population) from 1995 through 2002 as part of a continuing project to monitor sage-grouse populations. Changes in lek counts represent trends in breeding populations (Connelly et al. 2000c), but lek counts have been criticized because they may not always provide an accurate assessment of sage-grouse populations (Beck & Braun 1980). However, lek counts are an accepted method of monitoring these populations and have commonly been used to assess changes in populations (Johnson & Braun 1999, Connelly, Reese, Fischer & Wakkinen 2000b, Connelly et al. 2000c, LaMontagne, Irvine & Crone 2002). Previous telemetry research (Connelly et al. 1988, Wakkinen 1990, Apa 1998) allowed us to associate lek routes in our study areas with breeding populations.

Lek routes were surveyed three or more times annually during the breeding season (1 April-7 May) between 1995 and 2002, and all males observed on each lek were tallied. We compiled all lek data and checked for accuracy against original data cards recorded by observers in the field. Only routes that had been systematically counted using established procedures (Jenni & Hartzler 1978, Emmons & Braun 1984) were included in our database. Data from 19 lek routes counted over eight years (152 total routes) were used in our analyses. About 7% of these routes had missing values (e.g. a lek within a route was not counted or the data were missing in a given year), and these routes occurred in areas with different hunting seasons (closed, limited and moderate hunting) and during different years. Missing values were replaced by an average of the year before and the year after. If the missing value occurred at the end of the period (e.g. 2002), it was replaced by the preceding year's value. If the missing value occurred at the beginning of the period (e.g. 1995), it was replaced by the next year's value.

All data were tabulated by lek route, and routes were classified as representing populations subject to no hunting, limited hunting and moderate hunting. We then employed three different analytical approaches to assess the effect of changes in hunting regulations on rate of change of sage-grouse populations. First, we corrected the annual rate of change for pretreatment trends by subtracting the mean rate of change for the 1995-1996 period (prior to regulation change) from annual change values thereafter. We then compared rates of change among years and areas with different levels of exploita-

Table 1. Sage-grouse population change in response to different levels of exploitation in mountain valleys of southern Idaho, USA.

Season	Area	Mean number of males/lek 1995/96	2001/02	% change
No hunting	Upper Birch	6	17	183
	Lower Birch	14	30	114
	Total	20	47	135
1-bird bag	Crooked Creek	84	137	63
2-bird bag	Little Lost	64	98	53
	Lemhi	52	106	104
	Total	116	204	76

Table 2. Sage-grouse population change in response to different levels of exploitation in the lowland areas of southern Idaho, USA.

Season	Area	Mean number of males/lek 1995/96	2001/02	% change
No Hunting	East Big Desert	71	137	93
	Tractor Flats	64	105	64
	INEEL	34	65	91
	Total	169	307	82
1-bird bag	Shoshone Basin	94	111	18
	Brown's Bench	85	70	-18
	Plano	85	94	11
	Jacoby	80	108	35
	Curlew Valley	19	10	-47
	Rockland	13	5	-62
	Total	376	398	6
2-bird bag	Picabo Hills	65	89	37
	Timmerman	103	71	-31
	Paddleford Flat	60	83	38
	North Shoshone	61	63	3
	Bliss/Hill City	65	102	57
	Total	354	408	15

tion using a 3-factor analysis of variance. All interaction terms were non-significant, so we tested main effect terms for harvest levels, area (mountain valley and lowland), and year in a reduced model. Second, we averaged maximum male attendance for each lek route for 1997-1998 (first two years of regulation changes) and 2001-2002 (last two years of the study) and expressed them as ratios that were analogous to lambdas, the finite rates of change over the six-year interval. We then assessed population changes over that time period using a 2-factor analysis of variance on harvest levels and communities. Third, we regressed the natural log of lek attendance on year for each route and then treated each slope as an independent estimate of trend for sites subjected to the three levels of exploitation. The mean slopes for each level of exploitation were compared using a 2-factor analysis of variance for harvest level and community. All analyses were performed using SYSTAT V.10 (SYSTAT 2000. SPSS Inc., Cambridge, MA, USA). We considered differences significant if $P \leq 0.05$.

Results

We used five lek routes in the mountain valley areas and 14 routes in the lowland areas to examine sage-grouse breeding population change in response to hunting. Within the mountain valley areas from 1995-1996 to 2001-2002, numbers of males counted on all lek routes (N = 5) increased by ≥ 53% (Table 1). Of the 14 lek routes in the lowland area, 10 (71%) showed increases from 1995-1996 to 2001-2002 (Table 2). In the lowland areas, populations without hunting increased by an average of 82% (range: 64-93%), areas with limited hunting had an average increase of 6% (range: -62-35%), and those with moderate hunting increased by 15% (range: -31-57%) from 1995-1996 to 2001-2002 (see Table 2). Only the Bliss/Hill City lek route of the nine lek routes in areas open to hunting increased by > 50% from 1995-1996 to 2001-2002, but all lek routes (N = 3) in the areas closed to hunting increased by ≥ 64% (see Table 2).

Populations increased by an average of 103% (range: 53-183%) within the mountain valleys, regardless of hunting season, whereas lowland populations increased by an overall average of 21% (range: -47-93%), regardless of hunting season. However, statistical tests on rates of change were not significant ($P = 0.830$) between mountain valley and lowland areas (Table 3) despite these apparent differences because of large variation among areas and years within each treatment. A comparison of standardized rates of change indicated differences among years ($P = 0.020$) and areas having different hunting seasons ($P < 0.001$; see Table 3). Areas without hunting had greater increases (Bonferroni multiple comparisons: $P < 0.001$) than areas with 1-bird or 2-bird seasons (see Table 3), but areas with 1 or 2-bird seasons did not differ significantly ($P > 0.05$).

A comparison of the number of grouse counted on leks at the beginning of the regulation change (1997-1998) to the number counted at the end of the study (2001-2002) also suggested a difference among areas with different exploitation rates. Areas closed to hunting had

Table 3. Comparisons of rates of change among areas, treatments and years for sage-grouse in southern Idaho, USA.

Factor		F-value	df	P-value
Area (mountain valley vs lowland)		0.564	1, 123	0.830
Years		3.062	4, 87	0.020
Treatment		16.779	2, 87	<0.001
	Open vs closed			<0.001
	1-bird vs 2-bird			>0.05

Table 4. Mean trend of maximum number of male sage-grouse per lek (measured as slope) for 19 lek routes in lowland and mountain valleys subjected to three levels of exploitation.

	Mean Rate (SE), sample size[a]		
	No hunting[b]	1-bird season	2-bird season
Lowland	0.125 (0.012), 3, A	-0.038 (0.049), 6, B	0.026 (0.032), 5, B
Mountain valley	0.169 (0.031), 2, A	0.088 (-), 1, B	0.112 (0.028), 2, B

[a]Values followed by the same letter did not differ (P > 0.05).
[b]Areas without hunting had greater rates of increase than areas with hunting.

higher breeding population levels than those open to hunting, but the differences were not significant (ANOVA: $F_{2,15} = 2.581$, $P = 0.06$).

Trend analysis of rates of change of the breeding populations based on slopes of maximum count of males per lek route over time revealed differences between areas with different exploitation levels (ANOVA: $F_{2,16} = 4.976$, $P = 0.021$). Areas with no hunting had higher rates of increase than either 1 or 2-bird areas ($P = 0.018$; Table 4). However, rates of increase did not differ ($P = 0.458$) between areas with 1 and 2-bird seasons.

Discussion

Our data, analyzed through three separate but related approaches, suggest that limited or moderate hunting may slow the rate of increase for sage-grouse populations. Four of the 19 lek routes used for our study indicated decreasing populations, and these routes represented populations subject to hunting. However, 10 (71%) additional lek routes also represented hunted populations and these populations increased by an average of 42% during our study.

Although all three approaches used to analyze the response of sage-grouse populations to different harvest levels produced similar results, we did not consider any of these approaches as an ideal method for evaluating population response. Our analyses were based on lek counts, and this census technique may result in considerable variation due to weather, disturbance, and observer training (Beck & Braun 1980). Correcting the annual rate of change for pretreatment trends (i.e. prior to changes in hunting regulations) helped to standardize the measurements of treatment effects, but large annual variation in rates of change still made treatment differences among areas difficult to detect. Although our study was designed to minimize the chance of grouse moving among areas with different hunting seasons, some variation may have been due to these movements and some may have been due to grouse moving across state lines and being exposed to a second hunting season (J.W. Connelly, unpubl. data). Environmental variables (e.g. the amount of habitat loss or fragmentation) likely provided another source of variation. We minimized annual variation by expressing rate of change for each lek route based on the ratio of maximum male attendance at the end compared to the beginning of the treatment period. This facilitated detection of differences in response to harvest levels, but detection of differences between mountain valley and lowland areas was still difficult. Using the slope of the regression line for male attendance over time performed similarly to the ratio approach, but both of these methods were limited in power to detect differences among treatments by sample size because there was no replication within lek routes using these approaches. Nevertheless, the similarity of the conclusions drawn from the three approaches supports our contention that the relationships between breeding populations and harvest levels are valid.

Early research suggested that hunting had little impact on upland game by largely compensating for other forms of mortality (Allen 1954). More recently, numerous studies have challenged this assertion and suggested that it is possible for hunters to over-exploit upland game birds during the fall (Bergerud 1985, 1988, Gregg 1990, Ellison 1991, Dixon, Horner, Anderson, Henriques, Durham & Kendall 1996). Bergerud (1988) summarized evidence of additive mortality for blue grouse *Dendragapus obscurus*, white-tailed ptarmigan *Lagopus leucurus*, ruffed grouse *Bonasa umbellus* and greater prairie-chicken *Tympanuchus cupido,* and argued that hunting was additive to overwinter mortality.

Early work on sage-grouse similarly suggested that hunting had little effect on this species (Wallestad 1975, Braun & Beck 1985). However, sage-grouse may be more susceptible to overharvest than other upland game bird species, because they differ in their life history traits. Many species of upland game birds such as ruffed grouse, grey partridge *Perdix perdix*, and ring-necked pheasants *Phasianus colchicus* have relatively short life spans (1-2 years), high natural rates of mortality over winter (40-70%), and large clutch sizes of 10-17 eggs (Gullion 1984, Potts 1986, Petersen, Dumke & Gates 1988, Burger, Kurzejeski, Vangilder, Dailey & Schulz 1994, Christensen 1996, Giudice & Ratti 2001). Sage-grouse, in contrast, are long-lived (3-6 years), have low rates of overwinter mortality (2-20%), and produce relatively few young with average clutch size of 6-9 eggs (Schroeder, Young & Braun 1999). Autenrieth (1981) and Crawford & Lutz (1985) suggested that hunting may have some negative effects on sage-grouse populations. Johnson & Braun (1999) analyzed lek count and hunter harvest data and concluded that, up to some threshold level, hunting mortality was compensatory, but, at or beyond that level, exploitation of sage-grouse may be additive. Connelly et al. (2000a) also concluded that hunting losses are likely additive to winter mortality and may result in lower breeding populations. Finally, Wik (2002) suggested significantly reducing sage-grouse hunting in southwestern Idaho because of excessive mortality of females.

Although we had little evidence to suggest that hunting caused population declines, our results support the concept that hunting may be additive to overwinter mortality of sage-grouse. Large variation among mountain valley and lowland areas masked any differences in rates of change among populations within these areas. However, populations within the mountain valley areas increased at a relatively high rate regardless of hunting pressure. In contrast, declining and relatively stable populations occurred in less productive and sometimes fragmented habitat within lowland areas. Moreover, within the lowland area, populations in the area closed to hunting were separated from those with a moderate hunting season by a very large lava flow that apparently acted as a barrier to movements (Connelly et al. 1988, Wakkinen 1990). These populations generally occupied similar habitats, but the non-hunted populations increased at a rate that was > 5 times that of the populations with moderate hunting (see Table 2). Thus, exploitation may have a more pronounced effect on population recovery for sage-grouse occupying relatively xeric habitats that are close to human population centers, compared to relatively remote grouse populations occupying productive habitats.

Effects of exploitation may also be more severe for populations occupying highly fragmented habitats such as the Curlew and Rockland populations. These two areas represented a relatively large proportion (28%) of the total number of areas subject to limited hunting. Additionally, some grouse from a third area with limited hunting (Crooked Creek) migrated to Montana each year and were exposed to a second hunting season. Although these movements appeared to occur annually, we do not know what proportion of the Crooked Creek birds exhibited this behaviour. Inclusion of these areas may have confounded our analysis and prevented detection of differences between areas with limited and moderate hunting. Therefore, we are reluctant to conclude that hunting season structure (limited vs moderate) is relatively unimportant, but instead suggest that conservative seasons (1-bird bag, 7-day season) are appropriate for populations in xeric and fragmented habitats especially if they are relatively close to human population centers. The large increases in mountain valley populations that were subject to moderate hunting tend to further support the notion that habitat quality and access may influence a sage-grouse population's response to exploitation. Our findings agree with the observations of Autenrieth (1981) that sage-grouse populations occupying relatively xeric habitats near human population centers may be subject to overharvest. We also agree with Schroeder et al. (1999) and Connelly et al. (2000c) that hunting seasons for sage-grouse should be established with caution, and harvest rates should be relatively low. Although Connelly et al. (2000c) further recommended that harvest be prohibited when the entire breeding population is ≤ 300 birds, the sage-grouse population in Washington has not recovered following elimination of hunting in 1988 (Schroeder, Hays, Livingston, Stream, Jacobson & Pierce 2000). Thus, habitat management issues, not exploitation, are often the cause of population declines (Schroeder et al. 2000), and hunting restrictions should not be viewed as a remedy for all population ills. In many portions of the species' range, hunting restrictions combined with habitat conservation measures will likely be the most successful approach to recovering sage-grouse populations.

Acknowledgements - we thank all those people who conducted lek surveys over the past eight years. A review by T.P. Hemker improved an earlier draft of this manuscript. Funding was provided by the Idaho Department of Fish and Game and the United States Bureau of Land Management. This is a contribution from Idaho Federal Aid in Wildlife Restoration Project W-160-R and contribution 971 of the University of Idaho Forest, Wildlife and Range Experiment Station.

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