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Exploitation and greater sage-grouse *Centrocercus urophasianus*: a response to Sedinger and Rotella

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Recently, Sedinger & Rotella (2005) offered an insightful critique of our paper on the response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation (Connelly et al. 2003). We strongly agree with their assertion that refining our understanding of harvest effects on sage-grouse is an important question and welcome the opportunity to comment on their critique and perhaps more fully explain the strengths and weaknesses of our initial work (Connelly et al. 2003).

Sedinger & Rotella (2005) argued that correlation between population size and harvest regulations, combined with statistical issues, make it impossible to determine whether apparent population responses are the result of harvest regulations or density-dependent processes. They based their arguments on information taken from the

published literature and simulations using a density-dependent discrete logistic model. We have fundamental concerns with their approach that include: 1) a relatively narrow use of available literature; 2) a mischaracterization of our analysis; and 3) their data analysis and modeling. Below we attempt to address each of these areas.

Use of literature

Throughout their paper, Sedinger & Rotella (2005) argued that one reason it is difficult to understand the relationship between harvest and survival is because managers typically reduce harvest rates when populations are low and increase harvest rates when popula-

tions are high. They further questioned whether declining survival at high harvest rates might be due to the harvest rates themselves, or density-related effects. All papers cited to support their view dealt with harvest of waterfowl species (e.g. Nichols et al. 1984, Sedinger & Rexstad 1994), and they failed to cite any work on grouse or other upland game birds to support their statements. In North America, extensive and relatively complex processes have been developed for setting regulations for migratory game birds to allow involvement by multiple levels of government and use of annually updated population monitoring information (Blohm 1989, Smith et al. 1989). In the United States, annual regulations may change frequently and usually correspond with the current status of hunted populations (i.e. numbers of birds or population data). Since 1955, the U.S. Fish and Wildlife Service and the Canadian Wildlife Service have conducted annual aerial surveys, and ground counts in some areas to correct for visibility bias, during May to estimate numbers of ducks in more than 3.6 million km² of breeding habitat in the north-central United States, western and northern Canada and Alaska (Reynolds 1987, Smith 1995). Annual regulations are divided into either 'framework' or 'special' regulations. Framework regulations are the main tools used to adjust harvest levels at flyway or continental scales, and include framework dates (the earliest opening and latest closing dates), season length and bag limits (U.S. Department of Interior 1988). Special regulations modify framework regulations that are intended to influence harvest or hunter opportunity at finer spatial or temporal scales, or for individual species.

A general approach to upland game harvest management should also base harvest on abundance of the species, but this is rarely done. Instead, as Caughley & Sinclair (1994) suggested, most upland game harvest strategies have been developed through trial and error, and seasons for most small game species are kept relatively constant from year to year (Connelly et al. 2005). Strickland et al. (1994) reported that many states have de-emphasized collection of population data for upland game species "...because the lack of harvest impact indicates little need for the data".

Despite stable populations of greater sage-grouse from 1990 to 2003, Washington has maintained a closed season on the species from 1988 to the present, i.e. a 17-year period. Furthermore, from 1990 through 2004 (a 15-year period), Idaho has made only one significant change to the sage-grouse season and that was to change season structure to allow an assessment of effects of harvest (Connelly et al. 2003). After the study, two areas closed to hunting were open to a 1-bird bag limit in 2002.

During the Connelly et al. (2003) study, Idaho maintained the same regulations for a 5-year period from 1997 through 2001, regardless of population trend.

Similarly, from 1977 to 2004 (a 28-year period) bag and possession limits for blue grouse *Dendragapus obscurus*, ruffed grouse *Bonasa umbellus* and spruce grouse *Falcapennis canadensis* remained stable throughout Idaho. In South Dakota, bag and possession limits for ring-necked pheasants *Phasianus colchicus*, sharp-tailed grouse *Tympanuchus phasianellus*, greater prairie chickens *Tympanuchus cupido* and grey partridge *Perdix perdix* have not changed for at least the last 15 years. There are many other examples of maintaining stable regulations for upland game over an extended period of time (i.e. > 10 years). Thus the claim that greater (or more liberal) harvest regulations covary with population size is generally not supported for upland game birds and did not occur during the study we conducted (Connelly et al. 2003).

Characterization of analytical approach

Sedinger & Rotella (2005) claimed that Connelly et al. (2003) examined the effects of harvest on changes in lek size, collected data immediately following a drought and widespread population declines, and examined change in individual leks. All of these assertions mischaracterize our approach. We tabulated and examined data by lek route (a group of individual leks closely spaced and connected by movement of breeding birds) and clearly state so (Connelly et al. 2003: 336). Additionally, the comment about data collection being conducted in years immediately following drought and widespread population decline is misleading. We reported that following drought and widespread population declines, sage-grouse seasons were reduced in 1996. We actually collected data for many years before 1996. Moreover, subsequent analyses indicated the population decline was more perceived than real, and populations were generally stable since about 1987 (Connelly et al. 2004).

Sedinger & Rotella (2005) also claimed that we found that leks in the area closed to harvest grew more rapidly than those in areas open to hunting; however, we actually reported nothing about leks. We stated that areas closed to hunting had greater rates of increase of breeding populations than areas open to hunting. We also pointed out that exploitation apparently slowed population recovery. We used data from lek routes to examine these issues.

Some confusion may be due to mistakes in the sub-headings within Tables 1 and 2 in Connelly et al. (2003).

In both tables, the subheadings are 'mean number of males/lek' and they should be 'mean number of males/lek route'. Although we clearly explained this in the text, it is likely that the tables led to some misunderstanding.

Sedinger & Rotella (2005) further indicated that covariance between population size and harvest regulations existed during our study because: 1) more restrictive regulations were implemented and data collection began immediately after a population decline and 2) average lek sizes at the start of our study were smaller in unharvested areas than in areas with hunting seasons. Unfortunately, both of these observations tend to be misleading. More restrictive harvest regulations were implemented to better understand the effects of hunting on sage-grouse and not because of detailed knowledge of population trends. In the early to mid-1990s, concerns arose over the status of sage-grouse populations in Idaho and other western states. However, recent analyses indicated that statewide populations were relatively stable from the mid-1980s to 2003 so declines were more perceived than real (Connelly et al. 2004). Moreover, two of the three lek route areas closed to hunting in the lowland area had been closed for > 50 years because the area was designated as a national laboratory. These closures had nothing to do with sage-grouse populations. Designation of treatments was based on existing closures and knowledge of sage-grouse seasonal movements. We did not consider population size or trend and did not examine lek data prior to assigning treatments. Data collection within treatment areas began in most cases 20 or more years prior to changes in harvest regulations. The claim that average lek sizes in our study were smaller in unharvested areas at the start of the study is not entirely supported by the data. We agree this may be a valid criticism in the mountain valley areas, but we found no difference in mean lek sizes (ANOVA, $P = 0.77$; Table 1) in the lowland areas that constituted 67% of the unharvested leks analyzed. Additionally, Sedinger & Rotella (2005) relaxed their standard for significance

to $P = 0.09$ to show that differences in lek sizes were significant in contrast to the widely accepted standard of $P \leq 0.05$ that we (Connelly et al. 2003: 337) and most other researchers require.

Data analysis and modeling

An important principle of experimental design is to ensure that experimental units assigned treatments span the full range of conditions to which the conclusions are intended to apply. Lek routes assigned the no hunting treatment varied in initial mean male counts from a low of six males per lek route to a high of 71 males per lek route (Connelly et al. 2003: Tables 1 & 2). This is comparable to the range for the other treatments with the light harvest level (1-bird bag) also having two lek routes with initial means below 20 males per lek route.

Sedinger & Rotella (2005) provided a model for a sage-grouse population that provided provocative evidence that simulated populations experiencing density-dependent patterns of population growth could lead to erroneous evidence of negative harvest effects, but their results differed substantially from our analysis of real data. Their 10 repeated simulations of 15 or more years of data on population change are not exactly comparable to our five years of treatment data and two years of pretreatment data on 19 populations, and their ANOVA results and P-values are not really valid. Rather they are largely a function of the number of replications chosen, level of density dependence and differences in initial population sizes selected for each treatment. Note, however, the substantial differences from our analysis of real data. In particular our results showed no significant interaction term making our tests of main effects of areas, years and harvest treatments valid, whereas their interaction term is highly significant invalidating their tests of main effects such as harvest.

Figure 1 in Sedinger & Rotella (2005) shows mean initial lek size for different treatments, but mountain valley and lowland data are grouped together. They present the means of two years (1995 and 1996) for maximum counts on routes. However, if they want to express the relationship between harvest strategy and baseline population it would seem more meaningful to do so by stratifying by area (as we did) and using maximum male counts per lek route for 1996, the year before season changes were implemented. Each route represents a different number of leks counted and a different amount and quality of habitat. Thus, a better way to express baseline data would be to compare relative densities of grouse using males/lek rather than total males per lek route. Data on males/lek

Table 1. Mean number of sage-grouse males/lek at beginning of treatments (Connelly et al. 2003). The number of leks is given in parentheses.

Area/Year	Treatment		
	No hunting	1-bird	2-bird
Mountain Valley			
1996	3 (5)	9 (7)	19 (7)
1997	6 (5)	17 (7)	12 (7)
Lowland			
1996	14 (12)	10 (33)	11 (31)
1997	13 (12)	9 (33)	12 (31)

suggest that baseline populations were similar among treatments within the lowland area (see Table 1). Sedinger & Rotella (2005) correctly pointed out differences in the mountain valley area.

Sedinger & Rotella's (2005) plots of initial number of males per lek versus change in lek size provide very weak to non-existent support for their contention that rates of change are negatively density dependent as both non-harvested and lightly harvested populations show a positive relationship between changes in population size and initial number of males per lek (Sedinger & Rotella 2005: Fig. 2A & B). Only data from the medium harvest level (2-bird bag) suggest negative density dependence.

Figure 2 in Sedinger & Rotella (2005) purports to illustrate the relationship between change in lek size and initial lek size across a range of harvest treatments in our study. These data apparently were from Tables 1 and 2 in Connelly et al. (2003). However, because the mislabeled headings in the tables were mean males/lek rather than mean males/lek route, their analysis may not represent the relationship they stated. The influence of density dependence on impact of harvest, as Sedinger & Rotella noted, is a topic worthy of investigation. Continuing analysis of data on breeding populations of greater sage-grouse provides support for density dependence and further support for effects of exploitation on this species (E.O. Garton, unpubl. data).

Conclusions

Sedinger & Rotella (2005) emphasized the importance of understanding the role of density dependence in documenting the effects of exploitation on wildlife species. Although we certainly agree with this view, we also caution that investigators should strive to understand how density dependence would be expressed in sage-grouse or any other harvested species. Caizergues & Ellison (1997) reported that population growth in black grouse *Tetrao tetrix* is influenced more by adult survival than by either reproductive success or juvenile survival. Bro et al. (2003) demonstrated that reproductive success was a density-dependent phenomenon in grey partridge. Data on sage-grouse generally indicate relatively stable survival rates for adults and within Idaho fairly stable nest success rates regardless of population trend. We are not aware of any research that has been able to link changes in vital rates (e.g. nest success, nest initiation and survival rates) to sage-grouse population trends. Schroeder et al. (1999) concluded that if intrinsic factors (e.g. nest success and survival related to population density) influ-

ence sage-grouse populations they do so to a much lesser extent than extrinsic factors (e.g. weather and habitat). While discussing pheasant population trends, Edwards (1988) indicated that density-independent factors such as weather and agricultural programs influenced pheasant abundance. He cautioned that "We should not assume numerically stable or definable (closed) populations, and we should be slow to assume density dependence, inversity and regulation (as opposed to limitation) of abundance". Ellison (1991) concluded that there is little evidence for density-dependent breeding in tetraonids and that hunting may result in an age structure that lowers a population's productivity. Compensatory survival has been characterized as dogma within the field of wildlife management (Romesburg 1981, Warner 1992, Williams et al. 2004). Although upland game bird harvest has often been thought of as a compensatory form of mortality (Strickland et al. 1994), clearly there is a changing paradigm with respect to harvest management of upland game birds. A great deal more work is necessary before these relationships are fully understood.

We thank Sedinger and Rotella for their thoughtful critique of our paper. We hope that further dialogue will encourage research that will ultimately result in better understanding of harvest management and reliable conservation measures for game bird populations.

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