Effect of harvest on sage-grouse Centrocercus urophasianus populations: what can we learn from the current data?

SHORT COMMUNICATION

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Effect of harvest on sage-grouse *Centrocercus urophasianus* populations: what can we learn from the current data?

James S. Sedinger & Jay J. Rotella

Understanding the impact of human harvest is fundamental to the effective management of many wildlife populations. Such understanding has been elusive because harvest mortality may compensate for other sources of mortality when the mortality process is density dependent. This problem is exacerbated by the ubiquitous positive correlation between harvest regulations and population size: more harvest is allowed when populations are larger. Connelly et al. (2003) studied the impact of harvest regulations on sage-grouse *Centrocercus urophasianus* using three sets of regulations: closed season, 1-bird bag and seven-day season, 2-bird bag and 23-day season. Connelly et al. (2003) reported a generally negative correlation between harvest regulations and increase in number of males on leks for harvest regulations that ranged from a hunting closure to a 23-day season with a 2-bird bag. Because lek sizes were smaller where hunting was closed there was confounding between harvest and population density, making it difficult to distinguish harvest effects from those of population density. Based on a simple simulation the apparent effects of harvest on change in population size observed by Connelly et al. (2003) could be produced entirely by density-dependent phenomena. Additionally, λ (finite rate of population increase) was greater in areas with more restrictive harvest regulations. λ is a ratio of N_{t+1} to N_t, however, and there is a negative sampling covariance between λ and N_t; we expect λ to be larger when N_t is smaller based purely on this statistical fact. The study by Connelly et al. (2003) is an important attempt to study effects of harvest on population dynamics of sage-grouse. We do not argue that either additive mechanisms in survival or compensatory mechanisms in survival or reproduction influence the relationship between harvest and population dynamics of sage-grouse, but that correlation between population size and harvest regulations, combined with statistical issues make it impossible to distinguish between these two hypotheses in Connelly et al. (2003).

Key words: Centrocercus urophasianus, exploitation, harvest, population dynamics, sage-grouse

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Human harvest of wildlife has been a central issue in management of their populations for decades. For managers to effectively manage harvest, it is essential that they understand the impact of harvest on average survival rate at the population level. Errington & Hamerstrom (1935) proposed the idea of a harvestable surplus, in which habitat held numbers of a population that survived the most limiting season (typically winter in temperate North America) to below some threshold. Harvest of individuals above this threshold would have no effect on survival rate for the population as a whole because a number greater than that harvested would have died anyway. Anderson & Burnham (1976) formalized the concepts of additive and compensatory mortality for waterfowl harvest. Compensatory harvest mortality requires that harvest mortality reduces the mortality rate of the unharvested segment of the population such that there is no relationship between magnitude of the harvest and average survival rate in the population. Often, harvest is thought to be compensatory only below some threshold harvest rate that can be no greater than the mortality rate that exists in the absence of hunting (see Nichols 1991 for details). Additive harvest mortality, in contrast, adds to mortality in the population from sources other than hunting, resulting in reduced average survival at the population level in the face of hunting. A corollary of compensatory harvest mortality is that there must be some density dependence in the 'natural' mortality process.

Clearly, understanding the effect of harvest on annual survival in wild populations has important implications for managing these populations. In North America it has been difficult to understand the relationship between harvest and survival rates in harvested populations because managers typically reduce harvest rates when populations are low and increase harvest rates when populations are high (e.g. Sedinger & Rexstad 1994). Although managers view this approach as sound management, it completely confounds the effects of population density and harvest on annual survival. If survival rates decline at high harvest rates, is it because of the harvest rates themselves or because of the density-related effects of the corresponding high population level (Nichols et al. 1984, Nichols & Johnson 1989, Nichols 1991)?

Connelly et al. (2003) examined the effects of harvest of sage-grouse *Centrocercus urophasianus* in Idaho, USA, on changes in the sizes of leks in the studied populations. Understanding effects of harvest is an especially important issue for sage-grouse because their range has contracted significantly over the past several decades, and some local populations have declined (Connelly & Braun 1997, Schroeder et al. 1999, Connelly et al. 2000). Currently, all possible impacts on sage-grouse populations are being considered by managers.

Connelly et al. (2003) used three measures of population change to assess the effect of harvest regulations in two regions of Idaho on dynamics of sage-grouse populations. Data collection by Connelly et al. (2003:335) was conducted in the years immediately, "following a drought and widespread population declines". First, they examined response to hunting regulations of population rate of change for samples of individual leks. Specifically, they calculated rate of change in lek size before more restrictive hunting regulations were implemented and subtracted this rate of change from those calculated after regulations were implemented. Leks were assigned to one of three regulation packages: 1) closed season; 2) 7-day season with a 1-bird bag; and 3) 23-day season with a 2-bird bag. Second, Connelly et al. (2003) compared the maximum level of male attendance on leks during the first two years of implementation of more restrictive regulations versus the last two years of the study (four to five years after implementation of harvest treatments), calculated the increase and expressed it as λ, the finite rate of increase over the study. They then analyzed variation in λ in relation to region and hunting regulations using a two-factor Analysis of Variance (ANOVA). Third, they regressed the natural logarithm of lek attendance for each lek-survey route against year, calculated the slope (as a measure of population change over the study), and used ANOVA to assess variation in population change among regions and harvest treatments.

Connelly et al. (2003) found that leks in the area where harvest was closed grew more rapidly than did those experiencing harvest, although they found little difference between growth of leks experiencing 7-day sea-

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sons with a 1-bird bag and those experiencing 23-day seasons with a 2-bird daily bag. They concluded that hunting may slow the growth of sage-grouse populations and that hunting restrictions combined with habitat conservation may be the most successful approach to recovering sage-grouse populations.

We believe there are two fundamental underlying problems with using the results of Connelly et al. (2003) to conclude that harvest affects sage-grouse populations. The first issue regards covariance between harvest regulations and population size, which has been ubiquitous in regulation of wildlife harvest in North America (Nichols et al. 1984, Nichols & Johnson 1989, Nichols 1991, Sedinger & Rexstad 1994) and made it difficult, if not impossible, to discern the role of harvest in regulation of wildlife populations. The second issue is statistical; use of ratios or percentage changes to assess relative rates of population change can introduce statistical artifacts into population analysis (Eberhardt 1970, Raubenheimer 1995). Specifically, in this case λ has a negative covariance with N_{t+1} even in the absence of any biological relationship between the two parameters. These two issues introduce the same biases into assessments of population regulation, albeit for different reasons; they cause managers to overestimate the effect of harvest. We examine these issues with respect to Connelly et al.'s (2003) analyses and conclusions.

Covariance between population size and harvest regulations, i.e. greater harvest rates at higher population densities, confounds the effects of population density and harvest. If density-dependent processes reduce population increase because of constraints on survival or fecundity, then a population's trajectory under density-dependent constraints will appear the same as it would under harvest management. More dense populations will grow more slowly, either because they are harvested more heavily or because of density-dependent processes. Such covariance existed in the Connelly et al. (2003) study. First, more restrictive harvest regulations were implemented (and data collection began) immediately after the region's populations went through a widespread population decline. Thus, populations would be expected to rebound (do better after this period) under a simple density-dependent explanation that does not involve effects of harvest. This has important implications for interpreting results of pre- and post-treatment comparisons. Second, in Connelly et al. (2003), average lek sizes at the start of the study were smaller in unharvested areas than in areas subjected to harvest (P = 0.09 based on a 2-factor (harvest level and community) ANOVA comparing mean lek sizes at the start of the study; Fig. 1). This covariance has important implications for interpreting results from different treatments as once again a density-dependent explanation could replace an additive-mortality explanation. To illustrate the potential of density-dependent mechanisms to produce results similar to those of Connelly et al. (2003) we simulated several populations of sage-grouse using a simple density-dependent discrete logistic model:

$$N_{t+1} = N_t \left(1 + R\left(1 - \frac{N_t}{K}\right)\right),$$

in which both R and K were random numbers drawn at each time step from normal distributions, N(0.2,0.1) and N(100,10), respectively. Means and variances were selected to approximate those in Connelly et al.'s (2003) study. We simulated populations with beginning sizes equal to mean lek sizes in each harvest treatment at the beginning of the Connelly et al. (2003) study (Connelly
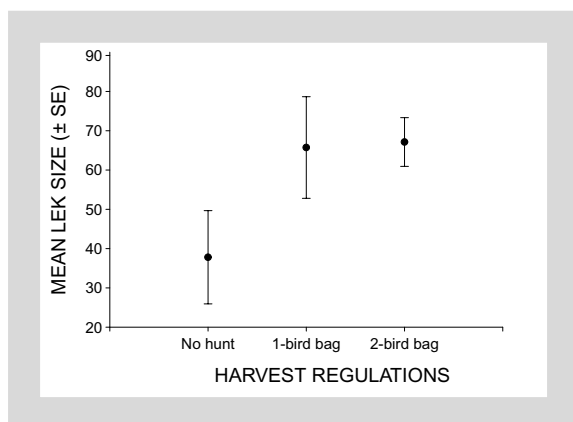

Figure 1. Relationship between harvest regulations and mean initial lek size in Connelly et al. (2003).

Table 1. Mean of 10 trials of two-factor ANOVA of population trends (corrected for pre-treatment trend) comparable to Table 3 in Connelly et al. (2003). Initial lek sizes and population trajectories approximated those in Connelly et al. (2003) assigned to closed harvest, 1-bird bag and 2-bird bag harvest regulations. We simulated (10 times) a density-dependent model of population dynamics using beginning lek sizes identified in Connelly et al. (2003). Because our goal was to assess the potential role of density dependence we simplified the model and excluded area effects. Note the substantial apparent effect of harvest treatment when harvest did not influence dynamics of these populations. The apparent effect resulted from slower growth in populations that were on average at higher density, which in Connelly et al. (2003) were assigned to harvest treatments.

Source of variation	df	MS	F	P
Year	4	0.009828	6.231	0.00012
Harvest	2	0.1092	69.21	< 0.00001
Interaction	8	0.004283	2.715	0.00835
Error	135	0.00157		

et al. 2003: Tables 1 and 2). We repeated the simulations 10 times. We then used the methods employed by Connelly et al. (2003) on these simulated populations to assess the role of harvest. It is important to recognize that in our simulated populations, harvest had no effect on population dynamics; only the density-dependent mechanism affected population dynamics.

In our simulated populations, those experiencing the highest harvest rates grew more slowly than those experiencing lower rates of harvest or no harvest (Table 1). In our simulated populations, however, harvest did not actually influence population dynamics because no harvest effects were included in the model. Thus, simulation results in Table 1 are entirely a result of a density-dependent process and indicate the potential for such a process to have produced the results reported by Connelly et al. (2003). Based on this simple simulation, alternative interpretations of their results are clearly possible and should be considered.

It is important to note that the role of density-dependence in our simulations was influenced by our selection of a specific value for the mean of K. The value we chose ($\mu = 100$) is near the upper end of the distribution of lek sizes for sage-grouse (Connelly et al. 2004) and exceeded mean lek size in 12 of 19 areas considered by Connelly et al. (2003). To the extent that we underestimated the appropriate value of K, our results overestimated the potential for density dependence to explain the results of Connelly et al. (2003).

It is also important to recognize that both our simulations and the analyses of Connelly et al. (2003) were based on counts of the number of males on leks. In both cases we are assuming that these counts reflect dynamics of the local population. While we cannot be certain that the relationship between lek counts and true population size is constant among areas, lek counts are typically the only survey data available, and they are the generally accepted method of monitoring sage-grouse populations (Connelly et al. 2000). To the extent that this assumption might be violated our results should be viewed with caution.

Comparing λs among leks assigned to different harvest strategies has the potential for bias if mean lek size varied among harvest treatments (see Fig. 1). λ is the ratio between population size at time t+1 (N_{t+1}) and population size at time t (N_t). Bias occurs because of the statistical covariance between a ratio and the denominator in the ratio (Eberhardt 1970). All other things being equal, we expect the ratio (λ in this case) to be negatively correlated with the denominator of the ratio at a level of r ~ -0.7 (Eberhardt 1970). Connelly et al. (2003) did not strictly examine the correlation between λ and
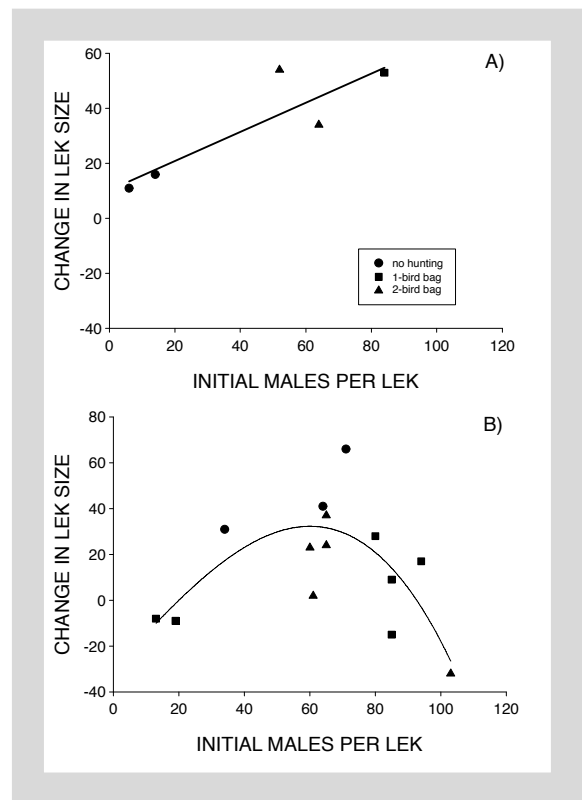

Figure 2. Relationship between change in lek size and initial lek size across a range of harvest treatments for sage grouse in Idaho. Data in A) are from mountain valleys in Connelly et al. (2003), and data in B) are from lowland areas in the same study.

population size. Rather, they used an ANOVA approach to compare λs among areas in which population size varied. Nevertheless, the principle provided by Eberhardt (1970) still applies; we expect λ to be smaller in areas where the initial population size was larger based on the statistical artifact created from these areas having a larger denominator when calculating λ. Thus, in Connelly et al. (2003), we would expect a negative correlation between λ (N_{t+1}/N_t) and harvest rate simply because sites without harvest had smaller initial N_t, whereas sites that experienced harvest had larger initial N_t.

Finally, as Figure 2 shows there is no consistent relationship between harvest regulations and absolute population growth in the Connelly et al. (2003) study. In fact, in mountain valleys, populations actually increased more rapidly when harvest regulations were more liberal (Fig. 2A), as pointed out by Connelly et al. (2003). In lowland areas (Fig. 2B), the pattern of increase is consistent with a pattern of density dependence. That is, rate of increase was highest at intermediate population levels and lowest at both low and high population levels, exactly the pattern one would expect under density de-

pendent population regulation. We note that there was no difference in population growth between populations experiencing 1-bird bags and short seasons and those experiencing 2-bird bags and longer seasons. Populations under closed seasons grew most rapidly, but these populations tended to be at intermediate levels where one might hypothesize that rate of population increase would be maximum, based solely on local population density. We recognize that it is most appropriate to measure rate of population increase on a per capita basis (i.e. λ). Because λ is a ratio, however, its use presents serious statistical problems as indicated above.

We laud the efforts of Connelly et al. (2003), an important attempt to assess the impact of harvest on sage-grouse population dynamics using experimental manipulation of harvest regulations. Overall, however, confounding between harvest regulations and population size, and the potential for statistical artifacts make it difficult to interpret the effects of harvest on sage-grouse population dynamics from this study. The statements made here neither espouse compensatory nor additive mortality in sage-grouse. Rather in our view, refinement of understanding of harvest effects on sage-grouse is an important question that will require decoupling regulations from population size (which was partially accomplished in this study). We also believe that direct assessment of the effect of harvest on the life-history stage directly affected by harvest, annual survival, will aid in the determination of harvest effects. To the extent, however, that density-dependent population regulation influences other life-history stages, such as juvenile recruitment (which if negatively related to density could, under some circumstances, allow populations to overcome additive harvest mortality), it will be necessary to study these aspects of sage-grouse life-history if it is important to understand the impact of harvest on population dynamics.

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