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Tools and Technology Article

Assessing Compensatory Versus Additive Harvest Mortality: An Example Using Greater Sage-Grouse

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ABSTRACT We used band-recovery data from 2 populations of greater sage-grouse (*Centrocercus urophasianus*), one in Colorado, USA, and another in Nevada, USA, to examine the relationship between harvest rates and annual survival. We used a Seber parameterization to estimate parameters for both populations. We estimated the process correlation between reporting rate and annual survival using Markov chain Monte Carlo methods implemented in Program MARK. If hunting mortality is additive to other mortality factors, then the process correlation between reporting and survival rates will be negative. Annual survival estimates for adult and juvenile greater sage-grouse in Nevada were 0.42 $\pm$ 0.07 ($\bar{x} \pm$ SE) for both age classes, whereas estimates of reporting rate were 0.15 $\pm$ 0.02 and 0.16 $\pm$ 0.03 for the 2 age classes, respectively. For Colorado, average reporting rates were 0.14 $\pm$ 0.016, 0.14 $\pm$ 0.010, 0.19 $\pm$ 0.014, and 0.18 $\pm$ 0.014 for adult females, adult males, juvenile females, and juvenile males, respectively. Corresponding mean annual survival estimates were 0.59 $\pm$ 0.01, 0.37 $\pm$ 0.03, 0.78 $\pm$ 0.01, and 0.64 $\pm$ 0.03. Estimated process correlation between logit-transformed reporting and survival rates for greater sage-grouse in Colorado was $\rho = 0.68 \pm 0.26$, whereas that for Nevada was $\rho = 0.04 \pm 0.58$. We found no support for an additive effect of harvest on survival in either population, although the Nevada study likely had low power. This finding will assist mangers in establishing harvest regulations and otherwise managing greater sage-grouse populations.

KEY WORDS *Centrocercus urophasianus*, compensatory harvest, exploitation, Markov chain Monte Carlo, survival.

The notion that mortality associated with predation might be compensated by reduced mortality from other causes dates at least to Errington's ideas about the threshold of security (Errington and Hammerstrom 1935, Errington 1945). Anderson and Burnham (1976) formalized approaches to understanding additive, versus compensatory, harvest mortality. Their effort was devoted largely to using band-recovery data to understand the relationship between harvest and mortality rates. A fundamental problem in such analyses is that parameter estimates in multinomial models covary when they are estimated from the same data. In band-recovery models (Brownie et al. 1985), recovery rates reflect harvest rates and are negatively correlated with survival estimates, even in the absence of a biological relationship between recovery and survival rates (Anderson and Burnham 1976). Consequently, analyses of band recoveries can produce a negative correlation between band-recovery rates and survival, consistent with expectation under additive harvest mortality, even when harvest is completely compensatory.

Ad hoc approaches to overcoming this problem have included splitting the data into independent data sets (e.g., using even- and odd-numbered bands), then examining correlations between band-recovery rate (an index of harvest) and survival parameters across data sets (Nichols and Hines 1983). An alternative, comparison of harvest and survival rates across populations, provides a relatively weak approach to assessing the functional relationship between harvest and survival because confounding factors could vary among populations. We would expect annual survival to be lower in populations experiencing higher harvest rates under a hypothesis of additive harvest mortality. Without true, experimentally implemented harvest regulations, it is not possible to control for confounding variables that could influence both harvest and survival rates (Nichols et al. 1984). Covariance between population density and harvest rates is an example of such confounding.

Recent availability of Markov chain Monte Carlo (MCMC) estimation approaches provides a mechanism for estimating process correlation between parameters, thereby eliminating the problem created by sampling correlation (Gilks et al. 1996, Cam et al. 2002). Consequently, MCMC provides a tool for assessing hypotheses about compensatory, versus additive, harvest mortality. Negative process correlation between harvest and survival rates is consistent with an at least partially additive harvest effect on survival, whereas process correlations >0 are consistent with a hypothesis that harvest mortality is fully compensated by other sources of mortality (Anderson and Burnham 1976). The MCMC methods have the advantage over classical numerical estimation procedures for parameter estimation from multinomial models because MCMC approaches produce parameter estimates that are not influenced by sampling covariance and are consequently unbiased (Link et al. 2002).

Compensation for harvest has received considerable attention with respect to grouse in Europe (Myrberget 1985, Ellison 1991, Smith and Willebrand 1999, Pedersen et al. 2004). Most of these studies have relied primarily on

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population responses to harvest (but see Smith and Willebrand 1999). Managers are most concerned about population-level consequences of their management actions, but use of population-level response to assess harvest effects adds substantial complexity because populations may exhibit numerous covarying responses to harvest or other management actions. For example, juvenile red grouse (*Lagopus lagopus scotica*) typically disperse from areas where most territories are occupied (Jenkins et al. 1964, 1967; Brøseth et al. 2005). Immigration may mask effects of harvest, or emigration may exacerbate them (Pedersen et al. 2004) to the extent that total harvest covaries with population density (e.g., Lindén 1981, Sedinger and Rexstad 1994, Sedinger and Rotella 2005).

Additionally, statistical confounding problems may be more likely when indirect measures are used. Pedersen et al. (2004) demonstrated an apparently strong additive effect of harvest on population rate of change in willow ptarmigan (*Lagopus lagopus*); higher harvest as a percentage of population size resulted in smaller increases in $\ln(N_{t+1}/N_t)$. Their result, however, was likely influenced by the fact that $1/N_t$ must have increased substantially more rapidly than $\ln(1/N_t)$, virtually ensuring Pedersen et al. (2004) would observe a negative covariance between harvest and change in population size, even in the absence of a biological relationship between harvest rate and λ. To see how this could create a negative correlation, remember that $\ln(N_{t+1}/N_t)$ equals $\ln(N_{t+}1) - \ln(N_t)$, then plot $-\ln(N_t)$ against $1/N_t$, which represents the relationship between abscissa and ordinate. This is a special case of induced correlation because the same N_t values are used for both the independent and dependent variables (Eberhardt 1970).

We used band-recovery data from populations of sage-grouse in Colorado, USA, and Nevada, USA, and MCMC methods to estimate band-recovery and survival rates and the process correlation between these parameter estimates. Our objectives were to 1) assess the potential for MCMC approaches to test hypotheses about additivity of harvest, and 2) assess the hypothesis that harvest represented an additive source of mortality in sage-grouse.

STUDY AREA

We captured sage-grouse in Nevada, primarily near water sources in the Montana Mountains (41°N, 118°W) on the Nevada side of the Oregon, USA, border. The Montana Mountains range in elevation from 1,310 m to 2,130 m and were characterized by communities dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain big sagebrush (*Artemisia tridentata vaseyana*), and low sagebrush (*Artemisia arbuscula*; appendix N, North Central Local Area Conservation Plan, greater sage-grouse conservation plan for Nevada and California, Nevada Department of Wildlife, unpublished data). Sage-grouse banded in Colorado were banded in the North Park area of north-central Colorado (41°N, 106°W; Zablan et al. 2003). Mean elevation was approximately 2,500 m and dominant vegetation was Wyoming big sagebrush (Zablan et al. 2003).

METHODS

We captured sage-grouse in Nevada during July–August 2001–2004 by night lighting (Giesen et al. 1982). We gave each individual a size 14 (F) or size 16 (M) metal band (Zablan et al. 2003). We assigned individuals to age classes (juv, yearling, and ad) and gender based on characteristics of wing feathers (Dalke et al. 1963). We recovered bands at check stations, which we placed in hunting areas for banded sage-grouse shot by hunters. Personnel of the Nevada Department of Wildlife (NDOW) provided letters explaining the project to all contacted hunters entering the hunt area. The NDOW personnel also attended a check station at the egress point for the hunt area during both weekends of the 2-week hunting season. Personnel also attempted to contact hunters in the field during the hunting season. Personnel from NDOW checked all hunter bags for bands at check stations. Wing barrels were provided at 4 locations along roads in the hunt area; hunters provided bands from shot sage-grouse and wings for estimating composition of the harvest at these wing barrels (Eng 1955). All sage-grouse hunters also received a harvest questionnaire.

Capture of sage-grouse in Colorado was described by Zablan et al. (2003). Individual sage-grouse in Colorado were also captured by night lighting, but in contrast to Nevada, sage-grouse were captured in spring near leks during 1973 to 1989. Extensive effort was made to recover bands from shot sage-grouse, similar to that in Nevada. Personnel from the Colorado Division of Wildlife operated check stations at 2 or 3 locations during both days of the opening weekend and the second Sunday of the 2-week hunting season during the first 9 years of the Zablan et al. (2003) study. Check stations in Colorado were operated only during the first weekend of the hunting season during the remaining 6 years of the Zablan et al. (2003) study. All hunters received a harvest questionnaire.

We lacked reward bands, which are necessary for estimating the proportion of bands from harvested birds that are reported (Nichols et al. 1995). We estimated the proportion of bands that were recovered through agency solicitation efforts and unsolicited reports by assuming that unsolicited band-reports represented 30% of unsolicited band recoveries (e.g., Nichols et al. 1995). This approach likely produced conservative estimates of reporting rates for these 2 studies because of the intensive hunter contact efforts, which should have substantially reduced the number of hunters that were uninformed about the importance of reporting bands.

We analyzed band recoveries from both populations using the Seber (1970) parameterization of band-recovery models in Program MARK (White and Burnham 1999). We also present analyses from the Brownie et al. (1985) parameterization for band recoveries from Nevada. The 2 parameterizations differ slightly from each other in that for the Brownie parameterization, band-recovery rates (f) represent the probability that a bird is shot, retrieved, and the band reported to the bird banding laboratory. Thus, because estimates of band-recovery rates are directly convertible to

estimates of harvest rate if band-reporting rates (i.e., proportion of bands retrieved by hunters reported to NDOW) are known, recovery rates can be used to directly estimate harvest rates (Brownie et al. 1985). For the Seber parameterization, reporting rates (r) represented the probability that a banded bird is found dead, and the band was reported (Seber 1970). Band recovery rates are approximately related to Seber (1970) reporting rates by the equation $f = (1 - S) \times r$, where S is annual survival.

Zablan et al. (2003) considered a suite of models, the most general of which allowed both survival and reporting rate to vary between sexes, among age classes, and with time. The most general model we considered for Nevada sage-grouse allowed for additive effects of age–gender and year. We could not consider more general models because band-recovery data for Nevada were too sparse. We used information theoretic approaches for model evaluation in analyses of the Nevada data (Burnham and Anderson 2002).

We used MCMC methods implemented in Program MARK to estimate process correlation between band-reporting rates and annual survival on a logit scale (White and Burnham 1999, White et al. 2008). The MCMC simulations provided a mechanism for sampling Bayesian posterior distributions to produce estimates of parameters (e.g., means, variances). We calculated the integral of the posterior to produce estimates of the distributions of parameters of interest (Gilks et al. 1996). The MCMC approach provides a mechanism for solving such integrals by sampling from candidate distributions using simulation and can be viewed as a tool for producing parameter estimates that would otherwise be difficult or impossible (Link et al. 2002). The advantage of this approach over standard maximum-likelihood estimation is that parameters (e.g., survival estimates) can be treated as random variables whose variances and covariances can be estimated (Link et al. 2002). In MARK, samples from candidate distributions are produced using a Metropolis–Hastings sampler (Gilks et al. 1996, White et al. 2008). In our case, MCMC allowed us to estimate process correlation between band-reporting rates and annual survival rates, free from the sampling correlation that exists between such estimates in standard maximum-likelihood estimation (Anderson and Burnham 1976).

We based MCMC estimation on models allowing annual variation in both reporting and survival rates and full interaction among age, sex, and year, for both Nevada and Colorado, which was necessary to estimate process correlation between survival and reporting rates across years. We simulated a single chain with 4,000 tuning samples and a burn-in period of 1,000 samples. We used 10,000 samples from the Markov chain to generate posterior distributions. We assumed prior distributions on survival and reporting rates were normal (0, 1.75) variables on a logit scale (White et al. 2008). We assumed prior distributions on process variances of survival and reporting rates on the logit scale were inverse γ (0.001, 0.001). The prior distribution on the correlation between survival and reporting rates on the logit scale was uniform (-1, 1). We report parameter estimates ($\pm$SE) from the band-recovery analysis for Nevada and estimates of process correlation ($\pm$SE) based on posterior distributions of survival and reporting rates for Colorado and Nevada. We estimated process correlation between harvest and survival rates separately for sage-grouse from Nevada and Colorado to avoid the potential that variables were confounded with both survival and harvest between the states, for which we did not account, and influenced our estimate of the correlation between survival and harvest. To assess the effect of the length of study on process correlation, we truncated the North Park, Colorado, data to produce data sets that were 10 years and 4 years long, in addition to the original data. We used the same analytical procedures for these truncated data as we used for the full data set to produce estimates of process correlation between survival and reporting rate and associated standard errors, which we report.

Table 1. Numbers of greater sage-grouse banded and recovered in the Montana Mountains, northern Nevada, USA, during 2001–2004.

		No. of recoveries			
Yr released	***n***	**2001**	**2002**	**2003**	**2004**
Ad F					
2001	40	5	1	1	0
2002	47		4	1	0
2003	46			3	1
2004	82				7
Ad M					
2001	17	1	0	1	0
2002	47		6	3	0
2003	38			3	1
2004	45				5
Yearling F					
2001	6	0	0	0	0
2002	15		0	1	0
2003	7			1	0
2004	18				0
Yearling M					
2001	1	0	0	0	0
2002	23		1	1	1
2003	9			1	0
2004	8				0
Juv					
2001	113	6	6	0	1
2002	222		22	7	6
2003	192			16	6
2004	116				18

RESULTS

We captured and banded 1,092 sage-grouse between 2001 and 2004 in northern Nevada, resulting in 137 recoveries through 2004 (Table 1). Zablan et al. (2003) banded 6,021 sage-grouse and reported recoveries of 961 individuals between 1973 and 1990 in their study. The most competitive models in the Zablan et al. (2003) study allowed for an additive effect of sex on annual survival and a quadratic trend in survival, which varied among age classes (Zablan et al. 2003, table 2). All competitive models in Zablan et al. (2003) allowed for sex, age, and temporal variation in survival and reporting rates. Reporting rates

Table 2. Performance of models of band recoveries for greater sage-grouse in northern Nevada, USA, 2001–2004. Models were based on the Seber parameterization for band recoveries implemented in Program MARK. Models include annual survival (S) and reporting rate (r), which is the probability that an individual is found dead and the band reported. Because banded greater sage-grouse were in a remote area in Nevada, and hunters were contacted by staff of the Nevada Department of Wildlife, all reported bands were associated with greater sage-grouse shot by hunters. Parameters held constant across years are indicated by (.), whereas a and t represent differences among adults plus yearlings, and juveniles, and annual variation, respectively.[a]

Model	ΔAICc	w_i	No. of parameters	Deviance
S(.), r(.)	0.00	0.41	2	40.75
S(.), r(a)	1.10	0.24	3	39.83
S(a), r(.)	1.91	0.16	3	40.64
S(a), r(a)	2.73	0.10	4	39.45
S(t), (a)	4.64	0.04	6	37.32
S(a), r(t)	5.59	0.03	6	38.27
S(a), r($a + t$)	6.29	0.02	7	36.94
S($a + t$), r($a + t$)	7.49	0.01	9	34.08

[a] ΔAICc, difference in Akaike's Information Criterion adjusted for small sample size; w_i, Akaike wt.

were best modeled using a linear time trend that differed across age and sex classes. Zablan et al. (2003, figs. 1, 2) reported substantial annual variation in survival (0.1–0.9) and reporting rate (<0.1–1.0), but a model allowing for full sex, age, and time interaction was not competitive, partially because it was so highly parameterized. A model in which both survival and reporting rates were held constant and did not vary among age classes or between genders for sage-grouse in Nevada was the best-supported model, receiving 41% of model weights (Table 2). Models allowing differences in survival or reporting rates between juveniles and adults plus yearlings received 40% of Akaike model weights. Annual survival estimates for Nevada sage-grouse age and gender classes pooled were 0.41 ± 0.054. Based on the Brownie parameterization, we estimated band-recovery rates averaged 0.09 ± 0.008 across years and age–gender classes, indicating that 9% of sage-grouse in the Nevada study area were harvested annually by hunters.

There was no clear relationship between annual survival rates and band-reporting rates across geographic locations or age and gender classes (Fig. 1). For example, yearling females in Colorado, which experienced the highest harvest rates, also had the highest annual survival rates. No bands from harvested grouse in Nevada were reported to NDOW outside of the solicitation process, thus, estimates of band-recovery rates provide a reasonable estimate of harvest rates in Nevada. For Colorado, we estimated that 91% and 82% of recovered bands were reported in 2 years (1976, 1977, respectively) for which sufficiently detailed information was available.

We estimated process correlation between band-recovery rate and survival rate on the logit scale to be $\rho = 0.68 \pm 0.26$ for North Park, Colorado, and $\rho = 0.04 \pm 0.58$ for northern Nevada. The estimate of process correlation for Colorado was consistent with a hypothesis of fully compensatory harvest mortality for that population. The estimate of process correlation for Nevada was much less precise than for Colorado and inconclusive with respect to a hypothesis of additive harvest mortality. Reducing the length of the data from Colorado from 18 years to 10 years and 4 years increased standard errors of our MCMC estimates of process correlation from 0.26 to 0.42 and 0.59,

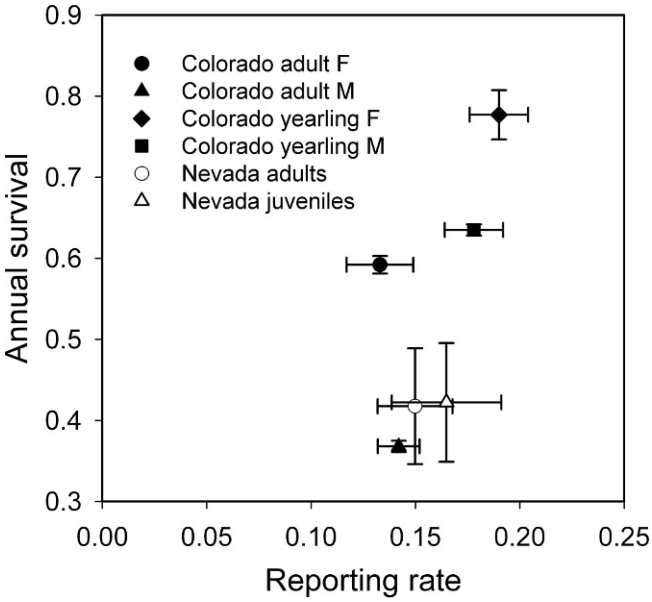

Figure 1. Estimates (±SE) of annual survival and reporting rates for greater sage-grouse from Colorado (1973–1990) and Nevada (2001–2004), USA. Colorado estimates from Zablan et al. (2003). Estimates were produced using the Seber parameterization for band recoveries in Program MARK.

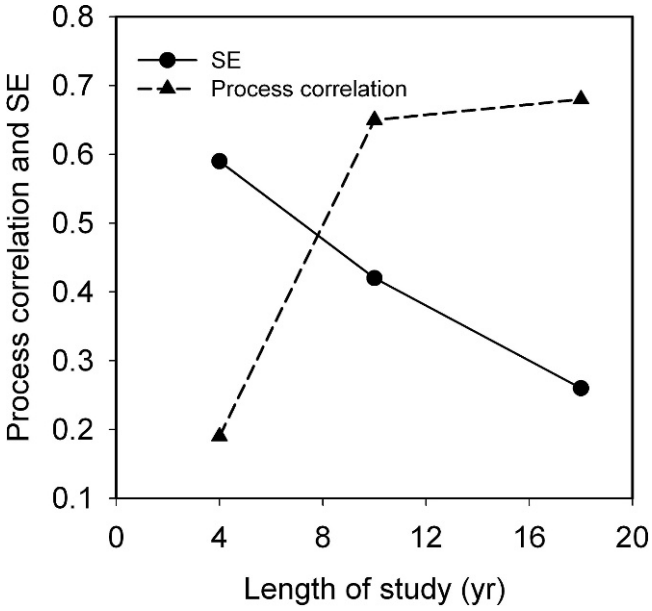

Figure 2. Estimated process correlation and standard error for banding studies of different length based on Markov chain Monte Carlo (MCMC) simulation in Program MARK. We banded greater sage-grouse in the Montana Mountains of northern Nevada, USA, 2001–2004, and in North Park, Colorado, USA, 1973–1989. We truncated the North Park Colorado data to produce data sets of 4 years and 10 years in length in addition to the entire data set of 18 years. We then fit an age × sex interactive model and estimated parameters in Program MARK. We used the MCMC simulation procedure to estimate process correlation and associated standard error.

respectively (Fig. 2). Point estimates of process correlation were robust to reduction of the data from 18 years to 10 years; estimated process correlation changed from 0.68 to 0.65 (Fig. 2), well within expected variation from the MCMC simulations. Reducing length of the band-recovery data to 4 years substantially changed our estimate of process correlation for the Colorado data to 0.19.

DISCUSSION

Estimates of process correlation between harvest and survival were either positive (CO) or near zero (NV); in neither area was there a negative process correlation required by a hypothesis of additive harvest mortality (Anderson and Burnham 1976). Process correlation for northern Nevada was estimated with relatively poor precision, a reflection of the relatively small number of recoveries (n = 137) and the short duration of the study (4 years). Additionally, our assessment of the effect of study duration on estimates of process correlation suggests that the relatively short duration of the Nevada study potentially caused us to underestimate process correlation between survival and reporting rates (Fig. 2). In contrast, the Colorado study (n = 961 recoveries, 17 estimates of survival) produced a reasonably robust and precise estimate of the correlation between harvest and survival probabilities. Visual examination of estimates of reporting rate and survival rate also do not indicate an additive effect of harvest on annual survival (Fig. 1). The 2 studies taken together do not support an additive effect of harvest on the annual mortality process in sage-grouse over the range of harvest rates experienced by these 2 populations. These studies also indicate that >10 years of banding and recoveries may be required to test hypotheses about additivity of harvest for sage-grouse.

The data we analyzed were not adequate for assessment of more complex hypotheses, including threshold effects of harvest, whereby harvest is compensatory below a particular level but becomes additive above that threshold. We can envision, however, experimental designs in which harvest rates are varied among spatial-temporal blocks, which would allow mangers to explore such hypotheses. We do not have a good foundation for simulations to assist with future study designs because neither study area produced a negative estimate of the harvest–survival correlation. Consequently, we do not have an estimate of the magnitude of the harvest–survival correlation under additive mortality, which is essential for simulations to assess sample size requirements for future studies. Clearly, the Nevada data set with 137 recoveries over 4 years did not produce an estimate of the harvest–survival correlation of sufficient precision to assess even strong additive harvest mortality, whereas the Colorado data, with 961 recoveries over 18 years, produced an estimate of process correlation that was sufficiently precise to detect even weakly additive harvest effects.

Negative associations between harvest and annual survival, suggestive of additive harvest mortality, have been observed in some waterfowl populations in North America (Smith and Reynolds 1992, Sheaffer et al. 2004, Sedinger et al. 2007; but see Sedinger and Rexstad 1994). For geese (Anserinae), the additive role of harvest in the annual mortality process is generally accepted (e.g., Sedinger et al. 2007). For ducks (Anatinae), however, harvest rates are virtually always confounded with population density; harvest rates are higher when populations are larger, so it is difficult to separate potential effects of harvest from those of density dependence (e.g., Sedinger and Rexstad 1994).

Earlier studies reached varying conclusions about the effect of hunting on sage-grouse populations. Braun and Beck (1985) and Wallestad (1975) concluded that harvest had little influence on sage-grouse populations, whereas Autenrieth (1981), Crawford and Lutz (1985), and Zunino (1987) believed that harvest could influence population dynamics in sage-grouse populations. Our conclusions differ from those in several other studies that concluded harvest mortality was additive. Fifteen percent and 42% of radiomarked male and female sage-grouse in southern Idaho, USA, were killed by hunting, and an additional 83% and 45% of males and females, respectively, were killed by predation (Connelly et al. 2000*a*). Mortality rates were low following the hunting season, providing little potential for compensation, and Connelly et al. (2000*a*) concluded that harvest mortality was likely to be additive to other forms of mortality. Connelly et al. (2000*a*) could not control for possible effects of radios on risk of harvest or predation mortality, which may have affected their conclusions. Sage-grouse in southern Idaho with radios had 23% (M) and 38% (F) higher harvest rates than sage-grouse that had received only metal bands (Connelly et al. 2000*a*, table 3). Connelly et al. (2003), in a different study, reported that leks increased more rapidly when harvest regulations were more restrictive, but Sedinger and Rotella (2005) showed that this result could have been caused by density-dependent processes, rather than harvest effects.

We cannot, however, rule out ecological differences in the mortality processes among Colorado, Nevada, and Idaho. We have observed the lowest monthly survival to occur during October–December on 2 different study areas in Nevada (Sedinger et al. 2010; J. S. Sedinger, University of Nevada–Reno, unpublished data), in contrast to low survival during spring–summer in Idaho (Connelly et al. 2000*a*). Our results indicate, however, that banding studies and MCMC estimation, especially combined with temporal–spatial variation in harvest rates, provide a reasonable approach to understanding the effect of harvest on sage-grouse populations.

Harvest rates and survival rates were remarkably similar between North Park, Colorado, and northern Nevada, with the exception of higher survival by females in North Park, Colorado compared with sage-grouse from northern Nevada. The generally positive association between survival and harvest rates suggests that environmental conditions that favor sage-grouse survival may also be consistent with greater harvest rates. We note that harvest rates were typically near or below general guidelines for sage-grouse harvest of 10% (Braun and Beck 1985, Connelly et al.

2000*b*). Our findings suggest these guidelines may be generally consistent with compensatory harvest mortality for many sage-grouse populations.

Our findings differ from those of some recent European studies of grouse, which concluded that harvest of grouse was largely additive. Harvest rates in many studies of willow ptarmigan are >20% of the fall population (Ellison 1991, Smith and Willebrand 1999, Pedersen et al. 2004). It is possible that at harvest rates >20%, harvest becomes at least partially additive (Anderson and Burnham 1976) in these populations, despite conclusions to the contrary for some populations (Jenkins et al. 1964, Ellison 1991). There are potential statistical artifacts in one assessment of harvest additivity at harvest rates >20% (Pedersen et al. 2004). Studies relying on radiotags to estimate harvest and survival estimates (e.g., Smith and Willebrand 1999) could not control for potential effects of the radios on either parameter, which can be variable (Miller et al. 1995, Steenhof et al. 2006, Terhune et al. 2007). Harvest rates may be correlated with local density, and it is possible that harvest is confounded with other density-related population processes, such as emigration and immigration. It is not clear how such confounding might affect harvest–survival relationships, but confounding could certainly influence indirect assessments (e.g., changes in N in shot and unshot areas) of harvest effects.

We believe that assessment of hypotheses about the effects of harvest on populations will be most powerful when harvest rates can be controlled and direct estimates of survival examined under preplanned harvest regimes. Direct assessments of the demographic trait influenced by harvest (i.e., annual survival) are most likely to yield clear results, uncompromised by confounding changes in other demographic parameters or ecological variables. Data from the populations we studied were not generated with the goal of examining additive versus compensatory mortality hypotheses, but we believe they demonstrate the potential power of using individually marked animals, combined with preplanned harvest regulations and MCMC estimation, for discriminating between these 2 important hypotheses.

MANAGEMENT IMPLICATIONS

Our results indicate that assessing process correlation between survival and harvest requires banding for ≥ 10 years. At harvest rates <11%, harvest is unlikely to have an important influence on local population dynamics of sage-grouse. Because most sage-grouse populations are harvested at rates comparable to, or lower than, those we analyzed, harvest is unlikely to have an important effect on the dynamics of these populations. Consequently, other factors, such as habitat, human development, and predation, should be considered as important factors influencing sage-grouse populations. We suggest that MCMC estimation in Program MARK, combined with well-designed banding studies, provides a useful approach for understanding the effect of harvest on local populations.

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