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Source: Wildlife Biology, 2018(1)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00362>

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# Estimating sex-ratio, survival, and harvest susceptibility in greater sage-grouse: making the most of hunter harvests

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We analyzed banding (3259) and recovery (six years) data from a hunted population of greater sage-grouse *Centrocercus urophasianus* in northwestern Moffat County, Colorado to examine vulnerability to hunter harvests and annual survival of adult and hatch-year (juvenile) birds. Additionally, we combined the recovery data with hunter-harvested wings and applied the Lincoln estimator to provide unbiased estimates of tertiary sex-ratio. Our results yielded the following findings: juveniles were harvested at twice the rate of adults, but harvest vulnerability was similar between adult males and females. Annual survival of juveniles was highly variable but similar between sexes. Sex ratios of adults and juveniles largely conformed to previously assumed proportions despite having adjusted those estimates with harvest rates. We suggest there is potential to effectively model populations of game birds using a combination of band recovery and hunter-harvested samples of species that can be readily captured, marked and have reasonable harvest rates.

The greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse), a lekking game bird species of the sagebrush (*Artemisia*) ecosystem, was once widespread throughout the Intermountain West and harvested in every state in which it occurred (Reese and Connelly 2011). Long-term contraction of its distribution (56%) and more recent declining trends have led to unprecedented conservation efforts to maintain populations and their habitats (USFWS 2013). Research efforts to increase our understanding of the species' demography have been commensurate with increased conservation and management (Garton et al. 2011, Taylor et al. 2012). However, there are limited data on survival and harvest rates of hatch-year (HY) birds (Taylor et al. 2012), and unbiased estimates of tertiary sex ratio (Atamian and Sedinger 2010). Generally, tertiary sex ratio is reserved to describe that of the breeding cohort; we use it here to refer to the sex ratio of both juveniles transitioning to breeding age class, and adults. Recruitment of hatch-year birds (i.e. production) and tertiary sex ratio are foundational to the understanding of avian population dynamics. Sage-grouse are relatively long-lived for a gallinaceous bird, and population dynamics are often most sensitive to adult survival (Taylor et al. 2012). However, recruitment and, perhaps more specifically, survival

of juveniles is frequently the principal driver of regulating population growth. Estimates of these demographic rates remain elusive for this species in some cases (Taylor et al. 2012). Population parameters are important for modeling population dynamics in response to natural (e.g. wildfire) or anthropogenic perturbations (e.g. energy development) and conservation (e.g. hunting).

Understanding age- and sex-specific susceptibility to harvest is vital to establishing hunting regulations and adaptively managing populations. Currently, there is a paucity of data on juvenile vulnerability to hunter harvest (Beck et al. 2006, Caudill et al. 2014), but the body of information on adult sage-grouse is becoming well founded (Connelly et al. 2000, Zablan et al. 2003, Broms et al. 2010, Sedinger et al. 2010). Adult harvest rates vary between 5 and 10% and appear to be similar between males and females (Zablan et al. 2003, Sedinger et al. 2010). Survival of juveniles to first breeding (i.e. recruitment) is poorly understood. However, the few studies that have examined juvenile survival from autumn (–Sep–Nov) to first breeding generally indicate that over-winter survival is similar to that of adults (Beck et al. 2006, Battazzo 2007, Caudill et al. 2014, Apa et al. 2017). Given the short-term ( $\leq 3$ -year) duration of these studies, we are lacking information on annual variation in recruitment (but see Blomberg et al. 2014).

Hunter-harvested wildlife affords an opportunity to collect data on vital rates that may otherwise be logistically or cost prohibitive (Broms et al. 2010, Dusek et al. 2014). We used six years of band-recovery and composition of age

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and sex information from sage-grouse wings collected from hunters in Moffat County, Colorado (1978–1983). We used a novel application of the Lincoln estimator (Lincoln 1930, Alisauskas et al. 2014) to generate an unbiased estimate of tertiary sex-ratio and production using band recoveries and wings collected from hunter-harvested birds. Our primary objective was to examine age-specific patterns of survival and harvest rates of male and female sage-grouse. Specifically, we sought to provide estimates 1) of juvenile survival to adulthood, as this parameter is not well described in the literature, 2) of harvest rates for juvenile and adult sage-grouse, and 3) of the tertiary sex-ratio.

## Study area

We studied sage-grouse in Moffat County which is in the northwest corner of Colorado adjacent to Utah on the west and Wyoming on the north. Our efforts were concentrated at Blue Mountain (adjacent to Utah on the west), Cold Spring Mountain (adjacent to Utah on the west and Wyoming on the north), northcentral Moffat County (adjacent to Wyoming on the north), and eastern Moffat County including a small portion of Routt County on the east (both adjacent to Wyoming on the north). However, for brevity we refer to the study area as Moffat County. These areas varied in elevation with the highest at Blue Mountain and Cold Spring Mountain = ~ 2785 m, lowest = ~ 1525 to 2000 m in the northcentral portion of the county (Braun et al. 2015). All areas had extensive areas dominated by big sagebrush *Artemisia* spp. with understories of native forbs and grasses with some aspen *Populus tremuloides*, mountain shrubs (*Amelanchier* spp., *Purshia* spp., *Rosa* spp.), and small trees (*Juniperus* spp.). Some agricultural fields (barley, oats, wheat, native hay) occurred at lower elevations.

## Methods

### Capture

Sage-grouse were located and captured using spotlights and long-handled nets (Giesen et al. 1982) near lek sites during the breeding season and in known summer ranges during July and August using, walk-in drive traps (Giesen et al. 1982) and bumper-mounted (Latcher and Latcher 1964) and stationary cannon nets (Braun 1976). Each bird was classified to an age and sex category based on body size and diagnostic plumage characteristics (Braun and Schroeder 2015). Once age and sex were ascertained, each bird was marked with a uniquely numbered aluminum band provided by the Colorado Division of Wildlife (CDOW) and released where captured. The CDOW did not have an IACUC protocol prior to about 1990, however, guidelines of Gaunt et al. (1987) were followed for appropriate care while capturing and handling sage-grouse.

### Data recovery

Wings were obtained from hunter-harvested sage-grouse at three hunter check stations and 16 wing barrels (Hoffman and Braun 1975) located at major access points to areas where

sage-grouse were commonly hunted. They were labeled as to site of collection and stored frozen until thawed and classified to age and sex (Braun and Schroeder 2015). Bands were obtained at check stations, in wing barrels, and through return of hunter questionnaires as well as personal contacts such as walk-ins and reported through the mail or via the phone. All hunters were required to obtain a permit prior to hunting during 1978–1980 which allowed a 100% questionnaire survey about hunting activities including: area of hunting, dates of hunting, number of grouse harvested/lost, a question about recovery of banded birds, etc. (Braun 1981). Data sheets were prepared for each band reported and were later transferred to digital files for storage and manipulation. Hunting seasons generally varied between 9 (1978), 16 (1979, 1981–1983), and 25 days (1980), beginning on the second Saturday of September each year. Hunters were allowed three birds per day and six in possession (Braun et al. 2015).

## Statistical approach

We used Brownie parameterization of age-structured recovery models to estimate annual recovery rates ( $f$ ) of male and female sage-grouse (Brownie et al. 1985). The Brownie parameterization provides estimates that can separate birds reported from hunter harvest ( $f$ ) from other sources of mortality ( $m = 1 - S - f$ ) (Cooch and White 2014). We included age-class at banding ( $age$ ; adult or juvenile) and time-dependence ( $t$ ) to investigate the effects of age and annual variation on survival ( $S$ ). We modeled recovery probability  $f$  as a function of time ( $t$ ),  $age$  and  $sex$ . Because of the relatively short duration of our study, and the absence of capture and release of juvenile birds in the final year, we limited time-dependence in our model set. Specifically, we constrained  $S$  to estimate temporal variation in  $f$  and vice versa. This approach enabled us to elucidate some of the temporal variation in survival and harvest, and potential changes in sex-ratio over time. However, this approach limits inference of  $S$  and  $f$ , especially under the Brownie parameterization because  $f$  contains some information about mortality and constraints on either parameter and necessarily makes assumptions about the pattern of variation in the unconstrained parameter (Cooch and White 2014). Mark–recapture analyses were conducted in Program MARK (Cooch and White 2014).

Model selection was used to identify the most parsimonious model from which to estimate age and sex specific parameters of survival and harvest. After examining the fit of the global model, models with fewer parameters were fit to the data. The number of potential models was large and we used a hierarchical procedure to guide model fitting (Lebreton et al. 1992). In both  $S$  and  $f$ , we started with additive models with main effects only (e.g.  $sex + age + t$ ). Model selection was based on Akaike's information criterion adjusted for small sample sizes ( $AIC_c$ , Burnham and Anderson 2002). Models where  $\Delta AIC_c < 2$  from the best fit model ( $\Delta AIC_c = 0$ ) were considered equally parsimonious. The ratio of  $AIC_c$  weights between two models was used to quantify the relative degree that a pair of models was supported by the data (Burnham and Anderson 2002). All parameter estimates (including means) are presented with 95% CIs otherwise noted.

Table 1. Number of greater sage-grouse captured, banded and released in Moffat County, CO 1978–1983.

Age and sex	1978	1979	1980	1981	1982	1983	Total
Adult male	49	764	597	11	21	36	1478
Adult female	36	168	150	31	45	14	444
Juvenile male	217	136	154	81	72	0	660
Juvenile female	206	177	167	70	57	0	677
Total	508	1245	1068	193	195	50	3259

We applied the capture–recapture Lincoln (1930) estimator for closed populations to provide unbiased annual ( $t$ ) estimates of abundance ( $N$ ) for each age ( $i$ ) and sex ( $j$ ) of a harvested population (Alisauskas et al. 2009). The Lincoln–Peterson capture–recapture estimator of abundance for closed populations is

$$\hat{N} = n_2 / \hat{p}_2$$

where  $n_2$  is the number of animals captured in the second of two sampling occasions, and  $\hat{p}_2$  is the ratio of recaptures to animals captured on the first occasion. The estimator of population size,  $N$ , from hunter harvest was

$$\hat{N}_t = \hat{H}_t / \hat{h}_t$$

where  $H_t$  was an estimate of harvest for year  $t$ , and  $h_t$  was the estimated probability that a bird alive at the time of banding in year  $t$  was harvested in year  $t$ . In the context of our work, the number of wings reported was the equivalent of  $H_t$  and  $f$  was the equivalent of  $h_t$ , assuming a band reporting rate of 1.0. Thus, from  $N_{ij}$  we then estimated annual sex-ratio and age-ratios (i.e. production, HY: AHY females) in the harvest as the ratios of male and female population size or juveniles per adult. We note that the assumption that band reporting rates = 1.0 could be violated but not as long as band-reporting rates were the same for both males and females or for juveniles and adults. We used the delta method (Powell 2007) to estimate confidence intervals for sex and age-ratios estimated from the Lincoln calculations. For count data from wings, we used Wilson’s confidence intervals as an estimate of variance for each ratio as it provides excellent coverage of the ratio estimators (Hagen and Loughin 2008).

## Results

In total, 3259 sage-grouse were captured and banded from 1978–1983. Sixteen birds were removed from the study because of recovery not associated with harvest. Hunters

Table 2. Number of greater sage-grouse wings reported from hunter harvests in Moffat County, CO, 1978–1983.

Age and sex	1978	1979	1980	1981	1982	1983	Total
Adult male	150	446	354	198	93	196	1437
Adult female	398	635	526	477	256	448	2740
Juvenile male	585	592	498	366	257	450	2748
Juvenile female	624	719	622	491	358	492	3306
Total	1757	2392	2000	1532	964	1586	10 231

harvested and reported 368 sage-grouse bands (3243 available for harvest) to the Colorado Division of Wildlife (Table 1). Hunters provided 10,231 wings from which age and sex of individual birds could be classified (Table 2).

Model selection based on  $AIC_c$  indicated the best fit model for estimating temporal variation in survival ( $S^{Adsex+t}$ ,  $S^{JuvC+t}$ ,  $f$  age) was one with age specific recovery rates, but similar rates between sexes in each age class (Table 3). The model also indicated sex specific survival of the adult class, but juvenile survival was best estimated as one probability for both sexes. The same model but with sex specific survival of juveniles was not well supported ( $\Delta AIC_c = 5.56$ ). The best fit model for estimating temporal variation in recovery rate ( $S^{Adsex}$ ,  $S^{JuvC}$ ,  $f$  age +  $t$ ) was one with age-specific recovery rates, but similar rates between sexes in each age class (Table 3). However, a competitive model ( $\Delta AIC_c = 1.82$ ) was one in which sex-specific recovery rates were estimated for each age class, but this model was 2.47 times less likely than the best model. Because of our temporally limited data and relatively small effect sizes, we defaulted to make inference from the simpler model rather than use model averaging.

Annual variation in survival and recovery rates was greatest among the juvenile age class (Table 4). Generally, recovery rates were twice ( $\hat{f} = 0.112$ , 95% CI: 0.097–0.131) that of adult sage-grouse ( $\hat{f} = 0.063$ , 95% CI: 0.053–0.073), and survival of juveniles was 13 to 40% less than that of adult

Table 3. Recovery models used to examine the effects of age survival of male and female greater sage-grouse in Moffat County, CO, 1978–1983. Model fit is described with deviance (Dev), the number of parameters ( $K$ ), the difference in Akaike’s information criterion corrected for small sample size from the best fit model ( $\Delta AIC_c$ ), and  $AIC_c$  weights ( $w_i$ ). Model structure estimated annual survival ( $S$ ) for adult ( $S^{Ad}$ ) and juveniles ( $S^{Juv}$ ), and probability of recovery ( $f$ ). The letter  $c$  denotes that a parameter was estimated as constant within a particular age or sex of birds, and  $t$  indicates an additive time effect. Additive models (+) included only main effects.

Model	$\Delta AIC_c$	$w_i$	$K$	Dev.
$S^{Adsex}$ , $S^{JuvC}$ , $f$ age + $t$	0.00	0.619	10	103.05
$S^{Adsex}$ , $S^{JuvC}$ , $f^{Adsex+t}$ , $f^{Juvsex+t}$	1.82	0.249	11	102.86
$S^{Adsex+t}$ , $S^{JuvC+t}$ , $f$ age	3.78	0.094	9	108.84
$S^{Adsex+t}$ , $S^{JuvC+t}$ , $f^{Adsex}$ , $f^{JuvC}$	5.62	0.036	10	108.67
$S^{Adsex+t}$ , $S^{JuvC+t}$ , $f^{Adsex}$ , $f^{Juvsex}$	5.71	0.034	10	108.75
$S$ age, $f$ age + $t$	10.92	0.003	9	115.97
$S^{Adsex}$ , $S^{JuvC}$ , $f^{Adsex}$ , $f^{Juvsex}$	37.71	0.000	6	148.80
$S^{Adsex}$ , $S^{JuvC}$ , $f^{Adsex}$ , $f^{Juvsex}$	42.34	0.000	6	153.43
$S$ age, $f$ t	45.24	0.000	8	152.31
$S$ age, $f^{Adsex}$ , $f^{Juvsex}$	45.46	0.000	5	158.55
$S$ age, $f$ age	46.33	0.000	4	161.43
$S$ t, $f$ age + $t$	49.31	0.000	8	156.38
$S$ c f c	70.53	0.000	2	189.64

Min  $AIC_c = 2818.1$

Table 4. Survival probabilities ( $S$ ) and recovery rates ( $f$ ) estimated from greater sage-grouse band recovery data using Brownie parameterization, Moffat County, CO, 1978–1983.

	Adult male		Adult female		Juveniles	
	$S^a$	95%CI	$S$	95%CI	$S$	95%CI
1978	0.866	0.637–0.960	0.938	0.799–0.983	0.554	0.332–0.756
1979	0.361	0.240–0.504	0.569	0.397–0.726	0.098	0.038–0.230
1980	0.252	0.156–0.380	0.440	0.273–0.622	0.061	0.021–0.162
1981	0.141	0.060–0.298	0.278	0.138–0.480	0.031	0.008–0.106
1982	0.804	0.373–0.966	0.905	0.560–0.986	0.440	0.125–0.812
Overall <sup>b</sup>	0.356	0.270–0.452	0.609	0.457–0.742	0.310	0.209–0.432
	$f^c$	95%CI	$f$	95%CI	$f$	95%CI
1978	0.052	0.036–0.075	0.055	0.037–0.082	0.106	0.079–0.141
1979	0.060	0.048–0.075	0.063	0.048–0.083	0.121	0.094–0.155
1980	0.072	0.058–0.089	0.076	0.058–0.098	0.143	0.113–0.180
1981	0.048	0.034–0.069	0.051	0.034–0.075	0.098	0.069–0.138
1982	0.010	0.004–0.021	0.010	0.005–0.023	0.021	0.010–0.044
1983	0.045	0.023–0.086	0.048	0.024–0.092	0.092	0.049–0.168
Overall <sup>d</sup>	0.063	0.053–0.076	0.060	0.044–0.079	0.112	0.097–0.131

<sup>a</sup>Annual survival was estimated from the model  $S^{Adsex+t, S^{juvc}+t, f \text{ age}}$

<sup>b</sup>Overall survival was estimated from the model  $S^{Adsex, S^{juvc}, f \text{ age}}$

<sup>c</sup>Annual recovery rate was estimated from the model  $S^{Adsex, S^{juvc}, f \text{ age}+t}$

<sup>d</sup>Overall recovery rate was estimated from the model  $S^{Adsex, S^{juvc}+t, f^{Adsex}, f^{juvc}}$

males and females, respectively. Because we constrained our temporal trend to additive models only, we are limited in our inference about temporal variation. These additive models indicated that survival was greatest at the beginning of the study and steadily declined until the penultimate year (Table 4). On average, adult females had the highest survival ( $\hat{S} = 0.609$ , 95%CI: 0.457–0.742) followed by adult males ( $\hat{S} = 0.356$ , 95%CI: 0.271–0.452), and then juveniles ( $\hat{S} = 0.310$ , 95%CI: 0.209–0.432).

Our population estimates averaged 29 611 over the study period (Table 5). From those estimates we derived tertiary sex-ratio for adult and juveniles. Sex ratio was generally skewed toward females in both adults (range = 1.352–2.607 females per male, Fig. 1A–B.) and juveniles (range = 1.016–1.320 females per male, Fig. 1C–D). However, statistically the tertiary sex ratio of juveniles was not measurably different from 1:1 based on Lincoln estimates (Fig. 1C). Adult sex ratios estimated from counts of wings alone were generally 11% greater than those based on Lincoln estimates (Fig. 1B). Juvenile sex ratio estimates were 6% greater in wing count data than those based on Lincoln estimates (Fig. 1C). Because of the differences in age-specific band recovery rates, estimates of production based solely on wings were on average 1.2 juveniles per adult female greater than those adjusted for the band recovery rate (Fig. 1E–F).

## Discussion

Our objectives were to provide insights to harvest rates of juvenile and adult sage-grouse and unbiased estimates of production and tertiary sex-ratios. Our study provided several key findings, 1) juvenile harvest rates were twice those of adults, 2) harvest vulnerability was similar between adult males and females, 3) survival of juveniles was highly variable, and 4) sex ratios of adults and juveniles largely conformed to previously assumed proportions despite having based those estimates on harvest rates (Braun et al. 2015).

Our analyses yielded novel insights about harvest mortality, indicating that juveniles were nearly two-times more likely to be harvested than adults, and adult males and females shared a similar vulnerability to harvest. The latter finding was contrary to anecdotal evidence from hunters which suggested that adult females exhibited substantially greater susceptibility to harvest than males (Braun et al. 2015). Beck et al. (2006) reported a harvest rate of 0.02 from 1 juvenile of 56 susceptible to hunter harvest in southeastern Idaho. Our findings were similar to harvest rates in Nevada and elsewhere in Colorado, with no differences in harvest rate between the sexes of adults (Sedinger et al. 2010). However, sub-adult (after-hatch year) birds did exhibit differences in harvest susceptibility between sexes, and compared to

Table 5. Fall population estimates of greater sage-grouse derived from an application of the Lincoln estimator to hunter-harvested wings and band recovery data, Moffat County, CO, 1978–1983.

	Adult male		Adult female		Juvenile male		Juvenile female	
	n	95%CI	n	95%CI	n	95%CI	n	95%CI
1978	2864	1821–3907	7215	4329–10 101	5502	3916–7088	5589	4002–7177
1979	7415	5794–9035	10 027	7285–12 770	4889	3651–6127	5659	4255–7063
1980	4911	3888–5934	6936	5126–8746	3476	2659–4293	4143	3203–5083
1981	4106	2624–5587	9388	5736–13 040	3721	2430–5013	4752	3164–6340
1982	9572	2022–17 121	24 955	4880–45 031	12 425	2820–22 031	16 404	3810–28 997
1983	4344	1496–7193	9424	3020–15 828	4 874	1830–7919	5071	1906–8236



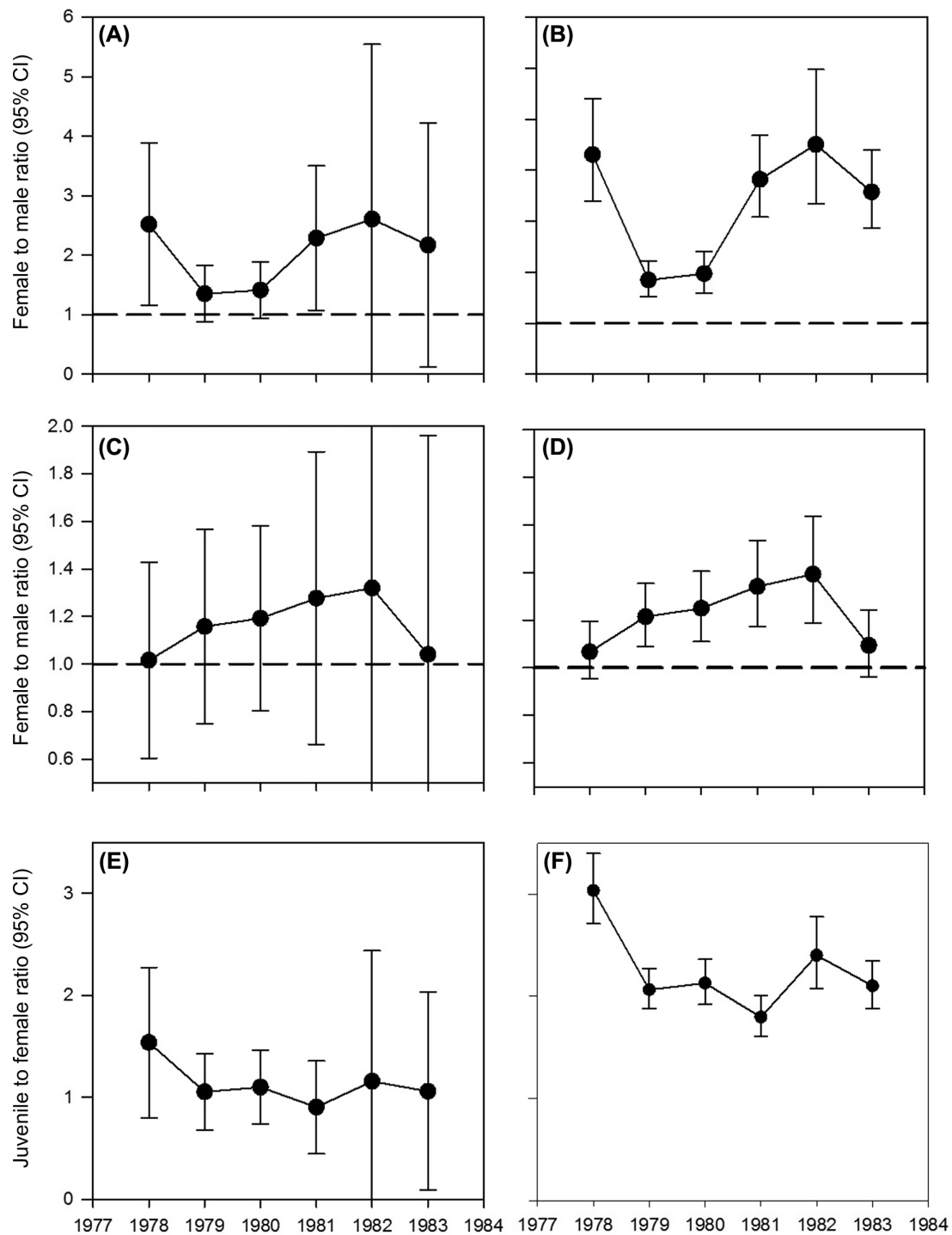


Figure 1. Annual estimates (95% CIs) of greater sage-grouse tertiary sex ratio for adults estimated from Lincoln estimator (A) and from counts of wings (B), juveniles estimated from Lincoln estimator (C) and from counts of wings (D), and production (juveniles to female ratio) estimated from Lincoln estimator (E) and from counts of wings (F), Moffat County, CO, 1978–1983.

adults (Zablan et al. 2003). Averaged across age and sex class, and year, our harvest susceptibility ( $\hat{f} = 0.083$  SE=0.005) was nearly equivalent to that found in Nevada ( $\hat{f} = 0.09$  SE=0.008). Sedinger et al. (2010) determined that harvest rates  $<0.10$  were compensatory to natural mortality. If that estimate is correct then harvest was compensatory for all cohorts in our study except for juveniles in 1979 and 1980 (Table 4). Caudill et al. (2014) reported greater harvest rates

(0.09 and 0.27 in 2008 and 2009, respectively) from radio-marked juvenile sage-grouse at Parker Mountain, Utah. Although sample sizes were limited ( $<50$  birds available for harvest) these higher rates may be reflective of susceptibility to harvest in geographically isolated populations (Gibson et al. 2011). Alternatively, these higher rates could be a result of increased vulnerability of radio-marked birds as has been observed in some waterfowl studies (Parker 1991).

Variation in post-fledging survival has been linked to body condition and climatic variation (Blomberg et al. 2014). Sage-grouse juveniles appear to have improved survival in years with cooler and wetter growing season conditions (Blomberg et al. 2014). Given the limitations with available climatic data, we were unable to link survival to such covariates. However, we found survival of juveniles to be highly variable and lower than studies of radio-marked birds (Battazzo 2007, Beck et al. 2006, Blomberg et al. 2014). Direct comparisons of our juvenile survival estimates are limited because telemetry studies followed juveniles to the first breeding season (Mar–Apr) and our estimates follow them to the subsequent hunting season. However, we transformed our annual estimates to monthly survival estimates ( $\hat{S}_{\text{month}} = \hat{S}^{1/12}$ ) and then projected those out seven months to provide comparable estimates. We estimated juvenile survival to first breeding (Oct–Mar) and it varied from 0.131 to 0.708. These estimates were considerably lower than those from radiomarked birds in Idaho ( $\hat{S} = 0.80$ , Beck et al. 2006) and Montana ( $\hat{S} = 0.91$ , Battazzo 2007), but similar between 2005 and 2008 for the same region of Colorado as our study ( $\hat{S}$  range of means 0.477 to 0.657, Apa et al. 2017). One limitation to these comparisons could be unaccounted for seasonal variation in survival with reductions during the breeding season. Thus, our study will tend to underestimate mean monthly survival compared to telemetry studies that monitored birds until the nesting season. While our data did not support sex specific survival rates of juveniles, recent work by Apa et al. (2017) demonstrated consistent measurable differences. Juvenile female survival was between 7 and 13 percentage points greater than for males, which was similar to our estimates (male  $\hat{S} = 0.258$ , female  $\hat{S} = 0.388$ ), albeit from a model not well supported in the data set. These data points lend support to previous hypotheses regarding differential physiological demands between the sexes that may result in the observed lower survival of juvenile male sage-grouse (Swenson 1986).

Our estimates of adult annual survival were comparable to those reported previously (Sedinger et al. 2010, Taylor et al. 2012, Dahlgren et al. 2016) with the exception of 1981 when adult male and female survival was  $< 0.14$  and  $0.30$ , respectively. Reduced annual survival has been linked to severe winter weather conditions (Anthony and Willis 2009). As measured by Anthony and Willis (2009), the winter of 1980 would have been considered severe in our study. Per the weather station at Craig, Colorado there were 31 days with temperatures  $< -18^{\circ}\text{C}$  and a snowpack of 917 cm. Although these were commensurate with lower survival, the winter of 1979 was more severe but adult survival was seemingly unaffected. Juvenile annual survival was only directly comparable to that of harvested birds in Nevada at  $\hat{S} = 0.40$  (Sedinger et al. 2010) and our estimates were considerably less ( $\hat{S} < 0.098$ ) in 3 of 5 years, and overall was 23% lower. Extrapolating estimates to first breeding from Idaho ( $\hat{S} = 0.68$ ) and Montana ( $\hat{S} = 0.80$ ) to annual survival suggests greater survival of juveniles in those populations (Beck et al. 2006, Battazzo 2007). However, such extrapolation assumes constant survival during the breeding season which typically is a period of high mortality and our estimates may be biased low. Nonetheless, if adjusted for

breeding season mortality we suggest juvenile survival estimates from other systems would remain considerably greater than our lowest annual survival estimates that were  $< 10\%$ .

Our estimates of tertiary sex-ratio of juveniles and adults are the first to be correctly adjusted for harvest susceptibility (Atamian and Sedinger 2010). Because our modeling indicated little variation in harvest rates within age classes it did not result in measurable differences in our estimates of sex-ratio from counts of wings alone. The juvenile sex ratio was essentially 1:1, and adults exhibited strong bias towards females in the population  $2.04$  (95%CI:  $1.45$ – $2.64$ , Braun et al. 2015). This pattern is reasonably supported by the differential in survival between the sexes (Connelly et al. 2011, Taylor et al. 2012). However, our adjusted estimates of production were considerably less (1.2 juveniles: female) than those generated from counts alone (Fig. 1D–E). While the trends of each data set tracked one another, the adjustment for harvest susceptibility may provide for a more accurate estimate of production. Additional work, perhaps a simulation study could assist in more clearly depicting the bias associated with using only count data.

We are encouraged by our approach and application of mark–recovery data to the Lincoln estimator in combination with hunter harvest information as a potential tool for reconstructing population sizes and age ratios of harvested populations (Alisauskas et al. 2014). Although contemporary harvest of sage-grouse may be more limited than in our study, there is potential for future application of these methods to hunted populations. Additionally, there appears to be some promise for other gallinaceous birds with greater harvests such as sharp-tailed grouse *Tympanuchus phasianellus*, gray partridge *Perdix perdix*, chukar *Alectoris alectoris* or quail *Callipepla* sp. that can be readily captured, marked and have reasonable harvest rates.

**Acknowledgements** – We especially thank Peter O. Dunn for sharing data and Howard D. Funk for encouraging the initiation of this project. We also thank the many temporary technicians who contributed over a period of years as well as permanent employees (Conservation Officers, Avian Researchers) of the Colorado Division of Wildlife.

**Funding** – Our field work during the 1978–1983 interval was supported by the Colorado Division of Wildlife through Federal Aid to Wildlife Restoration Project W-37-R.

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