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Successful Adult Willow Grouse are Exposed to Increased Harvest Risk.

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ABSTRACT Age and sex ratios in bag records are frequently used as indices of population composition for harvested populations. However, vulnerability to harvest may differ by age and sex thereby producing bias in population estimates. We assessed whether age and sex affected vulnerability to harvest for willow grouse (*Lagopus lagopus*) where adult density and brood size was known in the harvested populations. We collected bag records during 2 days of controlled hunting in 4 areas in 2 years (2007 and 2008) in Jämtland county, Sweden. We found that vulnerability to harvest was different for chicks and adults, but not between male and female adults. Hunters encountered broods at a higher rate than single birds compared to personnel conducting pre-harvest counts along line transects. Furthermore, the probability of shooting a grouse was higher in encounters of broods than individual grouse. Proportionally, we calculated about a 50% probability of a hunter shooting either a chick or an adult

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independent of encountering a single bird or broods of 2–10 grouse. Increasing adult density also increased the vulnerability to harvest for adults relative to chicks, independent of the chick to adult ratio in the pre-harvest population. The different vulnerability of adults and chicks to harvest observed in this study will dampen variation in age classes in bag records compared to the population, and we caution against extrapolation of age ratios in bag records to harvested populations.

KEY WORDS age ratio, bag limit, harvest vulnerability, hunters, *Lagopus lagopus*, selective harvest, sex ratio, willow grouse.

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If vulnerability to harvest is affected by age and sex in game species, the age and sex structure of the population will be biased when interpreted from harvest records (Skalski et al. 2005). Among the species in Galliformes, age and sex ratios in bag records are frequently used as indices for chicks per adult and sex-ratio in harvested populations. Several studies have reported that age and sex ratios in the bag can change during the hunting season (Helminen 1963, Bergerud 1970, Davis and Stoll 1973, Roseberry and Klimstra 1992, Durbian et al. 1999, Hansen et al. 2012), but few studies have compared the age and sex ratios in bag records with actual ratios of the harvested population. Among the Galliformes, vulnerability to harvest been investigated for bobwhite (*Colinus virginianus*; Pollock et al. 1989, Shupe et al. 1990) and red grouse (*Lagopus lagopus scoticus*; Bunnefeld et al. 2009). For bobwhite, both Pollock et al. (1989) and Shupe et al. (1990) used band recovery to assess vulnerability to harvest, and found that juveniles were more vulnerable to hunting than adults. Pollock et al. (1989) also showed an interaction of age and sex to the vulnerability of harvest. Bunnefeld et al. (2009) found that age and sex in bag records was biased compared to the pre-count population data. Hörnell-Willebrand et al. (2006) studied the temporal and spatial variation in chick production of willow grouse (*Lagopus lagopus*) using data from both bag records and line transect counts. The long-term bag records showed a similar distribution of chick to adult ratios in different areas, whereas counts showed larger variation in chick to adult ratios both within and between areas. Myrberget (1974) showed large annual and spatial variation in the chick to adult ratios in bag records for willow grouse, but the overall average (2.9 chicks/pair) was similar to the findings (2.8 chicks/pair) of Hörnell-Willebrand et al. (2006).

The willow grouse is one of the most popular small game species in Scandinavia. Populations show large annual fluctuations with variable breeding success and high rates of natural mortality (Marcström and Höglund 1980, Myrberget 1988, Smith and Willebrand 1999). Harvest rates can be substantial and over 50% harvest rates have been reported (Kastdalen 1992, Smith & Willebrand 1999, Willebrand et al. 2011). Willow grouse have small differences in the size and plumage characteristics between sex and age in the hunting season (late Aug–Feb), and birds are shot after being flushed from cover making it difficult to intentionally select for age or sex.

No studies exist investigating the mechanisms of the potentially different vulnerability between age groups and sexes in willow grouse (hereafter referred to as grouse) despite several reports suggesting a bias in the bag records compared to the harvested population. Here we present results from detailed grouse hunting data where grouse density and breeding success were estimated. We tested the hypotheses that the age and sex composition of grouse shot by hunters is unbiased compared to estimates of the hunted population determined by line transect surveys. We further investigated if the encounter rate of single grouse and broods was proportional to what was present in the hunted population.

STUDY AREA

We conducted our study in 4 areas in Jämtland county, Sweden that ranged in size from 54 km^2 to 174 km^2. Vegetation cover was dominated by alpine heath and shrub above the tree line and mountain birch (*Betula pubescens*) forest below the tree line. Areas were open for small game hunting from 25 August to the end of February with a daily bag limit of 8 grouse per hunter. Two thirds of all hunting took place the first 10 days of the season (Smith and Willebrand 1999). Grouse hunting in Sweden is mainly performed by hunters on foot with pointing dogs used to locate and flush grouse (Bergström et al. 1992). Study areas were the same as in Willebrand et al. (2011), where detailed description of harvest levels, hunting effort, and grouse demography from 1996–2007 were presented.

METHODS

Harvest Data

We conducted our experiment in 2007 (23–24 Aug) and 2008 (22–23 Aug). Hunters participating in the experiment were dedicated grouse hunters and hunting dog enthusiasts; this included 44 males and 11 females during 83 hunting days. Each day of the experiment, 6 to 8 hunters with pointing dogs entered the study areas. Hunters hunted separately and were free to search the area as they preferred, but had a daily bag limit of 8 grouse. Each hunter recorded data on all grouse encounters, including number of grouse seen and the number of grouse shot. We aged shot grouse based on molting following Bergerud et al. (1963) and determined sex by inspection of the gonads.

Grouse Populations

The first weekend in August, approximately 2 weeks prior to the hunt, we estimated total and adult density (birds/km^2) on each hunting area by line transect counts and distance sampling (Buckland et al. 2004, Hörnell-Willebrand 2005). We systematically placed parallel transect lines about 400 m apart covering the entire management area below 1,100 m in elevation. Experienced dog handlers trained in the distance sampling technique completed counts with the help of pointing dogs. We calculated chicks per pair from the total and adult density estimates.

Statistical Analyses

We assessed the vulnerability of chicks, adults, and sex to harvest using generalized linear models (GLM) with binomial errors. We used the proportion of adults and the proportion of adult males of all adult grouse in bag records for each area and year as response variables, and included adult density and the chick to adult ratio as explanatory variables. We did not include the sex of chicks in models because of the difficulty in sexing them.

We used a GLM with binomial errors to evaluate if the vulnerability of chicks and adults that were shot was dependent on brood size once grouse had been encountered. To test this hypothesis, we used the adult proportion bagged from different brood sizes as a response variable and the brood size they were shot from as the explanatory variable. Males in pairs that have successfully fledged chicks tend to stay with the brood (Martin 1984, Pedersen and Steen 1985), and we assumed that broods were composed of 2 adults and their chicks. Hunters did not report if they intentionally pursued scattered broods after an initial flush, and some recorded brood sizes possibly referred to a scattered brood or even a single chick. The sample size of adult males and females shot at different brood size encounters was too low to analyze.

To evaluate if hunters had a different probability in encountering individuals and broods of grouse than during counts along transect lines, we used a Fisher's exact test to calculate the odds ratio for a single grouse encounter during hunting versus transect counts in each area and year. We also used a Fisher's exact test to calculate the odds ratio for a grouse and an adult grouse to be shot when encountered as an individual versus in a brood in each area and year.

We evaluated all models by plotting residuals against predicted values of response variables and explanatory variables (Zuur et al. 2009, Zuur et al. 2010). We evaluated homoscedasticity by plotting the residuals from the regression in a Q-Q plot (Crawley 2007). We calculated the pseudo R^2 for all GLMs as a measure of explanatory power (Zuur et al.

2009). We carried out all analyses in the statistical software R (R Development Core Team 2010).

RESULTS

Pre-Hunt Populations and the Harvest

The pre-harvest grouse density estimates in the 4 areas and the 2 years varied between 7.3–35.7 grouse/km^2 (average CV = 23.8%), with 2.7–10.3 adults/km^2 and 0.7–5.8 chicks per pair. Adult density was not correlated with chicks per pair ($r < 0.01$, $P = 0.996$). The total bag consisted of 342 grouse: 161 adults (82 males, 74 females, and 5 unidentified grouse) and 181 juveniles (56 males, 72 females, and 53 unidentified grouse). Gonads of juveniles were less developed and more often damaged by shot or the retrieving dog compared to adults. In all areas and years, hunters had a lower and significant ($P < 0.05$) probability of encountering a single grouse (average odds ratio 0.37, range 0.28–0.53) than personnel counting grouse along transect lines. In 7 of 8 areas and years, we observed a lower probability of a hunter shooting a grouse (adult or juvenile) when encountering a single grouse relative to encountering a brood. This effect was only significant for 1 area and year (odds ratio 0.39, $P = 0.037$), however. Average odds ratio for the 6 non-significant comparisons was 0.70, and the odds ratio for the 1 area and year with a higher probability of shooting a grouse when encountered as a single was 1.65 ($P = 0.423$). We also found a lower probability of shooting an adult when hunters encountered a single grouse relative to broods of 2 or more individuals. Though, only significant for 1 area and year (odds ratio 0.06, $P = 0.001$). At 2 of our study sites, in different years, no adults were shot from single bird encounters. Average odds ratio of shooting an adult grouse in a single bird encounter relative to a brood for the 5 non-significant comparisons was 0.61. From the line transect counts we observed that 90% of the single grouse observed were adults, and we encountered chicks during 56% of the encounters that included adults.

Harvest Vulnerability

Vulnerability of adults to harvest relative to chicks increased with increasing adult density (β = 0.22, SE = 0.04, $Z_6 = 5.39$, $P < 0.001$, pseudo $R^2 = 0.93$; Fig. 1), but the chick to adult ratio in the pre-harvest population did not have any effect on the age ratio in the bag ($Z_5 = 0.002$, $P = 0.998$). In half of the bag records, the chick to adult ratio was 0.2–1 chicks/adult higher than the harvested population, whereas in the other half the chick to adult ratio was from 0.4–1.9 chicks/adult lower than the harvested population. The overestimation occurred at the lowest adult densities and vice versa for the underestimation. The only exception was at the second highest adult density where the chick to adult ratio in the bag was overestimated relative to the pre-harvest population estimate. Vulnerability to harvest for male and female grouse was unrelated to adult density ($Z_5 = -0.32$, $P = 0.747$) and chick to adult ratio ($Z_5 = -1.080$, $P = 0.280$) in the pre-hunt population. Average number of adult males per adult female in the bag records for the 2 years was 1.2, ranging from 0.8 to 1.7.

The vulnerability of chicks and adults to harvest was close to 1:1 and independent of the encountered brood size. The proportion of adults in the bag in brood sizes of 1 to 10 averaged 0.49, with a weak, but not statistically significant, negative trend (β = −0.06, SE = 0.04, $Z_8 = -1.42$, $P = 0.06$; Fig. 2). Brood size was truncated at 10 grouse, since we only had data on harvested grouse from 13 broods larger than 10 individuals. One adult was shot from a brood of 14 grouse.

DISCUSSION

Our results show that the age ratios of willow grouse in bag records was biased compared to density estimates from pre-harvest counts. The encounter frequency of single grouse was higher during pre-harvest counts than during hunting. The true difference was probably larger than estimated because chicks encountered and shot after an initial flush of a brood were recorded as single grouse. About 60% of the grouse shot were classified as single adults whereas 90% of observed single grouse during pre-harvest counts were adults. Hunters were more successful in bagging a grouse when encountering a brood compared to encounters of single grouse, and grouse from broods thereby became overrepresented in the bag.

Adult willow grouse show distraction display to divert the attention of predators from the chicks (Martin 1984, Pedersen and Steen 1985, Sonerud 1988, Martin and Horn 1993). The tendency for adult willow grouse to expose themselves will make them vulnerable to harvest and explain why the proportion of adults in the bag was independent of brood size. Hunters did not usually shoot more than 2 grouse when encountering a brood, and in initial brood encounters hunters would usually shoot at least one adult, resulting in an adult biased bag. This was counteracted by the fact that single adults are underrepresented in the bag records. Furthermore, in subsequent encounters of broods there must be a lower probability of an adult being shot than in first encounters, and more reencounters will result in a higher proportion of chicks in the bag. Few reencounters imply lower harvest rates, and Willebrand et al. (2011) showed that willow grouse populations experienced higher harvest rates in years with low density. This could explain why the proportion of adults in the bag decreased with decreasing adult density. The sex ratio of adult grouse in the harvest was in accordance with what has been reported earlier for willow grouse populations (Hannon 1983) and was not related to either the adult density or production in the pre-harvest population.

We conclude that the differences in vulnerability to harvest (single adults vs. adults with a brood; adults vs. chicks within a brood) can explain the close to identical distributions of chicks per adult in long-term bag records from different areas in Norway and Sweden (Steen et al. 1988, Willebrand and Hörnell 2001, Hörnell-Willebrand et al. 2006). This bias will vary with adult density, proportion of adults with a brood, average brood size, and harvest rate. Years with large average brood size and low harvest rate will greatly underestimate chicks per adult in the population, but it is difficult to see how the bias could be adjusted retrospectively.

MANAGEMENT IMPLICATIONS

Age ratio from harvested game birds is commonly used to estimate recruitment and improve the understanding of the demographics behind population change. Incorporating recruitment estimates from bag records in management models may result in poor predictions of population response if different age classes have different vulnerability to hunting as in this study.

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Figure 1.

Proportion of willow grouse adults in harvests by pre-harvest adult density in Jämtland county, Sweden, 2007–2008. The solid line is predicted from a generalized linear model and broken lines are 95% confidence intervals.

Figure 2.

Proportion of willow grouse adults in harvests by brood size of the encounters in Jämtland county, Sweden, 2007–2008. The solid line is predicted from a generalized linear model, broken lines are 95% confidence intervals.