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RESEARCH ARTICLE

Integrating Breeding Bird Survey and demographic data to estimate Wood Duck population size in the Atlantic Flyway

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ABSTRACT

The U.S. Fish and Wildlife Service (USFWS) uses data from the North American Breeding Bird Survey (BBS) to assist in monitoring and management of some migratory birds. However, BBS analyses provide indices of population change rather than estimates of population size, precluding their use in developing abundance-based objectives and limiting applicability to harvest management. Wood Ducks (*Aix sponsa*) are important harvested birds in the Atlantic Flyway (AF) that are difficult to detect during aerial surveys because they prefer forested habitat. We integrated Wood Duck count data from a ground-plot survey in the northeastern U.S. with AF-wide BBS, banding, parts collection, and harvest data to derive estimates of population size for the AF. Overlapping results between the smaller-scale intensive ground-plot survey and the BBS in the northeastern U.S. provided a means for scaling BBS indices to the breeding population size estimates. We applied these scaling factors to BBS results for portions of the AF lacking intensive surveys. Banding data provided estimates of annual survival and harvest rates; the latter, when combined with parts-collection data, provided estimates of recruitment. We used the harvest data to estimate fall population size. Our estimates of breeding population size and variability from the integrated population model ($\bar{N} = 0.99$ million, SD $= 0.04$) were similar to estimates of breeding population size based solely on data from the AF ground-plot surveys and the BBS ($\bar{N} = 1.01$ million, SD $= 0.04$) from 1998 to 2015. Integrating BBS data with other data provided reliable population size estimates for Wood Ducks at a scale useful for harvest and habitat management in the AF, and allowed us to derive estimates of important demographic parameters (e.g., seasonal survival rates, sex ratio) that were not directly informed by data.

Keywords: Aix sponsa, Atlantic Flyway, Breeding Bird Survey, count data, harvest, integrated population model, recruitment, survival, Wood Ducks

Integración de datos demográficos y del Conteo de Aves Reproductivas para estimar el tamaño poblacional de *Aix sponsa* en la ruta migratoria atlántica

RESUMEN

El servicio de pesca y vida silvestre de los Estados Unidos usa datos del Censo de Aves Reproductivas (BBS, por sus siglas en inglés) para ayudar en el monitoreo y manejo de algunas aves migratorias. Sin embargo, los análisis del BBS producen índices de cambio poblacional en vez de estimados del tamaño poblacional, lo que no permite su uso en el desarrollo de objetivos basados en abundancia y limita su aplicabilidad al manejo de la caza. *Aix sponsa* es una especie de importancia para la caza en la ruta migratoria atlántica pero es difícil detectarla durante censos aéreos debido a que prefiere hábitats con bosque. Integramos los datos de conteos de *A. sponsa* obtenidos en censos de cuadrantes terrestres en el noreste de Estados Unidos con datos del BBS a lo largo de la ruta migratoria atlántica, datos de anillamiento, datos de recolección de partes y datos de caza para derivar estimados de tamaño poblacional para la ruta migratoria atlántica. Los resultados superpuestos entre los censos intensivos de cuadrantes terrestres a menor escala y los del BBS en el noreste de EEUU proveen una forma de expresar los índices del BBS en una escala relativa a los estimados de tamaño poblacional, y usamos estos factores de escala para estimar los resultados de BBS en porciones de la ruta migratoria atlántica que carecen de censos intensivos. Los datos de anillamiento proveen estimados de supervivencia anual y tasas de caza, y cuando estos últimos se combinan con los datos de recolección de partes, se obtienen estimados de reclutamiento. Usamos los datos de caza para estimar el tamaño poblacional en otoño. Nuestros estimados de tamaño de la población reproductiva y de la variabilidad del modelo de población integrado ($\bar{N} = 0.99$ millones, DE $= 0.04$) fueron similares a los estimados del tamaño de la población reproductiva basados solamente en los datos de censos de cuadrantes terrestres de la ruta migratoria atlántica y del BBS ($\bar{N} = 1.01$ millones, DE $= 0.04$) entre 1998 y 2015. La integración de los datos del BBS con otros datos produjo estimados confiables del tamaño poblacional de *A. sponsa* a una escala útil para informar los niveles de caza y el manejo del hábitat en la ruta migratoria atlántica, y nos permitió derivar estimados de parámetros demográficos importantes (e.g. tasas de supervivencia estacional, proporción de sexos) que no son extraidos directamente de los datos.

Palabras clave: Aix sponsa, caza, Conteo de Aves Reproductivas, datos de conteos, modelos integrados de poblaciones, reclutamiento, ruta migratoria atlántica, supervivencia

INTRODUCTION

The Wood Duck (*Aix sponsa*) is a familiar and widely distributed waterfowl species that makes up a large percentage of the waterfowl harvest in the eastern U.S. (USFWS 2016a). The U.S. Fish and Wildlife Service (USFWS), in conjunction with Flyway Councils, promulgates harvest regulations for ducks at the Flyway scale (Figure 1). Joint Ventures and individual states set population and habitat goals for Wood Ducks at the Bird Conservation Region (BCR) and individual state scales. As a result, harvest and habitat management for Wood Ducks require abundance estimates at multiple spatial scales. Although large-scale intensive aerial surveys are conducted each spring over the breeding range of most ducks (i.e. the prairie pothole, parkland, and boreal forests throughout Canada and the north-central and far northeastern U.S.; USFWS 2015), Wood Ducks are not well represented in these surveys because they are difficult to observe from planes due to their affinity for densely forested areas during the breeding season and because the surveys do not cover a major portion of the Wood Duck breeding range (Bellrose and Holm 1994). To make up for this sampling weakness, a ground survey (the Atlantic Flyway Breeding Waterfowl Survey [AFBWS]; Heusmann and Sauer 2000, Sauer et al. 2014) is conducted each spring over a portion of the breeding range of Wood Ducks in the Atlantic Flyway (AF).

The North American Breeding Bird Survey (BBS; Sauer et al. 2003, 2017) spans the entire breeding range of Wood Ducks in the eastern U.S. Analysis of BBS data provides an index to population size that describes patterns of population change over time, but does not provide unbiased abundance estimates. The AFBWS, a systematic ground-based survey, provides an abundance estimate for Wood Ducks breeding in 11 states in the northeastern U.S. Zimmerman et al. (2015) used a hierarchical model to integrate survey data from the BBS and AFBWS to estimate Wood Duck breeding population size in the AF at the scale of individual states and BCRs. When aggregated to the AF scale, these estimates of population size yielded an overall mean similar to the estimated mean population size derived from a Lincoln–Petersen abundance estimator based on estimates of absolute harvest (from harvest surveys) and harvest rates (based on banding and encounter data; Alisauskus et al. 2009) of adult Wood Ducks in the AF. However, year-to-year fluctuations tended to be quite different, possibly because of sampling variance associated with each estimator, differential time steps (e.g., AFBWS/BBS = spring to spring, and harvest-based = fall to fall) and seasonal demographic rates, or bias in the harvest-based estimator due to annually varying migration from the Mississippi Flyway into the AF. Better inferences might be obtained by integrating survival and recruitment information with estimates of breeding population size and harvest through integrated population modeling, which could reduce bias and increase precision in estimates of abundance and demographic rates (Besbeas et al. 2005, Abadi et al. 2010, Kéry and Schaub 2012). Further, integrating multiple data sources could allow for the estimation of parameters that may be influencing population dynamics, but for which we do not have data to estimate directly (e.g., survival from spring to fall) and

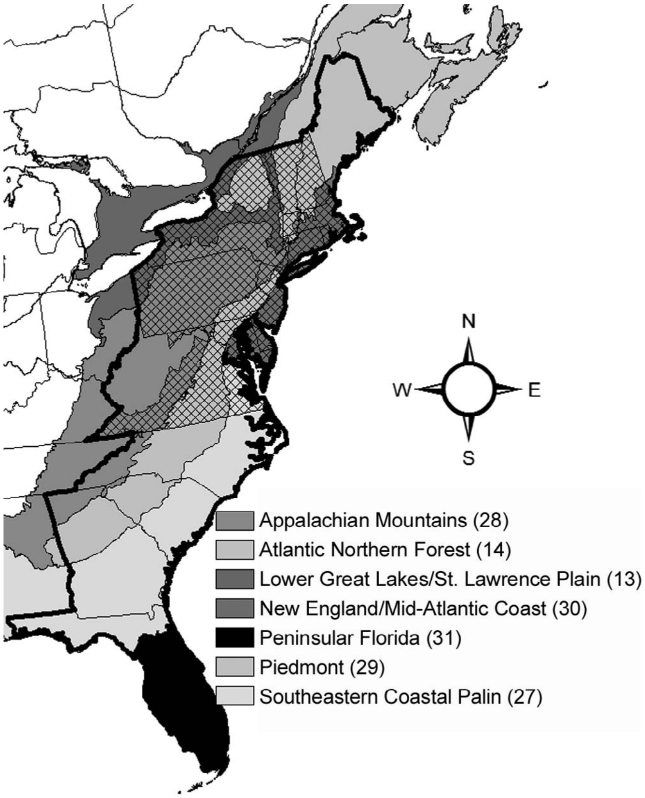

FIGURE 1. Bird Conservation Regions (BCRs) and spatial coverage of the Atlantic Flyway Breeding Waterfowl Survey (AFBWS; states with hatch marks) in the Atlantic Flyway. The Breeding Bird Survey (BBS) occurs in all states throughout the Atlantic Flyway.

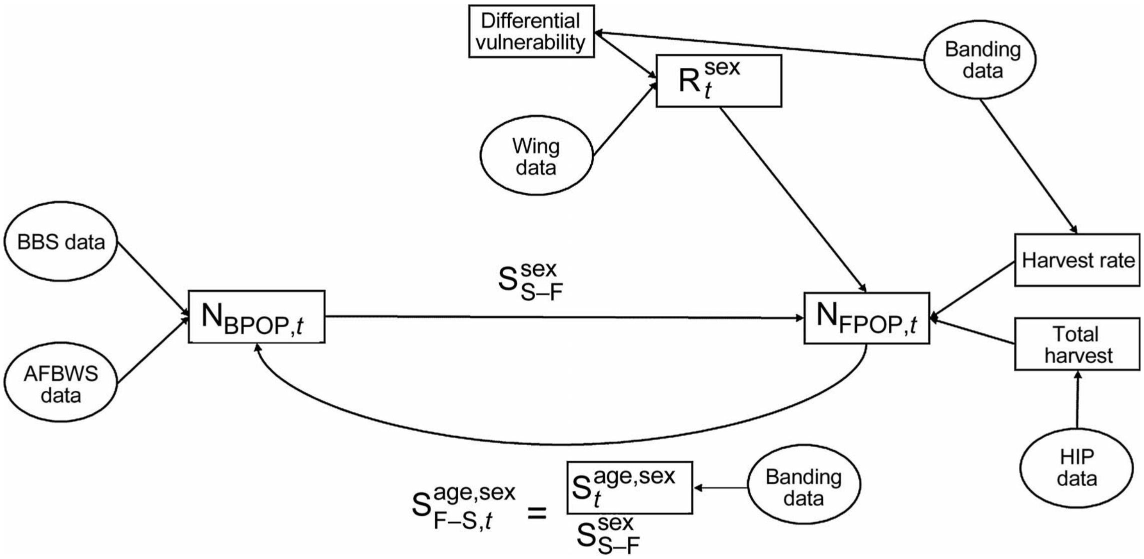

FIGURE 2. Full integrated population model and data used to estimate Wood Duck annual breeding population size ($N_{BPOP,t}$) in the Atlantic Flyway, 1998–2015. Ovals surround data sources and boxes surround parameters estimated from data. BBS = Breeding Bird Survey; AFBWS = Atlantic Flyway Breeding Waterfowl Survey; $N_{FPOP,t}$ = fall population size; S = survival (S = annual, S_{S-F} = Spring–Fall, S_{F-S} = Fall–Spring); and R = recruitment. Differential vulnerability refers to the vulnerability difference between juveniles and adults. Parameters are indexed by age (adult vs. juvenile), sex, and time (categorical year, *t*) effects when included in the model.

which may be important for reconciling differences in demographic rates estimated from different data sources (Abadi et al. 2010, Kéry and Schaub 2012). Here, we (1) update the integration of BBS and AFBWS data of Zimmerman et al. (2015; 1993–2013) with more recent data (1993–2015), and (2) integrate the combined BBS and AFBWS estimates with information from multiple monitoring programs to estimate a composite breeding abundance estimate for Wood Ducks throughout the AF from 1998 to 2015.

METHODS

Study Area

The U.S. portion of the AF spans the east coast from Florida to Maine (Figure 1). States from Virginia north to New Hampshire (excluding West Virginia) in the AF conduct waterfowl ground surveys (AFBWS) each spring within 1-km^2 plots established throughout each state. The AF encompasses all of BCRs 30 (New England/Mid-Atlantic Coast) and 31 (Peninsular Florida), and portions of BCRs 13 (Lower Great Lakes/St. Lawrence Plain), 14 (Atlantic Northern Forest), 27 (Southeastern Coastal Plain), 28 (Appalachian Mountains), and 29 (Piedmont) (Figure 1). Some portions of BCR 30 included salt marsh habitat, which we extracted from that BCR and analyzed separately for the AFBWS survey. All BCRs in the Atlantic Flyway included some overlap between AFBWS and BBS data except for Peninsular Florida.

Integrated Population Model

We developed a population model that integrated data on breeding population size (BBS and AFBWS data), survival (banding and encounter data), recruitment (harvest age ratio and differential vulnerability of adults and juveniles to harvest, from banding and encounter data), and fall population size (harvest and banding data) to jointly estimate abundance and demographic rates (Figure 2). These models can be useful in (1) assessing the overall consistency of the multiple data streams used in management, (2) estimating latent demographic parameters such as seasonal survival rates that are not directly estimable from available field data, and (3) providing more precise and likely less biased estimates of population size and demographic rates than if each data set were analyzed independently (Kéry and Schaub 2012). We used a discrete-time model with age and sex structure (Williams et al. 2002), with 2 age classes: juveniles and adults. Juveniles surviving to the following breeding season transitioned into the adult age class. Breeding adults that survive from spring to early fall (May to September) plus new recruits make up the fall population. Birds that survived to the following breeding season had to avoid death from both harvest and non-hunting mortality between fall and spring (Figure 2). For all parameters in the model, we specify age and sex cohorts with superscripts (AM = adult male, AF = adult female, JM = juvenile male, and JF = juvenile female), whereas subscripts indicate annual (*t*) or seasonal forms of parameters (BPOP =

breeding population size, FPOP = fall population size, S–F = spring to fall, and F–S = fall to spring).

We used a state-space modeling approach in a Bayesian hierarchical framework to estimate parameters within the model (Royle and Dorazio 2008, Kéry and Schaub 2012), and fit the model using Markov Chain Monte Carlo (MCMC) methods. Our integrated population model assumed that there was an unobserved true AF breeding population size ($N_{\text{BPOP},t}$) in year t that changed from year to year as a function of previous population size and demographic parameters, with normal process error on the log scale, and that the population was closed to immigration and emigration. This $N_{\text{BPOP},t}$ forms the mean of the observed population size from the integration of the BBS and AFBWS; it is distributed with means governed by demographic parameters and prior population sizes. We incorporated harvest data into the model, which can provide an estimate of population size during the early fall just after birds fledge (Otis 2006, Alisauskus et al. 2009). Specifically, we modeled changes in the latent, true population according to

$$N_{\text{BPOP},t} \sim \text{LogNormal}$$
$$\left(f \left[N_{\text{BPOP},(t-1)}, p_{(t-1)}, S^{\text{sex}}_{\text{S-F}}, \frac{S^{\text{age,sex}}_{(t-1)}}{S^{\text{sex}}_{\text{S-F}}}, R^{\text{sex}}_{(t-1)}, h^{\text{age,sex}}_{(t-1)}, H_{(t-1)} \right], \sigma^2_{\text{process}} \right)$$

where p = proportion of males in the breeding population, S = survival rate, R= recruitment (juveniles per adult), H = total harvest (numbers of birds), and h = harvest rate. We modeled the observation process as a function of the true underlying population size ($N_{\text{BPOP},t}$) based on the following relationship:

$$N^{\text{Observed}}_{\text{BPOP},t} \sim \text{Normal}\left(N_{\text{BPOP},t}, \sigma^2_{\text{sampling},t}\right)$$

where $\sigma^2_{\text{sampling}}$ was the sampling variance from the observed breeding population size estimates (see below).

We calculated an estimate of trend in breeding population size from 1998 to 2015 for the fully integrated population model using the definition described by Sauer and Link (2011):

$$B = \left(\frac{N_{\text{BPOP},2015}}{N_{\text{BPOP},1998}} \right)^{\frac{1}{2015-1998}}$$

We present the trend as percent growth per year (% = [B–1]×100). We were interested in comparing the trend calculated for the breeding abundance data to one expected from the demographic (survival and fecundity) data alone. Therefore, we calculated a trend based on just the demographic rates from 1998 to 2015 using a post-birth pulse, 2-age–class projection matrix. Assuming that fledged juveniles surviving the hunting season to the following breeding season transition into the adult age class, the characteristic equation is

$$\lambda_t = S^{\text{AF}}_t + S^{\text{JF}}_t \times R^{\text{F}}_t$$

We calculated the geometric mean of the λ_t and converted that to a percent change to compare with the trend in breeding abundance estimates (B) from the fully integrated model.

Breeding Population Size

We used a hierarchical model (Zimmerman et al. 2015) to estimate breeding population indices (birds per route) from the BBS data, and breeding population size from the AFBWS for strata (defined as the intersections of BCRs and states) throughout the Atlantic Flyway. We aggregated these estimates to the scale of BCRs where the BBS and AFBWS both provided data (i.e. overlap strata [OBCR]; e.g., BCR 28 in New York, New Jersey, Pennsylvania, Maryland, and Virginia contained both BBS and AFBWS data) and non-overlap strata (NBCR; e.g., BCR 28 in Georgia, North Carolina, and West Virginia contained only BBS data). We then calculated a single dimensionless scaling factor for each OBCR as the ratio of AFBWS population size estimates summed across years to the BBS indices summed across years. The scaling factors account for differences among the 2 platforms, including differences in detection rates between the BBS and AFBWS, bias associated with the roadside design of BBS routes, and reconciling the expansions used between the 2 surveys (i.e. BBS output is birds per route, whereas the AFBWS data are expanded from birds per area sampled to an abundance estimate). Therefore, the scaling factors relate the average index of birds per route to the total birds in a given region. After calculating the scaling factor, we multiplied the BBS indices in the NBCR by the scaling factor for the appropriate BCR to scale the indices to a population size estimate where AFBWS data were absent. The mean of the scaling factors across the BCRs was used to adjust the BBS indices for BCR 31 because no AFBWS data existed anywhere in that BCR. Specific details about the field and analytical methods for the BBS and AFBWS, as well as the integration of the 2 surveys, are described elsewhere (Heusmann and Sauer 2000, Sauer and Link 2011, Sauer et al. 2014, Zimmerman et al. 2015). We calculated trend estimates (B) based on just the AFBWS-BBS data from the 1993–2015 period to compare with published estimates from the 1993–2013 period.

Survival and Harvest Probabilities

We used banding and dead recovery data from the USGS Patuxent Wildlife Research Center Bird Banding Laboratory to estimate annual survival, recovery, and harvest rates of adult male, adult female, juvenile male, and juvenile female Wood Ducks. We based our analysis of banding and recovery data on pre-hunting–season banded birds (June–September), which were classified as normal wild-caught birds (bird status code 3), metal leg band only/control band in a reward band study/taken from artificial nest structure/spotlight (extra information codes 00, 04, 33, 70). All birds were given bands inscribed with either a toll-free number and mailing address, or a toll-free number and web address (band type codes 01, 08, 41, 53, and 81), and were banded in the U.S. portion of the AF. In addition, we filtered recovery data to include only birds found or shot dead (how obtained code 00, 01) during the hunting season.

We used the Brownie parameterization for dead recovery models (Brownie et al. 1985) to estimate annual survival and harvest probabilities from pre-season band-recovery information. We did not consider trends in annual estimates for demographic rates, so all time-varying models were categorical, where a subscript of t represented a model with a parameter for each year. Under this parameterization, the midpoint of the banding period defined the anniversary date for annual survival, representing the period from August 15 in year t to August 15 in year $t+1$. Our integrated population model incorporated various data sources entering the annual cycle at different periods of the year, so we needed to decompose the annual survival rates into their seasonal components. For example, our breeding population data were collected in May, so we needed to adjust those estimates to a fall flight (i.e. adults surviving from breeding season to the fall with probability S_{S-F}^{sex} plus new recruits in the fall population [see next section]) to reconcile those data with harvest-based estimates of the fall flight (Figure 2). We assumed that juveniles that survive the hunting season in the fall and the winter enter the subsequent breeding season as adults. Accordingly, we modeled survival from fall to spring with age- and sex-specific structure, whereas survival from spring to fall included sex structure but just one age class (adults). We did not have seasonal banding data to decompose annual survival rates $S_t^{age,sex}$ into seasonal components (S_{S-F}^{sex} and $S_{F-S,t}^{age,sex}$) to fit our integrated population data. We assumed that

$$S_t^{age,sex} = S_{S-F}^{sex} \times S_{F-S,t}^{age,sex}.$$

Therefore, if we know $S_t^{age,sex}$ and S_{S-F}^{sex} we can estimate $S_{F-S,t}^{age,sex}$. Because we had banding data to directly estimate $S_t^{age,sex}$ and no data to estimate S_{S-F}^{sex} directly, we assumed that spring to fall survival was temporally constant and used the breeding population data and fall flight to estimate the spring to fall survival as

$$S_{F-S,t}^{age,sex} = \frac{S_t^{age,sex}}{S_{S-F}^{sex}}.$$

We used reporting rates and their standard errors from Garrettson et al. (2014) to adjust recovery rates to estimate harvest rates for each cohort. Specifically, Garrettson et al. (2014) estimated Wood Duck reporting rates to be 0.73 (95% CI = 0.67–0.78), so we sampled reporting rates from a normal distribution with mean = 0.73 and variance = 0.00065 in each iteration of the MCMC updating. We calculated a concentration parameter for survival rates as a measure of relative dispersion (Link and Barker 2010:320):

$$\text{Concentration} = \frac{SD}{\sqrt{S \times (1 - S)}};$$

where SD = standard deviation and S = the estimated survival rate. We present the concentration parameter as an analogue to a coefficient of variation for binomial variables. We were interested in assessing the relative magnitude of annual variability of vital rates that was due to true temporal change in parameters (i.e. process variance) or sampling variance. Therefore, we used posterior distributions to decompose total variance of annual survival and harvest rates into process and sampling variance components following the approach outlined by Gould and Nichols (1998).

Recruitment

We used the methods described by Zimmerman et al. (2010) to derive sex-specific recruitment estimates using wings collected from the parts collection survey (USFWS 2016a) and the relative vulnerability of juveniles vs. adults to harvest (hereafter "differential vulnerability"), by sex, based on the harvest rates estimated above. Because our population model was cohort-specific, we estimated sex-specific recruitment estimates as

$$R_t^F = \frac{\frac{W_t^{JF}}{W_t^{AF}}}{\frac{h_t^{JF}}{h_t^{AF}}} \quad \text{and} \quad R_t^M = \frac{\frac{W_t^{JM}}{W_t^{AM}}}{\frac{h_t^{JM}}{h_t^{AM}}}$$

where W = number of wings collected and h = harvest rate, both of which are indexed by age and sex. Similar to the survival analysis, we did not consider trends, so parameters indexed by t represent categorical year effects. Units for the recruitment estimates are juvenile females per adult female and juvenile males per adult male. We estimated the total number of recruits for each sex by multiplying these recruitment rates by the total number of adult females and males in the fall population (e.g., $N_{FPOP,t}^{JF} = N_{FPOP,t}^{AF} \times R_t^F$). We calculated the total number of adult males and females in the fall population from the breeding population size, estimated proportion of males in the breeding population, and the survival from spring to fall:

$$N^{AM}_{FPOP,t} = N_{BPOP,t} \times p_t \times S^{M}_{S-F}$$

and

$$N^{AF}_{FPOP,t} = N_{BPOP,t} \times (1 - p_t) \times S^{F}_{S-F}$$

We calculated all p_t from the 1999–2015 period using the number of male and female Wood Ducks expected to survive to the following breeding season based on the fall flight (see below), harvest rates, and survival from fall to the following breeding season. We did not have estimates of p_{1998} from the model because we did not have data for the previous year's population size and demographic rates, so we estimated that as a latent parameter in the population model.

Fall Flight

We combined information from breeding population size, recruitment, spring-to-fall survival, and total harvest data (USFWS 2016a) derived from the Harvest Information Program (HIP) to estimate the fall population size of Wood Ducks. Our model and the harvest data provided 2 estimates of fall flight: the cohort-specific estimates of $N^{age,sex}_{FPOP,t}$ (estimated from breeding population size, proportion of males in the breeding population, spring-to-fall survival, and recruitment) described in the previous section and a harvest-based metric defined as the total harvest (H_t) of birds divided by the harvest rate (the Lincoln–Petersen estimator; Otis 2006, Alisauskus et al. 2009). To integrate these 2 estimates, we assumed the following likelihood for the harvest data:

$$H_t \sim \text{LogNormal}\left(\sum_{\text{cohort}} (N^{cohort}_{FPOP,t} \times h^{cohort}_t), \sigma^2_H\right)$$

The summation for the mean in the log-normal likelihood comes from the relationship: $H_t = N_{FPOP,t} \times h_t$. We adjusted the raw harvest data for bias associated with the HIP survey (Padding and Royle 2012) by multiplying total harvest estimates for each year by a bias correction sampled from a normal distribution with the mean and variance specified by Padding and Royle (2012; 0.73, 95% CI = 0.71–0.75).

Fitting the Model

We assumed vague priors for all parameters informed by data, and informed priors for parameters without data. We specified vague beta priors for annual survival and harvest rate parameters (i.e. dbeta[1,1]) and vague inverse gamma priors for $\sigma^2_{process}$ and σ^2_H (i.e. dgamma[0.001,0.001]). LeMaster and Trost (1994) estimated Wood Duck summer survival rates and reported a mean of 0.58 in the southern portion of their range and 0.85 in the northern portion. However, estimates varied widely among years and regions with values ranging from 0.44 to 1.00. A seasonal survival probability of 0.44 is likely an underestimate given that best estimates of annual survival for females are generally >0.50 (Nichols and Johnson 1990, Dugger et al. 1999, Kennamer and Hepp 2000). Therefore we assumed a uniform prior between 0.70 and 0.99 for spring to fall survival rates for males and females to accommodate the wide range of values observed in that study but still encompass biologically realistic values. We did not have data to directly inform p_{1998}, so we assumed a uniform prior between 0.5 and 0.75 based on information from Mallards (*Anas platyrhynchos*; USFWS 2016b) and treated it as a latent parameter in the model.

We used program JAGS (Plummer 2003) to fit our Wood Duck integrated population model. We limited our model to 1998 to the present because HIP was not initiated until 1998. We scaled all abundance and total harvest data to millions to help improve convergence. We ran 3 chains for 500,000 iterations and used 495,000 as a burn-in. We assessed convergence using the $\hat{R}$ statistic and assumed values <1.1 indicated adequate convergence (Gelman and Hill 2007). We saved the coda files to calculate correlations among parameters within the integrated population model (Kéry and Schaub 2012). We were specifically interested in comparing which demographic parameters correlated with population growth rates (Schaub et al. 2013) and whether individual demographic rates may have been correlated.

RESULTS

Population abundance estimates for Wood Ducks based on the integration of the BBS and AFBWS (without survival, recruitment, and harvest information) averaged 1.00 million between 1993 and 2015 with weak evidence of a slightly increasing trend (0.46% per year; 95% CI = –0.28% to 1.15%). The mean population abundance based on BBS and AFBWS between 1998 and 2015, which was used in the fully integrated population model, averaged 1.01 million with a similar trend as 1993–2015 (Figure 3). These abundance estimates were fairly precise with the mean CV of annual estimates = 13.15%. We observed similar trends between the AFBWS and BBS trends in most BCRs where the 2 surveys overlapped (Appendix Figure 6). The scaling factors (i.e. ratio of the summed BBS indices among years to the summed AFBWS abundance estimates among years) among most BCRs were also similar (Appendix Figure 7), with the mean scaling factor = 56.47 (95% CI = 45.23–70.38). The only exception was BCR 27 (Southeastern Coastal Plain), which had a scaling factor that was 70% smaller than the mean.

On average, 1,563 (SD = 433) adult male, 1,087 (SD = 301) adult female, 2,207 (SD = 569) juvenile male, and 1,907 (SD = 480) juvenile female Wood Ducks were

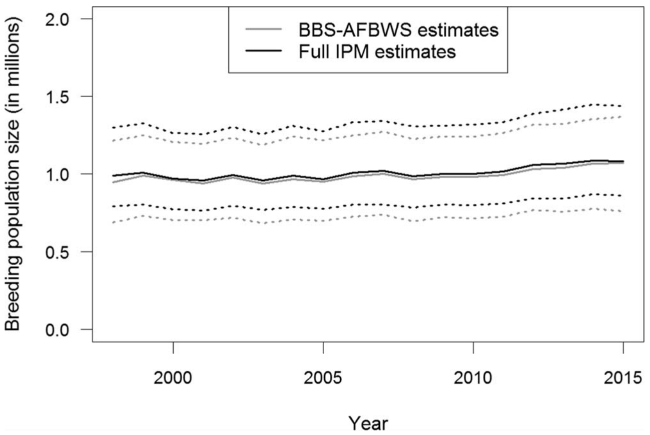

FIGURE 3. Population size estimates of Atlantic Flyway breeding Wood Ducks derived from (1) the original hierarchical model (Zimmerman et al. 2015), which integrates data only from the Breeding Bird Survey (BBS) and Atlantic Flyway Breeding Waterfowl Survey (AFBWS); and (2) the new integrated population model (Full IPM), which integrates both sets of survey data with demographic (e.g., survival and recruitment) and harvest data, 1998–2015.

banded each year between 1998 and 2015 in the AF. The total number of direct and indirect recoveries averaged 263 (SD = 100) adult males, 107 (SD = 43) adult females, 428 (SD = 175) juvenile males, and 243 (SD = 91) juvenile females per year. Based on these data, harvest rates appeared to increase for all cohorts beginning in 2009, but were greater for males than females and greater for juveniles within each sex class ($\overline{h^{AM}} = 0.11$, $\overline{h^{JM}} = 0.14$, $\overline{h^{AF}} = 0.07$, $\overline{h^{JF}} = 0.11$; Figure 4). Most of the annual variation in harvest rates appeared to be process variance (74%, 63%, 75%, and 56% for adult males, adult females, juvenile males, and juvenile females, respectively) rather than sampling variance. Estimated survival rates of males were 15% higher than those of females overall, but there appeared to be very little difference in survival between ages within sex classes ($\overline{S^{AM}} = 0.59$, $\overline{S^{JM}} = 0.59$, $\overline{S^{AF}} = 0.51$, $\overline{S^{JF}} = 0.52$; Figure 4). Most of the annual variation in survival was attributable to process variance for adult males (63%), adult females (68%), and juvenile females (62%), and sampling variance for juvenile males (59%). The relatively high proportion of sampling variance for juvenile males was surprising given the large number of bands released and recovered compared to those for other cohorts.

The USFWS received an average of 248 (SD = 64) adult male, 330 (SD = 72) juvenile male, 119 (SD = 36) adult female, and 222 (SD = 50) juvenile female wings of Wood Ducks harvested in the AF. We estimated the relative vulnerability of juveniles to adults to harvest (differential vulnerability; DV) annually and observed that, on average, juvenile females tended to be more vulnerable to harvest ($\overline{DV} = 1.55$ JF:AF) than juvenile males ($\overline{DV} = 1.35$ JM:AM; Appendix Figure 8). During most years, estimates of recruitment averaged slightly higher for females than males ($\overline{R^{F}} = 1.27$ JF:AF, versus $\overline{R^{M}}$ 1.03 JM:AM; Figure 5).

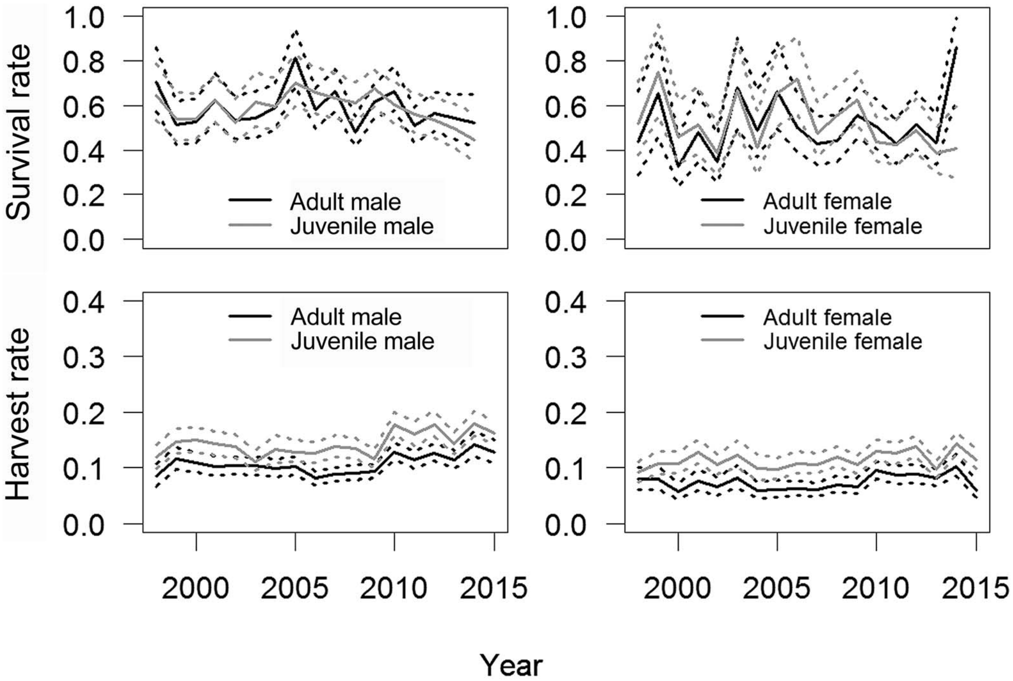

FIGURE 4. Annual survival (top 2 panels) and harvest rate (bottom 2 panels) estimates for adult and juvenile male and female Wood Ducks in the Atlantic Flyway, 1998–2015, derived from the integrated population model.

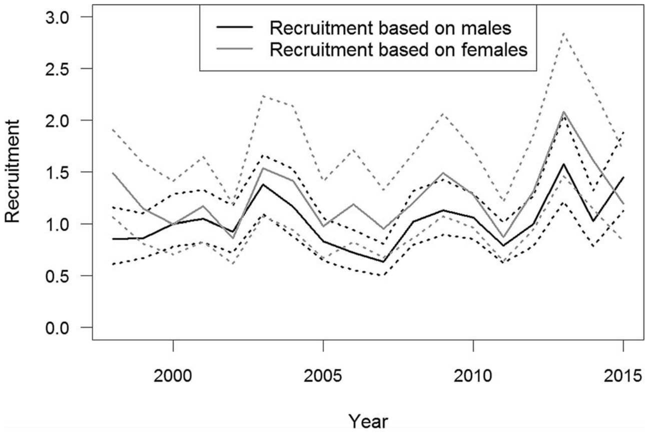

FIGURE 5. Annual recruitment estimates (male or female juveniles fledged per adult male or female, respectively) for Wood Ducks in the Atlantic Flyway, 1998–2015.

TABLE 1. Prior and posterior distributions for Wood Duck population parameters derived from an integrated population model and not directly informed by data in the Atlantic Flyway, 1998–2015.

Parameter [a]	Prior	Posterior median (95% CI)
p_{1998}	Uniform (0.50−0.75)	0.62 (0.50–0.74)
S^{F}_{S-F}	Uniform (0.70−0.99)	0.84 (0.71–0.98)
S^{M}_{S-F}	Uniform (0.70−0.99)	0.83 (0.71–0.98)
$\sigma^2_{Harvest}$	Gamma (0.001,0.001)	2.39 (1.26–5.06)
$\sigma^2_{process}$	Gamma (0.001,0.001)	12.07 (6.63–25.03)

[a] p = proportion males in the breeding population, S = survival, σ^2 = variance.

Although recruitment estimates have fluctuated from year to year, we did not observe an apparent trend in estimates for females or males (Figure 5).

The final integrated model incorporated the above demographic rates, total harvest, and estimates of 2 parameters not influenced directly by data (p_{1998} and S^{Sex}_{S-F}). Total annual harvest adjusted for bias ranged from approximately 193,860 to 330,731 in the AF between 1998 and 2015. Survival from spring to fall for adult male and female Wood Ducks was 0.83 (SD = 0.08) and 0.84 (SD = 0.08), respectively, and changed little from their prior distributions (Table 1). The estimated proportion of males in the breeding population averaged 0.63 and ranged from 0.51 to 0.69 from 1998 to 2015 (Appendix Figure 9). The posterior estimate of $p_{1998} = 0.62$ (95% CI = 0.50–0.74) was similar to the mean estimate and also did not appear to change much from the prior distribution (Table 1).

Integrating the different components of the model did not result in estimates appreciably different from the original abundance estimates based solely on the BBS-AFBWS data (Figure 3). The mean annual growth rate for the fully integrated population model from the 1998–2015 period was 0.66% yr^{-1} (95% CI = –1.69% to 3.01%), which was lower than the mean annual percent change based on survival and recruitment estimates ($\bar{x} = 14.23\%$, 95% CI = –9.85% to 45.04%). The mean fall abundance estimate using a Lincoln–Petersen estimator alone (i.e. using just harvest and harvest rate data) was greater (= 2.44 million) than the estimate of fall population size derived from spring breeding population (BBS-AFBWS), survival, and recruitment ($\overline{N_{FPOP}} = 1.72$ million; Appendix Figure 10), but incorporating the harvest data into the full integrated model did not appear to increase the overall fall population size in the full integrated population model. We found no evidence for correlations among the demographic (i.e. survival and recruitment) rates and annual growth rate (Appendix Figure 11A). We detected some evidence of weak negative correlations between some of the survival and recruitment estimates, and positive correlations between female-based recruitment and adult female survival and recruitment based on male and female data (Appendix Figure 11B).

DISCUSSION

Integrating the banding, recruitment, and harvest data provided estimates of breeding population size, overall trend, and annual fluctuations that were similar to the estimated time series based only on the BBS-AFBWS data. This suggests that the integrated BBS-AFBWS abundance estimates provided the strongest signal in the data or that fluctuations and trends associated with the demographic data were similar to the abundance data. The demographic data alone suggested a greater annual growth rate and higher annual variability than the BBS-AFBWS abundance estimates, so we suspected that integrating these components would have increased the overall trend and annual fluctuations in breeding population size compared to the raw breeding population data used in the model. Kéry and Schaub (2012) noted a similar relationship and concluded that their raw count data had relatively low sampling error, which led to that data source dominating the overall estimates. Neither survival nor recruitment was correlated with annual breeding population size estimates, and CVs for the demographic parameters were similar to CVs of the raw breeding population size. Therefore, the lack of a greater trend (as estimated from survival and recruitment alone) and lack of greater annual variability in the overall integrated estimates may be due to (1) negative correlations between survival and recruitment (e.g., tradeoffs between survival and reproduction in a population that is regulated by density dependence; Williams 1966, Bleu et al. 2016); (2) information from the AFBWS-BBS breeding population estimate (i.e. $N^{Observed}_{BPOP,t}$) providing the strongest signal among data streams; or (3) absorption of annual variation from the demographic parameters into the spring–fall survival estimate, which was not directly informed by data. Ultimately, however, we are encouraged that the full integrated population model provides similar breeding abundance estimates to the BBS-AFBWS data alone, and we suggest that incorporating the demographic data helps to justify the assumptions made in applying the abundance estimates to regions without AFBWS data.

We revised the full time series (1993–2015) of the population abundance estimate based on the integration of BBS-AFBWS data before combining with demographic rates. Our estimate of trend for the revised data is similar to the previous estimate derived for 1993–2013 (0.66%, 95% CI = –0.28% to 1.54%; Zimmerman et al. 2015). Despite the similarities in trend, we note that our overall time series of point estimates of population size were approximately 20% lower on average, which we attributed to 2 main factors. First, the scaling factor used to adjust BBS indices to the scale of abundance estimates derived from the AFBWS for BCR 29 was almost one-third of the original estimate in Zimmerman et al. (2015) and is much more precise and consistent with the other regions in the revised analysis. We suspect that the relative change in the scaling factor for BCR 29 was associated with the relatively small sample size of AFBWS plots in that BCR compared to other BCRs, which could lead to relatively large changes with a small addition of data. Second, portions of BCR 28 were inadvertently included in the southern section in the original analysis when strata estimates were aggregated to the larger scale for the BBS part of the model. Both of these factors reduced population size estimates in the southern portion of the flyway.

Harvest-based estimates of population size, when integrated with survival and recruitment information, had little influence on breeding population size in the integrated model, even though harvest-based estimators of population size indicated higher population sizes (during fall) during most years and more annual variability. This higher annual variation may be due to year-to-year differences in the spring-to-fall survival rates or reflect the imprecision in the estimates derived from data streams used in the analysis. Differences in scale and representativeness of both banding and harvest data can complicate the calculation of Lincoln–Petersen abundance estimates based on the ratio of total harvest to harvest rate. In addition, net immigration into or emigration out of the area used to produce the estimate can introduce bias (Alisauskas et al. 2009). In our case, we used harvest estimates from the AF and band recovery data from birds banded in the AF. The scales of these 2 datasets are appropriately matched. However, a fairly coarse analysis of direct and indirect band recoveries suggests that there is considerable net immigration by birds banded in the Mississippi Flyway into the Atlantic Flyway, especially by males (up to 40%), and especially those banded in the south (P. R. Garrettson, personal observation). Birds immigrating from the Mississippi Flyway to the Atlantic would be represented in the estimate of absolute harvest (H), but not in the sample of banded birds (Atlantic Flyway only) used to calculate harvest probability (h), resulting in a Lincoln–Petersen estimate that is biased high. We plan to further examine Wood Duck banding and recovery data for evidence of differential net movements among flyways and, if necessary, develop the adjustments needed to calculate an unbiased Lincoln–Petersen estimate for AF Wood Ducks (Alisauskas et al. 2014). Another possibility might be to extend our BBS-AFWBS model to the Mississippi Flyway, and couple that with a Lincoln–Petersen estimate and integrated population model that encompasses both flyways.

Wood Ducks were thought to be overharvested at the turn of the century (Bellrose 1976), so for much of the 20th century they were managed conservatively. From 1962 to 2007, the Wood Duck daily harvest limit was 2 birds per hunter per day in the Atlantic, Mississippi, and Central flyways, regardless of season length or the overall daily duck harvest limit, both of which fluctuated over this time frame. In 2008, the Wood Duck daily harvest limit was raised from 2 to 3 birds, based on an assessment that suggested the expected increase in harvest rate would not exceed Wood Duck harvest potential (Balkcom et al. 2010). The increase in adult male harvest rates is consistent with the 13% increase predicted by Balkcom et al. (2010). In addition, the pattern of higher increases in juvenile harvest than in adults in response to liberalizing harvest regulations is consistent with patterns seen historically in response to longer seasons (Kelley 1997). The overall pattern of higher harvest probabilities for males than females, and higher for juveniles than adults, is also consistent with previous work (Kelley 1997).

Wood Duck survival and recruitment rates vary spatially (Bellrose and Holm 1994), so a direct comparison to previous studies is difficult at the scale of our analysis. Our observed annual survival of Wood Ducks was higher for males than for females, which is similar to previous findings (Nichols and Johnson 1990, Otis and Dukes 1995), including slight declines in survival since the Wood Duck harvest limit was increased in 2008. Nichols and Johnson (1990) noted that survival rates were higher for adults than for juveniles in the northern portion of the AF, but the age classes had similar survival rates in the southern portion of the AF. Our observation of similar survival rates between age classes may reflect our estimation of survival at a larger, flyway scale that encompasses both northern and southern birds. Over the timeframe we examined, female age ratios were higher on average than male age ratios, but they tended to track each other over time, without an apparent trend. The lower male age ratios and lack of trend that we observed suggests that the sex ratio of adults is male-biased but now relatively stable. The higher variance of female age ratio estimates is likely due to a combination of lower sample sizes and potentially higher variability in female survival during the breeding season (Davis et al. 2007). Bellrose and Holm (1994) used the same methods to estimate AF-wide estimates of recruitment and observed a mean of 1.54 juvenile females per adult female from 1966 to 1985, suggesting higher recruitment during that period compared to our study period. Wood Duck densities were likely much lower during that earlier time frame, as the BBS suggests rapidly increasing trends in the Atlantic, Mississippi, and Central flyways during the 1980s and early 1990s, which likely explains those higher recruitment rates.

The posterior distributions for spring to fall survival and the proportion of males derived from the integrated population model did not change much compared to the prior distributions. These 2 parameters were the only ones not directly informed by data. Abadi et al. (2010) conducted simulations to assess the performance of integrated population models and noted that parameters not directly estimated from data were unbiased. LeMaster and Trost (1994) estimated summer survival for Wood Ducks in the northern and southern portion of the eastern U.S. (Mississippi and Atlantic Flyway) and found that estimates were higher in the northern portion of the flyway and varied among years. Their mean estimates of summer survival over all regions and years were about 80% for males and 72% for females. These estimates are lower than our spring-to-fall survival estimates, but difficult to compare because of differences in spatial coverage and time periods. A targeted effort to estimate spring-to-fall survival directly could help inform whether our latent estimates are biased. Further, because we suspect that the latent estimate of spring-to-fall survival may be influenced by differences in fall flight estimates derived from the breeding and harvest data, independent data on spring-to-fall survival could provide a better assessment of the relative contribution of these 2 estimates. We had hoped the other data streams in the model would help provide more precise posterior estimates of the latent parameters (Kéry and Schaub 2012), but the time series is not long enough or there is not enough variability in the overall dynamics to inform these parameters.

The BBS is a spatially expansive and intensive survey for all birds that is conducted each year but the counts are only indices of abundance, which can be of limited utility. The wide coverage and large sample sizes, however, make the BBS an extremely valuable survey for monitoring birds when the limitations imposed by the index counts can be overcome using additional information. Overlap between the BBS and other surveys can provide a means to convert the BBS indices to population size estimates over a variety of scales that are important for management. For example, the abundance estimates based on the integrated BBS, AFBWP, and demographic data that we present in this paper will likely be used to inform duck harvest management regulations in the Atlantic Flyway (F. A. Johnson personal communication). Similarly, BBS data for the Golden Eagle (*Aquila chrysaetos*) have been integrated with aerial survey data (Millsap et al. 2013) to support the Environmental Impact Statement for the eagle rule revision (USFWS 2016c). Runge et al. (2009) developed abundance estimates for Black Vultures (*Coragyps atratus*) by making assumptions about area sampled and bird activity patterns that have been used to inform levels of lethal and nonlethal control. We suggest that applying methods that we presented here will allow scientists to extract more reliable information from the BBS, making its use in management more rigorous and defensible.

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Ethics statement: We conducted this study in compliance with all applicable USGS study design and review protocols.

Author contributions: GSZ and JRS developed the idea and led the project. GSZ, JRS, GSB, and PKD developed the model and analytical techniques. GSZ and PRG wrote the original draft and all authors substantially edited the manuscript.

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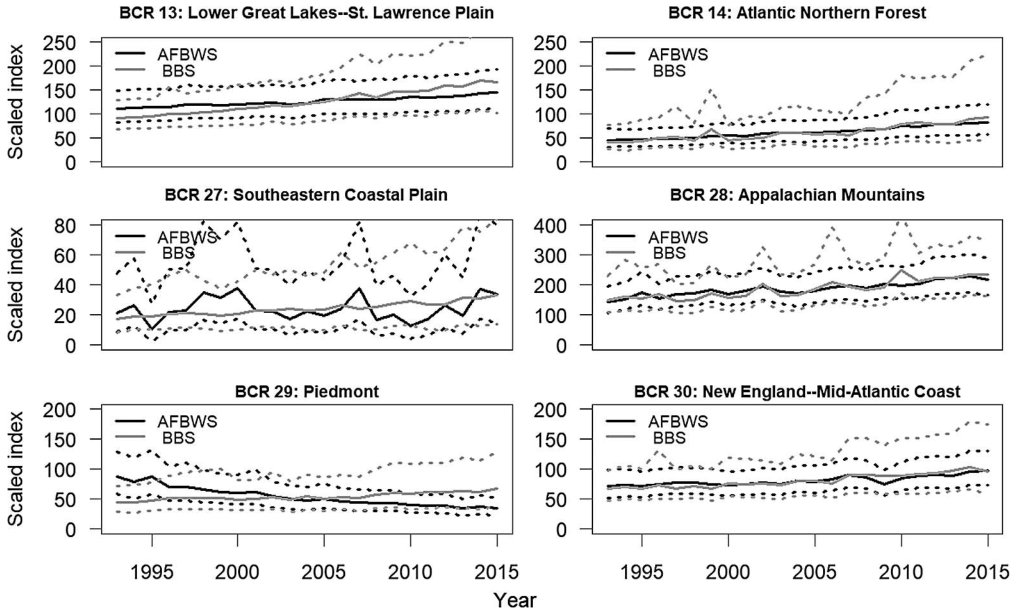
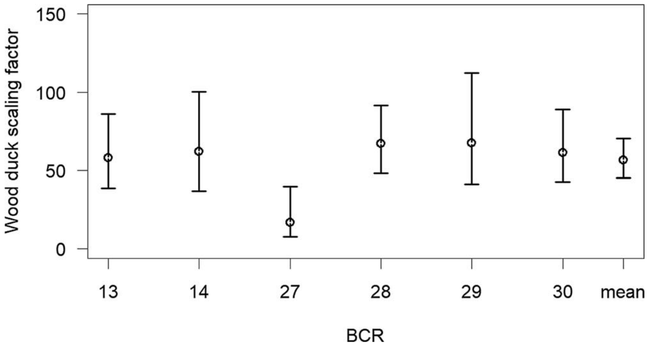
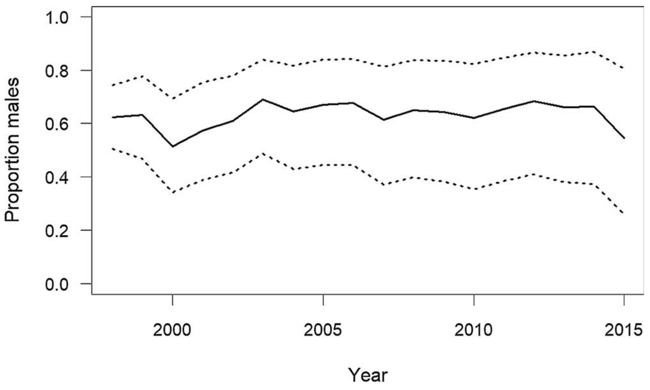


APPENDIX FIGURE 6. Comparison of trends in Wood Duck populations based on the Atlantic Flyway Breeding Waterfowl Survey (AFBWS) and the Breeding Bird Survey (BBS) where the 2 surveys overlap in Bird Conservation Regions within the Atlantic Flyway, 1998–2015. The BBS indices were arbitrarily scaled to the level of the AFBWS data (in 1,000s) so that the time series from each survey could be plotted together for comparing trends.

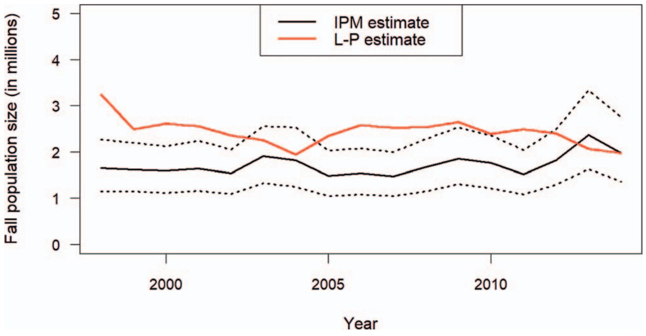


APPENDIX FIGURE 7. Adjustment factors estimated for scaling Breeding Bird Survey indices to population estimates based on Atlantic Flyway Breeding Waterfowl data by Bird Conservation Regions (BCR) in the Atlantic Flyway. BCR 13 = Lower Great Lakes/St. Lawrence Plain, 14 = Atlantic Northern Forest, 27 = Southeastern Coastal Plain, 28 = Appalachian Mountains, 29 = Piedmont, and 30 = New England/Mid-Atlantic Coast.

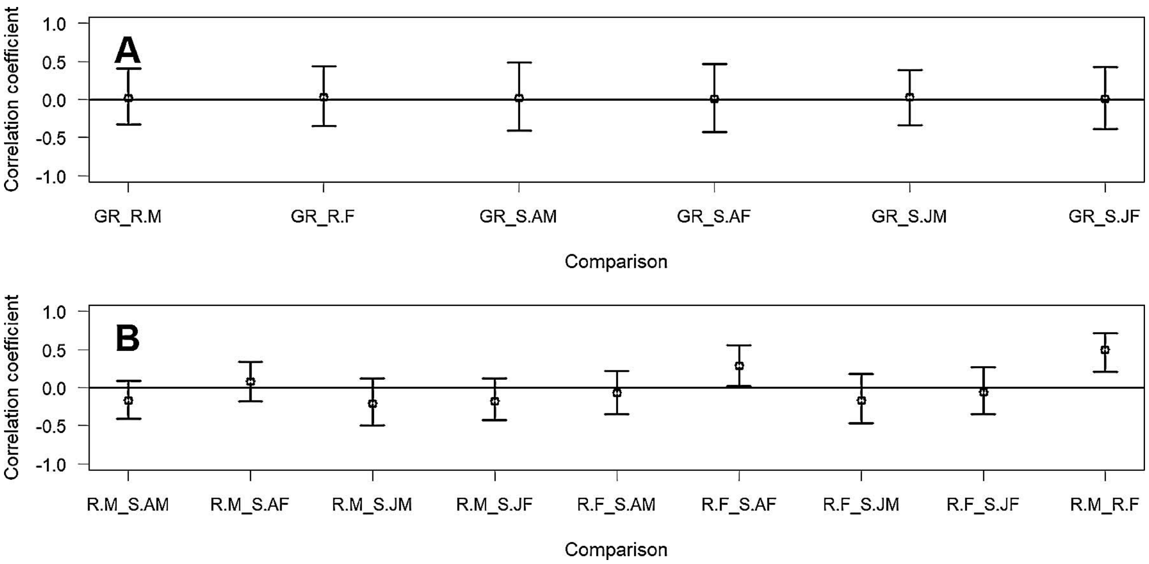
APPENDIX FIGURE 8. Estimates of annual differential vulnerability to harvest (juveniles relative to adults) for male and female Wood Ducks in the Atlantic Flyway, 1998–2015.



APPENDIX FIGURE 9. Estimated annual proportion of males in the breeding population of Wood Ducks in the Atlantic Flyway, 1998–2015.



APPENDIX FIGURE 10. Estimated fall population size of Wood Ducks in the Atlantic Flyway based on the integrated population model (IPM) and Lincoln–Petersen estimator (L-P), 1998–2014.



APPENDIX FIGURE 11. Correlations between parameters derived from integrated population model for Wood Ducks in the Atlantic Flyway, 1998–2014. (**A**) Correlations between growth rate (GR) and demographic rates (R.M = recruitment estimate based on males, R.F = recruitment estimate based on females, S.AM = adult male survival, S.AF = adult female survival, S.JM = juvenile male survival, and S.JF = juvenile female survival). (**B**) Correlations among demographic rates (R.M = recruitment estimate based on males, R.F = recruitment estimate based on females, S.AM = adult male survival, S.AF = adult female survival, S.JM = juvenile male survival, and S.JF = juvenile female survival).