Disentangling data discrepancies with integrated population models

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Abstract. A common challenge for studying wildlife populations occurs when different survey methods provide inconsistent or incomplete inference on the trend, dynamics, or viability of a population. A potential solution to the challenge of conflicting or piecemeal data relies on the integration of multiple data types into a unified modeling framework, such as integrated population models (IPMs). IPMs are a powerful approach for species that inhabit spatially and seasonally complex environments. We provide guidance on exploiting the capabilities of IPMs to address inferential discrepancies that stem from spatiotemporal data mismatches. We illustrate this issue with analysis of a migratory species, the American Woodcock (*Scolopax minor*), in which individual monitoring programs suggest differing population trends. To address this discrepancy, we synthesized several long-term data sets (1963–2015) within an IPM to estimate continental-scale population trends, and link dynamic drivers across the full annual cycle and complete extent of the woodcock's geographic range in eastern North America. Our analysis reveals the limiting portions of the life cycle by identifying time periods and regions where vital rates are lowest and most variable, as well as which demographic parameters constitute the main drivers of population change. We conclude by providing recommendations for resolving conflicting population estimates within an integrated modeling approach, and discuss how strategies (e.g., data thinning, expert opinion elicitation) from other disciplines could be incorporated into ecological analyses when attempting to combine multiple, incongruent data types.

Key words: American Woodcock; annual cycle; band-recovery; data integration; data integration for population models Special Feature; harvest; singing-ground survey.

INTRODUCTION

Accurate estimation of population parameters is essential to evaluate ecological theories, determine extinction risks, manage threats, adjust monitoring schemes, and predict responses to future environmental or management scenarios (Barlow 1995, Link and Sauer 2002, Hostetler and Chandler 2015). Yet, information on population dynamics and trends is fragmentary for many species, and can therefore be biased because of limited data across species' ranges and annual life cycles.

Few survey methods provide the geographic and temporal coverage needed for range-wide monitoring of vital rates. Studies that are conducted at broad spatial scales may lack consistent sampling effort and/or be minimally informative of demographic parameters (Davis et al. 2014, Zipkin and Saunders 2018). As a result, incomplete data are often used for estimation, prediction, and decision-making because they represent the best available information (Walsh et al. 2004, Grose 2014). Development of sound ecological theory and conservation strategies can be undermined if inferences stem from inaccurate parameter estimates resulting from the analysis of biased or incomplete data.

Integrated population models (IPMs) provide a flexible framework that can accommodate spatially or temporally incomplete data on abundance and population vital rates. IPMs incorporate disparate data types

(e.g., census, mark–recapture, and productivity) into a single, unified, dynamic model of the target population that can be used to simultaneously estimate population trajectories and the demographic processes that produce them (Besbeas et al. 2002, Schaub et al. 2007, 2015). By incorporating all available data on a population, IPMs overcome several limitations of independent analyses and account for multiple sources of uncertainty due to data limitations or environmental variation. IPMs are regularly used to compensate for data deficiencies, such as integrating locally sparse data from multiple study sites or sub-populations, enabling estimation of regional or metapopulation trajectories (Schaub et al. 2007, 2015, Brown and Collopy 2013, Davis et al. 2014). Simultaneously analyzing multiple data sets within an IPM can also address or reveal discrepancies among data sources (Maunder et al. 2006, Carvalho et al. 2017), in which two or more data sets provide differing inferences about a model state or process (Maunder and Piner 2017). Although inconsistencies in estimated population trajectories between survey methods are fairly common in natural populations, the use of IPMs to accommodate data discrepancies, as compared to deficiencies, has received much less attention (Maunder et al. 2017). The typical solution to data conflict is the elimination or statistical down weighting of the conflicting data sources (Maunder and Piner 2017). However, this approach does not resolve the underlying cause(s) of data discrepancies and may lead to incomplete or misleading population inferences (Wang et al. 2015), particularly when there is feedback among demographic processes. Synthesizing data sets that may describe separate population processes across space and time offers a powerful approach for resolving data inconsistencies by directly sharing information between conflicting data sets, rather than conducting post hoc comparisons of results from analyses using individual data sources. In this way, parameter estimates represent a weighted compromise between all available data sources.

Data discrepancies in population inferences can arise for several reasons. Inconsistencies could be introduced within the data collection process, such as non-random sampling in space or among ages/stages within a population. For example, due to the unstructured nature of some volunteer-based sampling programs (i.e., surveys can be conducted wherever and whenever the individual wants), biases can arise from variable survey effort or survey inconsistencies over time (Tulloch et al. 2013). Integrated modeling approaches can only partly resolve such biases; combining multiple data sets can dilute, but not eliminate, the inherent bias of a single data set (Nilsen and Strand 2018). Other discrepancies are the result of spatial or temporal variability in demographic processes across geographic and/or temporal extents. For example, census data from the North American Breeding Bird Survey (BBS), the Audubon Christmas Bird Count (CBC), and migration watch sites suggest a recent decline in abundance of American kestrels (*Falco*

sparverius sparverius), but population growth rates derived from these censuses vary across the subspecies' range (Wommack et al. 2015). In other systems, cross-scale interactions of both spatial and temporal variability may contribute to inconsistent population trends, as exemplified by the eastern North American monarch butterfly (*Danaus plexippus*) population. Census data on monarchs at their overwintering grounds in Mexico indicate a 19-yr downward trend (Ries et al. 2015). However, trend estimates from count data at summer Midwestern U.S. breeding sites have been inconsistent; some studies suggest declines in the northern extent of their breeding range (Stenoien et al. 2015, Saunders et al. 2017) while others have failed to detect any significant decreases in adult counts (Ries et al. 2015, Inamine et al. 2016). Issues of spatial scale mismatches may also lead to data set discrepancies, given that fine-scale indices may show contrasting trends compared to large-scale indices. Bobolinks (*Dolichonyx oryzivorus*), a grassland bird of conservation concern in North America, experienced significant provincial-level declines across much of their breeding range in Canada, according to data from the BBS and the Committee on the Status of Endangered Wildlife in Canada. However, recent work demonstrated that a majority of local bobolink populations have not strongly declined at finer scales over the same temporal interval (Ethier and Nudds 2015), suggesting a more optimistic trend than that obtained from analyses at broader spatial scales.

Here, we illustrate issues of data discrepancies with a case study of American Woodcock (*Scolopax minor*), a migratory game species of conservation concern in the United States. Continental-scale surveys of displaying male American Woodcocks indicate declines of approximately 0.6–1.1% per year in the central and eastern populations (Seamans and Rau 2017). However, estimates of annual population change based on fecundity and survival rates, as measured from harvest and banding data (Krementz and Bruggink 2000, Zimmerman et al. 2010), suggest that woodcock populations should be declining by ~17% per year (see Appendix S1 for more details). This discrepancy has yet to be addressed, precluding understanding of range-wide dynamics and development of robust management strategies. Although there have been analyses of American Woodcock population dynamics based on breeding surveys (Thogmartin et al. 2007, Sauer et al. 2008), localized nesting studies (Roboski and Causey 1981, McAuley et al. 1990), seasonal survival from radio telemetry (Longcore et al. 2000), harvest surveys (Padding et al. 2010), and band-recovery analyses (Krementz et al. 2003, Mayhew and Luukkonen 2010), there have been few attempts to combine these data (e.g., Zimmerman et al. 2010, Sullins et al. 2016) and no attempts to use an IPM for a population-level analysis.

Our primary objective is to illustrate how integrated population models can be used to account for discrepancies in ecological data through analysis of four

independent American Woodcock data sets. We synthesize long-term (1963–2015), continental-scale band-recovery, harvest, Parts-collection Survey, and Singing-ground Survey data (Fig. 1A and Appendix S1: Fig. S1 illustrate spatial distributions of data sets) into an IPM to identify (1) long-term population trajectories for both the eastern and central population units; (2) which periods of the annual cycle and stage-sex classes exhibit the lowest and/or most variable survival rates; and (3) which demographic rates (fecundity, juvenile survival, adult survival) constitute the main drivers of population change. Given our findings, we then highlight how IPMs can accommodate data set inconsistencies resulting from scale mismatch and spatiotemporal variability, two common
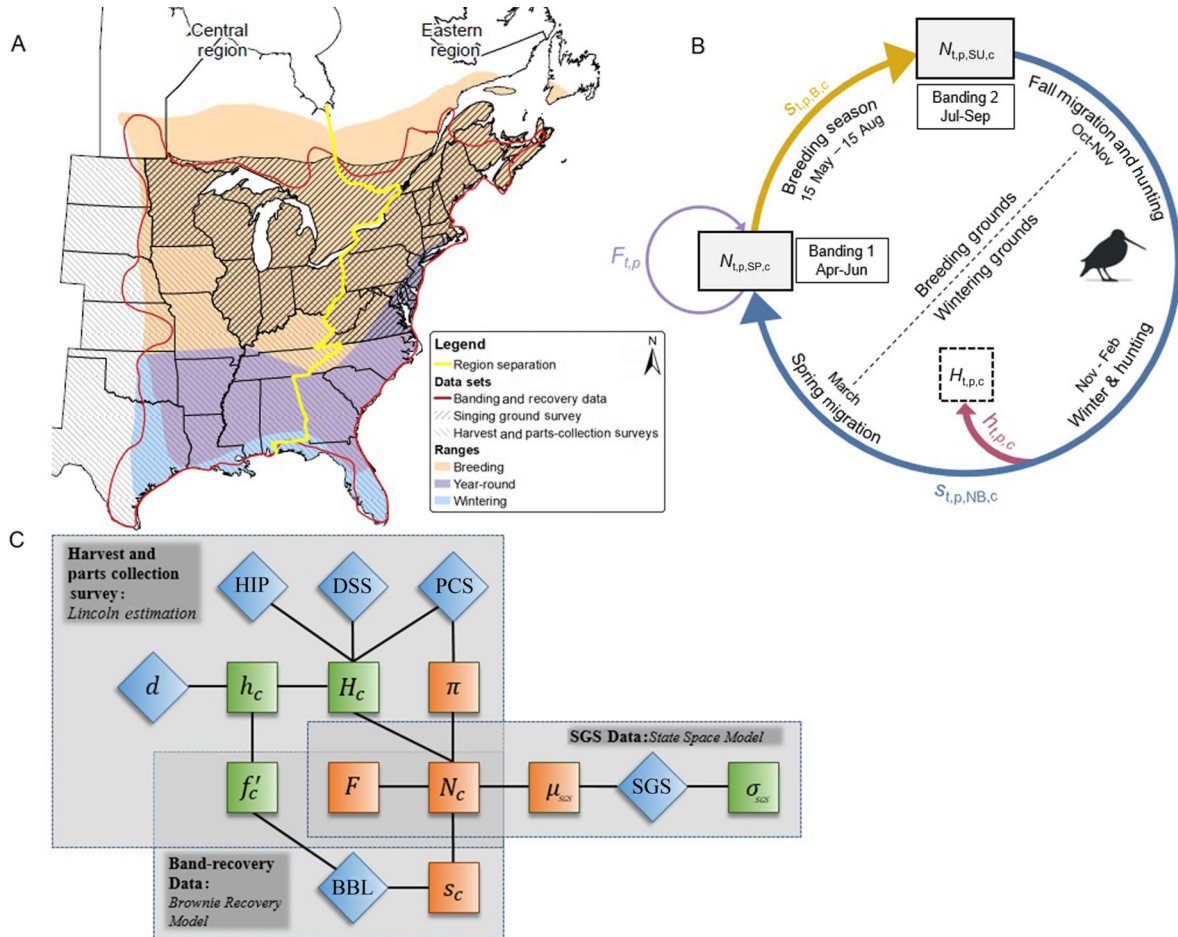

FIG. 1. (A) Delineation of American Woodcock central (left of yellow line) and eastern (right of yellow line) population units. Singing-ground Survey coverage is represented by right hatching, whereas harvest (DSS and HIP) and Parts-collection Survey (PCS) data are represented by left hatching; areas of overlap are represented by cross-hatching. The band-recovery data collection area (U.S. and Canada) is outlined in red. American Woodcock breeding (orange), wintering (blue), and year-round (purple) ranges are also shown. (B) Annual life cycle diagram of the American Woodcock. Using data collected during two separate banding periods, we estimate seasonal abundances (N) during each year t for each population p (eastern, central) of each stage-sex class c (juvenile, adult male, adult female) during spring (SP; left gray box) and late summer (SU; top gray box) using total annual harvest estimates ($H_{t,p,c}$; bottom dashed box). Estimated demographic parameters include annual survival during the breeding ($s_{t,p,B,c}$; yellow arrow) and non-breeding ($s_{t,p,NB,c}$; blue arrow) seasons, per-capita fecundity ($F_{t,p}$; purple arrow), and harvest rates ($h_{t,p,c}$; pink arrow). Harvest occurs throughout the breeding, fall migration, and wintering areas. Juveniles that survive the non-breeding season in year t transition to adults in the spring of year $t + 1$. (C) Directed acyclic graph of the IPM for American Woodcock illustrating the connection between each data source and estimated parameters in the model. Demographic parameters are indicated by orange squares, observation parameters are indicated by green squares, and blue diamonds indicate data. Black lines specify dependencies between parameters and data. Submodels are represented with dashed gray boxes and titled with the corresponding data source and model structure. Notation: SGS, Singing-ground Survey index; HIP, Harvest Information Program; DSS, Duck Stamp Survey; PCS, Parts-collection Survey; d, band reporting rate; BBL, band-recovery data; σ_{SGS}, Singing-ground Survey process and observation error; π, juvenile sex ratio; f_c', direct recovery probability for each stage-sex class; h_c, harvest rate for each stage-sex class; H_c, number harvested in each stage-sex class; μ_{SGS}, population-level index of displaying males in spring; s_c, survival probability for each stage-sex class; F, per-capita fecundity; N_c, population abundance for each stage-sex class.

challenges in data integration (Pacifici et al. 2019). We conclude by providing recommendations for alternative methodological approaches in cases when the development of an integrated model alone does not resolve data set discrepancies (i.e., results in unrealistic or unidentifiable parameter estimates).

METHODS

Focal species and study region

American Woodcock are migratory, upland game birds, widespread east of the Great Plains and south of the open Boreal Region in North America (McAuley et al. 2013). Management of American Woodcock throughout the continental United States is divided into two distinct units: eastern and central breeding and wintering populations (Fig. 1A; Cooper and Rau 2014). Our data suggest minimal movement between these two regions (Appendix S1; but see Moore and Krementz 2017). We estimate sizes of both populations separately and at two distinct periods during the annual cycle when the majority of bandings occur (Fig. 1B): spring (April–June) and late summer (July–September). We define two seasonal survival periods between the two midpoints of 15 May and 15 August (Fig. 1B): breeding season (15 May–15 August) and non-breeding season (15 August–15 May). Woodcock are harvested throughout their range from September through February (i.e., early portion of the non-breeding season), with 92% of all harvest occurring during September through November.

Data sets

Four primary data sets are used to monitor woodcock populations (Fig. 1): (1) the banding and recovery program coordinated by the U.S. Geological Survey Bird Banding Laboratory (BBL) provides information on harvest and survival rates; (2) harvest surveys (Duck Stamp Survey [DSS] and Harvest Information Program [HIP]) measure hunter effort and the total woodcock harvest in each state; (3) Parts-collection Surveys (PCS) measure stage- and sex-specific composition of the harvest (Seamans and Rau 2017); and (4) the Singing-ground Survey (SGS) provides an index of relative abundance of displaying males throughout most of their northern breeding range (see Appendix S1 for additional details on each data source).

These four monitoring data sets provide inconsistent inference on woodcock population trends. Previous analyses of band-recovery data from 1967 to 1982 yielded estimates of annual survival rates ranging from 0.31 to 0.39 for juvenile females and 0.52 to 0.58 for adult females (Krementz and Bruggink 2000, Longcore et al. 2000, McAuley et al. 2013). Fecundity estimates based on harvest data collected over a longer time period (1963–2006) indicate a fecundity rate of 0.79 fledged females per adult female (Zimmerman et al. 2010). Combining these demographic estimates in a population projection matrix indicates that woodcock populations should be declining by ~17% annually (Appendix S1). This is in stark contrast to the Singing-ground Survey data, which suggest more modest long-term declines of $\leq 1\%$ per year in both population units since 1968 (-1.05%/yr in eastern, -0.56%/yr in central; Seamans and Rau 2017). This discrepancy among woodcock data sources could stem from either scale mismatch, spatiotemporal variability, or both. For example, comparisons of population inference from prior woodcock studies (Derleth and Sepik 1990, McAuley et al. 1990, Krementz et al. 2003, Zimmerman et al. 2010, Seamans and Rau 2017) are based on data collected over different temporal (1963–2006 vs. 1967–1982 vs. 1982–1984, 1968–2016) and spatial scales (Michigan-only vs. Maine-only vs. eastern and central population units vs. continent-wide). Demographic processes presumably vary across seasons and throughout the woodcock's range, as is typical of many migratory species (Sillett and Holmes 2002, Hostetler and Chandler 2015). As a result, independent analyses of the various data sets, collected during a single period of the annual cycle or within a limited geographical area, are unlikely to be representative of broad-scale, population-level trends and vital rates.

Banding and recovery data (BBL).—The USGS Bird Banding Laboratory has compiled banding and recovery data for woodcocks over the complete timeframe of our study period (1963–2015). These data inform seasonal survival and harvest probabilities for juveniles and adults in both population units. Woodcock bandings occur during all seasons, with most individuals banded during the spring (April–May, ~40%) or late summer (July–August, ~25%). We excluded bandings during October–March, which includes the hunting and migratory periods. The recovery period was defined as 1 September–28 February, and only birds that were shot by hunters (86% of all recoveries) were included in our analysis.

Harvest (DSS and HIP).—There have been two monitoring programs that collect information on the number of hunters and the number of woodcock harvested annually, which we use to estimate the total woodcock population sizes. From 1963 to 2001, the US Fish & Wildlife Service (USFWS) estimated the annual number of woodcocks that were harvested using samples of waterfowl hunters who had purchased a federal duck stamp (DSS; Padding et al. 2010). However, because woodcock hunters are not necessarily waterfowl hunters, the sampling frame for the federal DSS was incomplete with respect to woodcock harvest. In 1999, the USFWS implemented the Harvest Information Program (HIP), which directly sampled woodcock hunters (Raftovich et al. 2015). We combined early harvest estimates from the DSS with more recent harvest estimates from the HIP using a hierarchical model (Arnold, 2019) that corrects for the different data collection approaches to

estimate total annual U.S. harvest of woodcock during the full length of our study period (1963–2015).

Parts-collection Survey (PCS) data.—The Parts-collection Survey (PCS) provides information on the stage-sex class (adult vs. juvenile, male vs. female) of harvested individuals using wing data submitted by hunters (Seamans and Rau 2017). A sample of hunters submits one wing from each woodcock harvested. At the end of the hunting season, USFWS biologists identify the stage (juveniles are < 1 yr, adults are ≥ 1 yr) and sex associated with each wing (Martin 1964; Appendix S1). The PCS is conducted annually across both eastern and central population units. We used data from 1963 to 2015 to estimate both the proportions of each stage-sex class (e.g., juveniles, adult males, adult females) out of the total population (Zimmerman et al. 2010), as well as the adult sex ratio. We used these estimates in conjunction with the harvest and band-recovery data to estimate stage-sex class abundances.

Singing-ground Survey (SGS) data.—The Singing-ground Survey was developed to estimate changes in woodcock abundance by exploiting the conspicuous courtship display of male woodcocks. Surveys are conducted along fixed routes across the breeding range, where observers record the number of male woodcocks heard vocalizing. Population trends for both eastern and central population units have been regularly estimated from SGS index data (Sauer et al. 2008, Seamans and Rau 2017). We incorporate annual SGS indices from 1968 to 2015 into our analysis and summarize routes by state/province and population (17 states/provinces within the eastern population unit; 8 states/provinces within the central population unit) to inform the population size of adult males in spring, and to calculate a derived annual population growth rate of males. This allowed for direct comparison with estimates obtained from prior analyses of SGS data alone over the same time period (Sauer et al. 2008, Seamans and Rau 2017).

Integrated population model

We estimated annual and seasonal survival probabilities and fecundity, as well as population sizes, growth rates, and adult sex ratios for American Woodcock in eastern and central U.S. population units by developing an integrated population model (Besbeas et al. 2002, Schaub et al. 2007). Our IPM uses a two-sex, stage-structured formulation with both biological (state) and observational processes. The biological process of the model is informed by seasonal population sizes via population projection matrices. The parameters of interest are estimated using the available data in three submodels (i.e., observational processes): (1) a Brownie band-recovery model to estimate stage-sex-specific survival and recovery probabilities using the BBL data; (2) a Lincoln estimation model for stage-sex-specific abundances using recovery probabilities and harvest data (DSS, HIP, and PCS; Alisauskas et al. 2014); and (3) a state-space model informing adult male abundance in spring using SGS data.

Biological process model

Projection matrices.—We assumed that breeding begins at age 1 and used two population projection matrices (Appendix S1) to decompose population dynamics into seasonal processes of adult (male, female) and juvenile survival and fecundity (Fig. 1B). These parameters were assumed to be the same for all individuals within a stage class (i.e., no individual heterogeneity; see Plard et al. [2019] for an IPM that incorporates individual-level processes), but were allowed to differ by population unit (central, eastern), season (spring, late summer), and year (1963–2015). Because woodcocks are polygynous and males provide no parental care, we did not specify a formal "marriage function" within our model, as in some two-sex population models (Veran and Beissinger 2009, Miller and Inouye 2011).

Our annual life cycle model of the American Woodcock describes seasonal abundances of adult males ($N_{t,p,k,\mathrm{MA}}$), adult females ($N_{t,p,k,\mathrm{FE}}$), and juveniles ($N_{t,p,k,\mathrm{JV}}$) of both sexes at two time periods annually (Fig. 1B): spring and late summer. The t index represents year (1963–2015), p represents population unit (eastern, central), k represents season (spring, SP; late summer, SU), and c represents stage-sex class (juvenile, JV; male, MA; female, FE). For the season index k, we use spring (SP, April–June) and summer (SU, July–September) in reference to state variables (e.g., $N_{t,p,k,c}$) because population abundances are estimated at the midpoints of the two banding periods (i.e., 15 May and 15 August; Fig. 1B), whereas we indicate survival ($s_{t,p,k,c}$) during the two transitional periods of breeding (B; 15 May–15 August) and non-breeding (NB; 15 August–15 May).

Seasonal population sizes of adult males were estimated via the following processes:

$$N_{t,p,\mathrm{SP,MA}} = N_{t-1,p,\mathrm{SU,MA}} \cdot s_{t,p,\mathrm{NB,MA}}$$
$$+ \pi_{t,p} \cdot N_{t-1,p,\mathrm{SU,JV}} \cdot s_{t,p,\mathrm{NB,JV}} \quad (1)$$

$$N_{t,p,\mathrm{SU,MA}} = N_{t,p,\mathrm{SP,MA}} \cdot s_{t,p,B,\mathrm{MA}} \quad (2)$$

where $s_{t,p,k,c}$ is the survival probability during year t of individuals in population p during season k (breeding B, non-breeding NB) in stage-sex class c, $\pi_{t,p}$ is the estimated proportion of juveniles that are male (i.e., sex ratio), and $N_{t-1,p,\mathrm{SU,JV}}$ is the estimated population size of juveniles in each population during summer. Thus, spring abundance ($N_{t,p,\mathrm{SP,MA}}$) includes adult males from the previous summer that survived the non-breeding season (which includes hunting and winter) as well as fledged juveniles that survived the previous non-breeding season and matured to adult males. Abundance in late summer ($N_{t,p,\mathrm{SU,MA}}$) is the number of males in spring that survived through the breeding season. Eqs. 1

and 2 are structurally identical for seasonal populations of adult females, except $\pi_{t,p}$ is replaced by $1 - \pi_{t,p}$, which is the estimated proportion of juveniles that are female.

Juvenile abundance is similarly described in two seasons (Fig. 1B): pre-fledged young in spring ($N_{t,p,\text{SP,JV}}$) and young in late summer that successfully fledged during the breeding season ($N_{t,p,\text{SU,JV}}$):

$$N_{t,p,\text{SP,JV}} = N_{t,p,\text{SP,FE}} \cdot F_{t,p} \tag{3}$$

$$N_{t,p,\text{SU,JV}} = N_{t,p,\text{SP,JV}} \cdot s_{t,p,B,\text{JV}}. \tag{4}$$

The total population size of juveniles in spring ($N_{t,p,\text{SP,JV}}$) is the product of the number of adult females in spring and per-capita fecundity ($F_{t,p}$). The total population size of juveniles in summer ($N_{t,p,\text{SU,JV}}$) is the number of juveniles in spring that survive through the breeding season ($s_{t,p,B,\text{JV}}$).

Estimation of life cycle parameters

Brownie recovery submodel.—We used the banding and recovery data (BBL) to estimate season-specific adult male, adult female, and juvenile survival probabilities within a Brownie recovery model (Brownie et al. 1985; Fig. 1C). To do this, we created a multidimensional band-recovery array (referred to as an m-array; Kéry and Schaub 2012) consisting of 12 subcomponent arrays, conditioned on (1) banding period, spring or late summer; (2) stage-sex class, juveniles (birds aged as either pre-fledged juvenile or < 1 yr old at banding), adult males (male birds aged as at least 1 yr old at banding), or adult females (female birds aged at least 1 yr old at banding); and (3) population unit, eastern or central. The last column of the m-array tallies the total number of individuals that were not recovered for a given banding period, class, and population unit. We also compiled a separate array of total birds banded during each year, banding period, stage-sex class, and population unit, which was provided as data to parameterize the multinomial likelihood for the observational component of the IPM (see *Data Availability* for model code available on Zenodo).

The direct recovery rate of banded birds $f'_{t,p,c}$ in each year t and population unit p for each stage-sex class c is defined as

$$f'_{t,p,c} = r_{t,p,c}/b_{t,p,c} \tag{5}$$

where $b_{t,p,c}$ is the number of newly banded birds and $r_{t,p,c}$ is the number of $b_{t,p,c}$ that were harvested and reported during the first hunting season following banding (Brownie et al. 1985; Model 0). Because we included woodcock banded during two different seasons (Fig. 1B), we were able to estimate seasonal (breeding and non-breeding) and annual survival probabilities ($s_{t,p,\text{AN},c}$; season $k = \text{AN}$ for annual). We estimated breeding season (15 May$_t$–15 Aug$_t$) survival using data from spring-banded birds and annual survival (15 Aug$_t$–15

Aug$_{t+1}$) using data from both banding seasons, and then calculated non-breeding season (15 Aug$_t$–15 May$_{t+1}$) survival as

$$s_{\text{NB}} = s_{\text{AN}}/s_B. \tag{6}$$

If spring-banded individuals survive the breeding season (with probability $s_{t,p,B,c}$), they are available to be harvested and reported with probability $f'_{t,p,c}$ during the first hunting season after banding (i.e., probability of encounter is the product $s_{t,p,B,c} \times f'_{t,p,c}$). However, for birds banded in late summer, the encounter probability is simply $f'_{t,p,c}$, which presumes no mortality between banding and start of harvest. We assume that surviving spring-banded birds have the same probability of being harvested as summer-banded birds; thus, seasonal survival can be directly estimated (Brownie et al. 1985; model H8). The recovery probabilities of banded individuals during subsequent harvest periods (i.e., indirect recoveries) are the product of cumulative survival probabilities (to the current harvest period) and indirect recovery rates.

Lincoln estimation submodel.—We estimated seasonal population abundances at time of banding (spring or late summer) for all three stage-sex classes (juveniles, adult males, or adult females) in each population unit using Lincoln estimators (Alisauskas et al. 2014), which represent two-sample mark–recapture models: $\hat{N} = m_1 m_2/r_2$, where m_1 is the number banded ($b_{t,p,c}$), m_2 is the number harvested ($H_{t,p,c}$), and r_2 is the number of harvested birds that were originally banded in m_1 ($r_{t,p,c}$). We estimated $H_{t,p,c}$ by apportioning total harvest ($H_{t,p}$) from annual harvest surveys (DSS and HIP) into stage and sex components: $H_{t,p,c} = \rho_{t,p,c} \times H_{t,p}$, using wing data from the Parts-collection Survey (PCS) to estimate proportional harvest $\rho_{t,p,c}$ (Zimmerman et al. 2017). Although m_1 and m_2 can be biased by differential vulnerability to banding or harvest, respectively, use of recaptures in the denominator controls for differential encounter probabilities and can provide unbiased estimates of population size and composition (Alisauskas et al. 2009). We added stochasticity to the Lincoln estimators by assuming that the number of harvested individuals $H_{t,p,c}$ was a binomial random variable

$$H_{t,p,c} \sim \text{binomial}\left(N_{t,p,c}, h_{t,p,c}\right) \tag{7}$$

where $h_{t,p,c}$ is per-capita harvest probability (Alisauskas et al. 2009). We estimated $h_{t,p,c} = f'_{t,p,c}/d_t$, where $f'_{t,p,c}$ is the direct recovery rate from our Brownie submodel and d_t is the annual probability of band reporting, provided as data in our model (Appendix S1; also see Zimmerman et al. 2017).

Singing-ground Survey (SGS) state-space submodel.—To further inform population size of adult males in spring ($N_{t,p,\text{SP,MA}}$), we incorporated annual Singing-ground Survey data via a state-space framework

(Fig. 1C). We estimated $\mu_{t,p}$, a population-level index of displaying males in spring, from 1963 to 2015 using annual SGS index data ($\text{sgs}_{t,j}$) collected in state/province j (within both population units; Fig. 1A; also see Seamans and Rau 2017:Table 2), such that

$$\text{sgs}_{t,j} \sim \text{Norm}(\mu_{t,p}, \sigma^2_p) \qquad (8)$$

where σ^2_p is the variance of the SGS index across states/provinces and years within each population unit p. We link $\mu_{t,p}$ to the annual population growth rate of male woodcocks ($\lambda_{t,p,\text{MA}}$) estimated in spring by assuming that both estimators follow similar annual trajectories:

$$\mu_{t,p}/\mu_{t-1,p} = N_{t,p,\text{SP,MA}}/N_{t-1,p,\text{SP,MA}} = \lambda_{t,p,\text{MA}}. \qquad (9)$$

Integration of submodels and estimation of fecundity

The three submodels are linked to the biological (state) process model through shared parameters of population abundances (N; Fig. 1C), and Brownie and Lincoln submodels are additionally linked through direct recovery rates (f'). We multiplied the likelihoods from our three IPM submodels (Brownie recovery, Lincoln estimator, and SGS state-space) to obtain the joint likelihood. Although we did not include explicit nest monitoring data in our model, as is typical in many avian IPMs (Schaub et al. 2015, Saunders et al. 2018), we were able to estimate annual per-capita fecundity ($F_{t,p}$) by combining the data sets and exploiting our model structure (i.e., Eq. 3). We additionally constrain fecundity by assuming that mean clutch size per female is uniformly distributed between zero and four, based on known woodcock breeding ecology (McAuley et al. 2013). Our fecundity estimates represent age ratios during spring banding (i.e., pre-fledged brood sizes) and hence do not incorporate summer mortality of juveniles.

Estimating population growth and correlations with demographic rates

We assessed the relative contributions of demographic processes (i.e., annual survival of juveniles, adult males and females, as well as fecundity) to variation in annual total population growth ($\lambda_{t,p}$), defined as the adult population size (male + female) during spring in year $t + 1$ divided by the adult population size in the previous year t:

$$\lambda_{t,p} = \left(N_{t+1,p,\text{SP,MA}} + N_{t+1,p,\text{SP,FE}}\right) / \left(N_{t,p,\text{SP,MA}} + N_{t,p,\text{SP,FE}}\right). \qquad (10)$$

To do this, we calculated the correlation coefficient (r) and associated 95% credible interval between the annual demographic parameters and the population growth rates, using estimates from each model iteration (i.e., full posterior sample), as well as the probability that the

correlations were positive $P(r > 0)$ (Schaub et al. 2015, Saunders et al. 2018).

Model fitting

We estimated the demographic parameters using the joint likelihood with a Bayesian approach (Schaub et al. 2007, Kéry and Schaub 2012). To calculate posterior distributions for parameters, we used Markov chain Monte Carlo (MCMC) in the program JAGS (Plummer 2003), implemented using R (package jagsUI; Kellner 2016, R Core Team 2017). We ran three independent chains of 400,000 iterations with a burn-in period of 350,000 iterations and an adaptation phase of 10,000 iterations; chains were thinned by 10, giving us 15,000 samples from the posterior distribution. We used vague priors for all parameters, with the exception of initial population sizes (constrained by independent Lincoln estimates; Arnold 2019) and mean recovery rates (constrained to a maximum of 0.1, given mean values of 0.03; Krementz et al. 2003). Model convergence was assessed using the $\hat{R}$ statistic (Gelman and Hill 2006) and visual inspection of chains; convergence ($\hat{R} \leq 1.06$) was obtained for all parameter estimates. Posterior distributions are summarized by their mean and 95% credible interval (CI). We also generated full posterior distributions for the derived parameters (population growth rates and correlations between demographic parameters and growth rates). The data and JAGS/R code for fitting the IPM are available on Zenodo (see *Data Availability*).

RESULTS

Population abundances and trajectories

Our integrated population model estimated that both the central (Fig. 2A) and eastern (Fig. 2B) woodcock populations declined over the time period of our study (1963–2015). Mean annual population growth rates over the study period ranged from 0.81 (CI 0.61–1.07) to 1.18 (CI 0.92–1.50) in the central population unit, with highly variable annual growth rates over the study period (Fig. 2C). In the eastern population unit, mean annual growth rates ranged from 0.89 (CI 0.72–1.07) to 1.08 (CI 0.91–1.26) and were highly variable during the first 30 yr, but stabilized (i.e., averages near 1.0) in the last 20 yr of the study (Fig. 2D). The central population exhibited less precise estimates of annual growth rates than the eastern population (Appendix S1: Fig. S2). The geometric mean of annual growth rates for both the central (0.99, CI 0.74–1.31) and eastern (0.99, CI 0.81–1.20) populations suggest a decline of about 1% annually over the 53-yr study period with minimal annual process variation (SD of the 52 annual estimates, 0.08 and 0.03, respectively).

We derived annual population growth rates for adult males within our IPM during spring to compare with annual SGS trend estimates reported by USFWS since
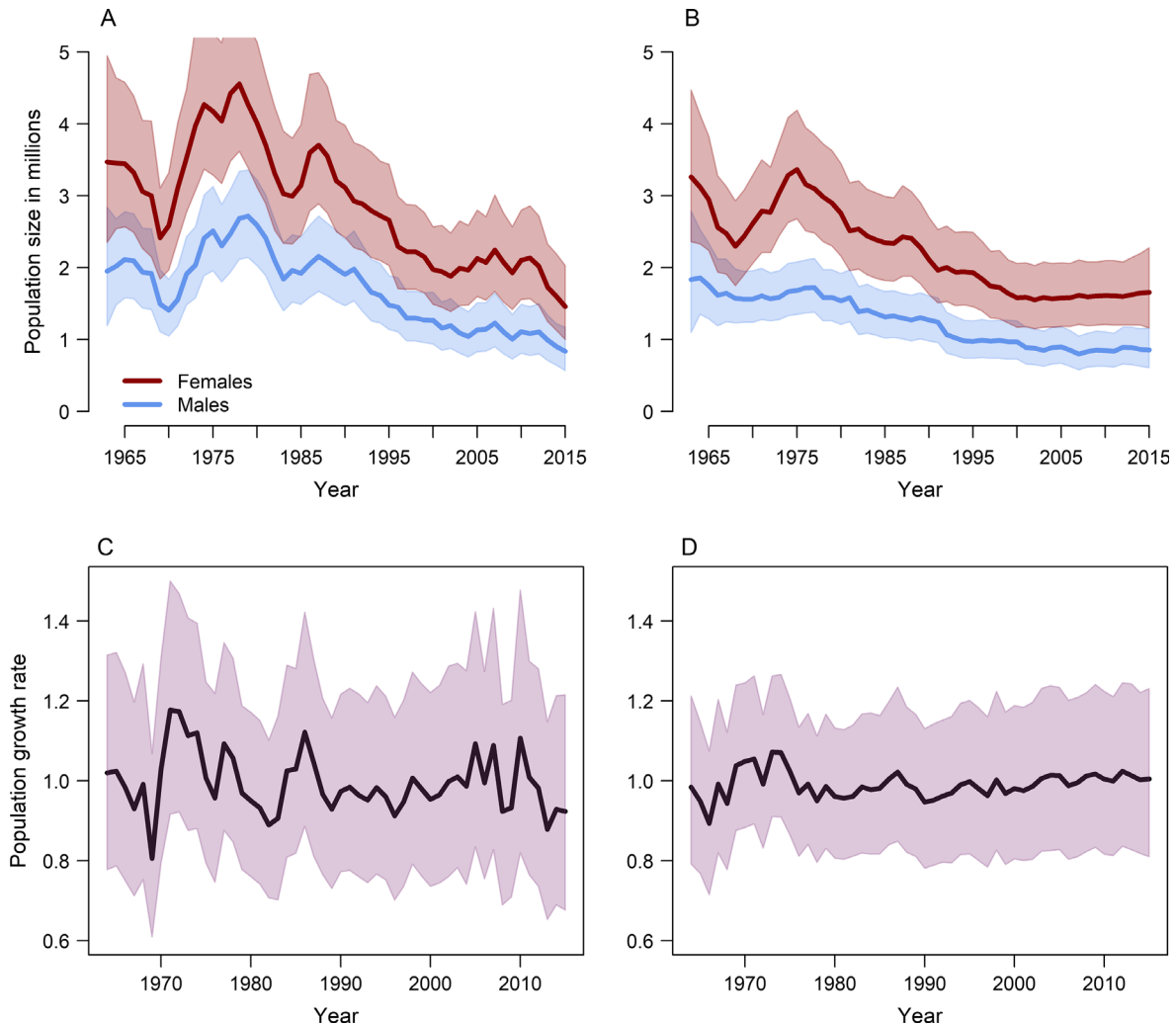
FIG. 2. Spring (April–June) estimates of adult male (blue) and female (red) population sizes (top row) and annual population growth rates (λ_t; bottom row) of American Woodcock during 1963–2015 in (A and C) central and (B and D) eastern population units. Population size estimates are shown in the millions. Shading represents 95% credible intervals.

1968 (Appendix S1: Table S1). Our mean annual growth rates during 1968–2015 for central (0.99, CI 0.72–1.36) and eastern (0.99, CI 0.76–1.28) males in the spring were virtually identical to those estimated from SGS indices alone (0.99 and 0.99). Our IPM results are in agreement with the reported long-term SGS trends (Seamans and Rau 2017), even though SGS data were only a small component of our IPM (Appendix S1). Thus, our findings suggest that spatiotemporal variabilities in the banding and/or harvest data sets are leading to overestimation of population declines with those data sets (i.e., ~17% vs. 1% decline per year).

Annual SGS estimates were only moderately correlated with the spring male population growth rates obtained from our IPM in both the central ($r = 0.35$) and eastern management units ($r = 0.38$). Additionally, estimated annual sex ratios show a long-term decline in the proportion of males within both the eastern and central populations (Appendix S1: Fig. S3), a result that has not been shown in prior analyses of individual data sources and could be contributing to the apparent discrepancy among data sets. Failure to account for temporal variation in adult sex ratios within woodcock population models could lead to overly confident inferences on population-level trends.

Population demographic rates

To address data set discrepancies stemming from spatial variability, we compared stage-sex-specific vital rates between the two population units. For both central and eastern populations, annual female survival was considerably higher than male survival, both of which were higher than juvenile survival (Fig. 3A; see Appendix S1:

Fig. S4 for season-specific survival rates of each stage-sex class). Annual survival estimates in the eastern population were lower than those of the central population for all three classes (Fig. 3A), which is consistent with lower mean breeding season survival for juveniles (0.40 vs. 0.57; Fig. 3B) and males (0.79 vs. 0.97; Fig. 3B) in the eastern population compared to the central population. Non-breeding seasonal survival estimates were comparable for adult males and females across the two populations (Fig. 3C). However, mean non-breeding season survival of juveniles was lower in the central population than in the eastern population (0.64 vs. 0.76; Fig. 3C). The eastern population exhibited higher average spring fecundity (3.03 juveniles per adult female, CI 2.62–3.50) compared to the central population (2.33, CI 2.05–2.64). To compare our fecundity estimates with those based on age ratios measured during summer banding (Zimmerman et al. 2010, Seamans and Rau 2017), we also derived mean estimates of late summer fecundity $[F_{t,p}*s_{t,p,B,JV}]$ for the eastern and central population units as 1.20 (CI 0.98–1.44) and 1.33 (CI 1.13–1.57), respectively.

Survival of adult males was fairly stable over the duration of the study period, whereas juvenile and female survival were more variable in both populations (Fig. 4A–C). Specifically, juvenile and female non-breeding survival rates demonstrated the greatest temporal variability in both population units (Appendix S1: Fig. S4). Annual fecundity was stable in the eastern population, but estimates in the central region were considerably more variable (Fig. 4D; Appendix S1: Table S2). See Appendix S1: Table S3 for a complete list of mean parameter estimates and associated credible intervals of woodcock population sizes and vital rates for each population, season, and stage-sex class, along with measures of annual process variation.

Drivers of population change

For both populations, all demographic rates were positively correlated with population growth rates (Fig. 5). Among the four demographic rates, fecundity ($r = 0.76$) had the highest correlation with growth rates of the central population, followed by juvenile and female survival ($r = 0.37$ for both parameters); adult male survival had only a weak correlation ($r = 0.07$) with population growth. In the eastern unit, population growth was most strongly correlated with adult female survival ($r = 0.65$) and juvenile survival ($r = 0.54$), followed by fecundity and adult male survival ($r = 0.18$). In all cases, the 95% credible intervals excluded zero and the probabilities of a positive correlation were nearly 1.0, except for adult male survival in both populations and fecundity in the eastern population unit (Fig. 5). Prior studies have hypothesized that long-term declines in both woodcock populations may be related to declines in fecundity, yet our results indicate that fecundity is a primary demographic driver only within the central population.

DISCUSSION

Integrated population models are regularly used to accommodate data deficiencies (e.g., missing demographic information, lapses in time series), but here we use IPMs to evaluate data set inconsistencies without omitting any of the seemingly contradictory data sources. This approach allowed us to identify sources of spatiotemporal discrepancy in independent analyses and to quantify long-term woodcock population trends across their continental range. Previous studies using data from only a single monitoring program were unable to characterize woodcock population dynamics across their full annual cycle and geographic range, resulting in inconsistent inferences on population trends (Roboski and Causey 1981, Derleth and Sepik 1990, McAuley et al. 1990, Krementz et al. 2003, Zimmerman et al. 2010, Seamans and Rau 2017). For example, survival and fecundity values were estimated from harvest and band-recovery data over a period of considerable variability in demographic rates during the 1960s–1980s (Figs. 2 and 4; Krementz and Bruggink 2000, Kelley 2001, Zimmerman et al. 2010), leading to potential issues of temporal scale mismatch in estimates of population growth rates. Used alone, these data likely
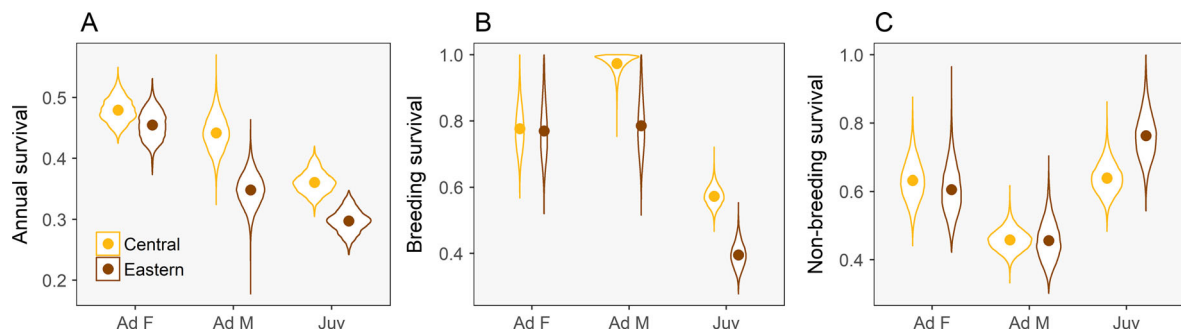

FIG. 3. Violin plots of the posterior distributions of (A) annual survival, (B) breeding season survival, and (C) non-breeding season survival for adult female (Ad F), adult male (Ad M), and juvenile (Juv) American Woodcock in the central (yellow) and eastern (brown) population units during 1963–2015. Circles represent mean estimates.
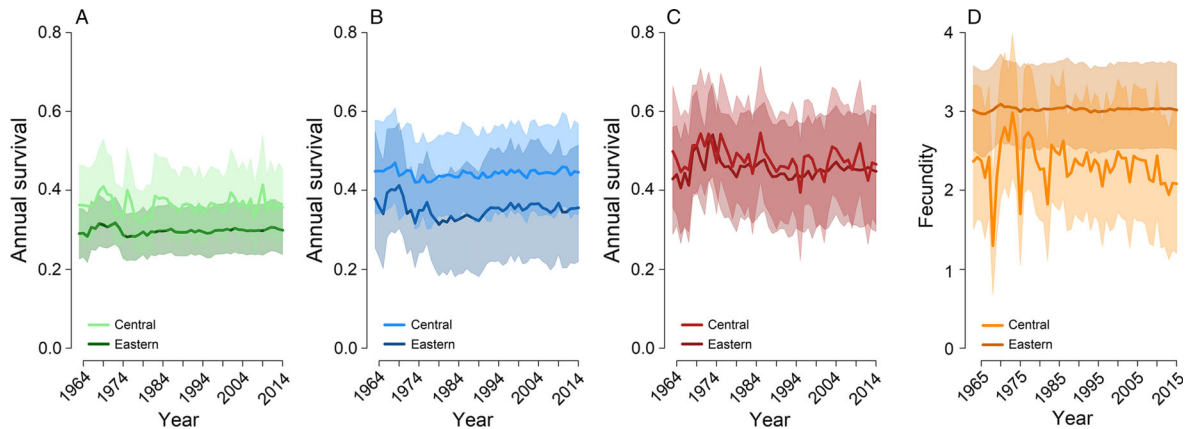
FIG. 4. Estimates of annual survival probabilities of (A) juvenile, (B) male, and (C) female American Woodcock, as well as (D) annual fecundity in central (light colors) and eastern (dark colors) population units from 1963 to 2015. Shading represents 95% credible intervals.

overestimate the rate of population decline, providing a discrepancy with trend estimates from other data sources collected across different spatial locations and time periods. Combining all woodcock data into an IPM allowed us to resolve this discrepancy and determine that both the central and eastern populations have declined at an average rate of approximately 1% annually since 1963 (Fig. 2), consistent with long-term monitoring data from the Singing-ground Surveys (Seamans and Rau 2017). We were able to attribute these declines to juvenile and

female survival (in both populations) and fecundity (particularly in the central population).

Our model suggests that the eastern population has stabilized in the last several decades while the central population has continued to decline (Fig. 2), results that have not been documented with analyses of any of the individual data sets and that demonstrate the importance of accounting for spatial variability. Estimates of mean adult annual survival from our IPM (Fig. 3) were similar to values obtained when analyzing band-recovery
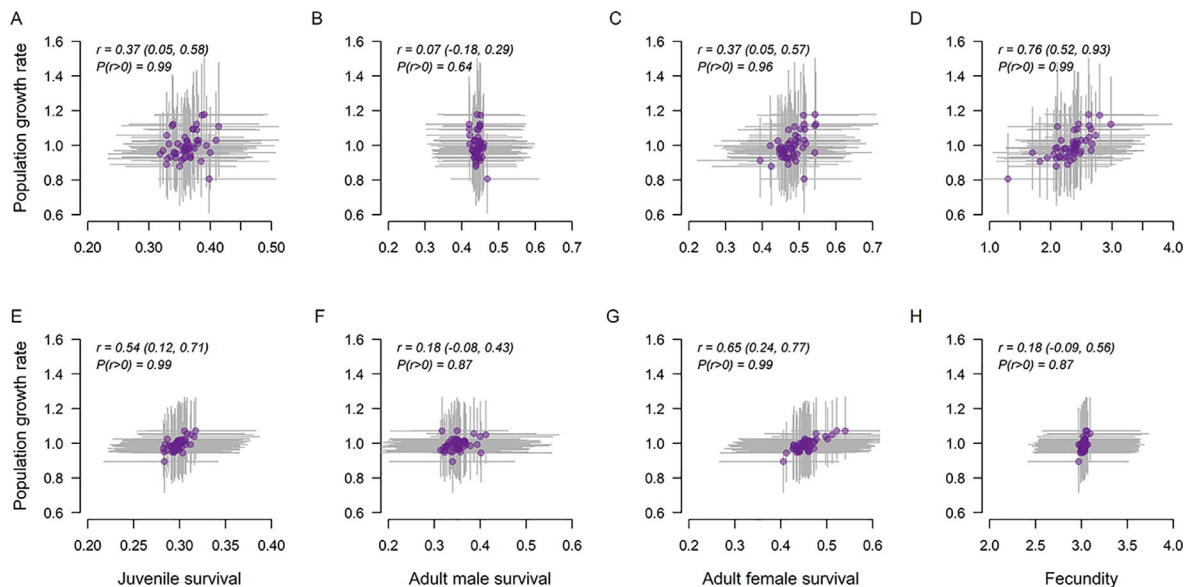

FIG. 5. Annual posterior means of the central (top row) and eastern (bottom row) population growth rates (spring) plotted against the annual posterior means of the estimates for (A and E) juvenile annual survival, (B and F) adult male annual survival, (C and G) adult female annual survival, and (D and H) fecundity from an IPM of American Woodcock during 1963–2015. Posterior means of the correlation coefficients (r), associated 95% credible intervals and probabilities that estimates are positive $P(r > 0)$ are given. Horizontal and vertical lines show the limits of the 95% credible intervals for each annual estimate.

data separately (Krementz and Bruggink 2000, Krementz et al. 2003), as were our fecundity estimates (adjusted to account for summer mortality; Zimmerman et al. 2010, Seamans and Rau 2017); however, estimates of juvenile annual survival were underestimated using band-recovery data alone (Krementz and Bruggink 2000, Krementz et al. 2003). Temporal and spatial variability in woodcock monitoring methods and effort likely also contributed to discrepancies in trend estimates. For example, although band-recovery data are available for the duration of the study period, recovery rates are low for several decades of the time series (Appendix S1: Fig. S5); also, half of all banding effort in the eastern population occurred during a 7-yr window (1968–1974) and 70% of all banding data for the central population came from Michigan. Hence, long-term survival estimates based on analysis of band-recovery data alone (Krementz and Bruggink 2000, Krementz et al. 2003) may be informed by data that are not spatially or temporally representative of the entire population and time series. Thus, data availability issues may be causing discrepancies in population inferences, especially regarding juvenile survival.

The Singing-ground Survey data, which tracks breeding males, is the primary monitoring program used to estimate population trends for American Woodcock (Seamans and Rau 2017). Although the average population growth rates estimated from SGS indices alone matched those from our IPM, annual sex ratios show a long-term decline in the proportion of males in both the eastern and central populations (Appendix S1: Fig. S3), indicating that the use of SGS indices alone for woodcock population monitoring may become problematic if male abundance is no longer representative of the total population. Continuing to synthesize data sets and update integrated modeling results can provide comprehensive monitoring of population stage-sex composition, vital rates, and ultimately long-term trends.

Guidance for resolving data discrepancies with IPMs

The involvement of multiple monitoring programs can lead to a relative wealth of communal data, yet the challenge remains that multiple data sets are rarely going to converge upon identical parameter estimates due to heterogeneity in population processes across space and time, as well as different assumptions and sampling biases inherent in each data set. When combining multiple data types, beginning with a conceptual model of the target population's life cycle and a diagram describing how each data source can be used to inform demographic parameters (Fig. 1B, C) can provide a clear understanding of how to maximize use of all data (Schaub and Abadi 2011). Identifying pertinent biological processes can highlight potential discrepancies that may arise given collection protocols, such as issues of spatial scale mismatch (i.e., local vs. continental data sets) and temporal variability (i.e., disparate observation/monitoring methods over time). In our case study, the Singing-ground Survey data (measured as singing males/route during the spring) and harvest data (measured as all stage-sex classes harvested during the fall) are not collected on a scale that can be easily translated to population abundance. Yet, we were able to include both these data sets in our IPM by linking annual trend estimates of spring males across submodel components. Although SGS indices only contributed a small piece of information (male abundance in spring), inclusion of these data within our IPM enabled us to tackle the root of the apparent discrepancy by directly sharing information between conflicting data sets, rather than conducting a post-hoc comparison of results from individual analyses.

Continued development of integrated modeling approaches to include data types that are limited (e.g., indices) or uninformative on their own can be useful to compensate for data discrepancies. For example, the PCS data in our woodcock example provide information on population size and structure, fecundity, survival, and vulnerability to harvest (see Koons et al. 2017). However, without the integration of band-recovery and harvest survey data (Zimmerman et al. 2010, Alisauskas et al. 2014), none of these parameters are identifiable from PCS data alone. Intensive data types, such as stage-structured counts or spatially explicit capture–recapture data, may be expensive to collect, and therefore only available over limited spatial or temporal extents. However, such data can be information rich. Incorporation of partial data types into integrated modeling frameworks can help describe state processes that are otherwise difficult to infer with typical observational data (Zipkin and Saunders 2018).

In many instances, such as our woodcock case study, simply combining all available data sources into an integrated modeling framework will be enough to resolve discrepancies that may rise from analyses of individual data sets. In situations where synthesis of conflicting data sources results in model failure (e.g., unrealistic and/or unidentifiable parameter estimates, lack of model convergence, estimates biased towards the most data-rich source), ecologists may consider borrowing methods from other fields to resolve discrepancies. Such methods include (1) data weighting (done in fisheries stock assessments; Francis 2011); (2) data subsetting and thinning (a geospatial technique, Freschi et al. 2014); (3) data supplementing (done in the social sciences; Foster et al. 2016); or (4) expert opinion elicitation (employed in psychology; Taylor et al. 2017), which can be used to formulate priors in Bayesian analyses (Murray et al. 2009).

In data weighting, estimates from data or methods that offer more reliable information receive higher weights in a model and thus contribute to inferences disproportionately (Srivathsa et al. 2018). Although data weighting can be misused (Francis 2011), it can also be a valuable approach in instances where there are known variations in quality among different data types. Data

thinning is another useful method for addressing issues related to high-volume data types that may introduce bias through sheer availability (Freschi et al. 2014). This approach could be applied to integrated ecological models where the volume of a given data source renders analysis prohibitive, or where additional data points from a given data type provide only a marginal improvement on inferences. Utilizing publically available data, such as "scraping" web-based data, can provide data to supplement deficiencies by capitalizing on data mining techniques (Bharanipriya and Prasad 2011). Such methods have only recently been introduced in ecology and present computational and analytical challenges (e.g., accounting for sampling biases from volunteer-collected data; Sullivan et al. 2014), but offer potentially powerful avenues for incorporating "big data", such as opportunistic species sightings by the public (e.g., eBird), into integrated modeling frameworks (Robinson et al., *in press*). Similarly, eliciting expert opinion can be a useful approach in cases where deficient data prohibit the ability to build reliable statistical models. When formulated as informed priors in a Bayesian analysis, for example, expert opinion can modify or strengthen patterns exhibited by empirical data sets that are limited in size and scope (Murray et al. 2009). Informed priors may also originate from comparative studies, such as reviews of vital rates in closely related taxa (e.g., global reviews of survival rates in shorebirds; Méndez et al. 2018) or larger-scale studies that use allometric scaling (e.g., survival vs. body mass relationships in birds and mammals; McCarthy et al. 2008).

Characterizing population dynamics and trends can be challenging, as it is difficult to measure all relevant parameters across a population's range. Available data may be representative of only a subset of a population through space and time. The spatiotemporal scope of ecological research has expanded greatly over the last few decades, necessitating more efficient data collection and advanced analytical methods. Integrated population modeling offers a useful approach for taking advantage of all available data on a target population. Yet, with the synthesis of disparate data types comes difficulties bridging discrepancies that arise from issues of scale mismatch, as well as spatial and temporal variability. We provide a foundation for resolving conflicting data streams in population modeling by (1) mapping out a target population's life cycle coupled with a diagram of the parameters shared among data sets (Schaub et al. 2007) to identify spatial and/or temporal discrepancies; (2) integrating partial, limited, conflicting, and/or apparently "uninformative" data types (Maunder and Piner 2017); and (3) adopting analytical approaches outside the field of ecology (e.g., data thinning and data weighting) when the aforementioned tactics prove ineffective. IPMs can also be used within an adaptive monitoring framework such that future data collection efforts can be guided in a way that reduces sources of uncertainty. Vital rates that are estimated with low precision, for

example, can be the focus of spatially and temporally targeted studies (e.g., telemetry) that can test the validity of IPM-based predictions and allow for model updates going forward. Through these techniques and further method development, ecologists can improve demographic parameter estimation, enabling accurate assessment of population trends at broad spatial scales, as well as identification of drivers of long-term population dynamics.

LITERATURE CITED

Alisauskas, R. T., K. L. Drake, and J. D. Nichols. 2009. Filling a void: abundance estimation of North American populations of arctic geese using hunter recoveries *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Environmental and Ecological Statistics 3:463–489.

Alisauskas, R. T., T. W. Arnold, J. O. Leafloor, D. L. Otis, and J. S. Sedinger. 2014. Lincoln estimates of mallard (*Anas platyrhynchos*) abundance in North America. Ecology and Evolution 4:132–143.

Barlow, N. D. 1995. Critical evaluation of wildlife disease models. Pages 230–259 *in* B. T. Grenfell, and A. P. Dobson, editors. Ecology of infectious diseases in natural populations. Cambridge University Press, Cambridge, UK.

Besbeas, P., S. N. Freeman, B. J. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58:540–547.

Bharanipriya, V., and V. Prasad. 2011. Web content mining tools: a comparative study. International Journal of Information Technology and Knowledge Management 4:211–215.

Brown, J. L., and M. W. Collopy. 2013. Immigration stabilizes a population of threatened cavity-nesting raptors despite possibility of nest box imprinting. Journal of Avian Biology 44:141–148.

Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data. U.S. Fish and Wildlife Service Resource Publication 156. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Carvalho, F., A. E. Punt, Y. Chang, M. N. Maunder, and K. R. Piner. 2017. Can diagnostic tests help identify model misspecification in integrated stock assessments? Fisheries Research 192:28–40.

Davis, A. J., M. B. Hooten, M. L. Phillips, and P. F. Doherty. 2014. An integrated modeling approach to estimating

Gunnison sage-grouse population dynamics: combining index and demographic data. Ecology and Evolution 4:4247–4257.

Derleth, E. L., and G. F. Sepik. 1990. Summer-fall survival of American Woodcock in Maine. Journal of Wildlife Management 54:97–106.

Ethier, D. M., and T. D. Nudds. 2015. Scalar considerations in population trend estimates: implications for recovery strategy planning for species of conservation concern. Condor 117:545–559.

Foster, I., R. Ghani, R. S. Jarmin, F. Kreuter, and J. Lane. 2016. Big data and social science: a practical guide to methods and tools. CRC Press, Boca Raton, Florida, USA.

Francis, R. C. 2011. Data weighting in statistical fisheries stock assessment models. Canadian Journal of Fisheries and Aquatic Sciences 68:1124–1138.

Freschi, V., et al. 2014. Geospatial data aggregation and reduction in vehicular sensing applications: the case of road surface monitoring. 2014 International Conference on Connected Vehicles and Expo (ICCVE). Wien, Vienna.

Gelman, A., and J. Hill. 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.

Grose, M. J. 2014. Thinking backwards can inform concerns about 'incomplete' data. Trends in Ecology and Evolution 29:546–547.

Hostetler, J. A., and R. B. Chandler. 2015. Improved state-space models for inference about spatial and temporal variation in abundance from count data. Ecology 96:1713–1723.

Inamine, H., S. P. Ellner, J. P. Springer, and A. A. Agrawal. 2016. Linking the continental migratory cycle of the monarch butterfly to understand its population decline. Oikos 125:1081–1091.

Kelley, J. R. Jr. 2001. American Woodcock population status, 2000. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

Kellner, K. 2016. jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses. Version 1.4.2. https://CRAN.R-project.org/package=jagsUI

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press, Cambridge, Massachusetts, USA.

Koons, D. N., T. W. Arnold, and M. Schaub. 2017. Understanding the demographic drivers of realized population growth rates. Ecological Applications 27:2102–2115.

Krementz, D. G., and J. G. Bruggink. 2000. Sources of variation in survival and recovery rates of American Woodcock. Proceedings of the Ninth American Woodcock Symposium, United States Geological Survey Information and Technology Report; 2000. United States Geological Survey Information and Technology Report 2000-0009, Laurel, Maryland, USA.

Krementz, D. G., J. E. Hines, and D. R. Luukkonen. 2003. Survival and recovery rates of American Woodcock banded in Michigan. Journal of Wildlife Management 67:398–407.

Link, W. A., and J. R. Sauer. 2002. A hierarchical analysis of population change with application to Cerulean Warblers. Ecology 83:2832–2840.

Longcore, J. R., D. G. McAuley, G. F. Sepik, and G. W. Pendleton. 2000. Survival of female American Woodcock breeding in Maine. Pages 65–76 in D. G. McAuley, J. G. Bruggink, and G. F. Sepik, editors. Proceeding of the Ninth American Woodcock Symposium 9. United States Geological Survey Information and Technology Report 2000-0009, Laurel, Maryland, USA.

Martin, F. W. 1964. Woodcock age and sex determination from wings. Journal of Wildlife Management 28:287–293.

Maunder, M. N., and K. R. Piner. 2017. Dealing with data conflicts in statistical inference of population assessment models

that integrate information from multiple diverse data sets. Fisheries Research 192:16–27.

Maunder, M. N., J. R. Sibert, A. Fonteneau, J. Hampton, P. Kleiber, and S. J. Harley. 2006. Interpreting catch per unit effort data to assess the status of individual stocks and communities. ICES Journal of Marine Science 63:1373–1385.

Maunder, M. N., P. R. Crone, A. E. Punt, J. L. Valero, and B. X. Semmens. 2017. Data conflict and weighting, likelihood functions, and process error. Fisheries Research 192:1–4.

Mayhew, S. L., and D. R. Luukkonen. 2010. Survival and recovery of Woodcock banded in Michigan, 1981–2004. Proceedings of the American Woodcock Symposium. Michigan Department of Natural Resources and Environment, Lansing, Michigan, USA.

McAuley, D. G., J. R. Longcore, and G. F. Sepik. 1990. Renesting by American Woodcocks (*Scolopax minor*) in Maine. Auk 107:407–410.

McAuley, D., D. M. Keppie, and R. M. Whiting Jr. 2013. American Woodcock (*Scolopax minor*). In A. Poole, editor. The birds of North America Online. Cornell Lab of Ornithology, Ithaca, New York, USA.

McCarthy, M. A., R. Citroen, and S. C. McCall. 2008. Allometric scaling and Bayesian priors for annual survival of birds and mammals. American Naturalist 172:216–222.

Méndez, V., J. A. Alves, J. A. Gill, and T. G. Gunnarsson. 2018. Patterns and processes in shorebird survival rates: a global review. Ibis 160:723–741.

Miller, T. E. X., and B. D. Inouye. 2011. Confronting two-sex demographic models with data. Ecology 92:2141–2151.

Moore, J. D., and D. G. Krementz. 2017. Migratory connectivity of American Woodcock using band return data. Journal of Wildlife Management 81:1063–1072.

Murray, J. V., A. W. Goldizen, R. A. O'Leary, C. A. McAlpine, H. P. Possingham, and S. L. Choy. 2009. How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. Journal of Applied Ecology 46:842–851.

Nilsen, E. B., and O. Strand. 2018. Integrating data from multiple sources for insights in demographic processes: simulation studies and proof of concept for hierarchical change-in-ratio models. PLoS ONE 13:e0194566.

Pacifici, K., B. Reich, D. Miller, B. Pease, and D. Huberman. 2019. Resolving misaligned spatiotemporal data with integrated distribution models. https://doi.org/10.1002/ecy.2709.

Padding, P. I., M. T. Moore, K. D. Richkus, and E. M. Martin. 2010. Estimating Woodcock hunter activity and harvest in the United States. Pages 29–35 in C. A. Stewart, and V. R. Frawley, editors. Proceedings of the tenth American Woodcock Symposium. Michigan Department of Natural Resources and Environment, Lansing, Michigan, USA.

Plard, F., R. Fay, M. Kéry, A. Cohas, and M. Schaub. 2019. Integrated population models: a powerful tool to embed individual processes in population dynamics models. https://doi.org/10.1002/ecy.2715.

Raftovich, R. V., S. C. Chandler, and K. A. Wilkins. 2015. Migratory bird hunting activity and harvest during the 2013–14 and 2014–15 hunting seasons. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ries, L., D. J. Taron, and E. Rendón-Salinas. 2015. The disconnect between summer and winter monarch trends for the

eastern migratory population: possible links to differing drivers. Annals of the Entomological Society of America 108:691–699.

Robinson, O. J., V. Ruiz-Gutierrez, D. Fink, R. J. Meese, M. Holyoak, and E. G. Cooch. I*n press*. Using citizen science data in integrated population models to inform conservation decision-making. Biological Conservation.

Roboski, J. C., and M. K. Causey. 1981. Incidence, habitat use, and chronology of Woodcock nesting in Alabama. Journal of Wildlife Management 45:793–797.

Sauer, J. R., W. A. Link, W. L. Kendall, J. R. Kelley, and D. K. Niven. 2008. A hierarchical model for estimating change in American Woodcock populations. Journal of Wildlife Management 72:204–214.

Saunders, S. P., L. Ries, K. S. Oberhauser, W. E. Thogmartin, and E. F. Zipkin. 2017. Local and cross-seasonal associations of climate and land use with abundance of monarch butterflies *Danaus plexippus*. Ecography 41:278–290.

Saunders, S. P., F. J. Cuthbert, and E. F. Zipkin. 2018. Evaluating population viability and efficacy of conservation management using integrated population models. Journal of Applied Ecology 55:1380–1392.

Schaub, M., and F. Abadi. 2011. Integrated population models: A novel analysis framework for deeper insights into population dynamics. Journal of Ornithology 152:227–237.

Schaub, M., O. Gimenez, A. Sierro, and R. Arlettaz. 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. Conservation Biology 21:945–955.

Schaub, M., J. Hirschheydt, and M. U. Grüebler. 2015. Differential contribution of demographic rate synchrony to population synchrony in barn swallows. Journal of Animal Ecology 84:1530–1541.

Seamans, M., and R. Rau. 2017. American Woodcock population status, 2016. US Fish and Wildlife Service, Laurel, Maryland, USA.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Srivathsa, A., M. Puri, N. Samba Kumar, D. Jathanna, and K. Ullas Karanth. 2018. Substituting space for time: empirical evaluation of spatial replication as a surrogate for temporal replication in occupancy modeling. Journal of Applied Ecology 55:754–765.

Stenoien, C., K. R. Nail, and K. S. Oberhauser. 2015. Habitat productivity and temporal patterns of monarch butterfly egg densities in the eastern United States. Annals of the Entomological Society of America 108:670–679.

Sullins, D. S., W. C. Conway, D. A. Haukos, K. A. Hobson, L. I. Wassenaar, C. E. Comer, and I.-K. Hung. 2016. American Woodcock migratory connectivity as indicated by hydrogen isotopes. Journal of Wildlife Management 80:510–526.

Sullivan, B. L., et al. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. Biological Conservation 169:31–40.

Taylor, P. J., S. Jones, C. D. Huntley, and C. Seddon. 2017. What are the key elements of cognitive analytic therapy for psychosis? A Delphi study. Psychology and Psychotherapy 90:511–529.

Thogmartin, W. E., J. R. Sauer, and M. G. Knutson. 2007. Modeling and mapping abundance of American Woodcock across the Midwestern and Northeastern United States. Journal of Wildlife Management 71:376–382.

Tulloch, A. I. T., K. Mustin, H. P. Possingham, J. K. Szabo, and K. A. Wilson. 2013. To boldly go where no volunteer has gone before: predicting volunteer activity to prioritize surveys at the landscape scale.

Veran, S., and S. R. Beissinger. 2009. Demographic origins of skewed operational and adult sex ratios: perturbation analyses of two-sex models. Ecology Letters 12:129–143.

Walsh, D. P., G. C. White, T. E. Remington, and D. C. Bowden. 2004. Evaluation of the lek-count index for greater sage-grouse. Wildlife Society Bulletin 32:56–68.

Wang, S. P., M. N. Maunder, T. Nishida, and Y. R. Chen. 2015. Influence of model misspecification, temporal changes, and data weighting in stock assessment models: application to swordfish (*Xiphias gladius*) in the Indian Ocean. Fisheries Research 166:119–128.

Wommack, E. A., R. D. Dawson, J. M. Shrimpton, and R. C. Bowie. 2015. Changes in population size and genetic diversity of a raptor species occurring in the boreal forest of Saskatchewan. Conservation Genetics 16:535–547.

Zimmerman, G. S., W. A. Link, M. J. Conroy, J. R. Sauer, K. D. Richkus, and G. S. Boomer. 2010. Estimating migratory game-bird productivity by integrating age ratio and banding data. Wildlife Research 37:612–622.

Zimmerman, G. S., J. R. Sauer, G. S. Boomer, P. K. Devers, and P. R. Garrettson. 2017. Integrating Breeding Bird Survey and demographic data to estimate wood duck population size in the Atlantic Flyway. Condor 119:616–628.

Zipkin, E. F., and S. P. Saunders. 2018. Synthesizing multiple data types for biological conservation using integrated population models. Biological Conservation 217:240–250.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2714/suppinfo

DATA AVAILABILITY

Data and code available from Zenodo: https://doi.org/10.5281/zenodo.2532006