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Regionally-explicit integrated population models developed for a migratory bird suggest biased demography, masking broader inference capacity

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ABSTRACT

Collecting representative demographic information to estimate wildlife population dynamics can be difficult, particularly for populations broadly distributed across heterogeneous landscapes. We developed an Integrated Population Model (IPM) to estimate spatially explicit demographic rates for mourning dove (*Zenaida macroura*) in Missouri, USA using 25 years of band-recovery data, harvest age ratios, and roadside counts across four distinct physiographic regions. We evaluated the impact of sampling schemes on demographic estimates using simulated data. Our model revealed substantial variation in survival probabilities among physiographic regions while productivity rates were similar (~2.5 juveniles produced per adult). Two regions with disproportionately high banding and harvest of doves likely biased previous state-wide estimates of survival low; adult and juvenile survival probabilities were 30% and 40% lower, respectively, relative to the other regions. Demographic inference based on these two regions alone would suggest that the subpopulation in Missouri faces extirpation, in contrast to more stable or even increasing trends in less heavily sampled regions. Our simulation results illustrated that large increases in the number of banded birds would be required to meaningfully reduce uncertainty in survival. We also found that the use of state-collected productivity data from intensively managed sites could bias productivity estimates high. We anticipate that conservationists could use this information as context in among-state coordination of harvest opportunities. More broadly, we encourage practitioners to test perceived biases in their sampling schemes and to use results gained in redesigning studies to reduce identified biases.

KEY WORDS: Integrated population modeling, sampling bias, harvest management, mourning dove, demographic heterogeneity

INTRODUCTION

Wildlife populations are shaped by a combination of demographic processes including survival, reproduction, and movement. The relative importance of these demographic rates often varies among life histories and across space and time (Morrison et al. 2022; Shinohara et al. 2023).

Quantifying the relative contribution of demographic rates to population growth rate allows practitioners to understand the proximate mechanisms of population change and their environmental drivers. Such linkages facilitate development or revision of targeted conservation plans for efficient allocation of resources and greatest impact on population trajectories (Arnold et al. 2018).

Quantifying the demography of species at the scale at which they occur is inherently challenging and typically not feasible for broadly distributed or highly mobile species. The status of wildlife populations is often reported at coarse or even range-wide spatial scales (Rosenberg et al. 2019; Cazalis et al. 2022; WWF 2024), yet there can be considerable spatial heterogeneity within populations across scales (Thorson et al. 2023; Smith et al. 2024). This is particularly true among migratory bird species, which experience varying selective pressures throughout their full annual cycle. Although their mobility may support high geneflow and thus limited differentiation between populations, individuals breeding, migrating, or over-wintering in different ecoregions can experience different sources of mortality, resource pressures, and environmental stochasticity. A possible alternative to focusing on range-wide metrics is to focus on regional information associated with subpopulations but this may obscure broader, population-level processes.

Hierarchical models are increasing in utility across ecology and have been used for a range of research endeavors, including to estimate population viability (Campbell et al. 2018), population

trends (Smith et al. 2024), and population dynamics (Drake et al. 2022; Nater et al. 2023). Integrated Population Models (IPMs) provide a statistical framework to facilitate demographic study of subpopulations while contextualizing demographic estimates in a larger population (Schaub and Abadi 2011; Zipkin and Saunders 2018; Saracco et al. 2022). IPMs are versatile in that researchers can structure models to account for spatial and/or temporal variation, incorporate uncertainty, and explore potential biases. This approach can support conservation plans for harvested species (Arnold et al. 2018), leading many wildlife management agencies to aim to incorporate IPMs in their harvest strategies (National Dove Task Force 2024).

The single most abundant and most harvested migratory game bird in North America is the mourning dove (*Zenaida macroura*), with an estimated 16.8 million birds harvested in the U.S. in 2023 alone (Seamans 2024). Mourning doves are studied and managed across the U.S. in management units, which are regions with coordinated federal and state practitioners who band doves for survival estimation, collect harvested wings to estimate productivity, and monitor harvest and abundance (National Dove Task Force 2024). While two-step population analyses for doves have been common over the last 30 years (e.g., survival models, then matrix models incorporating survival and productivity estimates), all management units are pursuing the development of IPMs to guide their harvest management decisions.

More than half of the overall dove harvest in the U.S. occurs within the Central Management Unit (CMU; Seamans 2024), which spans 14 states. Although the mourning dove population in the CMU is slightly declining, trends and survival estimates vary among states (Seamans 2024). Demographic estimates from Missouri are particularly divergent from surrounding states, with juvenile and adult survival estimates that are ~50% and ~25% lower than the CMU average, respectively. Despite low survival probabilities in Missouri, dove population survey data suggest

the population is stable there. This suggests that either the survival estimates for doves in Missouri are biased low or that the Missouri subpopulation has been buffered by doves produced elsewhere in the CMU, making it a sink population.

In many ecological studies, it is assumed that the individuals sampled reflect the broader population, in large part because there is no practical way of measuring or observing individuals not captured or detected. However, this assumption can lead to erroneous inferences if the sampled group differs substantially from the population (Pollock et al. 1990; Nichols et al. 1994; Stover et al. 2012). For example, the Missouri Department of Conservation (MDC) manages for doves primarily on state-owned land (conservation areas) to provide harvest opportunities by planting crops such as sunflowers that attract doves (Bonnot et al. 2011). Biologists at conservation areas with large numbers of doves can band a large sample of birds per unit effort in comparison to elsewhere. Hence, banding outside conservation areas is not common. However, it is possible that MDC management concentrates birds, increasing harvest rates, and lowering survival estimates for the state subpopulation. Taken together, these pieces suggest juvenile and adult survival may not be representative of the state population (Schulz et al. 2017).

In addition to the potential biases in dove banding data, bias could also meaningfully influence productivity estimates (Schulz et al. 2013). In hunted species, the collection of wings from hunters can provide information on the number of juveniles present in a population relative to adults, allowing for estimation of productivity in the population. Since naïve juvenile doves are more vulnerable to harvest (Schulz et al. 2013), a differential vulnerability factor is included in the CMU IPM (Brownie and Pollock 1985; Seamans 2024). However, if the age structure of the birds in harvested areas does not reflect the overall population age structure across the state,

productivity estimates could be skewed. This, in turn, could also contribute to lower survival estimates when these parameters are estimated jointly, as in IPMs.

The implications of bias in various data sources used in IPMs to estimate population dynamics are important to understand so that future work can be designed that directly accounts for biases and provides more accurate population estimates. In addition to providing a robust analytical framework to evaluate population dynamics, IPMs can be used to test scenarios that examine how changes in data distributions might influence key parameter estimates. These simulations can provide additional insight into the robustness of inferences and guide improvements in future study design. To this end, we built a state-level IPM to estimate demographic parameters for mourning doves in Missouri and examined spatial variation in survival, productivity, and population growth across four ecological regions within the state. We compared Missouri's IPM estimates to those from the broader CMU and then simulated different data collection scenarios to evaluate how the distribution and intensity of data collection efforts, particularly banding and productivity data, may influence demographic inference. We hypothesized that mourning dove demographic rates exhibited spatial heterogeneity within Missouri at sub-state scales and that regions containing intensively managed dove areas exhibited lower survival probabilities, reducing the state-wide survival estimates. We further hypothesized that juvenile survival probabilities exhibited larger discrepancies between regions due to their higher vulnerability to harvest. We therefore predicted that (1) regions with dove management areas exhibited higher mortality and higher productivity, and (2) regions with lower survival disproportionately influenced state-wide demographic estimates.

METHODS

Study area and physiographic regions

We split the state of Missouri into five physiographic regions following Partners in Flight (PIF) designations to account for expected differences in land use patterns and ecological conditions that could contribute to variation in dove demography. These PIF regions represent distinct ecological units that were developed to support region-specific bird conservation plans (Taulman & Smith, 2002, Figure 1). The five regions are Prairie Peninsula, Osage Plains, Dissected Till Plain, Mississippi Alluvial Plain, and Ozark-Ouachita Plateau (Figure 1).

The Prairie Peninsula region was historically a mosaic of tallgrass prairie, oak savanna, and riparian forest, but now is primarily composed of agricultural areas and riparian forest. The Osage Plains region was historically largely tallgrass prairie but is now largely agricultural. The Dissected Till Plain is moderately dissected, glaciated, flat-to-rolling terrain that slopes gently toward the Missouri and Mississippi River valleys. The Mississippi Alluvial Plain is dominated by bottomland hardwood forests. The Ozark-Ouachita Plateau is dominated by oak-hickory and pine forests.

Our study was mostly conducted on state-owned conservation areas across the PIF regions that support dove harvest opportunities (Figure 1). The Prairie Peninsula region covers the northeastern portion of the state and includes the Eagle Bluffs Conservation Area, the August A. Busch Conservation Area, and the Columbia Bottom Conservation Area. The Osage Plains region spans the southwestern portion of the state and includes the Robert E. Talbot Conservation Area, the Bois D'Arc Conservation Area, and the Reed Memorial Wildlife Area. The Dissected Till plain region covers the north and northeastern portions of the state and contains the Pony Express Conservation Area. The Mississippi Alluvial Plain covers the smallest area of the state and is located only in the extreme southeastern corner. Otter Slough Conservation Area and Ten

Mile Conservation Area are both located within this area. The Ozark-Ouachita Plateau region spans the central and south-central portion of the state. This area did not contain any public areas consistently participating in dove harvest management efforts and subsequently produced few data (Table 1); therefore data from this area were grouped with the closest region by county.

Data collection

Banding data

The U.S. Geological Survey Bird Banding Lab provided banding and recovery data for doves in Missouri between 1999 and 2023. The coordinates for each band record were used to align it to its corresponding physiographic region. Individuals that were ascribed as unknown age at the time of banding or were banded outside of Missouri were excluded from analysis. We retained all recovery records representing subsequent harvest of banded individuals, regardless of harvest location, and discarded live reencounters. We used data from 39,856 banded individuals (17,648 adults, 22,208 juveniles) between 1999 and 2023, of which 4,792 (12%) were recovered (Table 1).

Harvest composition

Information about harvest composition (i.e., the proportion of harvested birds that were adults vs. juveniles) was collected at both the state and federal level (Table 1). State harvest data were collected between 2005 and 2018 at conservation areas at the discretion of the area manager. Hunters that harvested birds on these conservation areas were required to submit wings from harvested birds immediately following their hunt and state biologists aged them at the end of the season. The state wing collection efforts yielded a total of 77,703 wings (15,590 adults, 51,001

juveniles, 11,112 unknown age). Federal data were collected through national mail surveys as part of the U.S. Fish and Wildlife Service Harvest Information Program (Raftovich et al. 2024). The federal wing collection for doves between 2007 and 2023 yielded 9,687 wings (2524 adults, 5673 juveniles, and 1490 unknown age). The harvest location for each wing was used to associate it with its corresponding physiographic region. There were no state data collected in the Ozark-Ouachita Plateau. The federal data from the Ozark-Ouachita Plateau were grouped into the next nearest region.

Count data

Mourning dove abundance was estimated using roadside survey data, collected by MDC Conservation Agents. Routes spanned ~32 km in length and were established in each county in Missouri, surveyed annually during 1-10 June (weather permitting). Observers in a vehicle traveling <32 km/h recorded all doves and flocks sighted. The physiographic region corresponding to each county was used to group roadside survey data for the analysis.

Analytical approach

We constructed an IPM to estimate state-level and region-specific demographic parameters for mourning dove in Missouri across four distinct physiographic regions across 25 years. The model had three sub-models: (1) a survival and harvest sub-model, (2) a productivity model, (3) a population density model.

For each region, we developed an annual stage-structured matrix model (Lefkovitch 1965; Caswell 2001) with two age classes (juvenile and adult) and a pre-breeding census to link

population density estimates to survival, harvest and productivity. We assumed that the region-specific demographic patterns came from a shared, state-wide distribution.

Survival/Harvest

We used a multinomial two-age (juvenile and adult) dead-recovery model to estimate survival and harvest probabilities using banding data (Brownie and Pollock 1985). We did not consider sex in survival and harvest estimation as mourning dove cannot be reliably sexed based on wings/plumage (Pyle 2022).

We assumed that region-specific adult survival (S_{a_s}) and juvenile survival (S_{a_j}) shared a normal distribution across all regions a . For example, adult survival probability was estimated as:

$$\text{logit}(S_{a_s}) \sim \text{Normal}(\mu_{a_s}, \sigma_s) \quad \text{Eq. 1}$$

where μ_a was the mean annual adult survival across all regions in the state on the logit scale and σ_s described among-region variation in adult survival. We incorporated temporal variation in demographic rates by assuming annual parameter values were drawn from region-specific normal distributions, such that:

$$\text{logit}(S_{a_{s,t}}) \sim \text{Normal}(\mu_{a_{s,t}}, \sigma_t) \quad \text{Eq. 2}$$

where $\mu_{a_{s,t}}$ was the region-specific, time-dependent adult survival probability and σ_t described region-specific variation in adult survival. We estimated annual adult and juvenile kill rate (defined as the proportion of birds within each age class that were killed, K_j and K_a , respectively) at the state and region level, as for adult survival.

We used a logit link for survival probability (S) and kill rate (K), such that:

$$\text{logit}(S_{a,s,t}) \sim \text{Normal}(\mu_{a,s,t}, \sigma_{a,s,t}) \quad \text{Eq. 3}$$

$$\text{logit}(K_{a,s,t}) \sim \text{Normal}(\mu_{a,s,t}, \sigma_{a,s,t})$$

199

200 We modeled separate recovery rates for adults (f_a) and juveniles (f_j) to account for differing
 201 vulnerability to harvest:

$$f_{j,t,s} = K_{j,t,s} \times (1 - Cr) \times R \quad \text{Eq. 4}$$

$$f_{a,t,s} = K_{a,t,s} \times (1 - Cr) \times R$$

202 where K was the kill rate, Cr was probability a bird was crippled (i.e., killed by a hunter but not
 203 retrieved), and R was the probability that a retrieved bird was subsequently reported.

204 *Productivity*

205 We defined productivity (γ) as the ratio of juveniles to adults in the fall population and informed
 206 our estimates using age ratios from harvested wing samples. We assumed that productivity
 207 followed a log-normal distribution with a state-wide mean such that:

$$\log(\gamma_{t,s}) \sim \text{Normal}(\mu_{\gamma_s}, \sigma_{\gamma_t}) \quad \text{Eq. 6}$$

208 where $\gamma_{t,s}$ was the productivity of a given region s in year t , μ_{γ_s} was the average productivity of
 209 the region, and σ_{γ_t} described annual variation. Both regional and temporal variation were drawn
 210 from a half-Cauchy distribution.

211 We assumed that the observed proportion of juveniles harvested (Ψ) was an outcome of age-
 212 specific kill rates (K_j, K_a) and the true ratio of juveniles to adults (γ) in the fall population at
 213 time t for a given region s , such that:

$$\psi_{t,s} = \gamma_{t,s} \times K_{j,t,s} / (\gamma_{t,s} \times K_{j,t,s} \times K_{a,t,s}) \quad \text{Eq. 7}$$

214

215 We then modeled the observed proportion of juvenile wings in the harvest for each year t and
 216 region s as:

$$juvenile\ wings_{t,s} \sim Binomial(\psi_{t,s}, Total\ wings_{t,s}) \quad \text{Eq. 8}$$

217 *Density*

218 We used roadside count data to estimate population density according to region s . To account for
 219 potential observation error in the roadside count, we used a state-space formulation. The latent
 220 (i.e., unobserved) density process was divided into two age classes: age 1 juveniles (i.e., the
 221 spring following their hatch during summer) and adults. The juvenile and adult densities at year
 222 $t+1$ for each region (s) were defined as the outcome of the productivity model, survival model,
 223 and population density the previous year:

$$Dens_{j,t+1,s} = \gamma_{t,s} \times S_{j,t,s} \times (Dens_{a,t,s} + Dens_{j,t,s}) \quad \text{Eq. 9}$$

$$Dens_{a,t+1,s} = S_{a,t,s} \times (Dens_{a,t,s} + Dens_{j,t,s}) \quad \text{Eq. 10}$$

224 We modeled the observed counts as a zero truncated normal distribution and as a function of the
 225 latent overall density ($Dens$) in year t and region s such that:

$$count \sim Normal(Dens_{t,s}, \sigma_{count_s}) \quad \text{Eq. 11}$$

226 where σ_{count_s} represented region-specific observation error in the road count survey.

227 *Model fitting*

228 We parameterized the IPM in a Bayesian framework (Schaub and Kery 2021) using the package
 229 nimble (de Valpine et al. 2017) in Program R (R Core Team 2024). We specified vague priors for
 230 all state-level random effects (i.e., hyper-parameters) and region-specific and annual region-
 231 specific standard deviations. We used an informative prior for the crippling rate (Cr) based on
 232 previously measured crippling rate of dove in Missouri (Schulz et al. 2013).

$$Cr \sim Uniform(0.25, 0.29) \quad \text{Eq.}$$

233 We ran four chains and 800,000 iterations with a burn-in of 200,000 and thin of 10, resulting in a
 234 posterior distribution for each parameter of 240,000 values. Model convergence was assessed
 235 using the R-hat statistic (Gelman and Hill 2006) and visual inspection of chains. Convergence
 236 (R-hat values < 1.1 and good mixing of chains) was achieved for all estimated parameter values.
 237 We report mean estimates with 95% credible intervals (CRI).

238 *Correlating demographic estimates with population growth rate*

239 We correlated juvenile survival, adult survival, and productivity with population growth rate in
 240 each region and compared the strength of correlations among regions using posterior
 241 distributions (Pearson 1896; Kéry and Schaub 2012). We report all correlation coefficients
 242 (Pearson's r) with 95% CRI.

243

244 **Development of scenarios**

245 To inform future monitoring of mourning doves in Missouri, we developed a suite of scenarios
 246 that reflected anticipated changes in data collection schemes from MDC, which is the state
 247 agency responsible for dove conservation planning. The state's monitoring program has
 248 supported the collection of banding data and conservation area-specific wing data (to supplement

federal productivity data collection). Recently, the discontinuation of state-level productivity data collection has prompted interest in optimizing banding effort to support future monitoring objectives. To test the anticipated impact of reductions in the amount of productivity data collected, we reran our IPM with data collected either only by the state or only through the federal monitoring program. All other components of the IPM remained constant.

We also used our IPM structure to explore the potential impacts of changes in banding effort. We created scenarios reflecting either an increase or decrease in banding effort. Using the posterior estimates of survival from the baseline IPM, we generated simulated m-arrays for each of the four regions that represented 25%, 50%, 100% (current), 125%, 150%, or 175% banding effort relative to the existing data. Banding effort was adjusted based on the actual number of bands deployed each year, with 100% being the same number of bands as our actual dataset. We then reran the IPM changing only the input banding data to learn the relative impacts of increases or decreases in banding effort.

RESULTS

Regional variation in demographic parameters

Productivity

Mean dove productivity estimated from 1999 to 2023 was 2.53 juvenile females per adult female (95% CRI 1.81-3.96) and similar among regions (i.e., credible intervals sufficiently overlapped; Figure 2). Productivity tended to be highest in the Mississippi Alluvial Plain (2.81, CRI 1.60-4.63) and lowest in the Osage Plains (2.17, CRI 1.34-3.40), with intermediate values in the Dissected Till (2.72, CRI 1.62-4.29) and Prairie Peninsula (2.41, CRI 1.45-3.83) region. We

found no consistent trends within or among region. However, the high degree of overlap among credible intervals suggested there were no spatial trends in dove productivity across Missouri when taking into consideration both the federal and state productivity data.

Survival and harvest

Mean annual survival probability for dove among all regions was consistently higher for adults (0.39, CRI 0.24- 0.57) than juveniles (0.19, CRI 0.10-0.36; Figure 2). Survival probabilities were highest in the Mississippi Alluvial Plain (juvenile mean: 0.23, CRI 0.13-0.36; adult mean: 0.47, CRI 0.35, 0.60) and Dissected Till (juvenile mean: 0.23, CRI 0.13-0.35; adult mean: 0.43, CRI 0.32-0.55), and lowest in the Osage Plains (juvenile mean: 0.15, CRI 0.18-0.36; adult mean: 0.30, CRI 0.33-0.40) and Prairie Peninsula (juvenile mean: 0.13, CRI 0.07-0.21; adult mean: 0.32, CRI 0.23-0.43). Although survival varied among regions, relative differences between age classes were consistent. Survival probabilities were relatively stable among years within each region, with no strong directional trends (Figure 2).

Mean kill rate among years and regions was 0.27 (CRI 0.18-0.41) for juveniles and 0.21 (CRI 0.07- 0.39) for adults. At the scale of the individual regions, the credible intervals between juvenile and adult estimates overlapped, although the Mississippi Alluvial Plain had moderately higher juvenile kill rates in some years (Figure 2).

Density

Mean density among regions was 0.90 doves/km² (Figure 2). Density was highest in the Mississippi Alluvial Plain (mean: 2.05, CRI 0.33, 4.98) and Dissected Till (mean: 1.41, CRI 1.14, 1.69), and lowest in the Osage Plains (mean: 0.07 doves/km², CRI 0.01, 0.22) and Prairie Peninsula (mean: 0.80 doves/km², CRI 0.01, 0.25). Densities were consistent in Dissected Till,

and slightly increased in Mississippi Alluvial Plain, but with a wide credible interval. Densities in the Osage Plains and Prairie Peninsula declined toward zero from 1999 to 2023.

Correlating demographic estimates with population growth rate

Correlations between demographic estimates and population growth rate (λ_t) suggested similar mechanisms for population change among regions (Figure 3). Among the demographic parameters we estimated, productivity was most strongly correlated with λ_t in each region, with the highest correlation coefficients in the Mississippi Alluvial Plain (mean r : 0.75, 95% CRI 0.46-0.93) and Osage Plain (r : 0.69, CRI 0.40-0.90), followed by Prairie Peninsula (r : 0.64, CRI 0.30-0.88) and Dissected Till (r : 0.56, CRI 0.17-0.87). Juvenile survival probability also was strongly correlated with λ_t in all four regions, although correlation coefficients were smaller than those for productivity and λ_t . The correlation between juvenile survival probability and λ_t was strongest at Osage Plain (r : 0.63, 0.26-0.86), followed by Prairie Peninsula (r : 0.59, CRI 0.21-0.84), Mississippi Alluvial Plain (r : 0.58, 95% CRI 0.20-0.83), and Dissected Till (r : 0.50, CRI 0.10-0.79). Adult survival probability was not strongly correlated with λ_t (i.e., 95% credible intervals for correlation coefficients overlapped zero in all cases; Figure 3).

Scenarios

Productivity scenarios

The state-wide mean productivity estimate when the IPM was informed by state data alone was 2.83 juvenile females per adult female (CRI 1.97-4.66), as compared to 2.05 juvenile females per adult female (95% CRI: 1.16, 4.67) based on the federal productivity data alone. The regional estimates for the state data only scenario were 2.97 (CRI 1.74-4.82) in Dissected Till, 3.31 (CRI

315 1.82-5.59) in Mississippi Alluvial Plain, 2.41 (CRI 1.42-3.98) in Osage Plain, and 2.69 (CRI
316 1.52-4.54) in Prairie Peninsula. The regional estimates for the federal data only scenario were
317 2.38 (1.44, 3.74) in Dissected Till, 1.63 (0.86, 2.87) in Mississippi Alluvial Plain, 1.48 (0.83,
318 2.49) in Osage Plain, and 1.98 (1.14, 3.26) in Prairie Peninsula (Figure 4).

319 The state-wide mean survival probability was 0.18 (CRI 0.11-0.32) for juveniles and 0.39 (CRI
320 0.24-0.56) for adults when estimated from the state data only and 0.22 (0.10, 0.45) for juveniles
321 and 0.39 (0.25-0.57) for adults when estimated from the federal data only. Regional juvenile
322 survival probabilities estimated from the state data alone were 0.21 (CRI 0.12-0.32) in Dissected
323 Till, 0.21 (CRI 0.35-0.60) in Mississippi Alluvial Plain, 0.15 (CRI 0.08-0.23) in Osage Plain, and
324 0.13 (0.07-0.22) in Prairie Peninsula. Regional adult survival probabilities estimated from the
325 state data alone were 0.43 (CRI 0.31-0.56) in Dissected Till, 0.48 (CRI 0.35-0.60) in Mississippi
326 Alluvial Plain, 0.31 (CRI 0.22-0.40) in Osage Plain, and 0.32 (CRI 0.22-0.44) in Prairie
327 Peninsula. For the estimates based on the federal data alone, regional juvenile survival estimates
328 were 0.26 (0.16, 0.38) for the Dissected Till, 0.30 (0.17-0.45) for the Mississippi Alluvial Plain,
329 0.15 (0.09-0.23) for the Osage Plain, and 0.13 (0.08-0.21) for the Prairie Peninsula. Regional
330 adult survival estimates based on the federal data alone were 0.43 (0.33-0.54) for the Dissected
331 Till, 0.48 (0.37-0.58) for the Mississippi Alluvial Plain, 0.31 (0.23-0.39) for the Osage Plain, and
332 0.33 (0.24-0.42) for the Prairie Peninsula.

333 Regional density estimates and the associated precision varied between the state and federal data.
334 For the estimates based on state data alone, estimated densities were highest in the Mississippi
335 Alluvial Plain (mean: 1.88, CRI 0.33-4.52), followed by Dissected Till (mean: 1.44, CRI 1.16-
336 1.75), with lower densities in Osage Plain (mean: 0.08, CRI 0.01, 0.26) and Prairie Peninsula
337 (mean: 0.10, CRI 0.01-0.32). The density estimates based on federal data alone were highest in

the Dissected Till (mean: 1.41, CRI: 1.17-1.67), followed by Mississippi Alluvial Plain (mean: 1.08, CRI 0.03-4.59), with lower densities in the Osage Plain (mean: 0.056, CRI 0.008-0.156) and PP (mean: 0.067, CRI 0.009-0.191).

Banding effort scenarios

Banding effort influenced the precision of our model survival estimates as measured by the 95% CRI width relative to baseline (100%) effort (Figure 5). Across regions, reducing banding effort in half increased CRI widths by 36% for adults and 22% for juveniles. Further reductions to 25% banding effort increased CRI widths by 57% for adults and 75% for juveniles and caused model convergence issues ($R\text{-hat}$ values > 1.1). A moderate increase in banding effort to 125% of current effort resulted in a 7% and 4% reduction in mean credible interval width for adults and juveniles, respectively. Further increases to 150% and 175% banding effort reduced credible intervals by 14% and 20% respectively for adult survival estimates. For juvenile survival estimates, the increases to 125% and 150% reduced mean credible interval width by 19% with less than 0.3% increase between 125% and 150%. Precision at the state level was not strongly impacted by banding increases or decreases.

DISCUSSION

We formed an integrated population model (IPM) to estimate mourning dove population dynamics across four physiographically-unique regions and 25 years in Missouri, USA to determine causes for discrepancies between like-for-like demographic estimates for the state of Missouri relative to the surrounding 13-state area, the latter of which are consistently higher. Our IPM revealed regional differences in dove demography across Missouri, including lower annual survival probabilities in areas more heavily managed for doves and density estimates in the same

360 areas trending toward local extinction. Productivity was similar among regions and to previous
361 estimates in the Central Management Unit (CMU, i.e., the among-state region that informs
362 continental dove harvest regulations and includes Missouri; (Tomlinson and Dunks 1993; Schulz
363 et al. 2013). Productivity and juvenile survival were proximate mechanisms for population
364 change of mourning dove across regions in Missouri, with adult survival showing minimal
365 correlation with population change.

366 Wildlife populations must balance the cost of current reproduction on future reproduction with
367 longer-lived species theoretically having lower incentive to invest in short-term reproduction
368 (Williams 1966). In practice, these tradeoffs and life history strategies can vary greatly among
369 and within species (Culina et al. 2019; Chang et al. 2024). Although adult survival can be an
370 important demographic rate (Schorcht et al. 2009; Chitwood et al. 2015; Nousiainen et al. 2025),
371 in the absence of large variation in annual adult survival even the populations of long-lived
372 species may be largely driven by productivity and juvenile survival (Genovart et al. 2018;
373 Pfeiffer and Schaub 2023). Our finding that productivity and juvenile survival drive mourning
374 dove population change aligns with life-history expectations for this short-lived species, as
375 individuals typically live one to two years (Otis et al. 2008). Given that a large proportion of the
376 population will only have one breeding season in which to reproduce, there may be limited
377 fitness benefits to delaying reproduction in favor of reproduction in future years. Additionally,
378 our annual estimates of adult survival exhibited no trends over time, further supporting the
379 expectation that juvenile survival and productivity would largely explain population growth.
380 Despite laying only 2 eggs on average per clutch, mourning doves can be highly productive in a
381 single breeding season by rearing multiple broods (Otis et al. 2008). They can begin nesting
382 early, as they are able to produce crop milk for their nestlings rather than depend on insect

emergence, can have multiple broods active at the same time, and renest relatively quickly due to reuse of nest sites and minimal nest construction (Westmoreland et al. 1986). Although our results are generally consistent with our expectations of dove life history theory, the annual density (and thus population growth rates) for two of the regions was lower than expected based on observed densities. These low-density estimates were likely driven by biased survival estimates in these two regions stemming from non-representative data collection (see further discussion below).

Achieving a representative sample in any plant or wildlife demographic study can be difficult to verify. Even in the absence of bias from sampling design or human observations, bias can stem from a number of sources such as the behavior of individuals sampled (Biro 2013; Johnstone et al. 2021), phenological characteristics of sampled individuals (Kendall et al. 2011), spatial heterogeneity (Fahrig and Nuttle 2005; Ten Caten and Dallas 2025), or timing of sampling (Piironen et al. 2023). Species which are both broadly distributed and sustain large population sizes are particularly susceptible to bias as it is typically impossible to sample a large proportion of the population and to evenly distribute sampling effort spatially. The mourning dove exemplifies these challenges, as it occurs across nearly every state and province in North America and numbers ~350 million individuals in the contiguous U.S. alone. Fewer than 0.01% of mourning doves in the U.S. are banded and demographic estimates are made at the scale of U.S. states or coarser (Seamans 2024), potentially obscuring underlying demographic patterns relevant to conservationists. By reducing the scale to ecological regions within Missouri, we were able to illustrate that demographic rates varied among regions. Although our state-wide survival probabilities were similar to those from the CMU IPM (mean adult survival 0.19 vs 0.15, juvenile survival 0.39 vs 0.36, respectively; Seamans 2024), we found substantial variation

in survival estimates among physiographic regions. Juvenile survival probabilities ranged from 0.13 in the Prairie Peninsula (northeastern region) to 0.23 in the Mississippi Alluvial Plain (southeastern region) and adult survival ranged by as much as 0.17 between regions. Adult survival was highest in the Mississippi Alluvial Plain (0.47), which was approximately the CMU average (0.48), suggesting that adult survival is not consistently low across the state.

Nearly 70% of banded birds in our analyses came from the Prairie Peninsula and Osage Plains (Table 1), which had consistently lower survival probabilities compared to other regions and nearby states. These regions contain the Columbia Bottom Conservation Area and the James Reed Memorial Wildlife Area (Figure 1), which have the highest numbers of birds harvested among state-monitored areas. Because these areas are managed to provide resources for doves and are state owned, they provide an opportunity for managers to band large numbers of doves with fewer man-hours and without land access limitations. Given the size of the overall dove population, large numbers of doves must be banded to support monitoring efforts. However, our results suggested that these data may not be representative of the population as a whole. Both the Prairie Peninsula and Osage Plain regions had density estimates that did not reflect the observed dove densities, likely driven by survival estimates that were ~40% lower than the rest of the state. Birds banded in higher harvest conservation areas in Missouri may be at a greater than average risk of mortality (Schulz et al. 2017), and by sampling heavily in these regions, the overall state survival estimates may be biased low, in turn forcing density estimates near zero. Alternatively, these regions may also be demographic sinks, reliant on an influx of birds from elsewhere in Missouri or surrounding states to prevent the extinction of the subpopulation.

Our scenarios for productivity illustrated the potential biases stemming from non-representative sampling. State-managed wing data, collected at high-harvest sites, produced consistently higher

age ratios than federal data, suggesting an overrepresentation of juveniles. This effect was particularly pronounced in the Mississippi Alluvial Plain, causing a substantial shift in productivity estimates there, while other regions remained more stable. Although there were overlapping CRI between the state-only and federal-only productivity scenarios at the state level, regional productivity estimates based on data collected at the conservation areas were as much as double those produced from the federal data, considering all other inputs constant. Because the absolute number of wings collected at the conservation areas was much greater than the federal collections, when both inform the model, the state-based wing data will have a stronger effect. One potential explanation for the higher proportion of juveniles at the conservation areas is that they support higher juvenile production. If such areas act as "super producers" that would not exist without intensive management, then harvest from these areas likely exerts limited demographic pressure on the broader population (i.e., beyond the conservation area). The state collected productivity data also gave rise to greater interannual variability in the estimates, creating greater potential for more rapid shifts in population size if they are not offset by survival.

Our simulated banding effort scenarios revealed little gain in precision of survival estimates with increased banding effort at the state level, likely due to regional differences in demographic parameters. Regional estimates of survival were improved with greater banding effort, however, there was not a substantial increase in precision of juvenile survival probability until 175% more juveniles were banded, compared to the actual number banded. At 175% effort, the precision for juvenile and adult survival probability improved dramatically. The apparent increase needed to improve juvenile survival probabilities likely stems from the age structure of the population. Although there were ~20% more juveniles banded than adults in total number, our productivity

estimates suggest that there should be 2 to 3 juveniles per adult in the population. Consequently, there was less sampling coverage for the juveniles than the adults despite more juveniles being banded overall. Our simulated results provide context that the current banding effort is sufficient to precisely estimate adult survival probability, but may be insufficient to precisely estimate juvenile survival probability.

Because our work suggests that demographic estimates for doves in Missouri are biased due to banding near conservation areas, we believe that a more even distribution of banding effort across the state would lower the bias, as birds could be banded away from high-harvest conservation areas. Our modeling framework was only able to account for spatial heterogeneity at the regional level. However, broader sampling could support finer scale spatially explicit modeling in the future. In the case of the Prairie Peninsula and Osage Plains regions, the natural differences between sub-populations seem overshadowed by sampling bias. Given the lower sampling coverage for juvenile doves, efforts targeting this age class such as banding nestlings may be considered to improve survival estimation. Further field studies are needed to evaluate whether the higher proportion of juveniles at conservation areas reflect higher productivity at these sites or whether food resources during the hunting season may be drawing in juveniles from surrounding areas.

More broadly, these results remind us to seek representativeness in demographic sampling designs and contextualize the challenges of developing inferences about populations based on focal site information. Concentrated monitoring at sites where access is feasible and where active management is on-going offers clear logistical advantages yet can unintentionally bias locations that are not demographically representative of the population as a whole. This is particularly true in large populations with large ranges encompassing multiple ecoregions. Our IPM framework

475 provides practitioners with an approach for estimating both state and sub-state (regional)
476 demographic rates to robustly investigate the extent to which spatial heterogeneity may influence
477 population-level inference. Allowing regional demographic rates to vary from the state-wide
478 average revealed patterns and discrepancies that would have been obscured by a single pooled
479 estimate, highlighting the importance of assessing monitoring frameworks at multiple scales.

Table 1. Sample sizes by regions of the productivity and banding datasets.

	Banded	Wing	Wing	Band
	birds	return –	return –	recoveries
Year Range	1999-2023	2005–2018	2003–2022	1999–2023
Dissected Till	4,140	9,619	1,871	434
Prairie Peninsula	13,675	6,625	1,451	1,408
Osage Plains	17,477	40,282	1,131	2,234
Ozark-Ouachita	1,267	0	1,139	86
MS. Alluvial Plain	8,092	10,065	810	772

Figure legends

Figure 1. Map of the physiographic regions in the state of Missouri with each region represented in a different color. The conservation areas that contributed data are noted. ABCA – August A. Busch Conservation Area; BDCA – Bois D’Arc Conservation Area; CBCA – Columbia Bottom Conservation Area; EBCA – Eagle Bluffs Conservation Area, OSCA – Otter Slough Conservation Area; PECA – Pony Express Conservation Area; RMWA – James A. Reed Memorial Wildlife Area; TACA – Robert E. Talbot Conservation Area; TMCA – Ten mile Pond Conservation Area.

Figure 2. Annual estimates of key demographic parameters for Mourning Doves across four regions in Missouri, USA: DT = Dissected Till Plain, MAP = Mississippi Alluvial Plain, OP = Osage Plains, and PP = Prairie Peninsula. Each row represents a different parameter—productivity, survival, kill rate, and density—with columns corresponding to the four regions. Estimates for adults (red) and juveniles (blue) are shown where applicable, with shaded areas representing 95% credible intervals. Dashed horizontal lines in the productivity, survival, and kill rate panels indicate grand mean estimates across all regions (i.e., not accounting for regional differences). Density estimates are shown from 1999 to 2024; all other parameters span 1999 to 2023.

Figure 3. Posterior mean correlations between demographic rates (adult survival, juvenile survival, and per capita productivity and λ (population growth rate)). Adult survival did not credibly affect the population.

507

508 Figure 4. Key demographic estimates for Mourning Doves across four regions in Missouri, USA:
509 DT = Dissected Till Plain, MAP = Mississippi Alluvial Plain, OP = Osage Plains, and PP =
510 Prairie Peninsula. Each row is labeled with its corresponding productivity scenario (i.e. federal
511 productivity data only or state productivity data only). Survival estimates for adults (red) and
512 juveniles (blue) include shaded areas representing the 95% credible intervals and the overall
513 mean across regions is represented by a dashed line.

514

515 Figure 5. Survival estimates and 95% credible intervals based on each banding effort scenario for
516 each region in Missouri USA: DT = Dissected Till Plain, MAP = Mississippi Alluvial Plain, OP
517 = Osage Plains, PP = Prairie Peninsula, state = state wide mean. Credible intervals decreased as
518 banding effort increased and the effect was more pronounced in the regions with higher initial
519 banding effort (thereby increasing the raw number of bands added or subtracted from each
520 scenario).

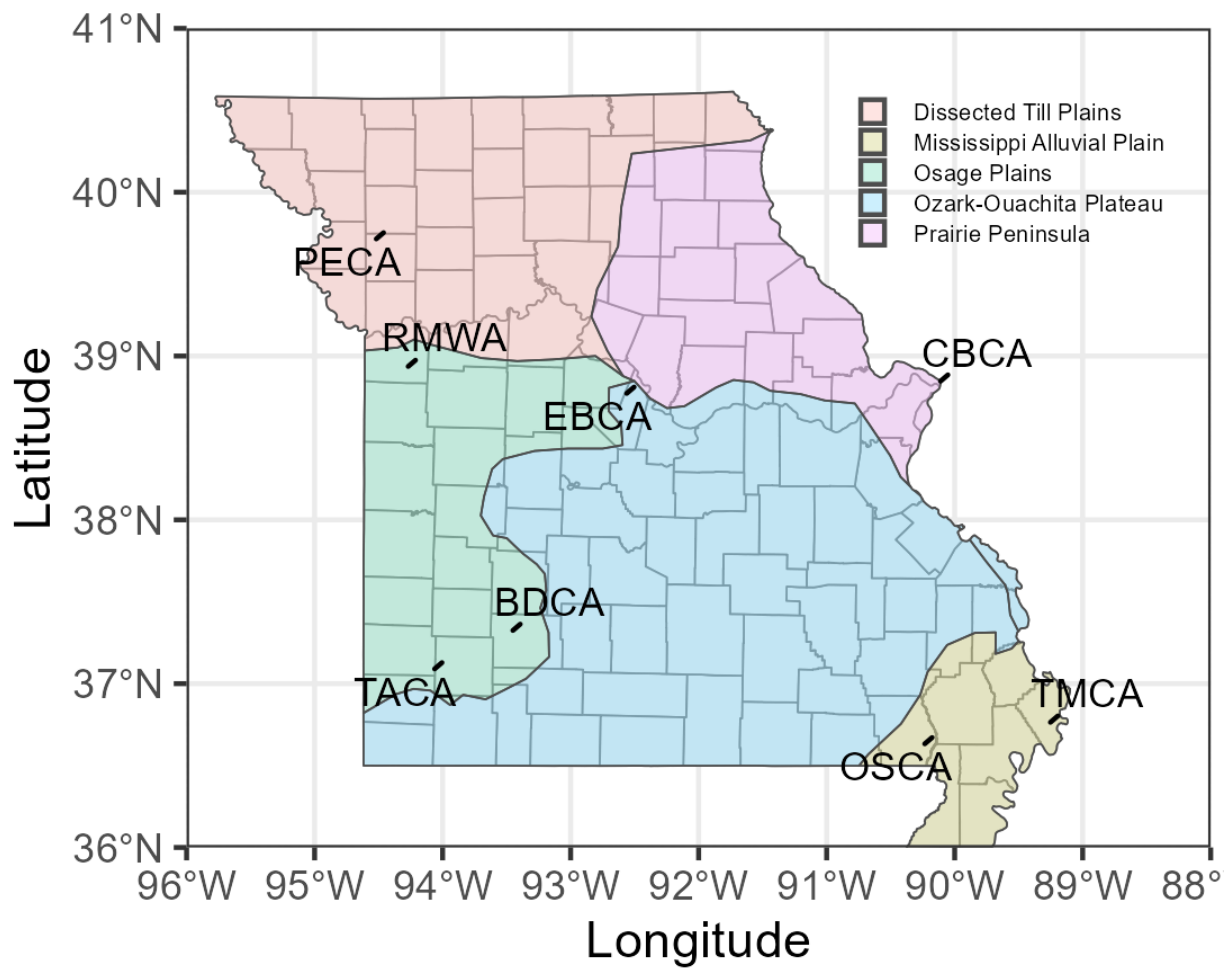


Figure 1.

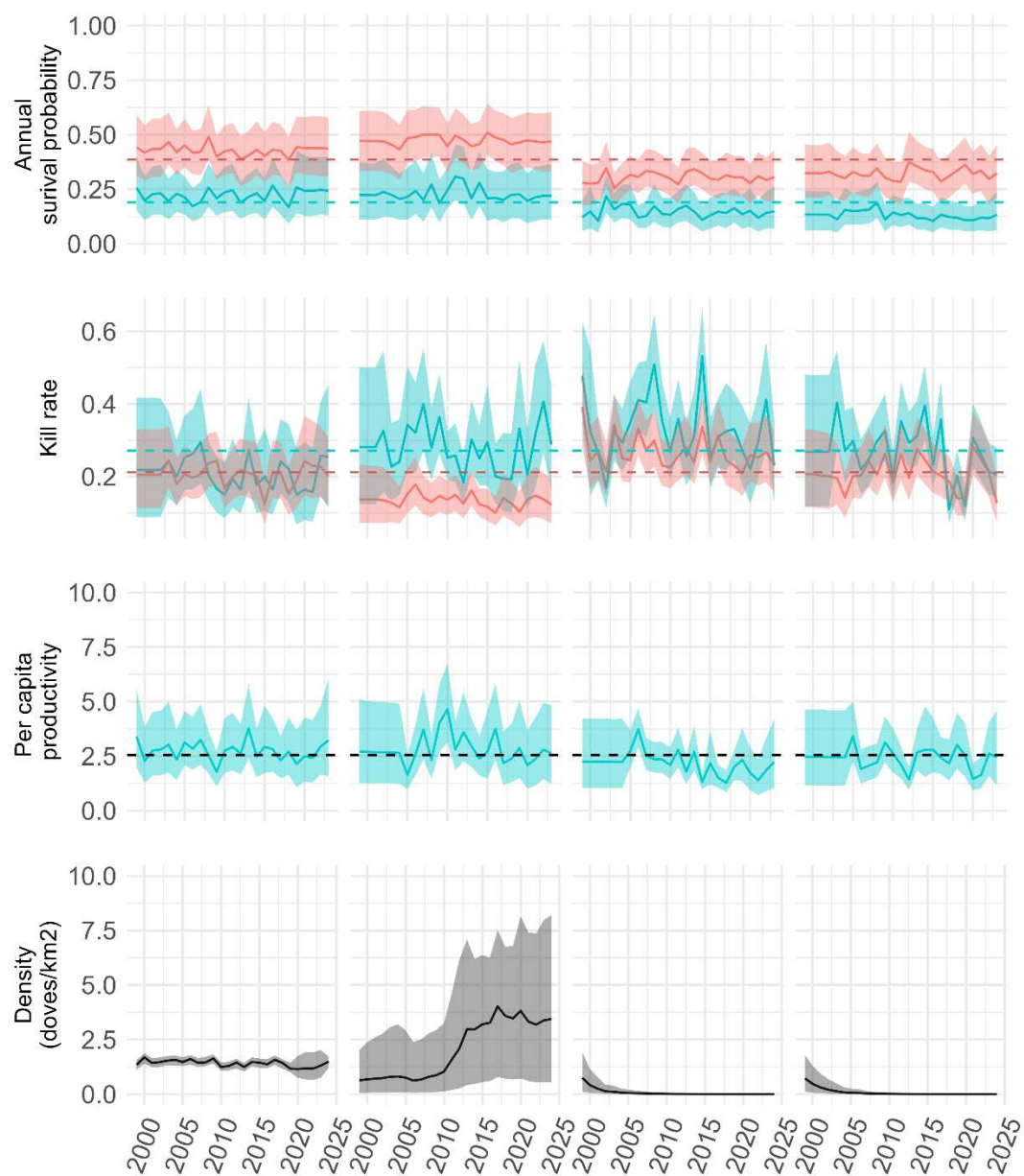


Figure 2.

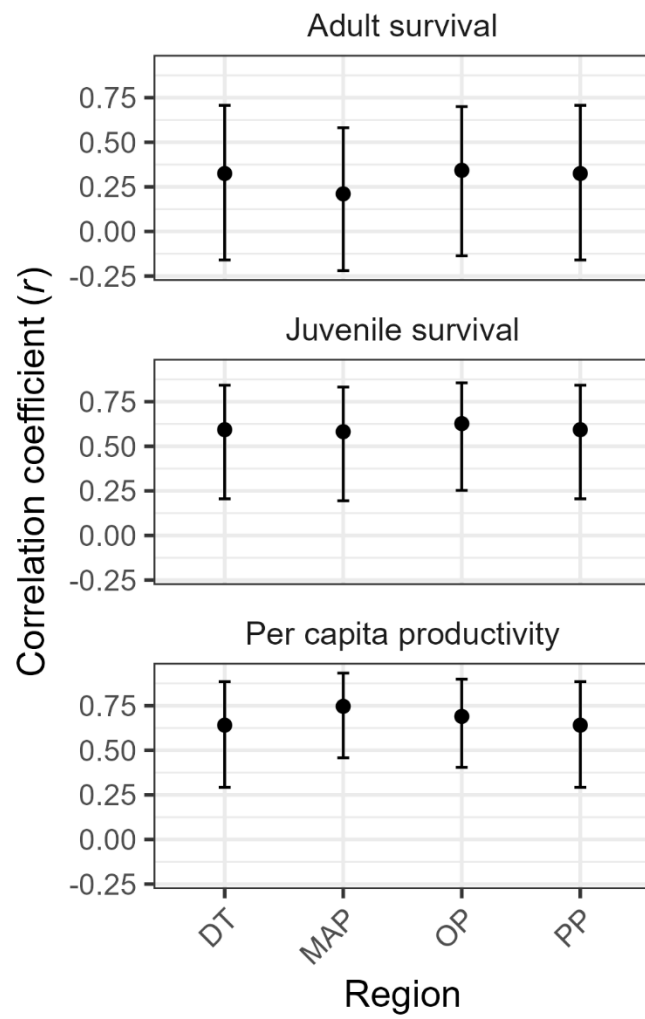


Figure 3.

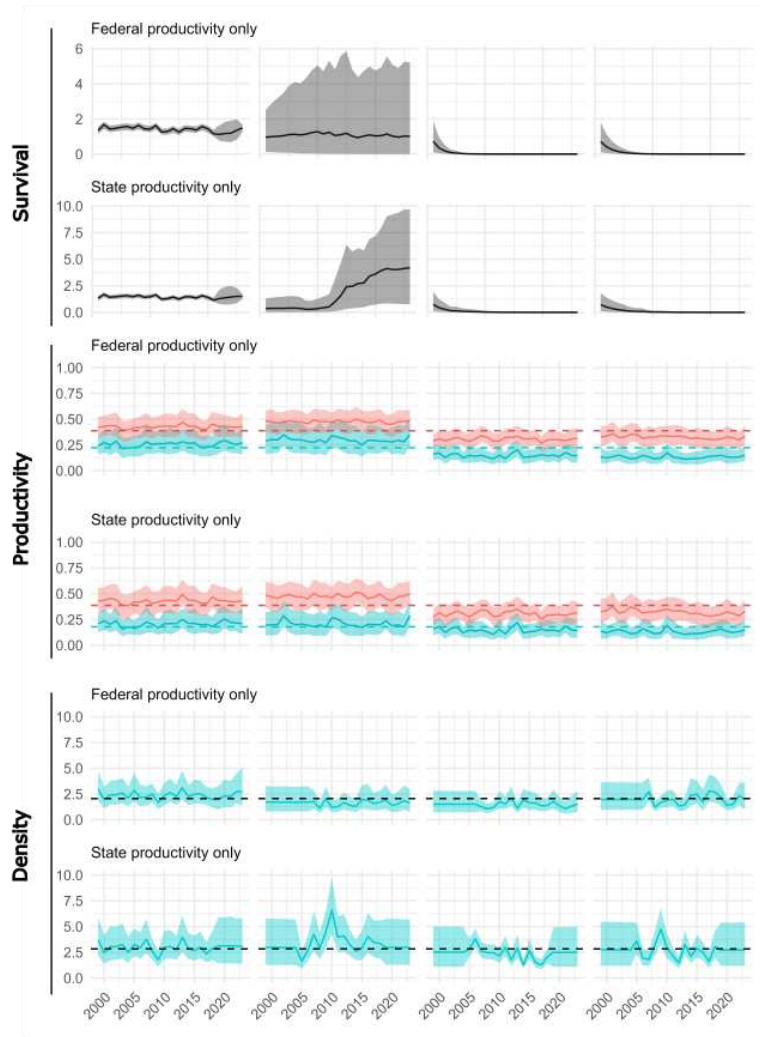


Figure 4.

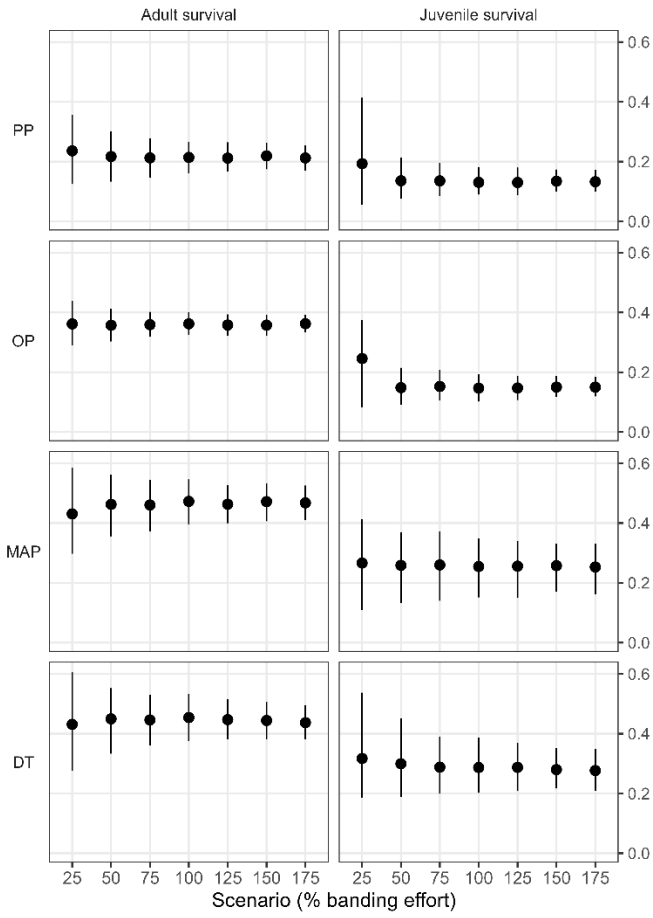


Figure 5.

521 **DECLARATIONS**

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530 **Conflicts of interest**

531 Not applicable.

532 **Ethics approval**

533 Not applicable.

534 **Consent to participate**

535 Not applicable.

536 **Consent for publication**

537 Not applicable.

538 **Availability of data and material**

539 Banding and recovery data are publicly available through the United States Geological Survey
540 Bird Banding Lab. Federal productivity data are available from the United States Fish and
541 Wildlife Service (Parts Collection Survey). Missouri survey and productivity data are available
542 by request from the Missouri Department of Conservation.

543 **Code availability**

544 Model code is provided in Electronic Supplementary Materials.

545 **Authors' contributions**

546 Author contributions: All authors contributed to idea development and manuscript writing. EE
547 performed the statistical analysis. Data were collected by the Missouri Department of
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