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Evaluation of seasonal site-level demography and management for northern bobwhite using integrated population models

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ABSTRACT

Understanding the effects of landscape management on northern bobwhite (*Colinus virginianus*) population growth requires information on seasonal- and stage-specific demographic parameters linked across the full annual cycle. We evaluated site-level seasonal dynamics and population growth of bobwhites in southwest Missouri and compared differences between three extensively and two intensively managed sites from 2016 to 2019. Extensively managed sites were continuous tracts of native prairie. Intensively managed sites were composed of smaller native and non-native grassland units interspersed with strip crops, food plots, and woody field borders. We radio-marked adults and broods to estimate survival and productivity, conducted spring whistle counts to estimate abundance and developed a two-season, two-stage, two-sex integrated population model to estimate population dynamics. The number of young hatched per female-incubated nest was greater on the three extensively managed sites compared to the two intensively managed sites. Six-month period survival of adults during the breeding season was also greater on the three extensively managed sites compared to the two intensively managed sites. One hundred-day juvenile breeding season survival varied among sites and was highest on Talbot, compared to juvenile breeding season survival on the other four study sites. Six-month, non-breeding season period survival was lowest on the two smallest extensively managed sites, Stony Point Prairie and Shelton Conservation Area compared to non-breeding season survival on the other three study sites. Annual changes in bobwhite abundance were weakly correlated with female fecundity, though this positive relationship was stronger on extensively managed sites. Intensively managed sites exhibited low mean fecundity and breeding season adult survival relative to those that resulted in a stable population. Populations across sites declined from 2016 to 2019 and estimates of annual population growth rates overlapped across sites. Differences between observed changes in bobwhite abundance and estimates of observed demographic rates at some sites suggest unmeasured processes such as movement or bias associated with data and model assumptions influenced estimated vital rates. Overall, our integrated population model was an effective tool for understanding site-level seasonal dynamics and population growth of bobwhites. Based on comparisons of demography between extensively and intensively managed sites, we suggest increased native grassland cover managed with prescribed fire, low intensity grazing, and high mowing may increase bobwhite nesting success and breeding season adult survival, however, achieving stable or increasing rates of population growth may also require increased juvenile breeding season and non-breeding season survival.

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1. Introduction

Evaluating seasonal contributions to annual population dynamics is critical for management of species given seasonally specific threats (Hostetler et al., 2015; Villellas et al., 2015) and the dependent nature of ecological processes occurring across seasons. Only recently have research efforts focused on evaluation of seasonal components in a full annual cycle framework (Marra et al., 2015). Seasonal threats to animal populations may include changes in predator communities, habitat disturbances, or weather patterns. Evaluating seasonal dynamics in an annual framework allows study of carry-over effects, which are processes occurring in one season that explain reproductive success or survival in a subsequent season (Harrison et al., 2011). These intra-annual processes driving annual dynamics can be accounted for in a periodic population model to better understand temporal variation in vital rates regulating population growth (Hunt and Tongen 2017, Rushing et al., 2017).

Population age structure and composition may also affect the contribution of vital rates to population growth. Hence, researchers often incorporate age-structured demographic information in their models but rarely account for male and female composition. Single-sex, female-based population models assume either (1) sexes exhibit similar vital rates, or (2) female dynamics drive population change. Male and female survival, however, may differ due to behavioral and/or environmental interactions. Moreover, in species where males either contribute to or limit reproductive success, biased sex ratios may influence annual fecundity rates, violating the assumption of female dominance (Caswell and Weeks 1986; Gerber and White 2014). Two-sex population models are necessary to evaluate population viability where vital rates differ between males and females, and where sex ratios may be skewed or vary due to those differences. Integrated population models (IPMs) provide a holistic approach for leveraging multiple data types to quantify demographic mechanisms of population change while accounting for age and sex structure, and testing hypothesized drivers (Rushing et al., 2017; Weegman et al., 2017, Zhao et al., 2019).

Northern bobwhite (*C. virginianus*; hereafter bobwhite) are an early successional, shrub-obligate upland gamebird of the eastern United States. Bobwhite have low annual survival and rely on high productivity and recruitment to maintain populations (McConnell et al., 2018). Bobwhite exhibit a flexible mating system in which both females and males can incubate nests and attend broods as pairs or independently over a relatively long breeding season that allows for multiple nesting attempts (Roseberry and Klimstra 1984; Curtis et al., 1993; Burger et al., 1995b). Bobwhite complete their full life cycle on a single landscape, but are exposed to seasonally-specific threats (Stoddard 1931; Brennan et al., 2014; Janke et al., 2017). Bobwhite have experienced long term, rangewide population declines largely explained by habitat loss, fragmentation, and degradation (Leopold 1931; Brennan 1991; Hernández et al., 2013). In Missouri, abundance has declined by 80% since 1967 and rate of loss has accelerated over the past 15 years (Sauer et al., 2017). Local exceptions to rangewide declines occur on landscapes purposefully managed for wildlife (McConnell et al., 2018). Population recovery on an altered landscape requires a better understanding of the influence of management strategies on full annual cycle dynamics.

Traditional wildlife management approaches for bobwhite often incorporate agricultural strip crops, food plots, and woody field borders among fragmented grassland units and have been applied to many public and private lands (hereafter "intensively managed sites"; Williams et al., 2004). The conservation efficacy of intensively managed sites relative to larger continuous tracts of native grasslands has not been examined. Management of large native grasslands with fire and low-intensity grazing, provide bobwhite with a mosaic of habitats suitable for nesting, brood-rearing, foraging and cover (hereafter "extensively managed sites"; Taylor et al., 1999a, Richardson et al., 2020). By contrast, agricultural cover on intensively managed sites may reduce nest success and adult survival during the breeding season and reduce usable space for bobwhite during the non-breeding season (Taylor et al., 1999b; Potter et al. 2011; Janke et al. 2013). Also, proximity to mature woody edges on intensively managed sites may reduce brood success (Sinnott et al. 2021b), however the availability of woody vegetation is important during the non-breeding season as protective cover (Janke et al., 2015; Mosloff et al., 2021). Bobwhite population growth may be correlated with non-breeding season survival, breeding season adult survival, and number of young hatched (Folk et al., 2007; Sandercock et al., 2008; Gates et al., 2012; Williams et al., 2012; Rosenblatt et al., 2021).

We evaluated bobwhite population dynamics across the full annual cycle at five sites in southwest Missouri. Land management differed among sites; two sites were intensively managed and three sites were extensively managed. We leveraged whistle count, nest monitoring, and radio-telemetry data in a joint analysis of abundance, fecundity, and seasonal survival to inform population management of a rapidly declining gamebird on public lands. Our objectives were to develop a two-season, two-stage (*i.e.*, juveniles and adults), two-sex integrated population model to estimate population dynamics to (1) evaluate site-level variation in seasonal vital rates and annual changes in bobwhite abundance on intensively and extensively managed sites, and (2) identify seasonal- and sex-specific vital rates driving annual population change. We predicted bobwhite populations on extensively managed sites would have greater fecundity and seasonal survival probabilities compared to intensively managed sites. We predicted that as a species with an especially fast life-history strategy characterized by high fecundity and low annual survival rates, bobwhite population growth would be most correlated with the number of young hatched and survival of young to fall recruitment. We also evaluated how model parameterization handles unmeasured demographic and influences vital rate estimates. We predicted vital rates with the least data would be most sensitive to change caused by parameterization. Our study represents a unique approach to addressing landscape-scale effects of management on full-annual cycle demography using an unusually complete dataset across the annual cycle of an upland game bird.

2. Materials and methods

We estimated seasonal age- and sex-specific survival and fecundity, as well as abundance and population growth for bobwhite in the eastern tallgrass prairie region of southwest Missouri, USA from 1 May 2016 to 1 May 2019 (Fig. 1). The gently rolling plains of this region were once dominated by tallgrass prairie interspersed with oak (*Quercus* spp.) woodlands and savannas. While the historical prairie landscape has been heavily modified by agriculture, this region was identified by the National Bobwhite Conservation Initiative as having high potential for bobwhite recovery (Palmer et al. 2011).

Our study sites included five Conservation Areas managed by Missouri Department of Conservation (MDC). Shawnee Trail Conservation Area (1471 ha) and Robert E. Talbot Conservation Area (1764 ha) were intensively managed sites, which incorporated small units (<1–24 ha) of agriculture and woody vegetation to provide food and cover for wildlife among grassland units maintained with fire, low-intensity grazing, and mowing (Fig. 2A, Fig. 2B). Shelton Memorial Conservation Area (129 ha), Stony Point Prairie Conservation Area (388 ha) and Wah'Kon-Tah Prairie (1226 ha) were extensively managed sites characterized by continuous tracts of native grassland maintained with fire, grazing, and mowing (Fig. 2A, Fig. 2C). While all sites included grassland units that were burned and grazed, the land cover composition and species richness of grasslands were distinct between intensively and extensively managed sites. Native grasslands on intensively managed sites were either native grass plantings or reconstructed prairies and species richness in these units ranged from fewer than 50 to 100 plant species. These grasslands were also smaller (4–28 ha) and fragmented by woodland or agricultural management units. By contrast, native grasslands on extensively managed sites were larger (>100 ha) continuous native

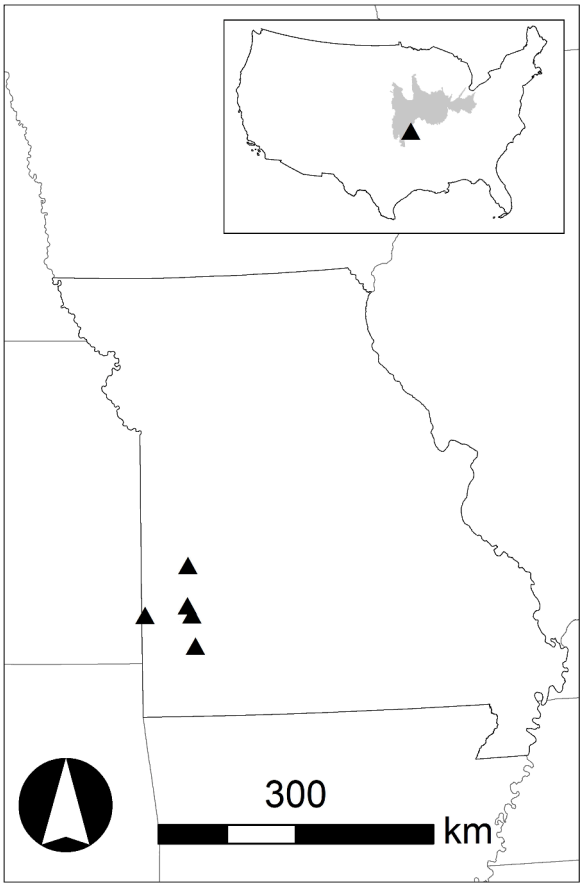

Fig. 1. Study area in which we evaluated site-specific variation in northern bobwhite full annual cycle demography at five Conservation Areas (▲) managed by Missouri Department of Conservation within the eastern tallgrass prairie region (gray) of southwest Missouri, USA, 2016–2018.

prairie and included of over 200 native plant species. While species richness was greater on extensively managed sites compared to intensively managed sites, grassland structure was similar across all sites due to similar disturbance regimes applied. All conservation areas used low-intensity grazing practices consisting of 1 animal unit per 4–5-acres for 90 to 120 days from April to August. Grazing units were rested every 1–4-years. All areas also used patch burn grazing, whereby 1/3 of each unit was burned annually or biannually followed by a rest period. Prescribed burns occurred September–April every 1–3-years. For the purposes of our study, we assumed Shawnee Trail and Talbot represented intensive management and Shelton Memorial, Stony Point Prairie, and Wah'Kon-Tah Prairie represented extensive management. We acknowledge that this is an observational study and that other factors beyond our control, such as study-area size and harvest pressure, differed among sites. Private lands surrounding these Conservation Areas were largely converted to tall fescue (*Festuca arundinacea*) pastures and row crop fields.

Hunting was permitted on all five study sites, except for the southern half of Wah'Kon-Tah Prairie. Hunting season opened 1 November and closed 15 January on all sites, except Talbot. Hunting season on Talbot closed 15 Dec and only half-day hunting was permitted. We did not have data on variation in harvest pressure across sites and years.

2.1. Data

We collected survival, fecundity, and abundance data on our five study sites beginning in February for three complete years 2016–2018 in cooperation with MDC. We captured bobwhite using funnel traps in February and March and fitted with uniquely numbered leg bands and 6-g necklace style radio-transmitters (<5% of adult body mass) with an expected battery life of 9-months (model AWE-QII from American Wildlife Enterprises, Monticello, FL, USA). Radio-marked adult bobwhite were tracked at least three times per week to monitor adult breeding season survival. We located nests during the breeding season when adults were tracked to the same location on consecutive days. We monitored nest fate and the number of eggs hatched per radio-marked adult to estimate fecundity. Once nests hatched and initial brood size was determined based on egg count, brood attending adults were

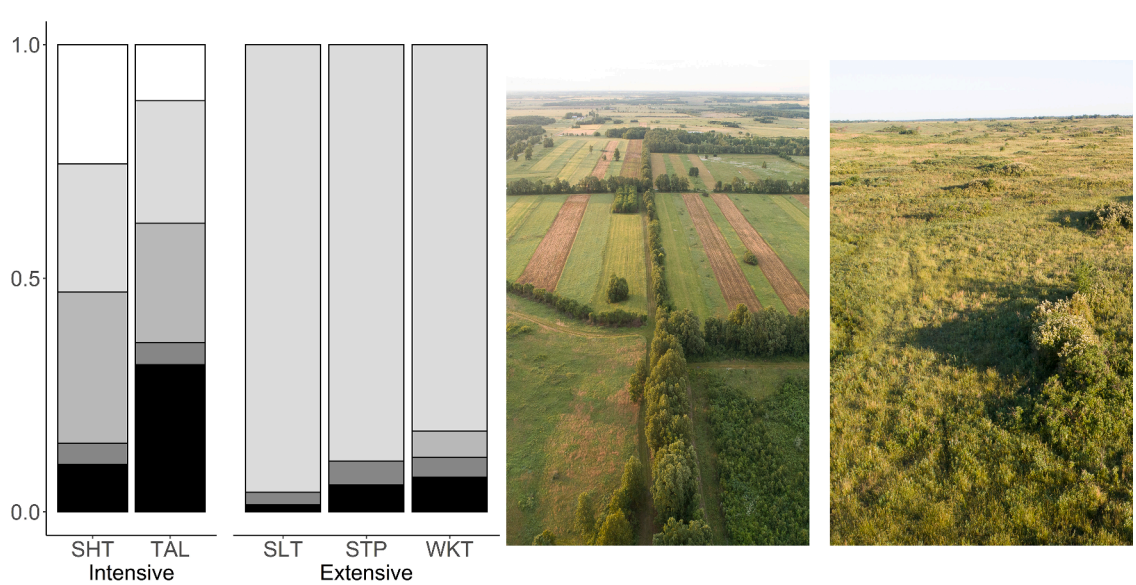

Fig. 2. Vegetation composition varied among the five study sites in which we estimated seasonal demography and annual dynamics of northern bobwhite in southwest Missouri, USA 2016–2019. A) All sites included native grassland cover (NatGr) and shrub cover. Two intensively managed sites had more agricultural crop (Ag), non-native grassland cover (NonNGr), and tree cover compared to the three extensively managed sites. B) Intensively managed sites employed fine-scale management practices that included strip crops, food plots, and linear wooded edges among grassland units. C) Extensively managed sites were continuous tracts of remnant or reconstructed prairies managed with fire, grazing, and mowing to maintain native grassland habitat (photo by David Stonner, courtesy of the Missouri Department of Conservation).

tracked daily. Broods were captured using the corral method before sunrise at around 20-days old (Smith et al., 2003), the number of young surviving from hatch was recorded, and one to six juveniles per brood were fitted with backpack transmitters using the suture technique (Terhune et al., 2020). Transmitters weighed 0.6- to 0.8-g with an expected battery life of 45 to 60 days respectively and were <4% of juvenile body mass (AWE-QC-0.8 and AWE-QC-0.65, American Wildlife Enterprises, Monticello, FL, USA; Sinnott et al., 2021a). We captured bobwhite using funnel traps in September and October and radio-marked adults and juveniles for non-breeding season survival estimates using the same protocols as spring trapping (Mosloff et al., 2021). Two pulses of trapping in the fall and early spring each year helped ensure adequate sample sizes of birds were available for monitoring in both the breeding and nonbreeding seasons. Capture and handling protocols were approved by the University of Missouri Animal Care and Use Committee (Protocol 8766).

MDC conducted bobwhite spring whistle counts 15 May–1 July 2016–2018 on Shawnee Trail ($n = 16$ listening stations), Shelton Memorial ($n = 2$), Stony Point Prairie ($n = 8$), Robert E. Talbot Conservation Area ($n = 16$), and Wah'Kon-Tah Prairie ($n = 18$). Whistle count listening stations were established 800-m apart in a grid for complete coverage of each site. The number of males calling within 400 m were recorded during a 10-min period between sunrise and 9:00 A.M. during 1–3 visits annually to each station as an index of population size. Although whistle counts are an imperfect index of bobwhite abundance, they are widely used and we believe our surveys were adequate for this analysis for several reasons (Hansen and Guthery 2001). Surveys were repeated by trained wildlife professionals using a standard protocol (Yeiser et al., 2020). Additionally, 10-min surveys in areas with higher bobwhite densities compared to the surrounding landscape increased the likelihood individuals would be available for detection (Lituma et al., 2017). Finally, the IPM framework allows for the sharing of information across multiple datasets for greater precision in estimates of true abundance (Adabi et al. 2010).

2.2. Data analysis

We developed an IPM to evaluate site-level management effects on seasonal demography and annual population growth of bobwhite populations. We linked spring whistle counts with nest monitoring and telemetry datasets to estimate abundance, fecundity, and survival to explicitly account for processes underlying population change (Besbeas et al., 2002; Schaub et al., 2007; Schaub and Abadi 2011; Kéry and Schaub 2012; Zipkin and Saunders 2018; Fig. 3). We also quantified unmeasured processes that accounted for differences between measured demographic data and observed changes in abundance with a scaling parameter (Robinson et al., 2014). These processes may include unmeasured demographic rates such as immigration and emigration. They may also include unaccounted for effects of the observation process, such as bias caused by violations of model assumptions (Riecke et al., 2019).

A scaling parameter is a balancing term that quantifies the difference between observed and estimated population dynamics. When not all demographic components are directly informed by data a scaling parameter can be beneficial for obtaining reasonable vital rate estimates when unmeasured processes influence observed dynamics. The scaling parameter should be interpreted somewhat cautiously as it also can absorb other model variation. The scaling parameter was the proportional difference in annual population growth between observed changes in abundance estimated from count data and projected abundance based on survival and fecundity rates estimated from nest monitoring and telemetry data. The size of the scaling parameter reflects the magnitude of the discrepancy between annual demographic and count data. A negative estimate for the scaling parameter would indicate changes in population size were lower than what might be expected based on observed survival and fecundity rates, suggesting net emigration of individuals from a population. A positive estimate for the scaling parameter would indicate changes in population size were greater than what would be expected based on observed survival and fecundity rates, which may result from net immigration of individuals into a population

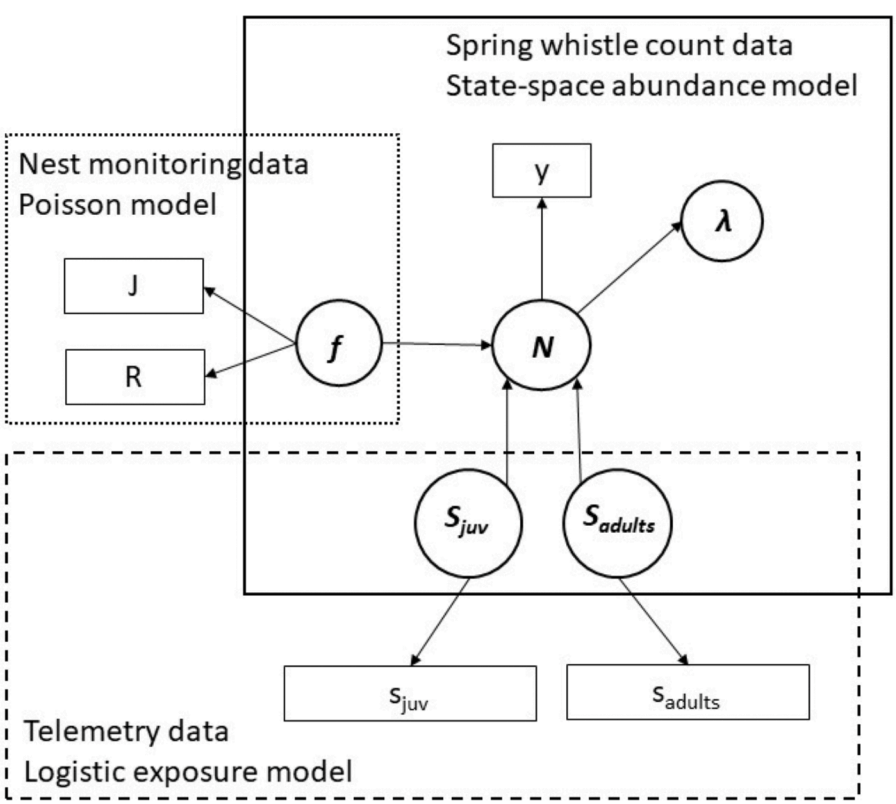

Fig. 3. Conceptual diagram of an integrated population model evaluating site-specific population dynamics of northern bobwhite in southwest Missouri 2016–2018. Small squares represent data for the number of young hatched per nest (J), the number of adults active during the breeding season (R), daily observations of survival (s), and the number of individuals detected during spring whistle count surveys (y). Circles represent demographic parameters estimated for fecundity (f), survival (S), abundance (N), and population growth (λ). Large square boundaries represent individual types of submodels used to estimate each demographic parameter.

or possibly negative effects of tagging on observed survival or fecundity rates.

We used a two-stage, two-sex periodic matrix design to account for seasonal demographic complexities across the full annual cycle (code available online in Supporting Information). Our matrix model allowed us to explicitly account for seasonal processes important in understanding intra-annual demographic sensitivities (Guthery et al., 2000; Doak and Morris 2010; Villellas et al., 2015; Hunt and Tongen 2017). We estimated demographic rates during both the breeding season (1 May–31 Oct) and non-breeding season (1 Nov–30 Apr). We accounted for differences in survival and productivity among groups of adults and juveniles, and males and females (Burger et al., 1995a; Sandercock et al., 2008). We included sex-specific productivity rates because bobwhite are polygamous, and both females and males contribute to fecundity as nest-incubating and brood-attending adults (Curtis et al., 1993; Burger et al., 1995ab). We fit our IPM in a Bayesian framework with a joint likelihood and prior probability distributions for estimates of abundance, survival, and productivity. We next describe each of the component likelihoods.

2.2.1. Count likelihood

We estimated population size within a Poisson binomial mixture model. For our observed counts of male bobwhite, we summed the total number of individuals heard calling at all listening stations during each round of replicated spring whistle count surveys i for each year t and site j. We estimated counts of female bobwhite abundance by multiplying male counts by the ratio of females to males captured during February and March funnel trapping in each year at each site. Spring whistle count data $C_{i,j,t}$ were described in a binomial regression (Eq. (1)) as part of the observation process within a state space model. Abundance $N_{j,t}$ was estimated as a function of the number of individuals detected on surveys and a constant detection probability p estimated using replicated counts. The true but unknown population size $N_{j,t}$ was described by a Poisson distribution (Eq. (2)) in a system-process equation. This true population size was the sum of three annual processes: adult survival, juvenile recruitment, and a scaling parameter. The number of adults surviving the previous year $Nadult_{j,t}$ that survived breeding season ($Sadult.b_{j,t}$) and non-breeding season ($Sadult.nb_{j,t}$) was estimated as the outcome of a binomial distribution (Eq. (3)). The number of juveniles produced $f_{j,t}$ that survived that same period ($Sjuv.b_{j,t}$, $Sjuv.nb_{j,t}$) was estimated as the outcome of a Poisson distribution (Eq. (4)). The scaling parameter z accounted for uncertainty around unmeasured processes that resulted in differences between observed vital rates and changes in population size over time associated with immigration, emigration, or violation of model assumptions (Robinson et al., 2014; Riecke et al., 2019). Annual population growth rate $\lambda_{j,t}$ was derived from abundance estimates across age classes, males, and females (Eq. (5), code available online in Supporting Information).

$$C_{i,j,t} \sim binomial(p,\ N_{j,t}) \tag{1}$$

$$N_{j,t} \sim Poisson(Ntot_{j,t}) \tag{2}$$

$$Ntot_{j,t} = Nadult_{j,t} + Njuv_{j,t} + N_{j,t-1} * z$$

$$Nadult_{j,t} \sim bin(Sadult.b_{j,t-1} * Sadult.nb_{j,t-1}, Nadult_{j,t-1}) \tag{3}$$

$$Njuv_{j,t} \sim pois(f_{j,t-1} * Sjuv.b_{j,t-1} * Sjuv.nb_{j,t-1}) \tag{4}$$

$$\lambda_{j,t} = \frac{N_{j,t}}{N_{j,t-1}} \tag{5}$$

2.2.2. Productivity data and analysis

We defined fecundity $f_{t,j,k}$ as the number of eggs hatched per capita across all adult females and males active on 1 May in each year t at each site j by each sex k. While bobwhite exhibit a flexible mating system, nests were overwhelmingly attended by a uniparental incubator and did not receive biparental care even among breeding pairs. The number of eggs hatched contributed to either female or male fecundity depending on the sex of the individual incubating the nest. Adults who were alive 1 May, but did not incubate or hatch a nest were included in the count of adults in the fecundity ratio. The number of eggs hatched included first nests, renests after failed attempts, and, rarely, second successful nests. We estimated fecundity in a Poisson regression using nest monitoring observations of the total number of eggs hatched by females and the total number of eggs hatched by males $J_{t,j,k}$ across all adults active on 1 May each year for each site and sex $R_{t,j,k}$ (Eq. (6), Eq. (7), code available online in Supporting Information).

$$J_{j,t,k} \sim pois(\rho_{j,t,k}) \tag{6}$$

$$\rho_{j,t,k} = R_{j,t,k} f_{j,t,k} \tag{7}$$

2.2.3. Survival likelihood

We incorporated three known-fate logistic exposure likelihoods in our IPM to estimate seasonal, age-, and sex-specific survival (Eq. (8), code available online in Supporting Information). This generalized linear mixed model included a modified link function, which allowed interval length between survival observations (d) to vary without biasing estimates of daily survival (Eq. 9; Shaffer 2004, Shaffer and Thompson 2007). The three likelihoods included (1) breeding season juvenile survival, (2) breeding season adult survival, and (3) non-breeding season survival. All models estimating daily survival $S_{t,j,k,l}$ included additive fixed effects for year β_t, and site β_j (Eq. (10)). Each of the three models also included a unique intercept term α.

The breeding season adult and non-breeding season survival models included a fixed binary effect for sex β_k. Sex of juveniles hatched during the breeding season could not be determined and we assumed survival of male and female young from 1 May to 31 Oct were equal. The non-breeding season survival model included a fixed binary age effect for adults and juveniles β_l . To calculate 6-month period survival estimates for breeding season adults and all non-breeding season age and sex classes within the IPM, we exponentiated site- and year-specific female and male daily survival probabilities by 182 days.

Breeding season juvenile survival was estimated from hatch to 100 days old. Survival in the first 3 weeks of life prior to radio-marking individuals was determined within the logistic exposure framework based on the number of young hatched and the number of young captured at roost locations (Dahlgren et al., 2010; Schreiber et al., 2016, Sinnott et al. In press. While brood amalgamation is a potential source of uncertainty in early survival observations, we observed low rates of brood amalgamation (<4% of captured individuals) for broods < 3 weeks old based on differences between expected body mass and brood age during brood captures. Brood counts from captures at roost locations are a reliable method for estimating chick survival (Faircloth et al., 2005; Dahlgren et al., 2010). Survival for young greater than approximately 3 weeks old was estimated based on observations of radio-marked individuals, which are not affected by brood amalgamation. The breeding season juvenile survival model included a fixed quadratic effect for brood age in days. The quadratic effect captured low daily survival rates immediately post hatch which increased rapidly and then stabilized during the late developmental period. To calculate period survival for breeding season juveniles, we first calculated daily survival probabilities from hatch to 100 days old and then took the product of a vector of survival probabilities from age on day 1 to day 100. One hundred-day period juvenile summer survival estimates reflect the time from mean hatch date 24 July to the start of the non-breeding season 1 November.

We assigned vague priors for all fixed effects and intercepts (*e.g.*, $\beta_k \sim normal(0,\ 0.001)$). The logistic-exposure generalized-linear mixed model for non-breeding season adult survival ($Sadult.nb_{t,j,k,l}$) can be written mathematically as:

$$Sadult.nb_{t,j,k,l} \sim bernoulli\left(S_{t,j,k,l}\right) \text{Survival probability} \quad (8)$$

$$S_{t,j,k,l} = s^{d}_{t,j,k,l} \text{ Modified link function} \quad (9)$$

$$\text{logit}\left(s_{t,j,k,l}\right) = \alpha + \beta_t + \beta_j + \beta_k + \beta_l \text{ Linear predictor of survival} \quad (10)$$

2.2.4. Population projection

While we had count and demographic data for 2016 through 2018, we projected Bobwhite abundance and population change for 2019 by sampling from the posterior distribution of our 2018 demographic rates and estimated site-specific pre-breeding season abundance (Kéry and Schaub 2012; Oppel et al., 2014).

We fit our IPM in a Bayesian framework in Program R version 3.6.1 using JAGS via the JagsUI package (R Core Development Team 2021; Plummer 2003; Kellner 2019). We ran models using three chains, each containing 40,000 iterations including a burn-in of 10,000, and a thin rate of 5, yielding 18,000 total samples for parameter posterior distribution. We evaluated model convergence by inspecting trace plots for all parameters and checking for R-hat values of <1.1 (Brooks and Gelman 1998). We present posterior means and 95% credible intervals (CRI) of estimated parameters. We interpret effects such as sex and age as influential when their 95% CRI did not overlap zero. We calculated correlation coefficients (r) between demographic rates and population growth across their full posterior distributions, and we calculated the proportion of correlation coefficients > 0 (Pr(r>0)) as a measure of the evidence that a positive correlation existed between a demographic parameter and population growth. Finally, we compared seasonal age- and sex-specific survival and productivity estimates for each site and management strategy to a subset of posterior samples that resulted in a stable population (*i.e.*, we report the distributions of posterior samples that yielded $\lambda \geq 1.00$). Given variation in posterior estimates of all demographic rates, the subset of posteriors that resulted in a stable population provided perspective about thresholds of rates to target for population management (Sandercock et al., 2008).

3. Results

We tracked 766 juveniles and 618 adults during the breeding season, and 772 juveniles and 349 adults during the non-breeding season to estimate survival probabilities (Table S1). We monitored success of 276 nests incubated among 576 adults active on 1 May at the start of the breeding season across all years. MDC conducted three rounds of Bobwhite spring whistle counts on Shawnee Trail, Shelton Memorial, and Stony Point Prairie annually 2016–2018, two rounds on Robert E. Talbot Conservation Area in 2017. On Wah'Kon-Tah Prairie, MDC conducted three rounds of spring whistle counts in 2016 and two in 2017 and 2018. While the number of replicated counts differed among areas, the binomial mixture model was flexible enough to allow varying intensity in sampling effort.

Bobwhite site-level, seasonal survival and fecundity probabilities were highly variable from 2016 through 2018 (Fig. 4; Table S2). During the breeding season, the number of young hatched per female was greater than the number of young hatched per male. Across all sites and years, 58.4% of females active 1 May survived and incubated one or more nests, compared to only 16.5% of males. As a result, female fecundity was more than 4-times greater than male fecundity ($f_F = 3.26$, 95% CRI: 2.14, 4.52; $f_M = 0.68$, 95% CRI: 0.18, 1.27; Fig. 5; Table S2). There was 0.93 posterior support that adult male breeding season survival was greater than adult female breeding season survival ($Sadult.b_M = 0.40$, 95% CRI: 0.18, 0.61; $Sadult.b_F = 0.34$, 95% CRI: 0.13, 0.56; $\beta_k = 0.17$, 95% CRI: -0.05, 0.39; Fig. 5). In line with our hypotheses, female fecundity was greater on the three extensively managed sites ($f_{SLT} = 3.48$, 95% CRI: 1.86, 5.00; $f_{STP} = 4.54$, 95% CRI: 2.79, 6.24, $f_{WKT} = 3.73$, 95% CRI: 2.30, 5.49) compared to the two intensively managed sites ($f_{SHT} = 2.41$, 95% CRI: 0.68, 5.85; $f_{TAL} = 1.94$, 95% CRI: 1.18, 2.74). Breeding season adult survival was also greater on the three extensively managed sites ($Sad.b_{SLT} = 0.42$, 95% CRI: 0.24, 0.60, $Sad.b_{STP} = 0.40$, 95% CRI: 0.24, 0.55, $Sad.b_{WKT} = 0.49$, 95% CRI: 0.33, 0.63) compared to the two intensively managed sites ($Sad.b_{SHT} = 0.26$, 95% CRI: 0.13, 0.41, $SadF.b_{TAL} = 0.26$, 95% CRI: 0.12, 0.41; Fig. 5, Fig. 6; Table S2). While we predicted breeding season juvenile survival would be highest on the three extensively managed sites, there was significant overlap in credible intervals across site estimates and an intensively managed site, Talbot, had the highest mean rate for breeding season juvenile survival ($Sjuv.b_{TAL} = 0.33$, 95% CRI: 0.19, 0.52; Table S2).

During the non-breeding season survival was again higher in males than females ($S.nb_M = 0.30$, 95% CRI: 0.13, 51, $S.nb_F = 0.24$, 95% CRI: 0.08, 0.44; $\beta_k = 0.20$, 95% CRI: 0.01, 0.40; Fig. 5). While we predicted juvenile survival would be lower than adult survival, age did not have a credible effect on non-breeding season survival ($\beta_l = 0.07$, 95% CRI: -0.17, 0.31). Additionally, while we predicted non-breeding season survival would be greater on extensively managed sites, we found significant overlap in credible intervals of site estimates (Fig. 5). Talbot, an intensively managed site, had the highest mean non-breeding season survival, followed by Wah'Kon-Tah, the largest extensively managed site ($S.nb_{TAL} = 0.39$, 95% CRI: 0.22, 0.55, $S.nb_{WKT} = 0.28$, 95% CRI: 0.15, 0.42; Table 1; Fig. 4). The two smaller native grassland sites, Stony Point Prairie and Shelton Memorial had the lowest non-breeding season survival ($S.nb_{SLT} = 0.20$, 95% CRI: 0.06, 0.37, $S.nb_{STP} = 0.22$, 95% CRI: 0.10, 0.36; Table S2; Fig. 5).

Annual population growth rates across all sites showed a declining trend ($\lambda_{total} = 0.74$, 95% CRI: 0.69, 0.79) and annual estimated changes in abundance matched declines observed on whistle count surveys over the 3-year study period (Fig. 7). Credible intervals of these estimates across sites and between land management strategies overlapped. We found the geometric mean of population growth was greatest on the larger extensively managed sites, Wah'Kon-Tah Prairie ($\lambda_{WKT} = 0.76$, 95% CRI: 0.70, 0.83) and Stony Point Prairie ($\lambda_{STP} = 0.77$, 95% CRI: 0.68, 0.86) and lowest on the smallest extensively managed site, Shelton Memorial Conservation Area ($\lambda_{SLT} = 0.65$, 95% CRI: 0.49, 0.80). Population growth rate was modestly greater on extensively managed native grassland sites ($\lambda_{EXT} = 0.76$, 95% CRI: 0.70, 0.82) compared to intensively managed sites that incorporated traditional, fine-scale management practices ($\lambda_{INT} = 0.70$, 95% CRI: 0.64, 0.77; Fig. 6).

To evaluate the influence of seasonal vital rates on annual population growth, we calculated correlations between each demographic rate and population growth. Among extensively managed sites, two vital rates had $a \geq 0.90$ probability of a positive correlation with population growth: female fecundity ($r = 0.60$, 95% CRI: −0.10, 0.83) and juvenile breeding season survival ($r = 0.50$, 95% CRI: −0.18, 0.82; Table S3). We found only a weak correlation between female fecundity and population growth rate across all sites and years ($r = 0.17$, 95% CRI: −0.09, 0.53; Table S4).

We compared site-level vital rate estimates to the subset of posterior samples that resulted in a population growth rate ≥1.0 to identify which seasonal vital rates most limited population growth at each site. Female fecundity and adult breeding season survival at intensively managed sites were lower than rates that resulted in a stable population growth rate (Table S2; Fig. 3). Non-breeding season survival at two extensively managed sites, Shelton and Stony Point, were also lower than rates that resulted in a stable population growth rate (Table S2; Fig. 3).

The scaling parameter contributed substantially to per-capita rates of population change ($z = 0.53$, 95% CRI: 0.46, 0.60; Fig. S2) and likely included unmeasured demographic rates such as immigration and/or error induced by violations of model assumptions. Missing abundance data for some sites in some years precluded estimation of a scaling parameter estimating year and site-specific differences between demographic and count data. When the IPM included a scaling parameter, vital rate estimates from the IPM closely matched estimates produced by independent survival and fecundity models. Without the scaling parameter, vital rates informed by less data (*i.e.*, juvenile breeding

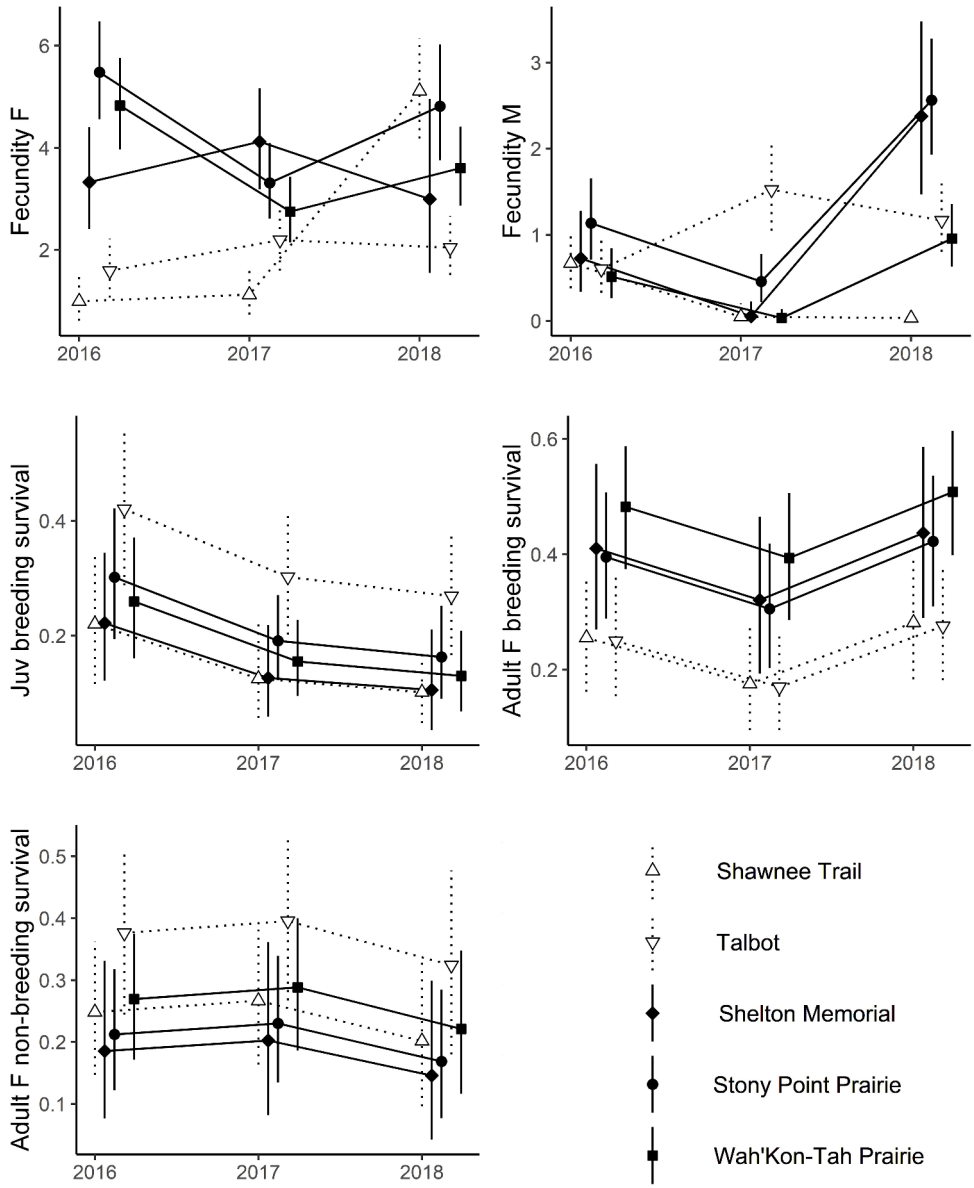

Fig. 4. Estimated northern bobwhite population demographic rates for extensively managed sites Stony Point Prairie, Wah'Kon-Tah, and Shelton Memorial (solid), and intensively managed sites Shawnee Trail and Talbot Conservation Areas (dotted) in southwest Missouri, USA 2016–2018.

season survival and non-breeding season survival) were high compared to estimates produced in an independent survival model (Fig. S1), while estimates of annual population growth were relatively low (Fig. S2). Additionally, without the scaling parameter, all vital rates had >0.90 probability of a positive correlation and the strongest correlations corresponded to vital rates informed by less data (again, juvenile breeding season survival and non-breeding season survival; Table S4).

4. Discussion

IPMs are the newest approach to evaluating full annual cycle population dynamics and over the past ten years their utility and flexibility have been increasingly tested and developed. IPMs have been used to estimate unobserved demographic rates, and their relationships to environmental conditions, and population change (*e.g.*, Abadi et al., 2010). We constructed a site-based, full-annual cycle, two-sex, two--stage, IPM that included a scaling parameter to account for unmeasured demographic processes. We evaluated the effects of landscape-scale differences in management practices on the full-annual cycle demography of bobwhite. While the sensitivity of IPMs to latent or data-poor processes is more recently being acknowledged and evaluated (Riecke et al., 2019; Weigers et al., 2022), our unique dataset with nearly complete data across all life stages and seasons suggests understanding of full annual cycle population dynamics is highly sensitive to unobserved demographic processes.

Previous studies evaluating bobwhite population dynamics within an IPM framework have used long-term, incomplete demographic datasets to evaluate weather effects on the highly variable dynamics of the bobwhite full annual cycle in population strongholds of northern and southeastern portions of the species' range (McConnell et al., 2018; Rosenblatt et al., 2021). Our IPM evaluated site-specific vital rates and population growth across two intensively managed sites and three extensively managed sites in a population centrally located within the species' range. Estimates for all seasons and life stages were informed by data and we used a scaling parameter to quantify unmeasured processes influencing estimated population dynamics. We found significant

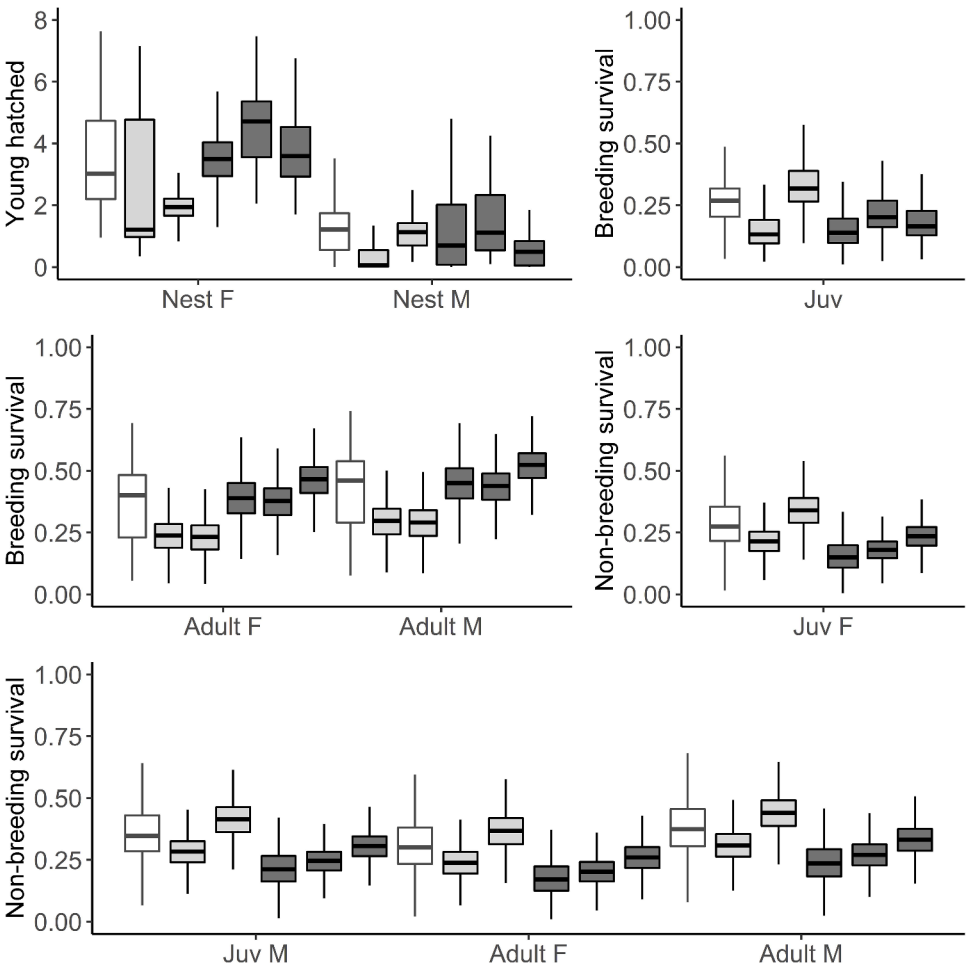

Fig. 5. Boxplots of posterior distributions of northern bobwhite fecundity (top) breeding season survival (1 May–31 October; center) and non-breeding season survival (1 November–30 April; bottom) across all years for each site in southwest Missouri. The first box plot for each vital rate represents a subset of posterior samples that resulted in a stable population growth rate (white; $\lambda \geq 1.00$). Observed site-level vital rates are then given in the following order for each vital rate: Shawnee Trail and Talbot (light gray, intensively managed sites), then Shelton Memorial, Stony Point Prairie, and Wah'Kon-Tah Prairie (dark gray, extensively managed sites). Fecundity were estimates of the number of young hatched per female-incubated nest (Nest F) and male-incubated nest (Nest M). Posterior distributions of breeding and non-breeding season survival estimated 6-month period survival probabilities for juveniles and adult females (Adult F). Posterior distributions of non-breeding season survival estimate survival probabilities for juvenile females (F) and adult females (Adult F).

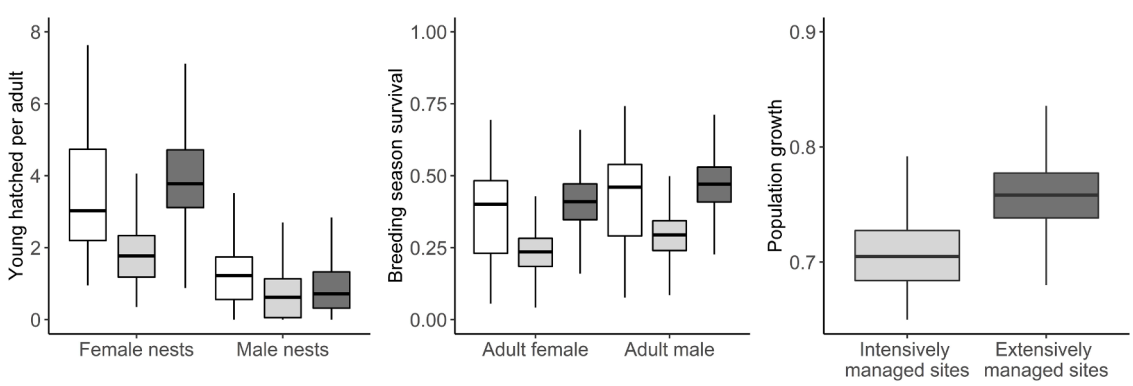

Fig. 6. Boxplots comparing estimates of northern bobwhite fecundity, breeding season adult survival, and population growth rates in southwest Missouri, USA 2016–2018. Posterior samples of demographic estimates were pooled across samples that resulted in a stable population (white), intensively managed sites (light gray), and extensively managed sites (dark gray).

differences in estimates of vital rates that were data poor with and without a scaling parameter. We also found relationships between vital rates and annual changes in population growth were sensitive to the inclusion of a scaling parameter. While IPMs can estimate vital rates where data are missing, our results highlight the sensitivity of any latent or data poor demographic parameter estimates which may absorb variation from multiple unmeasured demographic processes or data bias. These demographic estimates should be interpreted cautiously.

We found bobwhite populations on extensively managed sites composed of intact native prairies hatched more young per female and had greater breeding season adult survival compared to intensively managed sites composed of strip crops, woodlands, and native grass plantings and reconstructed prairies with lower plant richness compared to intact prairies. Age- and sex-specific differences in seasonal survival probabilities as well as male contributions to reproductive success underscored the importance of accounting for population structure and composition in evaluation of bobwhite full annual cycle demography. We did not find strong correlations between vital rates and population growth for all sites and years pooled, however, management strategies were associated with site-specific differences in vital rates limiting

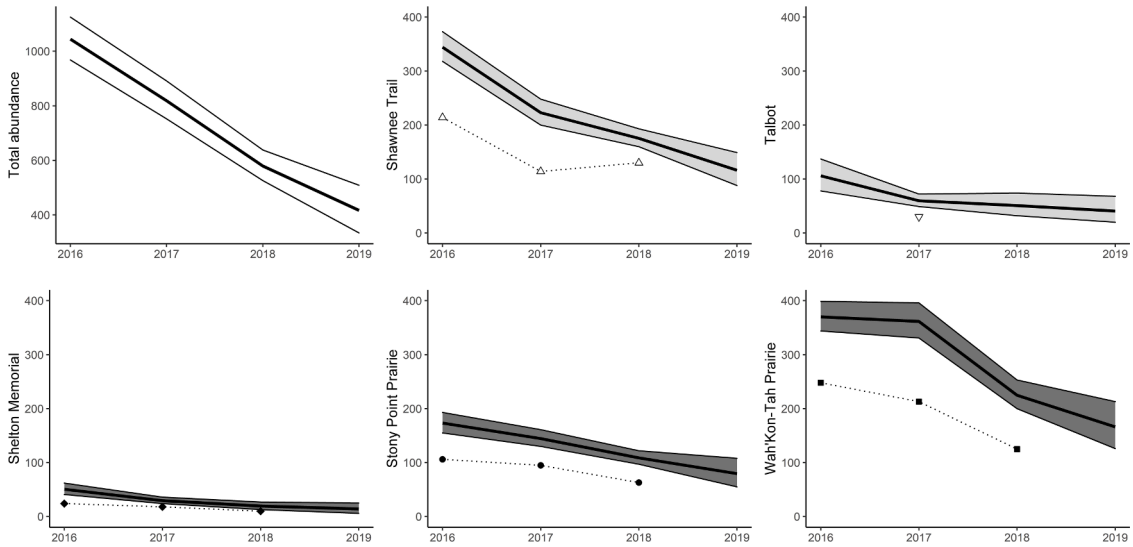

Fig. 7. Mean estimates (solid line) and 95% credible intervals (ribbon) of total northern bobwhite spring abundance in southwest Missouri, USA 2016–2019 (white), and site-specific abundance estimates for two intensively managed sites Shawnee Trail and Talbot Conservation areas (light gray), and three extensively managed sites Shelton Memorial, Stony Point Prairie, and Wah'Kon-Tah (dark gray). Estimated declines in abundance match observed declines in the maximum number of individuals detected during annual spring whistle counts (points, dotted line).

population growth. For example, female fecundity and breeding season adult survival on intensively managed sites were lower than rates from posteriors that resulted in a stable population. While non-breeding season survival was lower on extensively managed sites that effect may have been driven by low survival on the two smallest sites. We also found significant differences between estimated vital rates and observed annual changes in bobwhite abundance due to unmeasured processes which may have included movement of individuals into a population or biased data and violations of model assumptions. Unmeasured demographic processes will be discussed further below.

4.1. Population growth

While there was overlap in site-level estimates of population growth, results weakly suggested annual population growth rates were greater on extensively managed sites compared to intensively managed sites. While our seasonal demographic rates were within the range of previous studies that investigated declining bobwhite populations, population growth rates were well below those required for a stable population (Sandercock et al., 2008; Janke et al., 2017; McConnell et al., 2018). Annual indices of bobwhite abundance are highly variable, and even long-term "stable" populations experience multi-year periods of decline and growth (McConnell et al., 2018). Regional population strongholds are also vulnerable to periods of population decline (Rosenblatt et al., 2021). Long-term monitoring of these bobwhite populations would be needed for a robust assessment of population viability (Ross and Weegman 2022).

4.2. Breeding-season fecundity

While males contributed to productivity through nest incubation and brood rearing, the proportion of males that incubated a nest and the number of young hatched per male was a fraction of per capita female fecundity during the breeding season. Male fecundity was also not correlated with population growth. We found female fecundity was greater on extensively managed sites compared to intensively managed sites. On intensively managed sites the number of young hatched per female were low relative to estimates that resulted in stable populations. As an r-selected species with low annual survival, we expected fecundity to influence population growth rate (Sæther and Bakke 2000; Stahl and Oli 2006; Folk et al., 2007; Gates et al., 2012; Taylor et al., 2012). We found a weak correlation between changes in abundance and the number of eggs hatched from female-incubated nests on extensively managed sites composed of native grasslands managed with prescribed fire and grazing. However, there was no correlation on intensively managed sites or among sites and years. Lack of correlation may be due to a declining bobwhite population trajectory in southwest Missouri. For stable populations of r-selected species, fecundity may explain variation in population growth, but in declining populations, survival can have a stronger influence on changes in abundance (Meats 1971; Sandercock et al., 2008; McConnell et al., 2018). While we did not estimate effects of environmental covariates, greater availability of native grassland vegetation and reduced mature tree cover may increase fecundity on intensively managed sites (Taylor et al., 1999b; Potter et al. 2011).

4.3. Breeding-season juvenile survival

Long-term capture-recapture data from a stable population in the southeastern pine savannas of Tall Timbers Research Station in Florida estimated a 100-day period survival of 0.32 (95% CI: 0.18, 0.44; Terhune et al., 2019) based on mark-recapture of chicks banded around 2-weeks old. Breeding season juvenile survival in a northern population of bobwhite estimated as a latent variable within an IPM was 0.67 (95% CI: 0.03, 1.0). Breeding season juvenile survival in southwest Missouri based on radio-telemetry data were lower than those previous estimates (mean = 0.21, 95% CRI: 0.06, 0.45). Survival varied among sites and did not differ between intensively and extensively managed conservation areas. Juvenile survival was low relative to estimates that resulted in a stable population across all sites apart from Talbot. Juvenile survival is sensitive to habitat suitability and availability of brood habitat may be limiting on both intensive and extensively managed sites (Tanner et al., 2019). In southwest Missouri, broods selected for native grasslands that were burned and grazed on public lands as well as agricultural cover on intensively managed sites and private lands (Sinnott et al., 2021a). Both native grasslands managed with fire and grazing and agricultural cover in small strip crop fields were available to broods on Talbot. Bobwhite broods prefer habitat with bare ground, forb cover, and tall vegetation and survival is greatest on native grasslands managed with rotational fire and grazing (Taylor et al., 1999a; Sinnott et al., 2021b). Increasing the availability of native grasslands managed with fire and grazing and shrub cover may improve brood-rearing habitat and survival on both intensively and extensively managed sites (Taylor et al., 1999a; Brooke

et al., 2017; Sinnott et al., 2021ab).

4.4. Breeding-season adult survival

Adult breeding season survival was slightly lower for females than for males. While we did not compare survival of non-reproductive, incubating, and brood-rearing individuals, risks associated with reproductive behaviors may have contributed to lower female survival (Burger et al., 1995a). Other studies have found declining bobwhite populations to be sensitive to adult summer survival (Sandercock et al., 2008; Gates et al., 2012; Williams et al., 2012). We found adult breeding season survival was not strongly correlated with population growth across our sites during the study period. However, survival probabilities on intensively managed sites were lower than those on extensively managed sites and lower than those that resulted in a stable population. Breeding-season adult survival on these sites may increase with increased availability of grasslands and reduced use of forested areas (Taylor et al., 1999b; Lohr et al., 2011).

4.5. Non-breeding season survival

Previous field, simulation, and meta-analysis studies have found non-breeding season survival contributes disproportionately to abundance trends, especially for northern populations of bobwhite (Folk et al., 2007; Sandercock et al., 2008; Link et al., 2008; Williams et al., 2012; Rosenblatt et al., 2021). We found across all sites, except for Talbot, higher non-breeding season survival was required to achieve population stability.

Bobwhite face multiple pressures during the non-breeding season. Population density, covey dynamics, and landscape composition influence non-breeding season survival patterns. In winter, bobwhite benefit from grassland landscapes that provide permanent cover with ample shrubby vegetation (Williams et al., 2000; Lohr et al., 2011; Janke and Gates 2013; Janke et al., 2015; Mosloff et al., 2021). Thus, we expected winter survival to be highest on our native grassland sites, however, we found survival was highest on an intensively managed site (Talbot), followed by our largest extensively managed site (Wah'Kon-Tah Prairie). These sites are among the largest conservation areas in our study. Talbot has more woody cover than other sites; bobwhite select for woody cover in winter and it may increase survival (Janke et al., 2015; Mosloff et al., 2021). Wah'Kon-Tah Prairie is larger than the other two extensively managed sites, has proportionately more woody cover than Shelton Memorial, and half of the site is closed to hunting. Non-breeding season survival was lowest at the smallest conservation areas, Stony Point Prairie and Shelton Memorial. Small coveys, especially in low density populations, experience reduced winter survival if they remain isolated or must make large movements to find additional members (Williams et al., 2003a; Williams et al., 2003b; Williams et al., 2000; Janke and Gates 2013). Evaluating effects of area sensitivity, density dependence, and effects of vegetation, weather, and harvest pressure was beyond the scope of this study, but one or more of these factors may have contributed to site-level patterns in non-breeding season survival (Guthery et al., 2000; Williams et al., 2000; Williams et al., 2003b; Janke et al., 2015).

Our results would also benefit from further evaluation of survival during transitional periods between the non-breeding and breeding seasons. Greater sage-grouse experience reduced survival during these transitional periods between mid-winter and summer breeding seasons due to increased depredation (Blomberg et al., 2013a, Blomberg et al., 2013b). We do not yet know if non-breeding season survival probabilities are driven by winter processes (1 December–28 February) or changes during spring (1 March–30 April) when coveys break up and individuals establish territories. Achieving greater minimum non-breeding season survival would improve population viability.

4.6. Unmeasured demographic processes and other model uncertainties

A scaling parameter within our IPM quantified unmeasured demographic processes and improved accuracy of demographic rate estimation by accounting for differences in observed abundances and projected abundances based on vital rates (Robinson et al., 2014; Riecke et al., 2019). We assumed a constant rate for this scaling parameter due to limitations in our count data that prevented estimation of variation across sites and years. This may be a reasonable assumption as other studies have found scaling parameters among several species show low annual variation and there is evidence of consistent bias in telemetry-based estimates of bobwhite survival (Guthery and Lusk 2004; Robinson et al., 2014). The scaling parameter revealed significant differences between estimated demographic rates and changes in population size (0.53; 95% CRI 0.46, 0.60). Without the scaling parameter, demographic rates informed by the least data (juvenile breeding season survival and non-breeding season survival) were estimated high relative to estimates from independent submodels. Additionally, the correlation between these rates and annual changes in abundance was only credible without the scaling parameter. Our understanding of full annual cycle dynamics for bobwhite was significantly affected by variation in available data and parameterization of the model.

This difference between observed population changes and estimated demographic rates may be partly explained by immigration. While bobwhite populations are relatively sedentary, individuals can disperse distances >5-km within a season and declining bobwhite populations may rely on immigration for long-term persistence (Lohr et al., 2011). Movements to and from populations are difficult to quantify and may be measured directly through intensive marking and monitoring of new recruits or collecting genetic information (Millon et al., 2019).

This difference quantified by the scaling parameter may also be explained by violations of model assumptions. An assumption in radiotelemetry methodology is survival and reproduction of radio-marked individuals are observed perfectly and these rates are equal to that of unmarked individuals, however, this may not always be true (Body et al., 2017). Several studies have suggested telemetry-based estimates of adult bobwhite survival may be biased low (Cox et al., 2004; Guthery and Lusk 2004; Sandercock et al., 2008; Barron et al., 2010), although this may not be universal across studies (Palmer and Wellendorf 2007) and has not been evaluated for telemetry-based estimates of juvenile survival. We also assumed perfect detection of nests of radio-marked adults during the breeding season. If all nests were not detected by technicians, fecundity estimates may be biased low. Finally, we assumed daily survival rates were constant within the breeding and the non-breeding season and discounting any within-season temporal trends may bias period survival estimates derived from exponentiated daily survival rates (Weiser 2021).

Without additional genetic or capture-recapture data we are unable to separate contributions of immigration and potential biases associated with demographic data contributing to the scaling parameter within our IPM. We recommend integrating additional data types to better quantify immigration and designing telemetry analyses within a multistate framework to account for imperfect observations of survival and fecundity, for reduced potential bias (Devineau et al., 2014; Millon et al., 2019; Weegman et al., 2021).

5. Conclusions

Our study was constrained by the number of sites and years for which we could estimate demography because of the large field effort required to measure these parameters. Other site level attributes such as study area size and landscape context were to some extent confounded with management strategy and difficult to tease apart because of limited replication. The limited number of sites and years, the lack of environmental covariates, as well as bobwhite's highly variable demography may have contributed to wide credible intervals in site-specific

demographic estimates. Despite these limitations, we found multiple low seasonal vital rates resulted in annual declines in bobwhite abundance. Fine-scale habitat management practices such as establishment of food plots, field borders, and woody strips applied on intensively managed sites may not optimize habitat for nesting and adult breeding season survival. We encourage further research into environmental factors influencing these seasonal vital rates. We also encourage future studies to cautiously interpret latent demographic parameters and potential sources of bias that may influence those estimates.

CRediT authorship contribution statement

Emily A. Sinnott: Conceptualization, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Supervision. **Frank R. Thompson:** Conceptualization, Formal analysis, Investigation, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Mitch D. Weegman:** Conceptualization, Software, Formal analysis, Investigation, Resources, Writing – review & editing, Supervision, Project administration. **Thomas R. Thompson:** Conceptualization, Investigation, Resources, Writing – review & editing, Funding acquisition. **Alisha R. Mosloff:** Investigation, Data curation, Writing – review & editing. **R. Kyle Hedges:** Investigation, Resources, Data curation, Writing – review & editing. **Frank L. Loncarich:** Investigation, Resources, Data curation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.110211.

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