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ARTICLE

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American kestrel population trends and vital rates at the continental scale

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Abstract

The American kestrel (*Falco sparverius*, hereafter referred to as kestrel) has declined across much of its North American range since at least the mid-1960s. Kestrel population dynamics have been explored through a multitude of local studies and two broad reviews of available data. Across large geographic extents, however, the demographic cause(s) of kestrel population declines remain(s) largely unknown. As part of a collaborative effort to elucidate the drivers of kestrel population declines, we developed a continental-scale integrated population model using band-recovery data, productivity data, and Breeding Bird Survey indices from 1986 to 2019 to estimate indices of annual population sizes, survival, and productivity rates

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across the continental United States. We detected a decline in population size of ~1%–2% per year. Overall estimates of population growth from 1986 to 2019 suggest a 29% decline in population size (95% CI = −34% to −23%). There was little evidence of a trend in brood size. However, survival of juvenile birds (mean = −0.015, SD = 0.008 and mean = −0.024, SD = 0.010 for females and males, respectively) and adult males (mean = −0.016, SD = 0.010) in the summer declined, suggesting that these vital rates could be contributing to declines in populations over time. Winter adult survival rates (mean = −0.004, SD = 0.009 and mean = −0.009, SD = 0.010 for females and males, respectively) also declined but to a lesser extent than summer survival. For juvenile birds, winter survival increased (mean = 0.006, SD = 0.008 and mean = 0.002, SD = 0.009 for females and males, respectively); however, this was not enough to offset declines in summer survival and annual survival rates declined over the time series. Annual adult survival was also low relative to previous research on kestrel survival rates. Given the importance of survival to population trends, our findings provide support for several previously proposed broad classes of factors potentially contributing to observed population declines: declines in arthropod prey, second-generation rodenticides, neonicotinoid insecticides, and predation.

KEYWORDS
falcon, integrated population model, North America, population growth, population regulation, raptors

INTRODUCTION

American kestrels (*Falco sparverius*, hereafter referred to as kestrels) have been declining across most of their North American range at a steady rate of approximately −1.4% per year since the 1960s (Bird & Smallwood, 2023; Sauer et al., 2019). While this falcon has a range that spans the Western Hemisphere with large populations in southern South America, Mexico, and Caribbean regions, North America supports roughly 50% of the global population. Kestrels have been identified as a species of concern in 21 US state wildlife action plans (McClure et al., 2017) and are included in several regional lists of Birds of Conservation Concern by the U.S. Fish and Wildlife Service (USFWS, 2008). While there is concern regarding the long-term persistence of the American kestrel, it has not yet been listed on a national or continental Watch List of Partners in Flight (Rosenberg et al., 2016). However, identifying the demographic causes for a decline, before a species is of elevated concern across its range, can lead to less difficult and less costly intervention measures.

Kestrels are primarily associated with open country, grasslands, and pine savannahs, and grassland birds are among the most rapidly declining avian groups in North America (Rosenberg et al., 2019). American kestrels are but one of several grassland raptors in North America that are declining (e.g., ferruginous hawk, *Buteo regalis*, Rosenberg et al., 2019; short-eared owl, *Asio flammeus*, Miller et al., 2023; burrowing owl, *Athene cunicularia*, Conway, 2018). Although the loss of habitat is one hypothesized factor in the decline of grassland birds, the cause(s) of the kestrel decline, as well as causes of declines in other grassland raptors, remain(s) largely unknown. When it comes to the American kestrel, this is the case despite several local-scale studies and two broad reviews of available data (Bird & Smallwood, 2023; Farmer et al., 2006; McClure et al., 2017). Unlike other grassland raptors of conservation concern, there are numerous nesting studies and a relatively large banding dataset for the American kestrel across North America. As such, there is an opportunity to build population dynamic models with enough complexity to identify the demographic parameters contributing to the historical large-scale decline. Learning about the demographic causes of decline for kestrels may also provide some insights into declines of other related species.

Integrated population models (IPMs) are one type of analysis tool increasingly being used to guide conservation and management decision-making. IPMs integrate different data sources into a single model to describe population dynamics for a species (e.g., data on reproductive output, population counts, mark–recapture data; Abadi, Gimenez, Arlettaz, & Schaub, 2010). For raptors, IPMs have been used to set prescribed take levels from lawfully permitted activities including falconry (i.e., peregrine falcons, *Falco peregrinus*, U.S. Fish and Wildlife Service, 2023) and incidental take by energy infrastructure (golden eagles, *Aquila chrysaetos*, and bald eagles, *Haliaeetus leucocephalus*, Millsap et al., 2022; Zimmerman et al., 2022), as well as to investigate the conservation significance of nest augmentation programs (Eurasian kestrels, *F. tinnunculus*, Fay et al., 2019) and drivers of population dynamics (red kites, *Milvus milvus*, Pfeiffer & Schaub, 2022; Cooper's hawks, *Astur cooperii*, Millsap et al., 2023; Aplomado falcons, *Falco femoralis*, Rolek et al., 2022). IPMs have been recently used to explore population trends in local populations of the American kestrel that used nest boxes for breeding (e.g., Brown & Collopy, 2013; McClure et al., 2021). Nest boxes are a common management practice for augmenting kestrel populations regionally (Katzner et al., 2005). These studies demonstrated that immigration from individuals occupying the surrounding landscape (e.g., kestrels not nesting in nest boxes or from areas outside the study area) was important in maintaining nest box populations (Brown & Collopy, 2013). However, because of their local scale, these studies could not identify which of the primary demographic drivers, survival or fecundity, was deficient and thus necessitating immigration to maintain the local population (McClure et al., 2021). Declines in kestrel population size have occurred across their North American range, begging the question: what demographic rates are driving declines at this larger spatial scale?

Here, we built an American kestrel population dynamic model at the continental scale (1986–2019) to quantify trends in demographic processes. Building an IPM at the continental scale allowed us to focus on identifying potential demographic deficits leading to the need for immigration to maintain kestrel populations, thereby narrowing the potential large-scale drivers to age and sex-specific survival and fecundity. We also were able to estimate true rather than apparent (i.e., confounded with emigration) survival by parameterizing the model with dead recovery data rather than live recapture data (Gimenez et al., 2007; Kéry & Schaub, 2012). Furthermore, we were able to take advantage of banding pulses in the band-recovery data to estimate seasonal rather than simply annual survival rates. Our analysis elucidates the demographic rates that are likely driving the decline, significantly advancing our understanding of what may be happening to kestrel populations in North America.

METHODS

Data sources

Population size

For the count portion of the IPM, we used data from the North American Breeding Bird Survey (BBS) to quantify annual population changes of kestrels throughout the United States and southern Canada from 1986 to 2019. Sauer and Link (2011) provide full details of the survey design, field and analytical methods used in the BBS. Counts of adults from the BBS are analyzed using a log-linear regression model (details provided in Link et al., 2020; Sauer et al., 2013). The BBS analysis (Link et al., 2020) is conducted in a Bayesian framework and we were provided the posterior Markov chain Monte Carlo (MCMC) samples for each sample unit (i.e., 10,000 index estimates for each stratum and year) from the BBS office. We scaled each of these posterior samples by total area surveyed (Sauer & Link, 2011), aggregated among strata in the continental United States for each year, and then summarized the 10,000 estimates to generate summary statistics (mean and SD) for the indices used in our analyses. The final index used in the analysis represents the mean number of kestrels detected per route in the continental United States each year. We note that this index is not a measure of abundance each year. Rather, it represents a relative abundance each year that can be used to explore trends over time (Figure 1).

Band recovery

We acquired band and recovery data (Figure 2; Appendix S1) from the U.S. Geological Survey Bird Banding Laboratory (BBL) on 3 March 2021 to parameterize the survival submodel (Figure 1). Our recovery data consisted of bands found on kestrels that died and were reported to the BBL. We binned both band and encounter (hereafter, recovery) datasets into two age and two sex classes based on the BBL's age and sex codes. As in Ely et al. (2018), we treated AHY (after hatch year), SY (second year), ASY (after second year), TY (third year), and ATY (after third year) BBL age codes as after-first-year birds, hereafter referred to as adults (A). We treated HY (hatch year), J (juvenile), and L (local; i.e., nestlings) BBL age codes as first-year birds, hereafter

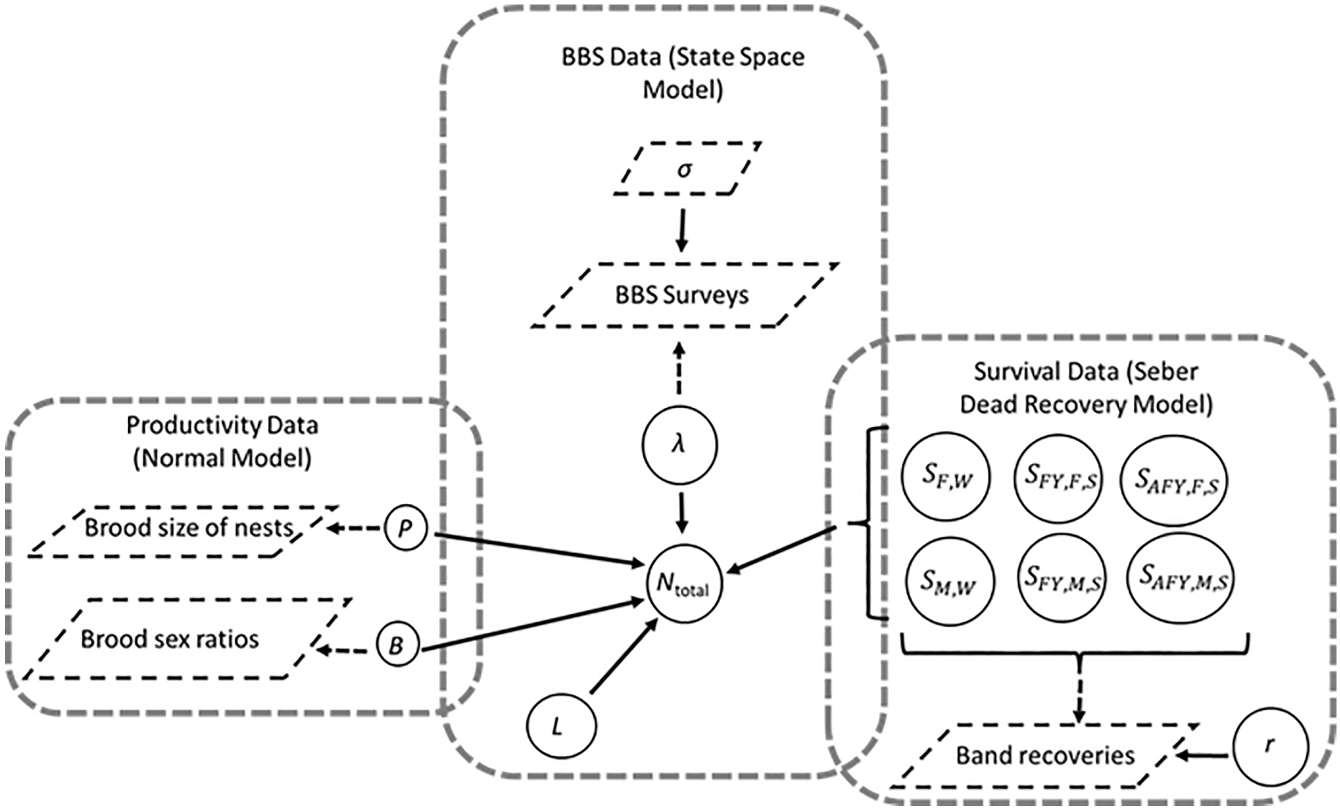

FIGURE 1 Directed acyclic graph of the continental-scale integrated population model for the American kestrel. Note that some demographic parameters are common to different sources of information. Estimated parameters are in circles, and the data are represented by rectangles. Arrows represent dependencies between nodes. Node notations: Band recoveries, data from the U.S. Geological Survey Bird Banding Lab; BBS Surveys, population count data collected through the North American Breeding Bird Survey (BBS); Brood size of nests and Brood sex ratios, data from a collection of small-scale studies estimating kestrel fecundity rates and data from the Bird Banding Lab, respectively; P, brood size; B, brood sex ratios; L, probability of a female fledging young; $S^{A,F,W}$, adult female winter survival; $S^{A,M,W}$, adult male winter survival; $S^{J,F,W}$, juvenile female winter survival; $S^{J,M,W}$, juvenile male winter survival; $S^{J,F,S}$, juvenile female summer survival; $S^{J,M,S}$, juvenile male summer survival; $S^{A,F,S}$, adult female summer survival; $S^{A,M,S}$, adult male summer survival; r, band recovery rate; N_{total}, population size; σ, population size SD; λ, population growth rate.

referred to as juveniles (J). Individuals with unknown age or sex were removed from this analysis.

We used multiple criteria to develop a final dataset from the BBL banding and recovery data for the survival submodel. We used banding and encounter data from 1986 to 2019 to align with the temporal scale of our productivity data (see *Fecundity* below). We retained only original banding records for wild-caught kestrels that were not marked or manipulated in additional ways that could have affected survival rates (e.g., with patagial tags or radio transmitters; Farmer et al., 2006). The last month of the BBL recovery file we received was February 2021. Thus, we removed any banding data after February 2020 so that all birds had a full year-long interval between banding and recovery. We filtered recovery data to exclude records where a bird's status or band type was uncertain. Some encounter records were missing the day of encounter; we retained those records and assigned the encounter day to be the 15th day of the month. We excluded records with encounter dates prior to the banding date.

We further subset the banding and recovery data into discrete seasons based on kestrel life history and the seasonal distribution of banding records. Most kestrels were banded in late spring and early summer at their nests, or on fall migration. By separately estimating survival for spring–summer and fall–winter, we were able to include kestrels that entered the capture history in either banding pulse. For juvenile birds, we retained records for a spring banding season from May to July. For adult birds, we retained records for a spring banding season from April to May. The fall banding season was the same for both age cohorts (September–October). This means that the summer period for juveniles is 15 June–1 October; for adults, it is 1 May–1 October and the winter period for juveniles is 1 October–15 June and for adults, it is 1 October to 1 May. The product of summer period survival rates (S^s) and winter period survival rates (S^w) for

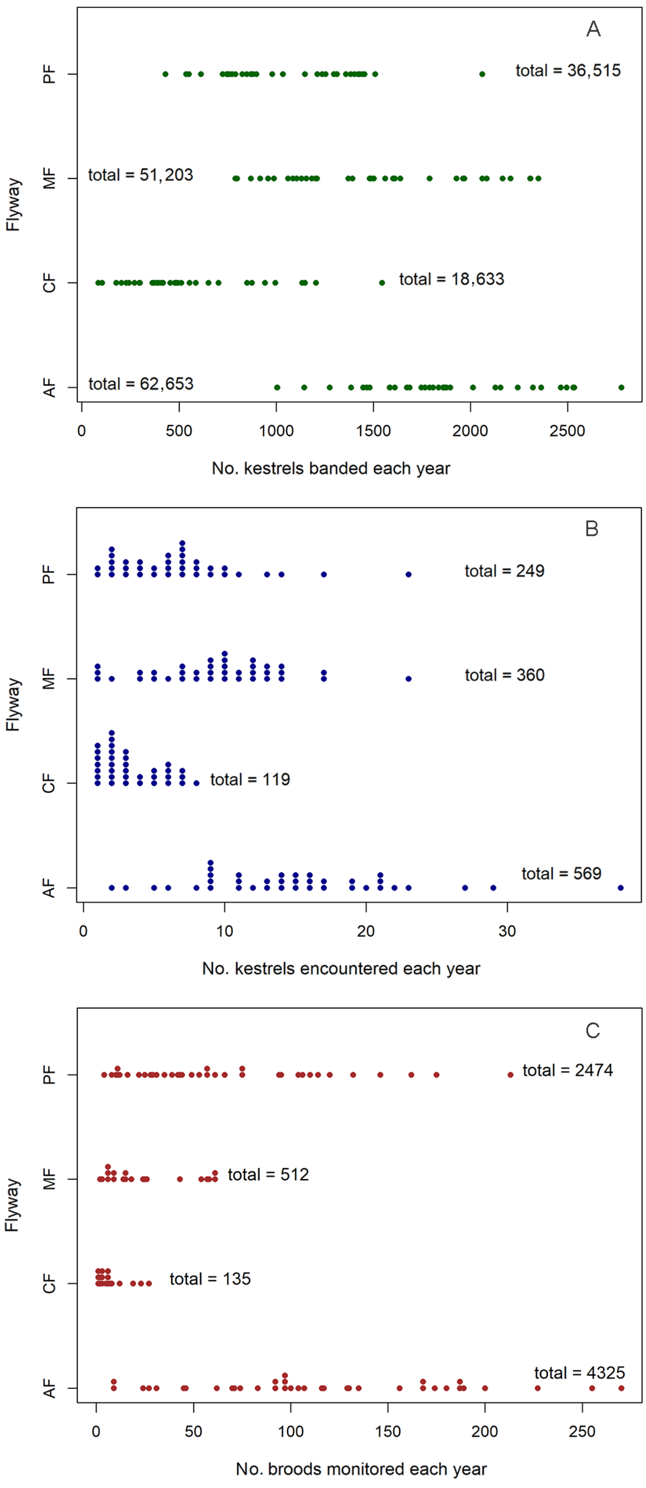

FIGURE 2 (A) The number of American kestrels banded each year by flyway (AF, Atlantic flyway; CF, Central flyway; MF, Mississippi flyway; PF, Pacific flyway), (B) number of kestrels recovered each year by flyway, and (C) number of broods monitored each year by flyway.

adults represents a year. In contrast, the seasonal survival rates do not represent a full year for juvenile birds (11 months) because they are banded after adults in the year in which they hatch and then become adults in the subsequent spring, in the year after they hatch. Therefore, to compare annual survival rates for juvenile to adult birds, we exponentiated the product of the two period survival rates for juveniles: $(S^{w} \times S^{s})^\wedge(12/11)$.

After filtering the banding and encounter data by the criteria described above, we had 109,893 juvenile spring banded birds (range = 1926–4595 annually) and 29,459 juvenile fall banded birds (range = 253–2187 annually). In addition, we had 18,651 adult spring banded birds (range = 247–934 annually) and 3435 adult fall banded birds (range = 49–196). During this time span, 1283 bands from this pool were recovered (n = 1123 juveniles and 160 for adults), with moderate inter-annual variation in recoveries (range = 0–13 for juvenile spring banded birds, 0–4 for juvenile fall banded birds, 0–4 for adult spring banded birds, and 0–2 for adult fall banded birds).

Fecundity

To parameterize the fecundity submodel (Figure 1), we contacted kestrel researchers (n = 14) at universities, government agencies, and nongovernmental organizations to request fecundity data (Figure 2; Appendix S1). We received fecundity datasets from 10 studies from across all four U.S. Fish and Wildlife Service Migratory Bird Program administrative flyways. In addition to the fecundity datasets from individual researchers, we acquired kestrel fecundity data from the Peregrine Fund's American Kestrel Partnership database and the Cornell NestWatch Program database (Bailey et al., 2024). In total, we used 10,056 individual kestrel nesting records between 1986 and 2019 to inform our fecundity submodel. Fecundity records included brood counts between 18 and 24 days of age (~80% of fledging age as recommended by Steenhof & Newton, 2007). Nest failures were included in the data as brood counts of zero.

We used banding data from the BBL (described above) to inform a brood sex-ratio model within the fecundity submodel (Figure 1). Kestrels are sexually dimorphic in plumage and generally can be accurately sexed by the time they are old enough to be banded. We assumed that banding was not biased towards either sex. Thus, sex ratios of banded nestling kestrels in the data reported to the BBL should provide an accurate measure of sex ratios in broods. We filtered banding data to select only kestrels banded as nestlings and for which sex was determined and recorded. The ability to sex young could be sex-linked (i.e., one of the sexes might be determinable at an earlier age, which would bias the unknown-sex young in favor of the other sex), so we filtered the data to exclude all kestrels banded on the same day under the same permit number and at the same location if there were any unknown-sex young among the birds banded. This likely eliminated some broods that could have been included in our analysis, but it was a conservative approach to ensure that only broods where sex was determined for all young were used. We further filtered the data to select only birds banded over the years of interest in the IPM (1986–2019). We used a simple binomial model for this analysis, with model inputs consisting of counts of all young in broods that met our filtering criteria and counts of males in those broods.

Integrated population model

The continental-scale IPM we developed for kestrels was based on three submodels: (1) a survival submodel using band recovery data; (2) a recruitment submodel based on brood counts from nest surveys; (3) a stage-structured population model (Caswell, 2001) that combines age- and sex-specific survival and recruitment estimates with the annual indices from the BBS each spring. When integrated in the same model, these datasets and submodels produce joint estimates of population size (or an index of population size), demographic rates and recovery parameters. We used a hierarchical modeling approach to link the data-generating processes with an ecological process model that describes the true but latent population processes (Kéry & Schaub, 2012; Figure 1).

State-space population size model

A key component of integrated population modeling is the process model that links population size to underlying demographic parameters. In our case, N is an index of population size estimated by the model rather than the true population abundance. Our process model was a pre-breeding, stage-structured Lefkovitch matrix model (Caswell, 2001) with two stages for each sex: juvenile females, juvenile males, adult females, and adult males:

$$N_{t+1}^{J,F} = N_{t+1}^{A,F} \times (1 - B_{t+1}) \times P_{t+1} \times L,$$

$$N_{t+1}^{J,M} = N_{t+1}^{A,F} \times B_{t+1} \times P_{t+1} \times L,$$

$$N_{t+1}^{A,F} = N_t^{A,F} \times S_t^{A,F,W} \times S_t^{A,F,S} + N_t^{J,F} \times S_t^{J,F,W} \times S_t^{J,F,S},$$

$$N_{t+1}^{A,M} = N_t^{A,M} \times S_t^{A,M,W} \times S_t^{A,M,S} + N_t^{J,M} \times S_t^{J,M,W} \times S_t^{J,M,S},$$

$$\overline{N}_{t+1} = N_{t+1}^{A,F} + N_{t+1}^{A,M},$$

$$N_{t+1} \sim \text{normal}\left(\overline{N}_{t+1}, \sigma^N\right) \text{T}(0,),$$

$$\sigma_N^2 \sim \text{inverse} - \text{gamma}(0.001, 0.001).$$

Here, $\overline{N}_{t+1}$ is the expected value of the truncated normal distribution (i.e., the summed abundance estimates) and σ_N^2 is the process variance. B represents the proportion of males in a brood, P represents brood size at fledging, and L represents the probability of a female breeding; see Fecundity sub-model section for details. Seasonal survival rates are represented by S, with age class indicated by the first superscript (A, adults; J, juveniles), sex indicated by the second superscript (F, female; M, male) and season indicated by the third superscript (W, winter; S, summer). Here, superscripts provide labels of age class and sex for parameters and do not indicate exponentiation unless otherwise indicated.

We assumed $N_1 \sim \text{lognormal}(\mu_{1986}, \sigma_{1986})$, where μ_{1986} and σ_{1986} were the mean and standard deviation on the log scale, respectively, calculated from the 10,000 MCMC samples scaled to the continental United States in 1986. We assumed equal sex ratio for adult males and females in year one ($N_1^{A,M} = N_1 \times 0.5$ and $N_1^{A,F} = N_1 \times 0.5$). We chose to start the time series with an equal sex ratio of adults because we had no basis for assuming otherwise; in subsequent years, the sex ratio was updated based on the model outputs. For the prior on juvenile male and female abundance in year one, we used the estimated overall mean brood size (intercept in our brood size model on the logit-scale, β^p; see below) and the proportion of males in brood (intercept in our logit-linear proportion of males in brood model on the probability scale, p_0; see below): $N_1^{J,M} = N_1^{A,F} \times p_0 \times \beta^p$ and $N_1^{J,F} = N_1^{A,F} \times (1 - p_0) \times \beta^p$.

We used annual indices from the BBS (described above; Link et al., 2020; Figure 1) as our count data. We specified the observation model as:

$$\text{BBS}_t \sim \text{normal}\left(N_t, \sigma_t^{\text{BBS}}\right),$$

where N_t is the adult population index, BBS_t is the observed mean BBS index each year, and σ_t^{BBS} is the observed standard deviation of the BBS index each year across all BBS routes. These annual indices account for variation in observer, survey route, observer experience, and year that may influence the number of birds seen each year on each route. Because our demographic parameters are represented as rates, so long as the annual indices accurately capture population dynamics from year to year, they provide an appropriate time series for our IPM. Notably, the BBS indices are produced with an estimate and standard error that can be aggregated at various spatial scales (e.g., flyway, continent) and allow for propagating this relevant source of uncertainty in the IPM.

Prior to fitting the integrated model, we evaluated submodels (survival, brood size, brood sex ratio) separately outside of the IPM to determine the version of each submodel to include. For each submodel, we considered four different temporal structures: (1) static with respect to time, (2) a simple linear time trend, (3) annual random effects, and (4) a combination of a linear time trend with annual random effects.

Survival submodel

We used the Seber (1970) dead recovery model to estimate seasonal survival and band-recovery rates. For the band-recovery submodel, we knew that banding efforts and reporting methods have changed over time, so we included a temporal trend and random effect to accommodate this heterogeneity in recovery rates. We formatted the recovery data as m-arrays ($\boldsymbol{m}$) where each row represented a cohort of kestrels banded and released in year t and each column represented the number of kestrel recoveries from that cohort each season-year (i.e., two seasons per year). For each cohort, there is an additional column to represent the number of kestrels never recovered during the time series. We had a separate recovery matrix for each combination of age class (a; juvenile, adult), sex (s; male, female), and season (b; fall, spring). Each row in the band-recovery matrix ($\boldsymbol{m}$) is modeled as following a multinomial distribution, where:

$$\boldsymbol{m}_b^{a,s} \sim \text{multinomial}\left(R_b^{a,s}, \boldsymbol{\pi}_{\boldsymbol{b}}^{a,s}\right)$$

The releases, R, were vectors of the total bandings for each year (length = number of years) for each age class, sex, and season. The cell probabilities, $\boldsymbol{\pi}$, were matrices based on a combination of an age/sex/season-specific mean ($\mu^s_{a,s,b}$) and trend ($\alpha^s_{a,s,b}$) for survival rate (s), and an age-specific mean recovery rate $\left(\mu^r_a\right)$ with annual random effects (ε^r_t). We modeled survival using the logit link as follows:

$$\text{logit}\left(s_t^{a,s,b}\right) = \mu^s_{a,s,b} + \alpha^s_{a,s,b} \times t$$

We also modeled recovery using the logit-link:

$$\text{logit}(r_t) = \mu^r + \alpha^r \times t + \varepsilon^r_t$$

We specified an uninformative prior probability distribution for the variance (inverse-gamma(0.1, 0.1)) and also specified minimally informative prior distributions for the intercept (μ^s and μ^r) and slope (α^s) parameters (normal(0, $\sigma^2 = 2.72$); see Northrup & Gerber, 2018).

When fitting models to empirical data, we used the deviance information criterion (DIC) to select the best (i.e., lowest DIC) survival submodel to use within the full IPM (Appendix S2: Table S1). The best survival submodel based on DIC included survival probabilities that varied by cohort (age and sex) and season, with a cohort and season-specific linear time trend. We initially included temporal random effects; however, these parameters were poorly estimated (i.e., wide credible intervals primarily reflecting the prior distributions), and so we removed these random effects from the final survival model. We used a simulation study to explore our ability to recover parameter estimates for the top survival model (Appendix S3).

Fecundity submodel

In addition to the four different model structures, we also explored three different probability distributions for estimating brood size: (1) a truncated normal distribution; (2) a Poisson distribution; and (3) an overdispersed Poisson distribution. For all models, we included an upper bound of 8 (the maximum observed brood size plus one). The truncated normal model with a random effect of year had the lowest DIC among the models evaluated (Appendix S2: Table S2). The final model for brood size (P) is as follows:

$$P_i \sim \text{normal}\left(\mu_{\text{year}[i]}, \sigma^2\right) T(,8),$$

$$\sigma \sim \text{uniform}(0, 10),$$

$$\mu_t = \beta^P + \varepsilon^P_t,$$

$$\beta^P \sim \text{normal}(0, 2.72),$$

$$\varepsilon^P_t \sim \text{normal}\left(0, \sigma_P^2\right),$$

$$\sigma_P \sim \text{uniform}(0, 10),$$

where i indexes each nest monitored, β^P is the intercept, and ε^P_t is the random year effect describing the expected brood size of each nest.

To estimate the breeding probability of female kestrels each year, we included a single latent parameter (L; Figure 1) in the state-space component of the IPM. Although we had limited data to inform L, IPMs can reliably estimate a single latent parameter without direct data if there is information about the parameter in other data supplied for the model (Abadi, Gimenez, Ullrich, et al., 2010; Schaub & Abadi, 2011). In our case, there appeared to be sufficient information in the other data used in our IPM to estimate L. Because breeding probability was a latent parameter, we could not evaluate support for various submodels. Rather, we evaluated the IPM for each of the four different model structures for L. Models with additional temporal complexity, compared to the static model, led to poor MCMC performance.

We modeled brood sex ratio data using a binomial model as:

$$B_t \sim \text{binomial}(\text{NB}_t, p_0)$$

where B_t is the number of male nestlings banded, NB_t is the total number of nestlings banded, and p_0 is the proportion of the broods that are males. The model with the lowest DIC was the model that was static with respect to time (Appendix S2: Table S3). We used a uniform(0, 1) prior probability distribution for p_0.

Model fitting in a Bayesian framework

We fit models in a Bayesian framework by implementing MCMC sampling in program R 4.2.3 (R Core Team, 2023) using the R package runjags (Denwood, 2016). Following an initial adaptation and burn-in phase of 6000 iterations, we fit IPMs with three chains, each chain of length 625,000 with a thinning rate of five to reduce autocorrelation, retaining 375,000 iterations to describe the posterior distribution. We evaluated model convergence using the Gelman–Rubin diagnostic (Rhat <1.1 indicates adequate convergence) and by inspecting trace plots (Appendix S4: Figure S1). Additionally, we sampled the posterior distribution until the MC error, as a percentage of the posterior standard deviation, was <5%. To assess the model fit, we conducted posterior predictive checks for each submodel by calculating a fit statistic for each empirical dataset and a dataset simulated under the assumptions of our model. For the survival and brood size models, we used the Freeman–Tukey fit statistic; and for brood sex ratio, the sum of squares of the Pearson residuals. We used the ratio of the fit statistic (i.e., the Bayesian p value, Gelman et al., 2004) to assess model fit, with values close to 0 or 1 indicating a lack of fit. We report posterior means and 95% credible intervals (CI; 2.5% and 97.5% quantiles) for focal parameters.

Matrix modeling

We quantified the relative influence of each population parameter on the population growth rate λ by computing lower level parameter elasticities from the population matrix using the vitalsens function in the popbio R package (Stubben et al., 2012). The pre-breeding population matrix was only based on female kestrels and was built as:

$$\begin{bmatrix} (1-B)\times P\times L\times S^{J,F,W}\times S^{J,F,S}, & (1-B)\times P\times L\times S^{J,F,W}\times S^{J,F,S} \\ S^{A,F,W}\times S^{A,F,S}, & S^{A,F,W}\times S^{A,F,S} \end{bmatrix}$$

We conducted analyses outside of the IPM by using 10,000 samples from the posterior distribution for each parameter, across all years, to account for uncertainty in the data-generating processes and in parameter estimation.

RESULTS

Survival

The largest declines in survival were for juveniles and adult males in the summer (Table 1, Figure 3). In comparison, adult female summer survival declined less precipitously throughout the time series. Winter survival for adults declined slightly, whereas for juveniles, it appeared to increase over the time series. Adult males had the highest average annual survival rate over the entire time series (mean = 0.61, 95% CI: 0.52–0.69), followed by adult females (mean = 0.52, 95% CI: 0.47–0.58), juvenile males (mean = 0.39, 95% CI: 0.32–0.46), and juvenile females (mean = 0.38, 95% CI: 0.32–0.46). However, for juveniles there was considerable overlap in credible intervals each year (Figure 4). Recovery rates were low but increasing throughout the time series (Table 1, Figure 5).

Posterior predictive checks indicated some lack of fit for band recovery models (Bayesian $p = 0.01$ for adult females and adult males banded in spring, and Bayesian $p = 0.97$ for adult females and 0.99 for adult males banded in fall). There was no evidence of a lack of fit for juvenile band recovery models (Bayesian $p = 0.13, 0.34, 0.85, 0.70$ for juvenile females banded in spring, juvenile males banded in spring, juvenile females banded in fall, juvenile males banded in fall, respectively). Even in our simulation study, there were often datasets for which the models did not fit the data well ($0.1 < p$ or $p < 0.9$; Appendix S3: Figure S1). However, our simulation study demonstrated our ability to reliably recover underlying parameter values despite lack of model fit (i.e., coverage was nominal for all parameters).

TABLE 1 Estimates of the posterior mean, lower 2.5% credible interval (LCI), and upper 97.5% credible interval (UCI) for population parameters for our integrated population model for American kestrels in North America from 1986 to 2019.

Submodel	Parameter	Mean	LCI	UCI
Brood size	Intercept	2.843	2.688	2.992
	Annual random effect SD	0.423	0.316	0.567
	Overall SD	1.984	1.952	2.016
Proportion of males in brood		1.208	1.207	1.209
Probability of initiating a nest		1.278	1.256	1.297
Survival	Intercept (AFW)	1.133	0.750	1.540
	Intercept (AMW)	1.277	0.895	1.667
	Intercept (JFW)	0.328	−0.003	0.662
	Intercept (JMW)	0.166	−0.164	0.505
	Intercept (AFS)	0.905	0.588	1.225
	Intercept (AMS)	1.727	1.334	2.134
	Intercept (JFS)	1.038	0.671	1.429
	Intercept (JMS)	1.628	1.189	2.088
	Slope (AFW)	−0.004	−0.022	0.014
	Slope (AMW)	−0.009	−0.029	0.012
	Slope (JFW)	0.006	−0.009	0.021
	Slope (JMW)	0.002	−0.016	0.019
	Slope (AFS)	−0.002	−0.017	0.012
	Slope (AMS)	−0.016	−0.036	0.004
	Slope (JFS)	−0.015	−0.031	0.000
	Slope (JMS)	−0.024	−0.045	−0.003
Recovery	Intercept (r)	−5.174	−5.391	−4.950
	Slope (r)	0.016	0.005	0.027
	Annual random-effect SD	0.254	0.174	0.357

Note: Survival model parameters are denoted by age, sex, and season (*J*, juvenile; *A*, adult; *F*, female; *M*, male; *W*, winter; *S*, spring). Note that proportion of males in brood, probability of initiating a nest, survival and recovery parameters are reported on the logit scale.

Productivity

We found moderate inter-annual variation in brood size (Figure 6). Our model estimated mean annual brood size, including unsuccessful nests, was 2.84 (95% CI: 2.69–2.99; Table 1). Brood sex ratio did not differ greatly from 50:50 (mean = 0.50, 95% CI: 0.50–0.50). The probability of a female breeding was relatively high (mean = 0.78, 95% CI: 0.68–0.90). Posterior predictive checks suggested adequate fit for the brood size (Bayesian $p = 0.42$) and brood sex ratio (Bayesian $p = 0.13$) models.

Abundance and population growth rate

Although mean population growth rates (λ) estimated by the IPM were close to one (geometric mean = 0.987, 95% CI: 0.984–0.990), more of the posterior density was below one in almost every year during the time series (Figure 7A). Furthermore, point estimates were below one for twice as many years as they were above one. Overall estimates of population growth from 1986 to 2019 suggest a 29% decline in population size (95% CI: −34% to −23%). Latent estimates of the total BBS index from the model, which include banding and recruitment data in addition to BBS data, generally match the raw BBS indices well, which suggests concordance in kestrel trends among demographic rates and the BBS indices (Figure 7B).

Matrix modeling

Adult survival had the greatest proportional impact on population growth rate, relative to juvenile survival and any parameter related to productivity (Table 2). Mean estimates of the net reproductive rate (number of females

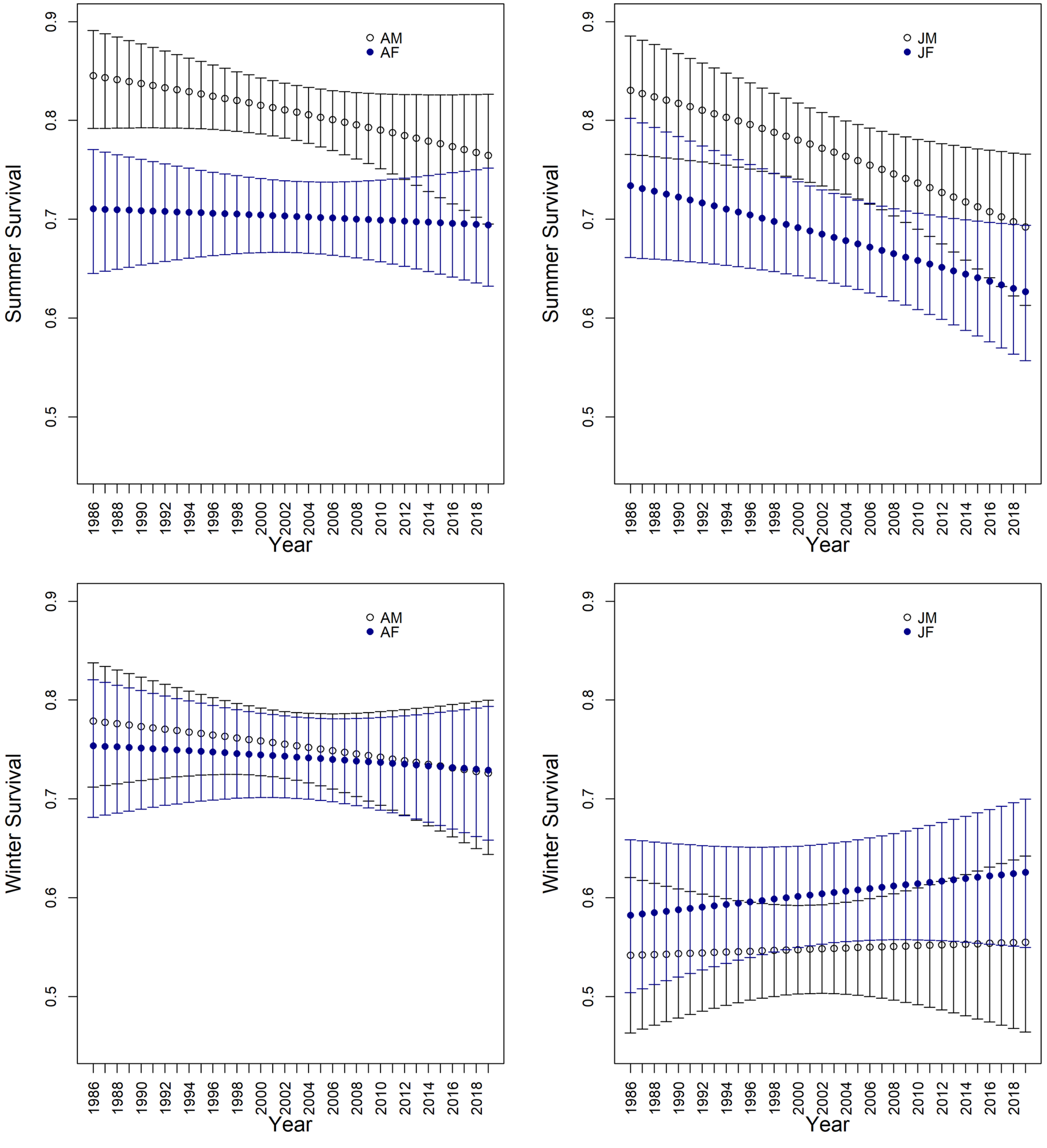

FIGURE 3 Estimated seasonal (winter or summer) survival (mean and 95% CIs) for adult male (AM), adult female (AF), juvenile male (JM), and juvenile female (JF) American kestrels in North America from 1986 to 2019.

a female would be expected to produce in her lifetime) were decreasing (0.97), but 95% credible intervals overlapped 1. The proportion of juvenile to adult birds was relatively even (mean = 0.47 and 0.53, respectively). Population growth rate from the matrix model suggested an average rate of decline of ~2% per year, but the 95% CIs overlapped one.

DISCUSSION

Our analysis revealed several aspects of survival that could contribute to the long-term decline in kestrel populations in the continental United States. First, summer survival for juvenile birds and adult males declined over the time series at a rate of ~1%–2% per year. Second,

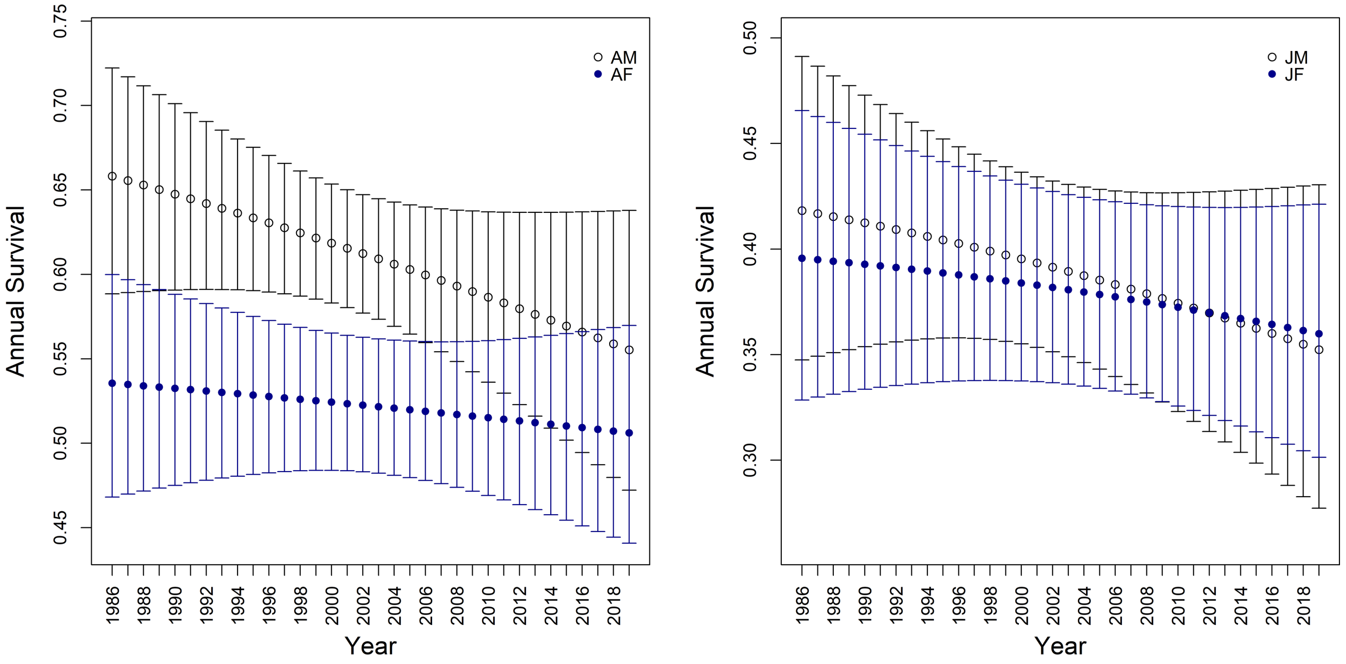

FIGURE 4 Estimated annual survival (mean and 95% CIs) for adult male (AM), adult female (AF), juvenile male (JM), and juvenile female (JF) American kestrels in North America from 1986 to 2019.

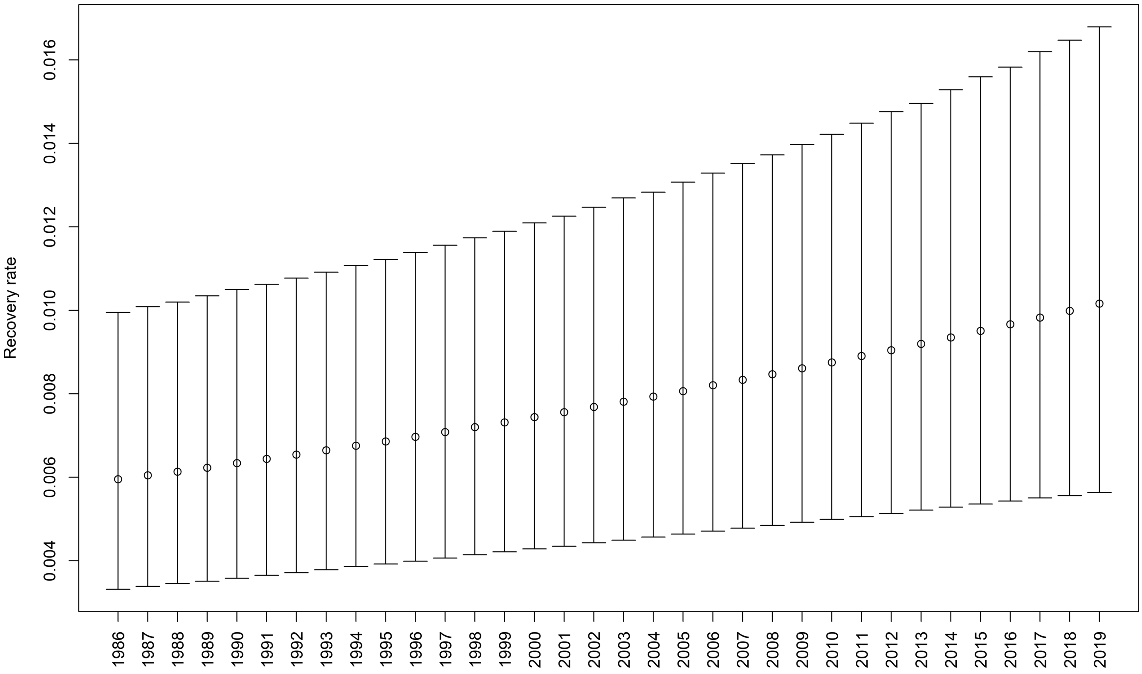

FIGURE 5 Recovery rates with 95% credible limits for American kestrels in North America based on band recoveries from 1986 to 2019.

the overall adult survival rates we observed, particularly for adult females, were lower than contemporary survival rates for most other similar-sized species in the genus *Falco* (e.g., 0.66–0.72 for Eurasian kestrels, Dobson, 1987; Fay et al., 2019; 0.78 for the Mauritius kestrel, *F. punctatus*, Nicoll et al., 2003; and 0.65–0.72 for the lesser kestrel, *F. naumanni*, Prugnolle et al., 2003; Serrano et al., 2005). In a review of raptor survival rates, Newton et al. (2016) described the relationship between body mass and survival. For a diurnal raptor of similar body size to adult American kestrels (~100 g), we would expect a higher annual survival (~70%) compared to what

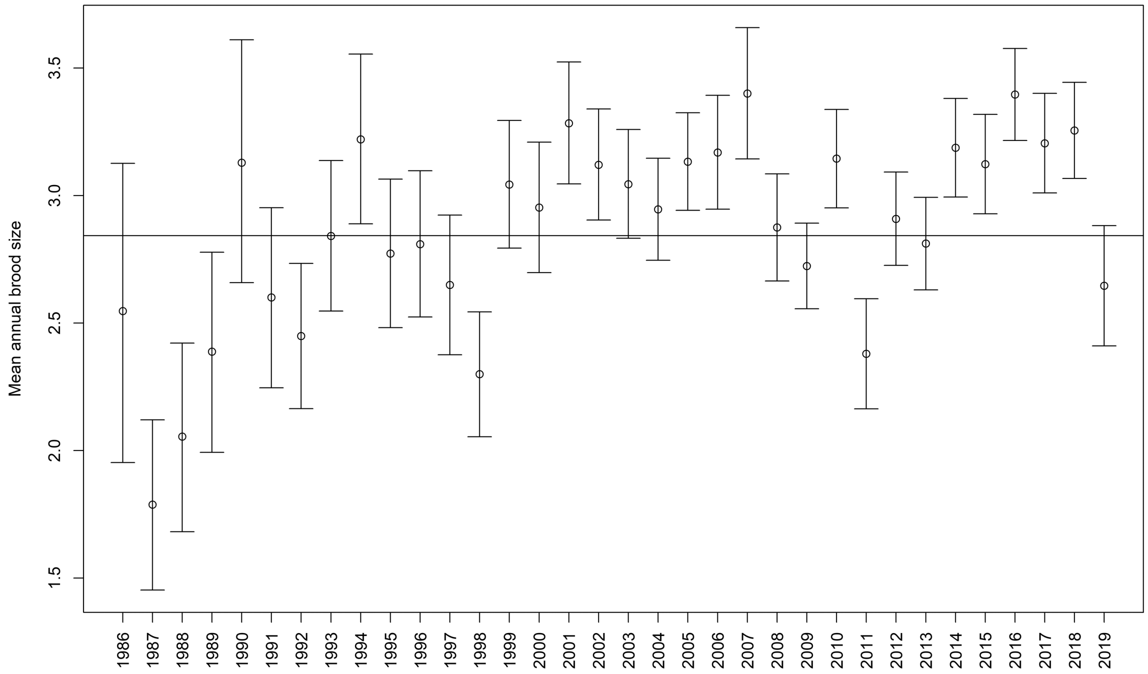

FIGURE 6 Estimated mean annual brood size and 95% CIs by year from 1986 to 2019 for the American kestrel in North America.

we found using our IPM (mean survival ~50%–60%). These observations suggest that some factor or factors related to the summer survival of juveniles and adult males, and the annual survival of adults, particularly adult females, have contributed to the long-term decline. Interestingly, winter survival for juveniles appears to be increasing in our study, so it is possible that higher winter survival could eventually compensate for low survival in other seasons and stabilize the population trend. Previous work demonstrated a positive relationship between warmer winter temperatures and apparent survival (Callery et al., 2022).

Our estimates of adult survival rates were very similar to apparent survival rates reported from six recent kestrel IPMs by McClure et al. (2021). Furthermore, at least one other study on kestrel survival found similar differences between males and females, whereby after-hatch-year male apparent survival tended to be greater than after-hatch-year female apparent survival within western North America (Callery et al., 2022). Compared to McClure et al. (2021), our estimates of juvenile survival were higher. We attribute the difference in estimates of juvenile survival to emigration being confounded with survival in the McClure et al. (2021) study, which is most likely to negatively bias estimates of juvenile survival given typical natal dispersal distances in kestrels (McCaslin et al., 2020).

As noted above, our assessment of elasticities of the lower level demographic rates shows that adult survival has the greatest effect on kestrel population growth rates, a finding also noted by McClure et al. (2021). The apparent chronically low survival of adult female kestrels is thus a potentially important factor relative to the long-term population decline. The high importance of adult survival is typical in raptors but is most pronounced in longer lived species like eagles (Millsap et al., 2022; Zimmerman et al., 2022). In smaller raptors with shorter life spans, other demographic parameters can have a substantial influence on population growth rates. In American kestrels, the effect of juvenile survival on population growth rates is also meaningful. This is in part because the age structure of the population is nearly evenly divided between juvenile and adult birds. Thus, the long-term decline in juvenile survival in summer has also likely influenced changes in population size.

Bird and Smallwood (2023) recently reviewed factors postulated to have contributed to the decline in American kestrel populations in North America. Of the seven factors they listed, five are potentially germane to kestrel survival: (1) declines in abundance of arthropod prey (e.g., common grasshoppers, Welti et al., 2020), particularly with respect to seasonal trends relative to kestrel breeding; (2) the continued use of second-generation rodenticides (Rattner et al., 2011; Rattner & Harvey, 2021); (3) the direct and indirect effects of neonicotinoid insecticides (Radvanyi et al., 1988); (4) increases in human population density; and (5) Cooper's hawk predation. With respect to the latter issue, Coooper's hawk populations declined in the middle of the 1990s likely due to DDT contamination (Pattee et al., 1985), but

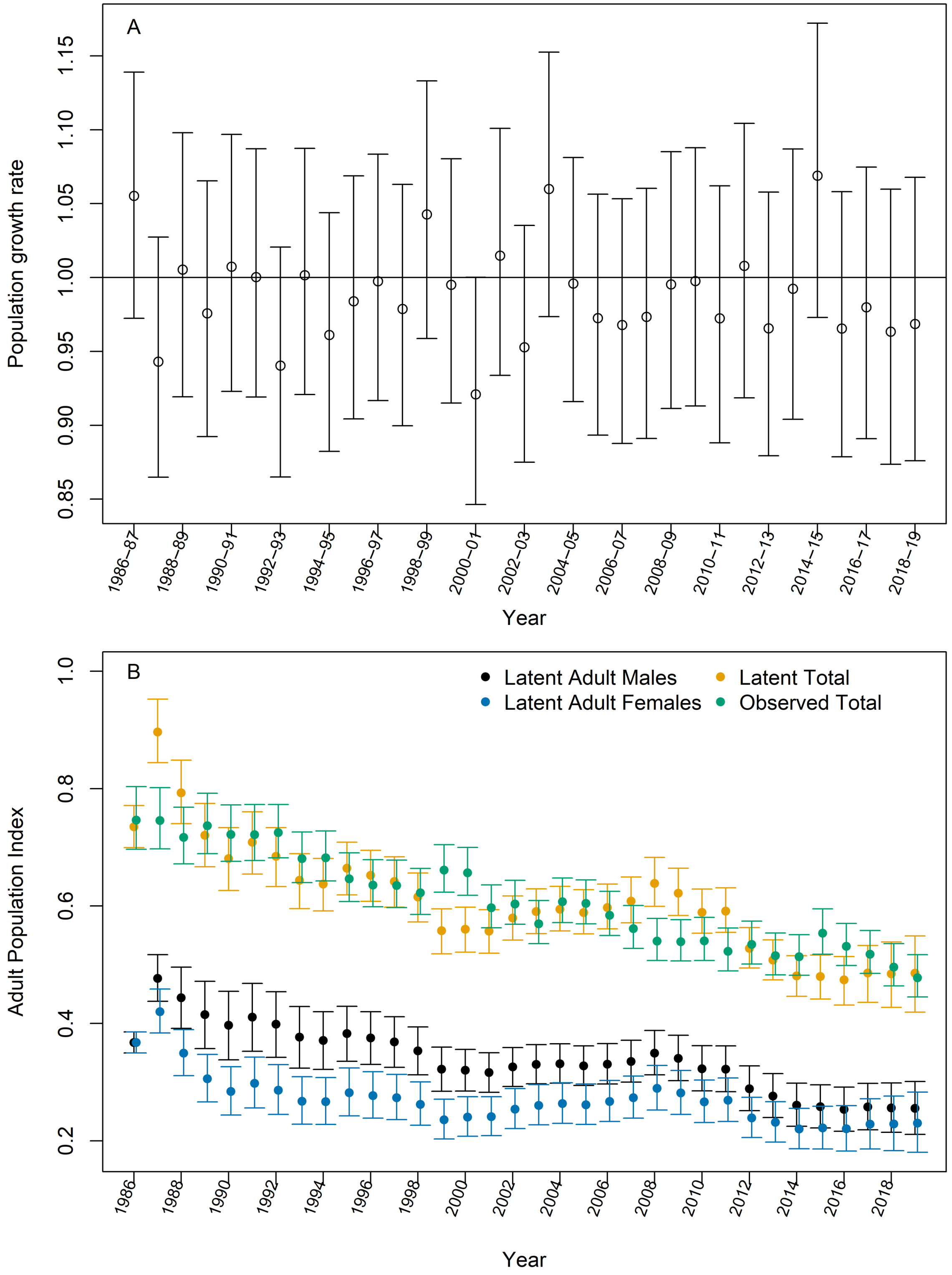

FIGURE 7 (A) Estimated population growth rate (λ) each year and (B) adult population index (mean and 95% CIs) from 1986 to 2019 for the American kestrel in North America. The horizontal line at 1 indicates a stable population that is neither increasing nor declining. The observed total comes from the Breeding Bird Survey data, whereas the latent total is estimated within the integrated population model.

populations have since recovered, and most of that recovery coincided with the timing of this study (Bednarz et al., 1990). Additionally, Cooper's hawks are known to prey on kestrels, and some hawks target nest boxes (Millsap et al., 2013). Thus, Cooper's hawk predation is a plausible potential cause of low kestrel survival during the period of decline. Increases in human population density since the 1960s are likely correlated with an increase in the distribution and abundance of some predators, including outdoor domestic cats and raccoons that tend to do well in human-modified landscapes. In a similar vein, an increase in human population density in North America has meant an expansion in vehicular traffic, which also poses a mortality risk to raptors (Bishop & Brogan, 2013). In the eastern United States, there is also evidence of a trade-off between adult survival and reproduction, with earlier nesters experiencing lower survival rates (Callery et al., 2022). Given the narrow window of resource availability for raising young in the east, this trade-off may lead to a continued decrease in adult survival, as adults are unable to shift the timing of reproduction with changing climate.

We found moderate annual variation in model-estimated productivity parameters, but there was no meaningful temporal trend for any measure of reproduction. Our overall estimate of mean brood size (2.84) is similar to what has been reported in the literature, but our estimate of the number of fledglings per female is on the low end of what has been reported previously (Table 3). We attribute this latter pattern to the fact that we were able to fully account for breeding propensity by including a latent parameter in our IPM that attempted to estimate

TABLE 2 Mean, SD, lower 2.5% credible interval (LCI), and upper 97.5% credible interval (UCI) of population growth rate (λ), proportion of first-year (FY) and after-first-year (AFY) age classes within the population, net reproductive rate (number of females produced by a female in her lifetime), and lower level elasticities associated with each vital rate for American kestrels in North America from 1986 to 2019.

Metric	Mean	SD	LCI	UCI
Population growth rate	0.98	0.08	0.82	1.13
Proportion FY	0.47	0.05	0.36	0.54
Proportion AFY	0.53	0.05	0.46	0.64
Net reproductive rate	0.97	0.32	0.47	1.71
FY survival elasticity	0.47	0.05	0.36	0.54
AFY survival elasticity	0.53	0.05	0.46	0.64
Fecundity elasticity	0.47	0.05	0.36	0.54
Proportion breeding females elasticity	0.47	0.05	0.36	0.54
Probability of female in brood elasticity	0.47	0.05	0.36	0.54

TABLE 3 Estimates of the brood size of successful nests (Brood size), number fledged per nesting attempt (Fledged), and the number of nests searched (Sample) from studies of the American kestrel in North America.

Manuscript	Location	Time	Model	Sample	Brood size	Fledged
This study	North America	1986–2019	IPM	NA	3.87	2.17
Varland and Loughin (1993)	IA USA	1988–1992	None	212	3.1	2.9
Katzner et al. (2005)	PA USA	1993–2002	None	270	2.9	2.73
Steenhof and Peterson (2009)	ID USA	1986–2006	None	543	4	2.6
Shave and Lindell (2017)	MI USA	2012–2015	None	18	NA	3.8
Snyder and Smallwood (2023)	NJ USA	1995–2021	None	696	3.1–4.5	2.25–3.97
Smallwood and Collopy (2009)	FL USA	1989–1993	None	>158	2.2–2.8	1.9–2.75
Eschenbauch et al. (2009)	WI USA	2004–2008	None	160	NA	2.89
Strasser and Heath (2013)	ID USA	2008–2009	None	73	3.9	NA
McClure et al. (2021)	FL, ID, PA, NJ USA	1992–2014	IPM	61–217[a]	NA	2.64–3.1
Miller et al. (2019)	FL USA	2019	None	17	3.4	2.2
Beatty et al. (2022)	FL USA	2018–2019	None	85	2.6	NA

Note: If used, the statistical model (Model) is also provided (IPM, integrated population model).

[a] Annual sample size.

the probability of this event. Despite not having any data to directly inform this probability, we were able to estimate this parameter with a reasonable amount of precision (Table 1). Thus, we do not believe the comparatively low number of young fledged per female that we estimate is problematic; rather, it is more realistic because it considers female breeding propensity. Our findings support the assertion of McClure et al. (2021) that declines in kestrel populations are unlikely to be the result of deficiencies in reproduction.

We used BBS indices as the count data for our IPM, taking advantage of the ability of IPMs to use indices of abundance rather than true abundance to derive inference on population status and demographic rates. As expected, model estimates of population growth rates and annual adult abundance indices provide evidence that kestrel populations have been declining at the scale of North America. Our estimate of a mean ~1%–2% annual rate of decline from 1986 to 2019 is similar to the 1.4% annual decline estimated from the BBS alone (1966–2019) by Bird and Smallwood (2023) and the 1.2% per year decline reported for the United States (1966–2022) by Hostetler et al. (2023). Both sources of population trends for kestrels suggest that rates of decline vary regionally and temporally, with some evidence that the extent of kestrel population declines may be abating in some regions. Recent analyses based on eBird checklist data provide additional support that population trends vary regionally, with much of the kestrel distribution in the United States west of the 100th meridian still in decline while the decline appears to have abated in the eastern United States (2007–2021; Fink et al., 2022). Because we relied on abundance indices as the count data in our IPM, we cannot provide estimates of true abundance. Although abundance indices are sufficient for developing an IPM, we would need additional datasets that allow us to correct for detection probability to estimate true abundance (e.g., Stillman et al., 2023). Future analyses using our IPM at smaller, regional scales could help elucidate these finer scale patterns in population trends and status.

The continental-scale IPM we developed will serve as the basis for evaluating hypotheses as to the causes of declines in kestrel survival rates over the last several decades. We expect that the causes of decline will vary spatially, and we are currently working to scale down this continental model. In doing so, one of the modeling challenges will be dealing with immigration and emigration among smaller geographic areas, like previous kestrel modeling efforts. One advantage of using band recovery data is that we should be able to separate emigration from survival and estimate rates of immigration into a focal population (e.g., the Central flyway). However, the quantity of band recoveries decreases at smaller spatial scales, making estimation of population parameters more difficult. As such, we are currently exploring the efficacy of combining band recoveries with live recaptures to improve our ability to estimate survival rates (Barker, 1997, 1999; Burnham, 1993). Although there are many live resight records for kestrels in the BBL data, given the heterogeneity in resight rates, we expect physical recapture data will be the only live recapture data that are feasible to include in our model (Cohen et al., 2014). In addition to limitations in the BBL data at sub-continental scales, BBS data are more limited in some portions of the kestrel range (Sauer et al., 2019). We are exploring the use of eBird Status and Trend products to improve the resolution of the count data included in our IPM (Fink et al., 2022). These products are more limited in temporal scale (i.e., currently available from 2007 to 2021), but provide impressive spatial resolution (~3 km^2) and are available for the entire North American continent. In this way, we hope to elucidate ecological drivers of ongoing declines in kestrel survival rates to better inform potential management interventions that could reverse this trend.

AUTHOR CONTRIBUTIONS

Paige E. Howell, Brian A. Millsap, and Abigail J. Lawson conceived the study idea and prepared the project proposal. Paige E. Howell, Brian A. Millsap, and Guthrie S. Zimmerman acquired data from public repositories or through direct requests from the research community. Productivity datasets were collected and curated for analysis by Jessi L. Brown, Julie A. Heath, John A. Smallwood, Karen Steenhof, Ted Swem, Karl E. Miller, and Christopher J.W. McClure. Paige E. Howell, Brian A. Millsap, and Guthrie S. Zimmerman developed the integrated population model and analyzed data, with intellectual contributions from Kristin P. Davis, Fitsum Abadi, Jessi L. Brown, Julie A. Heath, Brian W. Rolek, Christopher J.W. McClure, and Jean-Francois Therrien. Paige E. Howell and Brian A. Millsap wrote the manuscript; all co-authors provided a critical review of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Howell, 2025) are provided at https://doi.org/10.6084/m9.figshare.25605861.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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