RESEARCH ARTICLE

Evaluating population viability and efficacy of conservation management using integrated population models

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Abstract

1. Predicting population responses to environmental conditions or management scenarios is a fundamental challenge for conservation. Proper consideration of demographic, environmental and parameter uncertainties is essential for projecting population trends and optimal conservation strategies.

2. We developed a coupled integrated population model-Bayesian population viability analysis to assess the (1) impact of demographic rates (survival, fecundity, immigration) on past population dynamics; (2) population viability 10 years into the future; and (3) efficacy of possible management strategies for the federally endangered Great Lakes piping plover *Charadrius melodus* population.

3. Our model synthesizes long-term population survey, nest monitoring and mark–resight data, while accounting for multiple sources of uncertainty. We incorporated latent abundance of eastern North American merlins *Falco columbarius*, a primary predator of adult plovers, as a covariate on adult survival via a parallel state-space model, accounting for the influence of an imperfectly observed process (i.e. predation pressure) on population viability.

4. Mean plover abundance increased from 18 pairs in 1993 to 75 pairs in 2016, but annual population growth ($\bar{\lambda}_t$) was projected to be 0.95 (95% CI 0.72–1.12), suggesting a potential decline to 67 pairs within 10 years. Without accounting for an expanding merlin population, we would have concluded that the plover population was projected to increase ($\bar{\lambda}_t = 1.02$; 95% CI 0.94–1.09) to 91 pairs by 2026. We compared four conservation scenarios: (1) no proposed management; (2) increased control of chick predators (e.g. *Corvidae, Laridae*, mammals); (3) increased merlin control; and (4) simultaneous chick predator and merlin control. Compared to the null scenario, chick predator control reduced quasi-extinction probability from 11.9% to 8.7%, merlin control more than halved (3.5%) the probability and simultaneous control reduced quasi-extinction probability to 2.6%.

5. *Synthesis and applications.* Piping plover recovery actions should consider systematic predator control, rather than current ad hoc protocols, especially given the predicted increase in regional merlin abundance. This approach of combining integrated population models with Bayesian population viability analysis to identify limiting components of the population cycle and evaluate alternative management strategies for conservation decision-making shows great utility for aiding recovery of threatened populations.

1 | INTRODUCTION

As global climate change, emerging infectious diseases, invasive species and unprecedented rates of habitat loss continue to threaten wildlife populations (Brodie, 2016; Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016; Fisher, Gow, & Gurr, 2016; Maclean & Wilson, 2011), accurately describing and predicting how populations fluctuate under varying environmental or management conditions is increasingly critical. Conserving small and declining populations requires biologists to make decisions regarding complex ecological systems in the face of considerable uncertainty (Duarte, Pearl, Adams, & Peterson, 2017). Ecological and demographic stochasticity often limit assessment of population responses to environmental and management-related drivers with purely mechanistic frameworks (Williams, Nichols, & Conroy, 2002). Probabilistic approaches are needed to predict population trends and possible risks associated with management decisions. Typically, the uncertainty captured by these approaches relates only to the stochasticity of the modelled dynamics, but full consideration of demographic, environmental, and parameter uncertainties can reduce bias in estimates of population persistence (Melbourne & Hastings, 2008), lead to optimal conservation management (Johnson et al., 2013) and reveal specific data collection priorities to reduce that uncertainty (Maslo & Fefferman, 2015).

Population viability analysis (PVA) is a useful approach for identifying changes resulting from management decisions relative to baseline conditions (Beissinger & Westphal, 1998). Despite its ubiquity, accounting for parameter uncertainty in PVAs is challenging and traditional PVAs have been criticized for failing to separate sampling and process variance in estimates of demographic parameters (Green & Bailey, 2015; Heard, McCarthy, Scroggie, Baumgartner, & Parris, 2013). Bayesian population viability analysis (BPVA) has emerged as a powerful approach for overcoming limitations of classical PVA by allowing straightforward propagation of parameter uncertainty through the use of posterior probability distributions for parameters in population projections (Kéry & Schaub, 2012; McCarthy, 2007; Servanty, Converse, & Bailey, 2014). BPVAs can also be extended to incorporate uncertainty into conservation decision-making by evaluating prospective management scenarios in terms of probability of persistence or predicted population size (i.e. management modelling; Converse, Moore, & Armstrong, 2013; Lyons, Runge, Laskowski, & Kendall, 2008).

Bayesian approaches to PVA have primarily been pursued in the context of occupancy and mark–recapture modelling (Green & Bailey, 2015; Heard et al., 2013; Hegg, MacKenzie, & Jamieson, 2013; Servanty et al., 2014), but recently developed integrated population models (IPM) offer a unique opportunity to merge parameter estimation using multiple data types (e.g. census, mark–recapture, productivity, telemetry) with projection in a Bayesian framework (Kéry & Schaub, 2012). IPMs combine several data types collected on a given population into a single analysis to assess trends and drivers of population dynamics (Besbeas, Freeman, Morgan, & Catchpole, 2002; Brooks, King, & Morgan, 2004; Schaub & Abadi, 2011). By combining parameter estimates informed by multiple datasets into a single likelihood, the uncertainty around all demographic parameters is accounted for in a unified modelling framework. IPMs provide an ideal mechanism for incorporating uncertainty into BPVAs, yet few studies have focused on forecasting population abundances within this framework (but see Oppel et al., 2014).

We present a coupled IPM-BPVA approach to assess the (1) relative impact of demographic processes (survival, fecundity, immigration) on past population dynamics; (2) population viability 10 years into the future; and (3) efficacy of several possible management strategies for the federally endangered Great Lakes piping plover *Charadrius melodus* population. Since listing under the U.S. Endangered Species Act (ESA) and the Canadian Species at Risk Act (SARA) in 1986 (United States Fish and Wildlife Service [USFWS], 1985), the Great Lakes plover population has fluctuated between 17 and 75 known breeding pairs. Despite current management efforts, the population is far from the federal recovery goal of 150 pairs and continues to be threatened by avian and mammalian predation (U.S. Fish and Wildlife Service, 2003). However, the degree to which predation pressure impacts population growth and viability has never been explicitly quantified. We extend our IPM-BPVA to incorporate an imperfectly observed, temporally varying covariate (e.g. latent predator abundance) that may be influencing demographic rates and thus population viability. The methodological challenges of assessing predator abundances across broad spatial scales have largely precluded inclusion of predator-driven processes from PVAs (but see Stringham & Robinson, 2015), despite the considerable potential impacts on prey dynamics (especially for shorebirds; Colwell, 2010; Jackson, Fuller, & Campbell, 2004) and implications for management (Wilson, Gil-Weir, Clark, Robertson, & Bidwell, 2016).

We synthesized long-term (1993–2016) population survey, nest monitoring and mark–resight data to estimate and project annual demographic rates and population abundance, including predation-related effects on these quantities, while simultaneously accounting for environmental and demographic uncertainty. We also demonstrate how BPVA can propagate parameter uncertainty through predictions of population viability under different management options. This integrative method for evaluating alternative conservation strategies can serve as a tool in identifying key limiting components of the population cycle and as a guide in management decision-making to aid recovery of threatened populations.

2 | MATERIALS AND METHODS

2.1 | Study area and management

The Great Lakes population of piping plovers nests on wide, sparsely vegetated sand and cobble beaches along the shoreline of Lakes Michigan, Superior, Ontario and Huron (U.S. Fish and Wildlife Service,
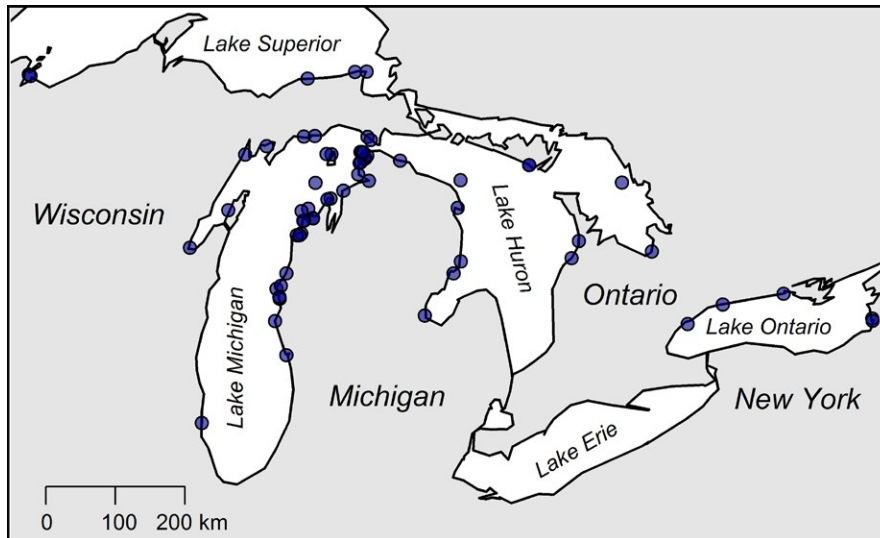
FIGURE 1 Distribution of major piping plover nesting locations in the Great Lakes region during 1993–2016. Our analysis integrated three distinct data types (population survey, nest monitoring and mark–resight) collected from all sites shown [Colour figure can be viewed at wileyonlinelibrary.com]

2003), and winters primarily along the U.S. Atlantic coastline ranging from North Carolina to Florida and the Bahamas (Gratto-Trevor et al., 2012; Stucker et al., 2010). Selective predator control (i.e. deterrence protocols, trapping, culling) of the primary avian predators of both young and adult piping plovers (American crow *Corvus brachyrhynchos*, common raven *Corvus corax*, herring gull *Larus argentatus*, merlin *Falco columbarius* and ring-billed gull *Larus delawarensis*) occurs intermittently and only at permitted nesting locations. Occasional trapping of mammalian predators (American mink *Neovison vison* and red fox *Vulpes vulpes*) also occurs at nesting sites, but at low frequencies and only when problem individuals can be identified. No predator control efforts occur on the wintering grounds, although increasing numbers of predators (cat *Felis catus*, coyote *Canis latrans*, dog *Canis lupus familiaris*, fox *Vulpes* and merlin) are reported to occur year-round at wintering locations (U.S. Fish and Wildlife Service, 2003). Our study used data from all known Great Lakes nesting locations during 1993–2016 (Figure 1).

2.2 | Demographic data collection

2.2.1 | Population monitoring data

Surveys were conducted by a network of contributing partners at historical, recent and potential nesting habitats during late April to early August annually from 1993 to 2016 (Figure 1). We used the total number of unique breeding pairs (i.e. individuals that renested following nest loss were not considered members of a new pair) observed each year as the population count data, which reflect the number of breeding females. Thus, we refer to total population sizes as the number of breeding pairs, rather than number of individuals, a count that excludes fledglings (i.e. individuals <1 year old).

2.2.2 | Annual productivity

Upon discovery of nesting birds, investigators placed predator exclosures around nests and erected warning signs and twine fences to

indicate local beach closures (U.S. Fish and Wildlife Service, 2003). Every 1–4 days, monitoring teams recorded nesting activities of colour-banded adults (Brudney, Arnold, Saunders, & Cuthbert, 2013), including locations of nests, counts and fates of eggs, hatch dates and number of chicks that survived to fledging age (*c.* 23 days old; Saunders, Arnold, Roche, & Cuthbert, 2014). We used the total number of fledglings observed each year, in conjunction with the number of surveyed broods, as productivity data.

2.2.3 | Banding and resight data

Piping plovers were banded using US Geological Survey (USGS) metal bands and Darvic colour bands (Avinet, Dryden, NY, USA). Adults were marked with unique colour combinations, whereas chicks were marked with brood-specific colour combinations that did not allow for individual identification without recapture. Unmarked or brood-marked (i.e. previously marked as chicks) incubating adults were trapped on the nest and given individual-specific colour combinations; chicks were caught by hand. We used data from 2,460 individuals first banded as chicks (2,328 individuals) or adults (132 individuals) during the 24-year study period. Resights were recorded every year during the breeding season (Saunders et al., 2014). We considered each breeding season as a separate encounter occasion to estimate annual juvenile and adult survival probabilities. Several unmarked adults were observed in the population each year (*c.* 2–6 annually), suggesting possible immigration from the largely unmarked Atlantic Coast and Great Plains populations or that birds hatched at unmonitored Great Lakes sites, despite efforts for regionwide survey coverage.

2.3 | Merlin count data collection

Previous work demonstrated that adult plover survival in the Great Lakes region has been negatively associated with annual abundance of eastern North American merlins (Saunders et al., 2014), and disappearances of breeding adults are most frequently attributed to

predation by merlins (Roche, Arnold, & Cuthbert, 2010). We obtained raw annual counts of merlins migrating through Hawk Mountain in Pennsylvania during autumn (August–December) and through Whitefish Point in Michigan during spring (March–May) throughout the 24-year study period (www.hawkcount.org). Migration through Hawk Mountain is thought to be the primary route of merlins leaving their breeding grounds in the northern United States heading to the south-eastern U.S. Atlantic coast and South America (www. hawkmountain.org) and can thus serve as an index of annual merlin population size. We combined estimates from the two locations via a state-space model (Kéry & Schaub, 2012) to approximate a latent annual index of abundance across the piping plover's entire range (Saunders et al., 2014), which we used as a covariate in our model of the plover population.

In building our IPM, we also tested for the effects of hurricane and spring temperature covariates. A prior study has demonstrated that adult plover survival is negatively related to annual hurricane activity on the south-east U.S. Atlantic coast where Great Lakes birds overwinter and somewhat positively related to minimum spring temperatures on the non-breeding grounds (Saunders et al., 2014). However, we did not find support for a significant association of either variable with adult survival and did not include these effects in the final version of the model (see Appendix S1 for more details).

2.4 | IPM framework

We estimated survival probabilities, productivity, population growth rates, abundance and immigration for the Great Lakes piping plover population by developing an IPM (Kéry & Schaub, 2012; Schaub & Abadi, 2011). Our female-based IPM utilizes a stage-structured formulation and is comprised of three subcomponent models: a state-space model using the annual population survey, a fecundity model using the nest monitoring data and a mark–recapture model using the data from colour-banded adults and chicks.

2.4.1 | Latent population model

We built the IPM assuming that breeding begins at age one, the sex ratio at fledging is even, and survival rates between sexes are identical (Saunders et al., 2014). Although some piping plovers exhibit delayed maturity, most female plovers in the Great Lakes population start breeding at 1 year and then breed annually thereafter (Saunders et al., 2014). We therefore assumed that all surviving juveniles matured to adults at age one. We utilized a stage projection matrix model with a pre-breeding census, which decomposes population dynamics into a state process as a function of adult and juvenile survival probabilities, annual fecundity and immigration (Figure 2). These parameters were assumed to be the same for all individuals within a stage class (i.e. no individual effects).

The life cycle model of the plover population includes three categories of adults (Figure 2): (1) age 1 individuals, locally produced fledglings that survived and recruited into the population (N_1); (2) age 2+ individuals that had been part of the breeding population in the
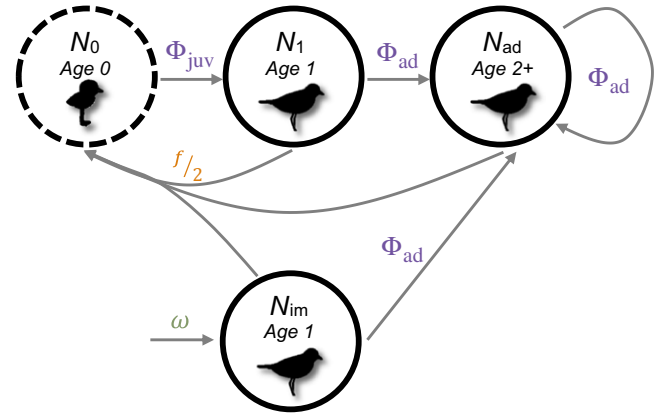

FIGURE 2 Life cycle diagram of the Great Lakes piping plover population. The three population segments of adult females (solid circles) which sum to the total estimated population size (N, measured as breeding pairs) each year are as follows: 1-year-old individuals who had been observed in the population as fledglings (N_1), individuals older than 1 year who had been previously observed in the population (N_{ad}) and immigrants (N_{im}). The annual number of fledglings (N_0) is also estimated within the model (dashed circle), but is not included in estimates of the total population size because we use a pre-breeding census. Estimated demographic parameters include age-specific survival (Φ_{juv}, Φ_{ad}), fecundity (f) and immigration (ω). Parameters are colour-coded according to the data types that contribute to their estimation; f (orange) is informed by both population survey and nest monitoring data; Φ (purple) is informed by both population survey and mark–resight data; and ω (green) is informed by population survey data [Colour figure can be viewed at wileyonlinelibrary.com]

previous year (N_{ad}); and (3) immigrants, breeding individuals new to the study area (N_{im}). Implicit in our population model is a juvenile stage (N_0) in which the fledgling population size is dependent on f_t, the number of individuals produced per female in year t and the total population of breeding adults: $N_{0,t} = \left[N_{1,t} + N_{ad,t} + N_{im,t} \right] \frac{f_t}{2}$. We incorporated demographic stochasticity into the model by allowing stage-specific abundance to vary according to stochastic processes:

$$N_{1,t+1} \sim \text{Poisson}(N_{0,t} \cdot \Phi_{juv,t})$$

$$N_{ad,t+1} \sim \text{Binomial}(N_{1,t} + N_{ad,t} + N_{im,t}, \ \Phi_{ad,t})$$

$$N_{im,t+1} \sim \text{Poisson}(\omega_t)$$

Here, $\Phi_{juv,t}$ and $\Phi_{ad,t}$ are apparent survival probabilities from year t to $t + 1$ of young (from mean banding age of c. 9 days old to age one) and adults, respectively, and ω_t is the annual number of immigrants entering the population (Schaub & Fletcher, 2015). We included environmental stochasticity by allowing all demographic parameters (survival, fecundity and immigration) to vary annually using random effects by assuming that the year-specific realized values were derived from normal distributions with a mean and variance that we estimated (e.g. $f_t \sim \text{Normal}\left(\mu_f, \sigma_f^2\right)$; see code in Appendix S2 for more details). We also included an effect of regional merlin abundance on adult plover survival as merlins are the primary predator of adults rather than

smaller, younger individuals. We chose to parameterize immigration as a number rather than a rate, which prevents overestimation when immigration is relatively small (Schaub & Fletcher, 2015). The total population size (i.e. number of breeding pairs) in year t is as follows:

$$N_t = N_{1,t} + N_{ad,t} + N_{im,t}.$$

2.4.2 | Estimation of model parameters

We used a hierarchical state-space model to partition the observed time series of breeding pair count data into a population process and an observation error component (De Valpine, 2003; Kéry & Schaub, 2012). The true number of breeding pairs in the population is linked to the survey data via an observation process that accounts for imperfect detection during population surveys. We modelled the observation process as a normal distribution conditional on the state process:

$$y_t \sim \mathrm{Normal}(N_{1,t} + N_{ad,t} + N_{im,t}, \tau_{obs})$$

where y_t is the number of observed breeding pairs in year t and τ_{obs} is the sampling error or variance in annual detection probabilities. To estimate apparent survival probabilities from individual mark–resight data, we used a Cormack–Jolly–Seber open-population live-recapture formulation (Kéry & Schaub, 2012; Schaub, von Hirschheydt, & Grüebler, 2015). We estimated survival probabilities by assuming that annual survival during the first year of life ($\Phi_{juv,t}$) was different from annual survival for birds older than 1 year ($\Phi_{ad,t}$). We assumed that resight probability was not dependent on age because all birds were >1 year old when they were first recaptured. The nest monitoring data were used to estimate fecundity (f_t), or the number of fledglings raised per adult female. The annual number of observed fledglings (j_t) was assumed to follow a Poisson distribution constrained by the number of surveyed broods in each year (b_t), such that $j_t \sim \mathrm{Poisson}(b_t f_t)$. See Appendix S2 for code and additional details.

We multiplied the likelihoods from the three different submodels (state-space, mark–recapture and productivity) to obtain the joint likelihood and estimated parameters from the joint model (Besbeas et al., 2002; Buckland, Newman, Thomas, & Koesters, 2004). We treated our datasets as independent, but since the survey methods are designed to obtain data on every individual, many individuals may be included in more than one (and possibly all three) data types. However, because the survey methods for this population are exhaustive and because previous work has demonstrated minor impacts on the accuracy of parameter estimates from non-independent, moderate-sized datasets (Abadi, Gimenez, Arlettaz, & Schaub, 2010), we assumed dataset independence.

2.4.3 | Estimating an index of merlin population size

We used a state-space formulation to estimate an index of annual merlin abundance, the covariate on $\Phi_{ad,t}$. We modelled merlin population dynamics using raw annual counts from Hawk Mountain and Whitefish Point observatories during 1993–2016. We estimated an index of latent merlin regional abundance (X_t) using both sets of observations s from the two observatories in each year t ($x_{t,s}$) such that:

$$x_{t,s} = \log(X_t) + \varepsilon_t$$

$$\varepsilon_t \sim \mathrm{Normal}(0, \sigma_x^2)$$

where σ_x^2 is the residual error that incorporates not only observation errors, but also the lack of fit of the state equations (Kéry & Schaub, 2012). We modelled annual changes to the true, latent merlin abundance using a stochastic population growth rate, s_t:

$$\log(X_{t+1}) = \log(X_t) + s_t$$

with $s_t \sim \mathrm{Normal}(\bar{s}, \sigma_s^2)$. We then included the annual latent merlin abundance estimates (standardized to $\bar{X} = 0$ and $\sigma = 1$) as a covariate on adult plover survival.

2.4.4 | Estimating population growth and its correlation with demographic rates

We calculated annual population growth rates (λ_t) for breeding pairs by dividing the total population size of breeding pairs (N_t) in year $t + 1$ by the total population size in year t:

$$\lambda_t = (N_{1,t+1} + N_{ad,t+1} + N_{im,t+1})/(N_{1,t} + N_{ad,t} + N_{im,t})$$

We used the geometric mean of log-transformed annual λ_t estimates (Oppel et al., 2014; Williams et al., 2002) to estimate the historic (1993–2016) and prospective (2017–2026) growth rates. To assess the relative contributions of the four demographic processes to variation in population growth, we correlated population growth rate with juvenile survival probability, adult survival probability, fecundity and immigration (Schaub, Jakober, & Stauber, 2013; Szostek, Schaub, & Becker, 2014; Tempel, Peery, & Gutierrez, 2014). We also correlated population growth rate with the annual index of merlin abundance to further quantify the influence of predation pressure on piping plover population dynamics. We calculated both the correlation coefficient (r) between each of these parameters and the growth rate (λ_t), using the mean estimates from each model iteration, and the probability that they were positive $P(r > 0)$ or negative $P(r < 0)$.

2.4.5 | Assessing population viability and efficacy of management alternatives with a BPVA

We assessed the viability of Great Lakes piping plovers by projecting the population size for 10 years into the future (2017–2026). Ten years represents the time frame used by the USFWS to project populations and assess reclassification criteria, and predictions greater than this duration are rarely meaningful given considerable uncertainty due to error propagation (Oppel et al., 2014). To make predictions, we augmented our datasets with NAs for the future years for both the piping plover population survey data and the merlin observational data, and then projected these values as part of the model fitting process (Kéry & Schaub, 2012; Oppel et al., 2014). We calculated the following derived quantities: (1) cumulative probability of annual population

quasi-extinction (i.e. ≤15 breeding pairs remaining, approximate population size outlined in ESA listing) and (2) probability that the population size in 2026 would be smaller than in 2016, the last year for which we have data.

We evaluated different management options by comparing both predicted cumulative quasi-extinction probability and total population size (N_t) in 10 years. We also calculated the probabilities that the scenarios with management would result in a larger population size in 2026, as compared to the size predicted under a null scenario (i.e. none of the proposed management options were implemented). For the null scenario, we forecasted population sizes and vital rates using the methods described above. We compared the null scenario to the following hypothetical management alternatives: (1) increased control of chick predators (e.g. *Corvidae, Laridae*, mammals) with the effect of a 20% increase in the number of fledglings; (2) increased control of merlins via reduction in their annual abundance by 20%, with the effect of increasing annual adult plover survival rates; and (3) simultaneous effects of both chick predator and merlin control (see code in Appendix S3 for details). Estimation of demographic parameters and population sizes from 1993 to 2016 was the same under all scenarios; only predictions into the future differed. We designed our management scenarios to reflect realistic conservation considerations that may be implemented by USFWS (V. Cavalieri, USFWS Endangered Species Biologist & Great Lakes Piping Plover Coordinator, pers. comm.).

2.4.6 | Model fitting

We fitted the IPM and BPVA using a Bayesian approach (Kéry & Schaub, 2012; Schaub, Gimenez, Sierro, & Arlettaz, 2007; Schaub & Abadi, 2011). To calculate posterior distributions for parameters, we used Markov chain Monte Carlo (MCMC) in the program JAGS (Plummer, 2003), implemented using the R package "jagsUI" (Kellner, 2016; R Development Core Team). We ran three independent chains for 400,000 iterations after a burn-in of 200,000 iterations and thinned chains by 10 to reduce autocorrelation (Link & Eaton, 2012). All prior probabilities were selected to be non-informative. Model convergence was assessed using the Rhat ($\hat{R}$) statistic (Gelman & Hill, 2006) and visual inspection of chains; convergence ($\hat{R} \leq 1.06$) was obtained for all parameter estimates. Model fit was assessed for each component model separately and is reported elsewhere (Saunders, Roche, Arnold, & Cuthbert, 2012; Saunders et al., 2014). Posterior distributions were summarized by their mean and 95% credible interval (CI) unless otherwise noted.

3 | RESULTS

3.1 | Abundance, demographic parameters and population growth

Our IPM estimated that the Great Lakes piping plover population increased from 18 breeding pairs (CI 15–21) in 1993 to 75 breeding pairs (CI 72–78) in 2016, tracking the observed population counts (i.e.

number of breeding pairs) very precisely (Figure 3a). The geometric mean of annual population growth ($\bar{\lambda}_t$) was clearly >1.0 ($\bar{\lambda}_t = 1.06$, CI 1.05–1.07), which translated to more than a quadrupling of the population size over the 24-year period.

Regional merlin abundance had a strong negative association with adult plover survival ($\beta_{merlin} = -0.29$, CI −0.73 to −0.06; see Appendix S1 for results regarding insignificant covariates), and the index of merlin abundance increased from 82 individuals (CI 55–109) to 126 individuals (CI 95–168) over the 24-year study period ($\bar{\lambda}_t = 1.02$; CI 0.98–1.07). Mean annual estimates of adult plover apparent survival ($\Phi_{ad,t}$) ranged from 0.71 to 0.86 (Figure 3b) with mean adult survival over the study period at 0.78 (CI 0.72–0.83). The lowest estimate of annual plover population growth ($\lambda_t = 0.86$) occurred during 2009–2010 when the index of merlin abundance was largest. Mean annual estimates of juvenile apparent survival ($\Phi_{juv,t}$) ranged from 0.17 to 0.29 (Figure 3b) with a mean value of 0.22 (CI 0.19–0.25) over the 24-year period. The average annual fledging rate (f) was 1.67 (CI 1.53–1.81) and was variable across years, ranging from 1.31 to 2.09 fledglings per female (Figure 3c). Precision on estimates of abundance, survival and fecundity was high (Figure 3a–c); estimates of immigration were the least precise due to lack of explicit data (Figure 3d). Immigration during 1993–2016 was low, with an expected number of 2.65 females (CI 0.14–5.32) entering the population annually (Figure 3d). Immigration varied considerably across years, with as many as 7.89 (CI 1.14–21.93) females estimated to have entered the population in 2002 (Figure 3d). Resight probability of banded individuals was relatively high ($p = .75$, CI 0.72–0.77) during the study period, reflecting the high search effort within the Great Lakes region.

All demographic rates were positively correlated with λ_t (Figure 4). Among the four demographic rates examined, juvenile survival had the greatest influence on population growth rate ($r = .42$), followed by fecundity ($r = .37$) and adult survival ($r = .34$); in all these cases, the 95% credible intervals excluded zero and the probabilities of a positive correlation were nearly 1.0 (Figure 4a–c). In contrast, the correlation between immigration and λ_t was only 0.31, and the credible interval overlapped zero (Figure 4d). The index of merlin abundance was negatively correlated with the plover population growth rate ($r = -.25$; Figure 4e), with a .99 probability of a negative correlation.

3.2 | Population viability and efficacy of management alternatives

The average plover population growth rate during 2017–2026 was predicted to be 0.95 (CI 0.72–1.12), leading to a projected decline from 75 pairs (CI 72–78) in 2016 to 67 pairs (CI 4–201) on average by 2026 (Figure 5a). A model without the merlin effect on adult survival projected an increase in plover abundance to 91 pairs (CI 42–169) on average by 2026 ($\bar{\lambda}_t = 1.02$, CI 0.94–1.09), albeit credible intervals for $\bar{\lambda}_t$ in both models overlapped 1.0. Incorporation of a temporally varying covariate into our IPM-BPVA led to greater uncertainty in $\bar{\lambda}_t$ such that the credible interval was considerably wider than in a model run that did not include a merlin effect on adult survival. We calculated the per cent of MCMC iterations in which the plover population was predicted to grow, decline or remain stationary by 2026 compared
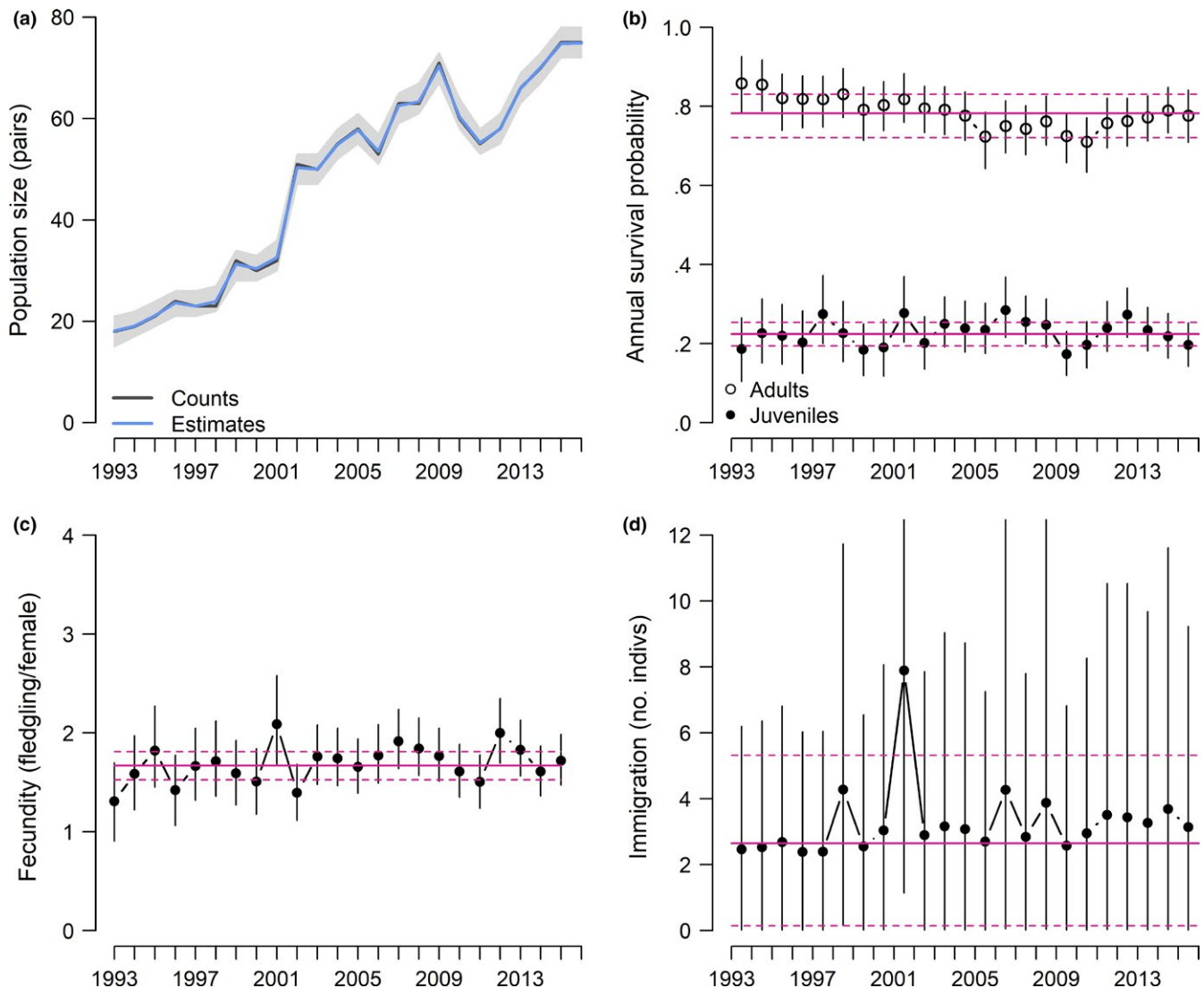
FIGURE 3 Estimates of (a) population size (number of breeding pairs, blue line) and 95% credible intervals (grey shading), compared to observed pair counts (surveys, black line); (b) annual survival probabilities of juveniles (closed circles) and adults (open circles); (c) fecundity (number of fledglings per female); and (d) immigration (number of individuals) during 1993–2016. Solid red lines indicate mean estimates with 95% credible intervals (dashed red lines) [Colour figure can be viewed at wileyonlinelibrary.com]

to the 2016 estimate. Our model projected that the population has a 32% probability of increasing in abundance (>78 pairs), a 63% probability of decreasing (<72 pairs) and a 5% probability of remaining the same (72 pairs ≥ N_{2026} ≤ 78 pairs). For comparison, the model without the merlin index projected that the plover population has a 60% probability of increasing, a 30% probability of decreasing and a 10% probability of remaining the same size as in 2016.

Despite a projected increase in the index of merlin abundance, the probability of quasi-extinction (≤15 breeding pairs remaining) of Great Lakes plovers by 2026 was estimated at an average of 11.9%. Future projected demographic rates were close to the means of the respective distributions estimated for 1993–2016 (Figure 5b–d). Mean annual adult plover survival was expected to decline, ranging from 0.76 to 0.66 (Figure 5e) as the index of regional merlin abundance was expected to increase from 126 individuals (CI 94–168) to 166 individuals (CI 63–379) by 2026 (Figure 5f; $\bar{\lambda}_t$ = 1.02, CI 0.94–1.12). Incorporation

of demographic and environmental stochasticity in our modelling approach resulted in annually increasing uncertainty in projections of future piping plover and merlin populations (Figure 5a,f).

Projections of population abundance and quasi-extinction probabilities differed among the four management scenarios, although there was considerable overlap in the credible intervals of estimates due to model uncertainty (Table 1). The chick predator control scenario (i.e. increased productivity) resulted in a larger average population size in 2026 compared to the null scenario (mean number of pairs: 91 vs. 67, respectively); quasi-extinction probability was reduced from 11.9% to 8.7% (Figure 6). The merlin control scenario (i.e. increased adult survival) yielded a predicted mean population size of approximately 117 pairs within 10 years (Table 1), and more than halved the quasi-extinction probability to 3.5% (Figure 6). Combining both management scenarios resulted in the greatest expected population size by 2026, with 156 breeding pairs on average (Table 1), as well as the lowest quasi-extinction probability of 2.6%
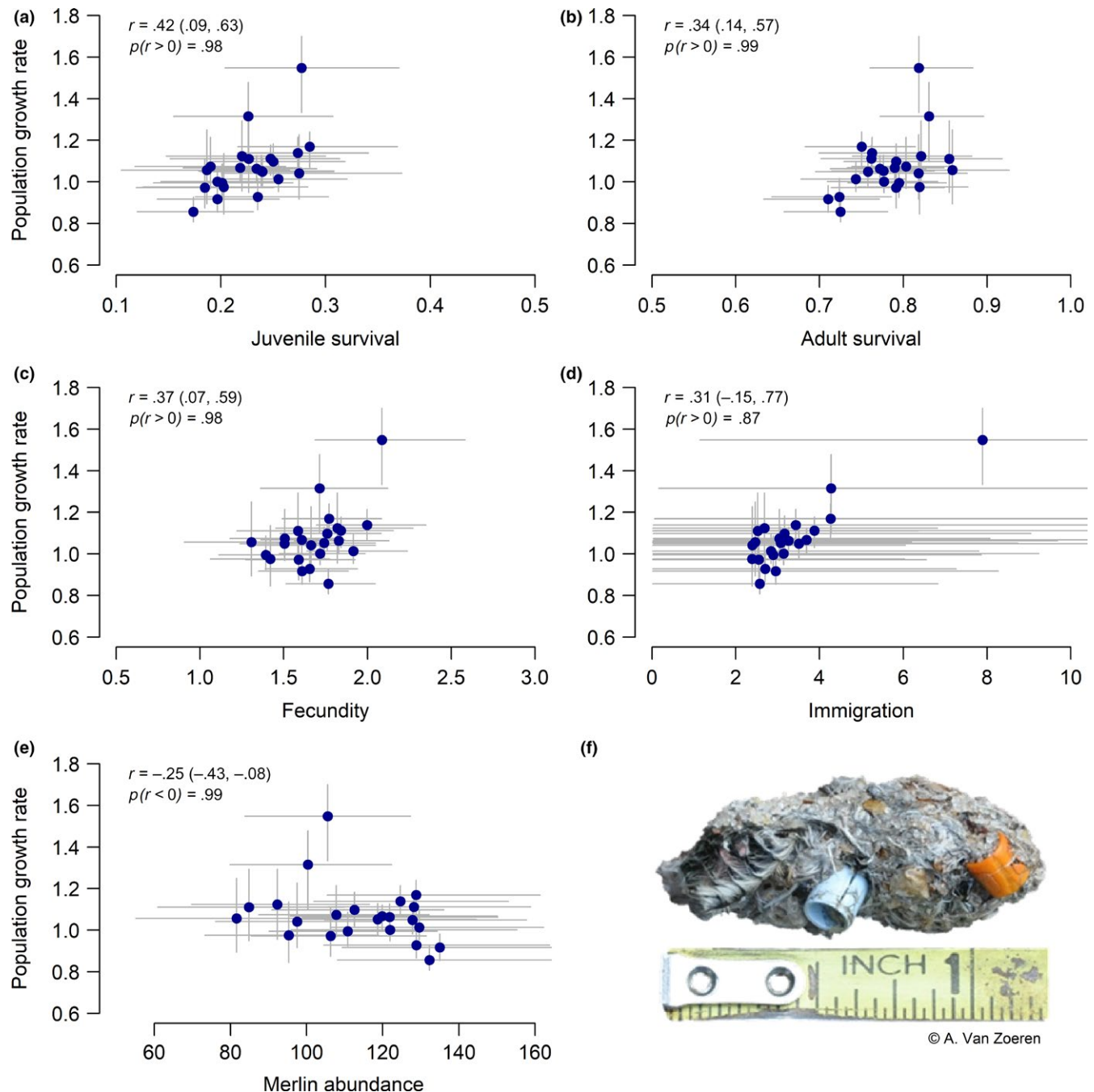
FIGURE 4 Posterior means of the estimated finite rate of population change (λ_t) plotted against the posterior means of the estimates for (a) apparent juvenile survival, (b) apparent adult survival, (c) fecundity, (d) immigration (number of individuals) and (e) an index of merlin abundance from an integrated population model for Great Lakes piping plovers during 1993–2016 (including latent merlin abundance on $\Phi_{ad,t}$). Posterior means of the correlation coefficients (*r*), associated 95% credible intervals and probabilities that estimates are positive *P*(*r* > 0) or negative *P*(*r* < 0) are shown. Horizontal and vertical lines show the limits of the 95% credible intervals for each annual estimate. (f) An image of a merlin pellet containing coloured leg bands from a Great Lakes piping plover (photograph courtesy of Alice Van Zoeren) [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 6). Moreover, there was a 97.1% probability that the combined scenarios would result in a larger population size in 10 years compared to the size under the null scenario; the probabilities that the other two scenarios would result in larger population sizes when implemented independently were each <95%, the conventional threshold for significance (Table 1).

4 | DISCUSSION

Despite uncertainty surrounding future projections of population abundance and demographic rates, our BPVA indicated that the Great Lakes piping plover population does not face a high and immediate risk of quasi-extinction under current conditions (*c.* 12%). Although
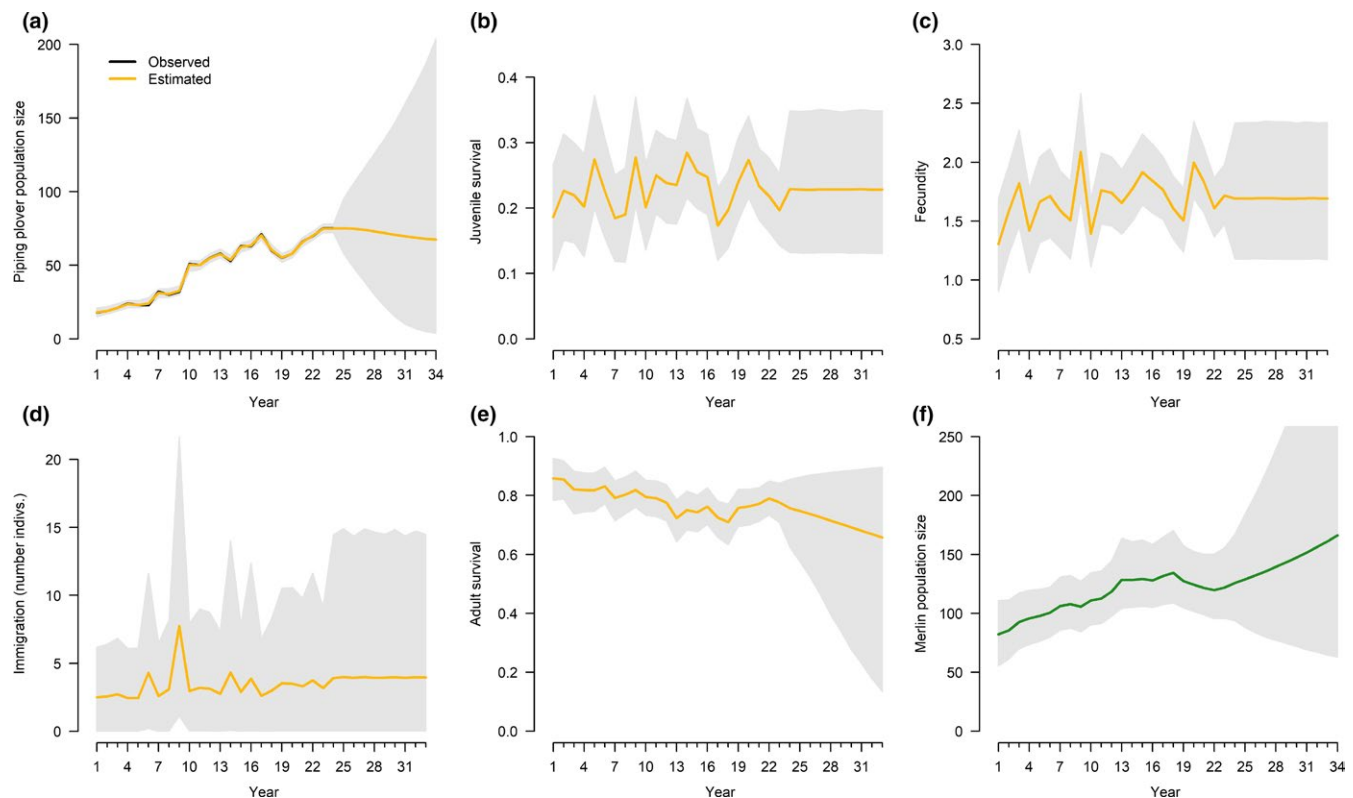
FIGURE 5 (a) Observed (black line), estimated (yellow line, years 1–24) and predicted (yellow line, years 25–34) population sizes of Great Lakes piping plovers, as well as (b–e) estimated and predicted demographic rates. (f) An estimated and predicted index of population size of eastern North American merlins (green line). Grey shading represents 95% credible intervals [Colour figure can be viewed at wileyonlinelibrary. com]

imprecise predictions of population size may not be ideal for long-term management, they capture the true environmental and demographic uncertainty surrounding both the biotic and abiotic factors influencing piping plovers and are more accurate than simpler models that do not take into account the simultaneous effects of multiple sources of uncertainty (Crone et al., 2013; Oppel et al., 2014). We could not account for all possible environmental influences on population viability, but our model indirectly captures some of the inherent variation in plover population responses to these factors through our inclusion of

environmental stochasticity (Ladin, D'Amico, Baetens, Roth, & Shriver, 2016). Our integrative framework can also serve as a guide for full-annual-cycle modelling efforts (Hostetler, Sillett, & Marra, 2015; Marra, Cohen, Loss, Rutter, & Tonra, 2015) that seek to incorporate several broad-scale processes, in addition to predation pressure, that are thought to influence plover population dynamics (e.g. persistently cold winter temperatures; Gibson et al., 2017).

One of the novel insights gained from our IPM-BPVA is the impact of regional merlin abundance on plover population viability. We

TABLE 1 Comparison of four management scenarios for the Great Lakes piping plover population: (1) null scenario or no proposed management; (2) chick predator control, resulting in a 20% increase in fledgling production annually; (3) 20% reduction in annual merlin abundance, resulting in increased annual adult survival; and (4) simultaneous implementation of both management strategies. Efficacy of each scenario was determined by the (1) relative population size (credible interval shown in brackets) predicted in 2026, compared to the null scenario; (2) cumulative quasi-extinction probability (≤15 breeding pairs remaining) within 10 years; and (3) probability that the given management scenario would result in a larger population size in 10 years relative to the null scenario, $P(N_{mgmt} > N_{null})$. All quantities were derived from 60,000 MCMC simulations

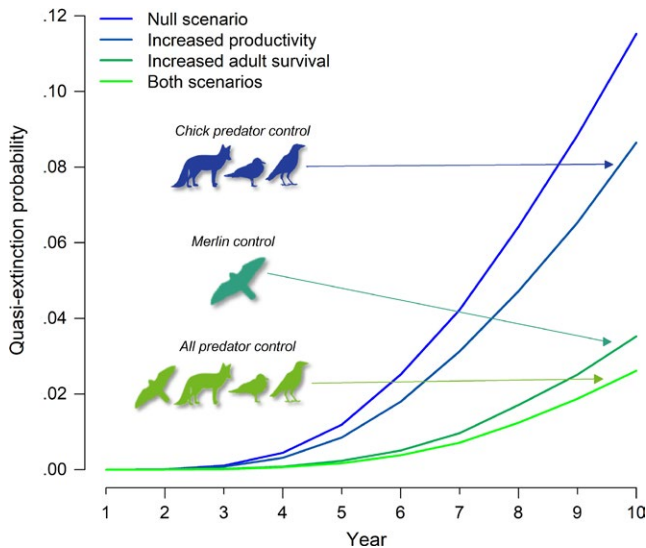| Scenario	Predicted population size (breeding pairs)	Quasi-extinction probability (%)	$P(N_{mgmt} > N_{null})$ (%)
Null scenario	67.3 [4–201]	11.9	—
Increased productivity [chick predator control]	90.5 [5–268]	8.7	78.7
Increased adult survival [merlin control]	116.5 [11–318]	3.5	91.2
Both management scenarios	155.5 [15–425]	2.6	97.1

FIGURE 6 Comparison of the cumulative quasi-extinction probabilities (≤15 breeding pairs remaining) of Great Lakes piping plovers 10 years into the future (2017–2026) under four management scenarios: (1) null scenario or no proposed management (light blue line); (2) chick predator control (e.g. mammals, *Laridae*, *Corvidae*), resulting in a 20% increase in fledglings annually (dark blue line); (3) 20% reduction in annual merlin abundance (i.e. adult predator control), resulting in increased adult survival (dark green line); and (4) simultaneous implementation of both management strategies (light green line) [Colour figure can be viewed at wileyonlinelibrary.com]

found a strong negative association of regional merlin abundance with adult plover survival, which scaled up to a moderately strong negative correlation ($r = -.25$) between the index of annual merlin abundance and plover population growth rates during the 24-year period. Because average merlin abundance was projected to increase over the next 10 years (Figure 5f), adult plover survival rates (Figure 5e), and consequently plover population size, were projected to decline (Figure 5a). Failure to account for merlin predation pressure would have led to overconfidence in a positive population trajectory, preventing prioritization of enhanced predator control strategies. Instead, accounting for merlin abundance generated a 63% probability that the plover population in 2026 would be smaller than in 2016, indicating that additional management strategies are needed to avert a potential population decline in the immediate future. Since management strategies can focus on improving a certain vital rate (e.g. fecundity, adult survival) or a combination of rates encompassing several life stages (Wisdom, Mills, & Doak, 2000), determining effective management actions should stem from evaluation of which potential management approach(es) is/are most likely to maximize projected population size and minimize quasi-extinction probability.

All of the conservation scenarios that we tested had a positive effect on piping plover population growth rates; however, only one resulted in attainment of the federal recovery goal (150 breeding pairs on average) by 2026: coincident control of chick predator and merlin populations. Simultaneous implementation of both predator control scenarios was also the only option that produced a >95% probability

that the resulting population size would be larger than under no proposed management. Recovery of the federally threatened Western snowy plover *Charadrius nivosus nivosus* population includes formal predator management at all nesting sites in Oregon, which has led to a significant improvement in chick survival as compared to similar sites in Washington, where predator management is not employed (Dinsmore, Gaines, Pearson, Lauten, & Castelein, 2017). Given the parallels between snowy plover and piping plover breeding biology, formalized predator management could be a similarly effective tool across Great Lakes nesting sites. Thus, we suggest that piping plover conservation efforts include development of selective control strategies that target the predator(s) most strongly impacting productivity and survival rates on a site-by-site basis. For example, certain nesting sites have consistently low adult survival due to heavy merlin predation pressure (e.g. sites in Michigan's Upper Peninsula), whereas others have consistently low chick survival due to high concentrations of chick predators (e.g. Ludington State Park). Focusing on improving survival rates during both life stages is the approach most likely to maximize population recovery and subsequent delisting.

Maintaining current ad hoc predator control procedures is especially concerning given that regional merlin abundance is predicted to increase over the next 10 years. However, our results relating an index of merlin abundance to adult survival are correlational. Additional studies explicitly estimating the impact of merlins on seasonal survival rates of plovers are needed (e.g. before and after control studies), as the manipulation of a given variable in the system may result in both direct and indirect effects on population demographic rates (Fieberg & Johnson, 2017). Although there is a mechanism behind the assumed causal link between piping plover abundance and regional merlin abundance (i.e. predator–prey dynamics; Figure 4f), our model only represents a probable influence rather than an explicit causation and our index of merlin abundance could be capturing some unknown variable(s) that may be impacting plover dynamics (MacNally, 2000). A previous study has demonstrated associations of annual hurricane activity and minimum spring temperatures on the non-breeding grounds with adult survival (Saunders et al., 2014), but we did not find support for an effect of either variable in this analysis (see Appendix S1 for more details).

Nevertheless, merlin populations in eastern North America have increased dramatically (Sauer, Link, Fallon, Pardieck, & Ziolkowski, 2013; Figure 5f of this study) and expanded their range (Niven, Sauer, Butcher, & Link, 2004). Our results, along with prior studies (Drake, Thompson, Drake, & Zonick, 2001; Murphy et al., 2003; Roche et al., 2010), suggest that piping plover population dynamics are, and will continue to be, markedly influenced by merlin predation pressure. Given the small size of the Great Lakes population, even a single active merlin nest at a populous plover nesting site can substantially reduce local breeding capacity, and consequently, annual productivity in the region (Roche et al., 2010). Yet because the merlin is listed as a threatened species in Michigan, additional precautions should be taken when considering alterations to their management strategy.

Temporal variation in the plover population growth rate was most strongly correlated with variation in juvenile survival (i.e. survival to 1 year old) and to a lesser extent with variation in local recruitment.

Variation in immigration was not a strong driver of population dynamics, likely because it was relatively constant over time (with a few exceptions; Figures 3d and 4d) and had the lowest precision. Therefore, conservation efforts focused on achieving high productivity and pre-fledging survival at the local site level (e.g. controlling chick predators, protecting established breeding sites) should be prioritized over broader management actions to promote exchange of adults between populations (e.g. restoring unused sites to attract new breeders; Saunders et al., 2012). IPM estimates of mean annual fecundity were variable, but consistently in the range of 1.5–2.0 fledglings per pair (Figure 3c), which is the specified recovery goal (U.S. Fish and Wildlife Service, 2003). Because this rate was the second strongest contributor to variation in population change and overlapped somewhat with juvenile survival, this result serves to emphasize the importance of isolating potential causes of chick mortality at the local scale (e.g. sites with higher incidents of predation) in order to boost population growth region-wide. Additionally, enhancing efforts to protect migratory, stopover and non-breeding habitats may improve juvenile survival post-fledging, contributing to population recovery. Although our results suggest that immigration is not the most crucial demographic process in this population, its contribution is not insignificant. For example, the large increase in population size observed in 2002 was attributed to a high influx of immigrants coupled with high estimated productivity, rather than abrupt increases in juvenile or adult survival (Figure 3). However, as a parameter not directly informed by data, immigration could also reflect any systematic biases in other vital rates; thus, the immigrant component of our model is more accurately considered "immigrants plus unknown variance."

Our coupled IPM-BPVA approach serves to achieve three important objectives for assessing the population viability of threatened species: (1) to account for demographic, environmental and parameter uncertainty in a single framework to provide more realistic credible intervals around predictions of future population viability; (2) to incorporate an imperfectly observed, temporally varying covariate on a key vital rate so that broad-scale processes (e.g. predation pressure) previously considered challenging to model can be included in population assessments; and (3) to allow for straightforward comparison of alternative management strategies within a flexible modelling framework.

The negative impact of growing predator populations on bird species has made predator management a critical component of avian conservation world-wide (Lavers, Wilcox, & Donlan, 2010; Smith, Pullin, Stewart, & Sutherland, 2010). Our approach, which considers multiple sources of uncertainty associated with a suite of management decisions, can be a useful tool to aid conservation biologists conducting population assessments and proposing management actions. Furthermore, our extension of the coupled IPM-BPVA incorporating latent abundance as a covariate on key vital rates can be used to model other imperfectly observed processes that may impact population growth and viability, such as prey availability (e.g. McGowan et al., 2011) or competitor abundance (e.g. Diller et al., 2016). As a whole, the framework presented here enhances the ability to describe and predict demographic responses of populations to varying environmental and management conditions, an increasingly pressing requirement for effective conservation.

AUTHORS' CONTRIBUTIONS

S.P.S. conceived the ideas, designed methodology with guidance provided by E.F.Z., analysed the data and led writing of the manuscript. F.J.C. provided support for data collection. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.j2906 (Saunders, Cuthbert, & Zipkin, 2018).

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SUPPORTING INFORMATION

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