



Breeding season management is unlikely to improve population viability of a data-deficient migratory species in decline

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ARTICLE INFO

Keywords:

Black tern
Data-deficient
Integrated population model
Management
Migratory species
Population viability

ABSTRACT

A major challenge in conservation is developing effective approaches to mitigate population declines in the face of ongoing environmental change. For migratory species, it is often more feasible to implement management during periods of stationarity, like the breeding season, when populations are less mobile. However, such management strategies are only successful if the demographic rates targeted (e.g., reproductive rates) contribute substantively to population growth. Thus, evaluation of population growth rate sensitivity to variation in demographic parameters is needed to determine the most effective conservation strategies. This is especially true for small and declining populations that require targeted and urgent action to mitigate declines under current and future environmental change. Here, we used a coupled integrated population model-Bayesian population viability analysis (IPM-BPVA) to estimate demographic rates and population viability within the context of climatic and management-related changes for a data-deficient, declining population of black terns in the Upper Midwestern United States. We found that current conservation efforts during the breeding season are unlikely to reverse the declines observed within the last decade (from an average of 307 breeding pairs in 2013 to 53 in 2022). Rather, interventions aimed at increasing adult survival are projected to reduce local extinction probability by 30–46 % compared to no additional management or management targeting other rates, depending on the climate scenario. Our results highlight the importance of enhancing management efforts for migratory species during migration and nonbreeding periods, which constitute a much larger, and generally riskier, proportion of the annual cycle compared to the breeding season.

1. Introduction

Growing anthropogenic pressures on the natural environment are increasing extinction risk for many of the world's species (Hoffmann et al., 2010; IPBES, 2019). One of the major challenges in conservation science is to determine how to manage populations effectively to mitigate and reverse ongoing declines. Natural resource managers have limited data and financial resources with which to base conservation decisions and must balance the feasibility of different strategies (e.g., targeting different life stages and demographic rates or periods of the annual cycle) with the potential benefit to a given species in the face of considerable uncertainty (Martin et al., 2018). Seasonal interventions

that correspond to relatively static periods of species' annual cycles are common strategies to maintain or increase population sizes (Runge et al., 2015). For migratory species, it is typically easier to implement management during periods of stationarity, such as the breeding season, compared to other times during the annual cycle when populations are more dispersed among heterogeneous landscapes. Interventions during the breeding season, such as predator exclusion (Smith et al., 2011) or predator removal (Lennox et al., 2018) to improve reproductive success, are typically easier to implement because such actions can be targeted over short time periods and within relatively small areas. Yet these management strategies are only effective for increasing population size if the demographic rates they target (e.g., reproductive rates) contribute

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<https://doi.org/10.1016/j.biocon.2023.110104>

Received 16 December 2022; Received in revised form 10 March 2023; Accepted 24 April 2023

Available online 12 May 2023

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substantively to population growth.

In long-lived species, population dynamics tend to be especially sensitive to variations in adult survival, while reproductive rates contribute substantially to the population dynamics of short-lived species (Sæther and Bakke, 2000; Gaillard and Yoccoz, 2003). Numerous studies have shown that adult survival has the strongest impact on population growth rates for slow-growing species or those characterized by late maturation, few offspring, and long life spans (see Manlik et al., 2016 for a review). Despite the known importance of adult survival to population growth in long-lived species, conservation management activities tend to be directed toward increasing productivity and survival of juvenile stages, largely because fecundity and subadult survival can be low and variable, while adult survival tends to be higher and more stable (Sergio et al., 2021). Demographic rates that most heavily influence population growth often exhibit low temporal variability (Gaillard and Yoccoz, 2003). Thus, achieving increases in adult survival may be difficult in practice (Sergio et al., 2021; Warret Rodrigues et al., 2021). Further, for long-lived migratory species, achieving increases in adult survival requires knowledge of threats or risk factors encountered during migration and nonbreeding periods (e.g., habitat loss and poaching) and potential interventions across large geographies, given that most of the annual cycle is spent outside breeding areas. Achieving increases in demographic rates, including adult survival, also depends on the magnitude of temporal variability in each rate and the efficacy of additional investments or management interventions in producing measurable improvements in those rates.

An evaluation of demographic rate sensitivity and the associated population-level benefits of various management interventions targeting different life stages is needed to determine the most effective conservation strategies, especially for small and declining populations that require targeted and urgent action. Unprecedented rates of both climate and land use change are accelerating population declines (Barnosky et al., 2011; IPBES, 2019), requiring conservation decision-making in the context of considerable uncertainty. Yet the demographic data required to rigorously estimate vital rates, as well as how changes in these parameters (e.g., due to variation in climatic or environmental conditions) affect population growth, are not typically available for the most imperiled populations (Oppel et al., 2014; Saunders et al., 2018). Rigorous analytical methods that can leverage fragmentary datasets to estimate demographic rates and simulate population viability under various scenarios are critical for abating or reversing current declines and minimizing the probability of future population collapses.

Demographic modeling, such as integrated population models (IPM) and population viability analysis (PVA) are increasingly used to estimate vital rates and their relationships to environmental variables, forecast population growth, future extinction, or quasi-extinction probability, and identify the most beneficial target demographic rates for management interventions to increase population size (Oppel et al., 2014; Saunders et al., 2021). Used together, integrated population model-Bayesian population viability analysis (IPM-BPVA) is a powerful method for merging parameter estimation using multiple types of data (e.g., count, mark-recapture, productivity) with population projection in a Bayesian framework (Saunders et al., 2018). For data-deficient species especially, it is important to utilize as much available data as possible to inform estimates of demographic rates, and IPMs offer a powerful approach for leveraging multiple data types to increase the accuracy and precision of estimates (Zipkin and Saunders, 2018). Here, we combined population survey, mark-recapture, fledgling counts, and nanotag data to develop a coupled IPM-BPVA to determine the factors influencing the decline of black terns (*Chlidonias niger*), a semi-colonial nesting waterbird, and whether current efforts focused on increasing productivity during the breeding season are likely to stabilize and/or recover a declining population in the Upper Midwestern United States (U.S.).

Waterbirds like black terns are typically long-lived, migratory species and are particularly vulnerable to climate change due to their reliance on wetlands that are sensitive to fluctuations in environmental

conditions (Sofaer et al., 2016). Black terns breed colonially in the north-central U.S. and across southern Canada and spend the nonbreeding period along coastlines from southern Mexico to northern South America (Heath et al., 2020). Black terns have declined by 2.4 % annually in the U.S. during 1966–2019 (Sauer et al., 2020) and are projected to lose 97 % of suitable nesting habitat in a major portion of their range by 2100 (Steen and Powell, 2012). Some regional declines are even more drastic; black terns declined by 7.6 % in Michigan, U.S. during 1966–2019 (Sauer et al., 2020) and have the most significant downward trend among Great Lakes marshbird species (Tozer, 2015). Despite dedicated monitoring and research efforts, estimates of demographic parameters, such as adult and juvenile survival probability and fecundity (survival from hatch to fledging), are hampered by the difficulty of locating cryptic nests and chicks under challenging field conditions (Marsh, 2020). Even when nests are located, accurate estimates of fledging success are difficult to ascertain as current methods to identify fledging involve counting flying juveniles during colony flushes, which can be extremely inaccurate when hundreds of birds take flight at once.

In addition to uncertainties regarding breeding season vital rates, nonbreeding season ecology is poorly understood for black terns as they spend much of the nonbreeding period at sea (Heath et al., 2020). Thus, we have little understanding of which time periods of the black tern annual cycle or life stages are most limiting and driving population declines. As a relatively long-lived species (average life span = 17.2 years; Myhrvold et al., 2016), adult survival of black terns is expected to have the greatest impact on population dynamics, yet for many of the practical reasons discussed, current management actions in the Upper Midwestern U.S. target early life stages to increase reproductive output (e.g., deployment of floating nest platforms, nest predator eradication, and increasing breeding habitat through invasive species abatement). Here, we aimed to determine whether such actions are likely to be sufficient in mitigating black tern population declines in the context of future environmental changes. We also assess the viability of nanotag tracking technology as a method for quantifying fledging rate as current methods are inexact and labor intensive. Specifically, our objectives were to: (1) estimate demographic rates (2013–2022) for black terns, (2) project population viability under realistic future climate and management scenarios, and (3) compare nanotag fledging rates to on-the-ground counts. Evaluating the efficacy of current and potential management strategies for population persistence in the context of global change will allow for enhancement of management strategies for this imperiled species within the Great Lakes region and beyond.

2. Material and methods

2.1. Data collection

Our study used data collected at the St. Clair Flats black tern breeding colony on Lake St. Clair, Michigan in the Great Lakes region of the U.S. This colony is monitored and managed by Detroit Audubon in collaboration with Audubon Great Lakes and Michigan Department of Natural Resources. Pre-breeding colony counts, mark-recapture, and fledgling count data were collected in 2013–2022 by 47 observers consisting of trained volunteers and staff technicians. Additionally, Avian NanoTags were deployed in 2019 and 2021 to assist in monitoring colony productivity. Local precipitation, water level, and storm event data were collected at Lake Saint Clair during the breeding season. We also aggregated data on global climate metrics (e.g., Southern Oscillation Index, North Atlantic Oscillation Index) to capture potential environmental factors influencing population dynamics during the nonbreeding period. Demographic and climate data collection are described in further detail below.

2.1.1. Demographic data collection

2.1.1.1. Pre-breeding colony counts. Observers monitored the black tern colony at St. Clair Flats in two-day periods every 7–10 days during 15 May–30 July each year (depending on weather and colony departure date). To determine breeding pair abundance annually, observers counted the number of adults flushed upon arrival at the colony during the peak of breeding when the maximum number of breeding adults was present at the colony during approximately 15–25 June (Fig. 1a [Adult count data]). We used half the adult flush counts as the observed breeding pair abundance each year.

2.1.1.2. Mark-recapture data. Adults and chicks were captured at nests and individuals were banded with a metal band and uniquely coded alpha-numeric color bands (Fig. 1a [Mark-recapture data]). Recaptures were recorded every year during the breeding season, and each season was considered a separate occasion for estimating annual demographic rates. We used the mark-recapture data to estimate juvenile and adult

apparent survival rates (see 2.2 below for details on model structure).

2.1.1.3. Fledgling counts. Technicians counted the total number of fledglings observed each year (fledgling counts) based on the number of hatch-year chicks confirmed flying (Fig. 1a [Fledgling count data]). Fledgling counts were completed by observers weekly from late July through early August. Exact dates varied somewhat by year based on when juveniles began fledging, which was dependent on nesting success and renesting attempts. We used the maximum weekly fledgling count to estimate fecundity rates (see 2.2 below for details on model structure).

2.1.1.4. Nanotag counts. We affixed nanotags on black tern chicks to track fledged young using the Motus Wildlife Tracking System (www.motus.org) during 2019 and 2021 (Fig. 1a [Nanotag data]). We deployed tags on a total of 35 black terns during the 2019 and 2021 breeding seasons ($n = 15$ deployed in 2019; 20 deployed in 2021). Prior to the breeding season, we set up three receiving towers around Lake St. Clair to track fledged individuals. Data beyond St. Clair Flats were

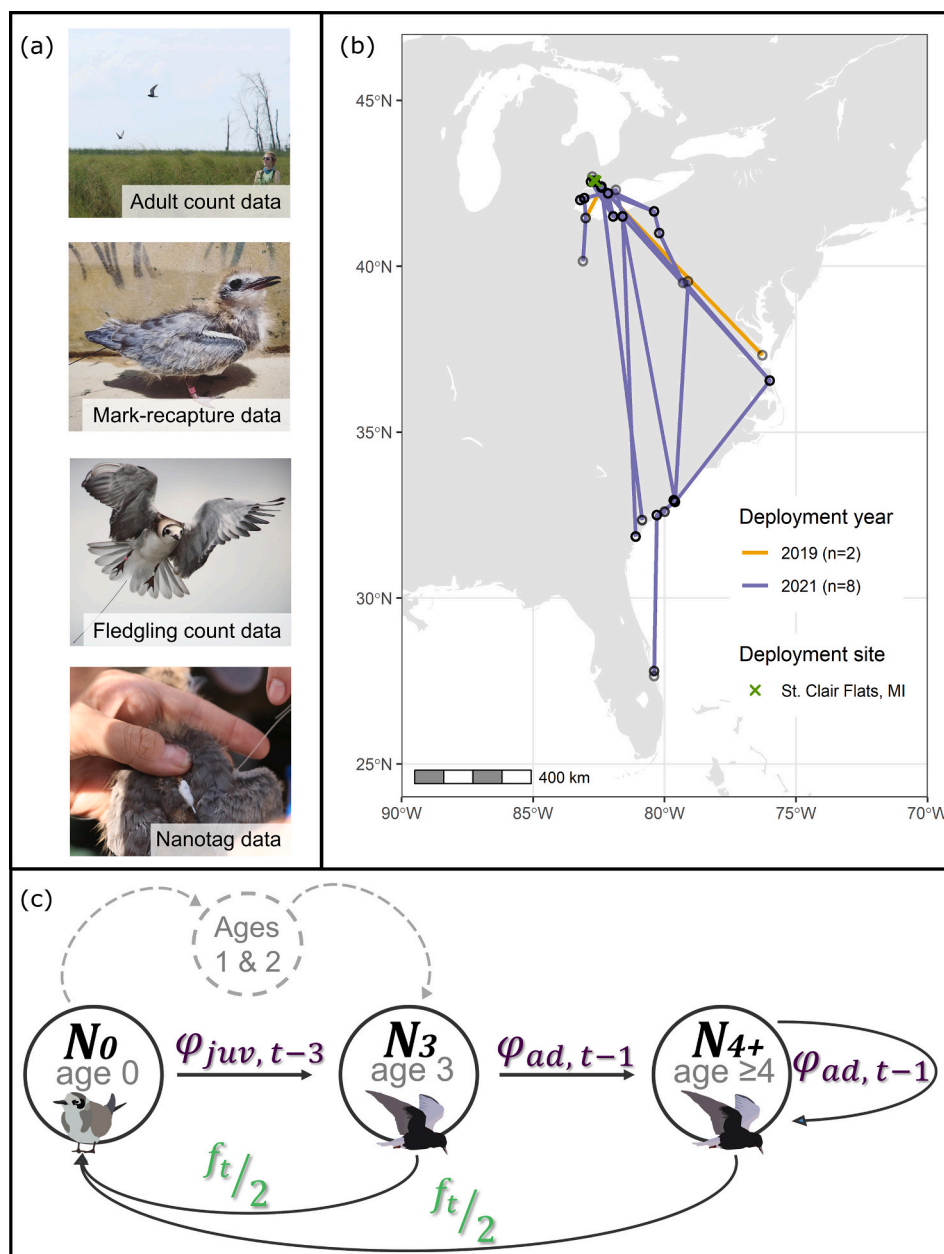


Fig. 1. (a) Adult black tern flush count [Adult count data], pre-fledged chick with color band and nanotag in St. Clair Flats (both adults and chicks were marked for inclusion in mark-recapture study) [Mark-recapture data], fledgling chick in flight [Fledgling count data], and nanotag attachment on pre-fledged chick [Nanotag data], (b) Fall migration routes for 10 black tern fledglings during 2019 (gold) and 2021 (purple). The St. Clair Flats deployment site is indicated by a green cross and detecting receivers are indicated by open circles. (c) Life cycle diagram of the black tern population with two adult stages: new 3-year-olds (N_3 ; minimum age at which young return to breeding grounds) and returning adults that had been observed previously in the population (N_{4+} ; 4+-year-olds). Annual estimates of demographic parameters include stage-specific survival (ϕ_{juv} , ϕ_{ad}) and fecundity (f). Parameters are color-coded according to the data types that contribute to their estimation; f (green) is informed by both population survey and nest monitoring data, and survival (purple) is informed by both population survey and mark-resight data. Note: ages 1 and 2 are shown in grey but annual survival of these age classes is not explicitly estimated. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

accessed through the coordinated Motus radio-telemetry network (Taylor et al., 2017). To generate maps of paths for tagged individuals, we summarized all detections per bird to represent presumed flight paths. We used the resulting maps and detection timings to (1) inform the suite of climate covariates we considered during the nonbreeding season (see below); and (2) compare fecundity estimates from the two data sources (i.e., on-the-ground fledgling counts vs. nanotagging data) to determine the efficacy of this technology for improving monitoring of pre-fledged and fledged young. See Appendix A for additional nanotagging details.

2.1.2. Climate data collection

We gathered data on both local and global climate metrics as potential drivers of black tern population dynamics. We tested for the effects of local variables on black tern annual fecundity, and local climate variables for St. Clair Flats included: (1) average annual lake water level (*WaterLevel*) during the breeding season (15 May–15 Aug.); (2) average daily precipitation (*Precip*) across the breeding season each year (15 May–15 Aug.); and (3) the annual number of storm events (*Storms*) recorded during the breeding season (15 May–15 Aug.). Each of these three metrics has been hypothesized to influence annual black tern productivity values by mediating changes to habitat availability (i.e., higher water levels result in reduced native vegetation for nest mats [Fuller, 2021]), and inundation potential, including nest washouts and resulting seiches from heavy rainfall events. Data on Lake St. Clair water levels were obtained from the Great Lakes Water Level Dashboard (U.S. Army Corps of Engineers [USACE], 2022), precipitation data were obtained from the nearest Community Collaborative Rain, Hail, and Snow Network (CoCoRaHS) weather station to the colony site at Lake St. Clair (New Baltimore [MI-MB9]; CoCoRaHS, 2022); and storm event data were obtained from the National Oceanic and Atmospheric Administration (NOAA) storm events database (NOAA Storm Data, 2022).

We also tested for the effects of broad-scale climate covariates on adult survival, including the Southern Oscillation Index (SOI; Elsner and Jagger, 2006) and the North Atlantic Oscillation Index (NAOI; Hurrell and Deser, 2009). These weather phenomena are associated with bottom-up processes that affect the abundance of lower trophic level species (e.g., phyto- and zooplanktonic species and fish (Stenseth et al., 2003)) and are correlated with seabird and waterbird survival (Szostek and Becker, 2015; Saunders et al., 2021). A positive SOI value is indicative of a La Niña cooling event, whereas a negative SOI value is indicative of an El Niño warming event (Elsner and Jagger, 2006). Although these weather events are strongly correlated with conditions in the central and eastern Pacific basins, they also are associated with weather patterns, including storm activity, in the Northern Atlantic, such that hurricanes and tropical storms in the Atlantic basin are more frequent during La Niña events (Bell and Chelliah, 2006). The North Atlantic Oscillation drives climate variability in eastern North America and affects freshwater (Straile et al., 2003), terrestrial (Mysterud et al., 2003), and marine environments (Drinkwater et al., 2003) in the northern hemisphere and has been associated with seabird population dynamics (Sandvik et al., 2005), including those species like black tern that winter in tropical latitudes (Szostek and Becker, 2015; Heath et al., 2020). Storm activity and paths in the North Atlantic are correlated with NAOI values, such that negative NAOI values in the months preceding the hurricane season are correlated with higher numbers of hurricanes and storms making landfall along the east coast and southeastern U.S. (Xie et al., 2005; Elsner and Jagger, 2006). Given that existing evidence indicates use of Atlantic coastal habitats by Michigan black terns for stopover and refueling during fall migration (see below; Fig. 1b) and the Gulf of Mexico region during the nonbreeding season (Fink et al., 2021), we sought to capture potential direct and indirect effects of these broad-scale climate indices experienced by individuals during these critical periods of the annual cycle.

We obtained monthly SOI values from the NOAA National Climate Data Center (NOAA, 2022), and we obtained monthly NAOI values from

the National Center for Atmospheric Research (University Corporation for Atmospheric Research [UCAR], 2022). Following prior studies (Saunders et al., 2021), we considered lagged effects of each broad-scale climate variable to capture possible indirect effects via bottom-up processes (e.g., abundance of prey), in addition to the possible direct effect of each variable on conditions during the migration and overwintering period within the annual time step. For the lagged variables (SOI_{t-1} and $NAOI_{t-1}$), we averaged monthly SOI and NAOI values across January–June of year $t-1$ preceding the hurricane season (1 June–30 November) of year $t-1$. For the current season (year t) migration and nonbreeding variables (SOI_t and $NAOI_t$), we averaged monthly SOI and NAOI values from September–December of year t and January–February of year $t+1$.

2.2. Integrated population model framework

We developed a female-based IPM to estimate population abundance, adult and juvenile survival probabilities, fecundity, and population growth rates for black terns breeding at St. Clair Flats. The IPM is composed of three submodels: a state-space model estimating annual abundance using the pre-breeding survey data, a Cormack-Jolly-Seber (CJS) model to estimate survival rates using the mark-recapture data, and a Poisson regression to estimate fecundity using the on-the-ground fledgling counts.

2.2.1. Population model

We used a female-based stage projection matrix model with a pre-breeding survey to decompose black tern demography into the state processes of adult and juvenile apparent survival and mean per-capita fecundity during 2013–2022. Parameters were assumed to be equal for all individuals within a stage class (i.e., no individual heterogeneity or differences among sexes). Given that our data were insufficient to estimate recruitment probabilities at multiple ages via a multistate capture-recapture framework, our model assumed a transition to adulthood at age three (Heath et al., 2020; with age 1 and age 2 juveniles included implicitly as an unobservable latent subadult stage), and that all adults could breed (Fig. 1c; life cycle diagram). Thus, ϕ_{juv} signifies the product of survival from fledging to 3-years old and transition to the adult stage, a rate which is estimated annually as new individuals become adults.

Our black tern life cycle model includes two categories of adults (Fig. 1c): (1) 3-year old individuals (N_3) and (2) individuals ≥ 4 -years old (N_{4+}). Our model also includes a fledgling stage (N_0), which depends on the number of adults and f_t , the number of female fledglings produced per female in year t (i.e., $f_t/2$, assuming an equal sex ratio of fledglings), but these individuals were not counted in the total breeding population size (N_{ad}). We included demographic stochasticity in our model by allowing stage-specific abundances to vary as a function of stochastic processes:

$$N_{0,t} \sim \text{Poisson}\left(N_{ad,t} \times \frac{f_t}{2}\right)$$

$$N_{3,t} \sim \text{Binomial}(N_{0,t-3}, \phi_{juv,t-3})$$

$$N_{4+,t} \sim \text{Binomial}(N_{3,t-1} + N_{4+,t-1}, \phi_{ad,t-1})$$

$$N_{ad,t} = N_{3,t} + N_{4+,t}$$

where $\phi_{juv,t-3}$ is the annual apparent survival probability of juveniles in year $t-3$ to year t , and $\phi_{ad,t-1}$ is the apparent survival probability of adults from year $t-1$ to t . Hereafter, all references to adult and juvenile survival results indicate apparent survival estimates.

We evaluated support for broad-scale climate variables (SOI_t , $NAOI_t$, SOI_{t-1} and $NAOI_{t-1}$) on adult survival and local climate variables on fecundity (*Precip*, *Storms*, and *WaterLevel*) via fixed effects. Due

to the low recapture rates of three-year old adults, we did not evaluate any covariates on juvenile survival. We used a forward selection process for the environmental variables on adult survival by first fitting univariate models to estimate separate effects of SOI_t , $NAOI_t$, SOI_{t-1} and $NAOI_{t-1}$ as follows:

$$\text{logit}(\varphi_{ad,t}) = \alpha_{ad} + \beta_{broad} \times BSCV_t + \varepsilon_t$$

where α_{ad} is mean adult survival, β_{broad} is the fixed effect of the broad-scale climate variable ($BSCV$: SOI_t , $NAOI_t$, SOI_{t-1} , or $NAOI_{t-1}$), and ε_t is the annual random effect for environmental stochasticity.

We carried forward any variables that had 85 % credible intervals (CI) that did not overlap zero (Arnold, 2010). We followed the same forward selection procedure for local-scale variables on fecundity ($Precip$, $Storms$, and $WaterLevel$) to determine the effect of local environmental conditions on breeding season reproductive success:

$$\log(f_t) = \alpha_f + \beta_{local} \times LSCV_t$$

where α_f is mean fecundity for fledgling counts, and β_{local} is the fixed effect of the local-scale climate variable ($LSCV$: $Precip$, $Storms$, or $WaterLevel$) on fledgling counts. We did not include random year effects on fecundity due to identifiability issues. The final top model included covariates supported at the 85 % confidence level and was used for estimating population viability (see below).

2.2.2. Estimating model parameters

We used a hierarchical state-space model to separate the observed time-series of pre-breeding survey counts into the biological process describing population size and an observation process (Schaub and Kéry, 2021). The true number of breeding pairs in the population is linked to the observed survey data through an observation process that incorporates imperfect detection during surveys. We modeled the observation process as a normal distribution conditional on the state process:

$$y_t \sim \text{Normal}(N_{ad,t}, \tau_{obs})$$

where y_t is the observed number of breeding pairs in year t and τ_{obs} is the observation error or sampling variance in annual detection probabilities.

We estimated annual apparent survival probabilities from individual mark-recapture data using a modified CJS submodel. We assumed that survival from fledging to age three ($\varphi_{juv,t}$) was different from survival probabilities for ≥ 4 -year-old individuals ($\varphi_{ad,t}$), and that recapture probability was the same for both new (age three; N_3) and returning breeders (\geq age four; N_{4+}) because all recaptured individuals were adults.

Fledgling count data were used to estimate fecundity (f_t), or the number of fledglings produced per female. The number of fledglings observed in each year, j_t , was assumed to follow a Poisson distribution constrained by the number of surveyed pairs R_t in each year (i.e., the number of pairs assessed for reproductive success):

$$j_t \sim \text{Poisson}(R_t \times f_t)$$

We also estimated fecundity from nanotag counts following the same procedure as above for fledgling counts (where the number of fledglings was constrained by the number of nanotagged individuals), but this fecundity estimate was not used in the IPM given the limited sample sizes in 2019 and 2021. Rather, we estimated fecundity from nanotagging data for comparison with the fecundity estimate from on-the-ground counts to assess whether deployment of nanotags is a comparable method to observing fledging in the field.

We multiplied the likelihoods of our three submodels (state-space, CJS, and Poisson regression model for on-the-ground fledgling counts) to obtain the joint likelihood. Although we treated datasets as independent, individuals are likely to be included in two or more datasets. For example, adult pair counts were used to estimate both population

size and fecundity. Despite partial dependency among datasets, recent work has demonstrated minimal biases in estimates from IPMs when datasets are partially or completely dependent (Weegman et al., 2021).

2.2.3. Assessing population viability

To evaluate the efficacy of various strategies to maintain and recover black tern populations in the Great Lakes region, we estimated population viability under a suite of climate and management scenarios. Current management efforts at St. Clair Flats include the use of artificial nesting platforms to increase hatching success and fledging rates, as well as habitat management to remove invasive species (*Phragmites australis*) and improve hemi-marsh conditions by creating floating mats of dead vegetation for nesting. These efforts focus on increasing fecundity, but we also tested management strategies targeting other demographic rates to assess population viability comprehensively (Table 1).

We evaluated population viability by projecting the number of breeding pairs for 10 years into the future (2023–2032) as part of the model fitting process (Schaub and Kéry, 2021; Saunders et al., 2021). To evaluate the impacts of management strategies focused on different rates in the context of potential future climate change, we tested 10 total scenarios that consisted of a combination of two climate scenarios and five management strategies (no additional management, increasing mean fecundity, increasing mean juvenile survival, increasing mean adult survival, and a combined scenario increasing all three demographic rates). For each of the 10 scenarios, we derived the following values for comparison: (1) probability that the population size in 2032 would be smaller than in 2022; (2) cumulative probability of annual population quasi-extinction (i.e., local extinction defined as ≤ 6 breeding pairs remaining, approximately 10 % of the minimum population size during the study period); and (3) the population growth rate from 2022 to 2032.

We assessed the response of adult survival to future climate scenarios

Table 1

We considered five potential management scenarios targeting different demographic rates: (1) increasing adult survival approximately 5 %, (2) increasing juvenile survival 10 %, (3) increasing fecundity by double, (4) a combined scenario with all three management strategies, and (5) a no additional management scenario. Scenarios were designed in consultation with black tern researchers and managers in Michigan (as part of the Great Lakes Black Tern Conservation Initiative) to represent the upper bounds of alterations in vital rates that could be possible under feasible management interventions targeting the different demographic rates. References are included as evidence to connect the given management scenarios with the potential interventions.

Management scenario	Potential interventions to achieve demographic rate increases	References
Increase adult survival 5 %	Adult predator control (e. g., avian predators); Buffer zones around stopover and nonbreeding season resting areas; Wetland restoration of historic breeding sites; Protection and enhancement of large wetland complexes at the landscape scale	Saunders et al., 2018; Althouse et al., 2019; Fuller, 2021; Naugle et al., 1999
Increase juvenile survival 10 %	Buffer zones around stopover and nonbreeding season resting areas; Wetland restoration of historic breeding sites	Althouse et al., 2019; Fuller, 2021
Double historic mean fecundity	Chick predator control; Floating nest platforms and exclosures to mediate water level changes; Increase available nesting habitat and improve habitat quality; Water level management to provide stable levels during the breeding season	Saunders et al., 2018; Tinbergen and Heemskerk, 2016; Zimmerman et al., 2002

by varying the top-supported broad-scale climate variable (BSCV) based on long-term (last 100 years; 1922–2021) and short-term (last 10 years; 2012–2021) means of the observed values of the climate index. We specified an informed prior distribution for future years of the index such that:

$$BSCV_{fut_i} \sim Normal(\mu_{st \text{ or } lt}, \tau_{BSCV}),$$

where $\mu_{st \text{ or } lt}$ is the short-term (*st*) or long-term (*lt*) mean and τ_{BSCV} is the variance in annual BSCV values that we specified using a bootstrap method (see code in Appendix B for details). In addition to the two climate scenarios described here, we also fit an additional climate scenario based on the 100-yr weak, positive trend of the BSCV (Appendix C).

To assess the efficacy of different management interventions, we manipulated fecundity, juvenile survival, and adult survival to represent possible strategies targeting different rates. We did not have suitable variables or proxies for management actions to consider as covariates for different interventions; thus, we manipulated the demographic rates directly to approximate the effects of such actions. The fecundity scenario doubled the historic mean fecundity (i.e., estimated fecundity during 2013–2022); the juvenile survival scenario increased survival to age three by 10 %; and the adult survival scenario increased adult survival by approximately 5 %. We also combined the three management scenarios to evaluate population viability if all three strategies were employed simultaneously. Scenarios were designed in consultation with black tern researchers and managers in Michigan (as part of the Great Lakes Black Tern Conservation Initiative) to represent the upper bounds of alterations in vital rates that could be achieved under feasible management interventions (Table 1).

2.2.4. Model fitting

We used a Bayesian framework for inference and parameter estimation, which allowed us to incorporate information from previous studies and existing data as weakly informative prior distributions for initial population sizes and demographic parameters. We specified priors for the initial population sizes of each stage class for the first three years (at most) of the time series (see code in Appendix B) based on the observed total population sizes in those years. Because available data were limited, we specified weakly informative priors for demographic parameters based on previous studies of black terns and similar tern species (Servello, 2000). We evaluated prior sensitivity by specifying a variety of means and variances for demographic parameters and found that results were robust to alternate prior specifications (see Appendix D for details). For survival parameters, we specified priors with beta distributions using $\alpha = 13.5$ and $\beta = 4$ for adult survival ($\varphi_{ad} \sim \text{Beta}(13.5, 4)$), yielding a mean = 0.77 and variance = 0.01 (equating to a prior distribution largely ranging from 0.5 to 1.0); and $\alpha = 3$ and $\beta = 12$ for juvenile survival ($\varphi_{juv} \sim \text{Beta}(3, 12)$), yielding a mean = 0.20 and variance = 0.01 (prior distribution ranging from 0.0 to 0.5; Appendix D, Fig. D1). We used a uniform prior (0–3) for fecundity, as average black tern clutch size is approximately 2.6 (Lislevand et al., 2007), but chick survival to fledging is relatively low (Heath et al., 2020). We used a diffuse, uniform prior (0–1) for recapture probability. We specified uniform priors for the standard deviation of the observation error in the counts of breeding pairs (0.5–50) and for the standard deviation of the random year effect on recapture probability (0–10). We used exponential priors with $\lambda = 1$ for the standard deviations of the random year effects on both adult and juvenile survival probabilities (see code in Appendix B).

We assessed overall fit of the IPM by comparing the demographic rates imputed from the IPM with the raw data, and we modeled the likelihood components for survival and fecundity independently to compare those independent estimates with those from the integrated analysis (Horswill et al., 2022; results not shown). We fit the IPM-BPVA (Schaub and Kéry, 2021) in program JAGS (Plummer, 2003), using the R

package jagsUI (Kellner, 2016). We ran three chains for 500,000 iterations after a burn-in of 400,000 iterations and thinned chains by 10, resulting in a posterior distribution of 30,000 values for each model parameter. Model convergence was determined using the Rhat statistic (Gelman and Hill, 2006) and visual inspection of chains. Convergence (Rhat values <1.1) was obtained for all parameter estimates. Posterior distributions were summarized by their means and 95 % credible intervals unless otherwise noted.

3. Results

3.1. Abundance, demographic parameters, and population growth

NAOI during January–June of the previous year ($t-1$) was the only covariate that met our model selection criteria and had a strong positive association with adult black tern survival ($\beta_{NAOI,t-1} = 0.94$, 85 % CI: 0.22, 1.62). No other covariate relationships were supported. We thus used a model with this single broad-scale covariate effect on adult survival for all subsequent analyses including estimating the demographic rates and population viability (see below). The black tern population was estimated to have decreased from 307 (CI: 289, 326) breeding pairs in 2013 to 53 (CI: 25, 82) pairs in 2022, which was generally consistent with the observed breeding pair counts (Fig. 2a). The observed counts were higher than the estimated population size in 2022 (Fig. 2a).

Mean fecundity from fledgling counts was 0.22 (CI: 0.20, 0.25), as estimated in the IPM, compared to 0.31 (CI: 0.16, 0.53), as estimated from the nanotag data (Fig. 2b); however, fecundity was defined slightly differently between these two data types and nanotag data were only obtained during two years of the time series (Appendix A). Variability in naïve fecundity rates from nanotagged individuals (number of fledglings recorded on receiving towers/total number chicks tagged) was high (2019: 0.13 and 2021: 0.40). On-the-ground counts of fledglings also exhibited similar variability, and naïve fecundity rates from fledgling counts (number of fledglings counted/number of pairs) ranged from 0.10 in 2019 to 0.34 in 2021 (Fig. 2b).

Mean juvenile survival (i.e., survival from fledging to age three) was 0.09 (CI: 0.02, 0.21) and varied from a low of 0.06 (CI: 0.004, 0.17) in 2018 and to a high of 0.11 (CI: 0.01, 0.54) in 2021 (Fig. 2c); there was considerable uncertainty in annual estimates given that this parameter encompasses multiple years and 1- and 2-year-olds are unobservable. Mean annual adult survival was 0.84 (CI: 0.75, 0.92). Somewhat surprisingly for a long-lived species, there was substantial year-to-year variation in adult survival, ranging from 0.55 (CI: 0.41, 0.71) in 2014 to 0.95 (CI: 0.78, 1.00) in 2016 (Fig. 2d).

3.2. Assessing population viability in the context of climate and differing management regimes

Under all 10 future scenarios, the population of black terns is expected to decline over the next decade (Table 2). The scenarios based on the past 100-yr and 10-yr means of the NAOI yielded relatively similar projections of population size under the different management scenarios, but across all management scenarios, the 10-yr mean of the NAOI (mean of the index for last 10 years [2012–2021] = 0.22) yielded larger projected population sizes than the 100-yr NAOI mean (mean of the index for last 100 years [1922–2021] = -0.03; Table 2, Appendix C). Across both climate scenarios, the null (no additional management) strategy produced the smallest projected population sizes and the highest quasi-extinction probabilities, followed by the strategies to increase fecundity and juvenile survival, which yielded similar population sizes and quasi-extinction probabilities (Table 2, Fig. 3, Appendix C). Increasing adult survival and the combined management scenarios produced the largest projected population sizes and lowest quasi-extinction probabilities (Table 2, Fig. 3, Appendix C).

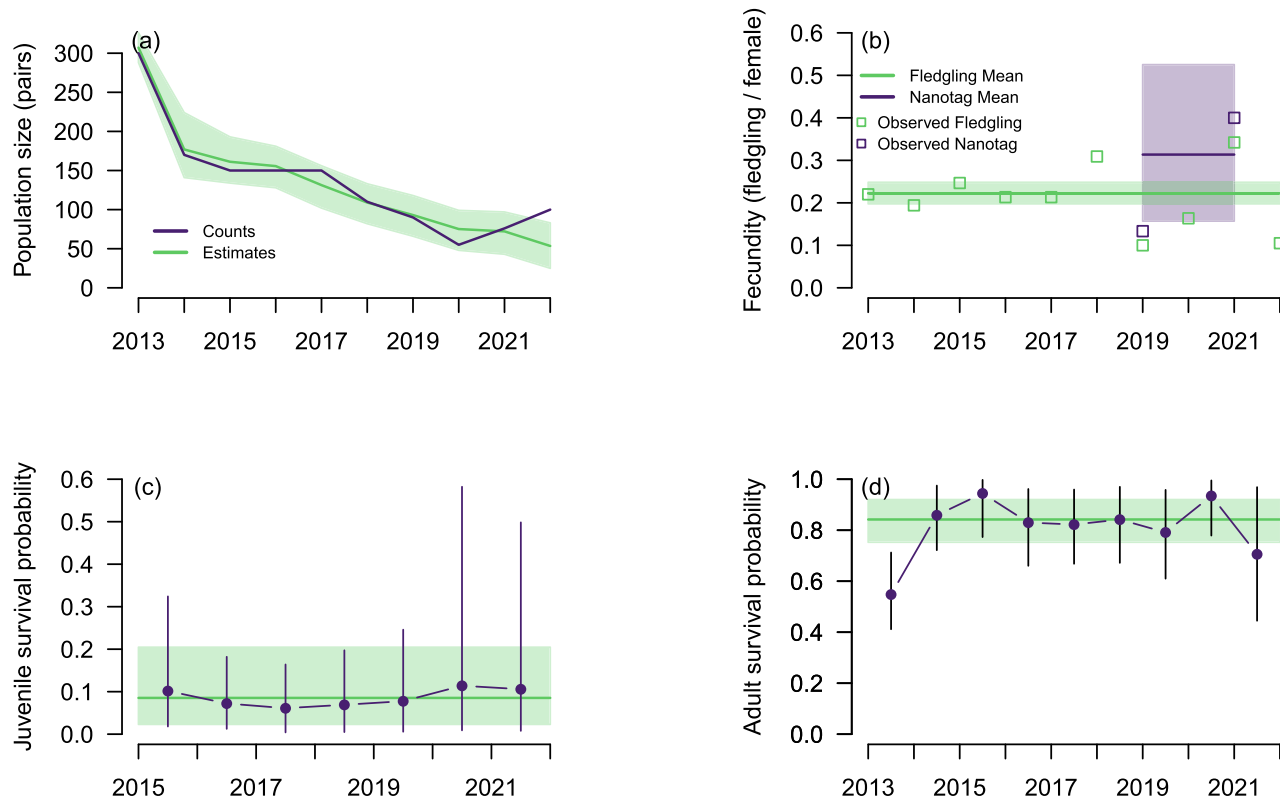


Fig. 2. Estimates of St. Clair Flats black tern (a) population size (breeding pair abundance estimates, green line) and 95 % credible intervals (light green shading) compared to observed pair counts (breeding season surveys, purple line); (b) fecundity (fledglings per female) estimated from fledgling counts (solid green line indicates mean estimate with shading indicating 95 % credible intervals) and nanotag count mean (purple line with shading indicating 95 % credible intervals). Open green boxes show the annual observed productivity from fledgling counts (observed fledgling count divided by observed breeding pair count), and open purple boxes show the annual observed productivity from nanotag counts (observed nanotagged fledgling count divided by the total number of nanotagged chicks); (c) juvenile survival probabilities (survival from fledgling to age three and recruitment probability); and (d) annual adult survival probabilities. Solid green lines indicate mean estimates with 95 % credible intervals (light green shading). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2

We considered two climate scenarios for future population projections based on the: (1) 100-year (1922–2021) mean of North Atlantic Oscillation Index (NAOI) and (2) 10-year (2012–2021) mean of the NAOI, as well as five management scenarios: (1) increasing adult survival approximately 5 %, (2) increasing juvenile survival 10 %, (3) increasing fecundity by double, (4) a combined scenario with all three management strategies, and (5) a no additional management scenario. For each scenario, we estimated the population size 10 years into the future; the probability that the population size in 2032 is less than the population size in 2022, $P(N_{2032} < N_{2022})$; the population growth rate from 2022 to 2032; and the local quasi-extinction probability (population size ≤ 6 breeding pairs remaining in 2032).

Nonbreeding season North Atlantic Oscillation Index (NAOI) scenario	Management scenario	Predicted population size (breeding pairs) in 2032 [95 % CI]	$P(N_{2032} < N_{2022})$	Population growth rate (N_{2032} / N_{2022}) [95 % CI]	Quasi-extinction probability
100-yr mean	Increase adult survival	10.0 [0–29]	1.0	0.18 [0–0.49]	39.8 %
100-yr mean	Increase juvenile survival	6.0 [0–24]	1.0	0.10 [0–0.37]	66.9 %
100-yr mean	Increase fecundity	6.0 [0–25]	1.0	0.10 [0–0.38]	67.5 %
100-yr mean	Combined scenario	14.5 [0–41]	1.0	0.27 [0–0.69]	27.3 %
100-yr mean	No additional management	5.1 [0–21]	1.0	0.09 [0–0.32]	72.8 %
10-yr mean	Increase adult survival	14.5 [0–36]	1.0	0.27 [0–0.59]	21.5 %
10-yr mean	Increase juvenile survival	9.8 [0–32]	1.0	0.17 [0–0.51]	43.6 %
10-yr mean	Increase fecundity	9.7 [0–34]	1.0	0.17 [0–0.53]	46.3 %
10-yr mean	Combined scenario	20.9 [1–49]	0.99	0.39 [0.02–0.83]	12.0 %
10-yr mean	No additional management	8.3 [0–29]	1.0	0.15 [0–0.45]	51.6 %

4. Discussion

We estimated black tern demographic rates and population viability within the context of climatic and management-related changes,

revealing that current conservation efforts during the breeding season are unlikely to reverse the ongoing decline of the St. Clair Flats population (Fig. 2a). Specifically, we demonstrated that interventions aimed at increasing adult survival are most likely to improve population

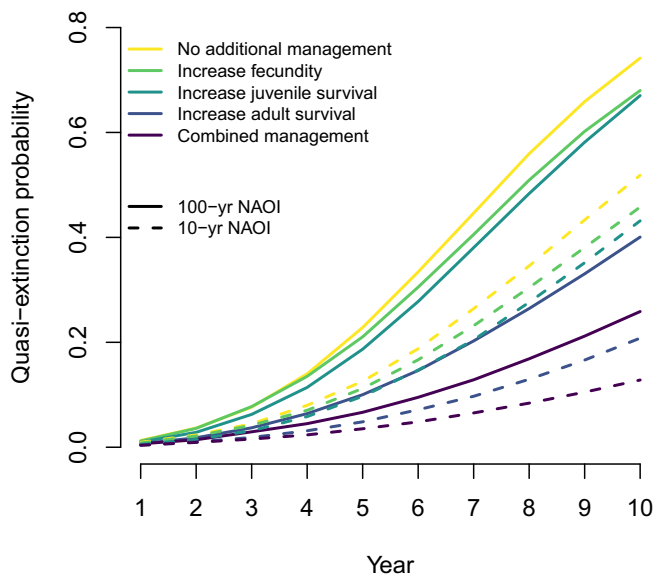


Fig. 3. Comparison of the cumulative quasi-extinction probabilities (≤ 6 breeding pairs remaining) of St. Clair Flats black terns 10 years into the future (2023–2032) under five management scenarios: (1) no additional management (yellow lines), (2) increasing fecundity by double (green lines), (3) increasing juvenile survival by 10 % (teal lines), (4) increasing adult survival by approximately 5 % (royal blue lines), and (5) a combined management scenario utilizing all three interventions (purple lines). Each of the five management scenarios were projected under two climate scenarios using the: (1) 100-year mean (1922–2021) of the North Atlantic Oscillation Index (NAOI; solid lines) and (2) 10-year mean (2012–2021) of the NAOI (dashed lines). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

viability by reducing quasi-extinction probability by 30–46 % compared to no additional management, depending on the NAOI scenario. These findings underscore the importance of enhancing monitoring and management efforts during migration and nonbreeding seasons, which constitute the longest periods of the annual cycle and when birds are the most vulnerable to migratory stressors and unfavorable weather and resource conditions (Marra et al., 2015). While this full annual cycle approach to conservation presents financial and logistical challenges across boundaries and agencies, our findings indicate that interventions targeting fecundity alone are unlikely to result in substantive changes to population size or reductions in local extinction risk (e.g., reduction of local quasi-extinction probability by ~5 % vs. no additional management).

For long-lived species like black terns, population dynamics tend to be especially sensitive to variations in adult survival (Sæther and Bakke, 2000), and demographic rates that most heavily influence population growth often exhibit low temporal variation (Gaillard and Yoccoz, 2003). In contrast to our expectations for long-lived species, we found substantial year-to-year variation in black tern adult survival (Fig. 2b). Yet, we note that we estimate apparent adult survival here, and some of the observed year-to-year variation in survival is likely due to permanent emigration. We hypothesize that the considerable temporal variation in adult survival rates is, in part, due to their acute sensitivity to environmental conditions and reliance on ephemeral and rapidly changing aquatic habitats and resources throughout the annual cycle (i. e., Great Lakes coastal wetlands during summer, changing marine environments in winter). Although it may be difficult to achieve increases in adult survival in practice, the annual variation in adult survival suggests there is potential for management efforts to improve this rate.

Migratory birds, like black terns, spend as much as 75 % or more of the year outside of their breeding ranges, and conditions during the nonbreeding period have carryover effects that influence survival and

reproduction during subsequent breeding seasons (Szostek and Becker, 2015). Stopover and staging sites are important energetic bottlenecks for migratory species (Warnock, 2010), and conditions at these sites can influence demographic rates during the rest of the year (McGowan et al., 2011). Our nanotagging results showed that Michigan-breeding black terns followed the Atlantic flyway during post-breeding migration (Fig. 1b) and used U.S. National Wildlife Refuges (NWR; e.g., Cape Romain NWR, SC; Mackay Island NWR, NC; and Pelican Island NWR, FL) as stopover sites. Future studies of black terns should focus on pinpointing important stopover and nonbreeding season sites to enact management and policy actions (e.g., protection of forage fisheries and offshore habitats from wind power development) that could benefit adult and juvenile survival. Only 9 % of the world's migratory bird habitat is protected from development or human disturbance, and much of this disparity occurs at migration stopover sites (Runge et al., 2015). Establishing buffer zones around prime habitats (e.g., beach closures) to protect resting flocks from anthropogenic disturbances could help migratory species conserve and build energy stores that are important for successful migration and future breeding seasons (Althouse et al., 2019).

We found evidence that positive NAOI in the migration/nonbreeding period preceding the breeding season ($NAOI_{t-1}$) exerts a positive influence on black tern adult survival, resulting in lower quasi-extinction probabilities under the more positive, short-term NAOI mean scenarios. Positive NAOI values are associated with mild, wet conditions in the eastern North America during the fall and winter seasons (Hurrell and Deser, 2009) and fewer hurricanes and storms making landfall along the east coast of the United States (Elsner and Jagger, 2006; Xie et al., 2005). We hypothesize that support for a lagged NAOI effect ($NAOI_{t-1}$) represents variations in the dynamics or composition of marine food resources available or conditions during the migratory and nonbreeding periods that might influence black tern adult survival, as opposed to direct, climate-induced mortality that would manifest as support for the unlagged NAOI variable ($NAOI_t$; Sandvik et al., 2005; Saunders et al., 2021). Predicting oceanic oscillations and their potential interactions with global warming is challenging and a relatively new field (Champanon et al., 2018), but several studies indicate that the NAOI will continue trending upward over the next 30–100 years (Delworth and Dixon, 2000; Gillett et al., 2003). Like the 10- and 100-yr NAOI means scenarios, our simulation of a weak, positive trend in NAOI values (Appendix C) also indicated that the black tern population is likely to continue declining over the next 10 years. However, if the NAOI continues to trend upward amidst climate change, black terns may ultimately benefit in the long-term, as our results also suggest that adult survival may be high in years with high NAOI values. Nevertheless, this is a correlational relationship rather than causative, so alternative measures (e.g., management actions) that can more directly improve low or highly variable vital rates are likely to be more effective at slowing or reversing the population decline.

As was expected for a long-lived species, manipulating fecundity had little influence on projected population sizes compared to survival parameters (Sæther and Bakke, 2000; Gaillard and Yoccoz, 2003). However, estimates of adult survival from our IPM were somewhat low and highly variable over the 10-year study period. Given that black terns are a relatively long-lived species, we expected that adult survival would influence population dynamics more heavily than fecundity and juvenile survival rates, and our results were consistent with this expectation. Yet, we also observed high variability in all rates and when coupled with relatively low adult survival, this limits potential for population recovery if no additional management efforts are enacted. Thus, interventions to stabilize fecundity remain important for buffering the population when adult survival is low or when local environmental conditions are poor. For example, recent high Great Lakes water levels have resulted in washouts and increased flooding during storm events, lowering black tern reproductive success and colony size at several colonies in the region (Fuller, 2021). Future efforts to stabilize and increase annual

fecundity could focus on refining nest platform designs to improve stability in fluctuating water levels and provide built-in exclosures to minimize predation as climate change continues to produce more unpredictable environmental conditions (Tinbergen and Heemskerk, 2016).

Although we were not able to include immigration in our model due to lack of data, immigration also likely plays an important role in buffering population declines (Brown and Kodric-Brown, 1977; Horswill et al., 2022). The observed population size in 2022 was higher than the estimated population size, and the observed population counts have been trending upward since 2020 while model estimates showed a negative trend during this time (Fig. 2a). Thus, it is likely that individuals may be immigrating into the population, but we were unable to parse the potential contribution of such a phenomenon due to lack of data. Management efforts to improve the amount and quality of available nesting habitat, such as eradication of invasive *Phragmites australis* to improve hemi-marsh conditions and creation of floating cattail (*Typha angustifolia*) mats to increase nesting substrate, could encourage colony-level recruitment.

Our results provide the first annual estimates of juvenile survival for Michigan black terns, a critical life stage that is frequently overlooked due to the difficulty of following fledged young before they return to the breeding grounds. Quantifying juvenile or subadult survival is particularly challenging in terns and many other waterbird species because individuals often do not return to breeding areas until they are three or more years old; thus, few juvenile survival estimates exist and information on how environmental conditions might affect survival during the early years of life is extremely limited in waterbirds (Monticelli et al., 2008). Compared to other tern species, juvenile survival in black terns (mean $\phi_{juv} = 0.09$ [CI: 0.02, 0.21]) appears to be generally similar, if not slightly lower. The mean juvenile survival rate of roseate terns (*Sterna dougallii*), which also return to breed at age three, is estimated as 0.15 but is assumed to be closer to 0.16–0.17 due to inter-colony movements (Spendlow, 1991). Similarly, multiple studies on common terns (*Sterna hirundo*) have reported mean juvenile survival (survival to age 4) between 0.07 and 0.14 (reviewed in Servello, 2000). Although our estimate of juvenile black tern survival is relatively imprecise due to limited data to inform this parameter, it is useful for comparing rates among species and for identifying reasonable goals for management interventions.

We assessed the efficacy of nanotags for recording fledgling counts versus on-the-ground counts. Given the challenges of confirming fledging in the field, even a coarse estimate of fledging success is likely more accurate than current on-the-ground observations of fledglings due to the difficulty of distinguishing fledglings from adults when the entire colony takes flight. Although we were able to obtain estimates of fecundity from nanotag data, the mean annual fecundity estimates from nanotags included considerable uncertainty. Nevertheless, the overlapping credible intervals of the fecundity estimates from these two observation methods serves as a proof-of-concept that nanotagging pre-fledged young can provide a valuable monitoring method for estimating annual reproductive success at black tern colonies. Additionally, our nanotagging results demonstrated the importance of Atlantic coastal habitats for juveniles that were refueling during fall stopovers, in contrast to eBird relative abundance maps that show the greatest abundances of black terns along the Gulf of Mexico coast in the fall (Fink et al., 2021).

The reality of many conservation and management-related questions is that the answer is often “more data are needed.” However, environmental change is threatening species with extinction now due to habitat loss, climate change, overexploitation, and pollution. Rapid implementation of effective conservation strategies is needed to combat these threats (Hoffmann et al., 2010). Conservation of many long-lived, migratory species is focused on increasing productivity, even though adult survival is often the most important demographic rate driving their population dynamics (Caswell, 2000). Indeed, our findings demonstrate

that management actions targeting adult survival were the most likely to improve population viability, and breeding season interventions alone are unlikely to abate ongoing population declines. While adult survival is generally a difficult vital rate to manipulate through management interventions, our estimates of black tern adult survival were variable over time, indicating the potential for management activities targeted at stopover sites and nonbreeding areas to improve this rate. Despite limited data for this rare and elusive species, we provided the first estimates of juvenile survival for Upper Midwest-breeding black terns and conducted a population viability analysis for the species that compared management strategies under different climate scenarios. Taken together, these results provide a foundation for advancing conservation decision-making for this imperiled species. More broadly, our coupled IPM-BPVA approach can be implemented for other data-deficient species in decline to evaluate the efficacy of management strategies both now and into the future.

Funding

Our funding partners include the Upper Mississippi River/Great Lakes Joint Venture, Michigan DNR, Detroit Audubon, Environment Canada, Indiana University, Detroit Zoo, Kalamazoo Nature Center, Lake St. Clair MetroPark & City of New Baltimore. Model development and data analysis were supported by a grant from the US Fish and Wildlife Service and the National Science Foundation (DBI-1954406).

CRediT authorship contribution statement

Kayla L. Davis: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Sarah P. Saunders:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition. **Stephanie Beilke:** Writing – review & editing, Project administration, Funding acquisition. **Erin Rowan Ford:** Data curation, Writing – review & editing, Funding acquisition. **Jennifer Fuller:** Data curation, Writing – review & editing. **Ava Landgraf:** Data curation, Writing – review & editing. **Elise F. Zipkin:** Conceptualization, Methodology, Writing – review & editing, Supervision.

Declaration of competing interest

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

Data availability

Model code is included in Appendix B, and full data and code are available on Github at https://github.com/zipkinlab/Davis_etal_2023_BioCons and is archived on Zenodo at <https://doi.org/10.5281/zenodo.7878956>.

Acknowledgements

We thank Todd Aleger, Jeff Costa, John Darling, Brandy Dybas-Berger, Jeremiah Heise, Dr. Alex Jahn, Joe Kaplan, Rich Keith, Isabel Krahling, Dave Moore, and Corey Wotring for their support and collaboration on this project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110104>.

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