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ADVANCING QUANTITATIVE APPROACHES FOR ESTIMATING AVIAN
POPULATION RESPONSES TO ENVIRONMENTAL CHANGE USING A
DATA-RICH SPECIES: THE AMERICAN WHITE PELICAN

by

Aimee Michele Van Tatenhove

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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ABSTRACT

Advancing Quantitative Approaches for Estimating Avian Population Responses to
Environmental Change Using a Data-Rich Species: The American White Pelican

by

Aimee M. Van Tatenhove, Doctor of Philosophy

Utah State University, 2024

Major professors: Erica F. Stuber, Ph.D. and Clark S. Rushing, Ph.D.
Department: Wildland Resources

Human-driven environmental change is impacting avian populations globally, and technological and analytical advancements are improving our understanding of how change drives population trends. However, estimating population dynamics and vital rates remains challenging for many species due to modeling limitations and sparse data. Improving methods to estimate these species' responses to change first requires validating new approaches on well-studied species. The American White Pelican (*Pelecanus erythrorhynchos*), a Nearctic migratory waterbird, has been studied extensively due to conservation concerns and human-wildlife conflict. As a large-bodied, data-rich species, pelicans are ideal for testing novel analytical methods using new or underutilized data sources. Yet knowledge gaps remain for pelican survival and connectivity, threats, and reactions to environmental change.

My research aimed to advance methods estimating avian survival, space use, and migratory connectivity, while improving understanding of pelican population drivers. In Chapter 2, I developed a joint recovery model to estimate regional connectivity and

survival using mark-recapture data. I applied this model to pelican banding data and found that pelicans often remain in the same region across seasons, with substantial variation in annual survival by region. In Chapter 3, I quantified environmental niche breadth and variability of pelicans. I found that pelicans do not track environmental conditions as a population, with notable variation in individual niches, suggesting that this population may be resilient to environmental change. Chapter 4 serves as a proof-of-concept. Here, I used machine learning to extract a pelican radar signature from weather radar using locations of GPS-tagged pelicans, then used this signature to predict locations of untagged pelicans and generate a pelican-airplane strike index at a local airport. Finally, I formally linked local pelican population dynamics to environmental variables in Chapter 5, by applying a state-space model to colony count data, then generating colony abundance forecasts under various management scenarios. Results suggested that land bridge formation between the colony and mainland is likely a driver of local breeding population declines. My research highlights variation in pelican response to environment depending on population and landscape scales examined, and presents improved approaches for estimating survival, migratory connectivity, and space use in avian species.

(215 pages)

PUBLIC ABSTRACT

Advancing Quantitative Approaches for Estimating Avian Population Responses to
Environmental Change Using a Data-Rich Species: The American White Pelican

Aimee M. Van Tatenhove

Advancements in wildlife data collection technology and analysis are helping us understand how human-caused environmental change is impacting bird species. Yet data collection for many species remains challenging, and often the data are difficult to analyze. Improved methods for collecting and analyzing avian data are needed to understand how species respond to environmental change. However, before applying new methods to poorly understood species, it is crucial to test methods on well-studied species to ensure their effectiveness. The American White Pelican is a well-studied species that is ideal for testing new analysis methods. Pelicans have been studied extensively due to conservation concerns and conflicts with humans. However, gaps still exist in our understanding of pelican survival and migratory destinations, threats, and reactions to environmental change.

My dissertation used pelican data to improve methods that estimate avian survival, identify environments bird species use, and measure how likely individuals are to migrate between regions. In Chapter 2, I developed a mathematical model to estimate how many pelicans migrate between North American regions and their resulting survival probabilities. I found that pelicans often remain in the same region year-long, with substantial variation in survival depending on location. In Chapter 3, I measured environmental conditions favored by pelicans and how this varied between individuals. I

found that pelicans do not rely on specific conditions as a population, and that individual use varies substantially, suggesting population resilience to environmental change.

Chapter 4 investigated the feasibility of extracting radar signatures of flying birds from weather radar using location data from GPS-tagged pelicans. Using this radar signature, I predicted locations of untagged pelicans across my study area and developed a pelican-airplane collision risk index for a local airport. In Chapter 5, I used a mathematical model to estimate how environmental conditions affected pelican colony abundance, then estimated future abundance under various management scenarios. I found that land bridge formation between the colony and mainland is a likely cause of abundance declines. My research offers improved analytical methods for avian populations, and highlights that birds may respond to environmental change differently depending on the landscape and population scales examined.

DEDICATION

To my mother.

Thanks for your tireless work to spark my curiosity and confidence.

I wish you could be here to see how far it has taken me.

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Innumerable people supported me throughout this degree, and my appreciation cannot be done justice in a few paragraphs. However, here's an attempt:

First, thank you Clark and Erica for being fantastic advisors. You played off of each other's strengths exceptionally well, and I feel incredibly fortunate to have grown as a scientist under your direction. Clark, thanks for encouraging my ridiculous ideas, for the bird and food adventures, for trusting me to step up to new challenges, and for guiding me along the way. You're an inspiration. Erica, thanks for welcoming me into your lab with open arms and for the incredible effort you put in to make sure I had funding and resources (and a corner office!). I'm eternally grateful.

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Thank you to my family for cheering me on and for refraining to ask how much longer my degree would take. You've all been incredibly supportive, even if you didn't really get why I wanted to go back to school *again*. Thanks Dad for your incredible strength, excitement, and encouragement, and for unabashedly celebrating the nerd I always have been. Thank you Jed for being so patient and supportive, and for not making

fun of my infantile computer skills. I'm still unable to explain to people what you do for a living.

Thank you to my friends, old and new. There are too many of you to thank directly in the space I have here, but I will never forget all of the incredibly fun adventures falling on our faces at Beaver Mountain, hiking up inadvisable slopes, birding in awful conditions, watching reality TV six feet apart, hounding Lake Restoration Solutions, hunting for epic rocks, chasing sharks and rays, and baking bonkers amounts of dessert. Thanks to you, my heart is full and my trail mix will always contain sand.

To all the wonderful folks at UPR, thank you for trusting me to learn the ropes of radio reporting. I never thought I'd get to become a real journalist and science communicator. The skills I learned and stories I was able to share changed me fundamentally for the better.

Thank you to Great Salt Lake. You taught me what it means to truly love and fight for a landscape and all of its inhabitants. And to the pelicans, thanks for keeping me humble. I don't think I'll ever be good at pelican captures, and I've come to terms with that shortcoming.

Funding played a huge role in my time at Utah State University, and without it, I wouldn't have been able to complete my dissertation. Thank you to the Fritz L. Knopf Fellowship, the Utah State University Ecology Center, Tracy Aviary, Great Salt Lake Audubon, the U.S. Geological Survey, the Utah Division of Wildlife Resources, and the Salt Lake City International Airport for generously supporting my research.

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Aimee Michele Van Tatenhove

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CHAPTER I

INTRODUCTION

Human-driven environmental change is impacting avian populations globally, but these impacts differ across populations, years, and seasons (Dunham *et al.*, 2021; Rushing *et al.*, 2021; Sillett *et al.*, 2000). Altered temperature and precipitation regimes, land-use changes, human-wildlife conflict, environmental contaminants, and disturbance drive avian population dynamics, space use, and demographics in complex ways, at varying spatial and temporal scales (Bateman *et al.*, 2020; Donnelly *et al.*, 2020; Eglington & Pearce-Higgins, 2012; Keith, 2005). However, avian response to environmental change—and the drivers underlying these responses—remain largely unidentified at scales relevant to management, conservation, and habitat protection for many species. Our ability to conserve struggling species depends on our ability to identify these diverse drivers and quantify and predict resulting changes in species' population dynamics at appropriate management and conservation scales (Davis *et al.*, 2023).

As avian tracking technology and statistical methods improve, so does our ability to identify drivers of population dynamics and to estimate population trends. New technologies are generating species-specific data of various types at unprecedented temporal and spatial resolutions (McKinnon & Love, 2018; Nathan *et al.*, 2022). With this accumulating wealth of data, we can begin to infer links between observed changes in demographic rates, range shifts, and space use, and their respective underlying drivers with the expanding toolbox available to analyze these datasets (Zipkin *et al.*, 2021). Improved integrative methods can expand the utility of data sources that may not yet

offer useful insight as standalone products (Zhao *et al.*, 2020). For example, machine learning can untangle non-linear effects of environmental conditions on populations (Cutler *et al.*, 2007), and computational and modeling advancements have allowed application of Bayesian methods to large datasets (e.g., de Valpine *et al.*, 2017). Spatial and temporal predictions are improving as well, as remotely sensed data increases in scope and resolution, further improving our understanding of avian population declines and informing targeted population management and conservation (Tredennick *et al.*, 2016). Considering we now have many well-studied avian species with increasingly large datasets available, data-rich species are ideal starting points with which to characterize population dynamics across multiple scales, relate demographics to underlying drivers, and to explore new ways of inferring population space use and demographic rates.

The American White Pelican (*Pelecanus erythrorhynchos*; hereafter “pelican”) is a migratory waterbird species that has been the focus of long-term study and management efforts since the 1960s. Abundant data across years and sites exist for this species, including long-term breeding colony count datasets across its range, high-resolution location data across the full annual cycle, and over a century of band reencounter data. Breeding colony counts have revealed both dramatic localized population declines and recoveries over the past century (Keith, 2005; King & Anderson, 2005; Moulton *et al.*, 2018; Murphy, 2005), and location data have quantified predation on aquaculture and game fish species, daily activity budgets, and high-use wintering habitats (King *et al.*, 2016; King & Werner, 2001). Banding reencounters collected across North America have characterized breeding colony fidelity and delineated the boundary of an eastern and western metapopulation (Anderson & Anderson, 2005; Hendricks *et al.*, 2002; Kijowski

et al., 2020). However, significant gaps still exist in our understanding of pelican population impacts from current and historical threats, regional survival, migratory connectivity, and expected reactions to rapid environmental change.

Historically, hypothesized threats to pelicans included habitat loss, disease, and the widespread use of pesticides (including DDT, toxaphene, endrin, and other organochlorine pesticides), exposure to which resulted in reduced nest success and direct adult mortality (Anderson *et al.*, 1969; Boellstorff *et al.*, 1985; Hendricks *et al.*, 2002). Conversely, proliferation of aquaculture within pelican wintering grounds has provided a steady food source for overwintering individuals in recent decades (King *et al.*, 2010), while wetland restoration and organochlorine bans may underlie range-wide population growth (Murphy, 2005). Current concerns include breeding colony disturbance (Moreno-Matiella & Anderson, 2005), human-wildlife conflict (Budy *et al.*, 2022; Kijowski *et al.*, 2020), and desiccation of foraging, breeding, and stopover sites, especially in the western United States (Moulton *et al.*, 2018). However, migratory behavior complicates our understanding of these threats and their effects on pelican populations. Band recoveries suggest that pelican metapopulations mix (Anderson & Anderson, 2005), but the extent to which mixing occurs and how it varies spatially remains relatively unknown. Population drivers in one location may affect only a portion of the pelican population or its entirety, depending on the extent of migratory connectivity, with significant implications for how we address conservation and management at local and population scales.

Given that pelicans are long-lived and highly reliant on disturbance-free waterbodies for breeding and foraging (Knopf & Evans, 2020), investigating pelican population drivers can provide unique insights into the long-term health of imperiled

aquatic habitats across the continent. In particular, saline water bodies and the surrounding wetlands that the western pelican population relies on for breeding and foraging provide significant ecosystem services and host a large number of species throughout the year compared to other aquatic ecosystems (Bobbink *et al.*, 2006; *Utah Wetlands Interpretive Network*, 2006; Wurtsbaugh *et al.*, 2017). Saline lakes are facing catastrophic declines globally (Saccò *et al.*, 2021; Wurtsbaugh *et al.*, 2017), and research into species using these habitats, including pelicans, may provide insight into how losing these landscape features may impact avian populations at local, regional, and intercontinental levels (Audubon, 2018; Conover & Bell, 2020). Great Salt Lake, Utah, provides a timely example of how saline lake declines may drive avian population dynamics at larger scales. Mineral extraction, encroaching development, and agricultural and urban water consumption threaten Great Salt Lake and its surrounding wetlands, that pelicans and other water-reliant avian species (e.g., waterfowl, waterbirds, and shorebirds) depend on for breeding, foraging, and migratory stopover habitat (Conover & Bell, 2020; Kijowski *et al.*, 2020). Great Salt Lake historically contained one of the largest, highly productive pelican breeding colonies in the western metapopulation, but near complete nesting failure and subsequent colony abandonment in summer 2023 underscores the severity of environmental impacts to avian populations using Great Salt Lake's resources. Rising salinity levels and historically low water levels are expected to continue to threaten pelican populations using Great Salt Lake, with implications for survival and population dynamics of the western pelican metapopulation, in addition to nearly 100 other water-reliant species Great Salt Lake hosts annually (Tavernia *et al.*, 2021).

As a data-rich species, pelicans are ideal candidates for quantifying effects of environmental change on population trends and to explore new data integration and analysis methods. In the following chapters, I leverage diverse data sources across multiple landscape scales to estimate pelican survival and migratory connectivity, quantify pelican niche and expected resilience to climate change, explore novel methods to estimate airspace use, and link declining pelican abundance to environmental drivers. This work fills significant knowledge gaps in our understanding of broad and fine scale pelican population dynamics and the environmental drivers underlying these trends. Furthermore, the methods detailed in the following chapters are applicable to species beyond pelicans, and may provide important stepping stones for future analyses of avian data.

Specifically, I employ a novel multistate joint recovery model (Chapter 2), parameterized in continuous time with pelican band reencounter data, to estimate pelican migratory connectivity and characterize survival by migratory strategy, then identify potential drivers of these differences range-wide. This modeling framework is computationally efficient and uses all pelican banding data available since routine pelican banding began in the 1960s, including data from non-reencountered individuals, to estimate band reencounter probabilities, survival, and migratory connectivity between the breeding and wintering ranges. By including data from individuals never seen again, this modeling framework reduces model bias to provide accurate estimates of survival and migratory connectivity and improve our understanding of spatially-explicit conservation needs (Cohen *et al.*, 2014; Korner-Nievergelt *et al.*, 2010).

Species environmental niche breadth and variability may underlie population-level responses to intensifying climate change (Carscadden *et al.*, 2020). Despite growing populations range-wide, pelicans' heavy reliance on water resources for breeding and foraging may limit their ability to adapt to environmental changes. Niche breadth and niche variability at individual and population levels may buffer environmental impacts at the species level (Fandos *et al.*, 2020), but how much niche use varies is unknown for the western metapopulation of pelicans. In Chapter 3, I quantify niche breadth and variability for pelicans across the Pacific Flyway to characterize expected pelican reactions to climate change. I use a multi-year GPS location dataset collected from multiple individuals across breeding and non-breeding ranges to calculate population- and individual-level niche characteristics. Furthermore, I compare my findings to a previous analysis conducted on the eastern metapopulation (Illán *et al.*, 2022) to characterize differences between metapopulations, with implications for management and expected population trends under climate change.

Broadscale weather radar is increasingly used as a tool to quantify avian migration, but has generally been restricted to species-agnostic measures (Guo *et al.*, 2023; Horton *et al.*, 2019). In Chapter 4, I explore the feasibility of combining information from individual-level GPS location data with broadscale weather radar data to build a species-specific radar signature of pelicans. I use an ensemble machine learning algorithm to characterize pelican radar signatures from NEXRAD weather radar data, then use this radar signature to predict pelican occurrence within radar airspace. This research is focused on airspace above Utah's Great Salt Lake, an important breeding and foraging site for pelicans within the western metapopulation. From these predictions, I

characterize spatial and temporal pelican airspace use above Great Salt Lake, to identify times and locations of high airspace use. I use these estimates to improve our understanding of habitat use throughout the breeding season and build a monthly pelican-airplane strike hazard metric at the Salt Lake City International Airport, a high-traffic airport located near important pelican foraging grounds.

Despite range-wide population growth, pelican breeding colony count data from across the Intermountain West suggests that pelican breeding populations are declining regionally. However, no attempts to formally tie population trends to environmental factors have been undertaken. Regional water limitations from a multi-decade drought (Williams *et al.*, 2022; Zhang *et al.*, 2021) and increasing agricultural and urban water consumption (Null & Wurtsbaugh, 2020; Wurtsbaugh *et al.*, 2016) are hypothesized to have driven declines, but other local and regional conditions may influence observed population dynamics. Using a long-term colony count dataset, I formally link environmental drivers to population declines and forecast population under relevant environmental and management scenarios (Chapter 5). I use a state-space modeling framework to appropriately account for over- and under-counting associated with colony counts, and quantify effects of both local and broadscale environmental drivers to inform the scope and aims of conservation and management strategies for this declining population. Finally, in Chapter 6, I conclude with an overview of my results and their importance to ecology and conservation.

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CHAPTER II

MODELING SURVIVAL AND CONNECTIVITY OF A MIGRATORY WATERBIRD
USING A CONTINUOUS-TIME, MULTI-STATE APPROACH

ABSTRACT

Survival may be driven by markedly different anthropogenic impacts and environmental conditions across the full annual cycle, including human development, habitat loss, pesticide use, drought, and disease. Understanding how and why survival rates vary spatially, and the degree of population interconnectivity between regions is crucial to crafting targeted conservation initiatives and for predicting future population dynamics. Even so, regional connectivity and variation in annual survival remain poorly understood for many species due to limited data or difficulties in analyzing existing datasets. One of these species, the American White Pelican (*Pelecanus erythrorhynchos*), is a large Nearctic waterbird that has experienced notable spatial variation in population trends across its range. Regional survival and connectivity are largely unexplored for this species despite the existence of long-term datasets from which survival and connectivity can be estimated.

Here, I describe a novel continuous-time joint recovery model applied to 63 years of band recovery and resight data from the North American Bird Banding Laboratory to quantify migratory connectivity and survival between American White Pelican summer and winter ranges. Band recovery data are typically modeled in discrete time, but band recoveries may occur at any point throughout the year, making continuous-time models more appropriate and computationally efficient for these data types. My approach also

efficiently handles large numbers of undetected individuals, which vastly reduces computational time for large band recovery data sets. Results from this analysis indicate that a majority of individuals remained in the region they were banded in throughout the year. Annual survival varied by migratory strategy, likely due to spatial variation in environmental conditions and anthropogenic impacts. Mean annual survival was high ($72.1\% \pm 0.9\%$) for individuals that were banded in and remained in the eastern United States throughout the year. Conversely, individuals that were banded in and remained in the western United States throughout the year experienced low survival ($48.4\% \pm 2.5\%$). These results offer important context for understanding historical pelican population dynamics, and may be used to inform current and future management strategies for American white pelicans across North America.

INTRODUCTION

Estimating survival and movement is critical to conserving avian populations as they decline globally. Migratory species have faced population declines of $> 25\%$ over the past half-century (Rosenberg *et al.*, 2019; Vickery *et al.*, 2023), and are in clear need of conservation programs that target factors driving negative population trends. However, survival and movement of migratory species are inherently linked, complicating our understanding of what is driving these declines. Individuals may encounter differing environmental conditions, resource availability, disease, and disturbance between migratory regions (Klaassen *et al.*, 2014; Paxton *et al.*, 2017; Rushing *et al.*, 2017), with implications for their survival depending on the set of conditions they encounter. Quantifying seasonal migratory connectivity—the degree to which areas within a species' range are linked by migratory movements of individuals—can reveal how population

trends are influenced by spatially heterogeneous conditions depending on the strength and spatial makeup of connectivity across populations (Cohen *et al.*, 2014; Cohen *et al.*, 2018; Robinson *et al.*, 2016). By understanding what percentage of a population moves and where, we can estimate movement-specific survival rates to identify relevant population drivers (Arnold *et al.*, 2018; Rushing *et al.*, 2021), understand source-sink dynamics across populations (Brawn & Robinson, 1996; Tittler *et al.*, 2006), and parameterize population models for use in conservation and management planning (Arnold *et al.*, 2018; Davis *et al.*, 2023).

Bird banding has a rich history in North America and Europe, and band reencounters have provided an important source of survival and movement data over the past century (du Feu *et al.*, 2016; Smith, 2013). Comprehensive banding programs, like that of the U.S. Geological Survey's Bird Banding Laboratory (BBL), compile avian banding data from researchers across the United States and Canada, and subsequent reencounter date, geographic coordinates (regardless of global location), and live or dead status of reencountered banded individuals. Banding records from these banding programs contain substantial data with which to estimate parameters across many sites, often going back decades, and are freely available for research use. Banding data have been used to parameterize adaptive harvest management models for waterfowl (Nichols *et al.*, 2007; U. S. Fish and Wildlife Service, 2021) and estimate survival and migratory connectivity across broad spatial and temporal scales, revealing conservation-relevant survival and movement patterns (e.g., Anderson & Anderson, 2005; Barker *et al.*, 2005; Fernández-Ordóñez & Albert, 2023; Robinson *et al.*, 2016).

Despite the wealth of information banding datasets contain, these data present considerable modeling challenges and are generally underutilized as a result (Korner-Nievergelt *et al.*, 2010; Korner-Nievergelt *et al.*, 2012). Long-term band reencounter datasets frequently contain tens to hundreds of thousands of individual encounter histories with numerous reencounters per individual, and therefore require computationally efficient modeling frameworks to analyze. Low and heterogeneous band reencounter probabilities inherent to these datasets may also make estimating regional survival and migratory connectivity difficult (Cohen *et al.*, 2014; Korner-Nievergelt *et al.*, 2012; Perdeck, 1977). Ecologists have long been seeking solutions for estimating these parameters from banding data, including through complex modeling frameworks and formulating band reencounter models within popular modeling software (e.g., Barker *et al.*, 2005; Brownie *et al.*, 1993; Robinson *et al.*, 2016). Until recently, most software programs used to estimate survival from band reencounter data collected continuously through time (e.g., M-SURGE (Choquet *et al.*, 2004), MARK (White & Burnham, 1999), and SURVIV (White, 1983)) were created to analyze VHF-based location data, which are often collected on a fixed temporal schedule. Creating custom analyses is often out of reach for many ecologists (Fouchet *et al.*, 2016; Rushing, 2023). As a result, continuous-time band data are frequently discretized for use in discrete-time frameworks by binning data into regular time periods (often seasons or years), defined *a priori* by researchers (e.g., Adams *et al.*, 2006; Heupel & Simpfendorfer, 2002), which typically results in information loss. Discretizing continuous-time reencounters may also cause parameter bias (Barbour *et al.*, 2013; Fouchet *et al.*, 2016; but see Pautrel *et al.*, 2023), especially when temporal bins are large, as individuals reencountered at the beginning of a bin are

modeled as having the same survival and reencounter probabilities as those reencountered at the end of a bin.

Here I introduce a continuous-time, multistate joint recovery model that estimates survival rates, live and dead reencounter rates, and migratory transition probabilities from band resight and recovery data. This modeling framework regards time between detections as a random variable, allowing for estimation of survival from irregularly spaced live and dead detections. Detection rates of marked individuals may vary spatially by observer effort and density, and failure to account for spatial variation may lead to parameter bias (Cohen *et al.*, 2014; Korner-Nievergelt *et al.*, 2010). Accordingly, I include data from both reencountered and non-reencountered individuals to estimate live and dead detection rates and migratory transitions by region. First, I use simulated banding datasets, generated from a range of ecologically plausible survival and detection probabilities, to demonstrate that the model produces unbiased estimates of survival and movement. I then apply the model to band reencounter data from American White Pelicans (*Pelecanus erythrorhynchos*; hereafter “pelican”), a Nearctic migratory waterbird species of research interest due to this species’ sensitivity to disturbance at breeding colonies and conflict with sport fisheries. Annual survival and regional transition probability estimates produced by this analysis are consistent with available published estimates and provide new estimates for regions previously lacking data. Together, survival and regional transition estimates reveal how spatially heterogeneous conditions across breeding and wintering grounds influence regional survival, and offer a roadmap to explore future research and conservation initiatives for the most beneficial effect on the overall population.

METHODS

Model description

This model considers individuals of any age that were captured alive and banded so that they may be subsequently identified as individuals at any point in time after the initial banding encounter. For each reencountered individual $i = 1, 2, \dots, N$, the time, state (alive or dead), and location of each encounter u are summarized as a history γ_i with length U_i . Time between encounters ($\Delta t_{i,u}$), in fractions of months, is modeled beginning at the individual's initial banding encounter as $t_{i,0} = 0$ through the end of the study period T , the date of the most recent band reencounter in the dataset. Initial banding encounters can occur any time during the study period. Based on where an individual is banded and subsequently migrates to, each reencountered individual is assigned a migration strategy m . Migration strategies are defined as the combination of the region an individual was initially captured and banded in ("banding region") and the region an individual migrates to ("migratory region"), where banding region $j \in 1, 2, \dots, J$ and migratory region $k \in 1, 2, \dots, K$. Individuals that are never reencountered or are only reencountered outside of focal seasons (e.g., an individual reencountered only in spring, when we aim to model summer to winter migration) are assigned an "unknown" migration strategy.

I use a multi-state framework and follow conventional joint recovery model definitions for three states: "alive", "recently dead", and "long dead" (hereafter, "dead"). I use the two dead states to distinguish between individuals that have died recently and are still recoverable on the landscape (e.g., not yet decayed), and those where individuals have been dead long enough that they are very unlikely to be reencountered (i.e., they have decayed and their bands are lost; Kéry and Schaub, 2012). This distinction accounts

for the differing recovery probabilities of individuals that are dead but not decomposed beyond recognition—especially important for large, white birds like pelicans, which are relatively easy to reencounter when dead but intact—versus recovery probabilities of bands from individuals that have decomposed completely. Migratory strategy-specific mortality hazard rates h_m (hereafter, “hazard rates”) govern the rate of transition between alive and recently dead states. Unlike discrete-time formulations of the model, in which individuals typically transition from the recently dead to the dead state after one interval, the continuous-time formulation allows individuals to make this transition at any point in time. I therefore also define a parameter ϕ that governs the transition rate from recently dead to dead and allow the model to estimate how long individuals remain in the recently dead state. I assume ϕ does not vary migration strategy. State transitions are governed by using 3 x 3 intensity matrix \mathbf{Q} for each migration strategy:

$$\mathbf{Q}_m = \begin{bmatrix} -h_m & h_m & 0 \\ 0 & -\phi & \phi \\ 0 & 0 & 0 \end{bmatrix}.$$

Individuals cannot transition out of the unobservable long dead state, and therefore the last row of \mathbf{Q} is all zeros.

Because detection rates are likely to vary spatially (Cohen *et al.*, 2014; Korner-Nievergelt *et al.*, 2010), and between states and tag type (e.g., metal leg bands only or leg bands and high-visibility auxiliary markers), live (p) and recently dead (r) detection rates are modeled as separate parameters, based on tag type status w and migratory strategy m of each individual. State-specific live and recently dead detection are modeled as 3 x 3 intensity matrix $\mathbf{\Lambda}$:

$$\Lambda_{w,m} = \begin{bmatrix} p_{w,m} & 0 & 0 \\ 0 & r_{w,m} & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

Long dead individuals (i.e., Λ [3, 3]) are considered unobservable and therefore have a detection rate of 0. Note that p and r are encounter rates, not probabilities, and are interpreted as the expected number of encounters within one unit time (i.e., month).

Finally, possible migration strategies are modeled as a $J \times K$ transition probability matrix Ψ :

$$\Psi = \begin{bmatrix} \Psi_{1,1} & \cdots & \Psi_{1,K} \\ \vdots & \ddots & \vdots \\ \Psi_{J,1} & \cdots & \Psi_{J,K} \end{bmatrix}.$$

On-diagonal elements represent the probability of remaining within a region, while off-diagonal elements represent the probability of transitioning from row region to column region. I assume that all possible transitions between regions are represented and that this is a closed population (i.e., no immigration into or emigration out of the study area by banded individuals occurs); therefore, Ψ rows must sum to 1.

To reduce model complexity, I regard all individuals that were never reencountered as having been banded at the same time for a given year and region—likely a reasonable assumption for species that are banded in large cohorts (e.g., colonial species). This sets the duration between banding date and the end of the study period to be identical for all individuals within a region and year, allowing the model to calculate a

single likelihood by annual cohort $c = 1, 2, \dots, C$ for each banding region. I set each cohort's banding date to equal the mean banding date for all individuals by region and year.

Likelihood estimation

By assuming \mathbf{Q} and $\mathbf{\Lambda}$ rates remain constant for individuals across the study period, rows of hazard rate matrix \mathbf{Q} sum to 0 and \mathbf{Q} elements are converted to probabilities over each Δt interval as $\exp\{\mathbf{Q}\Delta t\}$ (Rushing, 2023). Similarly, by assuming p and r remained constant, $\mathbf{\Lambda}$ elements are converted from detection rates to probabilities over each Δt interval as $\exp\{-\mathbf{\Lambda}\Delta t\}$. The likelihood of each reencounter u is:

$$\mathbf{\Gamma}_{i,u} = (\exp\{\mathbf{Q}\Delta t_{i,u} - \mathbf{\Lambda}\Delta t_{i,u}\} \mathbf{\Lambda}) \mathbf{\Psi}_{j,k} = (\exp\{(\mathbf{Q} - \mathbf{\Lambda})\Delta t_{i,u}\} \mathbf{\Lambda}) \mathbf{\Psi}_{j,k},$$

where $\mathbf{\Gamma}_{i,u}$ is a matrix with elements indicating the state-specific probabilities of being reencountered at time $\Delta t_{i,u}$. An individual's last detection to the end of the study period is similarly:

$$\mathbf{\Gamma}_{i,T-U_i} = (\exp\{(\mathbf{Q} - \mathbf{\Lambda})\Delta t_{i,T-U_i}\} \mathbf{\Lambda}) \mathbf{\Psi}_{j,k}, \tag{2.1}$$

where $\Delta t_{i,T-U_i}$ is the time between an individual's last reencounter and the end of the study period T .

In cases where an individual's migration strategy is unknown, the model estimates missing migration strategies by marginalizing over all possible strategies, conditional on

the individual's banding region. For example, the likelihood contribution for an individual banded in region $j = 1$ but without a known migration strategy would be modeled as:

$$\Gamma_{i,u} = (\exp\{(\mathbf{Q}-\Lambda)\Delta t_{i,u}\}\Lambda)\Psi_{1,1} + \dots + (\exp\{(\mathbf{Q}-\Lambda)\Delta t_{i,u}\}\Lambda)\Psi_{1,K} .$$

This individual's likelihood from U_i to T is similar to Eq. 2.1, except marginalized over all possible regional transitions:

$$\Gamma_{i,T-U_i} = (\exp\{(\mathbf{Q}-\Lambda)\Delta t_{i,T-U_i}\}\Lambda)\Psi_{1,1} + \dots + (\exp\{(\mathbf{Q}-\Lambda)\Delta t_{i,T-U_i}\}\Lambda)\Psi_{1,K} .$$

Each individual's contribution to the likelihood is:

$$L_i = \mathbf{f}_i \left[\prod_{u=1}^{U_i+1} \mathbf{\Omega}_{i,u} \right] \mathbf{1} ,$$

where \mathbf{f}_i is a vector indicating an individual's initial live or dead state (here, all individuals were first encountered as alive), $\mathbf{\Omega}_{i,u}$ is a 3 x 3 matrix containing hazard, live, and dead detection probabilities for each reencounter, and $\mathbf{1}$ is a 3 x 1 matrix containing all 1s (Jackson *et al.*, 2003). Because we cannot know an individual's live or dead state past its last reencounter, I also defined 3 x 3 matrix $\mathbf{\Omega}_{i,T-U_i}$ that contained all possible hazard, live, and dead detection probabilities, based on the individual's last observed state.

For individuals that were banded and never seen again, the model marginalizes over each possible migration strategy, conditional on banding region, to calculate the likelihood of not being encountered from the banding date T as:

$$\Gamma_{c,T-U_c} = \left(\exp\{(\mathbf{Q}-\Lambda)\Delta t_{c,T-U_c}\} \Lambda \right) \Psi_{1,1} + \dots + \left(\exp\{(\mathbf{Q}-\Lambda)\Delta t_{c,T-U_c}\} \Lambda \right) \Psi_{J,K} ,$$

where c is annual cohort $1, 2, \dots, C$.

The model calculates each non-reencountered cohort's contribution to the total likelihood as:

$$\mathcal{L}_c = \mathbf{f}_c [\mathbf{\Omega}_{U_c}] \mathbf{1} \times N_c .$$

where $\mathbf{\Omega}_{U_c}$ is a 3×3 matrix containing hazard, live, and dead detection probabilities for each cohort and N_c is the number of individuals in each cohort.

Simulations

To assess model performance, I simulated 100 pelican banding datasets using a range of values for h , p , r , ϕ , and ψ . I then quantified bias and precision of model estimates by calculating the mean difference between estimated and simulated values, and root mean squared error (RMSE) for all parameters. Each dataset contained encounter histories for 1,000 individuals, including never reencountered individuals. I randomly removed one third of known migration strategies for individuals that were reencountered at least once to simulate missing migration strategies in real world data. Simulated h , p , and r parameters were generated using a random effects structure for each

dataset, under the assumption that these parameters were generated by the same underlying process across all migration strategies. Mean hazard rates h were randomly selected from a $uniform(0, 0.06)$ distribution and mean values of p and r from $uniform(0, 0.01)$ distributions, which I considered ecologically realistic values (roughly approximate to annual h probabilities of 0.5 and annual p and r probabilities of 0.1; see Figure 2.2). Migration strategy-specific rates were then generated from a $normal(\log(\mu), 0.5)$ distribution, where μ represents the mean rate for h , p , and r parameters. I drew ϕ values from a $gamma(shape = 1, rate = 1)$ distribution, and I allowed ψ for each banding region to take on a range of values from 0–1, where all possible transitions must sum to 1. Diffuse $gamma(1, 20)$ priors were used for all parameters. Some simulated encounter history datasets contained very few reencountered individuals and were difficult for the model to converge on parameter estimates. I therefore refit any models that did not converge to new encounter history datasets until I had a total of 100 converged models.

Application to American White Pelican banding data

Pelicans are a widespread North American migratory waterbird species with an extensive long-term band reencounter dataset. Pelicans have attracted considerable conservation and management interest since the 1960s, due to their sensitivity to disturbances and perceived impact on sport fish populations. From the 1960s onward, pelican populations have been impacted by severe drought and changing precipitation regimes (Williams *et al.*, 2022; Zhang *et al.*, 2021), agricultural water diversions (Null & Wurtsbaugh, 2020; Wurtsbaugh *et al.*, 2016), predator disturbance (Moreno-Matiella & Anderson, 2005; Parnell *et al.*, 1988), degradation of breeding habitat (Anderson & King, 2005), and organochlorine pesticides (Keith, 1966, 2005). Pelican populations are

estimated to be increasing range-wide (Sauer *et al.*, 2019), but range expansion eastward (King & Anderson, 2005) and population declines at large western breeding colonies (Moulton *et al.*, 2018) suggest region-specific conditions may be driving populations in diverging ways. However, regional connectivity and survival of pelican populations remains poorly understood.

I applied the modeling framework described above to 63 years (1960–2022) of U.S. Geological Survey BBL pelican band return data, totaling 163,888 uniquely banded individuals, with 7,691 reencounters of 6,681 individuals. Pelicans have been banded routinely since the 1960s across the breeding grounds (United States and Canada Intermountain West and the Prairie Pothole regions). Banding typically occurs at breeding colonies in the summer, on hatch-year pelicans that have reached adult size, but have not yet gained the ability to fly. Pelicans were banded predominantly as juveniles across both eastern and western regions (percent banded as juveniles east = 99.9%, west = 99.0%). All banded pelicans receive a federal butt-end leg band with a unique identification number, and some individuals also receive field-readable auxiliary markers (e.g., high-visibility leg bands and wingtags), depending on when and where banding activities were conducted. I assumed that individuals experienced no tag effects (tags weighed under 3% of an individual's bodyweight) or tag loss.

Bird Banding Lab datasets include information about how bands are acquired and the condition of the banded bird at time of band reencounter, if available. Bands may be discovered many years after an individual died or reported without information about where bands were initially recovered, so I excluded 1,381 band recoveries from dead individuals with unreliable time and location of death (e.g., bands were reported after

being purchased online or were found unattached to a bird). I also excluded individuals with missing or improbable reencounter dates (e.g., reencounter month was listed as > 12; $n = 1,259$), individuals that were reported as having an unknown alive or dead state at time of reencounter ($n = 70$), and one individual that was recovered greater than 26.4 years after banding, which is the maximum recorded wild AWPE lifespan (Clapp *et al.*, 1982). Finally, I excluded two individuals with improbable reencounter locations (e.g., in the middle of the ocean) and three individuals with over 30 reencounters. Most of these encounters occurred over the course of 3–4 months in urban areas, and did not represent detection probabilities of other individuals within their respective regions.

I delineated three migratory regions of interest based on previously-defined metapopulation boundaries and predicted spatial differences in mortality and detection rates (Anderson & Anderson, 2005; Anderson & King, 2005; Figure 2.1): “east”, “west”, and “south”. A majority of individuals were banded during the summer, so I estimated summer to winter migratory connectivity between banding regions and migratory regions by removing individuals banded outside of summer months (June–September) and assigning migration strategies to individuals with reencounters occurring in the winter (November–March; Knopf & Evans, 2020) based on which migratory region they were reencountered in. For each banding region (east and west), individuals could use one of three migration strategies (east, west, south), resulting in a total of six migration strategies m (east-east, east-west, east-south, west-east, west-west, west-south). No pelicans were banded south of the US-Mexico border during the breeding season, therefore I set transition probabilities originating in the southern region to 0. A majority of reencountered individuals were not observed during winter months (~67%; 4,476 of

6,681) and could not be assigned a migration strategy. I treated the migration strategy of these individuals as missing data, allowing the model to estimate missing migration strategies. Given nearly all individuals were banded as juveniles, assigning unknown migration strategies to those recovered dead outside of winter months likely reduced occasions where bands were recovered from individuals that died at the colony after banding. This approach likely helps avoid overestimating the probability of remaining within a region throughout the year. Nearly all (~98%; 163 of 167) individuals that were reencountered during multiple winters used the same migration strategy across years, so I further assumed that once an individual chose a migration strategy, they did not deviate from that migration strategy in subsequent years.

I used the same random effects structure for h , p , and r parameters as in my simulations, under the assumption that survival and detection were generated by the same processes across migration strategies. Mean h , r , and p rates were modeled using gamma distributions (Table 2.1) and rates specific to each migration strategy were modeled with a $normal(\log(\mu), \sigma^2)$ distribution, where μ represents the mean rate across all migration strategies (and tag types, for p and r rates) and σ^2 is the variance for each parameter. Large monthly rates approach 1 when converted to annual probabilities, so I used a low variance of 0.005 for h , p , and r to pull migration strategy-specific monthly rates toward mean population rate parameter values.

I leveraged published estimates of pelican survival and reencounter probabilities to inform model parameters and to improve convergence. I incorporated these estimates into the model using informative priors for h , p , and r derived from previous studies of pelican survival and movement (Clark & DiMatteo, 2018; Hendricks *et al.*, 2002; J. Neill,

UDWR, written communication, 2016; Kijowski *et al.*, 2020; King & Grewe, 2001; Ryder, 1981; Strait & Sloan, 1975; see Table 2.1 for distributions). I translated published estimates to gamma priors by first converting annual survival, live resight, and dead recovery probabilities to monthly rates, then calculated the mean and standard deviation (sd) for each rate and converted these to gamma rate parameters as $1/(sd(h, p, r))^2/mean(h, p, r)$. The goal of these gamma rate parameters was to pull particularly high rate estimates toward realistic values in cases where the model had little information to estimate parameter values with, because moderate uncertainty in monthly rate estimates may translate to large uncertainty (and unrealistic estimates) in annual probabilities. However, I set all gamma shape parameters to 1, which did not restrict the lower bounds of the gamma prior distribution (Figure 2.2). I did not have published information available on annual recently dead to dead rates, so I placed a weakly informative $gamma(1, 30)$ prior on ϕ .

All models were fit in Stan (Carpenter *et al.*, 2017), using R package *rstan* (version 2.21.5; Stan Development Team, 2022) in R (v4.1.3 R Core Team, 2022), with 200 warmup, 500 total iterations, maximum tree depth of 10, initial step length of 0.1, target average acceptance probability of 0.9, and thinning of 1. Model convergence was established using \hat{R} values (chains with $\hat{R} < 1.1$ were considered to have converged; Brooks & Gelman, 1998) and visual inspection of trace plots.

RESULTS

Bias in parameter estimates based on simulated data was generally low for all parameters (Table 2.2), with the exception of the dead recovery rate r . Estimates of r

were biased high compared to simulated r values (bias (\pm sd): 0.007 ± 0.011 ; RMSE: 0.013), and bias increased as simulated r values approached zero (Figure 2.4).

High-visibility auxiliary tags were distributed unevenly across migration strategies, leaving some migration strategies (Figure 2.3) with little associated data to inform h , p , and r parameters for those strategies. However, missing migration strategies were relatively evenly proportioned by banding region (3,189 of 4,586 individuals (70%) in the eastern region and 1,287 of 2,095 individuals (61%) in the western region).

Mean mortality hazard rate h across all migration strategies was 0.038 (sd ± 0.014 ; see Table 2.3 for migration strategy-specific rates). Converted to annual probabilities, mean annual survival probability across all migration strategies was 0.630 (± 0.155). Annual survival probability was highest for the west-south migration strategy and lowest for the west-west strategy (Figure 2.5). Mean live resight rate p across all migration strategies was low (0.002 ± 0.003), resulting in a mean annual resight probability of 0.021 (± 0.030). There was high variation in p estimates associated with migration strategies for individuals tagged with high-visibility auxiliary markers (Table 2.3). Having high-visibility markers was associated with notably higher estimated live detection rates for east-east, west-east, and west-west migration strategies. Mean dead recovery rate r estimates were relatively high (0.033 ± 0.02), where mean annual dead recovery probability was 0.324 (± 0.230). Estimates of r varied by migration strategy and did not seem affected by presence of high-visibility auxiliary tags (Table 2.3). Recently dead to dead rate ϕ was constrained to be equal for all strata. Estimated ϕ rate was 0.922 (95% CI: 0.858–0.989), where individuals spent an average of 1.08 months in the

recently dead state and transitioned from recently dead to dead with an annual probability of 1.

The probability of remaining within a banding region from summer to winter was high (east-east: 0.789 (95% CI: 0.769–0.807); west-west: 0.641 (95% CI: 0.618–0.663); Figure 2.5), followed by migratory transitions from west-south (0.249 (95% CI: 0.228–0.270)) and east-south (0.202 (95% CI: 0.185–0.221)). Transitions from west-east regions were uncommon (0.111 (95% CI: 0.096–0.126)), and east-west transitions being extremely uncommon (0.009 (95% CI: 0.006–0.012)).

I did not formally compare computational efficiency to discrete-time model formulations or to model formulations that considered every non-reencountered encounter history separately. However, model run time for simulations and pelican banding data were reasonable: average simulation run time was 9.15 (sd \pm 6.31) minutes for capture histories of 1,000 total reencountered and non-reencountered individuals, and total model run time on pelican banding data was 2.18 hours. Simulations and the pelican band data model were run on a Windows 11 Pro 64-bit operating system with an 8-core AMD 3.8GHz processor and 64GB (2666 MHz) DDR4 memory.

DISCUSSION

I quantified migratory connectivity and spatial variation in annual survival using a novel continuous-time multistate joint recovery model, applied to 63 years of range-wide American White Pelican band reencounter data. The efficient formulation used in this analysis allowed me to quantify regional variation in survival associated with different migration strategies, which provided insights into regional threats experienced by white pelicans across the annual cycle. I found notable spatial variation in survival estimates by

migration strategy, indicating that the environmental conditions pelicans face in different regions during summers and winters may contribute to variation in survival, with implications for conservation and management by region and season.

Annual survival estimates revealed low survival for individuals that were banded in the western region and remained within this region over the winter months (Figure 2.1). Low survival in the western region may be due to poor wintering conditions, considering other migratory strategies originating in the west but wintering elsewhere had higher associated survival rates. The western United States has been subject to decades of drought and agricultural water diversions (Null & Wurtsbaugh, 2020; Zhang *et al.*, 2021), which have disproportionately affected saline lakes like California's Salton Sea (Audubon, 2018). The Salton Sea is a critical wintering site for up to 30% of the global American White Pelican population (Shuford *et al.*, 2002), but has experienced declining water levels and corresponding declines in food resources used by pelicans (Audubon, 2018). In contrast, west-south migratory connectivity was moderate, but survival associated with this migratory strategy was the highest across all migratory strategies. GPS data (Utah Division of Wildlife Resources [UDWR] unpublished data) suggest pelicans in western Mexico frequent large reservoirs with abundant roosting islands and foraging opportunities. These reservoirs are common throughout the region and ample favorable wintering habitat in the southern region may contribute to high west-south survival.

Pelicans remaining in the eastern region throughout the year had a nearly 24% higher survival rate compared to individuals that remained in the west throughout the year. The range of American White Pelicans is expanding eastward (King & Anderson,

2005) and may signal improving habitat and climate conditions for pelicans across the eastern region. Eastern pelicans that wintered outside of the eastern region had lower associated annual survival probabilities than those that remained in the east throughout the year, suggesting that high-quality wintering habitat and/or favorable climate exists in the eastern region for wintering pelicans. Aquaculture is prevalent in important pelican wintering areas along the Gulf Coast, and previous research has found easy access to abundant prey at catfish farms in the eastern region significantly improves pelican body condition (King *et al.*, 2010). Causes of low survival for individuals banded in the east and wintering in Mexico are currently unknown, and further research is needed to understand underlying drivers of survival for this migratory strategy.

Regional migratory transition probabilities revealed that pelicans predominantly remain in the region they were banded in between summer and winter. High connectivity within banding regions is likely due in part to the size of these regions, which encompass portions of both breeding and wintering grounds. Individuals remaining in banding regions from summer to winter may migrate, but do not leave a region's bounds (e.g., individuals banded at Great Salt Lake, Utah in the summer may migrate to the Salton Sea, California for the winter—both of which are located in the western region). Low connectivity between eastern and western regions supports the notion that the Continental Divide serves as a boundary between the eastern and western metapopulations of this species (Anderson & Anderson, 2005). Transition probabilities between eastern and western regions varied by the direction individuals migrated (i.e., east-west versus west-east), where 11.1% of individuals banded in the western region migrated to the eastern region, but fewer than 1% of individuals banded in the east migrated to the west.

Previous pelican band analyses and GPS tracking data have found that some western individuals from breeding colonies along the western metapopulation's eastern edge (e.g., Great Salt Lake and Yellowstone colonies) migrate along the eastern Rocky Mountains to the Gulf of Mexico, while the reverse (east-west migration) was rare (Anderson & Anderson, 2005; Diem & Pugesek, 1994; UDWR unpublished data). West-east connectivity is similar to that reported in a previous study that used BBL band reencounter data from 1921–1981 (10.6%; Anderson & Anderson, 2005), but east-west connectivity is much lower than previous estimates (3.7%; Anderson & Anderson, 2005), suggesting that pelicans were more likely to move westward before 1960, or that accounting for spatially heterogeneous reencounter rates has an appreciable effect on migratory connectivity estimates.

Strong migratory connectivity within the western region and its associated low survival probability are cause for particular concern. Pelicans that remain in the western region throughout the year (~64% of the western population) have only a 48.4% annual survival probability. This estimate reflects combined juvenile and adult survival, and therefore is likely lower than expected compared to adult-only survival estimates. Even so, this estimate is 8% lower than the next lowest survival probability (east-south migratory strategy), and pelicans of any age class that remain in the western region throughout the year likely experience lower survival rates than those that take other migration strategies. Large breeding colonies across the western metapopulation (e.g., Anaho, NV and Gunnison Island, Utah colonies), have declined notably in recent years (Moulton *et al.*, 2018), and declines at these colonies may be due in part to poor survival. The western metapopulation represents approximately 28% of the total American White

Pelican population (King & Anderson, 2005) and therefore declines in this region may impact both regional and range-wide population persistence as productivity declines at important breeding colonies, local adaptations are lost, and population genetic diversity shrinks (but see Oomen *et al.*, 2011; Reudink *et al.*, 2011).

Estimating migratory connectivity and survival from band reencounter data is difficult for three primary reasons: 1) reencounter data are often collected across areas with spatially heterogeneous reencounter rates, which may severely bias model estimates if not explicitly accounted for, 2) reencounter data may not contain information about where an individual spent its breeding or non-breeding season, only that the individual survived to be reencountered at its present location, and 3) banding datasets are often large, requiring computationally efficient methods to analyze. My model addresses these three issues. First, the model incorporates information from all banded individuals (including individuals never reencountered after banding), then estimates migratory connectivity, albeit at coarse spatial resolution, and annual survival based on regional live and dead reencounter rates. Second, my model estimates unobserved migration strategies by marginalizing over all possible migration strategies and associated survival, resight, and dead recovery values an individual might experience based on its banding region. Finally, I combine information from non-reencountered individuals to reduce the number of individual encounter histories the model must consider, and formulate the model in continuous time, which eliminates the need to consider discrete time periods of non-detections between detections when calculating survival likelihoods. Model estimates were generally unbiased when applied to a range of simulated parameter values (Figure 2.4). Dead reencounter rates were the exception, with bias in estimates of r tending to

increase as simulated r values approached zero. These results are consistent with those of Weegman *et al.* (2020), who found that models that estimates of dead recovery probabilities from joint-recovery models are biased high, especially when live resight probabilities are less than 0.1. Given that I drew p values from a $uniform(0, 0.01)$ distribution (approximately equivalent to annual live resight probabilities between 0 and 0.1), most simulated p parameter values were well below 0.1. However, simulations done by Weegman *et al.* (2020) found minimal bias in survival estimates, despite potentially large bias in r , consistent with my simulation results. Thus, although estimates of dead recovery rates from my model may overestimate the true recovery rates of American White Pelican bands, I expect the survival and migratory connectivity estimates to be unbiased and comparable across regions.

This modeling framework provides a computationally efficient method to estimate annual survival and migratory connectivity from large banding datasets with minimal bias, and results produced by my model, when applied to pelican banding data, offer important context for understanding how spatially heterogeneous conditions influence pelican survival and for managing populations of migratory species in the face of future threats across their annual cycle. Migratory connectivity was strong within banding regions, and conservation efforts focused on these regions may provide the largest benefits for improving and maintaining annual survival. Low annual survival within the western region may be driven by severe disease outbreaks and poor winter conditions at important non-breeding sites like the Salton Sea (Shuford *et al.*, 2002, Keith, 2005). Disease mitigation and conservation efforts focused on improving western wintering sites may improve survival outlook for the western region as a whole.

Conversely, high annual survival and migratory connectivity within the eastern region indicate conditions are favorable for pelican survival, and identifying drivers of high eastern survival may benefit the pelican population range-wide. Further investigation into population drivers, and exploration of pelican survival at finer scales than those examined here may reveal relevant conservation avenues for local populations. Application of this modeling framework to other species will leverage an underutilized data source, and close critical knowledge gaps to improve species conservation.

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TABLES AND FIGURES

Table 2.1: Prior and hyperprior distributions for h (mortality), p (live resight), and r (dead recovery) rate parameters. Gamma rates for each parameter were defined using published estimates of American White Pelican survival, live resight, and dead recovery probabilities, converted to rates. The mean rate across all migration strategies (and tag type, for p and r) for a given parameter is denoted by μ .

Parameter	Distribution	Reference
h	$\mu_h \sim \text{gamma}(1, 340)$ $h_{1:6} \sim \text{normal}(\log(\mu_h), 0.005)$	Clark & DiMatteo, 2018; Hendricks <i>et al.</i> , 2002; Ryder, 1981; Strait & Sloan, 1975
p	$\mu_p \sim \text{gamma}(1, 1625)$ $p_{1:12} \sim \text{normal}(\log(\mu_p), 0.005)$	Kijowski <i>et al.</i> , 2020; J. Neill, UDWR, written communication, 2016
r	$\mu_r \sim \text{gamma}(1, 23040)$ $r_{1:12} \sim \text{normal}(\log(\mu_r), 0.005)$	Hendricks <i>et al.</i> , 2002; King & Grewe, 2001

Table 2.2: Mean bias \pm standard deviation and root mean squared error (RMSE) across all 100 simulations of banding encounter histories for mortality hazard (h), live resight (p), dead recovery (r), and recently dead to dead (ϕ) rates, and regional transition probability (ψ). Bias is calculated as the mean difference between estimated and simulated values.

Parameter	Bias	RMSE
h	-0.006 ± 0.016	0.017
p	0.000 ± 0.003	0.003
r	0.007 ± 0.011	0.013
ϕ	-0.010 ± 0.064	0.065
ψ	0.000 ± 0.051	0.051

Table 2.3: Mortality hazard (h), live resight (p) and dead recovery (r) rate estimates and 95% credible intervals from American White Pelican banding data. Strata denote regional migration strategy¹ for h , p , and r rates, and whether an individual was or was not tagged with a high-visibility auxiliary tag at time of banding for p and r rates. Population row denotes mean and CI posterior estimates of the population-level random effects process underlying each regional migration strategy for h , p , and r . Individuals column indicates number of individuals observed using each migration strategy.

Strata	Individuals		h	p	r
Population	2,205	0.036 (0.034–0.039)	0.001 (0.001–0.001)	0.019 (0.017–0.021)	
EE - no tag	968	0.027 (0.026–0.028)	0.000 (0.000–0.000)	0.023 (0.021–0.025)	
EE - high vis tag	107		0.004 (0.004–0.005)	0.057 (0.049–0.066)	
EW - no tag	17	0.035 (0.030–0.040)	0.001 (0.001–0.001)	0.020 (0.016–0.025)	
EW - high vis tag	0		0.001 (0.001–0.001)	0.019 (0.015–0.024)	
ES - no tag	298	0.047 (0.041–0.054)	0.000 (0.000–0.000)	0.027 (0.023–0.030)	
ES - high vis tag	7		0.001 (0.001–0.001)	0.023 (0.018–0.030)	
WE - no tag	4	0.039 (0.034–0.045)	0.001 (0.001–0.001)	0.019 (0.015–0.023)	
WE - high vis tag	76		0.003 (0.003–0.004)	0.020 (0.016–0.024)	
WW - no tag	218	0.061 (0.056–0.065)	0.001 (0.000–0.001)	0.049 (0.044–0.055)	
WW - high vis tag	336		0.009 (0.008–0.010)	0.030 (0.025–0.033)	
WS - no tag	135	0.022 (0.020–0.023)	0.001 (0.000–0.001)	0.089 (0.075–0.105)	
WS - high vis tag	39		0.001 (0.001–0.001)	0.018 (0.015–0.022)	

¹Strata abbreviations signify migration strategies between summer banding region (“east” or “west”) to wintering region (“east”, “west”, or “south”). For example, “EE” signifies “east-east” migration.

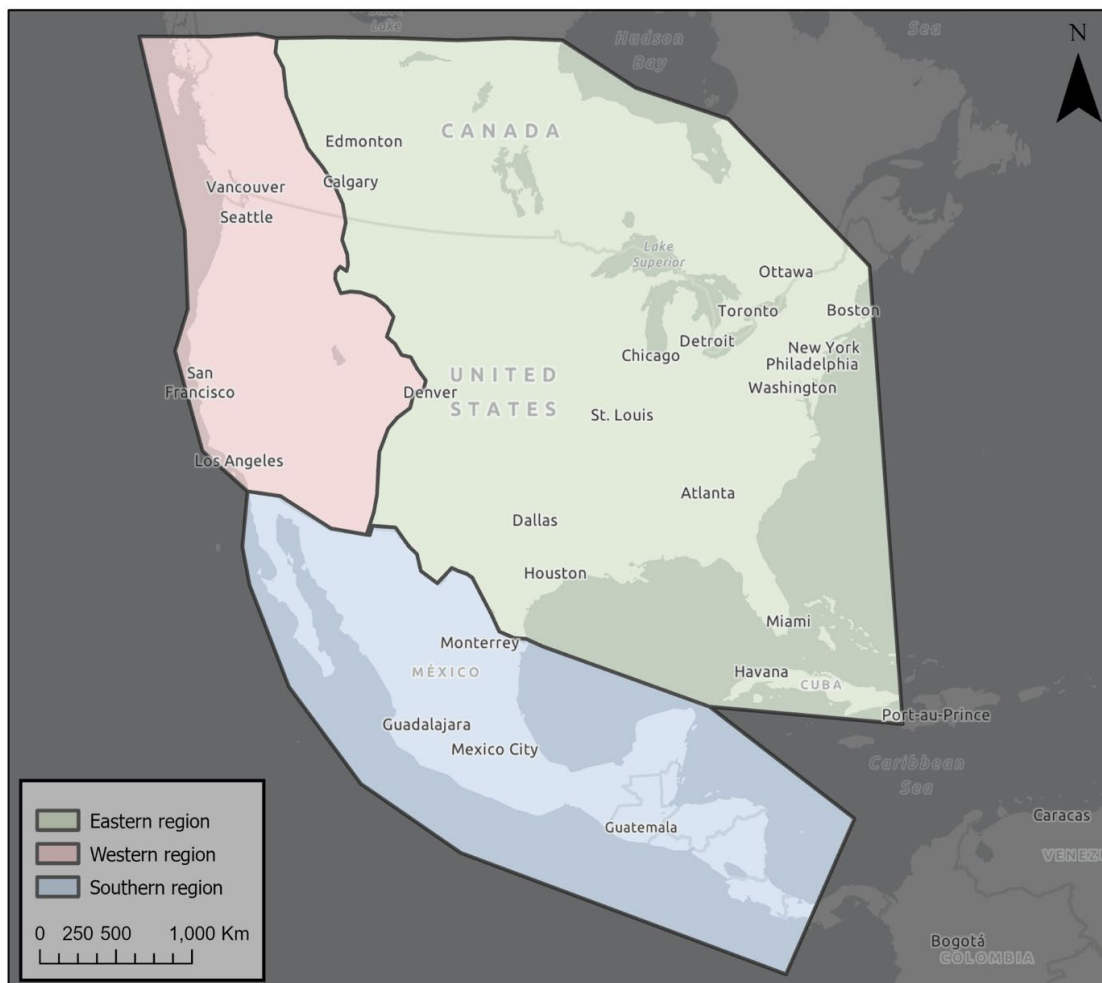


Figure 2.1: Boundaries of migratory regions encompassing all American White Pelican band returns from 1960–2022. The boundary between eastern and western regions was defined based on prior analyses of American White Pelican band returns (Anderson & Anderson, 2005; Anderson & King, 2005) and the northmost boundary of the southern region (along the US-Mexico border) represents differences in legal protections and expected observer effort between geopolitical regions.

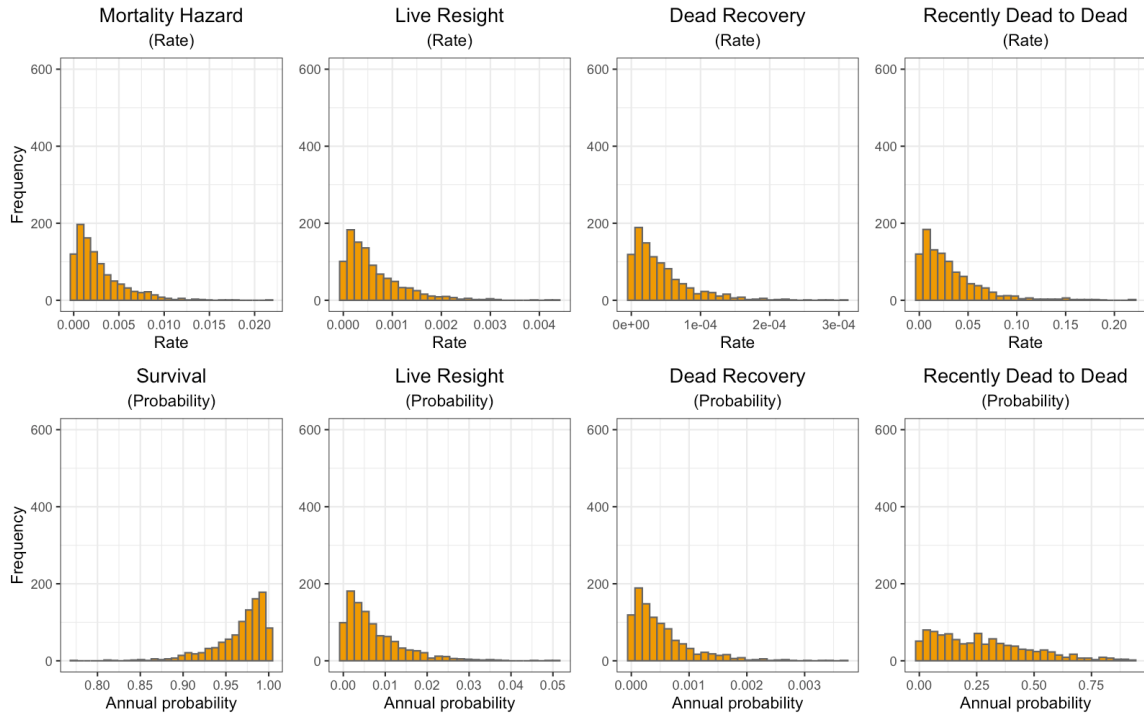


Figure 2.2: Informative gamma prior distributions for mortality hazard (h), live resight (p), and dead recovery (r) rates, generated using published annual survival, live resight, and dead recovery probability estimates (Table 2.1). No annual probability estimates were available for recently dead to dead rates (ϕ), on which I placed a weakly informative $\text{gamma}(1, 30)$ prior.

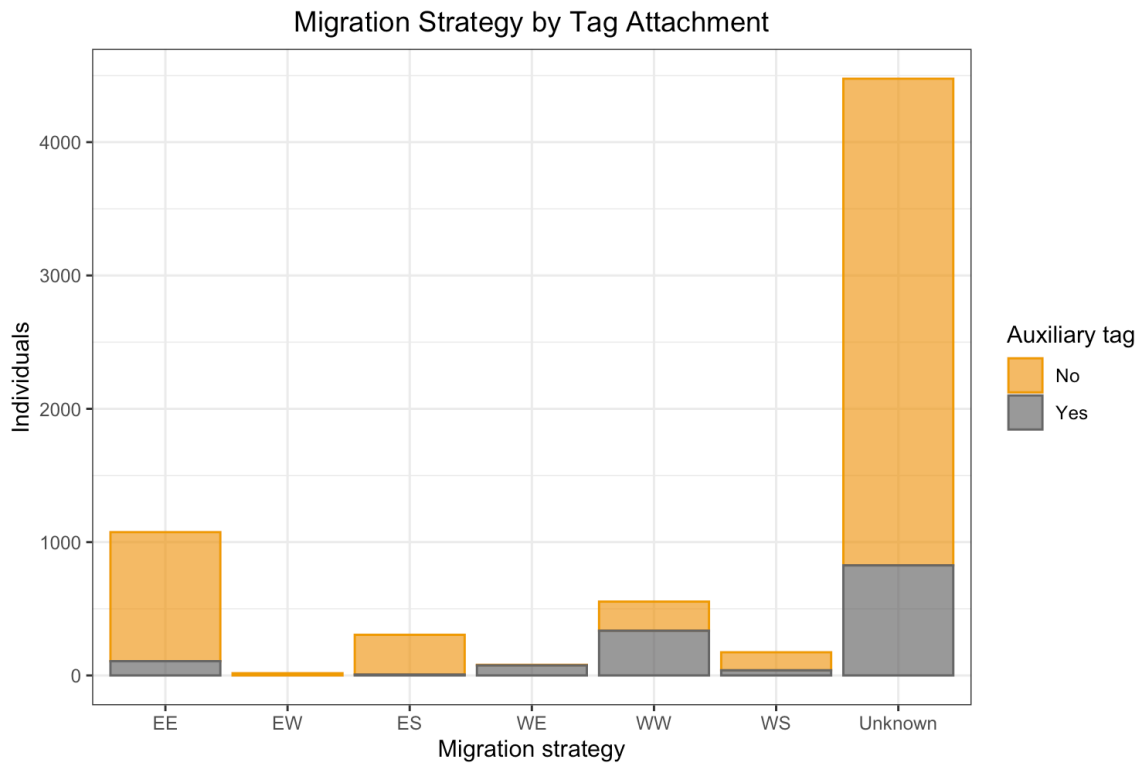


Figure 2.3: Number of reencountered pelicans by summer to winter migration strategy and whether individuals were fitted with a high-visibility auxiliary tag (e.g., wingtag or field-readable leg band) at time of banding. Migration strategy abbreviations signify strategies between summer banding region (“east” or “west”) to wintering region (“east”, “west”, or “south”). For example, “EE” signifies “east-east” migration.

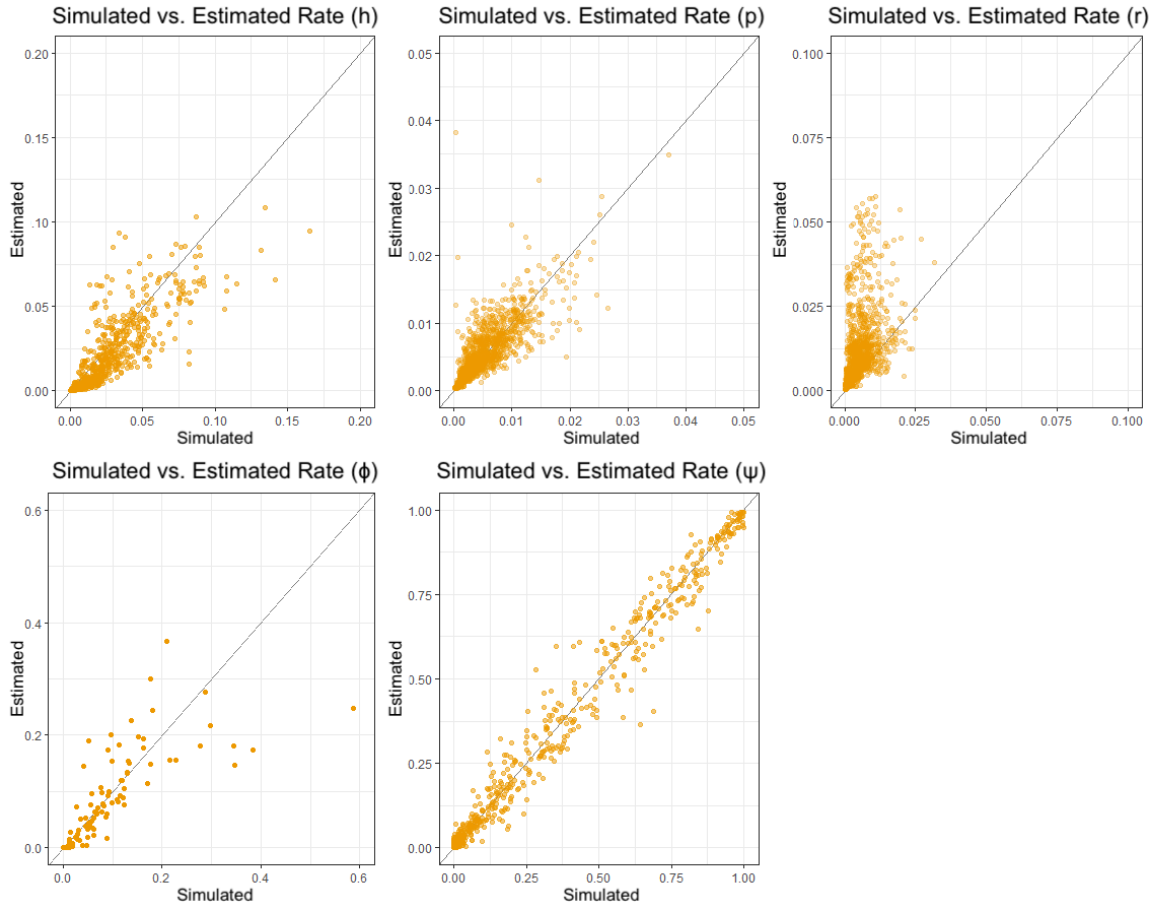


Figure 2.4: Parameter estimates from 100 simulated datasets of 1,000 banded individuals, generated using known values of mortality hazard (h), live resight (p), dead recovery (r), recently dead to dead (ϕ) rates, and regional transition probabilities (ψ). Orange points are the simulated (x-axis) versus estimated (y-axis) parameter values for each model.

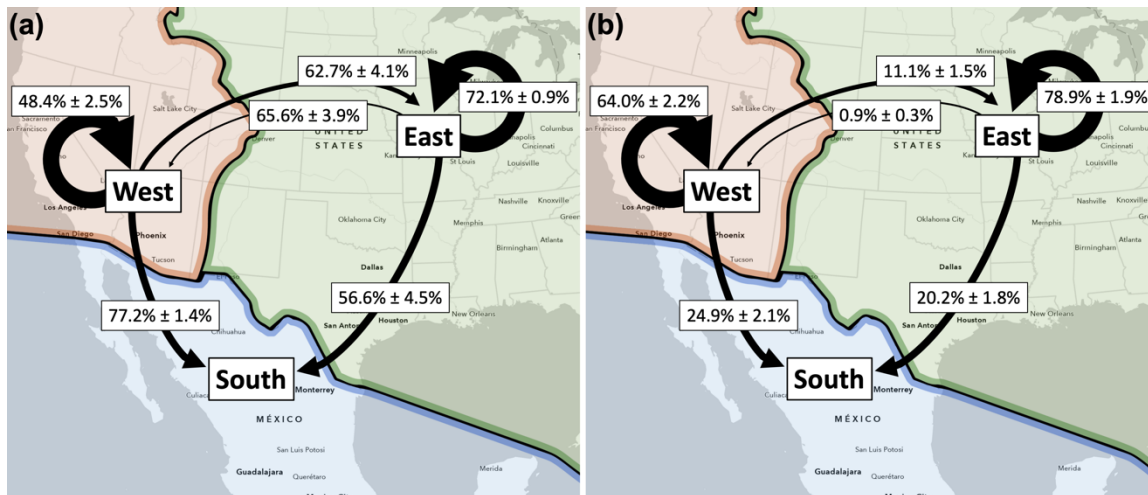


Figure 2.5: American White Pelican annual survival (a) and summer to winter migratory connectivity (b) by migration strategy. Arrows indicate direction of migration from summer (June–September) to winter (November–March) and line weight indicates strength of migratory connectivity. Colored boundaries indicate migratory regions. No individuals were banded in the southern region, and therefore migration out of this region was not possible.

CHAPTER III
MULTI-LEVEL ENVIRONMENTAL NICHE VARIABILITY OF THE AMERICAN
WHITE PELICAN

ABSTRACT

Variation in the environments used by individuals and across populations can provide insights into a species' potential response to environmental change. However, for most species, this variation in environmental (e.g., climate) conditions remains unquantified. For migratory species, measuring niche breadth (the range of environmental conditions within a niche) and variability (the degree of change in environmental conditions encompassed within a niche over time) between breeding and non-breeding seasons can reveal whether a species actively tracks its niche or displays seasonal plasticity. Migratory individuals tracking similar environments across seasons may be negatively impacted by environmental change unless they are flexible in their geographic range, whereas those that switch between environments may be more resilient. Similarly, populations with little variation in their realized niche may be negatively affected by environmental changes, while populations with greater variation in preferred conditions may be more buffered.

The American White Pelican (*Pelecanus erythrorhynchos*; hereafter, "pelican") has shifted its median breeding colony latitude northward over the past 50 years. However, the causes of this range shift and how populations might respond to future environmental change are unknown. I quantified population-level climate niche using four climate-related variables across 11 individuals and individual-level climate niche for 19 individuals within the Pacific Flyway using a multi-year GPS telemetry dataset. The

population showed moderate overlap between breeding and non-breeding range niches (Schoener's $D = 0.280$), but this overlap was not significantly greater than expected by chance, indicating that pelicans may not track climate niche and that seasonal pelican distributions might be driven by other factors.

A majority of individuals (68%) did not track climate niche between breeding and non-breeding regions, though there was high within-individual variation in niche overlap. This suggests that the population may be relatively resilient to environmental change. However, the breeding range niche breadth was more constrained than the non-breeding range niche, indicating that pelicans might not be fully utilizing available climate conditions within the breeding range, possibly due to an inability to shift range rapidly enough with to keep up with increasing temperatures. These findings underscore the importance of examining climate niche at both population and individual levels to understand potential resilience to environmental changes.

INTRODUCTION

Understanding species' adaptability to environmental change is crucial to conserving animal populations as land use and climate change transform ecosystems globally. Species inhabiting areas undergoing dramatic environmental shifts must be able to adapt to these changing environments, move to new areas that offer environmental characteristics they require, or risk extinction. Previous research has quantified species-level environmental niche breadth (i.e., the range of resources, habitats, or environments used by a species; Sexton *et al.*, 2017) as a way to measure current and expected adaptability to changing environments (Carscadden *et al.*, 2020; Castaño-Quintero *et al.*, 2024; Thorup *et al.*, 2017). Species with wide or seasonally variable environmental

niches (i.e., “generalists”) are expected to be more resilient to environmental change because altered environmental conditions are still likely to fall within their niche (Espindola *et al.*, 2019; Forsman & Wennersten, 2016). On the other hand, species with narrow, inflexible niches (i.e., “specialists”; Carscadden *et al.*, 2020) are expected to do relatively poorly in response to environmental change (Carscadden *et al.*, 2020; Kelly *et al.*, 2012). Quantifying species’ niche variability and breadth can provide important insights into which species may adapt to changing environments and those that must move with changing conditions or risk abundance, range, or demographic declines.

Past research has primarily characterized environmental niches at the species level under the assumption that individuals within a species share the same niche breadth and variability (Carscadden *et al.*, 2020). However, environmental niches may vary across subpopulations and even among individuals (Bastille-Rousseau *et al.*, 2017; Fandos *et al.*, 2020; Roughgarden, 1972), with implications for species persistence and speciation in changing environments (Carscadden *et al.*, 2020; Linhart & Grant, 1996; Plummer *et al.*, 2015). For instance, some individuals may display high levels of seasonal or inter-annual niche variation, while mean population niche breadth may remain static (e.g., white storks (*Ciconia ciconia*; Fandos *et al.*, 2020) and great black-backed gulls (*Larus marinus*; Maynard *et al.*, 2021)). As a result, niche variability may be missed when niche is evaluated at the species level only, leading to underestimates of species potential resilience to environmental change (Carlson *et al.*, 2021). Furthermore, examining niche across multiple population levels can contextualize species response to environmental change and inform species conservation at local and broad scales.

Migratory avian species may be subject to increasingly mismatched phenology and resource availability as climate change impacts different latitudes in diverging ways (Diez *et al.*, 2012; Mayor *et al.*, 2017; Rafferty *et al.*, 2020). As a whole, migratory avian species are faring particularly poorly, with estimated population declines across North America of 28.3% ($\pm 1.6\%$) since 1970 (Rosenberg *et al.*, 2019), and the Afro-Palaeartic of 26.7% ($\pm 5.2\%$) since 1980 (Vickery *et al.*, 2023). Migratory species are often assumed to track a specific set of environmental conditions across seasons (“niche tracking”; Gómez *et al.*, 2016; Plummer *et al.*, 2015; Tingley *et al.*, 2009; Zurell *et al.*, 2018). However, previous studies have shown that some migratory species may be predisposed to deal with environmental differences experienced in their seasonal niche, either through their wide niche breadth (e.g., Gómez *et al.*, 2016; Laube *et al.*, 2015) or niche variability between or within individuals (e.g., Martínez–Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Ponti *et al.*, 2020). Even so, niche quantification remains largely unexplored for most migratory avian species, limiting our understanding of expected species-specific reactions to environmental change or distributional shifts (Espindola *et al.*, 2019).

Historically, year-round individual-level location data were limited for most avian species due to weight limits on tracking devices and poor understanding of non-breeding ground space use (Kramer *et al.*, 2018; Webster *et al.*, 2002). Recent advances in tracking technology have provided large, high-resolution location datasets for large-bodied avian species for both breeding and non-breeding grounds. Combined with a wealth of remote sensing data and high-resolution climate projections, it is now possible to quantify niche breadth and variability at both the population- and individual-level, and to forecast

species distributions into the future (Espindola *et al.*, 2019; Fandos *et al.*, 2020; King *et al.*, 2022; Rodríguez-Rodríguez *et al.*, 2020). However, few studies have focused on potential avian response to environmental change across multiple populations, despite the increasing feasibility and utility of quantifying niche breadth and variability for local to broadscale species conservation decision support (Bolnick *et al.*, 2003).

In this study, I aimed to quantify individual- and population-level niche variability between seasonal ranges and metapopulations of American White Pelicans (*Pelecanus erythrorhynchos*; hereafter “pelican”), a large-bodied migratory waterbird. Pelicans have shifted median breeding colony latitude northward over the past 50 years (Moulton *et al.*, 2018), but whether this shift is in response to environmental conditions and how this population might respond to future environmental change is poorly understood. I used three years of pelican GPS data collected from individuals within the Pacific Flyway to examine whether pelicans tracked climate niche between the breeding and non-breeding seasons at either the individual or population levels. I used individual-level data to estimate realized climate niche breadth and variability of niche use between individuals. I also pooled individual GPS data across all study years to estimate population-level niche breadth, thereby estimating upper and lower bounds of climate conditions inhabited by this species. Additionally, some individuals were tracked across multiple years, allowing me to quantify intra-individual climate niche variation between years, to better understand niche variability and potential resilience to regional environmental change.

I hypothesized that pelicans within this study population would exhibit niche-tracking behaviors at the population level. Pelicans are reliant on shallow open-water foraging sites, whose availability and quality may be influenced by spatial or temporal

variations in temperature and precipitation (Dodds *et al.*, 2019; Donnelly *et al.*, 2020). As a population, shared needs for similar sites may result in broadscale climate niche tracking. Conversely, I expected pelicans would exhibit inter- and intra-individual variation in niche overlap and tracking behavior. GPS tracking data from pelicans within the Pacific Flyway shows large variation in home range sizes between individuals (Utah Division of Wildlife Resources [UDWR], unpublished data), potentially driven by preference for fine-scale environmental conditions (Fandos *et al.*, 2020) or habitat preferences and food availability (Ramos *et al.*, 2015).

METHODS

Study area and species data

American White Pelicans are a migratory North American waterbird species. Pelicans breed colonially across the Intermountain West and Prairie Pothole regions and winter across the southern United States, Mexico, and Central America. Prior band recovery analyses suggest that pelicans have display low dispersal across the Continental Divide (Anderson & Anderson, 2005). Populations on opposite sides of the Continental Divide likely encounter differing environmental conditions (Anderson & King, 2005; Moulton *et al.*, 2018) and food availability (King, 2005; King *et al.*, 2010), and have therefore been classified into two metapopulations (“eastern” and “western”; Anderson & King, 2005). In a prior analysis, Illán *et al.* (2022) examined environmental niche breadth and tracking behavior for GPS tagged pelicans within the eastern metapopulation. Consequently, I focused my analysis on the breeding and non-breeding regions of the western metapopulation (Figure 3.1) to quantify environmental niche use and tracking

behavior within this unexplored population, allowing for generalized comparisons between the two metapopulations.

I used GPS locations from 19 after-hatch-year pelicans captured and tagged by the UDWR in wetlands around the eastern periphery of Great Salt Lake, Utah. Historically, Great Salt Lake contained one of the largest breeding colonies of pelicans west of the Rocky Mountains, and serves as an important migration staging and stopover site for pelicans within the western metapopulation (Kijowski *et al.*, 2020). Individuals were captured between May and September 2016 to 2018 and fitted with GSM or ARGOS solar-powered GPS transmitters (Microwave Telemetry GPS/GSM 20-70), using custom-fit Teflon ribbon backpack harnesses (Dunstan, 1972). The GPS transmitters collected latitude, longitude, and elevation above sea level for all individuals at approximately one-hour intervals. All captures and transmitter attachments were conducted under IACUC protocol #2209, and U.S. Geological Survey Bird Banding Laboratory permit #21673.

Following methods detailed by Illán *et al.* (2022), I delineated "breeding" and "non-breeding" regions of the western pelican metapopulation for use in quantifying differences in seasonal niche breadth (see Figure 3.1). Pelicans typically migrate twice annually between northern breeding areas and southern non-breeding areas, often regardless of individual breeding status. However, migratory phenology varies substantially by individual, likely dependent upon age, sex, body condition, and environmental factors (Illán *et al.*, 2022; King *et al.*, 2022). Thus, assigning these as "summering" and "wintering" regions (common for many migratory species) may not be accurate. Furthermore, pelicans may exhibit long distance exploratory behavior between colonies and foraging locations in both breeding and non-breeding regions (UDWR,

unpublished data), making the transition from migration to seasonal residence unclear for this species. I defined the breeding region as the area encompassing all known locations of current breeding colonies within the Intermountain West and possible movements between them (Moulton *et al.*, 2018). For the non-breeding region, I defined the northern boundary as the southernmost latitude where pelicans display migratory behavior between breeding and non-breeding ranges. I used average net squared displacement calculated from GPS locations of pelicans tagged in the western metapopulation to define this boundary (Soriano-Redondo *et al.*, 2020). Net squared displacement calculates the squared distance between an individual's initial location and all subsequent locations. For migratory individuals, net squared displacement estimates typically follow a double-logistic curve, increasing as the individual migrates from the non-breeding range to the breeding range, leveling at a maximum distance on the breeding range, then falling to zero or near-zero as an individual returns to their prior non-breeding location. Seasonal residence and migratory behavior are then differentiated based on percent of total movement an individual makes between breeding and non-breeding regions (R package *migrateR*, version 1.0.9; Spitz, 2019; Spitz *et al.*, 2017). I defined the remainder of the non-breeding region based on a combination of prior metapopulation delineations (Anderson & King, 2005) and observed locations of GPS tagged pelicans.

I subset available pelican GPS data to individuals that remained within western metapopulation bounds during 2016–2018, thereby restricting the analysis to the climate niche space of the western metapopulation. I also only included individuals that had GPS locations available within both the breeding and non-breeding regions and that exhibited clear seasonal migration activity between regions (i.e., did not remain as a resident on the

breeding or non-breeding grounds across multiple seasons). Finally, to avoid oversampling environmental space for individuals or periods with GPS sampling intervals greater than once per hour, I thinned the GPS dataset to include one GPS location per hour, if available, for each individual per day.

Nineteen individuals were included in the individual-level analysis. Some individuals had GPS data spanning multiple calendar years, and I therefore classified GPS locations into migratory “bouts”, consisting of one season of breeding region locations and one season of non-breeding ground locations. Each bout began at the date of capture (or first arrival in the breeding region, if an individual had multiple seasons of data), and ended when an individual stopped transmitting or left the non-breeding region the next year. This ensured that individual analyses only contained GPS data from a single migration between the breeding region and non-breeding region, and allowed for comparisons of discrete migration events within individuals with multiple years’ worth of data. I also only included individuals with ≥ 150 GPS locations per migratory bout within each region, after temporal thinning, ensuring that each individual included was well over the minimum suggested presence points for the individual-level niche analysis (Guisan *et al.*, 2017; Zurell *et al.*, 2018).

For the population-level analysis, I pooled GPS data from the 11 individuals with greater than 1,000 locations available in both the breeding and non-breeding regions across the study period. I randomly subset each individual’s total locations to be equal to the individual with the fewest number of locations available by region ($n = 1,049$ points per individual) to avoid overfitting the model to individuals with more data.

Climate data

I used “Climatologies at High resolution for Earth’s Land Surface Areas” (CHELSA; Karger *et al.*, 2017, 2018) climate data available from the Swiss Federal Research Institute for Forest, Snow, and Landscape Research (<https://chelsa-climate.org/>). The CHELSA database contains high-resolution (30 arc second, or approximately 1 km resolution) climate data rasters with global coverage beginning in 1979. I used all monthly climate data variables available from the CHELSA 2.1 database (total monthly precipitation (mm), and mean, minimum, and maximum temperature (°C), by month) from January 2016 to December 2018, which aligned with coverage of the pelican GPS dataset. Accumulated precipitation has been associated with local lake levels, wetland foraging habitat and water availability, and species richness of wetland organisms including pelican prey species, both spatially and temporally (Dodds *et al.*, 2019; Donnelly *et al.*, 2020). Temperature may also influence water availability at important foraging sites through evapotranspiration (Donnelly *et al.*, 2020). Temperature extremes may impact pelicans directly by surpassing physiological heat and cold tolerances (Bartholomew *et al.*, 1953; Sovada *et al.*, 2014), while low temperatures may result in the ice over of open water sources that pelicans require for foraging (Illán *et al.*, 2022). These variables were also those used in the analysis conducted by Illán *et al.* (2022) on the eastern metapopulation. I filtered available rasters to only those containing pelican GPS locations, then cropped each raster to the breeding and non-breeding region.

Niche analysis

I extracted CHELSA climate raster cell values at the location and month of each pelican GPS location to represent environmental niche space used by pelicans on the

breeding and non-breeding grounds. To represent environmental niche space available to pelicans for use in the population analysis, I extracted all CHELSA climate raster cell values across the entirety of the breeding and non-breeding regions for each month that at least one pelican was present in that region. For individual analyses, I subset available environmental niche space to only include months where an individual was present in a given region. I then conducted a principal component analysis (PCA) of region-wide values from my four climate covariates to capture variation in available environmental niche space across the study area, using the *dudi.pca* function from R package *ade4* (version 1.7-22; Dray & Dufour, 2007; Thioulouse *et al.*, 2018). I retained the first and second principal components (PCs), then related environmental covariates at global, region-specific, and pelican location scales to each PC coordinate for use in describing used, available, and total environmental niche space.

I used R package *ecospat* (version 3.5.1; Broennimann *et al.*, 2023) to quantify population- and individual-level pelican climate niche. *Ecospat* first estimates species or individual occurrence densities spatially by mapping occurrences onto gridded environmental space during a season of interest. *Ecospat* then uses kernel smoothing methods to calculate occurrence densities for each grid cell within each study region. Environmental PCA values are also smoothed and rescaled for each grid cell. Finally, occurrence densities at each grid cell are divided by smoothed and scaled environmental values, which allows for direct comparisons of environmental niche across seasons, regions, and individuals, regardless of geographic extent (Broennimann *et al.*, 2012). Following Illán *et al.* (2022), I used a grid cell size of 100 km x 100 km (i.e., 100:1 ratio relative to the raster cell size of my environmental covariates).

Ecospat corrects for use of rare environments by assigning uncommon environmental values greater weights than more commonly observed values (Broennimann *et al.*, 2012), under the assumption that species use these areas less simply because they are rare. However, both the breeding (Intermountain West) and non-breeding regions (western Mexico) are characterized by highly variable environments and climatic extremes (Frankson *et al.*, 2022; Wise, 2012). Large grid cell sizes, like the 100 x 100km cells used in this analysis, may not always accurately represent environments used by pelicans, despite these environments' close proximity to pelican occurrences. Therefore, I thinned the environment considered during spatial gridding to exclude outlier environmental values outside of the 25th percentile (Guisan *et al.*, 2017), thus ensuring that highly rare environments (i.e., uncommon environmental values) were not over-represented within the analysis.

Based on occurrence densities and corresponding environmental characteristics, I quantified observed population-level niche overlap and individual-level overlap between regions using the Schoener's D overlap metric (Schoener, 1970). Schoener's D values of 0 indicate no niche overlap and 1 indicates complete niche overlap between breeding and non-breeding regions, corrected for occurrence density (Broennimann *et al.*, 2012). For context, similar studies have found Schoener's D of 0 to 0.75 between migratory regions (Fandos *et al.*, 2020; Illán *et al.*, 2022). I also calculated niche expansion (proportion of the breeding region niche that does not overlap with the non-breeding region niche), stability (proportion of the breeding and non-breeding region niches that overlap), and unfilling (proportion of the non-breeding region niche that does not overlap with the breeding region niche; Guisan *et al.*, 2014), where 0 indicates no overlap and 1 indicates

complete overlap. I calculated expansion, stability, and unfilling at both the population and individual levels.

To determine whether observed between-season niche overlap could be attributed to niche tracking, I conducted a niche similarity test (Broennimann *et al.*, 2012; Di Cola *et al.*, 2017; Warren *et al.*, 2008). The niche similarity test evaluates whether information on one seasonal niche (e.g., breeding) provides information on the niche of another season (e.g., non-breeding) beyond what can be expected from a null model. In this case, our null model is one where the four climate variables investigated here have no influence on pelican occupancy. To simulate "random" niches that were not determined by my climate variables, I randomly distributed pelican occurrence points across the breeding and non-breeding ranges and extracted their climate covariate variables.

Based on a simulation of 1,000 random niches, I calculated Schoener's D between each random niche and observed niches of the opposing season. If pelicans track their climate niche, then the Schoener's D value should be significantly higher than random, simulated Schoener's Ds (i.e., in the upper 5% of random, simulated Schoener's Ds; Warren *et al.*, 2008). Conversely, if seasonal distributions are caused by factors other than climate niche tracking, then the observed Schoener's D will not be significantly different from those generated by simulating pelican occurrence densities randomly, with no relationship with climate. To quantify how observed individual- and population-level niche dynamics compared to random niches, I compared expansion, stability, and unfilling metrics for each simulated versus observed niche following the methods described above. I also conducted the niche similarity test directly on randomly sampled versus observed environmental variables across the study period, to obtain estimates of

niche D, expansion, stability, and unfilling across single environmental predictors: total monthly precipitation, and minimum, mean, and maximum monthly temperature. All analyses were performed in R (version 4.3.1; R Core Team, 2023).

RESULTS

Net squared displacement

The net squared displacement analysis identified 34.8°N as the northernmost edge of the non-breeding region. GPS locations occurring north of this latitude and south of the defined breeding region were considered to be outside of the breeding and non-breeding ranges (i.e., migration range), and therefore were not considered in the analysis.

Population-level analysis

My population-level analysis was based on a total of 23,078 GPS locations from 11 individuals (breeding region = 11,539; non-breeding region = 11,539; Table 3.1). The first two components from the climate niche PCA explained 98.93% of total environmental variation, with PC1 and PC2 accounting for 75.28% and 23.65% of environmental variation, respectively. PC1 primarily described variation in temperature, while PC2 described precipitation (Table 3.2).

Observed Schoener's D between the breeding and non-breeding grounds combining all years was moderately low ($D = 0.280$). The niche similarity test indicated population-level niche overlap was not significantly higher than that of random available niche space (D mean (\pm sd) random = $0.120 (\pm 0.108)$, p -value = 0.092), suggesting no statistically significant population-level niche tracking behavior (Figure 3.2, Figure 3.3). Therefore, we cannot reject the null hypothesis that seasonal pelican distributions are

driven by factors other than tracking climate niche. I found that observed niche expansion and stability were significantly different (Figure 3.3) from random simulations from the background environment (expansion observed = 0.040, random expansion (\pm sd) = 0.585 (\pm 0.301), p-value = 0.001; stability observed = 0.960, random stability (\pm sd) = 0.415 (\pm 0.301), p-value = 0.001), while unfilling was not (Figure 3.3; observed = 0.219, random unfilling (\pm sd) = 0.715 (\pm 0.317), p-value = 0.134).

In addition to estimating niche variability with PCs, I also conducted the niche similarity test with each single environmental predictor to determine whether specific dimensions of the climate niche are tracked across seasons. Results suggested that pelicans did not track any one environmental variable alone (Table 3.3), but that expansion was significantly lower and stability was significantly higher than expected for minimum and maximum temperature compared to random simulations (p-values = 0.014 and 0.009 respectively). However, I found no evidence that Schoener's D or unfilling for minimum or maximum temperature were more different than expected (minimum temperature p-values: D = 0.119, unfilling = 0.101; maximum temperature p-values: D = 0.131, unfilling = 0.105).

Individual-level analysis

I estimated annual breeding and non-breeding range niche overlap with 74,204 GPS points from 19 individuals, for a total of 23 migratory bouts. Over all individuals, the climate niche PCA produced similar results to that of the population-level analysis (Table 3.2), with PC1 describing, on average (\pm sd), 75.42% (\pm 3.22%) of environmental variation, and PC2 describing an average of 22.27% (\pm 3.18%). PC1 represented temperature more so than precipitation, while PC2 reflected precipitation. Mean

Schoener's D between breeding and non-breeding regions across all individuals was low (mean = 0.201 ± 0.182), while mean niche expansion (0.441 ± 0.348), stability (0.559 ± 0.348), and unfilling (0.572 ± 0.301) were moderate, but with considerable inter-individual variation. The niche similarity test suggested that overall, Schoener's D was not significantly different from the random environment for a majority of individuals. However, six (32%) individuals displayed significantly greater climate niche tracking behavior than expected by chance (p-values < 0.05; Figure 3.2).

Interannual niche comparisons

Two individuals were tracked across two migratory bouts and one individual across three. The two individuals that were followed for two migratory bouts ("Hector" and "Loretta") displayed niche tracking behavior for both and for one of two migratory bouts, respectively. The remaining individual did not track environmental niche between breeding and non-breeding regions for any migratory bout (Table 3.4). Environmental conditions (PCs) varied significantly between years at each individual's used locations (all Wilcoxon rank sum test p-values < 0.001).

DISCUSSION

Using data from a multi-year American White Pelican tracking study, I show that pelicans in this study population do not appear to track the environmental niche between breeding and non-breeding seasons when the niche is quantified at the population level, but that the presence and degree of niche tracking behavior varies by individual. This study adds to a growing body of literature demonstrating that migratory species may display differing degrees of niche variability depending on the biological level examined,

and that care should be taken when drawing conclusions about niche variability and its implications for species-level response to rapid broadscale climate change when assessed at a single biological level. My findings of low niche expansion and high stability from the non-breeding to breeding region in relation to temperature suggest that temperature plays an important role in pelican niche breadth within the Pacific Flyway. This is in contrast to precipitation, despite this species' reliance on water for foraging and breeding activities. My findings complement and contrast previous work conducted on the eastern pelican metapopulation (Illán *et al.*, 2022), which, unlike the western population, found pelicans migrating between the Prairie Pothole Region and the Gulf of Mexico track temperature niche at the population level, but show similar niche tracking and switching behavior at the individual level as I found here.

Contrary to my population-level hypothesis, I did not find evidence that migratory pelicans track their climate niche between their breeding and non-breeding ranges. Population-level environmental niche tracking behavior in migratory species has been found in numerous studies (e.g., Fandos *et al.*, 2020; Nakazawa *et al.*, 2004; Tingley *et al.*, 2009), and has been used as an underlying explanation for population dynamics in response to shifting climate. However, the lack of niche tracking behavior at the population level does not necessarily imply that pelicans are switching niches between seasons. I found that niche expansion was significantly lower than expected, while niche stability was significantly higher than expected, based on the total environment available to pelicans. Conversely, niche unfilling was not significantly different from the available environment. Taken together, this suggests pelicans are not niche switching between breeding and non-breeding grounds, but instead are only occupying a portion of the niche

space available to them on the breeding grounds as compared to the non-breeding ground niche they occupy. True species expansions into new niche space appear to be relatively uncommon, and apparent niche shifts may instead be the result of niche unfilling (Strubbe *et al.*, 2013). Unfilling of migratory species' niches may be indicative of barriers to population dispersal or lags in colonization (Guisan *et al.*, 2014), suggesting that variables beyond those explored here may be limiting habitats available to pelicans within the Pacific Flyway.

When assessing each environmental variable separately, I found that population-level niche expansion from the non-breeding to breeding region was significantly lower and stability was significantly higher than expected in relation to minimum and maximum temperature. This observed niche unfilling of the non-breeding niche in the breeding region indicates that in the breeding region, pelicans do not use the full range of favorable temperatures available. Given that pelicans are reliant on water resources, the arid landscape in the Intermountain West may restrict pelican breeding and foraging to specific locales and therefore specific temperatures occurring at these sites (Anderson, 1991; Anderson & King, 2005; Moulton *et al.*, 2018; Figure 3.4). Additionally, I found that for all three temperature covariates, the population occupied on average cooler temperature niches on the breeding grounds as compared to the non-breeding grounds, but occupancy on the breeding grounds tended toward the warmest available temperatures in this region (Figure 3.4). Temperatures are increasing across the Intermountain West as climate change impacts increase (Joyce & Talbert, 2018) including at pelican nesting and foraging sites. Median breeding colony latitude for the western metapopulation has shifted northward by 114 km between 1960 and 2010

(Moulton *et al.*, 2018), and may indicate that pelicans are shifting their range northward to track suitable environmental conditions (i.e., temperature). However, tendency toward occupying the hottest available temperatures suggests that this population may not be able to colonize new areas fast enough to keep pace with rapid poleward temperature shifts (Román-Palacios & Wiens, 2020), resulting in reduced temperature niche breadth and mismatches between observed niche centroids and available temperatures on the breeding grounds. Thus, pelican populations at the southern edge of the western metapopulation's range (e.g., Great Salt Lake and Pyramid Lake breeding populations) may be disproportionately impacted by projected near-future increases in regional temperature (Hall *et al.*, 2021; Joyce & Talbert, 2018) as compared to more northerly populations, and may benefit from regular monitoring to detect decreases in colony health or abundance.

I found notable variation in individual-level niche tracking behavior at comparable—albeit slightly lower—levels to the eastern pelican metapopulation, with 32% (6 of 19) of individuals displaying niche tracking behavior during at least one migratory bout. Similarly, the eastern metapopulation analysis found 46% (6 of 13) of tracked individuals displayed niche tracking behavior. I also found limited evidence of intra-individual variability in degree of total niche overlap (Schoener's *D*), with one of three individuals tracked across multiple years changing niche tracking behaviors between migratory bouts. Individual-level variation has been suggested as a crucial factor underlying population-level adaptability to climate change, where the degree of individual-level variation is more indicative of species resilience to shifting environmental conditions than is the population-level niche breadth of a species (Etterson

& Shaw, 2001; Forsman & Wennersten, 2016). Additionally, populations with high individual niche variability may be less prone to extinction and show less variability in abundance, suggesting population resilience to change (Forsman & Wennersten, 2016).

Overall, the western metapopulation may fare relatively well in the face of climate change, either through individual variation in response to changing climate conditions or dispersal northward, but more detailed analyses may clarify species relationships with climate and other environmental conditions. This analysis examined niche using broadscale, remote-sensed temperature and precipitation data, but could benefit from additional variables relevant to pelicans, including water depth and prey abundance, when available, as these variables may more directly influence seasonal pelican distributions. Time-lagged effects of precipitation via snowmelt and water table recharge may impact conditions relevant to pelican use, including lake and wetland water levels (Wurtsbaugh, 2014), and inclusion of this information may benefit future analyses as well. Additionally, for species with a high degree of individual variation, like pelicans, drawing conclusions about niche breadth and variability from a handful of individuals may not accurately represent population-level niche. Leveraging tracking data from greater numbers of individuals will likely improve our understanding of population-level niche breadth and variability for pelicans and similarly variable species. Finally, accounting for habitat availability, biotic interactions, and diverging effects of climate change, which were not examined in this analysis, may provide greater detail about expected species' response to future climate impacts.

As species experience intensifying effects of climate change globally, clearer understandings of niche and expected resilience to environmental change are needed.

Conclusions from this analysis demonstrate the importance of quantifying niche at both population and individual scale when possible, and studies investigating niche variability and overlap between migratory regions should aim to quantify expansion, stability, and unfilling, in addition to Schoener's D. Estimating niche variability solely from a single species at the population scale may provide incomplete conclusions to expected species responses to changing environments, as resilience to broadscale climate change is likely dependent upon individual niche variability as well as niche breadth at metapopulation and species levels (Fandos *et al.*, 2020). For example, when examining Schoener's D only, we might conclude that the western pelican metapopulation is highly resilient to broadscale environmental change due to high individual-level variation in niche and no significant niche tracking behavior at the population level. However, additional information provided by examining niche expansion, stability, and unfilling indicates that southernmost pelican populations across the Intermountain West may be limited in their ability to escape or adapt to unfavorable environmental conditions as climate and land use changes intensify (Null & Wurtsbaugh, 2020; Williams *et al.*, 2022; Zhang *et al.*, 2021). Thus, leveraging multiple measures of niche across many biological scales may provide clearer understandings of species niche, and create accurate species distribution models, predict population dynamics, and create targeted conservation initiatives in the face of global losses in biodiversity.

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TABLES AND FIGURES

Table 3.1: Individual summaries of breeding and non-breeding region GPS location data, before thinning, by migratory bout. Each migratory bout consists of a single breeding region to non-breeding region transition, beginning at the date of capture (or first arrival in the breeding region, if an individual had multiple seasons of data), and ended when an individual stopped transmitting or left the non-breeding region the next year. Bolded individuals are those used for the population-level analysis.

ID	Capture Year	Sex	Migratory Bout	Breeding Region Locations	Non-breeding Region Locations
Abigail	2016	F	2016	1222	3250
Albus	2017	M	2017	1666	1288
Bridgette	2017	F	2017	1511	550
Cici	2017	F	2017	1506	2127
Deidra	2017	F	2017	1585	274
Eloise	2016	M	2017	1283	676
Everett	2016	M	2016	782	2420
Fiona	2017	F	2017	1469	1451
Fudd	2017	M	2017	1871	2463
Hector	2016	M	2016	1827	2627
Hector	2016	M	2017	2278	215
Jonah	2017	M	2017	1467	1049
Loretta	2016	F	2016	567	3696
Loretta	2016	F	2017	2707	2424
Miguel	2017	M	2017	2187	1171
Rachelle	2017	F	2017	636	1707
Rosalie	2016	F	2016	300	3192
Sylvester	2016	M	2016	1110	2781
Uma	2016	F	2016	926	2993
Uma	2016	F	2017	185	1085
Uma	2016	F	2018	1148	1115
Valerie	2017	F	2017	805	3584
Zeus	2017	M	2017	2255	603

Table 3.2: Variable loading factors from population- and individual-level principal component analyses. PC1 refers to the principal component (PC) that describes the largest amount of variation within the environmental dataset across pelican breeding and non-breeding ranges, and PC2 refers to the PC describing the second largest amount of variation. Individual-level analysis represents mean (standard deviation) PC loading across all individuals.

Component	Variable	Loading factor (population-level analysis)	Loading factor (individual-level analysis)
PC1	Total monthly precipitation	0.303	0.325 (0.237)
	Minimum monthly temperature	-0.975	-0.792 (0.556)
	Mean monthly temperature	-0.994	-0.817 (0.573)
	Maximum monthly temperature	-0.990	-0.807 (0.562)
PC2	Total monthly precipitation	0.953	0.913 (0.082)
	Minimum monthly temperature	0.168	0.182 (0.047)
	Mean monthly temperature	0.097	0.105 (0.062)
	Maximum monthly temperature	0.029	0.007 (0.080)

Table 3.3: Observed and estimated population-level niche overlap (Schoener's D), expansion, stability, and unfilling by environmental predictor. P-values indicate whether observed niche metrics differed significantly from estimates produced by comparing randomized breeding and non-breeding region niches generated from available background environments across the study area. Bolded text denotes statistically significant findings.

Predictor	Metric	Observed Niche	Simulated Niche (mean)	Simulated Niche (standard deviation)	P-value
Total monthly precipitation	Schoener's D	0.388	0.384	0.182	0.645
	Expansion	0.150	0.355	0.345	0.627
	Stability	0.850	0.645	0.345	0.627
	Unfilling	0.000	0.305	0.401	0.626
Minimum monthly temperature	Schoener's D	0.442	0.120	0.179	0.119
	Expansion	0.192	0.768	0.286	0.014
	Stability	0.808	0.232	0.286	0.014
	Unfilling	0.448	0.857	0.243	0.101
Mean monthly temperature	Schoener's D	0.383	0.171	0.215	0.215
	Expansion	0.220	0.685	0.325	0.071
	Stability	0.780	0.315	0.325	0.071
	Unfilling	0.426	0.744	0.331	0.213
Maximum monthly temperature	Schoener's D	0.367	0.105	0.171	0.131
	Expansion	0.147	0.761	0.282	0.009
	Stability	0.853	0.239	0.282	0.009
	Unfilling	0.343	0.834	0.297	0.105

Table 3.4: Observed and estimated niche overlap (Schoener's D) for individual pelicans tracked across multiple migratory bouts. P-values indicate whether observed niche overlap differed significantly from estimates produced by comparing overlaps between randomized breeding and non-breeding region niches generated from available background environments across the study area. Bolded text denotes significant findings.

ID	Migratory Bout	Observed Schoener's D	Mean simulated Schoener's D	P-value
Hector	2016	0.577	0.144	0.025
	2017	0.213	0.066	0.020
Loretta	2016	0.013	0.007	0.186
	2017	0.423	0.149	0.036
Uma	2016	0.131	0.066	0.196
	2017	0.019	0.005	0.103
	2018	0.097	0.131	0.482

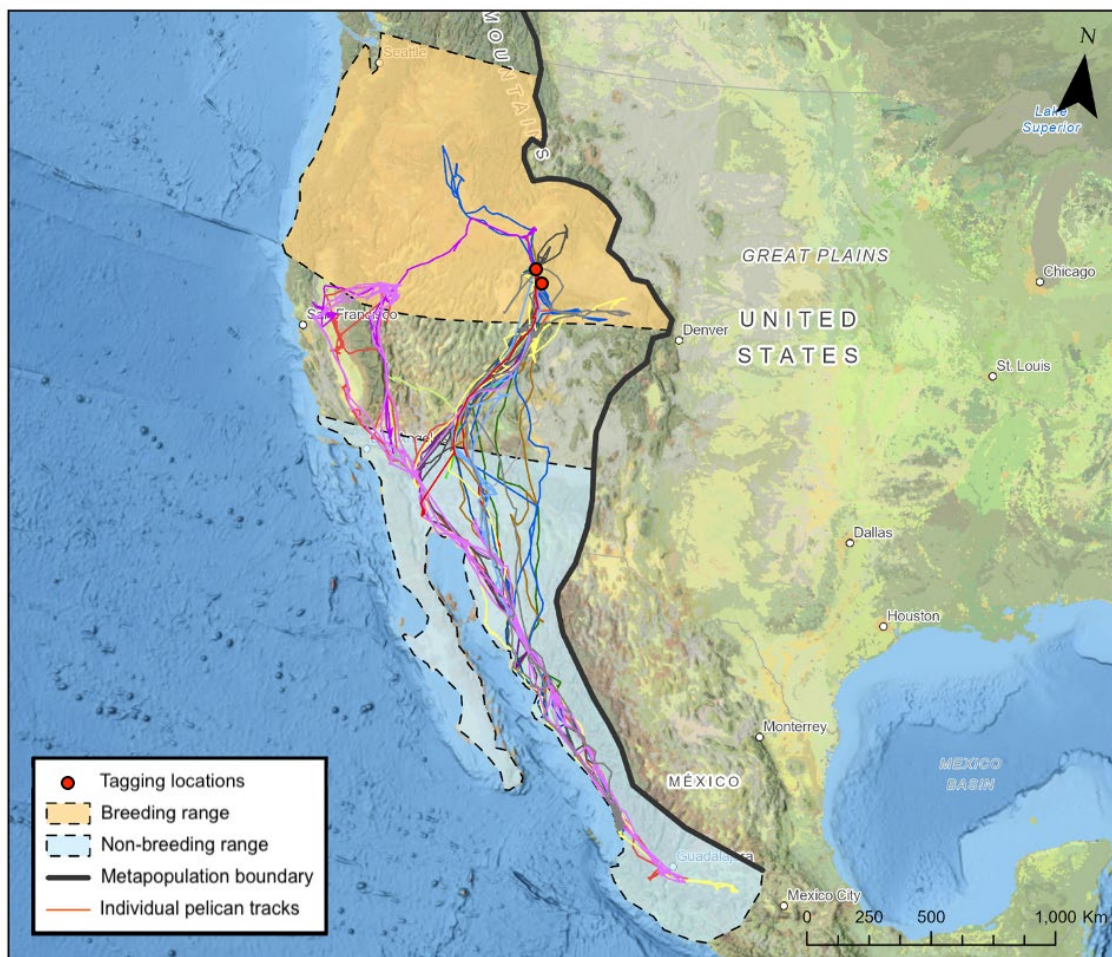


Figure 3.1: Western American White Pelican metapopulation breeding and non-breeding region boundaries. Red points indicate locations pelicans were captured and tagged with GPS transmitters (north: Great Salt Lake, Utah; south: Strawberry Reservoir, Utah). The heavy black line delineates the boundary of the western metapopulation considered in this analysis, while thin colored lines indicate individual pelican GPS tracks between 2016–2018.

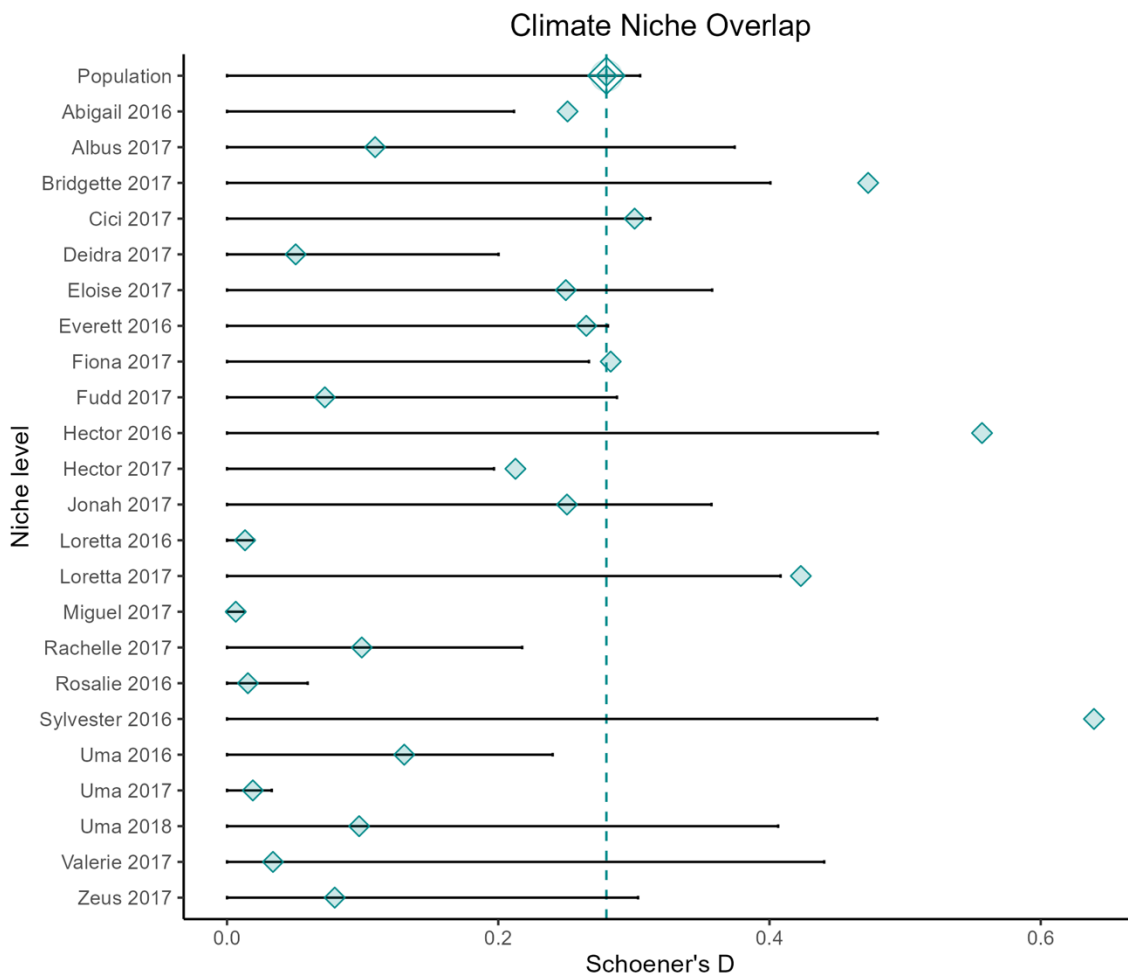


Figure 3.2: Niche overlap estimates (Schoener's D) between breeding and non-breeding regions. Estimates were based on environmental conditions at known used locations (blue diamonds) and 1,000 simulations where pelican "occurrences" were randomly generated without any relationship with climate variables (90% quantiles; black bars). Diamonds that do not overlap 90% quantiles indicate that observed ("used") niche overlap between breeding and non-breeding regions was greater than expected by chance if pelican occurrence was not influenced by climate variables, and can be considered seasonal "niche tracking". The vertical blue dashed line indicates the observed population-level mean niche overlap ($D = 0.280$). The y-axis indicates population-level (top row; double diamond) or individual-level niche estimates (single diamonds), with individual ID and migratory bout considered. Niche overlap estimates range 0–1, with 0 indicating no niche overlap and 1 indicating complete overlap between breeding and non-breeding regions.

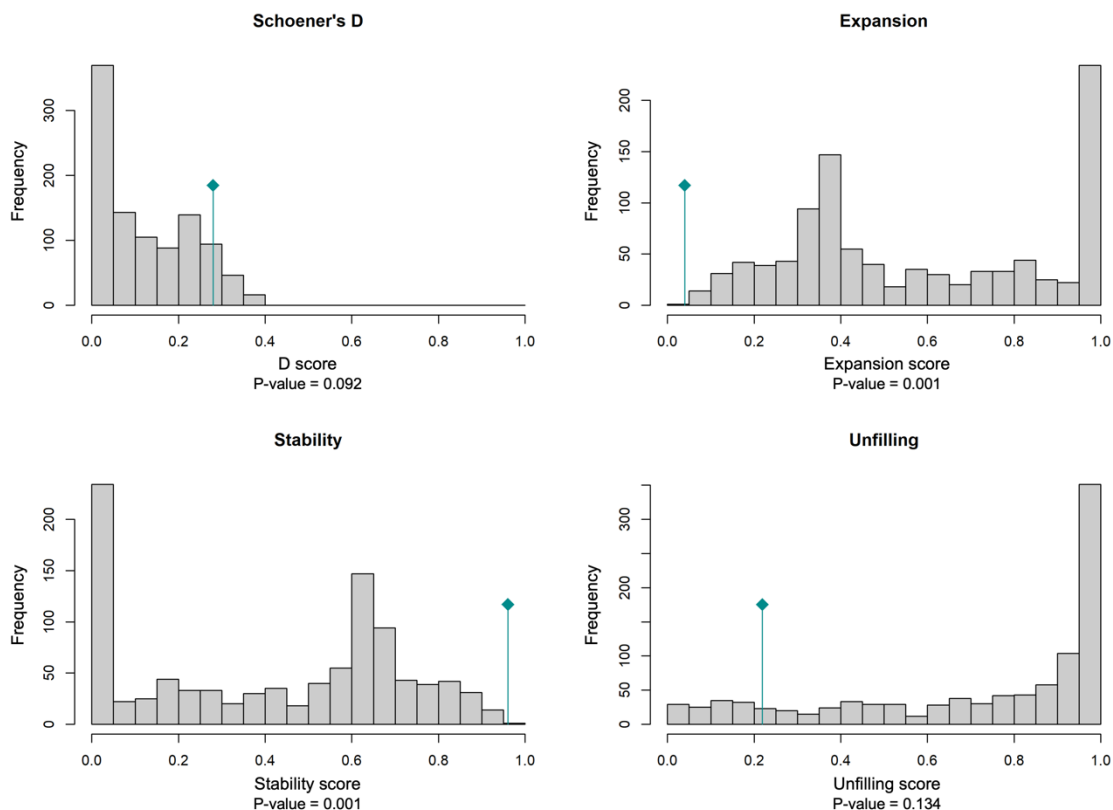


Figure 3.3: Population-level Schoener's D, expansion, stability, and unfilling compared to 1,000 simulated, random breeding and non-breeding region niches. Random niches were built from pelican "occurrences" that were randomly generated without any relationship with climate variables. Gray bars indicate frequency of calculated D, expansion, stability, and unfilling estimates from randomized niches and blue capped lines indicate observed population-level estimates for each metric. Schoener's D is the total niche overlap between breeding and non-breeding regions, expansion is the proportion of the breeding region niche that does not overlap with the non-breeding region niche, stability is the proportion of the breeding and non-breeding region niches that overlap, and unfilling is the proportion of the non-breeding region niche that does not overlap with the breeding region niche. All metrics range 0–1, with 0 indicating no overlap and 1 indicating total overlap.

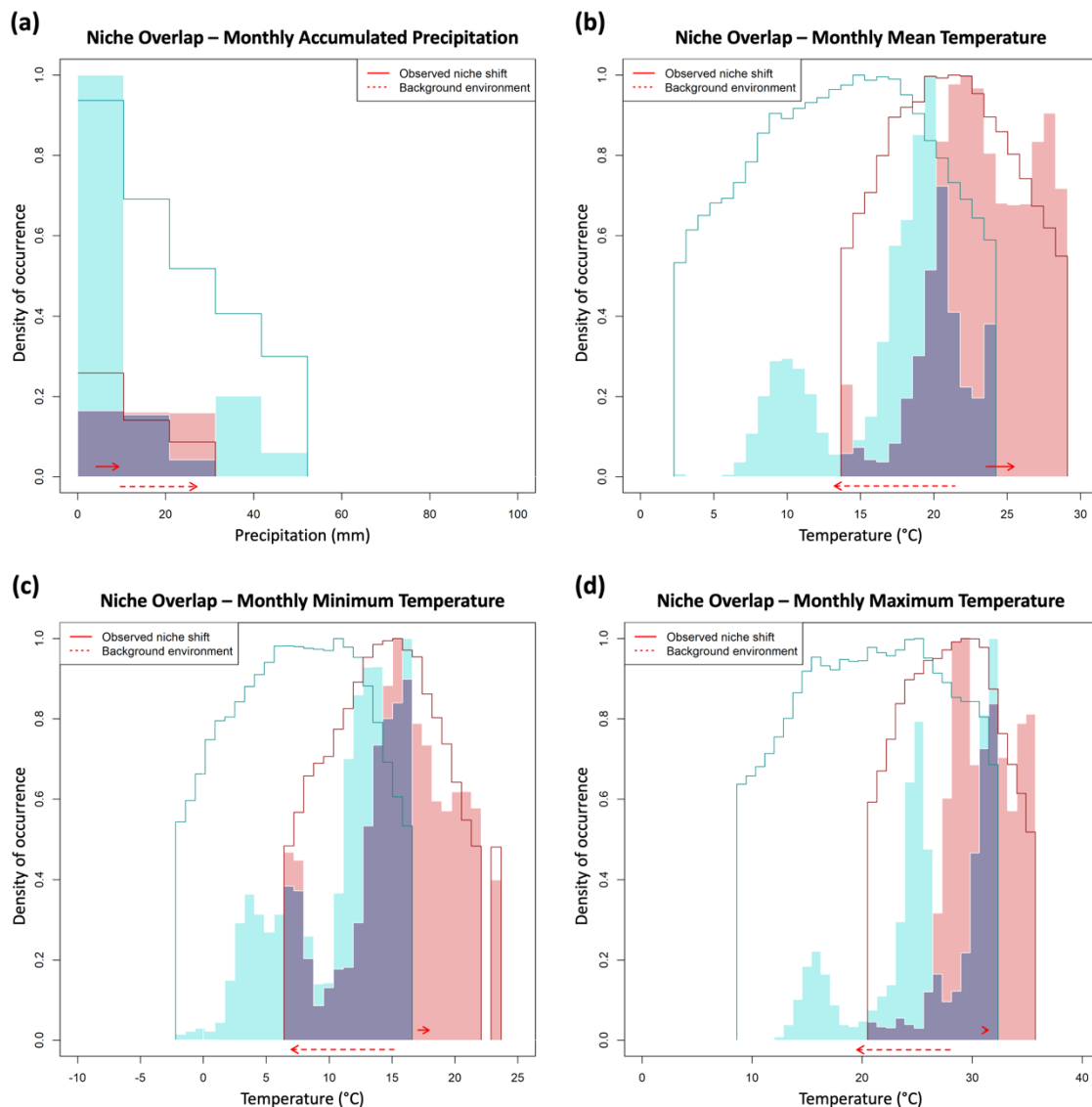


Figure 3.4: Occurrence density plots showing the shift of population-level niche centroid (solid arrow) and total available environment (dotted arrow) between the breeding (blue) and non-breeding (red) regions. Solid blue indicates realized pelican niche in the breeding region, solid red indicates realized pelican niche in the non-breeding region, and solid purple indicates observed niche overlap between regions. White areas outlined in blue and red indicate total available breeding region and non-breeding region environments, respectively.

CHAPTER IV

LEVERAGING WEATHER RADAR AND TRACKING DATA TO ESTIMATE
AIRSPACE USE OF A LARGE MIGRATORY BIRD

ABSTRACT

Population-level space use estimates are crucial for identifying important habitats and behaviors, and predicting population responses to global change. Space use estimates that are derived from individual-level tracking data may miss important movements and habitat use, depending on the particular individuals tracked. Weather radar has recently emerged as a potential valuable source of avian space use data across broad spatial areas and measures numerous individuals without the need for individual tracking. However, radar is predominantly used for multi-species analyses due to the challenge of extracting species-specific information from radar images, limiting its utility for species-specific conservation efforts.

To improve our ability to estimate species-specific population-level space use from existing data sources, I developed a modeling workflow that combines individual-level occurrence data and broadscale weather radar data. This workflow uses an ensemble machine learning algorithm trained on radar imagery at GPS locations collected from American White Pelicans (*Pelecanus erythrorhynchos*) above Great Salt Lake, Utah. The model uses radar-based information to predict pelican presence spatially within radar airspace to generate estimates of population-level space use by season. Given the significant bird-strike hazard posed by pelicans near Salt Lake City International Airport (SLCIA), I also developed a pelican-airplane strike hazard index based on hourly air traffic and radar data that identifies the hours most and least likely for a pelican strike to

occur. The modeling workflow achieved high prediction capability, with an Area Under the Curve of 0.982 and recall (true positive rate) of 0.739. Predictions from the best performing model suggested that pelicans are most likely to occur in Great Salt Lake radar airspace during the fall, once juvenile pelicans at the local breeding colony are old enough to fly. Pelican-airplane strike hazard was generated using an example month of airplane traffic data, and indicated that strike hazard was highest during afternoons, which coincided with peak daily airplane traffic. These findings have broad implications for utilizing archived radar data in avian population studies, enabling comparisons of population trends, high-use areas, and migration phenology across time periods.

INTRODUCTION

Population-level space use estimates have been crucial for defining our expectations of avian response to global change, from estimating species niche breadth (Illán *et al.*, 2022), to predicting seasonal species distributions (Williams *et al.*, 2017), and identifying critical nesting and stopover sites of sensitive species (McDuffie *et al.*, 2022; Schally *et al.*, 2022). Individual-level tracking has become increasingly popular in avian research with improvements in tracking technology, and avian spatial ecology has benefited tremendously from the resulting data (e.g., McKinnon & Love, 2018; Tonra *et al.*, 2019). However, population-level space use, especially in the case of cryptic or far-ranging avian species, may be difficult to accurately quantify from individual tracking data due to low detection rates and high individual variation in movement paths (Hüppop *et al.*, 2019). As a result, a primary challenge in avian ecology and conservation remains the population-level characterization of important movements and behaviors.

Understanding connectivity between populations can inform critical disease mitigation

(de Seixas *et al.*, 2022; Paolini *et al.*, 2023) and conservation initiatives (Fraser *et al.*, 2017; Gregory *et al.*, 2023; Rushing *et al.*, 2021), while variability and plasticity of movements may improve predictions of species' adaptability to climate and land use change (Beever *et al.*, 2017; Gilroy *et al.*, 2016; Sih *et al.*, 2012). Furthermore, understanding population movements and space use may allow us to obtain a clearer understanding of the likelihood and severity of human-wildlife conflicts before they occur (Bauer & de Iongh, 2005; Warrier *et al.*, 2021).

Broad-coverage weather radar has emerged as a powerful remote sensing tool for characterizing landscape-scale avian space use. Airspace comprises a critical part of available habitat for flight-capable avian species (Diehl, 2013; Hüppop *et al.*, 2019), and due to weather radar's broad sampling extent, radar data provide a snapshot of birds in flight across a large volume of three-dimensional airspace that other remote sensing technologies cannot. Weather radar data have been used to generate continent-wide migration forecasts (Van Doren & Horton, 2018), estimate timing and volume of avian migration across seasons and decades (Dokter *et al.*, 2018; Horton *et al.*, 2019; Nilsson *et al.*, 2019), and identify locations of communal bird roosts (Chilson *et al.*, 2019; Russell & Gauthreaux, 1998, Perez *et al.*, 2024). However, weather radar's landscape-scale perspective and difficulty in truthing radar observations to the species level has limited the utility of radar data for species-specific space use studies (Gauthreaux & Diehl, 2020; Hüppop *et al.*, 2019). Identifying species within weather radar images historically has been limited to expert knowledge about species-specific airspace-use characteristics and to instances of known species presence at a given time or location (Eschliman & Horton, n.d.; Gauthreaux & Diehl, 2020, Haas *et al.*, 2022). Expanding the utility of weather

radar to species-specific space use studies, beyond the narrow range of species identified using expert knowledge, requires broadening the scope of automated methods for classifying radar data to species.

Combining information from individual-level tracking data and broadscale weather radar data may improve the utility of weather radar for population-level species tracking. Radar imagery measures the physical characteristics of birds in airspace (e.g., shape, reflectivity, and velocity; Stepanian *et al.*, 2016), while concurrent individual-level tracking data provide information about what species the radar is observing. For instance, GPS tags could provide precise location data that may serve as a ground-truthing data source for remotely sensed species detections. By leveraging both individual and multi-species data, it may be possible to build species-specific radar signatures that can then be used to identify untracked individuals, especially when the species of interest is morphologically distinct from other species present.

Here, I developed a modeling workflow that identifies species-specific radar characteristics, then predicts relative presence probability of individuals within radar airspace. I used a random forests machine learning algorithm trained on GPS location data collected from American White Pelicans (*Pelecanus erythrorhynchos*; hereafter “pelicans”), a large waterbird species, to predict presence and location of individual pelicans within weather radar airspace over Great Salt Lake, Utah. My results demonstrate the utility of broad-coverage, freely-available Next Generation Weather Radar (NEXRAD) radar data to generate species-specific predictions of space use patterns. Pelicans are a considerable strike hazard for commercial airliners due to their large size and concentration in large flocks. I further demonstrate that pelican airspace

use can be predicted from radar imagery to create a species-specific bird-strike hazard index by hour and month for airplane flight paths in and out of the high-traffic Salt Lake City International Airport (SLCIA). By considering hourly air-traffic activity, this method identified areas and times of high airspace use and bird-strike risk at temporal resolution relevant to flight traffic plans. These results have broad implications for weather radar studies using archived radar data, allowing us to compare population trends, high-use areas, and migration phenology across time periods.

METHODS

Presence/pseudo-absence and radar data

American White Pelicans are a large migratory waterbird species with unique flight and behavioral characteristics, including large body size, congregation in large flocks, and high-speed flight (upwards of 110km/h; Utah Division of Wildlife Resources [UDWR] unpublished data), that make them well-suited for proof-of-concept radar studies. Pelican location data were collected from 74 satellite-tracked after-hatch-year pelicans captured and tagged by the UDWR. Pelican captures occurred in wetlands around the eastern periphery of Great Salt Lake during the breeding season (May–September) from 2015 to 2019, and in 2023. Captured individuals were fitted with GSM and ARGOS solar-powered GPS transmitters (Microwave Telemetry GPS/GSM 20-70 and Cellular Tracking Technology ES400W), using custom-fit Teflon ribbon backpack harnesses. The GPS transmitters collected latitude, longitude, and elevation above sea level for all individuals hourly between dawn and dusk for all individuals tagged between 2015–2019, and every 20 minutes between dawn and dusk for all individuals tagged in 2023. Pelican captures and transmitter attachments were conducted under IACUC

protocols #2209 and #12973, and U.S. Geological Survey Bird Banding Laboratory permit #21673.

The NEXRAD weather radar network consists of 160 federally operated radar stations spanning the contiguous United States that collect 360° scans of airspace with high-resolution, dual-polarized Doppler radar. The sole NEXRAD weather radar station with coverage over Great Salt Lake and its peripheral wetlands (KMTX; Figure 1), overlooks Great Salt Lake from Promontory Point, a ridgeline approximately 730 meters above the lake's surface. With a wide, relatively unobstructed radar viewshed available, I included the entirety of Great Salt Lake and the surrounding shoreline within the study area, for a maximum distance of approximately 100 km from the KMTX radar station (between latitudes 40.55 and 41.80 and longitudes -111.55 and -113.25; Figure 4.1).

I downloaded archived KMTX NEXRAD radar station Level II radar scans available at Amazon Web Services (available at: <https://noaa-nexrad-level2.s3.amazonaws.com/index.html>) for years 2015 to 2019 and 2023, using the *download_pvolfiles* function from R package *bioRad* (version 0.7.3; Dokter *et al.*, 2019). Level II radar scans are minimally processed, with the highest spatial resolution currently achievable by NEXRAD (~250 x 250 m image pixels; Brodzik, 2020). Radar scans were collected once per ten minutes using “clean-air mode”, which uses both long and short radar pulses to optimize sensitivity when there is little observed precipitation (NOAA, 2020). I chose scans at the minimum available radar beam angles (0.5° above horizontal for 2015–2019; 0° and 0.5° for 2023) at KMTX to capture a broad range of radar airspace, including low elevations, which I expected to contain the most pelican detections based on preliminary data exploration.

I processed radar scans into raster images of five radar variables useful in differentiating biological objects from precipitation in the atmosphere (Gauthreaux & Diehl, 2020; reflectivity factor (dBZ), differential phase (Φ_{DP}), correlation coefficient (ρ_{HV}), radial velocity (V_r), and differential reflectivity (Z_{DR}); see Table 4.1 for descriptions) using the vol2bird algorithm (Henja & Dokter, 2023).

I removed areas with high-elevation terrain that obstructed the radar beam using radar beam angle (0° beam angle = < 1,624 m above sea level; 0.5° beam angle = < 1,852 m above sea level) and an SRTM 90 m digital elevation model raster (Jarvis *et al.*, 2008). I also used a radar detection area filter generated by the National Weather Service (NWS) to exclude air space that lay behind high-elevation terrain (NWS Salt Lake City [@NWSsaltlakecity], 2020). Weather may mask animal presence in the airspace; therefore, I also used the depolarization ratio metric to filter out pixels suspected to contain weather (Kilambi *et al.*, 2018). Finally, I filtered radar images to only those collected within ± 2 minutes from pelican GPS location timestamps, to align as closely as possible with pelican observations.

I filtered the GPS dataset to local pelican observations that were detectable by the radar beam. I first filtered pelican GPS locations to those occurring within the study area between April and October ($n = 108,479$ GPS locations), encompassing seasonal migration and the breeding season (Knopf & Evans, 2020). I then filtered GPS locations by elevation to those that occurred within the radar detection area during a radar scan. Radar beams expand as they travel away from the radar emitter, thus I generated a radar detection area by calculating the elevation of the radar beam's center and the vertical width of the radar beam at a given location across the study area. I did so for both radar

beam angles and removed any GPS locations that occurred outside this area (0° beam angle: min = 1,533 m above sea level, max = 2,487 m; 0.5° beam angle: min = 2,010 m, max = 4,147 m). Most GPS locations lay outside (mostly below) the radar detection area or occurred in pixels excluded by weather and elevation filters, reducing the initial available GPS dataset to 93 pelican GPS locations within the radar detection area. Finally, radar scans may return missing values for some, but not all radar variables, depending on signal strength and scan type. The random forests algorithm used in this analysis cannot handle missing covariate values, so I further reduced the GPS dataset to only those GPS locations where no radar covariates were missing. This resulted in a final pelican GPS dataset of 23 presence locations from 16 individuals (male = 8, female = 8).

Random forests requires both presence and absence (or pseudo-absence) data to predict species presence (Cutler *et al.*, 2007). Pelican absence data were not available across the radar detection areas, so I generated pseudo-absence locations based on pelican space use patterns above Great Salt Lake. I first generated a population-level 99% autocorrelated kernel density estimate (AKDE) from all pelican GPS locations within the study area and study period with R (version 4.3.1; R Core Team, 2023) package *ctmm* (version 1.1.0; Fleming & Calabrese, 2023), which represents the geographic area used by the entire tagged population over the course of the study. I then randomly selected 10 locations per observed pelican GPS location from areas outside the population 99% AKDE as pseudo-absences ($n = 230$). Each selected location was randomly assigned a time and date that occurred within the study period. Because pelican absences were not observed and were therefore pseudo-absences, pelican occurrence probabilities generated from this analysis are regarded as relative probabilities (Phillips & Elith, 2013).

Model covariates

To distinguish pelican relative probability of occurrence, I extracted radar image pixel values for all five radar variables (Table 4.1) at the time and location of pelican GPS locations and at pseudo-absence locations (hereafter collectively, “presence-absence locations”). I also calculated mean pixel values of the eight pixels adjacent to each presence-absence location (i.e., neighborhood pixels) for each radar variable, to capture radar reflectivity data of pelicans that may have moved to an adjacent radar pixel between the time of GPS fix and the radar sweep or pelicans that occurred in a flock that spanned radar pixels. I included the following additional model covariates: scaled Julian date of each presence-absence location, time of day of each presence-absence location (rounded to the nearest hour), local annual pelican colony count, and annual tagging effort. Julian date and time of day were included to account for temporal variation in pelican movement and airspace use (Findholt & Anderson, 1995; King & Werner, 2001). To improve model interpretability, I scaled Julian dates to start on April 1st. Time of day was included at an hourly scale from 0–23, beginning at midnight. I included raw annual colony count data from the Great Salt Lake pelican breeding colony (Gunnison Island, Utah), collected by the UDWR, to represent the expected number of pelicans present within the study area by year. Previous combined counts of breeding and non-breeding individuals around Great Salt Lake suggest the total pelican population is on average four times the number of breeding individuals present (Paul and Manning, 2002), and colony counts are therefore not a direct measure of pelican abundance. However, counts may serve as a coarse index for the mean probability of detecting a pelican within radar airspace above Great Salt Lake. Annual tagging effort provided information about the

number of pelicans expected in radar airspace per tagged individual, and was calculated by taking the number of GPS transmitters deployed on pelicans at Great Salt Lake each year, divided by the total number of tagged pelicans across the study.

Random forests workflow

I used a random forests algorithm to predict the relative probability of pelican occurrence within radar image pixels from radar, temporal, and species-specific covariates. Random forests is a supervised ensemble machine learning algorithm that uses the outcome of multiple decision trees to vote on the class (e.g., presence vs. absence) of a given observation, based on a random subset of model covariates. Random forests is well-suited to classification problems and prediction using small datasets, because its ensemble and bootstrapping methods avoid overfitting models—a common drawback of standard decision tree frameworks—and therefore may be particularly appropriate for radar data analysis (Gauthreaux & Diehl, 2020; Zewdie *et al.*, 2019). Random forests is also useful in cases when relationships between data are non-linear, as can be the case with radar reflectivity data.

I used R package *randomForest* (version 4.7-1.1; Liaw & Wiener, 2002) to predict relative probabilities of pelican presence for use in classifying pelican presence and absence in airspace above Great Salt Lake. I used 1,000 trees, terminal node size of one, three available input features (i.e., covariates) at each split, and custom probability cutoff thresholds to account for class imbalance. Unbalanced data classes may result in machine learning classification algorithms achieving a “low” prediction error rate by classifying all samples as the majority data class (i.e., pelican absence in this analysis; Ali *et al.*, 2013; Elrahman & Abraham, 2013). To account for class imbalance, I calculated

and applied custom classification probability weights that adjust random forests' default threshold of 0.5 (e.g., below 0.5 = absence, above 0.5 = presence) up or down, limiting the number of samples predicted to be the majority class based on model training data. I did so by iteratively adjusting how many model variables were considered at each split on samples of radar data, then calculating the best balance of receiver-operator error (Kuhn & Johnson, 2013). Relative pelican presence probability was then predicted using the resulting probability weights.

I built a “baseline” model that included only radar and temporal covariates:

$$\text{Relative presence probability} \sim \text{pixel value}_i + \\ \text{mean neighborhood pixel value}_i + \text{time of day} + \text{date} ,$$

where i denotes radar variables dBZ, Φ_{DP} , ρ_{HV} , V_r , and Z_{DR} .

I also built a “count-effort” model, that included all components of the baseline model, as well as colony count and GPS tagging effort covariates:

$$\text{Relative presence probability} \sim \text{pixel value}_i + \\ \text{mean neighborhood pixel value}_i + \text{time of day} + \text{date} + \text{colony count} + \text{effort} .$$

I ran the models 10 times on 80% training and 20% testing data randomly split at each model run, to obtain mean receiver-operating characteristic (ROC) area under the curve (AUC), F2 score, and recall, which I used to rank each model's prediction capability on testing data. AUC measures the tradeoff between the model's precision (i.e., out of all of the pelican presences the model predicted, how many were actually

pelicans?) and recall (i.e., out of all pelican presences in my data set, the number correctly identified as pelicans). AUC scores range 0–1, where scores above 0.7 indicate a model does acceptably well at prediction, and anything above 0.9 as outstanding (Hosmer *et al.* 2013). The F2 score also ranges 0–1, with higher scores indicating greater prediction capability. F2 is similar to the more common F1 score, which measures the harmonic mean between precision and recall, therefore providing a measure of how well a model can accurately capture pelican presence. However, the F2 score weights the importance of recall to twice that of precision, which is useful in cases where maximizing recall is preferred over precision. To avoid selecting a model that under-predicted pelican presences (especially in the context of bird-strikes) to use for pelican presence prediction, I defined the best model as the single model iteration with the highest recall. In case of a tie between models, I selected the model with the highest AUC score and F2 scores. I also ranked each radar covariate’s importance for model prediction capability by calculating the decrease in each model’s predictive accuracy on out-of-bag data, when values of each variable are shuffled (“mean decrease accuracy”; Breiman, 2001).

Prediction case studies

I conducted a broad extent analysis, predicting expected seasonal relative probability of pelican occurrence in airspace over the Great Salt Lake study area (between latitudes 40.50 and 41.45 and longitudes -111.50 and -112.50; Figure 4.1), I applied the best-performing model to 30 randomly selected radar image rasters for each hour of the day, seasonally (spring: April–May, summer: June–August, fall: September–October; $n = 2,160$) across the study area. I then calculated the predicted median relative presence probability by season (spring, summer, fall). I also ground-truthed predictions

by predicting relative presence probability in radar pixels known to contain a GPS tagged pelican, and produced spatial estimates by season of relative presence probability across the study area.

I also conducted a localized analysis of pelican airspace use above the SLCIA. I delineated commercial airplane flight paths in and out of the SLCIA (Federal Aviation Administration, 2022), then overlaid the radar detection area to generate a zone where the radar beam and flight paths intersected (Figure 4.2). Within this area, I applied the best-performing model to 30 randomly selected radar image rasters for each hour of the day monthly across the study period ($n = 5,040$) to generate median relative presence probability by hour of the day and month. I also calculated an example hourly-by-month pelican-strike risk index at the SLCIA by dividing the estimated hourly number of flight arrivals and departures of any kind (e.g., commercial, cargo) by daily total flights, then multiplying by estimated hourly relative median pelican presence probability within the SLCIA radar detection area. In- and out-bound flight data at hourly resolution were only available from the SLCIA for January 2023, and I therefore used January flight data to estimate an example strike index for a single month (September) within the study period. Finally, I gathered total monthly airport traffic data (<https://slcairport.com/about-the-airport/airport-overview/air-traffic-statistics/>) for use in calculating real-world monthly expected pelican-strike hazard.

RESULTS

Model performance

Models were estimated based on a pelican presence/pseudo-absence dataset containing 23 pelican presence and 230 pelican absence locations, and radar and other

covariates. Custom classification probability weights were presence = 0.881, absence = 0.119 for both models, effectively weighting tree votes toward the less prevalent data class (i.e., presence data; Kuhn & Johnson, 2013).

Across all ten-fold model runs, both the baseline and count-effort models performed comparably. Both models performed well in terms of AUC (mean (\pm sd); baseline = 0.991 ± 0.009 , count-effort = 0.991 ± 0.013), but moderately in terms of F2 score (baseline = 0.440 ± 0.025 , count-effort = 0.426 ± 0.033) and recall (baseline = 0.674 ± 0.042 , count-effort = 0.657 ± 0.048). The top performing baseline and count-effort models, which were used for presence prediction (i.e., the highest performing model of ten runs), achieved AUC = 0.982, F2 = 0.464, recall = 0.739 (i.e., the model correctly predicts 73.9% of pelican GPS points) and AUC = 0.982, F2 = 0.489, recall = 0.739, respectively. Including additional count-effort information increased model performance in the F2 score by ~5%.

I ranked each covariate's importance in model prediction capability by calculating mean decrease in model predictive accuracy for each variable. Of the best performing run of the baseline model, mean ρ HV of neighborhood cells to GPS locations was the most important variable (Table 4.2), followed by mean V_r of neighborhood cells, then by mean Z_{DR} of neighborhood cells. Julian date and mean ρ HV of neighborhood cells were ranked highest for prediction capability for the count-effort model, followed by mean V_r of neighborhood cells.

Median (\pm sd) radar cell values at pelican presence and pseudo-absence locations for each top-ranked radar model were: neighborhood ρ HV (presence = 0.708 ± 0.155 , pseudo-absence = 0.756 ± 0.163), neighborhood V_r (presence = 0.875 ± 6.342 , pseudo-

absence = 1.500 ± 5.001), and neighborhood Z_{DR} (presence = 4.469 ± 3.243 , pseudo-absence = 5.348 ± 3.179).

Case studies

I used the best performing model across both model types (baseline and count-effort) and all ten-fold model runs to predict pelican relative occurrence probability for both case studies. Seasonal predicted relative probability of pelican presence, averaged across all hours, was lowest in the summer (median (\pm sd) = 0.144 ± 0.041 ; Figure 4.3), followed closely by spring (0.148 ± 0.027), and highest in fall (0.173 ± 0.028). During the spring, predicted median pelican relative presence probability across the study area was high nearest to the KMTX radar station, wetlands east of KMTX near the Bear River Migratory Bird Refuge, and to the west between KMTX and the Gunnison Island pelican breeding colony (Figure 4.1, Figure 4.4). Activity near KMTX and Gunnison Island lessened during the summer while activity increased to the east and south of Great Salt Lake. In fall, areas to the south of Great Salt Lake and along the Wasatch Mountain range to the east of Great Salt Lake were predicted to have the highest relative pelican presence probability.

The model correctly predicted pelican relative presence probability within pixels that were known to contain a GPS-tagged pelican (i.e., ground-truthed radar image pixels; Figure 4.5) 78.3% percent of the time, with a mean (\pm sd) predicted relative probability of 0.564 ± 0.106 .

Pelican presence estimates within SLCIA flight paths varied by month (Figure 4.6), with the lowest median relative presence probability occurring in June (median (\pm sd) = 0.127 ± 0.016) and highest in August (0.195 ± 0.022). Pelican presence predictions

also varied hourly across months (Figure 4.7). The lowest relative pelican presence probability across SLCIA airspace occurred at 03:00 in June (0.105 ± 0.014), and highest at 17:00 in August (0.202 ± 0.020).

Pelican-airplane strike hazard varied notably by hour across my example month (September, Figure 4.8a). High variability in air traffic across the day was a primary driver of strike risk, but peak air traffic roughly coincided with peak relative presence probability in the afternoons, further increasing strike risk during this period. Generally, across the day, the relative probability of striking a pelican in SLCIA airspace was the greatest between 08:00–11:00, 15:00–17:00, and 20:00–21:00. The lowest predicted strike hazard occurred at 01:00 with an estimated strike hazard of 0, as no in- or out-bound flights occurred during this time, while the highest occurred at 16:00 (median strike hazard = 0.014).

Monthly airplane traffic remained relatively stable across the study period (mean (\pm sd) monthly in- and out-bound flights = $26,588.71 \pm 728.24$), and therefore monthly strike hazard estimates did not differ greatly in magnitude from predicted pelican presence across SLCIA airspace (Figure 4.8b). The month with the lowest median strike hazard across the study period was June (median = 0.018 ± 0.002), and the highest was August (median = 0.029 ± 0.003).

DISCUSSION

I demonstrate that it is possible to achieve species-specific relative probability of occurrence within radar airspace, using a random forests algorithm trained on weather radar information and individual-level pelican GPS location data. My models achieved high AUC and reasonably high recall scores, but modest F2 scores, suggesting that the

models performed well at correctly identifying known pelican presence (i.e., true positives) in radar airspace, but may also classify non-pelicans as pelicans (i.e., false positives). However, because I only used pseudo-absences and not true absence data, it is unknown whether pseudo-absence locations predicted to contain a pelican were actually incorrect. Previous research has used weather radar data to identify airborne avian species (e.g., Gauthreaux & Diehl, 2020; O’Neal *et al.*, 2010; Russell & Gauthreaux, 1998), but to my knowledge, this is the first study to combine GPS location data and weather radar data for species-specific classification. Additionally, my analysis automated species-specific radar data extraction at known locations and generation of expected-absence data, removing the need for time-consuming hand-delineation of species presence and absence locations in radar images.

Both of the models I tested (a “baseline” model including only radar and time variables, and a “count-effort” model that also included tagging effort and local colony count data) performed comparably. Of the two additional variables I included in the count-effort model, colony count appeared relatively more important than effort (Table 4.2). However, including colony count information in my analysis improved the F2 score by < 5%, and obtaining colony count information (or other measures of population size) within radar study areas may be difficult or expensive to obtain for other avian systems. Depending on costs associated with gathering count data and the limited F2 score improvement, future studies may choose not to include such additional data.

Neighborhood ρ_{HV} , which indicates the diversity of sizes and shapes of airborne objects, and V_r , which may be used to separate non-meteorological objects from precipitation, were the most important radar variables for predicting pelican presence above the Great

Salt Lake basin. Birds and other biological scatterers often return lower ρ_{HV} values than precipitation (Gauthreaux & Diehl, 2020; Kumjian, 2013), whereas V_r may indicate speed and direction of birds in flight relative to a radar station. Species-specific characteristics of flight pattern, coupled with size and shape variation may enable us to identify species based on these distinguishing characteristics as captured in radar-based information.

Predicted airspace use across the study area was highest in the fall and lowest in the summer, followed closely by spring (Figure 4.3), corresponding with local pelican migration and nesting phenology (Knopf & Evans, 2020; Paul & Manning, 2002). Relative probability of pelican occurrence within radar airspace above Great Salt Lake was most variable in the spring, likely owing to variation in annual spring temperatures and individual migratory phenology. Airspace use also appeared to shift spatially by season. Springtime use was greatest between the Gunnison breeding colony and the closest foraging sites to the breeding colony, while use increased during the summer and fall at sites along the Wasatch Mountains and southerly Farmington Bay. Low spring and summer airspace activity coincides with pelican nesting phenology, when up to 20% of the local population may be engaged in time-intensive breeding and nesting activities (Knopf & Evans, 2020; Paul & Manning, 2002), limiting movements beyond those required for self- and offspring-provisioning. Water surrounding the Gunnison breeding colony is too salty to support fish and other potential pelican prey items (Kijowski *et al.*, 2020; Wurtsbaugh *et al.*, 2016), and as a result, the Bear River Migratory Bird Refuge and Willard Spur Waterfowl Management Area—state-managed wetlands just south of the Bear River Migratory Bird Refuge—serve as the nearest foraging grounds for adult

pelicans breeding at the Gunnison colony (Kijowski *et al.*, 2020). Increased activity in eastern and southern wetlands in the summer and fall may reflect reduced reliance on wetlands near the Gunnison colony as chicks mature, dispersal of fledged juveniles, and pre-migratory staging in these areas (Paul & Manning, 2002).

Quantifying bird-airplane strike hazard is becoming increasingly important as demand for air travel has increased. Pelicans have been involved in at least 33 plane collisions between 2004 and 2022 within the United States alone, costing airlines over \$17 million in airplane repairs and risking human injury or mortality (Dolbeer *et al.*, 2023). Of these pelican collisions, 27% occurred at the SLCIA (Federal Aviation Administration, 2023). Currently, avian species are becoming increasingly reliant on Great Salt Lake as a migratory stopover site (Wilsey *et al.*, 2017) and air traffic out of SLCIA is projected to increase (RS&H, 2022), likely resulting in increasing bird-plane strike risk through time. Monthly flight traffic in and out of SLCIA was fairly stable across study period months, and resultingly the strike hazard estimates mirrored seasonal pelican relative occurrence probability closely (Figure 4.8b), with August expected to be the worst month for potential strikes. Increased abundance of pelicans across the study area once chicks hatched at the Gunnison breeding colony have fledged (fall; Figure 4.3) and pre-migratory staging in eastern and southern Great Salt Lake wetlands near SLCIA (Figure 4.4; Paul and Manning, 2002) likely contribute to observed increases in strike hazard. Based on hourly flight data from January 2023, hourly pelican strike hazard was unsurprisingly largest during periods of high flight traffic, especially during afternoon hours when both flight traffic and relative probability of pelican presence was highest. Assuming hourly flight traffic remains similar across months, increased vigilance for

pelicans during the afternoon and evening hours is warranted, especially in high pelican abundance months of August and September.

Few pelican GPS locations aligned with NEXRAD radar sweeps during the study period, which severely limited the amount of pelican presence/pseudo-absence data available to train the random forests model. Pelicans spend a majority of their daily activity budget loafing or foraging at ground level (King & Werner, 2001), and even with an initial dataset of greater than 100,000 GPS locations, nearly all were collected at altitudes below areas the KMTX radar station could detect. Additionally, random forests machine learning algorithms are unable to handle missing data, which can be common in NEXRAD data, depending on signal strength and signal-to-noise ratio of radar scans. Removal of missing values from the KMTX radar data reduced my available model training dataset further. Given these data limitations, the model predicted pelican presence at a considerably better rate than random, but it still performed worse than previous bird-radar analyses with greater amounts of data available. For example, Gauthreaux & Diehl (2020) achieved 91% recall when using random forests to classify known radar detections of purple martins (*Progne subis*) into purple martin and “other” categories using 47,620 known occurrences of purple martins within radar airspace. Limitations of my model were notable in some of my spatial predictions, where large “hotspots” of high relative occurrence probability existed across seasons in unexpected areas, including over urban centers and mountain foothills. Upon further inspection, these hotspots were likely the result of persistent radar artifacts (e.g., ground and water clutter or airborne particulate point sources) that the model could not parse from pelican presences. Misclassification may also extend to other avian species if similarities between

pelicans and other Great Salt Lake species are large (e.g., waterfowl). Future analyses that use only the few most important radar variables may reduce the number of radar pixels containing missing values without sacrificing model performance, and efforts to develop methods for accurate data imputation could help improve model prediction capability. Including additional pelican location data as more individuals are collared over time will also likely reduce classification errors.

Pelicans are an ideal first species to explore whether extracting species-specific information from radar data is possible, but species-specific analyses are likely not limited to pelicans. Despite a small training dataset, my models achieved relatively high species-specific radar classification and prediction capability, which is promising for future applications of radar to avian GPS location data. Pelicans occur in high abundance around Great Salt Lake, and therefore my dataset of GPS locations within radar airspace may stand at the high end of what is currently available for most species. However, high-frequency GPS trackers have been successfully deployed on many other large-bodied avian species to date, including waterfowl, cranes, and raptors (e.g., Overton *et al.*, 2022), and known species occurrences within radar airspace are expected to grow over time as GPS trackers become increasingly capable of high-resolution fix rates. Furthermore, data collection for future GPS-radar analyses is likely easy to implement in near-future studies. Many new GPS transmitters can collect location data at the same frequency as NEXRAD radar sweeps (approximately once every 10 minutes). Aligning GPS fix rates with radar sweeps may reduce data loss and produce more detailed species-specific radar signatures, while still providing location data at frequencies relevant to research goals beyond GPS-radar analyses.

Given the proliferation of lightweight GPS tracking devices, planned NEXRAD improvements (National Weather Service, 2021), and increasingly sophisticated machine learning techniques, this chapter provides a glimpse into the future of radar's growing importance to ecological and conservation research. Numerous avenues for future species-specific radar research exist, including automated real-time species-specific forecasts and airspace use estimates of species continent-wide. Species that possess enough GPS data to generate species-specific radar signatures could likely support such real-time avian forecasts. Real-time NEXRAD data is freely available online and could be automatically ingested into a workflow that applies a random forests model to each radar image, generating a species-specific forecast of presence/pseudo-absence or relative probability of occurrence. Such real-time forecasts could be immensely useful for estimating bird-airplane strike hazard, relating species behavior to fine-scale weather conditions, and determining optimal times to power down wind turbines or turn off urban lighting to reduce bird deaths from infrastructure collisions. Furthermore, NEXRAD has extensive coverage across the United States, and data are collected similarly across radar stations. Expanding GPS-radar analyses to include multiple NEXRAD stations could provide a more comprehensive view of species-specific avian space use on a broader scale, with relatively minimal effort. Application to foreign radar networks or non-meteorological radar systems (e.g., aircraft surveillance radar) when possible may increase the utility of GPS-radar analyses further. Together, these future research avenues represent a significant step forward in understanding species-specific airspace use and abundance, and expansion and refinement of similar analyses warrants further exploration.

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scanning at a lower base elevation angle, lowering from 0.5° to 0.0°! We're very excited because this upgrade will support better coverage and weather detection across northern Utah! #utwx <https://t.co/tGkz02mKqK> [Tweet]. Twitter.

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TABLES AND FIGURES

Table 4.1: Descriptions and interpretations of dual polarized radar variables used for pelican presence prediction across Great Salt Lake radar airspace.

Radar variable	Abbreviation	Description
Reflectivity factor	dBZ	A logarithmic scale measuring the amount of transmitted power returned to the radar receiver from airborne objects. Provides information about the amount or reflectivity of objects in the air. Low values indicate few or low reflectivity objects, while high values indicate many or high reflectivity objects.
Differential phase	Φ_{DP}	A measure of how well synced horizontal and vertical radar waves are as they reflect from airborne objects. Provides information about the shape and concentration of objects in the atmosphere. Values increase with concentration and size of airborne objects.
Correlation coefficient	ρ_{HV}	The coefficient between power and phase of horizontal and vertical radar waves reflecting from airborne objects. Provides information about the diversity of size and shape of airborne objects. Lower values indicate variability, while higher values indicate uniformity in object size and shape.
Radial velocity	V_r	Velocity of airborne objects relative to the radar beam. Provides information on the speed and direction of airborne objects. Negative values indicate objects are moving toward the radar beam emitter, values near zero indicate movement perpendicular to the radar beam, and positive values indicate movement away from the radar beam emitter.
Differential reflectivity	Z_{DR}	The ratio between reflectivities measured by horizontal and vertical radar waves returning from airborne objects. Provides information about relative shapes of objects in the atmosphere. Negative values indicate objects are taller than they are wide, while positive values indicate objects are wider than they are tall.

Table 4.2: Variable importance to predicting pelican presence across Great Salt Lake radar airspace. Model performance for each variable was calculated by the observed decrease in prediction accuracy the model achieved when values of a given variable were shuffled (“mean decrease accuracy”). Greater values of raw performance decrease indicate greater variable importance to model prediction accuracy. “GPS” refers to radar variable values from pixels containing a GPS-tagged pelican and “neighborhood” refers to mean radar variable values from pixels adjacent to pixels containing a GPS-tagged pelican. Only the top six variables are shown.

Model	Best performing model run		Mean across all model runs	
	Variable	Raw performance decrease	Variable	Raw performance decrease
Baseline	ρ HV (neighborhood)	11.720	ρ HV (neighborhood)	10.653
	V_r (neighborhood)	10.121	V_r (neighborhood)	10.019
	Z_{DR} (neighborhood)	8.690	V_r (GPS)	8.362
	V_r (GPS)	7.683	Z_{DR} (neighborhood)	8.331
	Julian date	6.948	ρ HV (GPS)	8.138
	ρ HV (GPS)	6.780	Julian date	7.034
Count-effort	Julian date	12.421	Julian date	12.256
	ρ HV (neighborhood)	10.266	ρ HV (neighborhood)	9.931
	V_r (neighborhood)	8.848	V_r (neighborhood)	9.171
	Colony count	8.184	Z_{DR} (neighborhood)	8.101
	V_r (GPS)	7.929	V_r (GPS)	7.411
	ρ HV (GPS)	7.874	ρ HV (GPS)	6.962

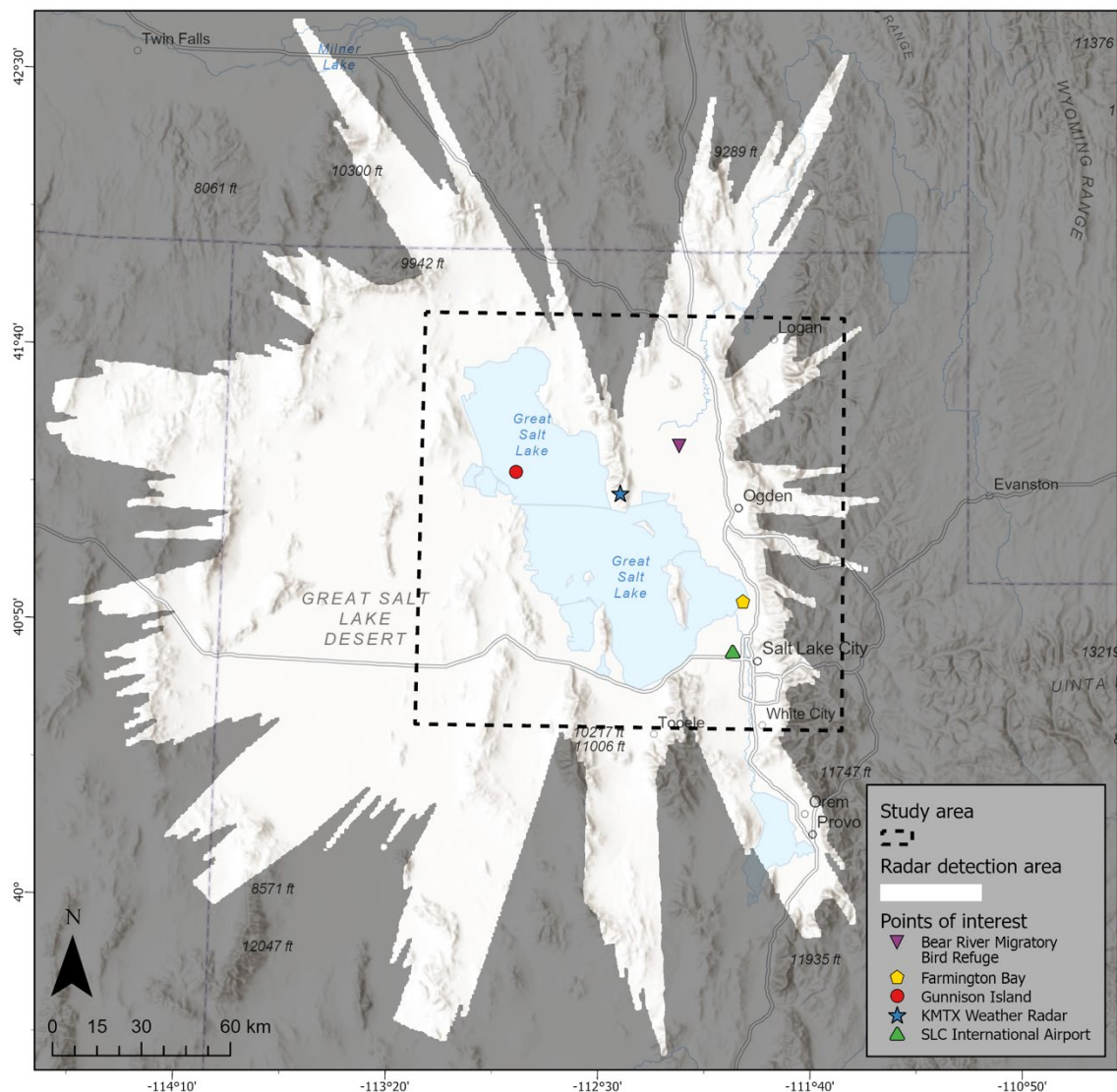


Figure 4.1: Radar detection area and points of interest across the Great Salt Lake basin. The KMTX NEXRAD weather radar station (blue star) overlooks Great Salt Lake from a ridgeline approximately 730 meters above the lake's surface. Pelicans nest colonially on Gunnison Island (red circle) and forage along the eastern periphery of Great Salt Lake at locations including the Bear River Migratory Bird Refuge (purple triangle) and Farmington Bay (yellow pentagon). The Salt Lake City (SLC) International Airport (green triangle) is a high-traffic airport that has experienced nine pelican-airplane strikes since 2004.

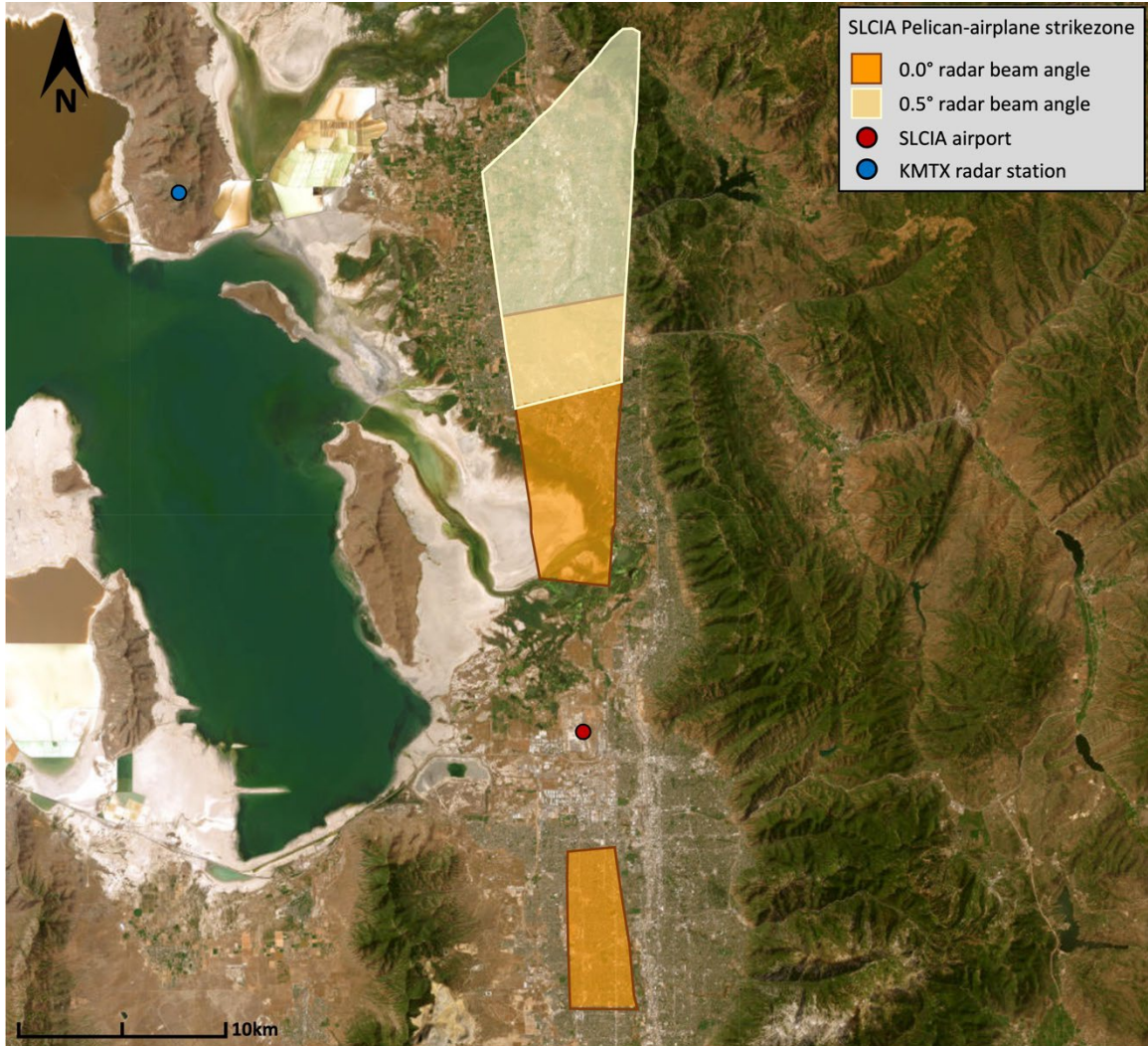


Figure 4.2: Intersection of airspace visible to the KMTX NEXRAD radar station and flightpaths in and out of the Salt Lake City International Airport (SLCIA). Orange polygons signify airspace within airplane flightpaths that are sampled by the radar station using a beam with 0.0° elevation above horizontal, and the off-white polygon signifies airspace sampled using a beam with 0.5° elevation above horizontal. The red dot indicates the SLCIA, and the blue dot indicates the KMTX NEXRAD station.

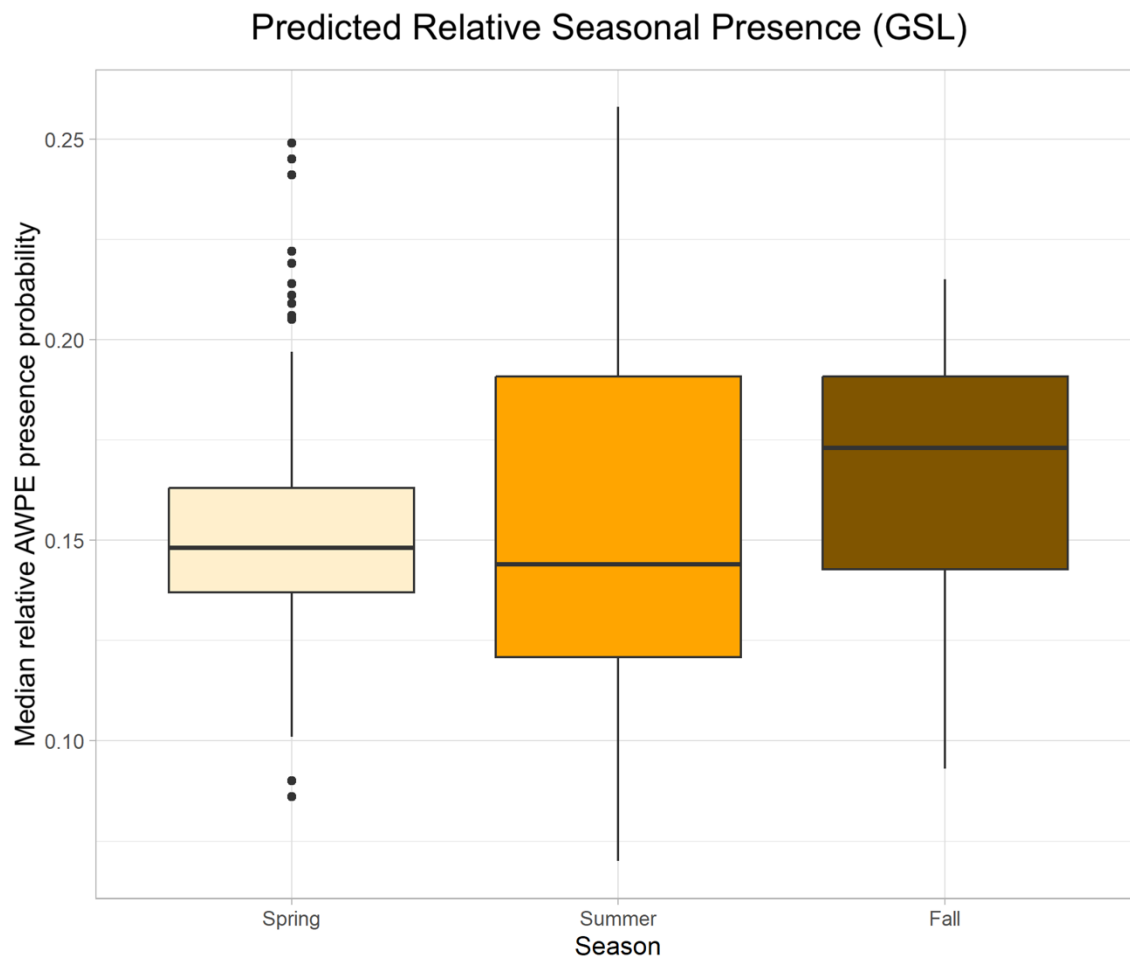


Figure 4.3: Median relative predicted American White Pelican (AWPE) presence probability across Great Salt Lake radar airspace by season across all study years. Predictions were produced using the best model run of ten from the count-effort model, but both models produced similar estimates.

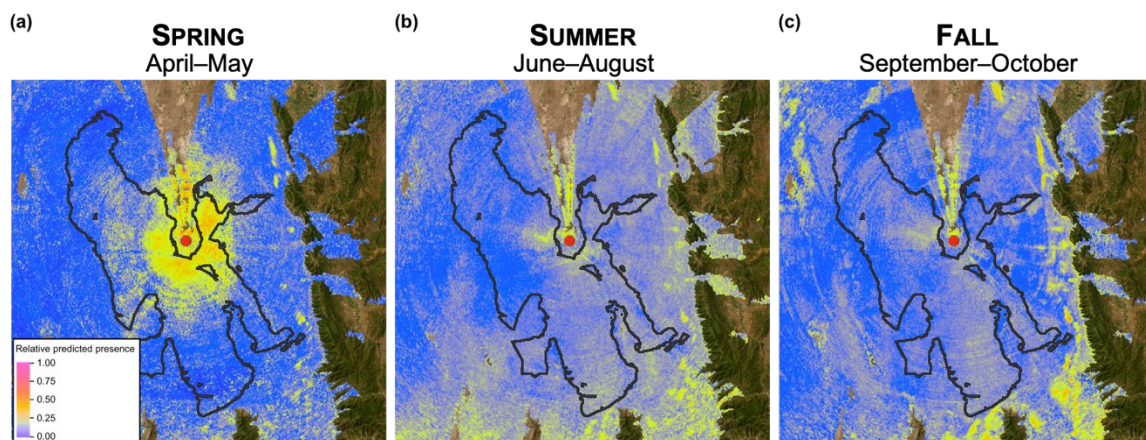


Figure 4.4: Spatial predictions of median relative pelican presence probability across Great Salt Lake radar airspace during the a) spring (April–May), b) summer (June–August) and c) fall (September–October) across all study years. Predictions were produced using the best model run of ten from the count-effort model, but the basic and count-effort models produced similar estimates.

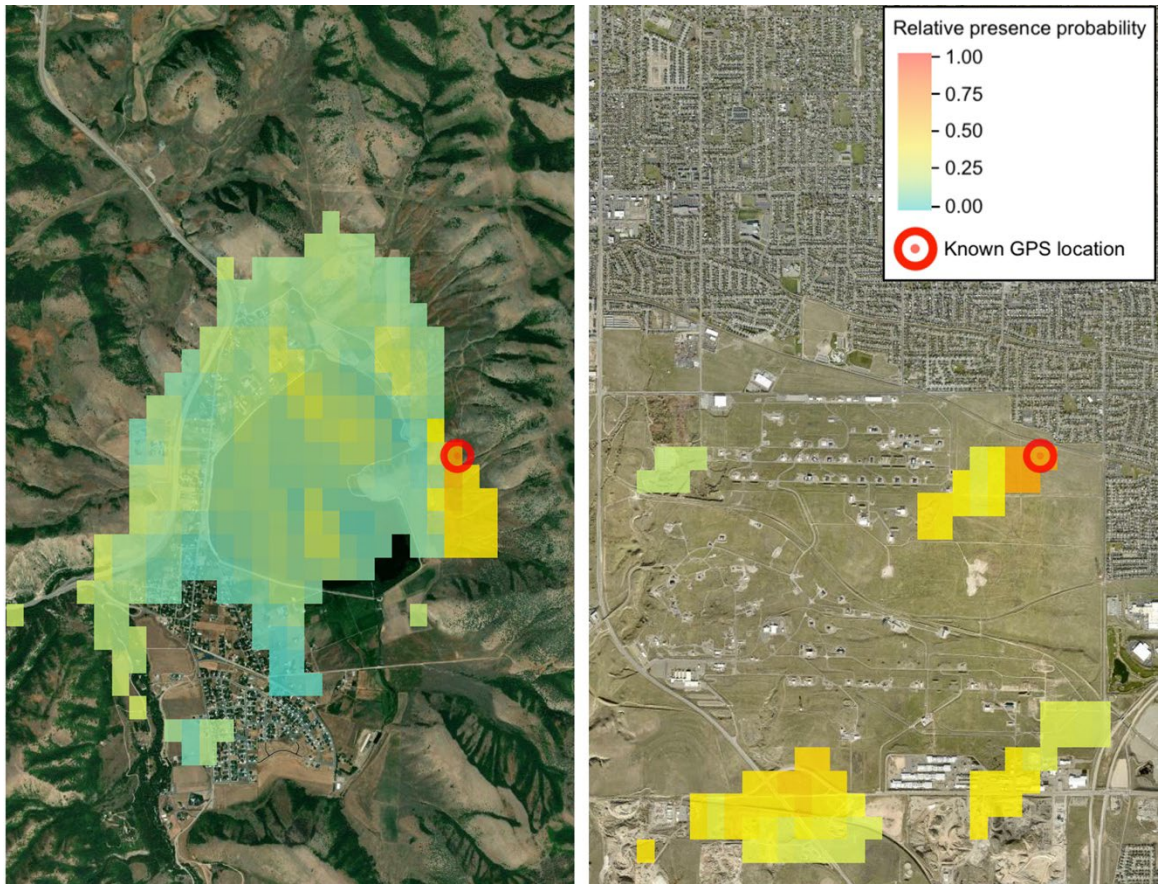


Figure 4.5: Examples of relative predicted pelican presence within 250 x 250 m radar pixels known to contain a GPS-tagged pelican. Images included here were produced using the best model run of ten from the count-effort model, but both the basic and count-effort models produced similar estimates.

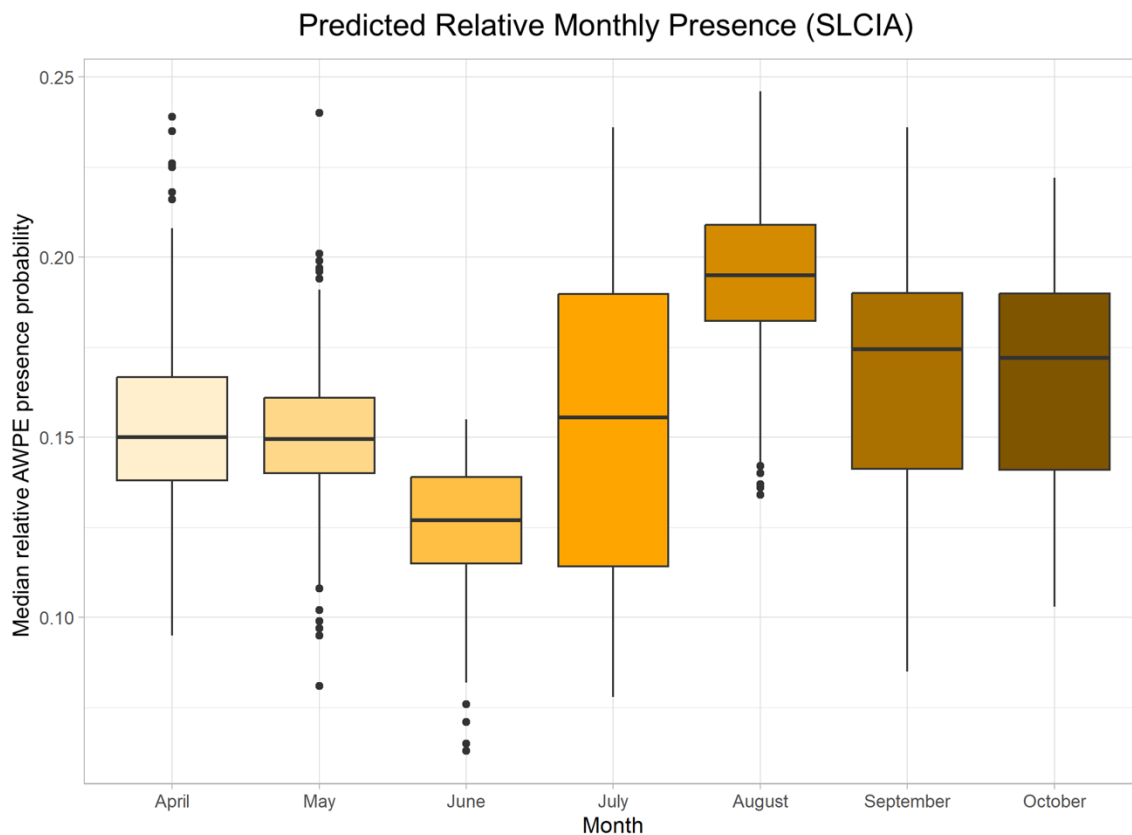


Figure 4.6: Median relative predicted American White Pelican (AWPE) presence probability across Salt Lake City International Airport (SLCIA) in- and out-bound airplane flight paths within radar airspace. Estimates are by month across all study years. Predictions were produced using the best model run of ten from the count-effort model, but both models produced similar estimates.

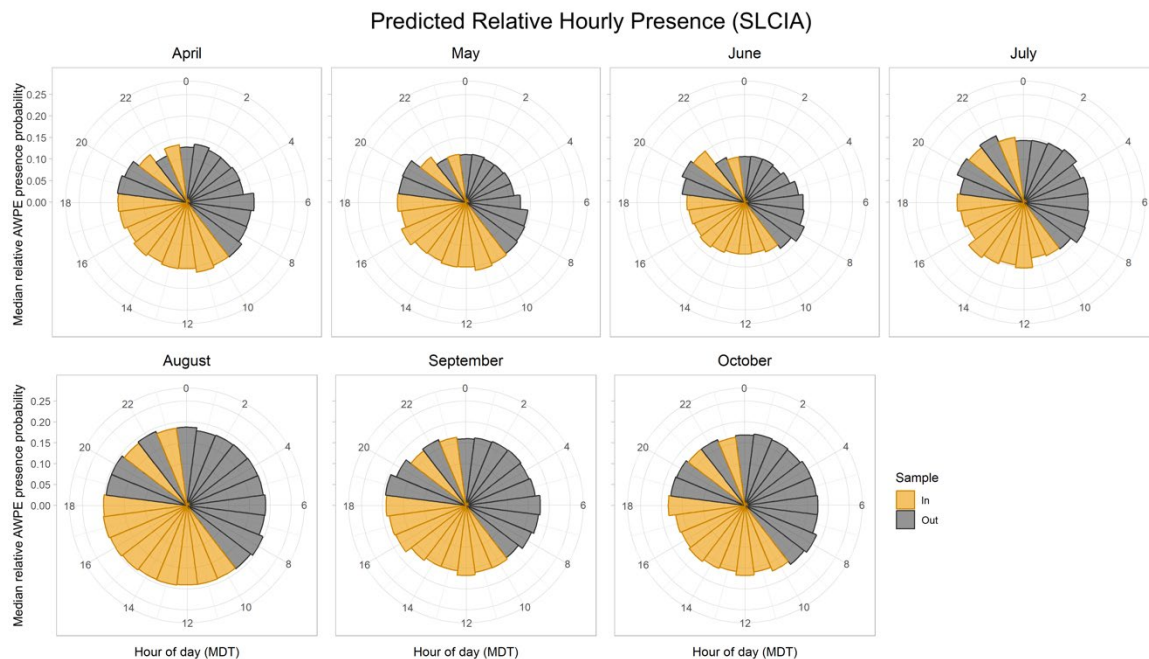


Figure 4.7: Median relative American White Pelican (AWPE) presence probability, predicted across Salt Lake City International Airport (SLCIA) in- and out-bound airplane flight paths within radar airspace (Figure 4.2). Bars represent median relative presence probability by hour across a 24-hour day, beginning at hour 0 (midnight). Concentric grid lines indicate the probability plot axis, beginning at 0 (plot center) and ending at 0.25 (outermost grid line). Estimates are by hour and month across all study years. Orange bars indicate hours with available model training data (i.e., pelicans occurred within the radar detection area during these hours; “in-sample”), while gray bars indicate hours without data available (“out-of-sample”). Predictions were produced using the best model run of ten from the count-effort model, but both models produced similar estimates.

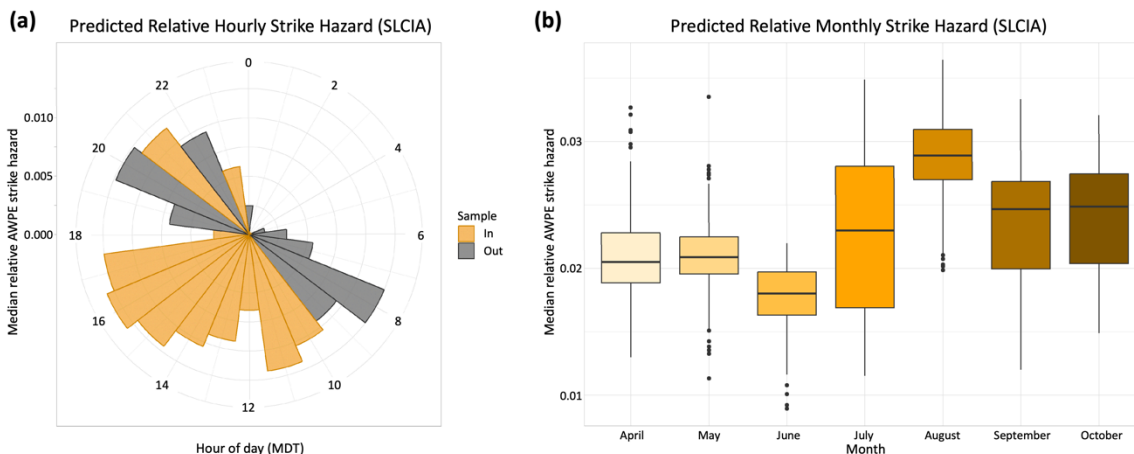


Figure 4.8: Median predicted American White Pelican (AWPE) bird-airplane strike probability across Salt Lake City International Airport (SLCIA) in- and out-bound airplane flight paths within radar airspace. Estimates were created by multiplying predicted pelican presence by in- and out-bound flight traffic for each time period. Hourly flight data were not available for all months, and therefore hourly estimates a) were produced using January 2023 hourly flight data and median predicted pelican presence for September across all years of the study period and are intended as an example only. Monthly estimates b) were produced using monthly 2023 flight data from SLCIA and median pelican predicted presence across all years of the study period. Predictions were produced using the best model run of ten from the count-effort model, but both models produced similar estimates.

CHAPTER V

SCALE-DEPENDENT POPULATION DRIVERS INFORM AMERICAN WHITE PELICAN MANAGEMENT IN A SHRINKING SALINE LAKE ECOSYSTEM¹

ABSTRACT

Shrinking saline lakes provide irreplaceable habitat for waterbird species globally. Disentangling effects of wetland habitat loss from other drivers of waterbird population dynamics is critical for protecting these species in the face of unprecedented changes to saline lake ecosystems, ideally through decision-making frameworks that identify effective management options and their potential outcomes. Here, I develop a framework to assess effects of hypothesized population drivers and identify potential future outcomes of plausible management scenarios on a saline lake-reliant waterbird species. I use 36 years of monitoring data to quantify effects of environmental conditions on the size of a regionally important breeding colony of American white pelicans (*Pelecanus erythrorhynchos*) at Great Salt Lake, Utah, USA, then forecast colony abundance under various management scenarios. I found that low lake levels, which allow terrestrial predators access to the colony, are probable drivers of recent colony declines. Without local management efforts, I predicted colony abundance could likely decline approximately 37.3% by 2040, though recent colony observations suggest population declines may be more extreme than predicted. Results from population projection scenarios suggested that proactive approaches to preventing predator colony access and

¹ Van Tatenhove, A.M., Neill, J., Norvell, R.E., Stuber, E.F., Rushing, C.S. *In press*. Scale-dependent population drivers inform avian management in a declining saline lake ecosystem. *Ecological Applications*.

reversing saline lake declines are crucial for the persistence of the Great Salt Lake pelican colony. Increasing wetland habitat and preventing predator access to the colony together provided the most effective protection, increasing abundance 145.4% above “no management” projections. Given the importance of water levels to the persistence of island-nesting colonial species, proactive approaches to reversing saline lake declines could likely benefit pelicans as well as other avian species reliant on these unique ecosystems.

INTRODUCTION

Across the globe, saline lakes and their peripheral wetlands are rapidly being lost due to water diversions, prolonged droughts, and rising temperatures (Wurtsbaugh *et al.*, 2017). Because they often occur in already water-stressed regions, saline lakes provide rare concentrations of water in otherwise arid landscapes, and their declines have outsized effects on the health of species reliant on these ecosystems (Moulton *et al.*, 2018; North American Bird Conservation and Initiative, 2022; Saccò *et al.*, 2021). In the United States alone, over half of saline lakes have decreased in surface area by > 50% since the late 1800s (Wilsey *et al.*, 2017). These dramatic lake level declines have shrunk aquatic habitats and exposed fragile lake beds, resulting in toxic dust storms (Goudie, 2014), billions of dollars in ecological clean-up costs (Ramboll Environ, 2016), and hemispheric-scale biodiversity loss (Conover & Bell, 2020). Shrinking saline habitats have been directly detrimental to plant and wildlife populations by destroying fisheries and extirpating plant and vertebrate species from critical habitats (Eimanifar & Mohebbi, 2007; Micklin, 2007). Despite growing interest in protecting these ecosystems, slowing

or reversing their declines will likely take years to achieve (Jacobs Engineering Group, 2019), further endangering the species that depend on them.

Colonial waterbirds that rely on saline lake ecosystems are particularly at risk of population declines as saline lakes shrink. Many of these species are well-adapted to saline habitats, and rely on saline lakes and their peripheral wetlands as stopover, breeding, and foraging sites (Saccò *et al.*, 2021; Wurtsbaugh *et al.*, 2017). Globally, shrinking saline lakes have been tied to population declines or local extirpation of numerous colonial avian species, including greater flamingos (*Phoenicopterus roseus*) in Iran's Lake Urmia (Sima *et al.*, 2021), and at least ten species in central Asia's Aral Sea (Joger *et al.*, 2012). Migratory species may be impacted most severely by saline lake habitat loss, because these areas often serve as final breeding or wintering destinations (e.g., Wilson's phalaropes (*Phalaropus tricolor*) in Laguna Mar Chiquita, Argentina), or serve as critical staging or refueling areas during seasonal migration (e.g., eared grebes (*Podiceps nigricollis*) in Great Salt Lake, USA).

Great Salt Lake is the largest saline lake in North America, and its location in the arid Great Basin, Utah, makes it an irreplaceable resource for migrating and breeding birds in the western hemisphere (Wurtsbaugh *et al.*, 2017). The lake and peripheral wetlands harbor large invertebrate and fish populations that feed up to ten million birds annually (Baxter & Butler, 2020). An estimated one-third of breeding and migrating birds in the western United States visit Great Salt Lake at some point in the year (Paul & Manning, 2002), including species of state and regional conservation concern (Sorensen *et al.*, 2020). Great Salt Lake water levels have shrunk dramatically since their peak in the 1980s, primarily due to agricultural water use (Wurtsbaugh *et al.*, 2016). These lake

level declines have compromised an estimated 40% of habitat used by invertebrate populations within the lake itself (Wurtsbaugh *et al.*, 2016), and have desiccated more than 80% of peripheral wetlands containing invertebrates, fish, and critical bird nesting habitat (Wurtsbaugh & Sima, 2022).

Decreasing water levels are frequently a primary driver of avian declines in saline lake ecosystems (Herbst & Prather, 2014; Micklin, 2007; Wurtsbaugh *et al.*, 2017), but for species of conservation concern, understanding how water levels and other drivers (environmental or otherwise) affect these populations is crucial to managing species appropriately. Water level declines may shrink breeding and foraging habitat directly (Diem & Pugsek, 1994; Moreno-Matiella & Anderson, 2005) or may allow predators access to previously isolated island breeding colonies (Moreno-Matiella & Anderson, 2005). Local weather and regional climate conditions may affect nest success, cause direct mortalities, or alter prey populations (Madden & Restani, 2005; Sovada *et al.*, 2014). Additionally, lagged effects of environmental conditions on a population through recruitment and survival may underlie interannual or long-term population dynamics (Evans *et al.*, 2023; Cornford *et al.*, 2023). For migratory species, conditions on the breeding or wintering grounds may produce carryover effects that also impact population dynamics across the full annual cycle in complex ways (Fayet *et al.*, 2016; Sillett *et al.*, 2000). With many possible competing hypotheses, decision-making frameworks that first quantify effects of threats that are within management control, then identify what actions may be most effective prior to enacting management on these species are ideal (Runge *et al.*, 2011).

Here, I investigate factors hypothesized to have contributed to American White Pelican (*Pelecanus erythrorhynchos*; hereafter “pelican”) population declines within the shrinking Great Salt Lake ecosystem, including declining lake levels, colony access by predators, and regional and local environmental conditions. I use long-term monitoring data from a population of pelicans that nest colonially within the shallow, hypersaline north arm of Great Salt Lake. Great Salt Lake pelican colony abundance has been declining since the late 1980s, but no formal assessment of its population drivers has been conducted to date. I also develop a population viability analysis (PVA) framework to forecast population abundance under alternative environmental and management scenarios, and apply it to Great Salt Lake pelican colony count data.

METHODS

Study site and colony counts

The Gunnison Island pelican breeding colony (Gunnison Island State Wildlife Management Area, Box Elder County, Utah, USA; Figure 5.1) is among the largest pelican colonies in western North America. At a peak count of approximately 20,000 breeding individuals, this population likely acts as a primary contributor to the western metapopulation of this species (Kijowski *et al.*, 2020), and is therefore important to the metapopulation’s persistence. Pelicans nest in small, dense subcolonies on benchlands around the island. Due to high water salt content and subsequent lack of forage fish near the breeding colony, pelicans nesting on Gunnison Island must travel > 45 km to forage in shallow wetlands in the U.S. Fish and Wildlife Service Bear River Migratory Bird Refuge and near the Salt Lake City International Airport along the eastern periphery of Great Salt Lake (Figure 5.1).

The Utah Division of Wildlife Resources (UDWR) began conducting colony counts opportunistically in 1963, and has conducted standardized fixed-wing aircraft counts of the Gunnison Island pelican population, beginning sporadically in 1976 and annually from 1980 to present. Counts were conducted in approximately the third week of May, during the pelican incubation period (J. Neill, UDWR, written communication, 2016).

Break-point analysis

Gunnison Island has experienced numerous and changing factors potentially influencing pelican abundance, including human disturbance and drought, and has displayed dramatic growth and interannual changes in abundance since colony counts began (Figure 5.2). I therefore expected that population drivers may act differently on colony abundance under different growth dynamics. I used a break-point analysis (Bahlai & Zipkin, 2020) conducted on all years of count data since regular, annual surveys began (i.e., 1980–2020) to identify the change in population trajectory between exponential growth and stable dynamics. The break-point analysis uses iterative model-selection to detect parameter value shifts in a population time-series by breaking time-series data into all possible subsets of four or more consecutive data points and fitting a population growth model to each. The analysis then evaluates all tested models using the Akaike information criterion for small sample sizes (AICc; Akaike, 1974) and identifies the best performing model (i.e., the model that contains the most explanatory break point combinations). I defined study period years as those years occurring after the best performing exponential-stable dynamics breakpoint.

Environmental covariates

I developed a set of environmental drivers hypothesized to influence pelican population dynamics (see Table 5.1 for full description of hypotheses). I hypothesized that local water levels may drive colony abundance by influencing availability of wetland foraging habitat and by facilitating predator access to colony habitat, especially in low water years (Anderson, 1991; Kijowski *et al.*, 2020). Extremely high water levels may also reduce available foraging area by making water too deep for pelicans to forage in (Anderson, 1991). However, within the study period, water levels in nearly all years were conducive to pelican foraging habitat (Artmann, 2017; Tarboton, 2017), and low water levels were expected to impact pelicans in future years, given overall regional water scarcity during this period. Therefore, I expected colony counts and water levels to have a linear relationship. I hypothesized that local spring temperatures may affect nest success, relating to chicks' cold stress limits (Evans, 1984). I also expected that negative density dependence indicates breeding gap years or dispersal to other nesting sites following years of high colony density, whereas positive density dependence reflects conspecific attraction and natal colony fidelity as first-time breeders choose breeding sites. Furthermore, I hypothesized that large-scale fluctuations in long-term temperature and precipitation regimes may influence breeding population dynamics through their influence on pelican survival and fecundity (Holmgren *et al.*, 2001; Sillett *et al.*, 2000; Stenseth *et al.*, 2002).

I obtained environmental data from sources with continual coverage across the study period as defined by the break-point analysis. I calculated annual mean breeding-season (April–July) water levels from monthly water level data at the U.S. Geological

Survey water level gage nearest to Gunnison Island (Great Salt Lake Near Saline, UT, USGS station no. 10010100, <https://waterdata.usgs.gov/monitoring-location/10010100/>) (U.S. Geological Survey, 2023). I derived a ‘land bridge presence’ indicator (an index of whether terrestrial predators have access to the island; Baskin & Turner, 2006; J. Neill, UDWR, written communication, 2016; Kijowski *et al.*, 2020) in years when Great Salt Lake water levels were below 1,278.5 m (measured in meters above sea level). I calculated mean minimum temperatures during April–July from monthly minimum temperature summaries collected at the Salt Lake City International Airport weather station (<https://w2.weather.gov/climate/xmacis.pp?wfo=slc>). I calculated mean annual Pacific Decadal Oscillation (PDO) index, an index of sea-surface temperature anomalies across the north Pacific Ocean, and Southern Oscillation Index (SOI), a climate index based on sea level air pressures in the tropical Pacific Ocean, from monthly indices (PDO: retrieved from the National Centers for Environmental Information, URL: <https://www.ncei.noaa.gov/pub/data/cmb/ersst/v5/index/ersst.v5.pdo.dat>; ERSST v5; SOI: retrieved from the NWS Climate Prediction Center, URL: <https://www.cpc.ncep.noaa.gov/data/indices/soi>). Pacific Decadal Oscillation and SOI have been implicated in continent-wide climate anomalies at annual and decadal scales (Mantua & Hare, 2002; Rasmusson & Wallace, 1983). I used annual colony size as a proxy for population density, as available nesting habitat stays relatively constant from year to year, despite fluctuating Great Salt Lake water levels changing the total exposed area of Gunnison Island.

Environmental covariates may act on a population immediately (e.g., direct mortality), or may have lagged effects on population dynamics (e.g., carryover effects). I

therefore included same-year effects (excluding density dependence, which depends on abundance of previous years) as well as one-, three-, and four-year lagged effects of all covariates in the model. Time lags were chosen based on pelican life history, where a lag of one year represents adult response to conditions in the previous year, while lags of three and four years represent recruitment of first-time breeders into the colony (Table 5.2).

Model description and fitting

I used a state-space modeling (SSM) framework to estimate latent true colony abundance as a function of current and time-lagged environmental covariates and density dependence, while accounting for over- and under-counting colony size (Auger-Méthé *et al.*, 2021; Newman *et al.*, 2014). I explored time-lagged effects by shifting covariate data toward the present by n lag years, while leaving count data associated with the years in which the data were collected (e.g., N_t reflects conditions at time $t-n$; Eq. 5.1). I first conducted a variance inflation factor (VIF) analysis on a model containing all covariates, to quantify multicollinearity in my predictors. All covariates had VIFs of less than five (James *et al.*, 2013), and I therefore included all covariates in my analysis. Due to the large number of hypothesized covariates ($n = 33$) and limited years of data ($n = 36$), I conducted a univariate screening procedure to reduce the number of covariates within my final (“global”) model. For the univariate screening, I ran individual models containing a single environmental covariate with all associated time lags (i.e., zero-, one-, three-, and four-year lags). My goal was to eliminate predictors with no effect on pelican counts, rather than to select only the strongest predictors (Grosbois *et al.*, 2008), and therefore I

set the inclusion level to any predictors with 80% credible intervals (CIs) not overlapping zero.

The co-occurrence of temporal trends in both population size and environmental covariates can lead to the detection of spurious relationships in regression-based analyses, where detected relationships between variables are a result only of overall trends and not of variation within these trends (Graham, 2003; Grosbois *et al.*, 2008). To strengthen inference about whether the environmental processes influence colony dynamics at an annual scale, I first removed temporal trends from covariate time-series by regressing each environmental covariate against year, then used model residuals as the annual covariate values in the SSM, so that values represent deviations from the mean trend and not the trend itself (Grosbois *et al.*, 2008; Rushing *et al.*, 2016).

Colony counts were log-transformed to linearize density-dependent terms (Auger-Méthé *et al.*, 2021; Royama, 1992), and covariates were modeled with the following process formulation:

$$\log(N_t) = \beta_0 + (1 + \beta_{N1})\log(N_{t-1}) + \beta_{N3} \log(N_{t-3}) + \beta_{N4} \log(N_{t-4}) + \beta_{X1} X_{1,t-0} + \dots + \beta_{Xi} X_{i,t-n} + z_{proc_t} \sigma_{proc} , \quad (5.1)$$

where N_t represents annual abundance at time t , β_0 represents a global intercept term, β_N terms represent density dependent slope coefficients expressed as a linearized autoregressive process (Royama, 1992), and β_X terms represent environmental covariate slope coefficients. Xs represent environmental covariates i , indexed by year t , with a time lag of n years, where $n = (0, 1, 3, 4)$. I modeled process variance using $z_{proc_t} \sigma_{proc}$ a

decomposition of process variance into an annually indexed normal distribution centered on zero multiplied by the standard deviation of process variance, which resulted in better convergence than alternative parameterizations.

I used the following observation model:

$$\log(y_t) \sim \text{Normal}(\log(N_t), \sigma_{\text{obs}}^2),$$

where y_t is the observed colony count in year t and σ_{obs}^2 is the observation error. Environmental covariate terms were given zero-mean normal priors, $\text{Normal}(0, 1.75)$, z_{proc_t} was modeled with a $\text{Normal}(0, 1)$ prior, and variance terms were given $\text{Gamma}(0.1, 0.1)$ priors.

The univariate screening procedure resulted in the following global model:

$$\begin{aligned} \log(N_t) = & \beta_0 + (1 + \beta_1)\log(N_{t-1}) + \beta_2\log(N_{t-4}) + \beta_3\text{waterlevel}_{t-1} + \beta_4\text{temperature}_t + \\ & \beta_5\text{temperature}_t^2 + \beta_6\text{bridge}_{t-1} + \beta_7\text{year}_t + z_{\text{proc}_{t-4}}\sigma_{\text{proc}}, \end{aligned}$$

where N represents annual abundance at time t , β_0 represents the global intercept, and β_n terms represent environmental covariate slope coefficients.

All models were estimated in R (version 4.3.1; R Core Team, 2023) with the package *NIMBLE* (de Valpine *et al.*, 2017; NIMBLE Development Team, 2022), using three chains with 100,000 iterations each, after 10,000 iterations of burn-in to achieve model convergence. To avoid influencing model outcomes from outside of the non-exponential growth phase determined by the break-point analysis, I did not consider

count data from prior to 1985. Therefore, incorporating density dependence time lags in the model left model years one through four without associated count data. I estimated these missing years of count data (i.e., $\log(N_{1:4})$), as well as parameter estimates z_{proc} , σ_{proc} , and σ^2_{obs} , using NIMBLE's default random walk sampler. I used NIMBLE's automated factor slice Markov chain Monte Carlo (MCMC) sampler ("AF_slice"; Tibbits *et al.*, 2014) for all slope parameters to improve convergence. Model convergence was established using \hat{R} values (chains with $\hat{R} < 1.1$ were considered to have converged; Brooks & Gelman, 1998) and visual inspection of trace plots. Data, projected environmental covariates, and associated novel code used in this analysis are available in USGS data and software releases (Van Tatenhove *et al.*, 2024a; Van Tatenhove *et al.*, 2024b).

I evaluated the global model's predictive performance using temporal holdout validation (Auger-Méthé *et al.*, 2021), using the first 28 years (80% of data; 1985–2012) as training data to estimate the model parameters, and the remaining eight years (2013–2020) as test data. To quantify model fit, I calculated root mean squared percentage error (RMSPE; Shcherbakov *et al.*, 2013) of predicted versus observed data in the test set and generated 95% prediction intervals (i.e., the interval within which 95% of future observations are expected to fall, accounting for both the uncertainty in estimating the mean and the variability of individual predictions around that mean).

Population Viability Analysis (PVA) and future environmental scenarios

I conducted a PVA using posterior samples generated by the fitted global model to project colony abundance to 2040 under five possible management scenarios (see Table 5.3 for description of all tested scenarios), where each year's latent true abundance

is estimated concurrently as the model samples, resulting in an estimated colony abundance time-series for each model iteration (total iterations minus burn-in = 90,000). Expected future water level and temperature trends, assuming no adjustments in local water resource management or significant changes in climate (i.e., “status-quo”) were generated by regressing observed 1985–2020 data for each continuous covariate against year, and extrapolating the estimated trend 20 years into the future. The land bridge was designated as “present” for any projected water levels below 1,278.5 m above sea level. To explore how individual environmental covariates might affect colony abundance, I also investigated scenarios where I held future water level and temperature values constant at the 1985–2020 mean. Incorporating expected natural fluctuations in projected covariates would likely provide more realistic projections of future pelican abundance. However, this approach provides a clearer picture of how each covariate alone affects future colony abundance. Furthermore, constant covariate values can be interpreted to represent management actions to stabilize water levels lake-wide or hypothesized effects of greenhouse gas reductions on local temperatures. Finally, to project colony response to removing the land bridge (e.g., installation of fencing or predator removal), I set all projected land bridge data to zero (i.e., not present). These forecasts do not account for changes in environmental conditions outside the scope of the global model or immigration and emigration dynamics.

RESULTS

Break-point analysis

The break-point analysis identified three points of population dynamics change in the time-series: 1985, 2012, and 2019 (Table 5.4). The latter two years were well outside

of the exponential growth phase identified by the break point analysis (Figure 5.2), and I therefore restricted the analysis to only years within the non-exponential growth phase (1985–2020). I chose to retain count data from years 2012–2020, even though 2012 and 2019 were identified as break-points, as they likely represent other potential ecological “breaks” besides exponential-stable dynamics.

Global model

After performing variable screening, I retained density dependence, land bridge presence, spring temperature, and water levels (Table 5.5, Table 5.6) in the global model. The model demonstrated high predictive performance (RMSPE = 0.677; Figure 5.3) in eight-year temporal holdout data.

I found strong evidence for a negative effect of land bridge presence at a one-year lag, negative density-dependence at one-year lag, and positive density-dependence at four-year lag (Table 5.6). I estimated that the colony declined approximately 20.5% following years where a land bridge was present (log mean = -0.229 ; 95% CI: -0.447 , -0.014) compared to years without the land bridge. Colony abundance displayed negative density dependence with a one-year lag, with abundance expected to decline by an average of 0.8% (log mean = -0.838 ; 95% CI: -1.114 , -0.503) for every one percent increase in colony size in the previous year. Conversely, I found strong evidence of positive density dependence at a four-year lag, with abundance expected to increase by approximately 0.6% (log mean = 0.621 ; 95% CI: 0.317 , 0.868) for every one percent increase in colony size four years prior. I found moderate evidence for a positive relationship between abundance and both minimum spring temperature and water levels. After accounting for temporal trends in colony abundance, my model estimated colony

abundance would increase on average by 5.8% (log mean = 0.056; 95% CI: -0.008, 0.122) for each degree Celsius of minimum spring temperature increase. Similarly, for each meter of Great Salt Lake water level increase, I would expect the population to increase by 9.7% (log mean = 0.093; 95% CI: -0.044, 0.236).

Population Viability Analysis (PVA)

Between 1985 and 2020, the Gunnison Island colony declined by a median value of 1.5% per year, with high interannual variability, resulting in a cumulative population decline of 17.9%. Under the PVA “status-quo” scenario (Table 5.3), the colony is predicted to further decline by 37.3% by 2040, to an estimated 5,062 individuals (95% CI: 1,490, 9,131; Figure 5.4). Under the “stabilizing spring temperatures” scenario, the population is projected to decrease 47.9% below 2020 levels (a further 17.1% decrease from “status quo” PVA estimates; Figure 5.4a to 4,201 individuals (95% CI: 954, 8,638). However, under the “land bridge elimination” scenario (Table 5.3), the pelican population is expected to increase to 9,993 individuals (95% CI: 3,411, 18,962) by 2040, an increase of 23.8% from 2020 estimates, and a 97.4% increase from the 2040 prediction for the “status quo” (Figure 5.4a). Pelican populations are expected to increase the most when both the land bridge is eliminated and water levels are returned to their 1985–2020 average, to an estimated 12,423 individuals (95% CI: 5,973, 19,638; a 53.9% increase from 2020 estimates and 145.4% increase from “status quo” PVA estimates; Figure 5.4b).

DISCUSSION

Using long-term monitoring data, I quantified effects of hypothesized population drivers on a declining colonial American white pelican population within a shrinking saline lake ecosystem. I also projected population abundance into the future under potential environmental and management scenarios to suggest possible management approaches for protecting this species into the future. This developed workflow may be translated to other avian species in declining saline lake ecosystems to quantify effects of hypothesized population drivers and identify future outcomes of plausible management scenarios. My case-study analysis indicates a direct link between Great Salt Lake declines and the decline of a regionally important American White Pelican colony, and highlights potential consequences of continued water level declines for the viability of this iconic species. The strong influence of local conditions on colony dynamics has important implications for the management of this species, suggesting that managers may be able to mitigate recent declines through local actions. However, without rapid management intervention, the PVA indicates that the Gunnison Island colony may go extinct within the 21st century.

I found strong evidence that land bridge presence is negatively related to colony abundance, supporting my hypothesis that Great Salt Lake's declining water levels impact population dynamics, likely by allowing terrestrial predators access to the previously predator-free island. Terrestrial predators, including red fox (*Vulpes vulpes*) and coyotes (*Canis latrans*) have been detected on Gunnison Island since 2017 (Kijowski *et al.*, 2020). Predator presence may dissuade waterbirds from nesting and often contributes to colony abandonment across colonial waterbird species (e.g., Parnell *et al.*,

1988), including pelicans (Moreno-Matiella & Anderson, 2005). I also found evidence of strong negative density dependence with a lag of one year, supporting my hypothesis that pelicans are likely limited by food or nesting sites, and therefore disperse from Gunnison Island to other breeding colonies or take breeding gap years following years of high colony density. Furthermore, I found evidence for positive density dependence with a time lag of four years. The mechanisms here are less clear but may be due to synergistic effects of natal colony fidelity (where pelicans hatched on Gunnison Island are likely to return to the colony as first-time breeders, reflecting colony abundance and nest success of their hatch year) and conspecific attraction common in colonial species like pelicans, influences Gunnison Island population dynamics.

While water levels were not a strong driver of colony abundance beyond their influence via land bridge presence, my PVA scenarios indicate that if Great Salt Lake water levels are increased in tandem with colony protection from predators, abundance could rebound toward historical levels faster than through management of either of these population drivers in isolation (Figure 5.4b). Alone, colony separation from the mainland (e.g., fencing or fladry installation) and/or predator control may offer a more immediate and relatively cost-effective solution to reversing population declines than refilling Great Salt Lake, a task requiring legislative, agricultural, and municipal cooperation across the Great Salt Lake watershed amid drought conditions and increasing human water use. However, a two-pronged approach could provide comprehensive protections for the breeding colony, wetland foraging habitat, and critical migratory stopover habitat that the Gunnison Island pelican population and other species rely on, well into the future.

Recent events at the Gunnison Island colony underscore the need for rapid management actions to address colony declines, and to view the PVA population decline estimates as conservative. While conducting a shorebird monitoring flight over Great Salt Lake in late June 2023, UDWR officials noted the near-complete abandonment of Gunnison Island by nesting pelicans. Previous colony abandonment or near-abandonments have occurred at Gunnison Island (Kijowski *et al.*, 2020), but the current 2023 abandonment is the first recorded instance where factors beyond human disturbance to the colony appear to have caused colony-wide nesting failure. This single-season abandonment may not represent complete colony extinction, but it does imply that the PVA may underestimate declines, which indicates that without management, colony abundance could decline by 37.3% by 2040. The PVA may underestimate these declines due to unexpected environmental shifts not captured in projected environmental covariates and emerging conditions not included within the model. Great Salt Lake is experiencing unprecedented changes as climate variability increases and human population growth further stresses water systems. Compounded effects of increasing water diversions and evaporation from Great Salt Lake as regional temperatures climb may cause future water levels to decline more quickly than projected (Hall *et al.*, 2021). Shifts in prey availability and increased predator activity may also lead to unexpected population dynamics like those observed in 2023. Unmodeled factors including disease and lake level management may impact population dynamics in unexpected ways as well. Since its widespread introduction into wild bird populations in 2021, highly pathogenic avian influenza (HPAI) infections have devastated colonially nesting bird species globally, including numerous pelican species (Alexandrou *et al.*, 2022; Lo *et al.*, 2022;

Ministerio de Salud, 2022). Highly pathogenic avian influenza has not been detected at the Gunnison Island colony, but has been confirmed in pelicans within Utah (Utah Division of Wildlife Resources Avian Influenza Dashboard, 2023), with the potential to affect nesting populations in the future. Finally, salinity level management for brine shrimp production may uncouple water levels within the lake's north arm from those in the south arm (Marden *et al.*, 2020), where most Great Salt Lake wetland habitat is located. In February 2023, a berm was placed across the causeway breach to prevent hypersaline water from flowing into the south arm and threatening Great Salt Lake's brine shrimp fishery. Until the berm is removed or other causeway breaches are constructed, water level gage measurements in the north arm of the lake, which were used in analyses presented here, may no longer represent conditions in the south arm, including at important pelican foraging sites.

Improving saline lake protections is expected to benefit avian biodiversity at a global scale. Given the recent record declines and expected continued anthropogenic impact on saline lake ecosystems globally, there is an urgent need to quantify how these ecosystems can be managed to conserve the biodiversity that relies on them. Ecological collapse of saline lakes occurring within high-use avian migration corridors, like Great Salt Lake in the Pacific Flyway, may have rapid, outsized impacts on species' survival and abundance, leading to flyway collapse (Conover & Bell, 2020; Micklin, 2007). Global initiatives are beginning to focus on these shrinking habitats (e.g., the recent National Park designation of Laguna Mar Chiquita, Argentina (Castellino, 2022) and the Saline Lake Ecosystems in the Great Basin States Program Act (2022)), but for large saline lakes like Great Salt Lake, the logistical and legal complexity of this process

means it will likely take years before measurable on-the-ground progress is made (Jacobs Engineering Group, 2019). Considering many of these ecosystems are facing imminent or ongoing habitat loss (Wurtsbaugh *et al.*, 2017), we may lose substantial hemispheric avian biodiversity unless immediate actions are taken to protect saline lake-reliant species. Restoration of desiccated saline lakes has shown promise in restoring migratory bird habitat and fisheries, and mitigating blowing toxic dust (Los Angeles Department of Water and Power, 2016; Micklin, 2016). However, proactive approaches to protecting saline lakes could limit irreversible biodiversity loss, reduce human and wildlife health impacts, and dramatically lower the cost of conserving the unique ecosystems these lakes harbor.

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TABLES AND FIGURES

Table 5.1: Hypotheses and predicted relation of potential environmental American White Pelican population drivers at the Gunnison Island colony, Great Salt Lake, Utah, from 1985–2020.

Driver	Scale	Hypothesis	Relationship	Citations
Colony abundance	Local	N decreases when previous year's N is large, due to individuals abstaining from breeding or moving to less crowded breeding colonies; N increases when N three or four years prior is large, reflecting the return of first-time breeders to the colony in numbers corresponding to hatch year cohort size	-/+	Moulton <i>et al.</i> , 2018
Mean annual Great Salt Lake water level	Local	N increases with increasing water levels as wetland foraging area increases	+	Doxa <i>et al.</i> , 2012
Land bridge presence	Local	N decreases with land bridge presence, due to terrestrial predator presence	-	Bunnell <i>et al.</i> , 1981; Kijowski <i>et al.</i> , 2020; Moreno-Matiella and Anderson 2005
Minimum spring temperature	Local	N increases as minimum spring temperatures increase, due to nestling intolerance of cold, then decreases due to nesting intolerance of extreme heat (i.e., a quadratic effect)	$-x^2$	Evans 1984; Madden and Restani 2005; Sovada <i>et al.</i> , 2014
Pacific Decadal Oscillation (PDO)	Broad	N decreases with positive PDO indices, which are indicative of colder, wetter conditions across multiple years	-	DeRose <i>et al.</i> , 2014; Wang <i>et al.</i> , 2010
Southern Oscillation Index (SOI)	Broad	N decreases with positive SOI indices, which are indicative of drier conditions across multiple years	-	Stagge <i>et al.</i> , 2023; Wang <i>et al.</i> , 2010; Wise 2010

Table 5.2: Hypothesized mechanisms underlying time lagged environmental drivers of American White Pelican population dynamics at the Gunnison Island colony, Great Salt Lake, Utah, from 1985–2020.

Time lag (years)	Mechanism	Citations
0	Driver affects N_t via annual fecundity or breeding conditions in year t	Rodenhouse <i>et al.</i> , 1997
1	Driver affects N_{t+1} via adult choice whether to breed at colony bases on colony conditions or food availability in year t	Tavernia <i>et al.</i> , 2021
3 & 4	Driver affects N_{t+3} or N_{t+4} via natal colony fidelity of N chicks fledged in year t	Tavernia <i>et al.</i> , 2021

Table 5.3: Population management scenarios and forecast environmental covariate data used to project population trajectories of American White Pelican colony abundance at the Gunnison Island colony, Great Salt Lake, Utah, between 2020 and 2040.

Scenario	Forecast environmental covariates		
	Water levels	Minimum spring temperatures	Land bridge
Status quo	Current trajectory continues	Current trajectory continues	Current status
Land bridge eliminated	Current trajectory continues	Current trajectory continues	Absent
Stable temperature and land bridge eliminated	Current trajectory continues	Constant at 1985–2020 mean (5.21°C)	Absent
Stable temperature	Current trajectory continues	Constant at 1985–2020 mean (5.21°C)	Present
Stable water levels and land bridge eliminated	Constant at 1985–2020 mean (1279.51m)	Current trajectory continues	Absent

Table 5.4: Break point analysis of pelican count data at the Gunnison Island colony, Great Salt Lake, Utah, from 1980–2020, using Bahlai & Zipkin’s (2020) dynamic shift detector. A population growth model is fit to years between each break (i.e., all possible subsets of 4 or more consecutive colony counts), from which AICc values (Individual AICc column) are calculated, then summed across the entire time-series (Total AICc column). The top performing model (bold) is the model with the lowest AICc.

Set of best performing models (lowest AICc)		
Breaks	Individual AICc	Total AICc
1985, 2012, 2019	104.344, 515.811, 126.234	752.389
1985, 2006, 2019	104.344, 398.690, 244.429	753.463
1985, 2011, 2019	104.344, 497.413, 146.255	754.012
Breaks tested		
Breaks	Break weights	Corrected weights
1983	0.042	0.053
1984	0.102	0.127
1985	0.385	0.480
1986	0.064	0.080
1987	0.028	0.034
1989	0.001	0.001
1990	0.001	0.001
1991	0.008	0.010
1992	0.004	0.005
1992	0.001	0.001
1994	0.003	0.004
1999	0.002	0.002
2000	0.035	0.044
2001	0.009	0.011
2002	0.009	0.011
2003	0.012	0.015
2004	0.007	0.008
2005	0.028	0.035
2006	0.155	0.194
2007	0.037	0.047
2008	0.029	0.036
2009	0.010	0.013
2010	0.005	0.006
2011	0.104	0.129
2012	0.205	0.256
2013	0.051	0.064
2014	0.019	0.024
2015	0.094	0.117
2019	0.802	1.000

Table 5.5: Univariate screening results and posterior state space model estimates (mean and 80% CIs) of Gunnison Island pelican count data and hypothesized population drivers. Bold rows indicate 80% CIs that did not overlap zero. Year was included in the global model to represent a year effect for all covariates. Spring temperature quadratic effect with a time lag of 1 year was not included because the main effect 80% CIs overlapped zero.

Covariate	Time lag	Mean	Lower 80% CI	Upper 80% CI
Density dependence	1-year lag	-0.754	-1.224	-0.324
Density dependence	3-year lag	0.026	-0.314	0.379
Density dependence	4-year lag	0.418	0.009	0.797
Density dependence	Year	-0.498	-0.967	-0.047
Land bridge presence	0-year lag	0.028	-0.177	0.236
Land bridge presence	1-year lag	-0.320	-0.512	-0.099
Land bridge presence	3-year lag	0.097	-0.143	0.288
Land bridge presence	4-year lag	-0.177	-0.405	0.111
Land bridge presence	Year	0.072	-0.673	0.780
Minimum spring temperature	0-year lag	0.050	0.013	0.082
Minimum spring temperature ²	0-year lag	-0.004	-0.020	0.011
Minimum spring temperature	1-year lag	-0.013	-0.043	0.016
Minimum spring temperature²	1-year lag	-0.016	-0.031	0.000
Minimum spring temperature	3-year lag	0.006	-0.026	0.037
Minimum spring temperature ²	3-year lag	0.008	-0.006	0.024
Minimum spring temperature	4-year lag	-0.025	-0.058	0.003
Minimum spring temperature ²	4-year lag	0.012	-0.006	0.028
Minimum spring temperature	Year	-1.194	-1.766	-0.523
PDO	0-year lag	0.027	-0.059	0.114
PDO	1-year lag	-0.081	-0.166	0.003
PDO	3-year lag	0.014	-0.080	0.109
PDO	4-year lag	-0.010	-0.114	0.096
PDO	Year	-1.013	-1.660	-0.367
SOI	0-year lag	-0.040	-0.154	0.074
SOI	1-year lag	0.082	-0.023	0.188
SOI	3-year lag	0.005	-0.099	0.109
SOI	4-year lag	0.098	-0.011	0.206
SOI	Year	-1.141	-1.765	-0.507
Water levels	0-year lag	-0.032	-0.083	0.020
Water levels	1-year lag	0.082	0.028	0.137
Water levels	3-year lag	-0.040	-0.099	0.020
Water levels	4-year lag	0.018	-0.064	0.099
Water levels	Year	-1.372	-2.074	-0.660

Table 5.6: Mean (log scale) state space model estimates and 95% credible intervals (CIs) of covariates included in the global model. Bold covariates indicate 95% CIs did not overlap zero.

Variable	Lag (years)	Mean Estimate	95% CI
Intercept	-	2.067	-0.923, 5.069
Year	-	-0.152	-1.007, 0.696
Density Dependence	1	-0.838	-1.114, -0.503
Density Dependence	4	0.621	0.317, 0.868
Land bridge presence	1	-0.229	-0.447, -0.014
Minimum spring temperature	0	0.056	-0.008, 0.122
Minimum spring temperature ²	0	0.029	-0.036, 0.094
Water level	1	0.093	-0.044, 0.236

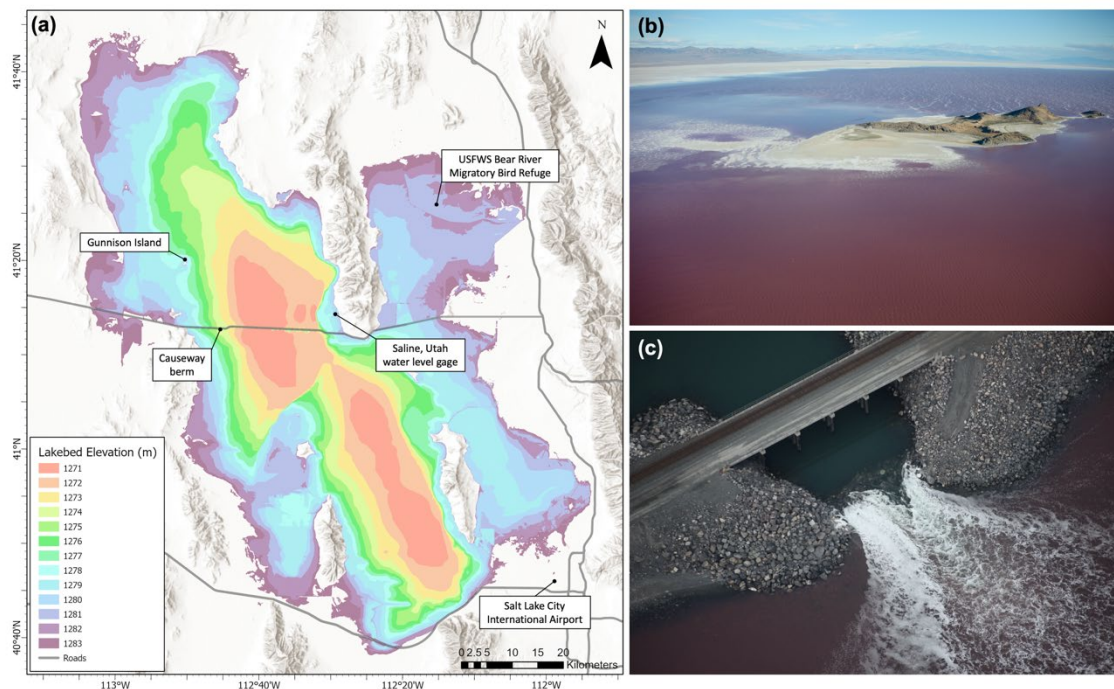


Figure 5.1: Notable features of Great Salt Lake, Utah, including locations of water level (Saline, Utah) and temperature gages (Salt Lake City International Airport), as well as foraging grounds nearest to the Gunnison Island pelican colony (U.S. Fish and Wildlife Service Bear River Migratory Bird Refuge). Photos depict (b) the land bridge that forms between Gunnison Island and the mainland when Great Salt Lake water levels fall below approximately 1,278.5 m above sea level, and (c) the railroad causeway berm that can be raised or lowered to adjust salinity and water levels of Great Salt Lake's north and south arms. Great Salt Lake bathymetry model credit: Tarboton (2017), digital elevation model credit: Jarvis *et al.* (2008), and photos credit: J. Neill, UDWR.

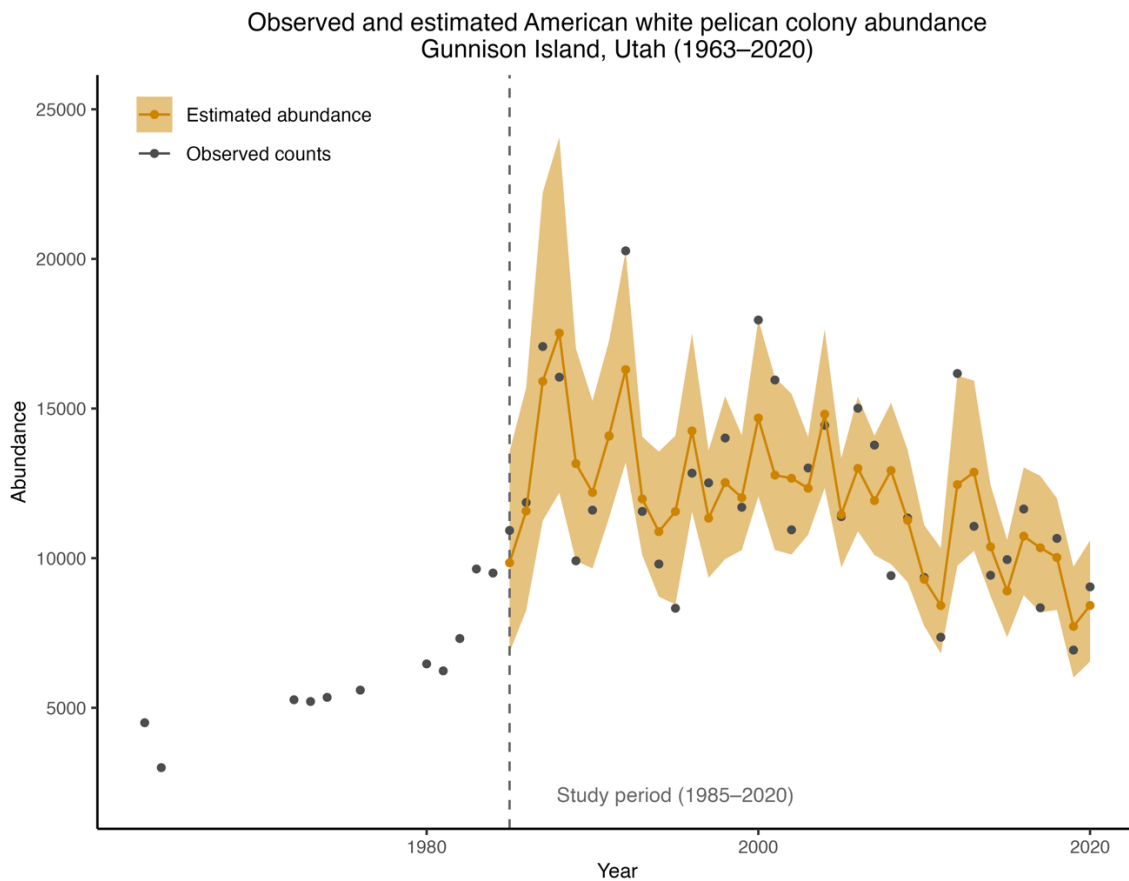


Figure 5.2: Observed counts from 1963–2020 (black dots) and estimated abundance from 1985–2020 (mean and 95% credible interval; orange) of the Gunnison Island pelican population. Only years from 1985–2020 (post-exponential growth) were included in the analysis, as the effects of population drivers may differ under different population growth dynamics.

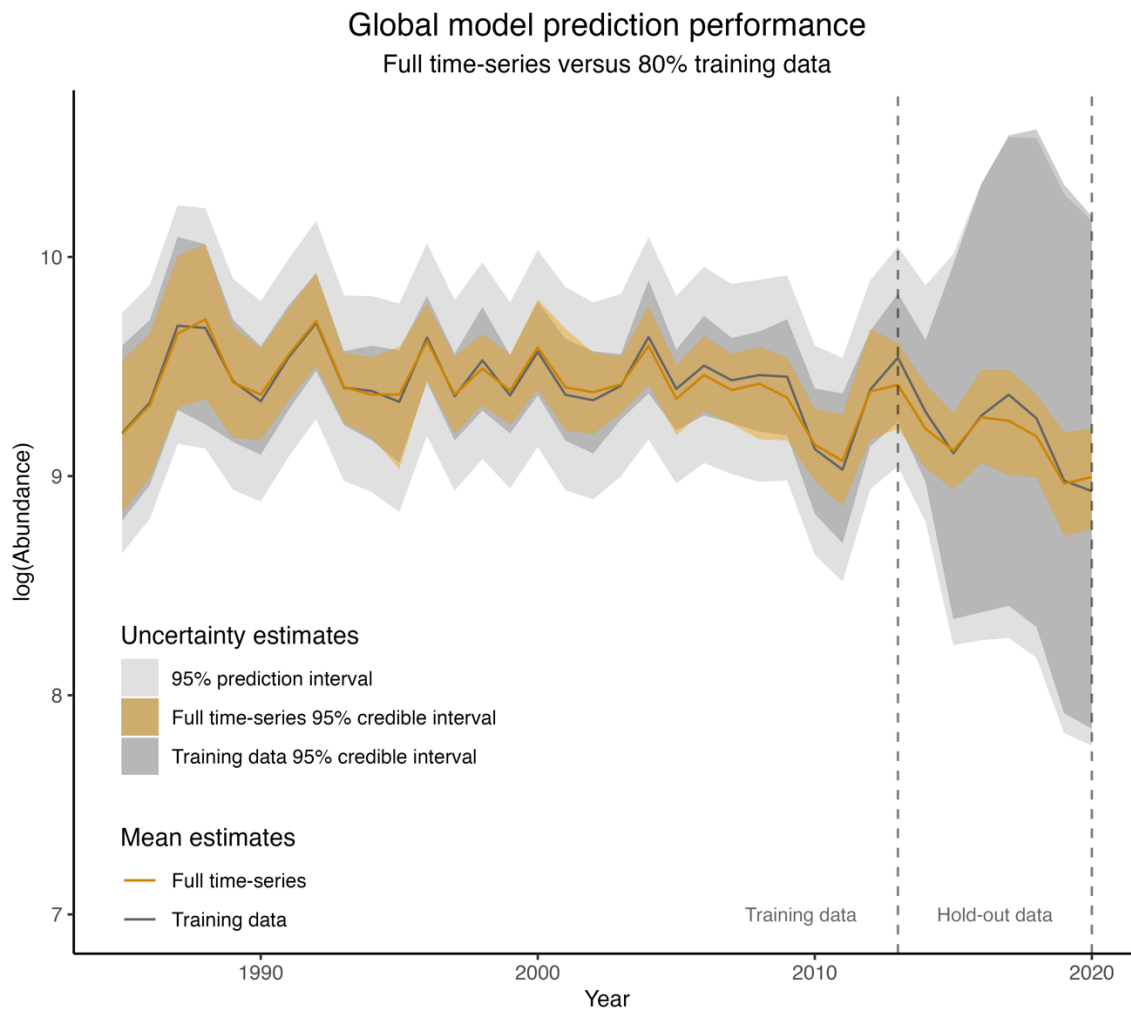


Figure 5.3: Predictive performance of the global state-space model. Performance was measured by fitting the model on 80% training data (years 1985–2012), then projecting the trained model onto remaining test years (years 2013–2020) to compare performance with a model fit on all years (orange). The global model fit only with training data (dark gray) had high predictive performance in hold-out data, with low error (RMSPE = 0.677), and was largely contained in the prediction interval (light gray).

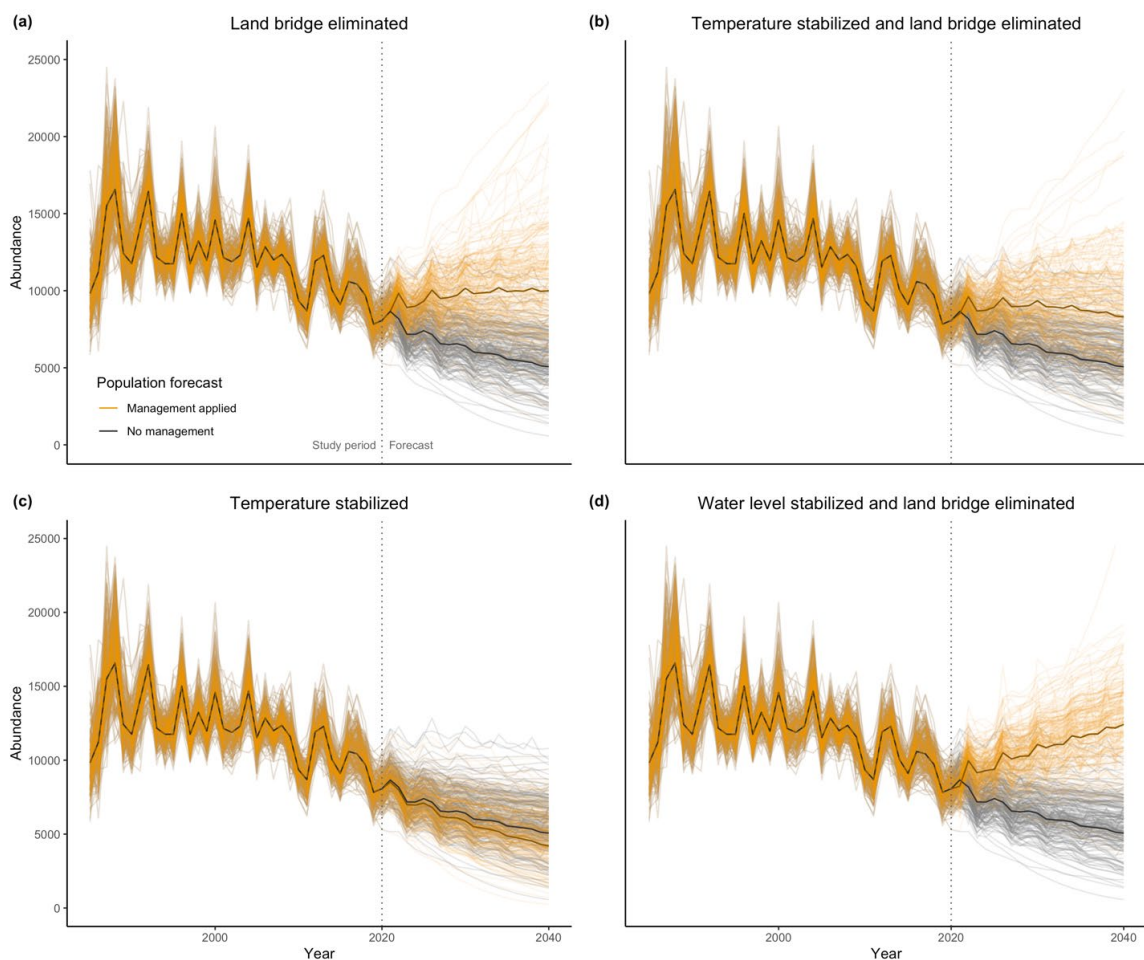


Figure 5.4: State-space model estimates of historical colony counts (“study period”, 1985–2020) and 20-year population viability analysis (“forecast”, 2021–2040) of the Gunnison Island American White Pelican breeding colony under selected environmental and management scenarios (Table 5.3). Thick opaque lines represent mean posterior estimates, while thin transparent lines are individual posterior estimates. Gray indicates estimated population trajectories if no management actions are taken (Table 5.3: “status quo”) and orange indicates population trajectories based on management scenarios listed in Table 5.3.

CHAPTER VI

DISCUSSION

Quantifying avian response to environmental change, and its underlying drivers, is difficult. Migratory species present an exceptional challenge, as these species may use heterogeneous landscapes across the full annual cycle, which are subject to differing environmental and anthropogenic conditions based on seasonality, climate, and local environmental laws. For migratory species with multiple populations, connectivity between these populations may be strong or weak, with implications for how heterogeneous conditions affect vital rates across multiple landscape scales (Cohen *et al.*, 2014; Cohen *et al.*, 2018). Furthermore, we often examine avian population response to environment at single biological scales: individual, sub-population, or population. These findings are crucial for describing avian response to climate and land-use change, but may not accurately describe avian response at all population levels (Carlson *et al.*, 2021). We may therefore miss important dynamics and context, limiting the impact and efficiency of conservation and management plans in the face of global population declines. My work attempts to build upon prior research addressing these issues, and explore improved avenues with which to quantify avian survival, migratory connectivity, and space use across multiple biological levels and landscape scales. This dissertation focused on American White Pelicans (*Pelecanus erythrorhynchos*), but the methods and conclusions drawn in the preceding chapters are applicable to many species beyond pelicans.

In Chapter 2, I advanced our understanding of how spatially-varied environmental conditions and migratory connectivity may influence species survival across a species'

range. I estimated regional annual survival and migratory connectivity from pelican band reencounter data, leveraging an existing, underutilized data source (Korner-Nievergelt *et al.*, 2010; Korner-Nievergelt *et al.*, 2012). I did so in a Bayesian joint recovery continuous-time framework, which incorporates information from individuals never reencountered after banding and estimates missing migration strategies, in order to utilize the most information possible from this dataset (Rushing, 2023). My findings demonstrate that pelican survival varies dramatically depending on what regions individuals reside in and migrate between, with important implications for how we manage pelican populations going forward. Pelican populations that remain in the western United States through the winter had up to 24% lower annual survival rates than those banded in the eastern region, perhaps due to poor conditions at overwintering sites like California's Salton Sea (Audubon, 2018; Shuford, 2002). The population that remained in the eastern region throughout the year, however, had the highest estimated annual survival of any migration strategy. High survival within this population may be the result of super-abundant food at aquaculture farms that has been linked to improved pelican body condition during winter months (King *et al.*, 2010). In addition to survival, I characterized migratory connectivity between summer and winter sites, and found that migratory connectivity was strong within banding regions (i.e., east and west). Considering nearly 64% of all pelicans banded in the western region remained in the western region over the winter, low survival rates associated with this migration strategy suggest local populations may be at risk of declines. Exploring potential causes of low survival rates associated with this migration strategy are crucial to proactively managing pelican populations in this region.

Chapter 3 explored niche breadth and variability of pelicans within the Pacific Flyway, with implications for expected pelican resilience to changing environmental conditions. I examined pelican occurrence across monthly precipitation and temperature conditions between the breeding and non-breeding grounds for this region, at both the individual and at the metapopulation level. I then compared these results to previous research conducted on the eastern metapopulation (Illán *et al.*, 2022). I found that individuals within the Pacific Flyway population (i.e., the western metapopulation) track climate niche between breeding and non-breeding grounds to varying degrees, but that the metapopulation as a whole does not appear to track climate niche. Few studies to date have examined niche across population levels (Carscadden *et al.*, 2020), and results from my research provide important context to how we conceptualize species niche breadth, variability, and expected response to climate change. Furthermore, I found that the western metapopulation did not occupy the full climate niche available in the breeding grounds, suggesting that this population may be limited in the areas it uses on the breeding grounds or that it may be experiencing barriers to dispersal and colonization of new sites, despite presence of favorable climate conditions across the breeding region. This effect was most noticeable in regard to temperature, indicating that this population may not be retreating northward fast enough to keep pace with poleward shifts in increasing temperature region-wide (Román-Palacios & Wiens, 2020). My findings add further support to the argument that pelicans in the western metapopulation may be disproportionately affected by climate and land-use changes as drought and water diversions increase across this region (Null & Wurtsbaugh, 2020; Williams *et al.*, 2022), especially at the southern edge of this population's range (Moulton *et al.*, 2018).

Linking avian space use and phenology to environmental drivers across broad scales requires improved tools to detect species presence and absence (Gauthreaux & Diehl, 2020; Stepanian *et al.*, 2016). In Chapter 4, I explored new methods to quantify pelican airspace use and phenology by combining information from pelican GPS location data with broadscale NEXRAD weather radar reflectivity data. To my knowledge, this is a method that has not been explored previously, but represents a promising avenue with which to estimate avian space use, phenology, and abundance. I characterized a pelican radar signature using ensemble machine learning, then used outputs from this model to predict pelican occurrence within radar airspace over Great Salt Lake, Utah. The model performed well, given extremely limited GPS location data within radar airspace. From the resulting predictions, I estimated relative seasonal pelican presence probability above Great Salt Lake. I found that predicted relative probability of pelican occurrence within radar airspace above Great Salt Lake was most variable in the spring, likely owing to variation in annual spring temperatures and individual migratory phenology. Predicted occurrence was highest overall in the fall, when chicks have gained the ability to fly and pelicans are staging in Great Salt Lake wetlands before fall migration. I also conducted a fine-scale analysis at the high-traffic Salt Lake City International Airport, where I predicted hourly pelican-airplane strike hazard for in- and out-bound air traffic. Twenty-seven percent of recorded pelican-airplane strikes in the United States have occurred at the Salt Lake City International Airport (Federal Aviation Administration, 2023), and air traffic is projected to increase with planned airport expansions as early as fall 2024 (RS&H, 2022; Wyatt, 2022), underscoring the need to mitigate pelican strike hazard at this location. I found that relative predicted pelican strike hazard was highest in the

afternoons and during fall months, and increased vigilance by airport wildlife crews or changes to flight schedules, if possible, to reduce flights during these times may reduce potential pelican-airplane strikes.

Finally, in Chapter 5, I formally linked population declines at Utah's Gunnison Island pelican breeding colony to environmental conditions. Population declines at this colony have been anecdotally linked to water level declines, predator disturbance, and food availability (Kijowski *et al.*, 2020), but my findings directly tie observed declines to formation of a land bridge from the mainland to the Gunnison Island colony and probable predator disturbance as a result. I found a strong effect of both positive and negative density dependence on interannual population variation, which has important implications for how we contextualize interannual changes in abundance (Doxa *et al.*, 2010; Moulton *et al.*, 2018) and suggests a link between natal colony conditions and abundance of first-time breeders returning to the colony. Furthermore, I projected species abundance into the future under various environmental and management scenarios, providing a roadmap for managers to use to conserve the pelican population at the Gunnison Island pelican breeding colony. Projections indicated that protecting the Gunnison Island colony from terrestrial predator access (e.g., via installation of fencing or fladry, or direct predator control measures) was beneficial to increasing colony abundance. Raising overall Great Salt Lake water levels (e.g., through regional water-saving measures, legislative initiatives, or water donations) in addition to colony protection measures provided the most benefit to colony abundance, likely through a combination of nesting site protection from predator disturbance and increases in available foraging area at important wetland foraging sites around Great Salt Lake.

My overarching goal for the research presented here was to improve our understanding of avian response to environmental change across spatial scales and heterogeneous landscapes, and in the process, improve and explore new tools with which to do so. American White Pelicans are an ideal system to study population responses and explore new methods given the large amount of data we have regarding their movements, habitat use, and abundance. My findings are largely in agreement with previous research on pelicans range-wide, but they provide additional, important context to population trends we are observing, and future expected responses to climate change. Moreover, my results underscore the clear need for continued study of this species in the face of rapidly changing environmental conditions, especially in the western metapopulation. American White Pelican populations are increasing as a whole, but the western metapopulation may be especially susceptible to increasing temperatures and drought, given its reliance on few, large breeding sites and possible limitations in its ability to make range shifts to keep up with changing favorable climate conditions. Future research and management of this iconic species should focus on understanding differences in population trends, range shifts, and survival between metapopulations, preventing terrestrial predator disturbance at breeding colonies, and increasing availability of high-quality wetland habitat year-round.

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Stepanian, P. M., Horton, K. G., Melnikov, V. M., Zrnić, D. S., & Gauthreaux, S. A. (2016). Dual-polarization radar products for biological applications. *Ecosphere*, *7*(11), e01539. <https://doi.org/10.1002/ecs2.1539>

Williams, A. P., Cook, B. I., & Smerdon, J. E. (2022). Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. *Nature Climate Change*, *12*(3), 232–234. <https://doi.org/10.1038/s41558-022-01290-z>

Wyatt, B. (2022). *SLC International Seeking 13 Retail and Restaurant Spaces for The New SLC-Phase 3*. Salt Lake City International Airport.

<https://slairport.com/assets/news/Procurement-Process-Underway-for-The-New-SLC-Phase-3.pdf>

CURRICULUM VITAE

Aimee M. Van Tatenhove

Department of Wildland Resources
 S.J. & Jessie E. Quinney College of Natural Resources
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 Website: www.avantatenhove.com
 Email: [aimee.van.tatenhove\[at\]usu.edu](mailto:aimee.van.tatenhove@usu.edu)

EDUCATION

- 2019 - present Ph.D. - Ecology**
 Department of Wildland Resources
 S.J. & Jessie E. Quinney College of Natural Resources
 Utah State University, Logan, Utah, USA
 Advisors: Dr. Clark S. Rushing & Dr. Erica F. Stuber
- 2010 - 2014 B.S. - Natural Resources**
 College of Agriculture & Life Sciences
 Cornell University, Ithaca, New York, USA
 Advisor: Dr. Patrick Sullivan

PROFESSIONAL APPOINTMENTS

- 2019 - present Fritz L. Knopf Doctoral Fellow - Graduate Research Assistant**
 Department of Wildland Resources & USU Ecology Center
 Utah State University, Logan, Utah, USA

Duties include designing and conducting original research on American white pelicans, including local population modeling, avian radar detection and presence prediction, and species distribution modeling; organizing lab group meetings and meeting topics; mentoring junior lab members; applying for research grants; planning setup and food prep for annual graduate retreat

- 2020 - 2023 Utah Public Radio - Science Reporter & Junior Editor**
 NPR-member station - Department of Agriculture and Applied Science
 Utah State University, Logan, Utah, USA

Duties include reporting on local and regional science, environment, and Great Salt Lake and Utah Lake water declines and development; conducting interviews; writing and editing scripts; recording and editing audio; creating web content; editing reporter scripts; leading news meetings and scheduling news content as needed

REFEREED PUBLICATIONS

Van Tatenhove, A.M., Neill, J., Norvell, R.E., Stuber, E.F., Rushing, C.S. **In press**. Scale-dependent population drivers inform avian management in a declining saline lake ecosystem. *Ecological Applications*.

Rushing, C.S., Van Tatenhove, A.M., Sharp, A.J., Ruiz-Gutierrez, V., Freeman, M.C., Sykes, P.W., Given, A.M., & Sillett, T.S. **2021**. Integrating tracking and resight data enables unbiased inferences about migratory connectivity and winter range survival from archival tags. *Ornithological Applications* 123 (2). doi: 10.1093/ornithapp/duab010 [[link](#)]

Fayet, A., Shirai, M., Matsumoto, S., Van Tatenhove, A.M., Yoda, K. & Shoji, A. **2019**. Differences in breeding success among neighbouring streaked shearwater subcolonies correlate with egg size and quality of parental care. *Ornithological Science*. doi: 10.2326/osj.18.189 [[link](#)]

Van Tatenhove, A.M., Filiberti, E., Sillett, T.S., Rodenhouse, N. & Hallworth, M. **2019**. Climate-related distribution shifts of migratory songbirds and sciurids in the White Mountain National Forest. *Forests* 10 (2): 84. doi: 10.3390/f10020084 [[link](#)]

Van Tatenhove, A.M., Fayet, A., Watanuki, Y., Yoda, K. & Shoji, A. **2018**. Streaked shearwater *Calonectris leucomelas* moonlight avoidance in response to low aerial predation pressure, and effects of wind speed and direction on colony attendance. *Marine Ornithology* 46: 177-185. [[link](#)]

Igic, B., Nunez, V., Voss, H.U., Croston, R., Aidala, Z., López, A.V., Van Tatenhove, A.M., Holford, M.E., Shawkey, M.D. & Hauber, M.E. **2015**. Using 3D printed eggs to examine the egg-rejection behaviour of wild birds. *Peerj* 3:E965. Doi: 10.7717/Peerj.965 [[link](#)]

Schulenberg, T.S., Arizmendi, M.D.C., Rodríguez-Flores, C.I., Soberanes-González, C.A., Behrstock, R.A. & Van Tatenhove, A.M. **2014**. Yucatan Nightjar (*Antrostomus Badius*), Version 1.0. In Neotropical Birds Online (T.S. Schulenberg, Editor). Cornell Lab Of Ornithology, Ithaca, New York, USA. Doi: 10.2173/Nb.Yucnig1.01 [[link](#)]

PRESENTATIONS

Invited Talks

Van Tatenhove, A.M., Stuber, E.F., Rushing, C.S. **2023**. Modeling survival and connectivity of a migratory waterbird in a continuous-time framework. Waterbird Society Annual Meeting, Fort Lauderdale, Florida, USA.

Van Tatenhove, A.M. **2022**. From Grantsburg to Utah. Grantsburg High School, Grantsburg, Wisconsin, USA.

Van Tatenhove, A.M. **2021**. A thirsty Great Salt Lake. Stokes Nature Center, Logan, Utah, USA.

Van Tatenhove, A.M. & Rushing, C.S. **2019**. Quantifying spatial and temporal population trends of North American pelicans. Waterbird Society Annual Meeting, Salisbury, Maryland, USA.

Van Tatenhove, A.M. **2019**. Pelicans through time and space. Stokes Nature Center, Logan, Utah, USA.

Van Tatenhove, A.M. **2019**. From Grantsburg to Utah. Grantsburg High School, Grantsburg, Wisconsin, USA.

Contributed Talks

Van Tatenhove, A.M., Neill, J., Norvell, R.E., Stuber, E.F., Rushing, C.S. **2023**. Scale-dependent population drivers inform waterbird management in an imperiled saline lake ecosystem. USU - USGS Coop Coordinators Meeting, Farmington, Utah, USA.

Van Tatenhove, A.M., Neill, J., Norvell, R.E., Stuber, E.F., Rushing, C.S. **2023**. Scale-dependent population drivers inform waterbird management in an imperiled saline lake ecosystem. The Wildlife Society UT/CO Chapter Annual Meeting, Grand Junction, Colorado, USA.

Van Tatenhove, A.M., Horton, K.G., Rushing, C.S., Stuber, E.F. **2022**. Weather radar as a tool to quantify local airspace-use of a large migratory waterbird. Waterbird Society Annual Meeting, Corpus Christi, Texas, USA. ****Won: Best Presentation Award**

Van Tatenhove, A.M., Horton, K.G., Rushing, C.S., Stuber, E.F. **2022**. Weather radar as a tool to quantify local airspace-use of a large migratory waterbird. American Ornithological Society Meeting, San Juan, Puerto Rico, USA. ****Won: Best Presentation Award**

Van Tatenhove, A.M., Rushing, C.S., Stuber, E.F. **2021**. Local versus broad-scale population drivers: a Bayesian state-space analysis of long-term American white pelican colony dynamics. Waterbird Society Annual Meeting, Virtual Meeting.

Van Tatenhove, A.M. & Rushing, C.S. **2021**. Local versus broad-scale population drivers: a Bayesian state-space analysis of long-term waterbird colony dynamics. American Ornithological Society Meeting, Virtual Meeting.

Van Tatenhove, A.M. & Rushing, C.S. **2020**. Quantifying spatial and temporal population trends of North American pelicans. North American Ornithological Conference, Virtual Meeting.

Van Tatenhove, A.M. & Rushing, C.S. **2020**. Quantifying spatial and temporal population trends of North American pelicans. Ecological Society of America Meeting, Virtual Meeting.

Van Tatenhove, A.M., Norvell, R., Conner, M., Kijowski, A., Brewerton, A., Neill, J., Moulton, C. & Green, M. **2019**. Conservation and management perspectives of American white pelicans within the Pacific flyway. Waterbird Society Annual Meeting, Salisbury, Maryland, USA.

TECHNICAL REPORTS

Van Tatenhove, A.M. **2016**. Kodiak: A successful seabird survey season. *U.S. Fish and Wildlife Service*. [[link](#)]

Stoner, K. & Van Tatenhove, A.M. **2016**. Kodiak: refuge doubles search effort for rare seabird nests. *U.S. Fish and Wildlife Service*. [[link](#)]

OUTREACH & MEDIA COVERAGE

ArcGIS Story Maps

Van Tatenhove, A.M., Juhlin, E., Dastrup, R.A. **2023**. Water for Wildlife: Dire consequences of a shrinking Great Salt Lake. *The Great Salt Lake Collaborative*. [[link](#)] ****Won: Society of Professional Journalists Top of the Rockies 2nd Place Award, Multimedia Story**

Radio Series

Van Tatenhove, A.M. & Juhlin, E. **2022**. Lake Effect: a storytelling initiative sharing impacts of Great Salt Lake. 30 episodes. *Utah Public Radio*. [[link](#)]

Selected Radio Pieces - full list available here [[link](#)]

Van Tatenhove, A.M. **2023**. Cache Valley Christmas Bird Count provides valuable data on avian populations. *Utah Public Radio*. [[link](#)]

Van Tatenhove, A.M. **2023**. Research ties worsening wildfires to bird mortalities. *Utah Public Radio*. [[link](#)] ****Won: Society of Professional Journalists Top of the Rockies 1st Place Award, Science and Technology Feature**

Van Tatenhove, A.M. **2022**. Cache Valley Christmas Bird Count successful, chilly. *Utah Public Radio*. [[link](#)] ****Won: Society of Professional Journalists 3rd Place Award, Radio–Best Use of Sound**

Van Tatenhove, A.M. **2022**. Increasing Great Salt Lake salinity predicted to impact Utah brine shrimp. *Utah Public Radio*. [[link](#)]

Van Tatenhove, A.M. **2022**. Utah State University brings academics and esports together. *Utah Public Radio*. [[link](#)] ****Won: Society of Professional Journalists 1st Place Award, Radio–General Feature**

Van Tatenhove, A.M. **2022**. A community science project studies the elusive, snow-loving rosy-finch. *Utah Public Radio*. [[link](#)] ****Won: Society of Professional Journalists 3rd Place Award, Radio–Environment**

Van Tatenhove, A.M. & Juhlin, E. **2022**. A deep dive into Utah Lake: Pt 1 & 2. *Utah Public Radio*. [[link](#)][[link](#)] ****Won: Society of Professional Journalists 2nd Place Award, Radio–Series**

Juhlin, E. & Van Tatenhove, A.M. **2022**. Boa Ogoi and the Bear River Massacre on Wednesday's Access Utah. *Utah Public Radio*. [[link](#)]

Van Tatenhove, A.M. 2021. Wild About Utah: the quiet importance of brine flies. *Utah Public Radio*. [[link](#)] ****Won: Society of Professional Journalists 2nd Place Award, Radio–Environment**

Van Tatenhove, A.M. 2021. Doughy Details: the science behind sourdough. *Utah Public Radio*. [[link](#)]

Van Tatenhove, A.M. 2021. Researchers track Utah's tiny hummingbirds. *Utah Public Radio*. [[link](#)]

Van Tatenhove, A.M. & Cornachione, H. 2021. A look at the impacts of insect decline, ways to counteract it. *Utah Public Radio*. [[link](#)]

Van Tatenhove, A.M. 2020. Christmas Bird Count: listening for owls. *Utah Public Radio*. [[link](#)] ****Won: Society of Professional Journalists 2nd Place Award, Radio–Best Use of Sound**

TEACHING EXPERIENCE

2020 Teaching Assistant - Utah State University

Applied Avian Ecology (WILD 5560; 3cr) led by Dr. Frank P. Howe

Designed from scratch and taught “Intro to population dynamics” and “Habitat distribution modeling with Maxent” labs; taught mark-recapture with emphasis on avian marking methods lecture; provided essay and quiz grades and feedback; provided support leading field trips

WORKSHOPS ATTENDED

2023 Introduction to Movement Ecology

Utah State University - one week course led by Dr. Kezia Manlove

Covered movement data set-up and cleaning, animal movement models, home range estimation methods, habitat selection, path segmentation (e.g., hidden Markov models for behavioral states), and methods for inferring connectivity.

2022 Introduction to GLMs and GLMMs for Life Science Grad Students

Utah State University - three day course led by Dr. Kezia Manlove

Covered link functions, likelihoods, prediction, model assumptions and performance, multilevel models, and implementation in a frequentist framework in R.

GRANTS AND FELLOWSHIPS

Total: \$137,055

2024

Travel Grant (\$500)

American Ornithological Society

- 2023 Research Grant (\$1650)**
Utah Division of Wildlife Resources
- 2023 Travel Grant (\$500)**
Waterbird Society Conference and General Meeting
- 2022 Travel Grant (\$700)**
Waterbird Society Conference and General Meeting
- 2022 Travel Grant (\$730)**
American Ornithological Society
- 2022 Research Grant (\$5000)**
Utah State University Ecology Center Research Award
- 2022 Research Grant (\$1000)**
Great Salt Lake Audubon Grant Program
- 2022 Research Grant (\$1000)**
Tracy Aviary Conservation Fund
- 2019 - 2023 Fellowship (\$125,000)**
Fritz L. Knopf Doctoral Fellowship in Avian Ecology and Conservation
- 2019 Travel Grant (\$375)**
Waterbird Society Conference and General Meeting
- 2019 Travel Grant (\$600)**
Utah State University Ecology Center

ACADEMIC AWARDS

- 2022 Student Presentation Award - The Waterbird Society**
Waterbird Society Annual Meeting, Corpus Christi, Texas, USA.
- 2022 Student Presentation Award - AOS Council**
American Ornithological Society Meeting, San Juan, Puerto Rico, USA.

PROFESSIONAL SERVICE

Professional Memberships

American Ornithological Society
Ecological Society of America
Pacific Seabird Group
The Waterbird Society

Reviews Provided

Ornithological Applications
The Waterbird Society

PROFESSIONAL SKILLS

Software & coding

R, JAGS, Nimble, Stan, unmarked, Maxent, ArcGIS Pro, MARK and RMark

Modeling

Bayesian state space models, multistate survival and movement models, ensemble machine learning

Field

Avian banding (passerines and pelicans), avian mist net extraction, point counts, nest searching, GPS backpack transmitter attachment, foothold trap deployment and use, bow net deployment and use, outboard motor operation, all-terrain vehicle operation, 4x4 vehicle operation

FIELD RESEARCH

2021 - 2023 Crew leader - American white pelican GPS-GSM transmitter deployment

Utah State University, Logan, Utah, USA

Led and trained volunteer field crew in capture of American white pelicans, attached GPS transmitters to pelicans, organized volunteer schedules, recruited volunteers, maintained trapping and transport equipment, organized trapping permissions on state and federal property

2019 - 2020 Banding assistant - passerines

Utah State University, Logan, Utah, USA

Extracted birds from mist nets for banding and light-level geolocator deployment, banded select passerine species with federal identification bands and RFID bands, maintained RFID equipped bird feeders, set up and took down mist nets

Total birds banded: 98; total birds extracted: 176

2018 Research assistant - alcid and procellariid productivity

U.S. Fish & Wildlife Service, Homer, Alaska, USA

Nest searched for petrel burrows, performed regular nest checks, collected repeat morphological measurements from petrel chicks, serviced nest cameras, mist netted for adult petrels, identified murre hatch dates from photos, digitized notebook data

- 2018** **Crew leader - avian point counts**
Smithsonian Migratory Bird Center, Hubbard Brook Experimental Forest, New Hampshire, USA
- Trained crew of four people in conducting avian point counts along transects, organized employee schedules based on weather and hiking conditions, trained employees in data entry, advised on safe practices while working alone outdoors*
- 2017** **Research assistant - streaked shearwater ecology**
Oxford and Hokkaido Universities, Awashimaura, Niigata Prefecture, Japan
- Nest searched, conducted regular nest checks on active burrows, captured adult shearwaters from burrows for GPS tag deployment/removal, assisted with GPS transmitter deployment/removal, serviced trail cameras, marked adult shearwaters for mark-recapture pilot study, collected moonlight level and colony attendance data*
- 2016** **Research assistant - Kittlitz's murrelet nesting ecology and near-shore marine bird surveys**
U.S. Fish & Wildlife Service, Kodiak, Alaska, USA
- Nest searched on rocky (up to 45°) slopes, maintained four remote field camps and associated gear in bear-dense area, assisted with murrelet banding, deployed and maintained nest cameras, recorded nest locations, conducted vegetation surveys at nest sites, digitized field notebook data, conducted near-shore transect counts of seabirds by species*