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Integrated population modelling improves the utility of partially aligned data

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Knowledge of demography is essential for understanding wildlife population dynamics and developing appropriate conservation plans under global change. However, population survey and demographic data (e.g., capture-recapture) are not always aligned in space and time, hindering our ability to robustly estimate population size and demographic processes. Integrated population models (IPMs) can provide inference for population dynamics with poorly aligned but jointly analysed population and demographic data. In this study, we developed an IPM for partially aligned population and demographic data, and applied this model to a migratory shorebird species, the snowy plover (*Charadrius nivosus*). Snowy plover populations have declined dramatically during the last two decades, yet the demographic mechanisms and environmental drivers of these declines remain poorly understood, hindering development of appropriate conservation strategies. We analysed 21 years (1998-2018) of partially aligned population survey, nest survey, and capture-recapture-resight data in three snowy plover populations (i.e., Texas, New Mexico, Oklahoma) in the Southern Great Plains of the US. By using IPMs we aimed to achieve better precision while evaluating the effects of wetland habitat (represented by Palmer drought severity index) and climatic factors (minimum temperature, wind speed) on snowy plover demography. Our IPM provided reasonable precision for productivity measures even with missing data, but population and survival estimates had greater uncertainty in years without corresponding data. Our model also uncovered the complex relationships between wetland habitat, climate, and demography with reasonable precision. The Palmer drought severity index had positive effects on snowy plover productivity (i.e., clutch size and clutch fate) and apparent survival, indicating the importance of protecting wetland habitat under climate change and other human stressors for the conservation of this species. We also found a positive effect of minimum temperature on snowy plover productivity, indicating

potential benefits of warmth during night on their population. Our study suggested that continuous population and capture-recapture surveys combined with segmented productivity survey data can be practical and useful for understanding population dynamics and underlying demographic processes in this and other species. Our modelling approach lays a foundation of allocating limited conservation resources for evidence-based conservation decision-making ~~under global change~~.

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Abstract

Knowledge of demography is essential for understanding wildlife population dynamics and developing appropriate conservation plans under global change. However, population survey and demographic data (e.g., capture-recapture) are not always aligned in space and time, hindering our ability to robustly estimate population size and demographic processes. Integrated population models (IPMs) can provide inference for population dynamics with poorly aligned but jointly analysed population and demographic data. In this study, we developed an IPM for partially aligned population and demographic data, and applied this model to a migratory shorebird species, the snowy plover (*Charadrius nivosus*). Snowy plover populations have declined dramatically during the last two decades, yet the demographic mechanisms and environmental drivers of these declines remain poorly understood, hindering development of appropriate conservation strategies. We analysed 21 years (1998-2018) of partially aligned population survey, nest survey, and capture-recapture-resight data in three snowy plover populations (i.e., Texas, New Mexico, Oklahoma) in the Southern Great Plains of the US. By using IPMs we aimed to achieve better precision while evaluating the effects of wetland habitat (represented by Palmer drought severity index) and climatic factors (minimum temperature, wind speed) on snowy plover demography. Our IPM provided reasonable precision for productivity measures even with missing data, but population and survival estimates had greater uncertainty in years without corresponding data. Our model also uncovered the complex relationships between wetland habitat, climate, and demography with reasonable precision. The Palmer drought severity index had positive effects on snowy plover productivity (i.e., clutch size and clutch fate) and apparent survival, indicating the importance of protecting wetland habitat under climate change and other human stressors for the conservation of this species. We also found a positive

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Key words: climate change, conservation, data integration, demography, human stressor, imbalanced sampling, population monitoring, wetland

Introduction

The knowledge of demographic processes is fundamental to learning about natural populations (Turchin 2003; Rockwood 2015). Due to continuous impacts of global change such as climate change and agricultural development on biodiversity patterns (Thomas *et al.* 2004; Foley *et al.* 2005; Parmesan 2006; Grimm *et al.* 2013) including population dynamics (Sæther, Sutherland & Engen 2004; Reist *et al.* 2006; Simmonds & Isaac 2007; Zhao *et al.* 2019), knowledge of demographic responses to environmental factors holds essential value in guiding conservation planning (Clark *et al.* 2001; Rushing *et al.* 2020).

It can be challenging to quantify population dynamics and underlying demographic processes with severely limited data. Inferences about demographic processes (e.g., survival) often relies on data of marked animals (e.g., capture-recapture data; Pollock 1991; Williams, Nichols & Conroy 2002), which can be difficult to collect. Furthermore, demography and population survey data are not always spatially and temporally aligned. Approaches that link population survey and demographic data are particularly useful when data are relatively sparse because they can potentially provide a comprehensive understanding of population dynamics and underlying demographic processes.

Integrated population models (IPMs) jointly analyse multiple types of data such as population survey, capture-recapture, and productivity information (Besbeas *et al.* 2002; Brooks, King & Morgan 2004; Schaub & Abadi 2011). These models can provide more accurate and precise parameter estimates than models that analyse each data type separately (Abadi *et al.* 2010; Schaub & Abadi 2011). Furthermore, IPMs can provide estimates of some parameters without direct data via sharing of information among data types (Besbeas *et al.* 2002; Tavecchia *et al.* 2009; Schaub, Jakober & Stauber 2013; Zhao, Boomer & Royle 2019). Consequently,

IPMs are particularly useful when data are sparse and unaligned or partially aligned in space and time (Saunders *et al.* 2019). IPMs have largely improved our understanding of natural animal populations (Schaub & Fletcher 2015; Ahrestani *et al.* 2017; Weegman *et al.* 2017; Zhao *et al.* 2019) and allow for the development of more effective and efficient conservation practices (Arnold *et al.* 2018; Zipkin & Saunders 2018; Zhao *et al*. 2020).

Many shorebird populations are sensitive to climate change (Van de Pol *et al.* 2010; Lehikoinen *et al.* 2013) because their key habitats (wetlands) are driven by weather and climatic factors (Sorenson *et al.* 1998; Sofaer *et al.* 2016; Zhao *et al.* 2016). Other types of human disturbance such as agricultural development may also lead to wetland habitat loss (Johnston 2013; Burgin, Franklin & Hull 2016; Donnelly *et al*. 2020). Consequently, shorebirds are threatened by multiple human stressors. For example, numerous North American shorebird populations have declined during the past half-century, likely due to degradation, fragmentation, and other kinds of human disturbance of wetlands (Howe, Geissler & Harrington 1989; Bart *et al.* 2007; Rosenberg *et al.* 2019). However, warming temperatures resulting from climate change may drive shorebird population dynamics by influencing incubation behaviour and partitioning of incubation duties, particularly during cold periods (e.g., at night), because warmer temperatures allow birds to reserve more energy for reproduction or survival (Van de Pol *et al.* 2010; Saalfeld *et al*. 2012). Greater wind speed during breeding seasons may increase physiological stress during incubation and accelerate water evaporation, and thus negatively impact shorebird demography and incubation success (Hilde *et al*. 2016).

The snowy plover (*Charadrius nivosus*) is a migratory shorebird species with breeding and wintering populations distributed along the Pacific Coast and Gulf Coast, as well as interior breeding populations in the Great Basin and Southern Great Plains (Page *et al.* 2009). Recent

studies have estimated a severe decline of the interior breeding populations in the Southern Great Plains (Andres *et al.* 2012; Saalfeld *et al.* 2013; Heath 2019). Knowledge of the demographic foundations and potential drivers of such a decline is essential for conservation planning of this species. However, knowledge gaps due to data limitations have hindered the development of effective conservation strategies.

In this study we developed an IPM analysing 21 years (i.e., 1998-2018) of partially aligned data for snowy plovers breeding within the Southern Great Plains. By using this modelling approach, we first aimed to achieve better precision of population and demographic estimates. We then evaluated the contributions of demographic processes to population growth. Lastly, we tested hypotheses regarding the drivers of productivity and survival, including wetland habitat, temperature, and wind speed. Based on our results, we provided recommendations for future population monitoring and conservation planning of snowy plover, and suggested prioritization of data collection schemes for conservation projects that often have limited resources.

Methods

Study area

Our study is located in the ecological region of the Southern Great Plains in Texas, New Mexico and Oklahoma (Figure 1), which encompasses semi-arid short and mixed grass prairie (Assal, Melcher & Carr 2015). More specifically, we studied 3 breeding populations in Texas, New Mexico and Oklahoma, respectively. Study sites included 3 privately owned saline lakes (i.e., A, B and C) and Muleshoe National Wildlife Refuge (NWR) in Texas, Bitter Lake NWR in New

Mexico, and Salt Plains NWR in Oklahoma. Details about the study sites can be found in Heath (2019).

Data collection

Population survey

For the Texas population, surveys were conducted weekly May through July at lakes A, B and C in 1998-2000, 2008-2010, and 2017-2018 (Figure 2), along transects that covered 3.2-3.5 km sections of shoreline (Heath 2019). Both the observers and survey areas were consistent within each year. Surveys began at approximately 08:00 and lasted 1-2 hours in days without abnormally high winds (i.e., wind speed >50 mph) or rain. For the New Mexico population, surveys were conducted biweekly and otherwise under the same protocol of the Texas population, in each year from 1999 through 2018.

For the Oklahoma population, annual surveys were conducted on a single day in early May from 2013 to 2017 at Salt Plains NWR. The entire salt flat area of Salt Plains NWR was divided into a total of 668 grids that were 300 m × 300 m, among which 100 were randomly selected for surveys. Biologists and volunteers were paired, and 10-12 grid cells were assigned to each pair to survey. Surveys were conducted along 300 m transects while birds within 75 m distance from the transects were counted. In addition to annual surveys, distance sampling was conducted at Salt Plains NWR during May-July in 2017 and 2018. The region was divided into three sub-regions (i.e., north, middle, south). The same grids of the annual survey were used, among which 9 (3 for north, 2 for middle, 4 for south) were randomly selected. Surveys were again conducted along 300 m transects, but in addition to counting birds with 75 m distance, the linear distance between the observed birds and the transects was also recorded.

136 More details about the population surveys can be found in Saalfeld *et al*. (2013) and Heath-
137 Acre *et al.* (2020).

138 *Nest survey*

139 We surveyed snowy plover nests at least once per week during the breeding season. Nests were
140 located by searching suitable habitat and observing adults incubating nests or flushing from or
141 returning to nests. The search effort was relatively consistent among study sites and years
142 (Conway, Smith & Ray 2005). Once a nest was located, clutch size (i.e., the number of eggs) and
143 ultimately clutch fate (success or failure) were determined and recorded. Nest surveys were
144 conducted in 1999-2000, 2008-2009, and 2017-2018 at lakes A, B and C, and in 1999-2000 and
145 2008-2009 at Muleshoe NWR for the Texas population, in 2017-2018 at Bitter Lake NWR for
146 the New Mexico population, and in 2017-2018 at the Salt Plains NWR for the Oklahoma
147 population.

148 *Capture-recapture-resight*

149 Adult snowy plovers were captured at feeding locations using mist nets and on nests using nest
150 traps (Conway & Smith 2000). Juveniles were captured within 24 hours of hatching, either by
151 hand in nests or with adult(s) after hatching. All captured individuals were banded with a
152 uniquely numbered U.S. Geological Survey aluminium band and a unique combination of colour
153 bands. Blood samples were collected during captures to identify sex (Saalfeld *et al.* 2013). The
154 identities of banded birds were recorded during subsequent captures or population surveys (see
155 above), yielding recapture and resighting information. The capture-recapture-resight surveys
156 were conducted in 1999-2000, 2008-2009, 2013-2014, and 2016-2018 at lakes A, B and C and
157 Muleshoe NWR for the Texas population, in 2013-2014 and 2017-2018 at the Bitter Lake NWR

158 for the New Mexico population, and in 2013-2018 at the Salt Plains NWR for the Oklahoma
159 population.

160 *Environmental data*

161 We considered Palmer drought severity index, minimum temperature, and wind speed as
162 potential drivers of snowy plover productivity and survival. Palmer drought severity index is a
163 measurement of the amount of surface water based on recent precipitation and temperature
164 (Palmer 1965). As Palmer drought severity index tends to be positively correlated with
165 precipitation and negatively correlated with maximum temperature (Appendix 1), it can be used
166 to represent wetland habitat availability that influences shorebird demography (Todhunter 1995;
167 Dinsmore 2008). High minimum temperature represented warmth during night, which may
168 influence snowy plover demography through energy reserves. We also considered wind speed
169 because greater wind speed may increase physiological stress during incubation and thus
170 negatively influence snowy plover survival and productivity. We also considered actual
171 evapotranspiration, precipitation, and maximum temperature, but these variables were highly
172 correlated with Palmer drought severity index and/or minimum temperature (Appendix 1), and
173 thus were not included in the model. We calculated the mean values of the above-mentioned
174 covariates during the breeding season (i.e., May-July) for each population and year and included
175 them in our IPM.

176 ***Modelling approach***

177 We developed an IPM to explain snowy plover population dynamics as a consequence of the
178 spatiotemporal variation in productivity and survival. Our IPM included three sub-models: a
179 population sub-model, a productivity sub-model, and a survival sub-model, which utilized

population survey, nest survey, and capture-recapture-resight data, respectively. We describe each sub-model and then the overall model below.

Population sub-model

We assumed that population size in region *i* in the first year, denoted $N_{i,1}$, followed a log-Normal distribution such that $log(N_{i,1}) \sim Normal(\mu_i^{[0]}, 0.1)$, in which $\mu_i^{[0]}$ was selected based on the population survey data of the corresponding region, and a small standard deviation of 0.1 was used. From the second year (i.e., $t \geq 2$), population size was assumed to follow a log-Normal distribution such that

$$log(N_{i,t}) = log\,(N_{i,t-1} \times 0.5 \times \phi_{i,t-1}^{[AM]} + N_{i,t-1} \times 0.5 \times \phi_{i,t-1}^{[AF]} + N_{i,t-1} \times 0.5 \times \gamma_{i,t-1} \times \pi_{i,t-1} \times 0.5 \times \phi_{i,t-1}^{[JM]} + N_{i,t-1} \times 0.5 \times \gamma_{i,t-1} \times \pi_{i,t-1} \times 0.5 \times \phi_{i,t-1}^{[JF]}) + \varepsilon_{i,t}^{[N]}, \quad (1)$$

in which $\phi_{i,t-1}^{[AM]}$, $\phi_{i,t-1}^{[AF]}$, $\phi_{i,t-1}^{[JM]}$, and $\phi_{i,t-1}^{[JF]}$ were apparent survival of adult males, adult females, juvenile males, and juvenile females, respectively, $\gamma_{i,t-1}$ was average clutch size, $\pi_{i,t-1}$ was clutch fate, and $\varepsilon_{i,t}^{[N]}$ were process errors that followed a Normal distribution of mean 0 and standard deviation $\sigma^{[N]}$. Note that we assumed that both adult sex ratio and clutch sex ratio were 1:1.

We then linked the population survey data with the true but latent population size. For the Texas and New Mexico populations, we assumed that population counts followed Poisson distributions such that $y_{i,t,k} \sim Poisson(N_{i,t} \times exp\,[\varepsilon_{i,t,k}^{[y]}])$, in which $y_{i,t,k}$ was the population count of population *i* in year *t* and date *k*, and $\varepsilon_{i,t,k}^{[y]}$ were observation errors that followed a Normal distribution of mean 0 and standard deviation $\sigma^{[y]}$.

For the Oklahoma population, we assumed that the grid-level (indexed by j) counts followed a Poisson distribution such that $y_{i,t,j} \sim Poisson(\frac{N_{i,t}}{668} \times exp\,[\varepsilon_{i,t,j}^{[y]}] \times p^{[ANN]})$ for the annual surveys from 2013 to 2017, in which the total population size was divided by the total number of grids (i.e., 668, see above), $\varepsilon_{i,t,j}^{[y]}$ represented the variation in local abundance among grid j, and $p^{[ANN]}$ was the detection probability for these annual surveys. We also assumed $y_{i,t,j} \sim Poisson(\frac{N_{i,t}}{668} \times exp\,[\varepsilon_{i,t,j}^{[y]}] \times p_{i,t,j}^{[DIST]})$ for the distance sampling in 2017 and 2018. Here we had $p_{i,t,j}^{[DIST]} = exp\,(-1 \times \xi \times d_{i,t,j})$, in which ξ was a decay parameter representing the assumption that detection probability would decrease when the linear distance between the birds and the transect, denoted $d_{i,t,j}$, increased (Royle *et al*. 2004).

Productivity sub-model

We assumed that clutch size and fate were functions of Palmer drought severity index, minimum temperature and wind speed. More specifically, we linked clutch size with these covariates using a multinomial logistic regression. We considered the probability of a clutch size n (denoted $\omega_{i,t}^{[n]}$) for n = 1, 2, and 3. Average clutch size was then calculated as $\gamma_{i,t-1} = 1 \times \omega_{i,t}^{[1]} + 2 \times \omega_{i,t}^{[2]} + 3 \times \omega_{i,t}^{[3]}$. We then had $\omega_{i,t}^{[n]} = \frac{\theta_{i,t}^{[n]}}{\sum_{n=1}^{3} \theta_{i,t}^{[n]}}$, in which $\theta_{i,t}^{[1]}$=1, and $\theta_{i,t}^{[2]}$ and $\theta_{i,t}^{[3]}$ were expressed as functions of the above-mentioned covariates such that

$$log\left(\theta_{i,t}^{[2]}\right) = \alpha^{[2]} + \beta_1^{[2]} \times PDSI_{i,t} + \beta_2^{[2]} \times MINT_{i,t} + \beta_3^{[2]} \times WIND_{i,t} + \varepsilon_{i,t}^{[2]}, \quad (2)$$

and

$$log\left(\theta_{i,t}^{[3]}\right) = \alpha^{[3]} + \beta_1^{[3]} \times PDSI_{i,t} + \beta_2^{[3]} \times MINT_{i,t} + \beta_3^{[3]} \times WIND_{i,t} + \varepsilon_{i,t}^{[3]}, \quad (3)$$

in which $PDSI_{i,t}$ was the Palmer drought severity index for region *i* and year *t*, $MINT_{i,t}$ was minimum temperature, $WIND_{i,t}$ was wind speed, and $\varepsilon_{i,t}^{[2]}$ and $\varepsilon_{i,t}^{[3]}$ were process errors that followed Normal distributions of mean 0 and standard deviations of $\sigma^{[2]}$ and $\sigma^{[3]}$, respectively. Note that we used intercept and slope parameters that were the same across the regions, which represented the assumption the demography-environment relationships were the same across regions. We also considered regressions with region-specific intercept and slope parameters such that $log\left(\theta_{i,t}^{[2]}\right) = \alpha_{i}^{[2]} + \beta_{1,i}^{[2]} \times PDSI_{i,t} + \beta_{2,i}^{[2]} \times MINT_{i,t} + \beta_{3,i}^{[2]} \times WIND_{i,t} + \varepsilon_{i,t}^{[2]}$ and $log\left(\theta_{i,t}^{[3]}\right) = \alpha_{i}^{[3]} + \beta_{1,i}^{[3]} \times PDSI_{i,t} + \beta_{2,i}^{[3]} \times MINT_{i,t} + \beta_{3,i}^{[3]} \times WIND_{i,t} + \varepsilon_{i,t}^{[3]}$ to allow for region-specific demography-environment relationships.

We linked clutch fate with the same covariates using a logistic regression such that

$$logit\left(\mu_{i,t}\right) = \alpha^{[f]} + \beta_{1}^{[f]} \times PDSI_{i,t} + \beta_{2}^{[f]} \times MINT_{i,t} + \beta_{3}^{[f]} \times WIND_{i,t} + \varepsilon_{i,t}^{[f]}, \quad (4)$$

in which process errors $\varepsilon_{i,t}^{[f]}$ followed a Normal distribution with mean 0 and standard deviations of $\sigma^{[f]}$. As in the regressions of clutch size, we also formed a regression with region-specific intercept and slope parameters for clutch fate.

Survival sub-model

We linked apparent survival with the same covariates mentioned above using a logistic regression such that

$$logit\left(\phi_{i,t-1}^{[C]}\right) = \alpha^{[C]} + \beta_{1}^{[C]} \times PDSI_{i,t} + \beta_{2}^{[C]} \times MINT_{i,t} + \beta_{3}^{[C]} \times WIND_{i,t} + \varepsilon_{i,t}^{[C]}, \quad (5)$$

in which $\phi_{i,t-1}^{[C]}$ was the apparent survival of cohort *C* (i.e., adult male, adult female, juvenile male, juvenile female) in region *i* and year *t*, and process errors $\varepsilon_{i,t}^{[C]}$ followed a Normal distribution with mean 0 and standard deviations of $\sigma^{[C]}$. We again considered a regression with region-specific intercept and slope parameters for apparent survival.

We also estimated the probability of recapture ($p^{[REC]}$) and resighting ($p^{[RES]}$). The likelihood of the individual encounter history data was then calculated using $\phi_{i,t-1}^{[C]}$, $p^{[REC]}$, and $p^{[RES]}$ values.

Model implementation

We implemented the IPM in a hierarchical Bayesian framework with posterior distributions obtained by Markov chain Monte Carlo (MCMC) computing in the software JAGS (Plummer 2003), which was called from R (R Development Core Team 2013) through the package "jagsUI" (Kellner 2015). We used vague priors Normal (0, 100) for any intercept and slope parameters, gamma (0.01, 0.01) for any precision parameters and the decay parameter in distance sampling, and uniform (0, 1) for any probability parameters. We used 5,000 iterations including 3,000 burn-in and 5 chains, yielding 10,000 posterior samples for each parameter. We checked the convergence of the MCMC computing using R-hat statistics and Gelman-Rubin diagnostics (Brooks & Gelman 1998). The R-hat statistics for each parameter were ≤1.02, and the chains were well mixed.

Post-modelling analysis

We conducted a hierarchical partitioning analysis (Mac Nally 1996) to understand the relative contributions of demographic parameters in describing population growth rates (Zhao, Boomer

& Royle 2019). Hierarchical partitioning is based on multiple linear regressions, in which population growth (i.e., $\frac{N_{i,t}}{N_{i,t-1}}$) was the response variable and demographic parameters were the predictors. This approach considers all possible models, each of which corresponds to a given combination of predictors. For each model, the joint contribution of the predictors is calculated. With such information, hierarchical partitioning allowed us to calculate the relative independent contributions of each demographic parameter on population growth. We used the full posterior samples to conduct these analyses to account for uncertainty in parameter estimates.

Results

Population and demographic estimates

Our results revealed population declines in the Texas and New Mexico populations, and potentially the Oklahoma population (Figure 3). Note that the Oklahoma population had a much larger population size (e.g., mean 1803.6, 80% C.I. 1600.1, 2038.1 in 2017) than the Texas (mean 82.6, 80% C.I. 74.1, 92.7 in 2017) and New Mexico populations (mean 23.7, 80% C.I. 21.2, 26.8 in 2017). However, the trend of the Oklahoma population was less clear due to the lack of population survey data in the early years.

Average clutch size (Texas: mean 2.62, 80% C.I. 2.02, 2.97; New Mexico: mean 2.65, 80% C.I. 2.02, 2.97; Oklahoma: mean 2.62, 80% C.I. 1.99, 2.98) and clutch fate (Texas: mean 0.36, 80% C.I. 0.10, 0.82; New Mexico: mean 0.40, 80% C.I. 0.09, 0.80; Oklahoma: mean 0.39, 80% C.I. 0.05, 0.90) were similar among populations, but declined during our study period (Figure 4). Apparent adult survival was greater than juvenile survival for both females and males for all study populations, but there was large uncertainty in estimates and no strong trends. Adult

female (Texas: mean 0.72, 80% C.I. 0.20, 0.99; New Mexico: mean 0.75, 80% C.I. 0.19, 0.98; Oklahoma: mean 0.73, 80% C.I. 0.13, 0.98) and adult male (Texas: mean 0.77, 80% C.I. 0.17, 0.99; New Mexico: mean 0.78, 80% C.I. 0.18, 0.99; Oklahoma: mean 0.73, 80% C.I. 0.17, 0.98) survival was ~73% and ~75% respectively, while juvenile female (Texas: mean 0.15, 80% C.I. 0.00, 0.81; New Mexico: mean 0.12, 80% C.I. 0.00, 0.82; Oklahoma: mean 0.09, 80% C.I. 0.00, 0.81) and juvenile male (Texas: mean 0.08, 80% C.I. 0.00, 0.73; New Mexico: mean 0.09, 80% C.I. 0.00, 0.68; Oklahoma: mean 0.06, 80% C.I. 0.00, 0.66; Figure 5) survival was < 15% for all populations, with high uncertainty.

Demographic contributions on population growth

Demographic parameters considered in our IPM had similar and substantial contributions to population growth rates (clutch size: mean 8.5%, 80% C.I. 2.0%, 30.8%, clutch fate: mean 9.1%, 80% C.I. 2.0%, 33.6%, adult female survival: mean 13.1%, 80% C.I. 2.2%, 47.2%, adult male survival: mean 14.9%, 80% C.I. 2.4%, 51.2%, juvenile female survival: mean 10.7%, 80% C.I. 2.2%, 39.4%, juvenile male survival: mean 10.6%, 80% C.I. 2.0%, 39.0%; Figure 6).

Drivers of demography

The results from the IPM with region-specific intercept and slope parameters showed little regional variation in demography-environment relationships (Appendix 2). Therefore, here we report the results of the model with universal intercept and slope parameters.

Palmer drought severity index had a positive effect on the probability of a clutch size of 2 (mean 0.65, 80% C.I. −0.53, 2.06) with moderate certainty and the probability of a clutch size of 3 (mean 1.54, 80% C.I. 0.61, 2.88) and clutch fate (mean 1.70, 80% C.I. 1.25, 2.15) with relatively high certainty. Minimum temperature also had a positive effect on the probability of a

clutch size of 2 (mean 0.21, 80% C.I. −0.31, 0.82) with moderate certainty and the probability of a clutch size of 3 (mean 0.83, 80% C.I. 0.36, 1.40) and clutch fate (mean 0.99, 80% C.I. 0.72, 1.24) with relatively high certainty. Wind speed positively influenced clutch fate (mean 0.40, 80% C.I. 0.13, 0.77) with relatively high certainty but not the probability of a clutch size of 2 (mean 0.11, 80% C.I. −0.58, 0.84) or 3 (mean 0.14, 80% C.I. −0.50, 0.86; Figure 7).

Palmer drought severity index also positively influenced survival (adult female: mean 0.46, 80% C.I. −0.29, 1.16; adult male: mean 0.29, 80% C.I. −0.61, 1.02; juvenile female: mean 0.89, 80% C.I. 0.07, 2.47; juvenile male: mean 0.66, 80% C.I. −0.21, 1.80) with moderate certainty. Minimum temperature (adult female: mean −0.12, 80% C.I. −0.74, 0.49; adult male: mean −0.23, 80% C.I. −0.95, 0.38; juvenile female: mean 0.07, 80% C.I. −0.69, 1.30; juvenile male: mean −0.36, 80% C.I. −1.65, 0.45) and wind speed (adult female: mean −0.13, 80% C.I. −0.77, 0.41; adult male: mean −0.05, 80% C.I. −0.68, 0.57; juvenile female: mean −0.04, 80% C.I. −0.68, 0.62; juvenile male: mean −0.05, 80% C.I. −0.72, 0.59) only had weak effects on survival (Figure 8).

Discussion

Our IPM provided reasonable precision for productivity estimates and uncovered the complex relationships between wetland habitat conditions, climate, and demography with partially aligned data. Our results showed that wetland habitat (represented by Palmer drought severity index) positively impacted productivity and survival of snowy plover, indicating the importance of protecting wetland habitat for the conservation of this migratory shorebird that breeds in a semi-arid environment. Our results also showed that minimum temperature positively influenced

productivity. Based on these results, we recommend continuous population and capture-recapture surveys combined with segmented productivity survey data for understanding population dynamics and underlying demographic processes when data collection is limited by time and/or financial resource.

Analysis of partially aligned data

Our study could only provide population and demographic estimates with reasonable precision using IPMs. IPMs have been increasingly used in understanding population dynamics and underlying demographic processes due to their capability of estimating parameters with unbalanced data (Saunders *et al.* 2019) or even without specific data (Besbeas *et al.* 2002; Zhao, Boomer & Royle 2019), at no substantial cost to bias or precision of parameter estimates (Weegman *et al*. 2020).

Previous work revealed that the responses of populations to environmental conditions may be region-specific (Forchhammer *et al.* 1998; Williams, Ives & Applegate 2003; Grøtan *et al.* 2009). However, these studies often focus on large spatial ranges that cover multiple ecological regions. Zhao, Boomer and Royle (2019) found that demography-environment relationships tend to be similar within ecological regions, but different among ecological regions. Because our study area lies in the Southern Great Plains, it is reasonable to assume that our three populations respond similarly to the environment. To test these hypotheses, we formed an IPM with region-specific demography-environment relationships, and the results confirmed our assumption of similar responses among populations. Based on these results, we used a model with universal demography-environment relationships, which provided an information-borrowing mechanism among populations. As data availability and quality were variable among populations (e.g., a relatively thorough population survey in New Mexico but demographic surveys in Texas), such

an approach allows us to achieve relatively reasonable precision for all three populations. We encourage practitioners to use information-borrowing approaches among populations when data are only partly aligned, such as in our study.

Even with the advanced IPM, uncertainty of population and survival estimates was still high in some years due to the lack of corresponding data. For example, Oklahoma population estimates from 1998 to 2012 had relatively high uncertainty due to lack of population survey data during this period. These results remind us that monitoring programs are still extremely important for gaining knowledge about wildlife populations, even with advantages from recent modelling techniques.

Environmental impacts

Our study revealed the demographic mechanisms for and environmental drivers of the declines of the snowy plover populations in the Southern Great Plains (Andres *et al.* 2012; Saalfeld *et al.* 2013; Heath 2019). Our study showed that wetland habitat, represented by Palmer drought severity index, had a strong positive effect on snowy plover productivity measures (i.e., clutch size and clutch fate) and a moderate positive effect on juvenile survival. Thus, the declines in snowy plover productivity and population size can be attributed, in part, to the change of wetland habitat. Like other shorebirds, snowy plover populations rely on wetland habitat (Conway, Smith & Ray 2005), where degradation or loss in wetland habitat may decrease their productivity or even survival (Saalfeld *et al*. 2011; Saalfeld *et al*. 2013). Wetland habitat loss could be driven by climate change (e.g. Sorenson *et al.* 1998; Sofaer *et al.* 2016) as well as other human stressors (Johnston 2013; Burgin, Franklin & Hull 2016; Donnelly *et al*. 2019; Donnelly *et al*. 2020). For example, the decline of the snowy plover population at Bitter Lake NWR may be driven by the

degradation of ground water sources in the Pecos River ecosystem related to agricultural development (Heath 2019).

Our study also reveals a positive effect of minimum temperature on snowy plover clutch size and fate. Increases in temperature are normally considered to lead to drier habitats and thus negatively impact shorebird populations. In our study area, maximum temperature is negatively correlated with Palmer drought severity index (Appendix 1). Even though we could not evaluate the effect of maximum temperature on snowy plover demography due to this correlation, the positive effect of Palmer drought severity index may indicate a negative impact of high temperature during day time on snowy plover demography. High temperatures not only could lead to increased evapotranspiration and drought but also may create a thermally stressful environment for nesting snowy plovers that necessitates incubating parents cooling eggs during daylight hours (Saalfeld *et al*. 2012). High minimum temperature, on the other hand, represents a relatively warm condition during night, which may benefit these birds (Van de Pol *et al.* 2010; Saalfeld *et al*. 2012). Further studies that are able to disentangle the multifaceted effects of climatic conditions on shorebird demography and behaviours are essential for a comprehensive understanding of the impacts of anticipated change on their populations, associated with climate change. Despite that we predicted a negative effect of wind speed on snowy plover demography (Hilde *et al*. 2016), we found that wind speed was positively correlated with clutch fate but not other demographic parameters. However, the relatively high uncertainty of the effect of wind speed indicated that further investigation is needed.

Interestingly, our results showed that productivity and survival of all cohorts had similar contributions on snowy plover population growth. Several studies showed that productivity tends to vary more and also contribute more to population growth (Alisauskas *et al.* 2004; Cooch *et al*.

2001; Taylor *et al.* 2012), although these studies focused on larger birds. Survival might play a more important role than productivity in smaller birds such as snowy plovers (current study) and insectivores (Zhao unpublished data). The relatively high uncertainty of population and survival estimates in some years, however, may have masked the differential contributions of demography on population growth, warranting further investigation.

Conservation implications

Conservation programs often have limited financial resources and practitioners are challenged to balance monitoring and conservation priorities. Demographic data (e.g., capture-recapture) are more expensive to collect than count data of unmarked populations yet are crucial for understanding demographic foundations of population dynamics. Recent studies showed that count data of unmarked animals can provide information for demography (Dail & Madsen 2011; Zipkin *et al.* 2014; Hostetler & Chandler 2015; Zhao, Royle & Boomer 2017). Furthermore, it would be ideal to jointly analyse count and demographic data to achieve comprehensive understanding and robust inference of population dynamics and underlying demographic processes (Zhao 2020). Our study showed that reasonable precision of demographic estimates could be achieved even with partially aligned data. In particular, productivity estimates had an overall reasonable precision even though nest survey data were available for only short periods. Previous researchers showed that productivity/recruitment could be estimated without direct data using IPMs (e.g., Besbeas *et al.* 2002; Zhao, Boomer & Royle 2019; Weegman *et al*. 2020). Survival estimates in Texas also had an overall reasonable precision despite the gaps in capture-recapture-resight data. Survival estimates in Oklahoma, however, had relatively high uncertainty during the first 15 years of our study period due to the lack of capture-recapture-resight data. Population estimates had relatively reasonable precision only for years with population survey

416 data. In particular, the Oklahoma population was much larger than the other two populations and
417 thus seems particularly important for the conservation of this species, which corroborates
418 previous work (Heath 2019). Yet the estimates of the Oklahoma population had high uncertainty
419 during the early years due to the lack of data, which largely hindered our ability to identify a
420 long-term trend for this population. Overall, it seems that a combination of continuous
421 population count and capture-recapture/resighting data with segmented nest survey data is
422 practical and useful for monitoring population status and developing appropriate conservation
423 strategies for this species.

424 Despite the imbalanced data availability, our IPM provided an understanding about the
425 environmental drivers of snowy plover in the Southern Great Plains. Our study revealed that
426 snowy plover demography and thus population dynamics are driven by wetland habitat
427 conditions, indicating the importance of wetland habitat conservation under climate change and
428 other human stressors such as groundwater mining and agricultural development (Conway,
429 Smith & Ray 2005; Heath 2019). Our study also showed that future warming may potentially
430 benefit snowy plover populations, at least in the short term (i.e., acknowledging that beyond a
431 certain point, increased temperatures will negatively influence snowy plover productivity;
432 Saalfeld *et al*. 2013). Understanding the multifaceted effects of climate on animal demography is
433 key for accurate forecasts of population responses, and thus appropriate conservation planning
434 under climate change (Clark *et al.* 2001; Petchey *et al.* 2015).

435 Taken together, our IPM lays a foundation of allocating limited conservation resources for
436 evidence-based conservation decision-making under global change. The benefits of out
437 modelling approach are not limited to our study species, as more studies should consider
438 balancing allocation of conservation resources between different types of data.

439

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640

Figure 1

Study area

Figure 1. The position of the Great Plains in the contiguous US (inner panel), and the positions of our study sites in the Southern Great Plains in Texas (Muleshoe National Wildlife Refuge [NWR] and lakes A, B and C), New Mexico (Bitter Lake NWR), and Oklahoma (Salt Plains NWR).

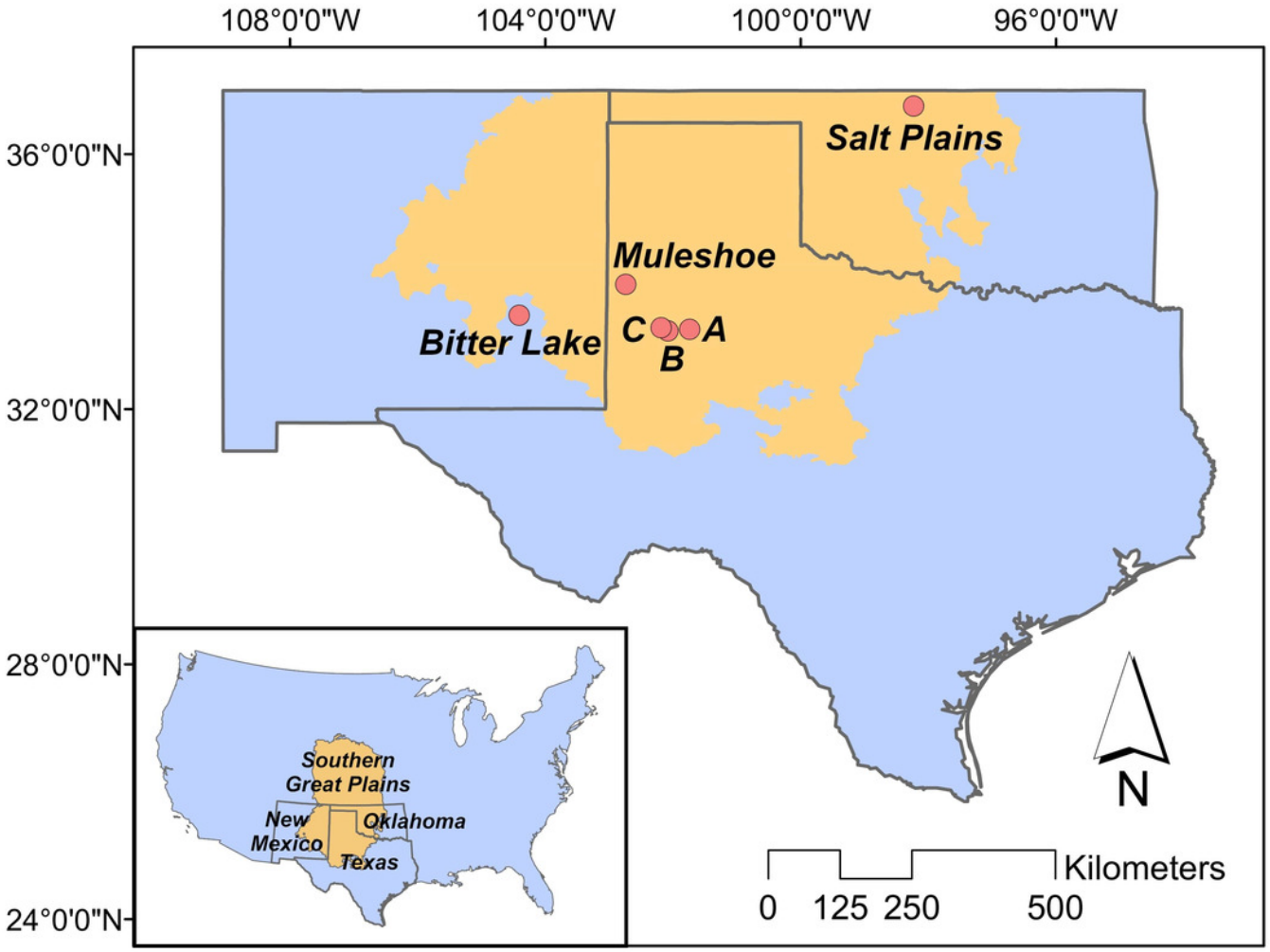


Figure 2

Data availability

Figure 2. The years in which each type of data (population survey, distance sampling, nest survey, and capture-recapture-resight) are available for each population (Texas, New Mexico, Oklahoma).

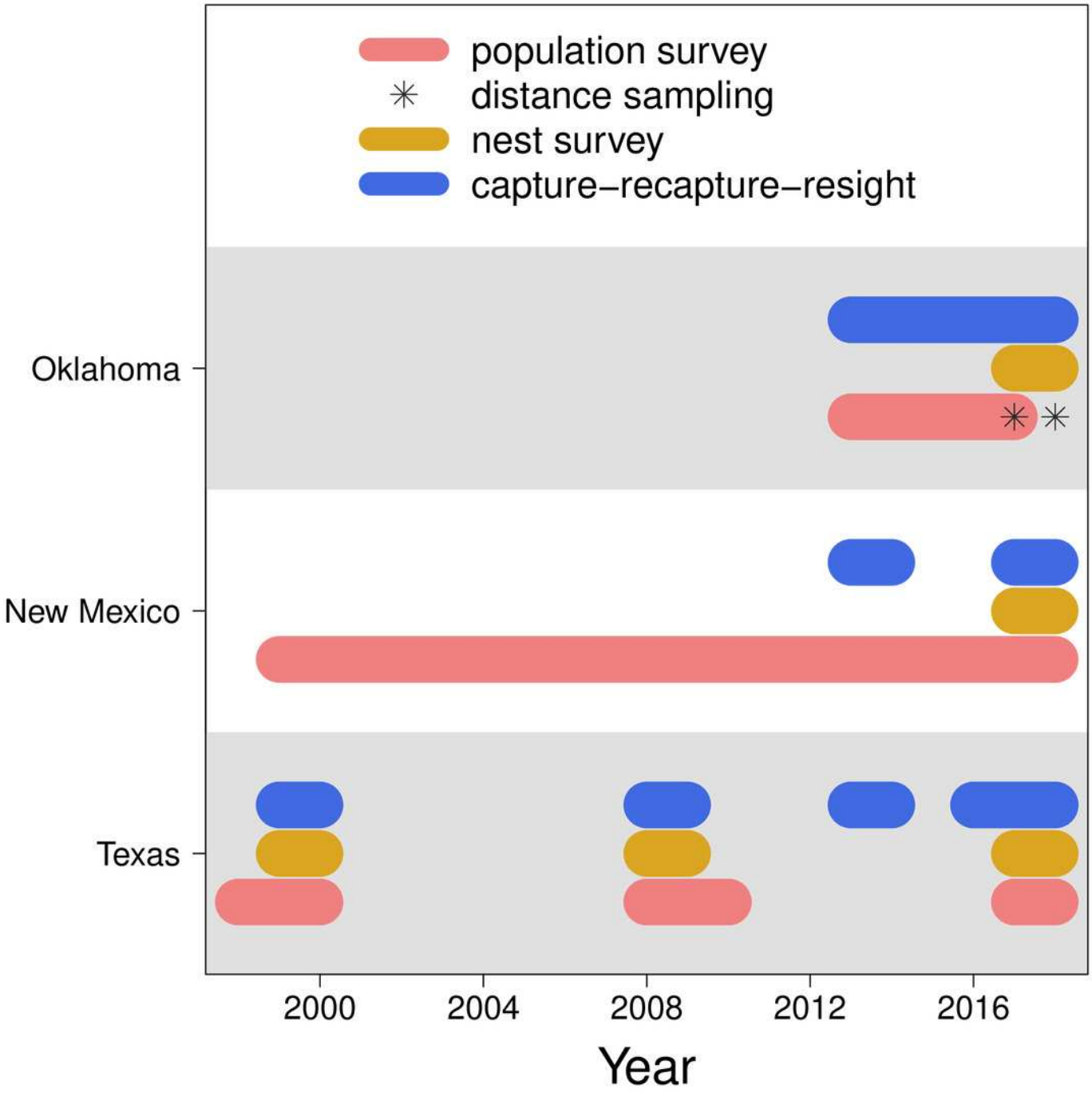

population survey
distance sampling
nest survey
capture–recapture–resight
Oklahoma
New Mexico
Texas
2000
2004
2008
2012
2016
Year

Figure 3

Population estimates

Figure 3. IPM estimated population trend (yellow line) and corresponding 80% Credible Interval (purple band) as well as population count data (red points) in Texas, New Mexico, and Oklahoma.

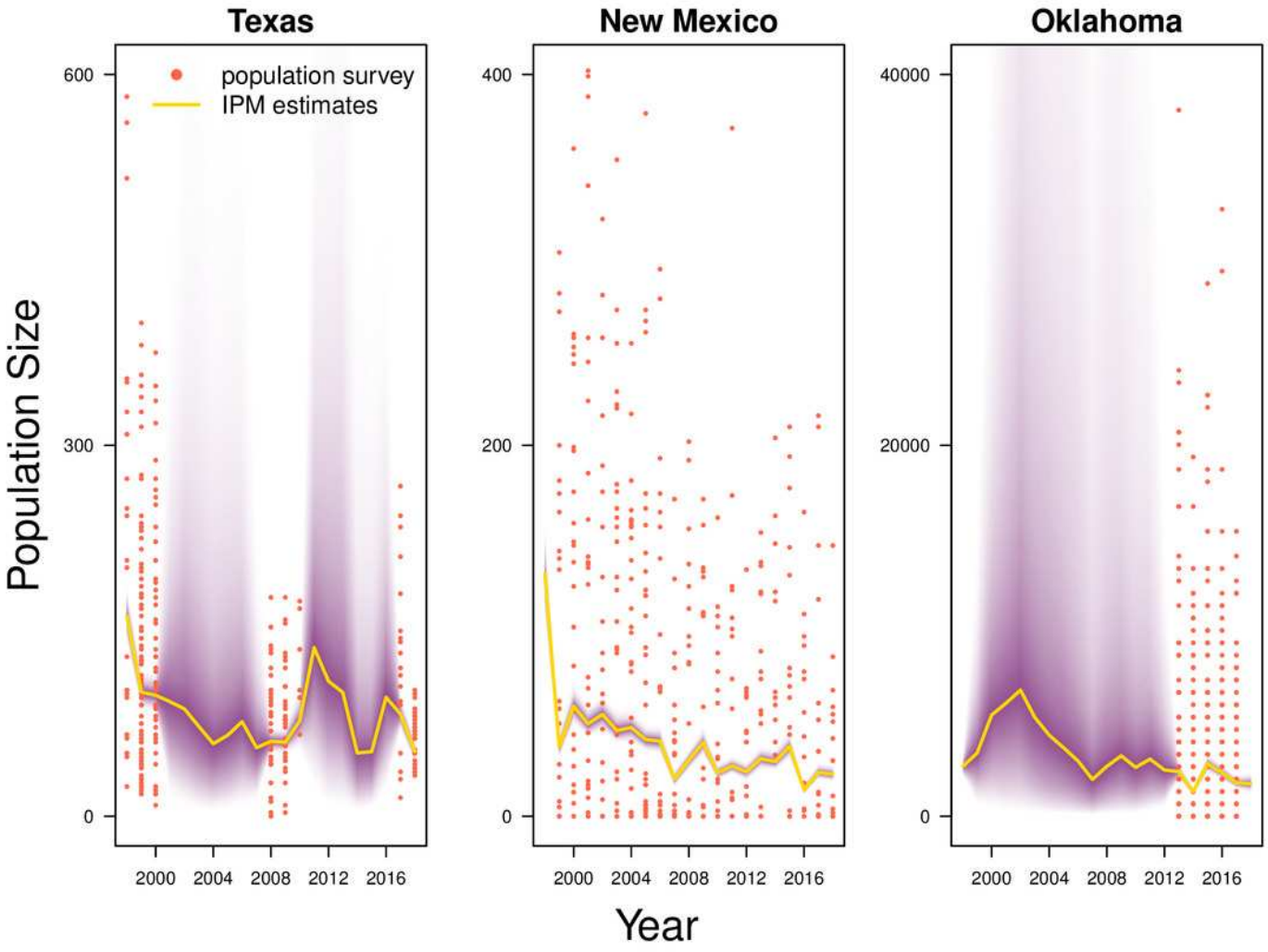


Figure 4

Productivity estimates

Figure 4. IPM estimated average clutch size and clutch fate (yellow line) and corresponding 80% Credible Interval (purple band) in Texas, New Mexico, and Oklahoma.

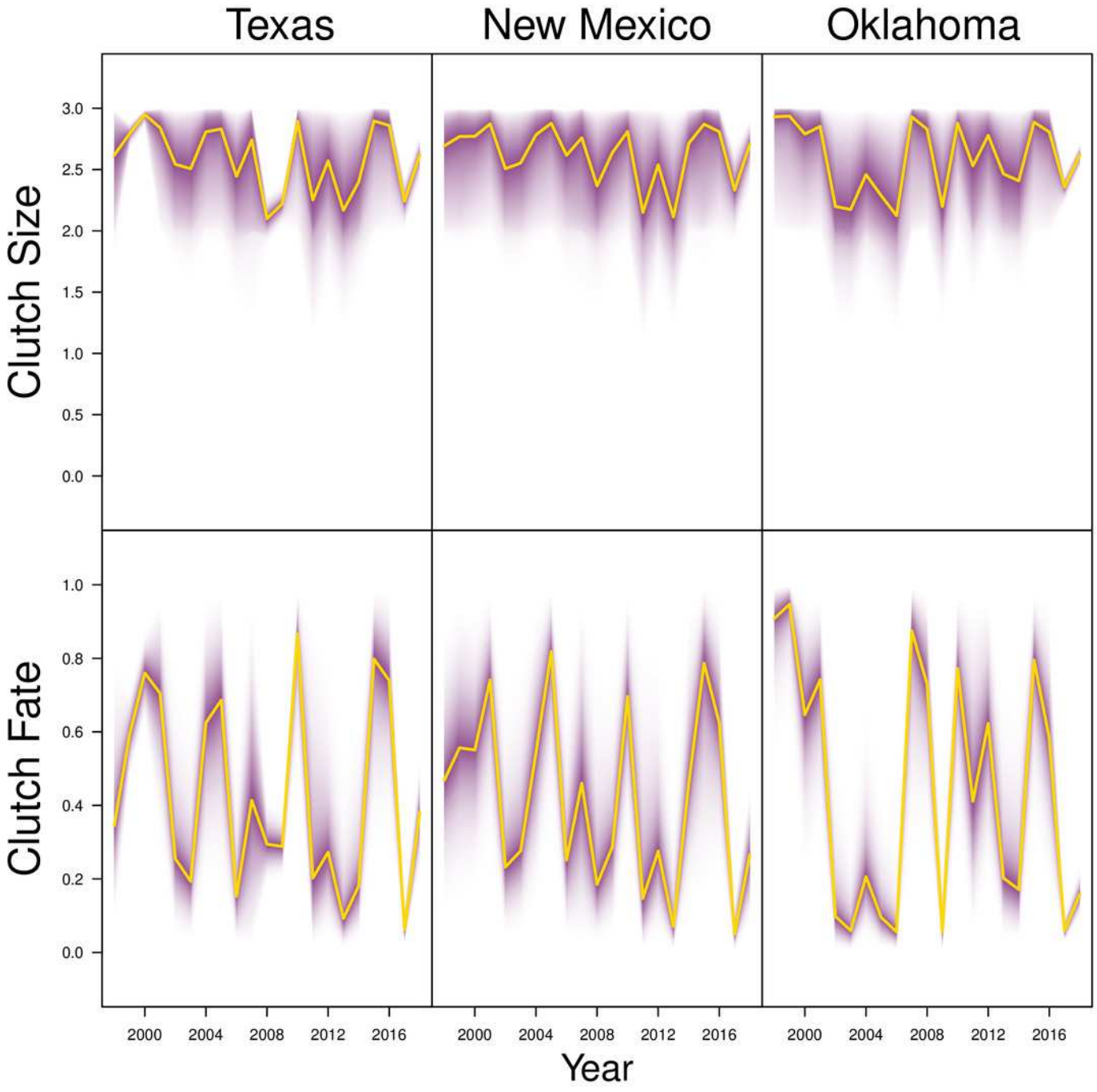

Texas
New Mexico
Oklahoma
Clutch Size
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Clutch Fate
1.0
0.8
0.6
0.4
0.2
0.0
2000
2004
2008
2012
2016
Year

Figure 5

Survival estimates

Figure 5. IPM estimated apparent survival of adult female, adult male, juvenile female and juvenile male (yellow line) and corresponding 80% Credible Interval (purple band) in Texas, New Mexico, and Oklahoma.

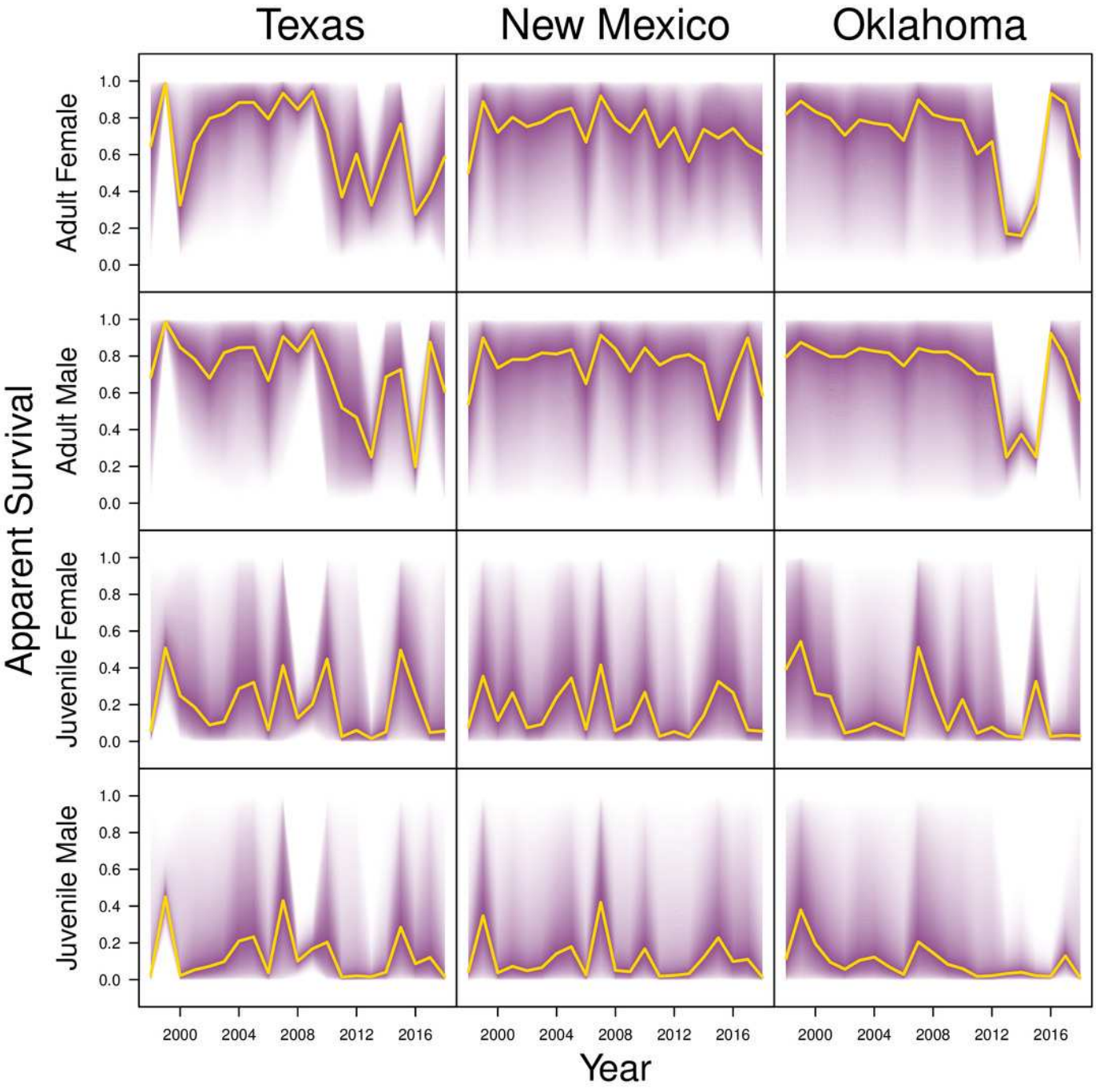

Texas
New Mexico
Oklahoma
Adult Female
Adult Male
Juvenile Female
Juvenile Male
Apparent Survival
1.0
0.8
0.6
0.4
0.2
0.0
2000
2004
2008
2012
2016
Year

Figure 6

Demographic contributions

Figure 6. The relative independent contribution of average clutch size, clutch fate, and apparent survival of adult female, adult male, juvenile female, and juvenile male on snowy plover population growth in Texas, New Mexico, and Oklahoma.

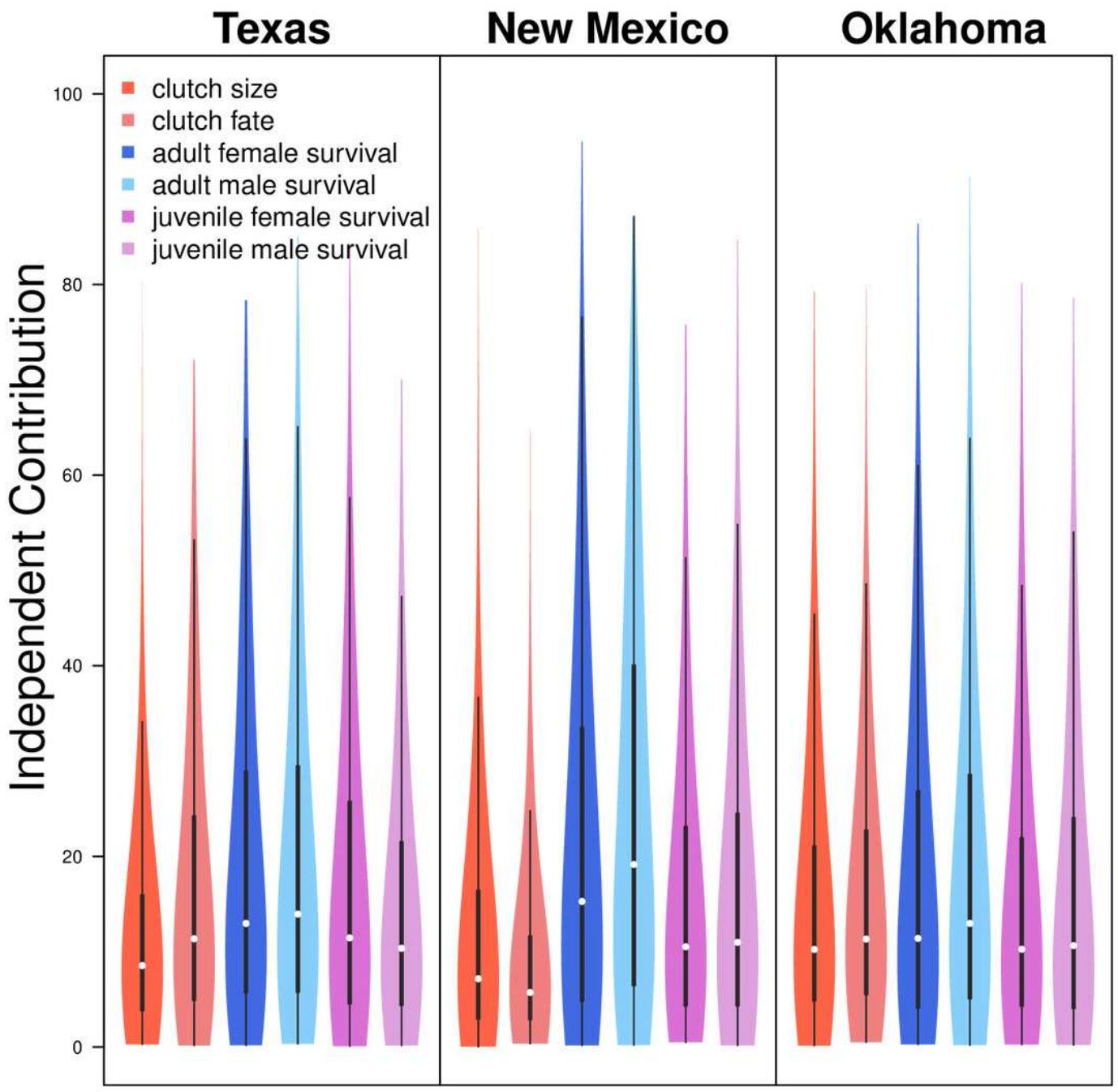

Texas
New Mexico
Oklahoma
clutch size
clutch fate
adult female survival
adult male survival
juvenile female survival
juvenile male survival
Independent Contribution
100
80
60
40
20
0

Figure 7

Drivers of productivity

Figure 7. Violin plots showing the posterior distributions of the slope parameters that represent the effect of Palmer drought severity index (PDSI), minimum temperature (min temp), and wind speed (wind) on productivity measures of snowy plover including the probability of a clutch size of 2 (C2) or 3 (C3), and clutch fate (FT).

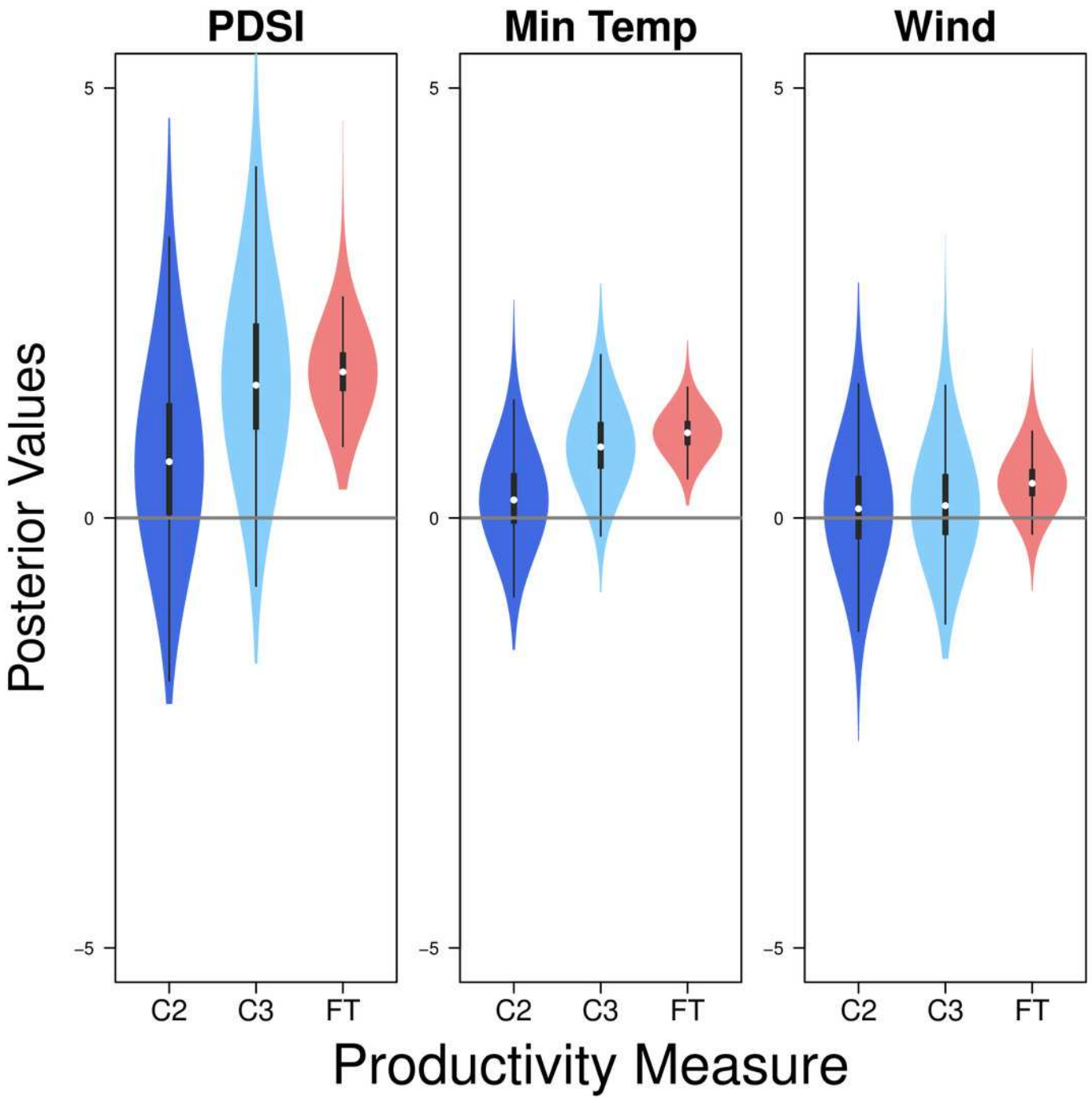
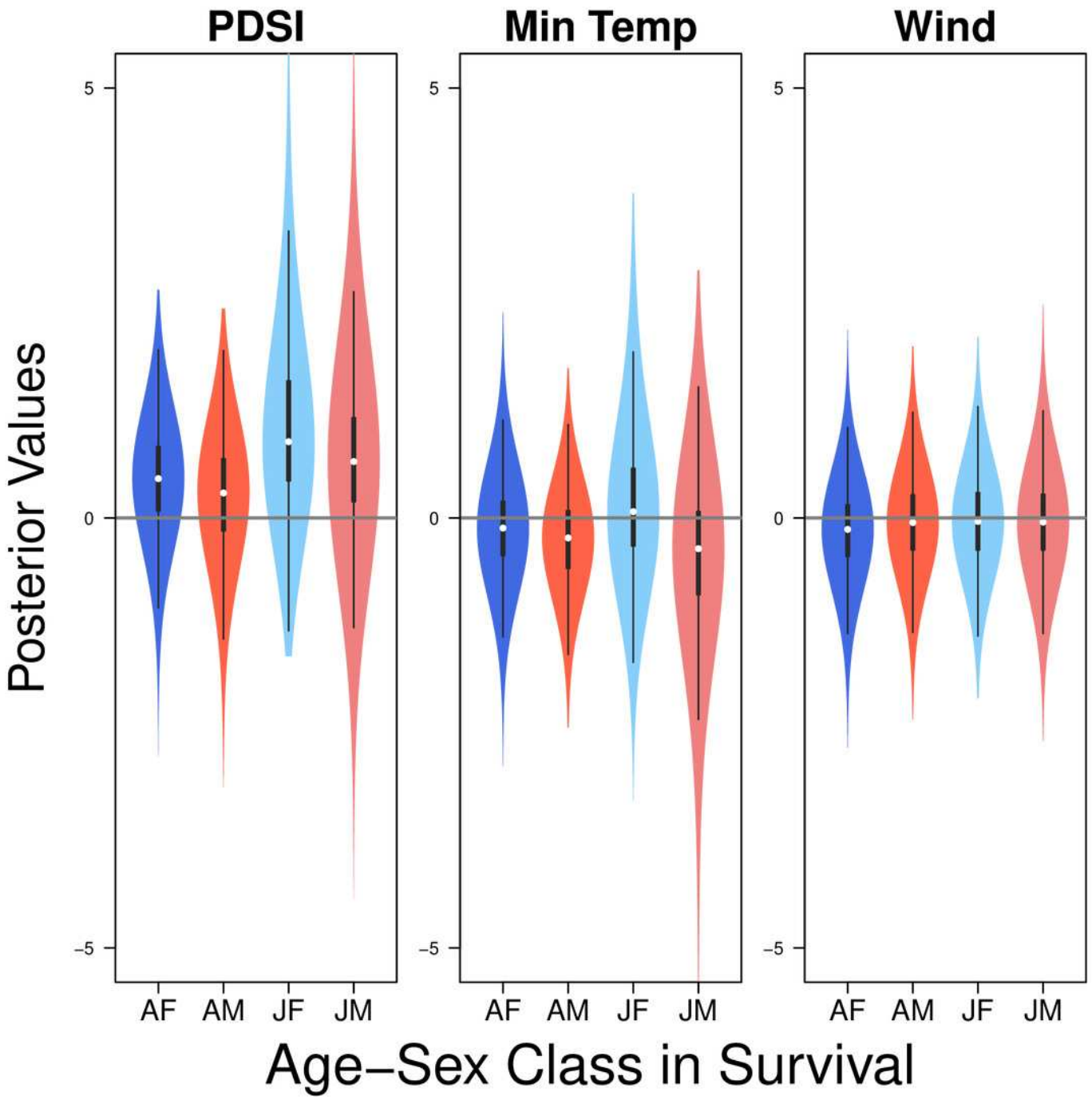

PDSI
Min Temp
Wind
5
0
−5
Posterior Values
C2
C3
FT
Productivity Measure

Figure 8

Drivers of survival

Figure 8. Violin plots showing the posterior distributions of the slope parameters that represent the effect of Palmer drought severity index (PDSI), minimum temperature (min temp), and wind speed (wind) on the apparent survival of adult female (AF), adult male (AM), juvenile female (JF), and juvenile male (JM) snowy plover.


PDSI
Min Temp
Wind
5
0
−5
Posterior Values
AF
AM
JF
JM
Age−Sex Class in Survival