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Associations of extreme weather, El Niño events, and streamflow with the annual apparent survival of a migratory riparian bird in the western United States

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Neotropical avian migrants are affected by environmental change throughout their full annual cycles. In the southwestern United States, these species rely on riparian corridors for food and water, for migration stopover sites, and as breeding grounds. Climate change imperils these essential ecosystems, with the southwest predicted to become hotter and more arid, thus resulting in more frequent extreme heat and drought. The tropical forests of Latin America, where many Neotropical migrants overwinter, face similar threats. The impacts of these changes on the demography of migratory riparian species remains poorly understood. We analysed 13 years of capture–mark–recapture bird banding data (2011–2023) from southern Utah to examine the effects of age-class and a range of environmental variables on the survival of a common migratory and riparian breeding bird, the Western Yellow-breasted Chat *Icteria virens auricollis*. We found that adult chats had a significantly greater probability of survival than first-year birds (mean survival adults: 0.53 ± 0.11; juveniles: 0.12 ± 0.07). While rates of survival differed for the two age-classes, the variability was closely matched across years, indicating that both adults and juveniles are impacted similarly by ecological factors. We also found that annual survival rates were particularly sensitive to the El Niño-Southern Oscillation (ENSO) cycle, with El Niño events being associated with reduced chat survival. This suggests a key negative impact of drier, hotter conditions during migration and on the wintering grounds in Central America—conditions that may become increasingly extreme with future climate change. We also found near-significant negative effects of breeding season heat events (% of days with maximum temperature exceeding the 90th percentile of a 30-year baseline) and spring precipitation, as well as a potential positive association between chat survival and breeding season streamflow. Our results not only demonstrate the importance of environmental variation across the full annual cycle of chats in driving variation in survival, but also highlight how future climate change may impact the demography of a key riparian species.

Keywords: avian demography, capture–recapture models, El Niño-Southern Oscillation, *Icteria virens auricollis*, Icteriidae, Neotropical migrant, Yellow-breasted Chat.

Climate change is expected to become one of the most impactful drivers of worldwide biodiversity loss over the next century (Heller & Zavaleta 2009, Wormworth & Şekercioğlu 2011, IPCC 2022, Mota *et al.* 2024), yet much research has focused on range shifts (e.g. Chen *et al.* 2011), changes in phenology (e.g. Gienapp *et al.* 2006) and physiology (e.g. Marshall *et al.* 2013). While ecologically important, these investigations do not directly assess changes in demographic rates that fundamentally determine species persistence (Selwood *et al.* 2015). Past work suggests that extreme

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events, such as heatwaves, can be more devastating to animal populations than a gradual rise in mean temperature, as the latter allows time for acclimatization, whereas heat waves occur suddenly, leaving no opportunity for such adjustments (Vasseur *et al.* 2014, Cooper *et al.* 2020). Furthermore, extreme heat events have been linked to declines in survival (Jiguet *et al.* 2006, Cruz-Mcdonnell & Wolf 2016), diminished foraging efficiency (du Plessis *et al.* 2012) and reduced reproductive capacity in birds and other animals (Walsh *et al.* 2019, Schou *et al.* 2021).

Species in arid regions face particularly substantial threats in a warming climate (Seager *et al.* 2007). The southwestern United States (U.S.) is considered a climate change 'hotspot', with increasing temperatures, aridity and interannual variability (Seager *et al.* 2007, Diffenbaugh *et al.* 2008, Diffenbaugh & Ashfaq 2010). Droughts also are predicted to increase in severity and frequency (Meehl & Tebaldi 2004, Seager *et al.* 2007) in a landscape where water availability is already naturally low and may be an ecologically limiting resource (Gaur & Squires 2018). Riparian corridors play a crucial role in providing resources and landscape connectivity (Seavy *et al.* 2009, Şekercioğlu 2009) and are disproportionately biodiverse given their small geographical footprint (< 2% of the total land area of the southwest; Szaro 1980, Bender 1982, Svejcar 1997). In the deserts of Utah, for example, more than 70% of bird species use riparian corridors for at least part of their life cycle (Parrish *et al.* 2002).

As climate change intensifies, the importance of riparian zones in buffering populations against extreme heat and drought is expected to increase (Seavy *et al.* 2009). However, riparian habitats are, themselves, being impacted by climate change in a range of ways, including changes in river hydrology with advancing snow melts, changing flood magnitudes and diminishing summer streamflow (Perry *et al.* 2020, Elias *et al.* 2021). These changes can shift riparian vegetation towards dominance by drought-tolerant tree species, such as invasive salt cedar *Tamarix* spp. (Johnson 2000, Stromberg *et al.* 2010), potentially reducing habitat quality and the effectiveness of riparian habitats as climate refugia (Seavy *et al.* 2009, Stromberg *et al.* 2010, Perry *et al.* 2020). There is consequently an urgent need to better understand how climate variation impacts species survival, and the extent to which climate extremes can contribute to population declines.

In this study, we explore impacts of environmental change on the survival rates of a breeding bird, the Western Yellow-breasted Chat *Icteria virens auricollis* (hereafter 'chat'), that is characteristic of riparian habitats in the Interior West of the U.S. As a Neotropical migrant, chats are affected by climatic conditions across their full annual cycle (Sillett & Holmes 2002, Moreno & Møller 2011), and events which happen during one phase of their life cycle may impact subsequent phases (Marra *et al.* 1998). Along with the predicted changes to breeding ground conditions, chats may face worsening conditions during migration and on their wintering grounds in Central America, with both a decrease in rainfall and an increase in temperature predicted in the future across this region (Imbach *et al.* 2018). The El Niño-Southern Oscillation (ENSO) has been shown to influence the survival and productivity of migratory passerines, and has been used as an indicator of migratory and wintering conditions for such species (Sillett *et al.* 2000, Mazerolle *et al.* 2005, Lamanna *et al.* 2012, García-Pérez *et al.* 2014). ENSO is a natural, cyclical climatic phenomenon occurring over several years, characterized by periodic fluctuations in winds and sea-surface temperatures across the tropical Pacific (NOAA 2023). In the Northern Hemisphere, the influence of ENSO is strongest during winter, with weak effects seen in summer (NOAA 2023). In particular, El Niño events result in drier, warmer weather during the winter in Central America, where chats spend the non-breeding season, and higher than average precipitation in the Southwestern U.S. (Lin & Qian 2019, Nigam & Sengupta 2021, NOAA 2023, Tonelli *et al.* 2024).

Using 13 years of capture–mark–recapture (CMR) data from southeastern Utah, we model the effects of breeding season weather conditions, streamflow and normalized difference vegetation index (NDVI) on annual chat survival. We also relate chat survival to ENSO to capture the impact of migratory and wintering conditions. We expect hotter, drier conditions across the annual cycle to correspond with reduced survival for both adult and first-year birds. Because first-year birds are often expected to have a lower rate of survival compared to adults owing to a general lack of experience and factors such as fledging date

(Naef-Daenzer *et al.* 2001, Cox *et al.* 2014, Beauchamp 2023), we predict that these young birds will be more strongly affected by climatic conditions. In addition, using NDVI and streamflow as proxy indicators for resource availability, we predict less green and less wet years to correspond with reduced survival. We evaluate the relative strength of each variable in influencing chat survival, generating novel insights into the potential impacts of climate variation on this species.

METHODS

Study site

The study was conducted in eastern Utah at the Bonderman Field Station at Rio Mesa in Grand County (38°47′56.7″N, 109°12′17.2″W; Fig. 1a), a 160-ha restricted-access site owned and operated by the University of Utah for field studies (Kittelberger *et al.* 2022, 2025). The site is located within a canyon of the Colorado Plateau, at 1280 m elevation, and classified as a 'lowland riparian' area (Parrish *et al.* 2002). The Dolores River runs through the site, feeding the riparian vegetation which extends roughly 30–70 m on each bank. Mist-nets for bird banding are located within this habitat (Fig. 1b). The predominant flora of the site includes salt cedar species, squawbush *Rhus trilobata*, Russian knapweed *Rhaponticum repens* and New Mexico privet *Forestiera pubescens*, along with scattered cottonwood trees *Populus fremontii* (Parrish *et al.* 2002, Kittelberger *et al.* 2022, 2025).

Study species

The Yellow-breasted Chat *Icteria virens* was once considered a wood-warbler in the family Parulidae, yet molecular phylogenetic studies led to the chat being placed into its own family, Icteriidae, in 2017 (Thompson & Eckerle 2022). Our study focused on the western subspecies *I. v. auricollis*, which breeds from the middle of the continental U.S. to the west coast, and north to southwestern Canada (Thompson & Eckerle 2022), and is generally confined to riparian and dense shrub habitat with cottonwoods *Populus* spp. and salt cedars (Brand *et al.* 2010). Adults are omnivorous, feeding on small invertebrates, and fruit and berries when available. The western chats migrate overland to winter in coastal areas of Chiapas and Oaxaca, southwestern Mexico (Mancuso 2020, Thompson & Eckerle 2022). During migration and overwintering, chats generally inhabit similar low, dense vegetation to that used on the breeding grounds.

Field data collection

Annual mist-netting has taken place at Rio Mesa every spring and autumn since 2011 during landbird migration (Kittelberger *et al.* 2022, 2025). The station follows standard Monitoring Avian Productivity and Survivorship (MAPS) protocols (Desante *et al.* 2016), with standardized banding effort undertaken each year from early April to mid-June, and mid-August to early November (Kittelberger *et al.* 2025). Sixteen 38-mm mesh mist-nets, measuring 12 × 2.5 m, are operated in fixed locations across 300 m of riparian habitat (Kittelberger *et al.* 2022, 2025). Banding is carried out on 10 out of every 12 days during the season, with nets opened 30 min before sunrise and checked every half-hour for 6 h before closing. The schedule is adjusted occasionally as a consequence of adverse weather conditions that could threaten the safety of the birds. After fixing an aluminium band on an individual's leg, the age and sex of each chat is determined, when possible (Pyle 1997, 2022), and morphological and life-history measurements including wing-length, fat score, breeding status and body-mass are also recorded.

Capture–mark-recapture data

The sampling period for this study is May to September each year, encompassing both the spring and autumn banding periods in order to cover both the breeding and post-breeding seasons. We constructed a capture history for each banded individual, consisting of one presence observation per individual per sampling period (i.e. combining spring and autumn banding). For this study, we have separated individuals by age-class, referring to birds in their first calendar year that were born during the breeding season of a given year as 'hatch-year' birds, while we treat individuals within the first year of their life (hatching-year and second-year/yearling birds following bird banding terminology—i.e. individuals that have not yet moulted into their basic plumage) as 'first-year' birds (Pyle 2022). Adult birds are individuals at least in their second calendar year, having already undergone at least one prebasic moult.

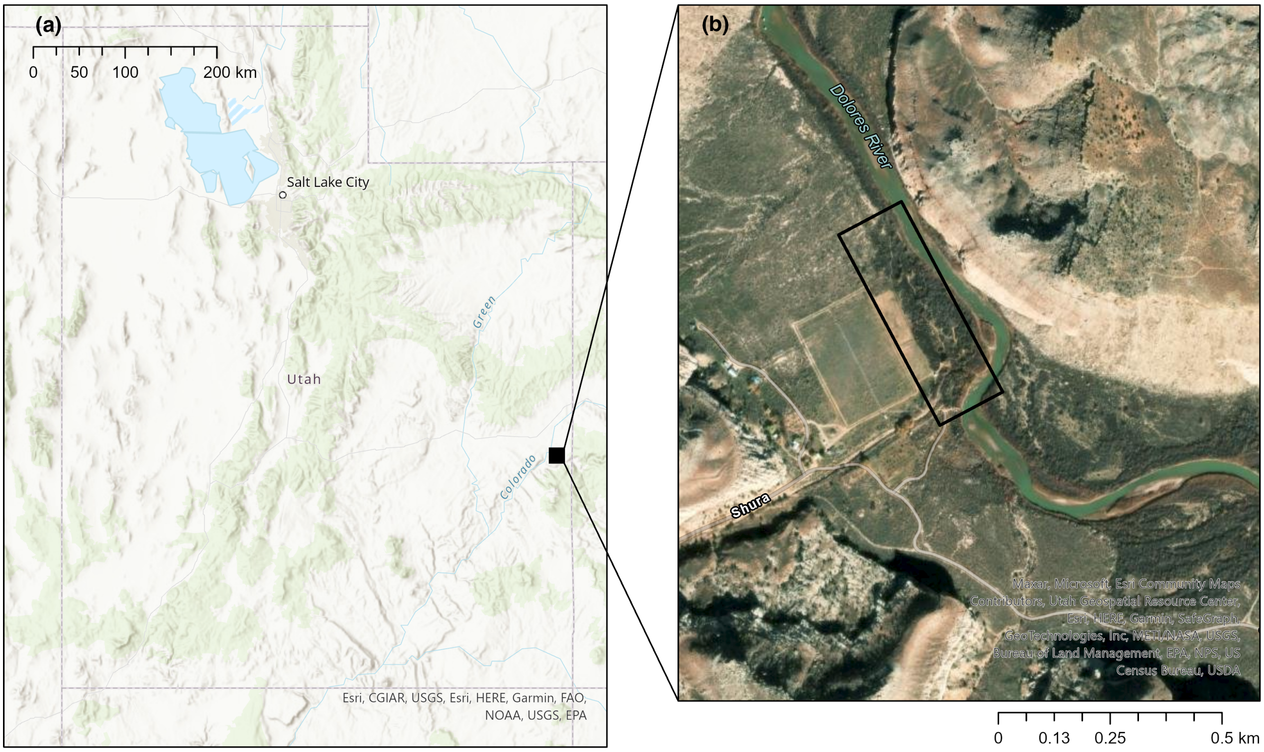

Figure 1. (a) Location of Bonderman Field Station at Rio Mesa in Grand County, Utah. (b) Site of annual bird banding along the Dolores River at Rio Mesa. Base maps obtained via ESRI (2023).

As we were interested in how age affects survival, we included first-year birds to examine the impact of age-class on survival, with any bird of an indeterminate age excluded from the dataset. As the site is located within the western migratory flyway, the sample is also expected to include transient individuals found moving through the region (La Sorte *et al.* 2014). Following the methods of Ryu *et al.* (2016) we therefore removed any birds encountered only once from our analysis, unless they met additional criteria suggesting resident status (namely birds with breeding signs of either a brood patch or cloacal protuberance, or birds captured in June, after the migratory period). Among 800 chats banded at Rio Mesa across the 13 years of the study (2011–2023), 552 individual chats met these inclusion criteria for the analysis.

Environmental variables

Weather

We calculated mean peak daily temperature (°C) and precipitation sum (mm) for each breeding season during the study period. Breeding season is defined as the period May to August inclusive, during which chats are known to be mating, nesting or raising young. Daily weather data for the study site were extracted from PRISM interpolated maximum and minimum temperature and total precipitation data (PRISM 2023) at a pixel resolution of 2.5 arc second, which equates roughly to a 4-km grid for the latitude of the study site.

Extreme temperatures have been shown to negatively affect survival (Jiguet *et al.* 2006, Mckechnie & Wolf 2010, Cruz-Mcdonnell & Wolf 2016, Latimer & Zuckerberg 2019), so we also calculated the annual percentage of days where daily peak temperature exceeded the 90th percentile from a 30-year base period (1991–2020) using Climpact (WMO 2017, Climpact 2021). In addition, we calculated spring (March–May inclusive) precipitation sum because riparian vegetation health has been found to be positively correlated with wetter spring conditions (Warter *et al.* 2023).

Streamflow

Streamflow rates for riparian zones in the region are dependent on snowmelt from surrounding mountainous areas, with the timing and magnitude of the melt impacting riparian vegetation growth and quality (Johnson 2000, Elias *et al.* 2021). In addition to altering riparian vegetation, changes in streamflow can result in bird heat stress or dehydration if surface water availability is reduced (Perry *et al.* 2020). To investigate the impact of streamflow fluctuations on survival, we obtained daily river discharge values in cubic feet per second for the Dolores River at Rio Mesa (USGS 2023) and took the maximum discharge rate for each breeding season across the study period.

Normalized difference vegetation index

NDVI was used as a proxy for resource (food and habitat) availability (Pettorelli *et al.* 2011), as it is strongly correlated with vegetation productivity (Zhang *et al.* 2003). It has been positively associated with survival (Grande *et al.* 2009), bird species richness (Hurlbert & Haskell 2003), increased breeding productivity (Saino *et al.* 2004) and population size (Wilson *et al.* 2011). To calculate NDVI for the study site, we used Terra Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI data from NASA EarthData (Didan 2015), restricted to a 1-km radius surrounding the banding site. Terra MODIS data are generated every 16 days at 250-m spatial resolution, with values ranging from −1 to +1, where negative values indicate absence of vegetation (Myneni *et al.* 1995). We smoothed the composites to reduce noise using a Savitzky–Golay filter (Cai *et al.* 2017) with the package ‘signal’ (0.07–7; Signal Developers 2013) in R Statistical Software (R Core Team 2023) and used the average maximum NDVI (hereafter ‘NDVI’) for each breeding season across the study period.

El Niño-Southern Oscillation index

Conditions for chats during migration and overwintering were evaluated using international ENSO indices. We used the global Multivariate ENSO Index (MEI.v2) from the Physical Sciences Laboratory (NOAA 2023) for each non-breeding season of the study period (monthly values from September to April inclusive) to calculate the average sea surface temperature and air pressure anomaly. Variations from normal ocean temperatures influence the tropical Pacific Ocean–atmosphere system, impacting weather and climate worldwide (NOAA 2023). MEI combines oceanic and atmospheric variables into a single index. Values fluctuate around zero, with positive values corresponding to El Niño events and negative values corresponding to La Niña events.

Survival modelling

We estimated apparent survival (ϕ) and probability of detection (P) using a hierarchical CJS model within a Bayesian framework (Cormack 1964, Jolly 1965, Seber 1965, Saracco *et al.* 2010). Apparent survival is the probability that an individual will be alive and present during the sampling period (t) if alive and present during the previous sampling period ($t - 1$) (Kéry & Schaub 2012), and is thus an underestimate of true survival as it does not account for emigration from the population or transient individuals present during sampling (Cilimburg *et al.* 2002, Gilroy *et al.* 2012, Ryu *et al.* 2016). CJS models make further assumptions: (1) bands are not lost, (2) individuals are recorded correctly, (3) marked and recaptured individuals represent a random sample from the study population, (4) all marked individuals have the same probability of recapture and survival, (5) individual survival and detection probabilities are independent, (6) sampling periods are short, and (7) recaptured individuals are released immediately. Our study design meets all assumptions except for that of short sampling periods. Because our capture period spans May to September each year, survival risk is effectively averaged across this timeframe, with each individual contributing a single observation per year. While this approach minimizes the impact of seasonal variation, it does not fully eliminate potential biases introduced by extended sampling windows, and survival estimates should therefore be appropriately interpreted.

The model includes a latent state process Z, describing the true state of individual i at sampling period t (either alive $Z_{i,t} = 1$, or dead $Z_{i,t} = 0$), and an observation process y, describing whether the individual is detected ($y_{i,t} = 1$) or not detected ($y_{i,t} = 0$), conditional on its true state. An individual’s first capture $Z_{i,f}$ is fixed at 1, and all subsequent occasions are modelled as Bernoulli trials. We allow survival probability ϕ_{t-1} to vary over time, with the latent state process described as follows:

$$Z_{i,t=1} = 1$$

$$Z_{i,t+1} \mid Z_{i,t} \sim \text{Bernoulli}\left(Z_{i,t}\phi_{t-1}\right)$$

The probability of detection $P_{i,t}$ and the state of the individual $Z_{i,t}$ dictates whether a chat is detected $y_{i,t}$ or not during a sampling occasion (only a living bird can be detected), with the observation process described as:

$$y_{i,t} \mid Z_{i,t} \sim \text{Bernoulli}\left(Z_{i,t}P_{i,t}\right)$$

We allowed for heterogeneity in both detection and survival rates during the study period by including year as a random effect in both survival and observation models. Failing to allow for variability in P has been found to lead to an overestimate of detection and an underestimate of survival (Clark *et al.* 2005). Survival probability was modelled as a logit linear function:

$$\text{logit}\left(\phi_{i,t}\right) = \alpha + \gamma_t + \beta_a * a_{(i,t)} + \beta_e * e_{(t)}$$

where $\phi_{i,t}$ is the survival probability for individual i at time t, α is the intercept, γ_t represents the random time effect, β_a is an effect of age (binary covariate, 1 for adult and 0 for hatch-year) and β_e is the effect of environmental variable e. To avoid overparameterizing the model, we analysed each environmental variable in a separate model, always retaining age as an additional covariate. While the variables were analysed separately, some were found to be correlated (precipitation sum and mean peak daily temperature [$r = -0.75$], and NDVI and streamflow rate [$r = 0.75$]; Table S1). The implications of these correlations are addressed in the Discussion. All variables were standardized by centring to have a mean of 0 and scaling to a unit standard deviation. This normalization allows for the comparison of coefficient sizes on the same scale.

We fitted models using JAGS (Plummer 2003), called from the package 'R2jags' (0.7–1; Su & Yajima 2021) in R Statistical Software (R Core Team 2023; see Appendix S1 for model code). Non-informative priors were used for all estimated parameters. For random year effect variances, a uniform hyper-prior was used (bounded 1–100), and normal priors with mean of 0 and precision of 0.0001 were used for all other parameters. We estimated posterior distributions using three chains of 25 000 iterations run in parallel. The first 12 000 iterations were discarded as burn-in, and every other sample was retained thereafter (thinning = 2), resulting in a final posterior sample size of 19 500. Model convergence was assessed using the Gelman–Rubin convergence statistic $\widehat{R}$ (Brooks & Gelman 1998) and the visual inspection of auto-correlation and trace plots. Convergence was considered successful with an $\widehat{R} < 1.02$ and with trace plots appearing stationary (Kéry & Schaub 2012). To assess model fit, we used a posterior-predictive check, following the methods of Gelman *et al.* (2000) and Chambert *et al.* (2014), whereby we visually compared the distributions of summed detection histories for observed data with the simulated detection histories generated by the model. Close similarity of the resulting distributions indicated good model-fit. For all model parameters, the mean of each posterior distribution is reported with 95% credible intervals (CRIs) and the proportion of the distribution above or below zero. Parameters with CRIs that do not overlap zero are interpreted as having strong evidence for an effect and may be considered 'statistically significant'. In addition, the magnitude of the effect can be inferred from the posterior mean and the width of the CRI, where narrower intervals indicate greater precision. A larger proportion of the posterior distribution to one side of zero indicates greater certainty about the direction of the effect.

RESULTS

Survival modelling

The mean annual apparent survival was consistently higher among adult birds than first-year birds, with an overall mean annual survival rate of 0.53 ± 0.11 for adults and 0.12 ± 0.08 for first-year birds, with considerable interannual variability in survival rates (Fig. 2). Across the study period, the mean annual recapture rate for chats was 0.36 ± 0.05. The 95% CRIs for the posterior distribution of the effect of age did not overlap with zero (Table 1; Fig. 4a), providing strong support for a positive effect of being an adult on survival.

We found a strong negative effect of ENSO on chat survival (Table 1; Fig. 3h). This was the only environmental parameter for which the posterior 95% CRI excluded zero (Table 1; Fig. 3). While adult birds were found to have a greater overall

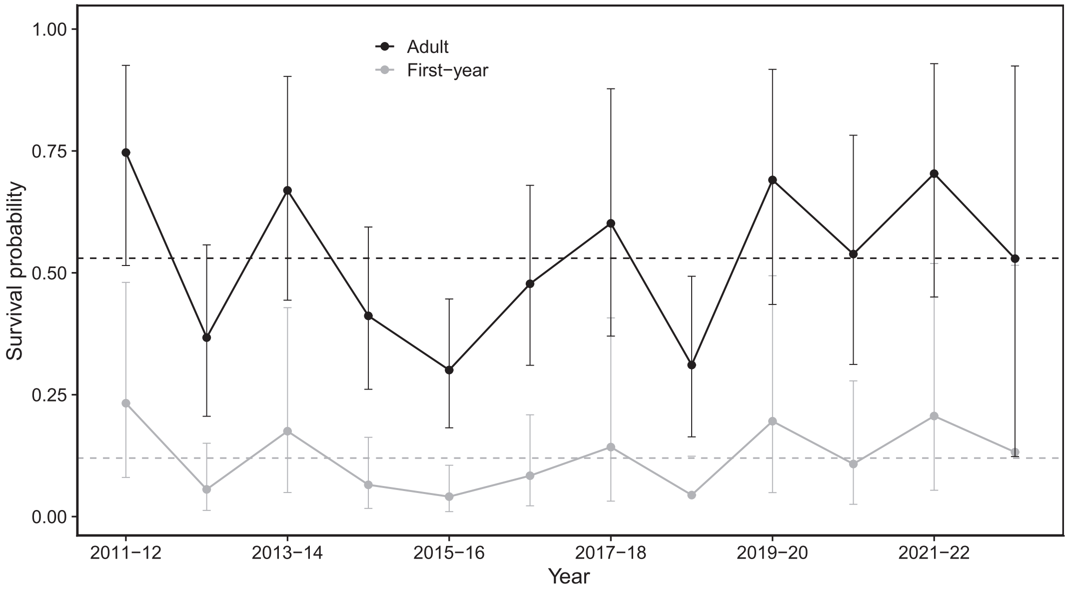

Figure 2. Mean annual apparent survival for adult (black) and first-year (grey) Western Yellow-breasted Chats in Rio Mesa, Utah, from 2011 to 2023 with 95% credible intervals. Sample in year t is indicative of the survival since the previous sample in year $t - 1$. Mean survival across the study period is indicated by the dashed lines.

Table 1. Posterior means for the effects of age and environmental variables with the lower and upper 95% credible intervals (CRIs) and the proportion of the posterior distribution to one side of zero for each variable.

	Posterior mean	SD	Lower 95% CRI	Upper 95% CRI	Prop. dist.
Age	**2.45**	**±0.51**	**1.50**	**3.50**	> **0: 1.00**
Peak daily temp.	−0.08	±0.36	−0.84	0.62	< 0: 0.58
Precipitation	−0.05	±0.34	−0.72	0.64	< 0: 0.58
Peak temp. > 90th%	−0.48	±0.35	−1.21	0.26	< 0: 0.94
Spring precipitation	−0.48	±0.35	−1.25	0.18	< 0: 0.93
Max streamflow	0.51	±0.39	−0.20	1.33	> 0: 0.92
NDVI	0.08	±0.38	−0.64	0.88	> 0: 0.58
ENSO	**−0.58**	**±0.26**	**−0.99**	**−0.14**	< **0: 0.98**

Bold indicates effects where the 95% CRI does not overlap zero.

chance of survival compared to first-year individuals, ENSO impacted both age-classes in a similar manner. El Niño events (positive ENSO values) were associated with lower survival probability, and La Niña events (negative ENSO values) with higher survival probability (Fig. 4a).

We found evidence of survival rates decreasing with percentage of days with peak temperature exceeding the 90th percentile (Table 1; Fig. 3d) and spring precipitation sum (Fig. 3e), and increasing with average streamflow rate (Table 1; Fig. 3f). Although the 95% CRIs for these variables overlap zero, a substantial proportion of the posterior distributions lay to one side of zero, indicating near-significant negative and positive effects, respectively. This suggests probable directional relationships, albeit with greater uncertainty compared to parameters with CRIs that fully exclude zero. As with ENSO, both first-year and adult birds were found to be associated similarly with these variables. The negative effect of percentage of days with peak temperature exceeding the 90th percentile suggests that years with more extremely warm days during the breeding season (Fig. 4b), and years with higher spring rainfall (Fig. 4c), may be associated with lower survival. The positive effect of streamflow rate suggests that years with higher river discharge may also be associated with higher survival (Fig. 4d). The posterior distributions for mean peak daily temperature, breeding season precipitation sum and NDVI all centred around zero

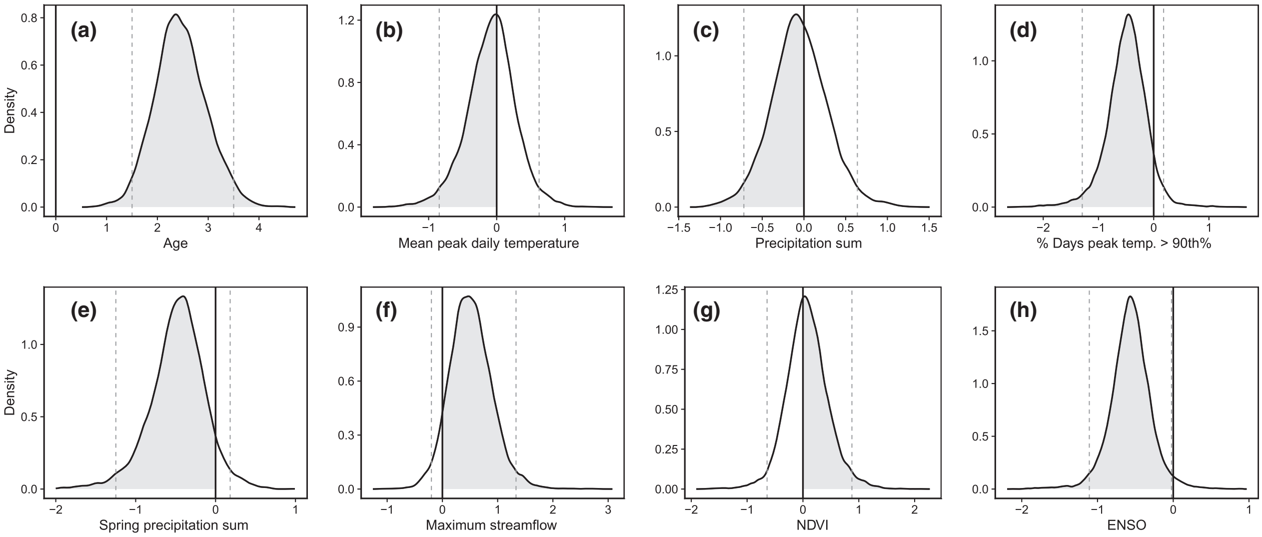

Figure 3. Posterior distributions for the effect of (a) age and (b–h) environmental variables on apparent survival of Western Yellow-breasted Chats. The *x*-axis represents the posterior distribution of regression coefficients. For age (a), this represents the effect of being an adult relative to a first-year bird. The *y*-axis represents posterior density. A solid line at zero indicates the point of no effect, allowing for the visual assessment of the distribution above and below zero. Dashed lines indicate 95% credible intervals (CRIs). The proportion of the posterior distribution above or below zero (shaded areas) highlights the strength and direction of the effect. Variables with CRIs that do not overlap zero are interpreted as having a statistically significant effect on apparent survival.

(Table 1; Fig. 3b,c,g), implying no discernible effect of these variables (Fig. S1).

DISCUSSION

We found strong annual variability in apparent survival for chats in the Southwestern U.S., with ENSO being the strongest predictor of survival probability among the environmental variables considered for both age-classes. El Niño events were associated with lower survival, suggesting a potential negative impact of adverse conditions for chats during migration and on their Central American wintering grounds. We also found evidence to suggest that chat survival is lower in years with a higher proportion of extremely warm days during the breeding season (i.e. temperatures > baseline 90th percentile), and in years with higher spring rainfall, but potentially higher in years with greater river discharge.

The effects of ENSO on chat survival (Fig. 4a) mirror those shown in other Neotropical migrant species such as Black-throated Blue Warbler *Setophaga caerulescens* (Sillett *et al.* 2000) and Yellow Warbler *S. petechia* (Mazerolle *et al.* 2005), as well as patterns shown in a wider study of riparian birds in the region (Neate-Clegg *et al.* 2022). For Neotropical migrants in the Pacific Northwest, however, survival rates and productivity have been shown to be higher during El Niño years (Nott *et al.* 2002, Lamanna *et al.* 2012), emphasizing the geographical variability of ENSO effects. As ENSO effects are most strongly felt during winter in the Northern Hemisphere (NOAA 2023, Tonelli *et al.* 2024), impacts on species are likely to vary strongly with differences in migration pathways and wintering ranges (Tonelli *et al.* 2024). For chats, El Niño creates hotter and drier than average conditions on the wintering grounds (Lyon & Barnston 2005, NOAA 2023), potentially increasing competition for scarce food resources (Strong & Sherry 2000, Smith & Robertson 2008). Such poor habitat quality during the non-breeding season can result in residual effects which carry over to subsequent seasons, influencing individual fitness (Marra *et al.* 1998). El Niño events have, likewise, been correlated with reduced physiological condition for long-distance migrants (Wolfe & Ralph 2009, González-Prieto & Hobson 2013, Paxton *et al.* 2014, Cooper *et al.* 2015), with climate oscillations having a greater overall impact on first-year birds than adults (Robinson *et al.* 2007).

Western Yellow-breasted Chats from across the breeding range overwinter in coastal southwestern

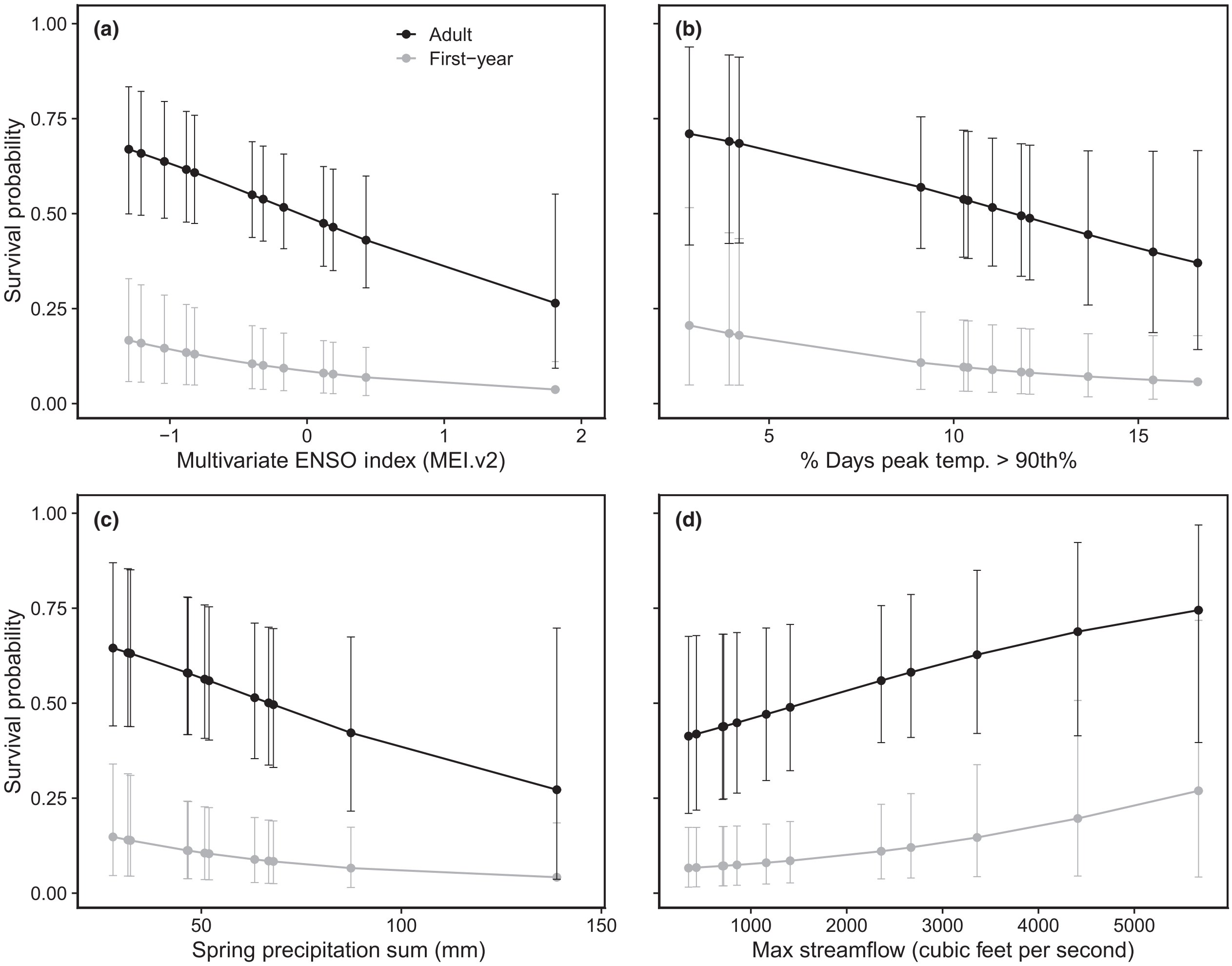

Figure 4. Relationships between apparent survival for adult (black) and first-year (grey) Western Yellow-breasted Chats and (a-d) the environmental variables found to have an association with apparent survival, shown with 95% credible intervals. Each point represents a sample year ($n = 12$) from the study.

Mexico (Lovette *et al.* 2004, Mancuso 2020), yet our findings are specific to the population in southeastern Utah and the edge of the Colorado Plateau. Our results should not be extrapolated to the entire breeding population, as regional variability in environmental conditions, such as those driven by ENSO, may lead to different effects on survival probability across the species' range. Although there is no clear consensus on how ENSO events are likely to change with climate warming (e.g. Maher *et al.* 2018, Fredriksen *et al.* 2020, Cai *et al.* 2021, Dieppois *et al.* 2021), the latest generation of climate models indicate increases in ENSO, rainfall and sea-surface temperature variability in a warmer world (Fredriksen *et al.* 2020, Yun *et al.* 2021). An uptick in the magnitude of El Niño events could, therefore, have adverse effects on the demographic parameters of chats, alongside many other migratory species in the Southwestern U.S.

We also found evidence suggesting that chat survival is negatively associated with extreme heat events during the breeding season, with a near-significant negative effect of the percentage of days surpassing the baseline 90th percentile of peak daily temperature (Fig. 4b). A previous study on riparian birds in the region also found a negative association between extreme heat and population growth for more than half of the focal species, but this was attributed to lower recruitment rates rather than adult apparent survival (Neate-Clegg *et al.* 2022). Extreme heat and water stress can have significant direct impacts on bird survival (Ma *et al.* 2015), alongside indirect effects on habitat quality and prey abundance (Bale *et al.* 2002, Pearce-Higgins *et al.* 2010). Accordingly, we found no evidence for any effect of mean peak daily temperatures on survival, suggesting again that extreme events (> 90th temperature percentiles) may be more impactful. As climate change is predicted to exacerbate temperature variability and extremes (Rahmstorf & Coumou 2011, Fischer & Knutti 2015, IPCC 2022), further research into the impact of extreme heat events on demographics is urgently warranted.

Alongside temperature, we found evidence of a potential positive association between streamflow rate and chat survival (Fig. 4d). Riparian ecosystem health is driven by multiple factors, including spring precipitation (Warter *et al.* 2023) and streamflow rate (Elias *et al.* 2021), the latter being highly sensitive to the timing and magnitude of upstream snowmelt (Johnson 2000, Elias *et al.* 2021). Climate warming is predicted to disrupt these dynamics, potentially causing mismatches between riparian seed dispersal and snowmelt (Perry *et al.* 2020). Such changes could reduce native tree abundance while promoting invasive species (Johnson 2000), further stressing riparian habitats and decreasing resource availability for chats and similar species. Although streamflow has not been directly related to survival in previous studies, decreased flow rates have been associated with declines in obligate riparian species abundance (Merritt & Bateman 2012, Hinojosa-Huerta *et al.* 2013, Cubley *et al.* 2020). These declines may result from resource-driven dispersal in drier years along with reduced habitat suitability, which is likely to have negative demographic effects for riparian birds.

NDVI, a widely used proxy for vegetation health and resource availability, was found to be strongly correlated with streamflow ($r = 0.75$) before analysis. Despite the correlation between streamflow and NDVI, and the observed relationship between streamflow and survival, there was no statistical evidence to support an association between NDVI and chat survival. This result aligns with previous findings by Neate-Clegg *et al.* (2022), who found that NDVI was positively correlated with population growth for several riparian species in the Southwestern U.S., but not chats. The lack of a detectable NDVI effect in our study may stem from the relatively coarse spatiotemporal resolution of available NDVI products. Nevertheless, the strong correlation between streamflow and NDVI highlights the broader importance of resource availability and habitat quality. Through its impact on riparian ecosystem health, streamflow is likely to have an indirect effect on demographic parameters of chats and other birds, extending beyond the scope of our analysis.

We additionally found a potential association between higher spring precipitation at Rio Mesa and lower chat survival (Fig. 4c). Although El Niño is associated with wetter and cooler conditions in the Southwestern U.S., it was not correlated with spring precipitation at Rio Mesa ($r = 0.26$). Notably, the rainiest spring recorded during the study period (2019, with 138.85 mm of precipitation—86.71 mm above the mean) did not coincide with a strong El Niño effect. With the peak year of rainfall excluded, a negative relationship with survival was still detected, albeit with greater uncertainty. High spring rainfall may impact chats during their migration and arrival period, which is a critical life stage for survival (González-Prieto & Hobson 2013, Drake *et al.* 2014). Alternatively, excessive rainfall could have indirect effects later on in the breeding season by altering vegetation structure and/or prey abundance. While NDVI serves as a useful proxy for these changes, no direct effect of NDVI on survival was detected in this study. This suggests that spring precipitation and its potential impacts on riparian ecosystems may affect survival through mechanisms not fully captured by NDVI.

As expected, we found substantial differences in apparent survival rates between first-year and adult birds, with first-year survival averaging 77% lower than adult survival. A fundamental difficulty in any apparent survival study is distinguishing between mortality and emigration (Kéry & Schaub 2012). In our study, first-year survival was substantially lower than the commonly assumed value of half of adult survival (Greenberg 1980, Donovan *et al.* 1995), which is likely to reflect higher rates of natal dispersal compared to breeding dispersal (Paradis *et al.* 1998). Few studies have examined site fidelity in chats, but they appear to show rates consistent with other migratory shrubland and forest birds (0.31 ± 0.05 for adults, 0.01 ± 0.05 for first-year birds;

Schlossberg 2009). The elusive nature of chats and their preference for dense vegetation often make them difficult to detect unless singing during the breeding season (Thompson & Eckerle 2022). McKibbin and Bishop (2012) reported similar site fidelity for chats but cautioned that estimates may be low owing to challenges in resighting. Without reliable estimates of site fidelity and dispersal rates, it is difficult to isolate the effects of mortality from emigration in a survival study.

Factors that impact individual bird survival are numerous, complicating the task of uncovering relationships between environmental variables and demographic rates. The findings of our study underscore the importance of considering age-class along with multiple effects of weather and other environmental influences across a species' annual cycle when conducting survival and/or demographic analyses, echoing prior research on a wide array of passerine species (e.g. Sillett & Holmes 2002, Wilson *et al.* 2011, Dybala *et al.* 2013, Drake *et al.* 2014, García-Pérez *et al.* 2014). While survival is a key aspect of population dynamics, understanding changes in productivity, recruitment and population growth would provide a more comprehensive view (Runge & Marra 2005). As found in previous research, certain environmental factors may have stronger effects on particular demographic parameters (e.g. affecting productivity more than apparent survival; Moreno & Møller 2011, Cruz-Mcdonnell & Wolf, 2016, Schou *et al.* 2021). However, the relatively small effective sample size in our study limited us to testing a single environmental variable in each model with age as a covariate. With more data, both temporally and spatially, future studies may allow for a more robust exploration of these interactions and their effects on survival and other demographic parameters.

CONCLUSIONS

We demonstrate a range of ways through which environmental variation can influence apparent survival throughout the annual cycle of the Yellow-breasted Chat, with a particularly clear role of ENSO cycles as an important correlate of chat demography in the Southwestern U.S. Uncovering the mechanisms behind the negative survival impact of El Niño events is an important priority, particularly as the magnitude of temperature and precipitation extremes associated with these events may increase in the future. The potential negative impact of extreme heat event frequency during the breeding season is also indicative of potential future risks from climate warning, as predicted for this and other riparian species that may be highly dependent on the availability of climatic microrefugia during such events (Seavy *et al.* 2009). Reductions in streamflow through riparian zones may also negatively impact chat survival, and this is likely to be through indirect effects on habitat quality and resource availability through the breeding season. Future environmental changes that may impact streamflow (e.g. changing meltwater phenology, upstream infrastructure development) should be carefully assessed for their potential negative impacts on riparian communities (Poff *et al.* 2011, Kittelberger *et al.* 2023). Refining our understanding of the impacts of environmental change on key demographic parameters will allow for a better understanding of the threats faced by these at-risk bird species in the future (Runge & Marra 2005).

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AUTHOR CONTRIBUTIONS

Liz Allocca: Conceptualization; methodology; formal analysis; investigation; writing – original draft; visualization; project administration; writing – review and editing. **James J. Gilroy:** Conceptualization; methodology; writing – review and editing; supervision; software; validation; resources. **Kyle D. Kittelberger:** Conceptualization; methodology; data curation; writing – review and editing; project

administration; funding acquisition; resources. **Çağan Hakkı Şekercioğlu:** Writing – review and editing; supervision. **Diana Bell:** Writing – review and editing; supervision.

CONFLICT OF INTEREST

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

ETHICS STATEMENT

All birds were handled and banded following the Bander's Code of Ethics and authorized under a Federal Bird Banding and Marking Permit held by the University of Utah.

Data Availability Statement

Data will be made available on request.

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SUPPORTING INFORMATION

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

Appendix S1. Survival model code.

Table S1. Correlations among environmental variables. All variables were analysed separately to avoid model overparameterization. Correlated variables are indicated in bold.

Figure S1. Relationships between apparent survival for adult (black) and first-year (grey) Western Yellow-breasted Chats and the environmental variables found to have no association with apparent survival, shown with 95% credible intervals. Each point represents a sample year ($n = 12$) from the study.