Long-term monitoring reveals the impact of changing climate and habitat on the fitness of cavity-nesting songbirds

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ABSTRACT

Long-term studies on the impacts of global change on reproduction are rare, even though reproductive output can respond more quickly than species' abundances or distributions. We explore the influences of habitat use and weather on fitness, by using an 11-year dataset of 2305 nesting attempts (7174 nestlings) across four species of cavity-nesting songbirds within California's Central Valley. Specifically, we modeled relationships between habitat type, maximum nesting season temperature, and winter/nesting season precipitation and nest site selection, reproductive success, and nestling weight for each species. We found that species selected nest sites based on species-specific habitat variables and that reproductive success and nestling weight peaked in selected habitats, suggesting an absence of ecological traps. Higher maximum nesting season temperatures were negatively associated with clutch size, reproductive success, and nestling weight for all species. For example, models predicted that the probability of successfully fledging tree swallows declined by 39 % and tree swallow nestling weight declined by 19 % when nests experienced the hottest versus the coolest maximum temperatures. In contrast, the effects of precipitation on reproductive outcomes varied by species and timing. We observed strong negative associations between nesting season precipitation and reproductive success/nestling weight in tree swallows and western bluebirds. Our findings suggest that, while habitat conversion to orchards has not resulted in ecological traps, predicted increases in temperature and spring precipitation may reduce the fitness of cavity-nesting songbirds in California. More broadly, our results highlight the importance of long-term monitoring when unravelling impacts of global change on fitness.

1. Introduction

Two of the primary threats to biodiversity worldwide are habitat conversion to agriculture, and climate change (Maxwell et al., 2016). Most studies explore the impacts of land use and climate (across years) or weather (within years) by measuring changes in species' abundances, occurrences, and/or distributions (Amano et al., 2020; Freeman et al., 2018; Furnas, 2020; Jarzyna et al., 2016; Møller et al., 2008; Northrup et al., 2019; Princé and Zuckerberg, 2015; Rushing et al., 2020; Saino et al., 2011). However, long-term studies of the impacts of global change on reproduction are rare, even though understanding fitness is key to understanding population dynamics. For example, studies of reproduction can help document ecological traps, where a species preferentially uses a habitat despite negative effects on its fitness (Battin, 2004; Gates and Gysel, 1978). Such studies can also act as early warning signals that a population may be in trouble, given that declines in reproduction often manifest before changes in species abundance, occurence, or distribution. Indeed, lag effects are important when studying both habitat conversion and climate change, as population-level responses to both stressors can often be quite slow (Devictor et al., 2012; Gibson et al., 2013; Lehikoinen et al., 2021). Finally, reproductive studies can also provide insight into how fitness may change as a function of extreme weather events, and thus indicate how populations may respond as the frequency and severity of extreme weather events increases with climate change (IPCC, 2022; Román-Palacios and Wiens, 2020).

Birds have been shown to be particularly impacted by land use and climate change, with each stressor affecting three-quarters and one-third of globally threatened avian species, respectively (BirdLife

International, 2018). Correspondingly, studies of the reproductive impacts of agriculture (Santangeli et al., 2018), habitat management (Shochat et al., 2005), and logging (Flaspohler et al., 2001; Robertson and Hutto, 2007) on songbirds have all revealed that birds can fall into ecological traps in that they may not always select nesting locations where they are most successful (Ben-Aharon et al., 2020; Demeyrier et al., 2016). Indeed, appropriate nest site selection is vital for avian fitness and can influence reproduction in a number of ways. First, well-hidden nests are better protected from predation and/or parasites (Li and Martin, 1991; Martin, 1993; Wesołowski and Tomialojc, 2005) as well as interspecies competition for nest sites (Nilsson, 1984). Second, parental foraging is tied to nest site selection (Stauss et al., 2005): because parents will only travel so far when foraging, nest site selection can determine the amount and quality of food available for nestlings (Bruun and Smith, 2003; Low et al., 2010). Third, the habitat surrounding the nest affects the nest's microclimate (Ardia et al., 2006; Dawson et al., 2005), with shaded nests more buffered against temperature extremes (both hot and cold) than more exposed nests. Erroneously assessing environmental cues when selecting nest sites can thus have large implications for avian reproduction. Fortunately, cavity-nesting songbirds will readily nest in artificial nest boxes, allowing researchers to experimentally place boxes in distinct environmental contexts, monitor them over many nesting seasons, and then link local habitat conditions to spatio-temporal variation in nest site selection and reproductive success (Purcell et al., 1997).

Cavity-nesting songbirds are also good model organisms for elucidating relationships between weather extremes and reproduction. The negative effects of cold snaps on nestling physiology (and survival) are well established (e.g., Garrett et al., 2022; Martin et al., 2017; Shipley et al., 2020; Winkler et al., 2013). There is also emerging evidence that temperature spikes can be harmful to breeding birds by both directly compromising nestling physiology (i.e., inducing hyperthermia) and by reducing resource provisioning to nestlings (Bourne et al., 2020; Conrey et al., 2016; Funghi et al., 2019; Schou et al., 2021; Zuckerberg et al., 2018). As a result, increasingly frequent and severe temperature spikes have been linked to the collapse of avian communities (Iknayan and Beissinger, 2018; Riddell et al., 2019, 2021). Precipitation extremes and timing can also have severe implications for avian reproduction. Rainfall early in the year may generate more abundant food resources later in the spring, thus benefiting nestlings (Morrison and Bolger, 2002) while heavy precipitation during nesting may decrease invertebrate food availability (McCarty and Winkler, 1999), resulting in smaller fledglings (Dawson and Bortolotti, 2000) and/or complete nest failure (Schöll and Hille, 2020). Similarly, drought may reduce primary productivity, and in turn, prey availability for foraging parents (Barras et al., 2021; Marcelino et al., 2020).

Here, we quantify the effects of habitat and weather on avian nest site selection, reproductive success, and nestling weight for four species of secondary cavity-nesting songbirds within California's Central Valley. Specifically, we present the first published results from a dataset of 2305 nesting attempts (7174 nestlings) by ash-throated flycatchers (*Myiarchus cinerascens* – migrant), house wrens (*Troglodytes aedon* – partial migrant), tree swallows (*Tachycineta bicolor* – migrant), and western bluebirds (*Sialia mexicana* - resident), systematically monitored across an average of 162 nest boxes per year for 11 years.

The Central Valley is an appropriate ecosystem for investigating the impacts of land use and weather extremes on avian reproduction. The region has experienced massive land-use changes and habitat loss over the past century, including the loss of over 90 % of its riparian land cover (almost entirely due to agricultural expansion; Katibah, 1984). The climate is Mediterranean, with hot, dry summers and cool, wet winters. It is regularly subject to extreme temperatures and variable rainfall patterns. Studies in the Central Valley may also provide a window into the effects of a warming future. Over the last 30 years, average maximum temperatures during the nesting season (i.e., March–July) in the Central Valley rose into the 98th, 97th, 88th, and 68th percentiles of

the maximum temperatures experienced across tree swallow, house wren, western bluebird, and ash-throated flycatcher ranges within the continental United States (Birdlife International, 2021; PRISM Climate Group, 2021). Looking forward, temperatures are expected to rapidly increase further, particularly during the summer, with average annual maximum temperatures predicted to increase by 3 °C by the end of the century, even under the moderate United Nations Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathway (RCP) 4.5 emissions scenario (Pierce et al., 2018). Annual precipitation is predicted to remain the same or increase slightly (Pierce et al., 2018), but to exhibit greater year-to-year volatility (Swain et al., 2018). Importantly, precipitation timing is predicted to change significantly for the region, with decreases in winter precipitation (November-January) and increases in spring precipitation (February–May), during the avian nesting season (Houlton and Lund, 2018).

Our work was guided by two overarching questions. First, we ask if species are most fit where they choose to nest or if, instead, we see evidence of ecological traps. We predicted that species select nest sites based on adaptation to habitat variables that optimize their nesting success, but that habitat changes caused by anthropogenic land uses might act as ecological traps (i.e., species will select boxes in orchards, but fitness will be lower in these boxes). Second, we ask how elevated temperatures, reduced winter rainfall, and increased springtime precipitation, all signatures of ongoing climate change in the region, may affect cavity-nesting songbird fitness. We predicted that high maximum temperatures negatively impact reproductive success as birds struggle to physiologically cope during the already hot, dry summers characteristic of the region's Mediterranean climate. We also predicted that decreases in winter precipitation would result in lower reproductive success because of lower net primary productivity the following spring and, in turn, lower invertebrate prey availability for foraging parents. Finally, we predicted that increases in spring precipitation would also correlate with lower reproductive success, due to both the increased energetic costs of thermoregulation during rain events and limited foraging opportunities.

2. Materials and methods

2.1. Study area

We explored the effects of habitat and weather extremes on secondary cavity-nesting songbird reproduction within the lower Putah Creek watershed in California's Central Valley. The region experiences a typical Mediterranean climate, with hot dry summers and mild wet winters. Based on NOAA weather station 30-year climate normals (1991–2020), the average annual temperature in Davis, CA (midway along the creek corridor) was 16.4 °C (ranging from 9.1 °C in winter to 23.3 °C in summer) and average annual precipitation was 486.7 mm, with 85 % of rain falling in winter and spring.

Specifically, our system of artificial nest boxes was located along a ~ 50 km stretch of lower Putah Creek that originates at the base of Monticello Dam (which forms Lake Berryessa), flows past the cities of Winters and Davis and through the Yolo Bypass Wildlife Area, and ultimately discharges into the Sacramento-San Joaquin Bay-Delta (Fig. 1). The Putah Diversion Dam also impounds the creek, diverting ~90 % of its water to Solano County. Much of the Putah Creek ecosystem can now be characterized as a deeply-incised creek channel supporting only a narrow strip of riparian forest bordered by orchards and row crops. Though semi-natural habitats still surround Putah Creek in its upper (western) reaches, most of the woodlands that formerly provided natural nesting cavities for birds adjacent to the lower and middle reaches have been felled and replaced with agriculture. Further, the few natural cavities that remain are regularly usurped by invasive species, primarily European starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*).

The Putah Creek Nestbox Highway was established in 2000 with the goal of augmenting nesting habitat for native cavity-nesting songbirds.
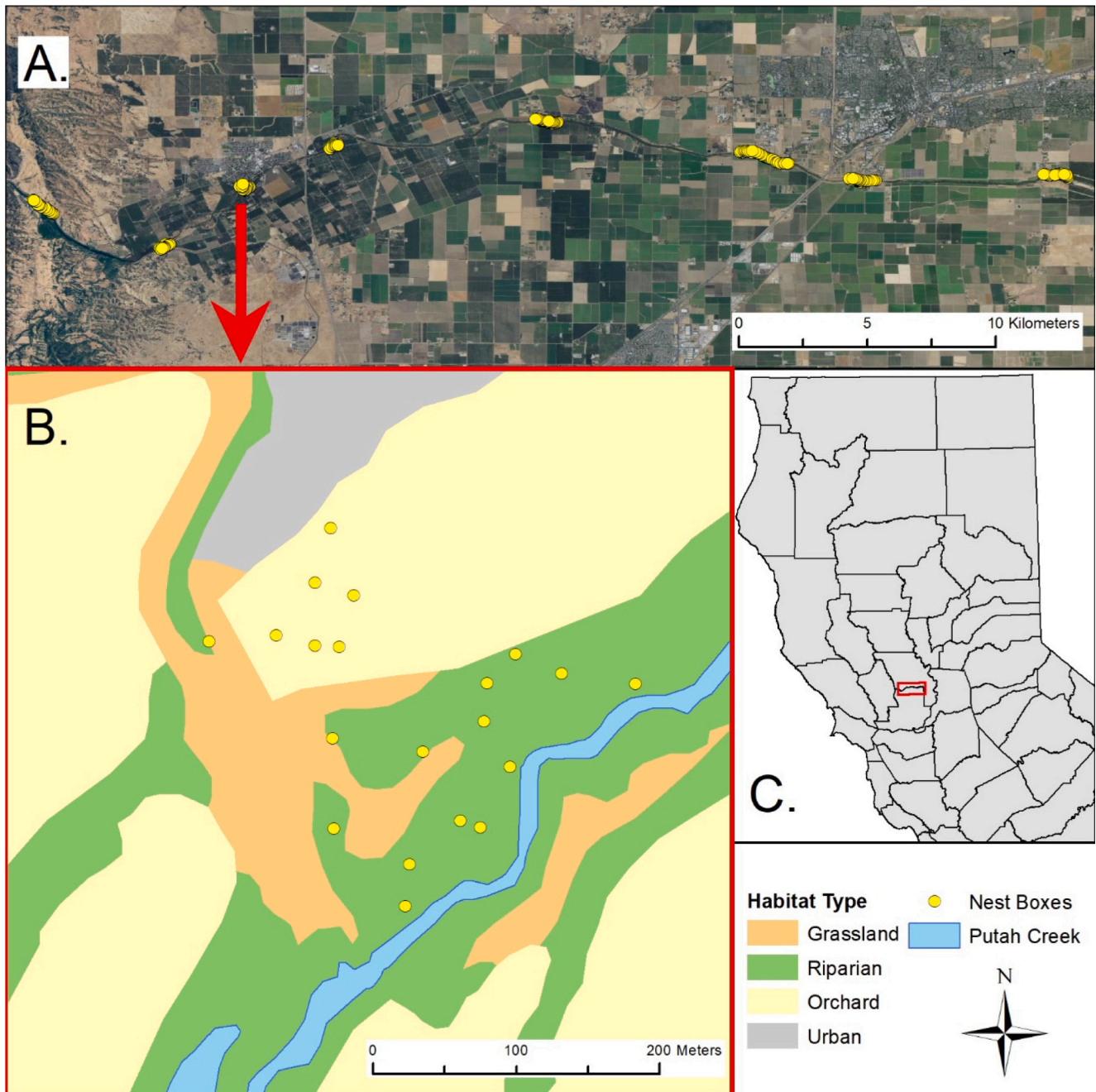
Fig. 1. A. Satellite image showing nest boxes distributed across the eight sites that constitute the Putah Creek Nestbox Highway in California's Central Valley in 2020. B. Red arrow indicates one of the study sites, as detailed in the map below, classified by habitat type alongside nest box locations. C. Inset map shows the location of the study area in northern California. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

This network comprises eight sites along Putah Creek, with an average of 20 boxes per site. Across the network, an average of 162 nest boxes (range 128–184) were monitored each year. Our data is drawn from 2004 to 2008 and 2015 to 2020 (Fig. 1). Boxes were laid out systematically at ~50 m intervals parallel to the creek in one to two linear rows depending on the site, with one row along the creek and a second along the outer edge of the riparian habitat. Occasionally, a third row was placed in nut orchards where orchards were adjacent to the riparian edge. Boxes were hung using orchid pot hangers from tree limbs around 3 to 4 m high (i.e., within the canopy) to help protect nests from heat, predators, and vandals.

2.2. Nest box data collection

The Putah Creek Nestbox Highway uses standard North American Bluebird Society nest boxes (www.nabluebirdsociety.org) that can accommodate a variety of small cavity-nesting passerines. The internal dimensions of a nest box are approximately $102 \times 140 \times 273$ mm. The box entrance hole is located three-quarters of the way from the bottom to the top of the box and the diameter is ~40 mm to accommodate the largest target species, ash-throated flycatcher, while excluding the invasive European starling. These nest boxes have historically hosted seven native cavity-nesting species: Bewick's wren (*Thryomanes bewickii*), oak titmouse (*Baeolophus inornatus*), white-breasted nuthatch

(*Sitta carolinensis*), ash-throated flycatcher, house wren, tree swallow, and western bluebird. However, the latter four species comprise the majority (>90 %) of nesting attempts and are therefore the focus of this study. House sparrows occasionally attempt to nest in boxes near urban areas, but eggs and nests are removed to discourage use (house sparrows are nonnative and therefore exempt from the Migratory Bird Treaty Act). A total of 2305 nesting attempts (defined as a clutch of at least one egg) were included in this analysis, comprising 217 attempts by ash-throated flycatchers, 368 by house wrens, 1141 by tree swallows, and 579 by western bluebirds.

Each year, nest boxes were visited every 7–10 days from March through August. During each visit, field observers recorded data on adult presence, nest development stage, number of eggs laid, whether incubation had begun, and number of nestlings present. Between four and seven days prior to the earliest estimated date of fledging, all nestlings were measured and banded. Field observers recorded body weight, wing chord length, tail length, and bill length (nares-to-tip) for each nestling. Median nestling age at banding for house wrens was 10 days, ash-throated flycatchers 11 days, tree swallows 13 days, and western bluebirds 14 days. Nestlings were left undisturbed between banding and fledging. Boxes are cleaned out before the beginning of each breeding season in February and after each nesting attempt, and diatomaceous earth was used to treat mite and ant infestations.

2.3. Environmental data

We collected data on seven environmental variables (four habitat and three weather) associated with each nest box during each year of the study. First, we quantified average median Enhanced Vegetation Index (EVI) values for the 30 m^2 pixel that intersected each nest box for each yearly nesting season (March 1st to July 31st) using the Landsat 5 TM Collection 1 Tier 1 8-Day EVI Composite (2004–2008) and Landsat 8 Collection 1 Tier 1 8-Day EVI Composite (2015–2020) in Google Earth Engine. EVI can be considered a proxy for net primary productivity (e.g., Myneni et al., 1997; Schloss et al., 1999; Wang et al., 2004). Second, we calculated the distance from the closest major paved road to each nest box as a proxy for traffic noise (McClure et al., 2013), using the 2019 Census TIGER/Line Shapefiles dataset (U.S. Census Bureau, 2019). Third, we estimated the distance from Putah Creek to each nest box, using data from the California Department of Fish and Wildlife's California Wildlife Habitat Relationships map, a remotely-sensed water classification map, and a line map of the midline of the creek. We created the water map by calculating the Normalized Water Difference Index from a June 2016 aerial image (National Agriculture Imagery Program), using green and near-infrared bands and assigning any pixels with a value greater than or equal to 0.3 as water (McFeeters, 2013). The midline of the creek was hand-digitized from the same imagery and buffered by 3 m to account for narrow portions of the creek where overhead vegetation obscured water pixels. Fourth, using ground-truthing data and satellite images (for nest boxes no longer installed), we characterized the habitat type of each nest box into three groups: grassland (*n* = 26 in 2020), orchard (*n* = 20 in 2020), and riparian woodland (*n* = 138 in 2020). Preparation of habitat variables was done using ESRI ArcMap v10.7.1.

Finally, we quantified three weather variables for each of the 2305 nesting attempts from daily National Oceanic and Atmospheric Administration (NOAA) weather data for the cities of Davis (Davis 2 WSW Experimental Farm, CA US; *n* = 82 in 2020) and Winters (*n* = 102 in 2020). The weather data used was selected based on proximity of weather station to the relevant nest box location. The mean distance between nest boxes and weather stations was 4.32 km. Average maximum daily air temperature during the nesting period for a given nesting attempt, as well as the sum of precipitation during the same period were calculated from weather data starting on the estimated first day of incubation and ending 30 days later (the average length of the entire nesting period across our entire dataset). To analyze the

relationship between temperature and nestling weight, we again calculated the average maximum daily temperature and sum of precipitation, but this time for the period between hatching and fledging, starting with the estimated hatching date and ending 14 days later (the average length from hatching to banding across the species in our dataset was 13 days). Finally, winter precipitation— fixed across all nesting attempts in each year— was calculated as the sum of all precipitation from October 1st of the prior year until March 1st (i.e., from the beginning to the end of winter rains).

2.4. Statistical analyses

We examined the relationship between the seven habitat and weather variables and nest site selection, reproductive success (i.e., clutch size and the probability of successfully fledging young), and nestling weight for each species separately. First, nest site selection was computed as a Bernoulli variable, with 'success' defined as at least one egg laid within a box and 'failure' defined as no nesting attempts made by a given species in a given year in that box. Second, clutch size was modeled with a truncated generalized Poisson distribution, as clutch size constituted underdispersed count data with no zeros (Brooks et al., 2019; Kendall and Wittmann, 2010). Third, the probability of successfully fledging young was computed as a binomial response variable, reflecting the number of eggs that did versus did not hatch and ultimately fledge. Finally, we assessed nestling body weight (in grams) with a Gaussian distribution, including age of nestling as a fixed effect to account for variation in the exact time chicks were banded and weighed. As the size of any given fledgling may be smaller in larger broods (Nur, 1984; Robinson and Rotenberry, 1991), we also included brood size as a predictor variable in all nestling weight analyses.

Importantly, average maximum daily temperature increases with the progression of each nesting season, and many nest boxes experience multiple nesting attempts within a nesting season. In addition, clutch size (Finke et al., 1987; Styrsky et al., 2000, 1999; Young, 1994), parental provisioning (Johnson et al., 2004), reproductive success (Drilling and Thompson, 1991), and nestling weight (Styrsky et al., 1999, 2000) may also decline later in the nesting season, confounding the effect of temperature on reproductive success. Thus, we ran one set of models using temperature only and a second set including day of year as a predictor variable. To account for the high correlation between temperature and day of year, we regressed nesting temperature on day of year and used the residuals as our predictor variable in the global model (i.e., departure from predicted average maximum temperature during the nesting period; Fig. S1).

We built generalized linear mixed models for each species and for each scaled and centered predictor variable. To account for interannual variability and spatial autocorrelation, we included random effects of year and 'nest box' nested within 'site.' We checked for multicollinearity of predictor variables and no model resulted in variable inflation factor values >3; thus, all fixed effects were retained in global models.

We created all possible subsets of the fixed effects in the global model and ranked them by sample-corrected Akaike Information Criterion (AICc). We report the standardized regression coefficient effect sizes for the top-ranked model for each species. We also include (in supplementary tables in Appendix A) all models within 2 AICc of the top model, as well as the null model (i.e., no fixed effects) and global model (i.e., all fixed effects) as references. Statistically significant relationships were defined as those with *p*-values <0.05 in the top model; marginally significant relationships were defined as having p-values between 0.05 and 0.1. All statistical analyses were conducted in R version 4.2.1 (R Core Team, 2022) using the "glmmTMB" (Brooks et al., 2017), "MuMIn" (Barton, 2022), and "performance" (Lüdecke et al., 2021) packages.

3. Results

Models revealed strong species-specific effects of both habitat and

weather on nest site selection, clutch size, nesting success, and nestling weight.

3.1. Clear relationships between habitat and nest site selection, but no indication of ecological traps

Habitat variables strongly influenced avian nest site selection, but differently for each species. Ash-throated flycatchers selected grassland boxes over orchard boxes (Tukey's HSD, $p = 0.0351$) and boxes further from the creek ($p = 0.0022$; Fig. 2 A – D; Tables S1-2). House wrens selected boxes in areas of high EVI ($p < 0.0001$), primarily in riparian habitat, less often in grassland, and rarely in orchards. In contrast, tree swallows selected boxes in areas with low EVI ($p = 0.0039$), but also close to the creek (p < 0.0001). However, no differences in nest site selection were observed among habitat types for tree swallows. Finally, western bluebirds tended to select boxes further from the creek ($p = 0.0002$), in grassland and orchard habitats (but rarely in riparian forests).

Ash-throated flycatchers produced significantly more eggs in grassland boxes over orchard boxes (matching their nest site selection; Tukey's HSD, $p = 0.0290$). For the remaining three species, habitat did not affect clutch size (Tukey's HSD, $p > 0.05$) (Fig. 2 E – H; Tables S3-4). Fledging success (Fig. 2 I – L) and nestling weight (Fig. 2 M – P) did not vary among habitats for ash-throated flycatchers. Habitat type did not affect tree swallow fledging success, but there was a marginally significant positive relationship between tree swallow nestling weight and nests in orchards (Tukey's HSD, $p = 0.06$). Western bluebirds had a higher proportion of eggs that resulted in fledglings in orchards compared to grassland or riparian habitats (Tukey's HSD, $p = 0.0034$ and $p = 0.0007$ respectively), but there was no effect of habitat on

nestling weight for this species. In contrast, house wrens did not fledge a single chick during their two nesting attempts in orchard habitats during our study. Median EVI, distance from roads, and distance from creek had varying effects on reproductive success and nestling weight (Tables S7-8; S11-12).

Generally, the habitat variables that predicted nest site selection also had the same directional relationship with reproductive success and nestling weight (or had no direct effect on fitness). For example, house wrens selected nest boxes in areas with high EVI over the nesting season and produced larger clutches of eggs in these sites (Tables S1-4). Similarly, western bluebirds selected orchard sites more often than riparian sites and had greater fledging success there (Fig. 2; Tables S1–2; S7–8). There were no statistically-significant deviations from this trend, indicating the absence of strong ecological traps in this system.

3.2. Average maximum temperature during nesting period drives several avian reproductive outcomes

Overall, higher maximum temperatures during the nesting season were correlated with lower avian reproductive success. For all four species, higher average maximum temperatures during the nesting period were correlated with smaller clutch sizes ($p < 0.05$; Fig. 3 A - D; Tables S3–4). However, effects were no longer significant after accounting for the fact that temperatures increase over the nesting season ($p > 0.05$; Fig. S3; Tables S5-6). Higher maximum temperatures had a negative, though non-significant, effect on fledging success for ash-throated flycatcher, a marginally significant negative effect for western bluebird ($p = 0.0553$), and a significant negative effect for tree swallow and house wren ($p < 0.0001$ and $p = 0.0009$ respectively; Fig. 3 E – H; Tables S7-8). However, when accounting for day of year,
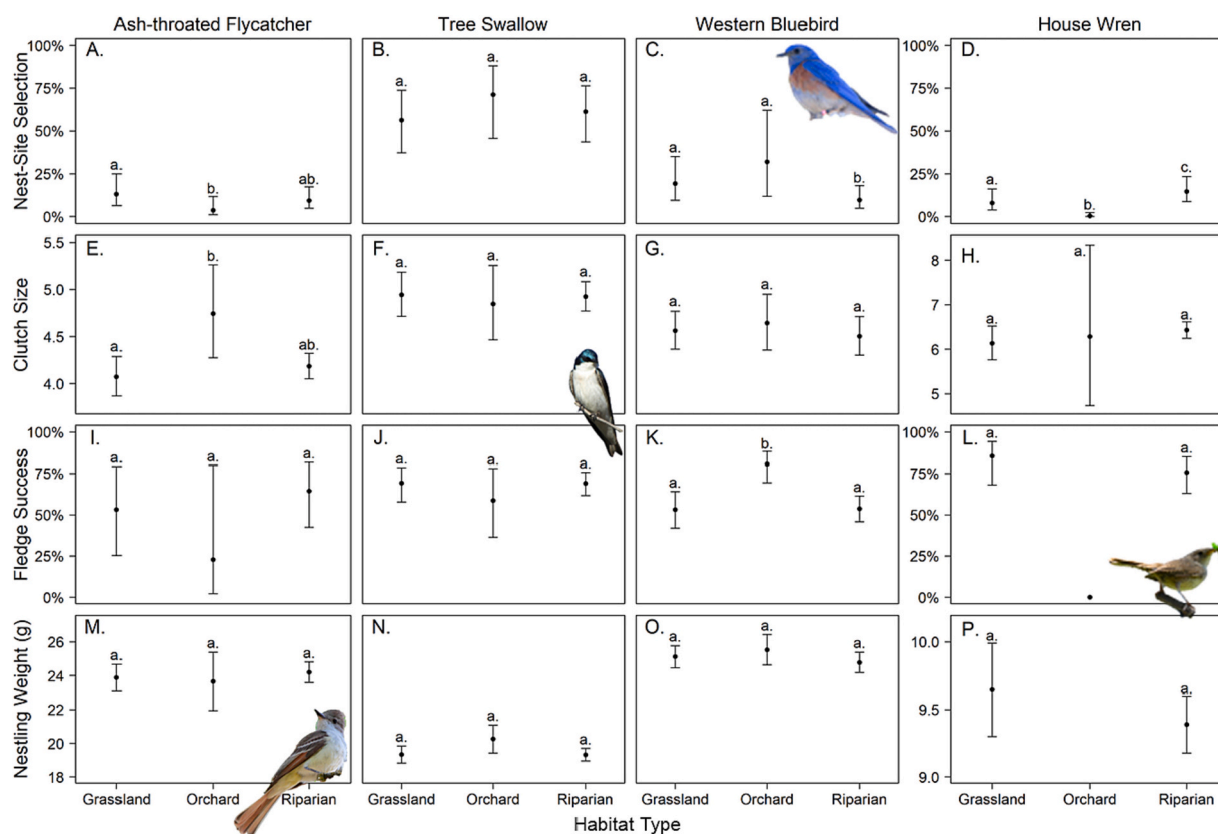

Fig. 2. Effects of habitat type on nest site selection (A – D), clutch size (E – H), fledging success (I – L), and nestling weight (M – P) for secondary cavity-nesting songbirds along Putah Creek. Lowercase letters indicate statistically significant differences between groups (Tukey's HSD, $p < 0.05$). Bars indicate 95 % confidence intervals. House wrens had only two nesting attempts in orchard boxes during the entire study period (the same individuals in the same year), and never successfully fledged a chick in an orchard.
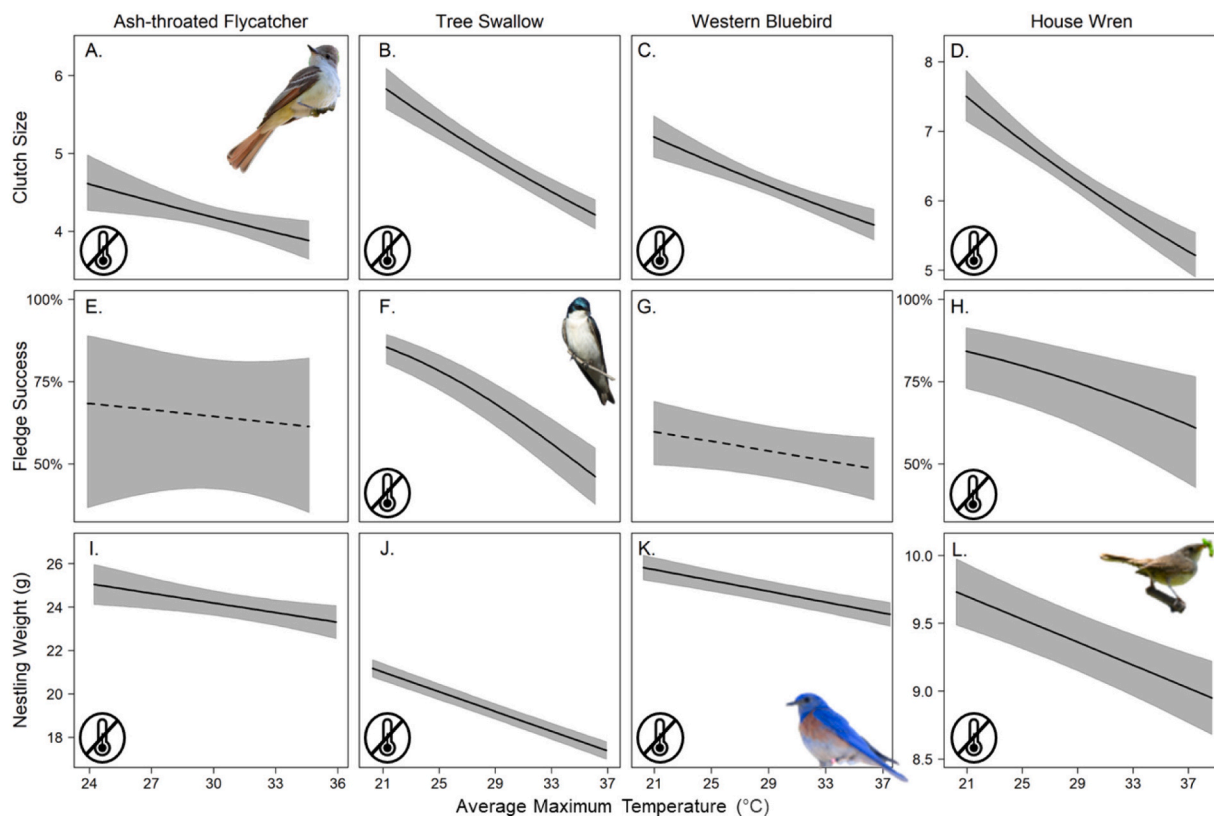
Fig. 3. Relationship between clutch size (A – D), fledging success (E – H), and nestling weight (I – L) and average maximum temperature during nesting attempts for secondary cavity-nesting songbirds along Putah Creek. Solid lines indicate statistically significant trends (p < 0.05). Thermometer icons indicate relationships that will likely be negatively impacted by future climate change in the Sacramento Valley (i.e., increasing temperatures). Negative impacts on nestling weight and fledging success remained after accounting for potential impacts of nesting date (Fig. S5).

maximum temperature residuals only had a statistically significant negative effect on western bluebird fledging success ($p = 0.0079$; Fig. S3; Tables S9-10). For all four species, higher average maximum temperature during the nesting period had a statistically significant negative effect on nestling weight (Fig. 3 I – L; Tables S11-12). After accounting for day of year, maximum temperature residuals still had a significantly negative effect on nestling weight for all species except western bluebird, where the effect was marginally significant ($p = 0.0537$; Fig. S3; Tables S13–14).

3.3. Winter precipitation has minimal impacts on reproductive outcomes

Winter precipitation was never included in a top model as a predictor for clutch size or fledging success for any species (Fig. 4 A - H; Tables S4; S6; S8; S10). Greater winter precipitation did, however, have a positive effect on nestling weight, but the effect was only statistically significant for house wren ($p = 0.0076$; Fig. 4 I – L; Tables S11-12) and was only included in the top model for tree swallow when accounting for the day of year ($p = 0.1596$; Tables S13-14).

3.4. Nesting season precipitation significantly lowers reproductive outcomes for two of the four study species but increases fitness for a third

Fledging success and nestling weights of tree swallows and western bluebirds significantly declined with increasing nesting season precipitation in models that did and did not account for the day of year (Fig. 5; Tables S7-14). Nesting season precipitation also had a significant, negative effect on the fledging success of house wrens ($p = 0.0170$) but was marginally significant after accounting for the day of year ($p = 0.0698$). In contrast, for ash-throated flycatchers, there was a significant

positive relationship between nesting season precipitation and fledging success ($p = 0.0009$) and marginally significant positive effect on nestling weight ($p = 0.0745$; Fig. 5; Tables S7–14). No significant effects were observed on clutch size for any species (Tables S3–6).

4. Discussion

4.1. Nest site selection and ecological traps

As predicted, we found that cavity-nesting songbirds did indeed select nest sites based on habitat variables, and that these variables were species-specific. Furthermore, these habitat variables tended to positively correlate with fledging success and nestling weight (Fig. 2; Tables S8; S12). Ash-throated flycatchers, house wrens, tree swallows, and western bluebirds all selected nest sites that resulted in higher reproductive success and larger nestlings, indicating that nest site selection in this system did not result in ecological traps. Furthermore, we found little evidence supporting our prediction that anthropogenic habitats might create ecological traps. For example, western bluebirds selected orchards for nesting and had higher reproductive success there compared with other habitats.

Our results match the findings of other studies showing that habitat variables predict species-specific nest site selection by cavity-nesting songbirds in California. For example, research in an oak woodland along California's Central Coast also found that house wren nest sites were associated with riparian vegetation and that western bluebirds nested away from riparian areas, selecting grasslands (Milligan and Dickinson, 2016; Purcell and Verner, 2008). Similarly, a study in oak woodlands at the San Joaquin Experimental Range also found that western bluebirds selected nest sites in open grasslands and oak
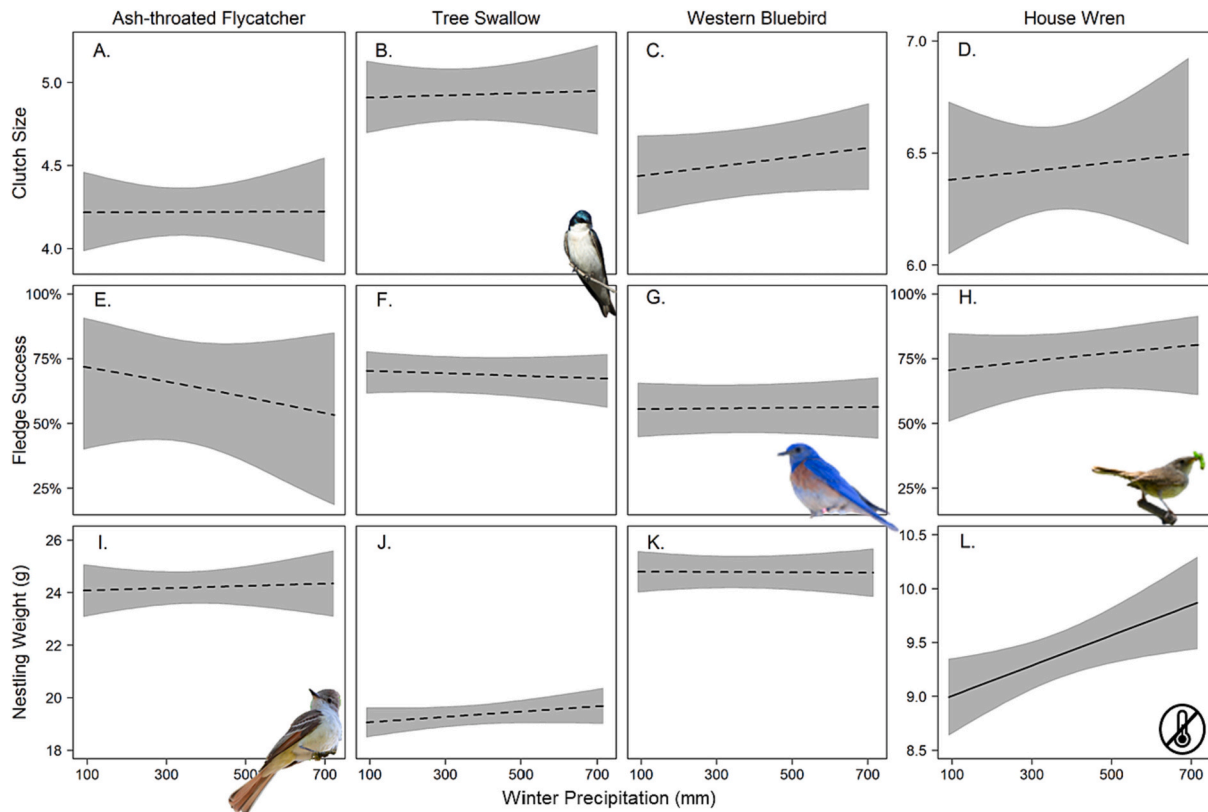
Fig. 4. Relationship between clutch size (A – D), fledging success (E – H), and nestling weight (I – L) and the sum of winter precipitation prior to the nesting season for secondary cavity-nesting songbirds along Putah Creek (October 1st to March 1st). Solid lines indicate statistically significant trends ($p < 0.05$). Thermometer icons indicate relationships that will likely be negatively impacted by future climate change in the Sacramento Valley (i.e., decreasing annual precipitation).

woodlands, whereas house wrens selected nest sites in areas of dense vegetation (Purcell and Verner, 2008). This mirrors our finding that house wrens selected nest boxes in areas with high EVI over the nesting season.

4.2. Climate change and the fitness of cavity-nesting birds

We predicted that increasing annual temperatures in California's Central Valley were likely negatively impacting the reproductive success and nestling weight of cavity-nesting songbirds. Supporting this prediction, we found, over our 11-year study, that higher average maximum temperatures during the nesting season were associated with smaller clutch sizes and reduced reproductive success and nestling weight for all species (Fig. 3; Tables S4; S8; S12). Our models indicated that average nestling weight of ash-throated flycatchers, house wrens, tree swallows, and western bluebirds declined by 7 %, 8 %, 19 %, and 9 % respectively, between the coolest (21.7 °C) and hottest (36.0 °C) average maximum air temperatures recorded during each nest's 30-day nesting period. Additionally, tree swallow fledging success declined 39 % (from 85 % to 46 %). Negative impacts on nestling weight and fledging success remained after accounting for potential impacts of nesting date (Fig. S3; Table S10; S14). For clutch size, we could not unravel the underlying mechanisms of lower reproductive success seen later in the nesting season: it could represent reduced female condition in later clutches, reduced food availability, or the (much) hotter temperatures that females experience later in the season.

Our results suggest that, in this California Mediterranean climate with hot dry summers, high maximum temperatures may be more detrimental to breeding birds than low minimum temperatures, even though most of the prior literature has focused on documenting the negative effects of cold snaps (DuBowy and Moore, 1985; McCarty and Winkler, 1999; Winkler et al., 2013). Increasing maximum temperatures

can affect reproductive success and nestling weight in several ways. Extremely high daytime temperatures can reduce invertebrate prey availability (Barras et al., 2021; Fletcher et al., 2013; Higgins et al., 2010); and decrease food provisioning for offspring as parents reduce their foraging rates to avoid the heat (Conradie et al., 2019; Cunningham et al., 2021). Additionally, exposure to high temperatures in the nest can also result in chick weight loss and mortality due to increased costs of thermoregulation (Bourne et al., 2020; Murphy, 1985; Riddell et al., 2019) and evaporative water loss (Albright et al., 2017).

Counter to our prediction, we found little evidence that winter precipitation positively influenced avian reproduction. We found only one significant positive association: house wren nestlings tended to be larger when preceding winters were wetter (Fig. 4; Table S12). For the other three species, negative results contradict other studies that found reproductive success increased with precipitation preceding the nesting season (Chase et al., 2005; Rotenberry and Wiens, 1991; Zuckerberg et al., 2018). A possible reason for this is that Putah Creek receives perennial flows from its upstream dams, thereby mitigating the effects of annual drought.

Our study supported the prediction that increased precipitation during the nesting period compromised reproductive success. Both tree swallow and western bluebird nestling weight and overall reproductive success were negatively associated with nesting period precipitation (Fig. 5; Table S8; S12). For example, our models predicted that the probability of successfully fledging tree swallows and western bluebirds declined by 45 % (from 73 % to 28 %) and 20 % (from 56 % to 36 %) respectively and that average nestling weights declined by 18 % (from 19.5 to 16.0 g) and 6 % (from 25.1 to 23.6 g) respectively when nests experienced the wettest (73.2 mm) versus the driest (no precipitation) nesting periods.

There are multiple pathways by which these negative associations may arise. Previous studies have indicated that food availability best
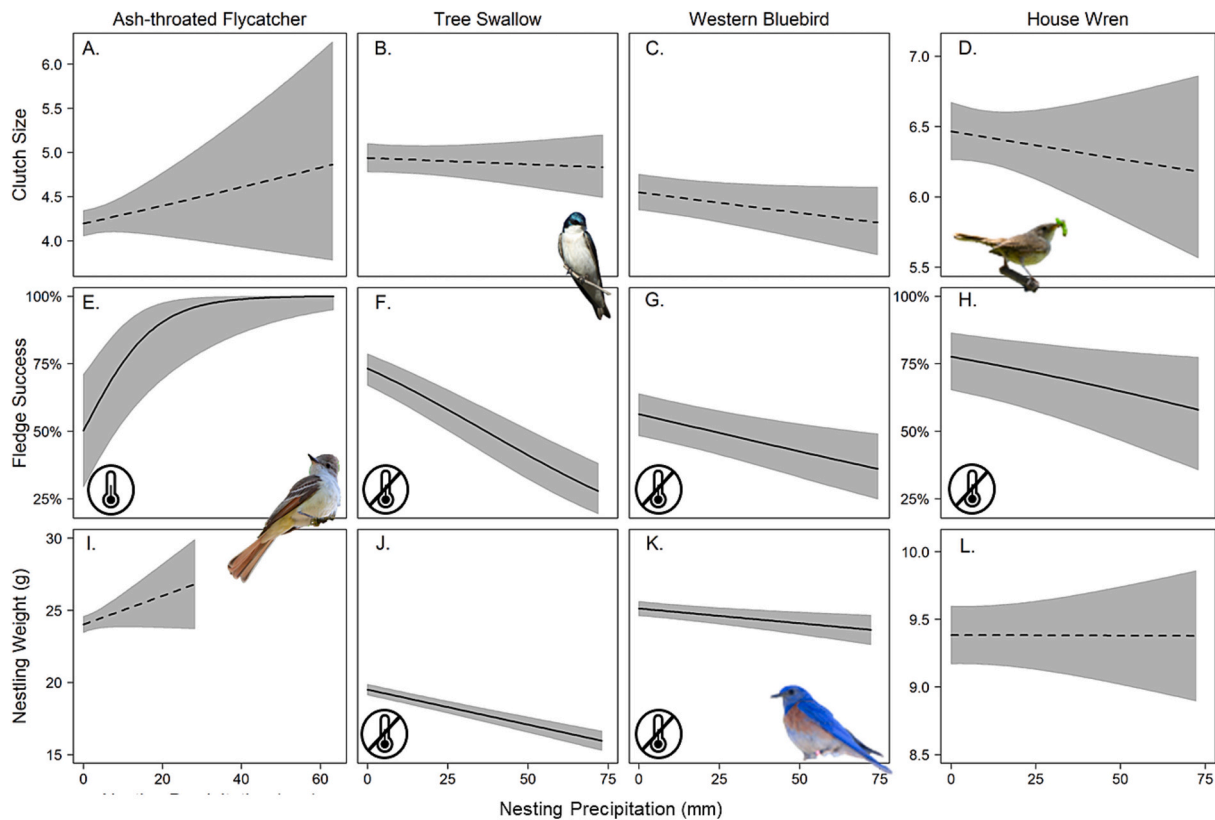
Fig. 5. Relationship between clutch size (A – D), fledging success (E – H), and nestling weight (I – L) and the sum of precipitation during nesting for secondary cavity-nesting songbirds along Putah Creek. Solid lines indicate statistically significant trends (p < 0.05). Thermometer icons indicate relationships that will likely be positively (regular icon) or negatively (crossed-out icon) impacted by future climate change in the Sacramento Valley (i.e., increasing spring precipitation).

predicts tree swallow nestling growth (Ardia, 2006; Quinney et al., 1986) and that precipitation during the nesting season may have negative effects on the availability of the aerial arthropod prey base that they rely upon (i.e., aerial insects are less active during rain events). Furthermore, parental visits to the nest to feed young may decline during periods of precipitation, further reducing food availability for nestlings (Öberg et al., 2015; Radford et al., 2001). Flooding may also drive black rats (*Rattus rattus*) and other predators into the trees (Whisson et al., 2007), where they concentrate predation on nesting birds. Finally, the interaction between precipitation and low temperatures may increase the cost of thermoregulation for nestlings, leading to decreased growth and higher mortality (Radford and du Plessis, 2003).

4.3. Limitations and future studies

There are several limitations to our study that could be addessed in future studies. First, our study does not measure microclimate associated with the nests. This may be important as nests within riparian forests, grasslands, or orchards are all likely to experience very different local temperature, humidity, precipitation, and disturbance regimes (Williams and Newbold, 2020). The mostly closed-canopies evaluated in this study might be expected to be buffered against these environmental and climatic factors (de Frenne et al., 2019). Future studies could monitor nest site microclimates through temperature and humidity sensors inside and outside nest boxes. Second, nesting in other more intensive anthropogenic habitats (e.g., row crops and urban areas) adjacent to Putah Creek could be examined. These areas are considerably hotter, having little or no canopy cover, and so thus may be more vulnerable to climate change (de Frenne et al., 2019; Suggitt et al., 2011). Interestingly, we noted that western bluebirds showed greater reproductive success in orchards. Understanding how these anthropogenic habitats might act as surrogates for natural forests in fragmented ecosystems

could be important to conservation and restoration. Finally, additional studies could explore the exact mechanisms relating habitat and climate to the fitness of cavity-nesting songbirds in our system, such as the impacts of land use, temperature, and precipitation on food availability and provisioning rates, predation, parasites, and direct physiological effects on nestlings.

5. Conclusion

Our results complement a rich portfolio of studies exploring the relationships between habitat, nest site selection, and reproductive success in cavity-nesting birds, but is the first (to our knowledge) that expressly links both habitat *and* weather extremes to reproductive success and nestling weight. Our findings suggest that cavity-nesting songbirds do indeed select nest sites based on habitat variables. These variables generally correlate with reproductive success and nestling weight, suggesting an absence of ecological traps in the habitats examined here. This is an encouraging finding, validating ongoing efforts to bolster cavity-nesting bird populations in anthropogenic systems, for the benefit of humans (e.g., insect pest control; Jedlicka et al., 2011, 2014; Shave et al., 2018) and the birds themselves (Dybala et al., 2018; Finch et al., 2019; Norris et al., 2018).

Less optimistically, our results suggest that the predicted effects of climate change in California's Central Valley, particularly increased nesting season temperature and spring precipitation, are likely to have broad and mostly negative impacts on cavity-nesting songbird reproductive success and nestling weight. Mediterranean species are known to be among the most sensitive of any group to changes in land use and climate (Newbold et al., 2020), and, globally, the biome has experienced some of the greatest rates of habitat loss and fragmentation (Jacobson et al., 2019; Riggio et al., 2020) while being one of the least protected (Dinerstein et al., 2017). This region may act as a bellwether for

Mediterranean systems more broadly, as individuals nesting in the Central Valley already experience some of the most extreme temperatures of any individuals of the same species across the Continental United States. Ultimately, species persistence in these systems in the face of the predicted effects of climate change will require phenological (e.g., nesting earlier in the season) and/or physiological (e.g., increased thermal tolerance) adaptations, and may be assisted by habitat restoration efforts that focus on providing thermal refugia (e.g., increased tree cover).

CRediT authorship contribution statement

Jason Riggio: Conceptualization, Methodology, Writing – original draft, Visualization. **Andrew Engilis:** Writing – review & editing, Supervision, Funding acquisition. **Hanika Cook:** Investigation, Data curation, Writing – review & editing, Project administration. **Evelien de Greef:** Investigation, Data curation, Writing – review & editing, Project administration. **Daniel S. Karp:** Conceptualization, Methodology, Writing – review & editing. **Melanie L. Truan:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

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

Data availability

Our data is included in Appendix B

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109885.

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