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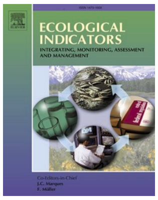

Original Articles

The importance of high streamflow and bank erosion for the Bank Swallow, a sentinel species of alluvial river systems

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ABSTRACT

Lowland alluvial rivers are rich in biodiversity, yet many are highly degraded, constrained by dams and riprap, and no longer support robust natural communities or critical ecosystem services. Restorative actions are needed, as are ecological indicators for evaluating their effectiveness. We evaluated factors that regulate the population growth rate of Bank Swallows to inform strategies for its recovery and to assess its value as an indicator of riparian ecosystem health. In North America, over the past 50 years, this species, which depends upon erosion for its cutbank breeding habitat, has declined at a rate considered extreme. Understanding the causes of this decline and identifying feasible recovery actions is an urgent conservation priority. In our 25-year study of the Bank Swallow population on the Sacramento River, the breeding population fluctuated widely but declined at an average overall rate of 1.5 % per year. Periodic high streamflow played an important role in maintaining the population, and its effect on the population growth rate was time-lagged by 1 year. This suggests that high flow conditions may have improved rates of Bank Swallow reproductive success and/or survival, leading to increased recruitment into the breeding population in the subsequent year. We also found evidence for density-dependent population growth, suggesting that when the breeding population was large, high-quality nesting habitat was limiting. Our study establishes the critical importance of high streamflow and bank erosion to maintaining Bank Swallow breeding populations. In so doing, it informs recovery strategies for the species and the rivers it inhabits and identifies the Bank Swallow as an appropriate indicator of alluvial river ecosystem processes.

1. Introduction

Hotbeds of biodiversity (Strayer and Dudgeon 2010), and purveyors of myriad ecosystem functions and services (Petsch et al. 2022), lowland alluvial rivers and their associated floodplains are amongst the most important of habitats on earth—for both people and nature (Tockner and Stanford 2002). Yet many of the world's large rivers are in a state of decline or are already considered "non-functional" (Palmer et al. 2008, Erwin 2009) due to historic degradation and ongoing mismanagement (Jakubínský et al. 2021). Most lack environmental protections (Abell et al. 2017), and many are plagued with flow regime alterations caused by dams, diversions, channelization, bank armoring, construction of artificial embankments that contain high flows (levees), and extractions of water and sediment (Fuller et al. 2015, Best 2019). Lost is the ecological integrity of these systems and ecosystem services they once provided.

Notable progress has been made on some rivers to restore important aspects of ecosystem function (Neilsen 2002; Friberg et al. 2016); however, for many others the situation is worsening from continued degradation forced by increasing human population pressures including climate change (Best 2019). Restorative actions are needed yet will only be effective at scale if they are based on an understanding of the hydrobiological processes that underpin freshwater ecosystems and the distinct threats they are facing. When drivers of population change are

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addressed with appropriate actions, degraded freshwater ecosystems can improve, but having appropriate indicators and targets to guide the process is critical (Tickner et al. 2020).

The Bank Swallow (*Riparia riparia*; also known as the Sand Martin) may be a suitable indicator of the ecological health of many alluvial river systems within its broad Holarctic breeding distribution. Most breeding colonies of this migratory passerine are found on eroding cutbanks of low-gradient, meandering rivers and streams (Garrison and Turner 2020). In North America north of Mexico, this species declined by 3.7 % yr^{-1} from 1966 to 2019, resulting in a 94 % loss characterized as "extreme" (Sauer et al., 2020). Their dependence on cutbanks for reproduction suggests a direct influence of river function on their population dynamics, and a potential opportunity for flow management to help recover this declining aerial insectivore and the river systems they depend upon. Here, we examine evidence for the role of streamflow and other factors in influencing the population dynamics of Bank Swallows on the middle Sacramento River in Northern California, the southern edge of the species breeding range. Most of this breeding population occurs within a 161-km reach of the river between Red Bluff and Colusa (Garrison et al. 1987). Annual monitoring of this species, listed as Threatened under the California Endangered Species Act, has shown high annual variability in breeding population size, and more research has been called for to better understand the underlying drivers of these patterns (Girvetz 2010).

Bank stabilization projects that involve the placement of large rocks and demolition concrete (hereafter riprap) on riverbanks to halt erosion have been identified as the greatest threat to Bank Swallow population viability in California (California Department of Fish and Game CDFG, 1992). They have been implicated in the extirpation of Bank Swallows from central and southern California (Garrison et al. 1987, Small 1994), and have caused harm to this species on the Sacramento River where egg and chick mortality, at times numbering in the thousands, was observed when riprap was dumped directly on top of breeding colonies (Schlorff 1997). Rapid colonization by breeding Bank Swallows after riprap is removed (Golet et al. 2003, Melcer 2021) suggests that high quality nesting habitat may be limiting in this system. However, the large annual fluctuations in breeding population sizes that have been observed cannot be explained by this factor alone given that riprap extent has changed incrementally over time. Other factors influencing reproductive success and survival during the breeding season, or survival during migration and overwintering, may also be contributing, including some (e.g., streamflow) that can be managed.

Annual variation in streamflow has also been suggested as a factor shaping Bank Swallow population dynamics (Garcia et al. 2008). High flows erode sloped banks and create steep surfaces into which swallows excavate their nesting burrows. Fresh cut, steep banks appear to be preferred and may improve reproductive success by reducing burrow parasite loads and nest predation (Haas et al. 1980, Garrison and Turner 2020). On the Sacramento River, Bank Swallow colonies are found more consistently in locations that have more bank erosion (Garcia 2009); however, evidence for effects of flow on swallow population dynamics has been mixed. The probability of new colonies forming and existing colonies disappearing both increased with peak river discharge of the preceding winter (Wright et al. 2011), but neither mean nor peak flow were found to be good predictors of the number of colonies or the number of burrows within them (Garcia 2009). These results suggest that variation in streamflow is not a good predictor of the breeding population size. Previous analyses have not, however, considered time-lagged effects of flows on population dynamics, as might be manifested if they affect breeding habitat quality, resulting in improved reproductive success and population growth when 1-year old birds return to the colonies to breed the following spring.

Drought may also influence population dynamics on the Sacramento River, although its effects have varied among populations studied elsewhere. Among Bank Swallows that migrate from England and Europe to Africa, drought was associated with reduced food availability and adult survival during the non-breeding season (Cowley and Siriwardena 2005, Norman and Peach 2013, Mondain-Monval et al. 2020). In contrast, adult survival in Hungary was not related to rainfall in their wintering range, but breeding populations declined in low rainfall years due to lower recruitment of first-time breeders and reduced immigration from elsewhere (Szép 1995a, Szép 1995b).

Our objectives were to evaluate long-term trends in Bank Swallow breeding population size on the middle Sacramento River and the role of streamflow, drought, and density-dependent reproductive success in Bank Swallow population dynamics, incorporating time-lagged effects. Our 25year survey dataset is well suited to addressing these questions because it includes years of both extreme drought and floods. Based on our findings we recommend management interventions to help recover the species and suggest that the Bank Swallow be viewed as a sentinel of biodiversity health on the Sacramento River and potentially other lowland alluvial river ecosystems within its range.

1.1. Background

The North American Bank Swallow nests in colonies ranging from 10 to over 3,000 active nests (this study), and winters in Central and South America. Preferred nesting habitat is on tall, steep banks in burrows dug a meter or more deep in alluvial, friable soils with appropriate texture and grain size (Humphrey and Garrison 1987). They appear to prefer to nest in freshly eroded banks (Haas et al. 1980), although remnant burrows are sometimes reused (Garrison 1989). How reuse of burrows influences nest success is an important research question (Sinclair et al. 2020).

On the Sacramento River, breeding Bank Swallows arrive at the colonies starting in early April, with some birds initiating burrow excavation soon thereafter (Garrison and Turner 2020). Excavation usually takes 4–5 days to complete (Sieber 1980, Turner and Rose 1989). Following a rainy winter with high flows few remnant burrows may remain. For example, only ~3 % were observed after the wet winter of 2011 (Wright et al. 2011). Nest building may continue until mid-June (Wright et al. 2011). Eggs have been observed from late April until early July, with chick presence in nesting burrows peaking in mid-May (Wright et al. 2011). Typical clutch size is 3–6 eggs, with 4 or 5 eggs being most common (Garrison and Turner 2020). Although return rates of juveniles to their natal colonies are not well established, previous research suggests they typically enter the breeding population after their first winter, with females being somewhat less likely to do so than males (Freer 1979, Holmes et al. 1987). Breeding site fidelity of adults is also in need of more study, however, annual survival rates determined by live recoveries and life table analyses for juveniles and adults was 40 % or below in five of six studies from Europe and North America (Garrison and Turner 2020).

In 1986, concern over observed impacts to Bank Swallow breeding colonies from Sacramento River bank stabilization projects led the California Department of Fish and Game (CDFG; now the California Department of Fish and Wildlife, CDFW) to initiate a comprehensive colony survey of the Sacramento and Feather Rivers. Within this survey area, ~70 % of the nesting population was found to occur along a 161-km reach of the Sacramento River between Red Bluff and Colusa (Garrison et al. 1987). In 1986, this reach supported over 25,000 burrows, including two very large colonies of ~3,200 burrows each (Garrison et al. 1987).

Since the annual Sacramento River colony surveys first began, approximate 10-year updates on the status of the breeding population have been provided (Schlorff 1997, Garcia et al. 2008). The first reported that between 1986 and 1996 total burrow counts declined by 56 %, and the number of colonies dropped 28 %. These declines were cause for concern because they dropped the population below a viability threshold of 10,000 pairs below which an isolated population was expected to have a > 33 % risk of extinction in the next 50 years (Buechner 1992). Through 2007, the population showed signs of recovery but remained below historic levels (Garcia et al. 2008). This context establishes the importance of examining more recent survey data, identifying factors driving population swings, and using this knowledge to develop conservation strategies.

2. Methods

2.1. Study area

The Sacramento River is California's largest river, supplying approximately 80 % of freshwater flowing into the Sacramento and San Joaquin River Delta (California State Lands Commission 1993). Its 62,000 square kilometer watershed provides a critical source of water for people and habitat for a wide variety of wildlife species. Historically, the river was lined by ~325,000 ha of riparian forest; however, over 95 % has been lost (Katibah 1984). Shasta Dam, located above the study area, constrains the river's flow regime and associated natural processes that promote habitat succession and regeneration; however, during storm events tributary inputs below the dam sometimes produce high flows that drive geomorphic processes. Active flow management that is done to support the ecosystem is largely focused on improving habitat conditions for threatened and endangered fish species.

Levees and riprap degrade the floodplain and in-channel habitat of the Sacramento River by confining two-thirds of the river's linear extent. However, the Red Bluff to Colusa stretch (Reaches 2 and 3, Fig. 1), where most of the Bank Swallows nest, is largely alluvial. There is less natural geologic control of river meander (Singer and Dunne 2001), and levees, where present, are setback from the river's banks in many places, creating hydraulically connected floodplains. Here the river also has less riprap on its banks, allowing natural riverine processes of bank erosion, point bar deposition, and the natural shifting of river bends (meander migration) to take place. Riparian conservation and restoration efforts have primarily focused on this section of the river because the degradation here is more easily reversible than in other areas (Golet et al. 2013, Holl and Golet 2020).

The watershed experiences a Mediterranean climate that is strongly affected by El Niño Southern Oscillation (ENSO) and Pacific-North America (PNA) teleconnection climatic patterns (Redmond and Koch 1991; Cayan et al. 1999). It typically experiences hot, dry summers and variably wet winters. Periods of drought have become more severe in recent years as the climate has warmed, but so too have atmospheric river systems, creating a hydroclimatic whiplash effect (Swain et al. 2018).

2.2. Bank Swallow colony surveys

In the first two years (1986 and 1987) that Bank Swallow colony surveys were conducted on the Sacramento River, CDFG surveyed all main channels from Redding to Verona (344 river km, Fig. 1). Since then, except in 2006, annual surveys have taken place between Red Bluff and Colusa (161 river km), the core breeding area for Bank Swallows in California. Located within this zone are the 4,142-hectare US Fish and Wildlife Service (USFWS) Sacramento River National Wildlife Refuge, for which the Bank Swallow is a Trust Species (USFWS 2005), and the 1,526-hectare CDFW Sacramento River Wildlife Area. Bank Swallow surveys were identified as an ongoing monitoring need in the Comprehensive Conservation Plan for the Refuge (USFWS 2005).

Between 1986 and the present, data collection methods changed such that results are not strictly comparable between pre-1999 and later surveys. Earlier surveys took place over extended periods lasting 1–2 months, whereas the latter ones were completed in a week or less during early June when chicks are typically present, and breeding activity is high at the colonies (Wright et al. 2011).

We analyzed survey data from Red Bluff to Colusa (reaches 2 and 3, Fig. 1) that were collected from 1999 to 2023. Over this 25-year period, surveys were conducted on two consecutive days in early to mid-June by a crew of four people that followed a standardized protocol developed by the Bank Swallow Technical Advisory Committee (Bank Swallow Technical Advisory Committee (BANS-TAC), 2017). The range of survey dates across all years of the study was June 4-June 16. Surveys involved travelling downstream by boat, examining both banks for the presence of colonies, defined as clusters of two or more burrows in a cutbank. Colonies were considered separate if gaps between them were > 161 m.

Colonies were classified as active when chick(s) were observed, or at least one adult was seen flushing from or flying into a burrow. Inactive colonies were not included in the breeding population index. At the active colonies, only burrows that appeared to be in use during the current breeding season were counted. These burrows were sufficiently deep (appearing "inky black"), free of debris, and lacked spider webs. Their entrances tended to have smooth edges and often showed claw drag marks and fecal droppings on the landing runways.

Although the proportion of burrows that appeared to be in use varied among colonies and between years, likely driven in part by the extent of erosion events during the previous winter, our strict monitoring protocol ensured that burrow counts represent a useful index of breeding population size. We make no assumption about the proportion of counted burrows that are currently occupied, but assume that the proportion is consistent across years such that the percent change in burrow counts is a useful index of the population's growth rate. Our methods follow the recommendation of Wright et al. (2011) to use unconverted burrow counts whenever possible as a rough abundance index to avoid introducing an additional variable (occupancy) and its associated uncertainty.

Burrow counting was done simultaneously and independently by two observers and repeated as needed until counts were within 10 % of each other. Counts at individual colonies took from several minutes to over an hour depending upon the number of burrows, lighting conditions and other factors. Burrow counts used in our analyses are the average of the two observers' totals of burrows that appeared to be in use for each active colony, and sum totals of the averaged counts for each year across all colonies in survey area. These burrow counts are assumed to be a good index of current year breeding population size (Humphrey and Garrison 1987, Schlorff 1997, Moffatt et al. 2005, Girvetz 2010; Wright et al. 2011, Garrison and Turner 2020).

2.3. Conceptual model and hypotheses

To better understand factors driving population dynamics of Bank Swallows on the Sacramento River, we developed a conceptual model illustrating potential effects of environmental conditions (specifically streamflow and drought) and population density, on variation in the population growth rate, through hypothesized effects on immigration/emigration, reproductive success, and survival (Fig. 2).

In developing this model, we assumed that the growth rate in the number of Bank Swallow burrows between subsequent breeding seasons *t-1* and *t* was directly influenced by reproductive success in year *t-1,* survival during the non-breeding season between years *t-1* and *t*, and whether or not surviving chicks and adults returned to breed on the Sacramento River in year *t* (i.e., rates of immigration/emigration).

Based on prior research, our conceptual model focuses on four distinct hypotheses that may contribute to changes in population size from breeding season *t-1* to *t*:

H1) Higher flows in the winter rainy season immediately preceding the breeding season (i.e., during the same year *t*) create higher quality breeding habitat due to increased bank erosion, which leads to increased immigration to the Sacramento River for breeding.

H2) Higher flows in the winter rainy season of the prior year (year *t-1*) create higher quality breeding habitat resulting in increased reproductive success in year *t-1* leading to more adults in the breeding population in year *t*.

H3) More severe drought conditions in the prior year's breeding season (year *t-1*) lead to lower reproductive success resulting in fewer

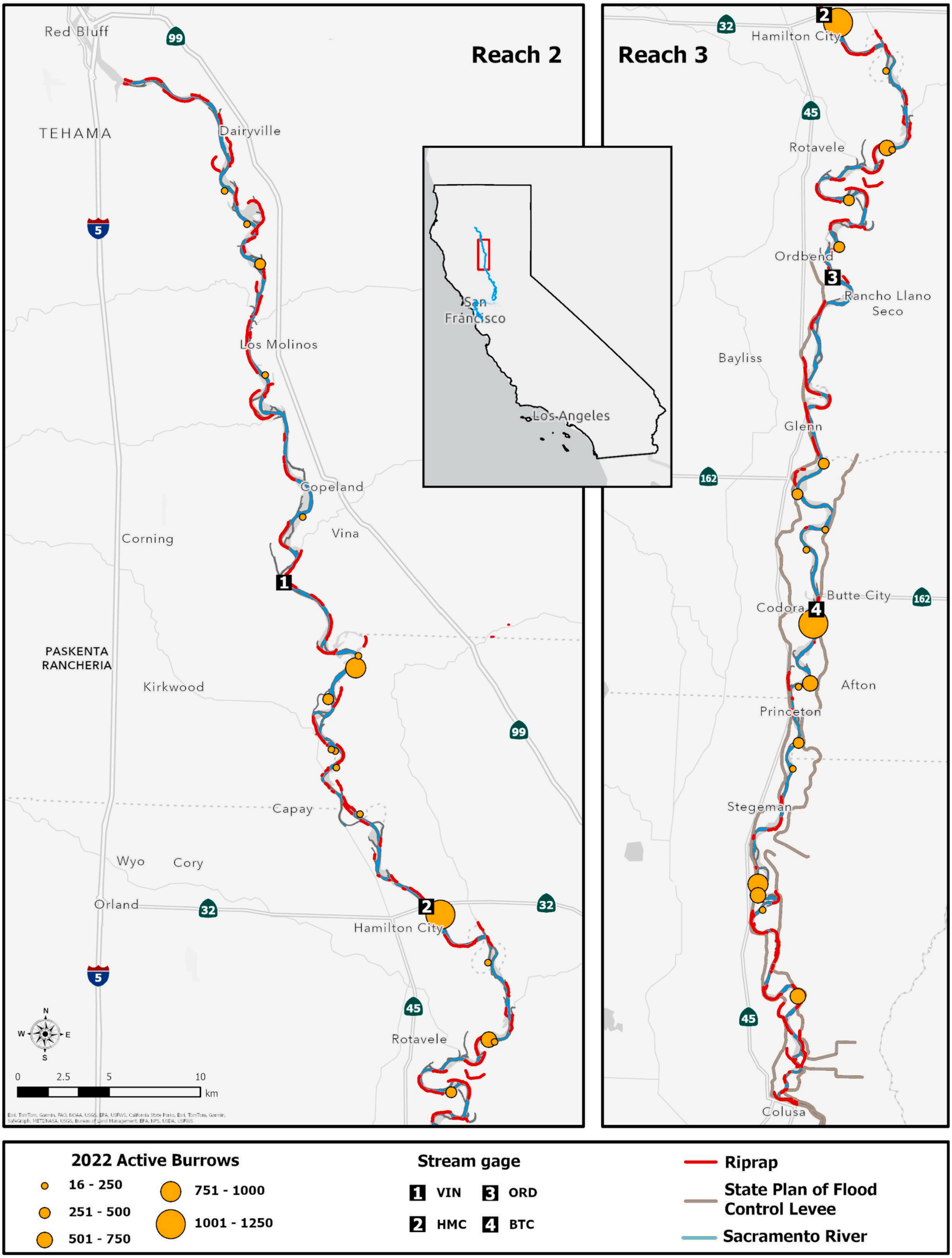

Fig. 1. Location of the study area showing active Bank Swallow nesting colonies, riprapped banks, and flood control levees. Inset map shows its location within California, USA. Left panel is the northern section, and right panel is the adjoining southern section (with overlap). Defined by river kilometers (RKM) above the confluence of the Sacramento and San Joaquin rivers, Reach 2 (RKM 391–296) is from the Red Bluff Diversion Dam to Ordbend Bridge, and Reach 3 (RKM 296-230) continues southward to Highway 20 at Colusa. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

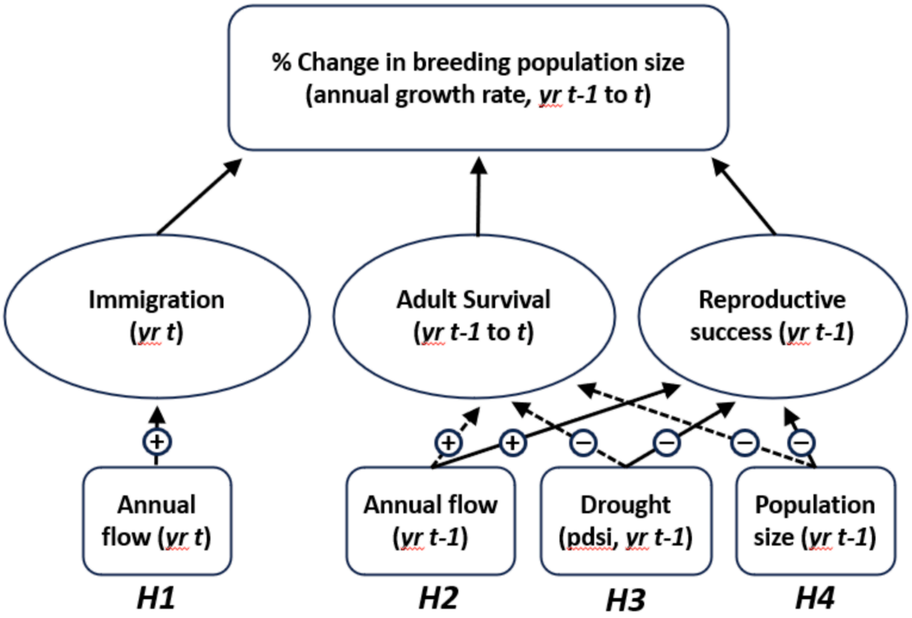

Fig. 2. Conceptual model for the variation in Bank Swallow annual growth rates, showing the four hypotheses evaluated in this analysis: *H1*. Effects of current year's annual flow on the number of adults returning to Sacramento River colonies to breed. *H2*. Effects of the previous year's annual flow on reproductive success. *H3*. Effects of drought conditions during previous breeding season on reproductive success. *H4*. Effects of population size during the previous breeding season on reproductive success (density-dependence, where N = number of burrows). In all cases reproductive success is considered inclusive of chick survival and recruitment. Also shown are hypothesized (dotted line) relationships between parameters of *H2*, *H3* and *H4* and adult survival. See methods for details.

young being recruited into the breeding population in year *t*.

H4) Larger total breeding population sizes on the Sacramento River in the prior year (year *t-1*) lead to lower reproductive success, due to density-dependent factors affecting large colonies.

In addition to influencing reproductive success, hypotheses 2–4 may also affect adult survival (as indicated in Fig. 2), although we expect that their effect sizes would be smaller than what is experienced by the chicks. By choosing to breed, adult Bank Swallows expose themselves to unavoidable risks, which may vary under differing environmental conditions. Life history theory predicts that to maximize lifetime reproductive success, short-lived bird species with relatively high annual fecundity (such as the Bank Swallow) should show an increased willingness to trade their own survival for that of their offspring, compared to longer-lived bird species (Williams 1966, Stearns 1992). Previous studies have found survival costs of reproduction in the closely related Cliff Swallow (*Petrochelidon pyrrhonota*) (Brown and Brown 2004).

Although reproductive success in Bank Swallows is not generally expected to be food-limited (Garrison 1998), drought conditions may affect food availability and hence reproductive success and nestling survival. This may particularly be true in California's Mediterranean climate (Dybala et al. 2013), although the Sacramento Valley is heavily subsidized with agricultural water deliveries, even in dry years. More generally in insectivorous songbirds, reductions in food availability during the breeding season has been shown to have moderate effects on chick body condition and strong effects on reproductive success (Grames et al. 2023). Drought has also been shown to have adverse effects on multiple life history stages in birds, including adults (Albright et al. 2010, Saracco et al. 2018, Oswald et al. 2021).

In addition, Bank Swallow breeding performance may be driven by variation in the total quantity of high-quality nesting habitat, which has likely diminished over time as the extent of riprap on the banks increased (Girvetz 2010, Golet et al. 2013). Availability of suitable nesting habitat is recognized as a major factor affecting the size and distribution of Bank Swallow breeding populations throughout their range (Cramp 1988, Turner and Rose 1989, Szép 1991).

2.4. *Data analysis*

2.4.1. *Model covariates*

To assess H1 and H2, we compiled mean daily streamflow data from four river gages spanning the Sacramento River study area: Vina Bridge (VIN, river km 352), Hamilton City (HMC, river km 321), Ord Ferry (ORD, river km 296), and Butte City (BTC, river km 271) (https://cdec.water.ca.gov/dynamicapp/wsSensorData). For each gage, we calculated the sum of the daily mean flow during each water year. A water year in California is a 12-month period that runs from October 1 to September 30. The water year is named for the calendar year it ends in. For example, the 2000 water year began on October 1, 1999, and ended on September 30, 2000.

During the years of our study, on average more than 88 % of the flows > 15,000 cfs (the minimum erosion threshold for the study reach [Larsen et al. 2006]) occurred in the first half of the water year (October-March). Additionally, the flow volumes on days that exceeded this threshold were 48 % greater during this period compared to the second half of the water year, April-September. Thus, most of the high flows in the study reach occurred in winter prior to the Bank Swallow breeding season.

The annual streamflow totals at each of the four stations (Fig. 1) were highly correlated with each other, so we calculated the mean value. We also considered the daily mean flow above the Larsen et al. (2006) minimum erosion threshold. However, values for the total flow and the total flow above 15,000 cfs in each water year were highly correlated (Pearson's $r = 0.98$). We therefore retained only total annual flow as a model covariate. For H1, we considered the effect of total annual flow during the same water year ($flow_t$). This includes the winter immediately preceding the breeding season when most high flows occur. For H2, we considered the effect of total annual flow during the previous water year ($flow_{t-1}$).

To assess H3, we compiled monthly values for the Palmer Drought Severity Index (PDSI) from NOAA for the "Sacramento Drainage" climate division in California. The PDSI incorporates monthly temperature, precipitation, and soil–water holding capacity data to represent the severity of dry and wet spells, with values ≥ 2 considered moist and values ≤ -2 considered to represent drought (Palmer 1965). For each water year, we calculated the mean of the monthly PDSI values for the Bank Swallow breeding season, April through August. For H3, we considered the effect of drought during the previous water year ($pdsi_{t-1}$).

Finally, to assess H4, we used model-derived estimates of the prior year's breeding population size (N_{t-1}), informed by the prior year's observed burrow count totals (y_{t-1}), as a predictor representing the effect of density-dependent reproductive success on the population growth rate.

We log-transformed $flow_t$ and $flow_{t-1}$ to reduce the influence of a few years with extreme values, and then centered and scaled the values of $flow_t$, $flow_{t-1}$, and $pdsi_{t-1}$ to have a mean of zero and standard deviation of 1. There were no strong correlations between any of these three variables ($|\text{Pearson's } r| < 0.55$).

2.4.2. Population model

To evaluate the relative importance of each of our hypotheses, we fit a dynamic population model implemented in JAGS 4.3.1 using the R package *rjags* (Plummer 2003, Plummer 2023, R Core Team 2023). We modeled the annual growth rate from year *t-1* to *t* (R_t) and the mean burrow count in year *t* ($\overline{N}_t$) as:

$$log(R_t) = r_{max} + \beta_1 * flow_t + \beta_2 * flow_{t-1} + \beta_3 * pdsi_{t-1} + \beta_4 * (N_{t-1}/1000) + \beta_5 * t$$

$$\overline{N}_t = R_t * N_{t-1}$$

where r_{max} represents the maximum growth rate of the population when the population is small, and β_1, β_2, β_3, and β_4 represent the effect size of each of our hypothesized predictors on the annual growth rate: $flow_t$, $flow_{t-1}$, $pdsi_{t-1}$, and N_{t-1} (thousands), respectively. We also included β_5 to represent the effect of any underlying long-term trend in growth rate by year (*t*). We considered β_4 to represent the strength of density-dependence, and as analogous to $-r_{max} / K$, where *K* is the carrying capacity of the study area for the breeding population.

To account for additional process error, we treated N_t as a lognormal random variable with mean $\log(\overline{N}_t)$ and constant variance σ_p^2:

$$N_t \sim lognormal\left(log(\overline{N}_t), \sigma_p^2\right)$$

To account for additional observation error, we treated the observed burrow count in each year *t* (y_t) as a lognormal random variable with mean $\log(N_t)$ and constant variance σ_o^2:

$$y_t \sim lognormal\left(log(N_t), \sigma_o^2\right)$$

We also estimated the starting value of *N* in the year 1999 from the observed value as:

$$N_{1999} \sim lognormal\left(log(y_{1999}), \sigma_o^2\right)$$

We used vague normal prior distributions for all β parameters (mean 0, variance 10^2 on the log scale), and we used a vague uniform prior distribution for r_{max} (ranging −2 to 2 on the log scale) and all variances (σ_p^2 and σ_o^2, ranging 0 to 5).

We estimated the posterior distributions for all model parameters using Markov chain Monte Carlo (MCMC). We fit 3 chains, each with 40,000 initial samples discarded for adaptation and burn-in. We accumulated an additional 100,000 samples from each chain, retaining every 25th sample. We evaluated convergence of the three chains using the Gelman-Rubin diagnostic (Gelman and Rubin 1992, $\hat{r} < 1.05$) and visually inspecting the trace plots. We calculated the residuals between the observed (y_t) and expected (N_t) burrow counts in each year and found no evidence of autocorrelation in the residuals by year. We also conducted posterior predictive checks by calculating the sum of the squared residuals over all years for each MCMC sample, as well as the sum of the squared residuals between y_t^{new} and N_t, where y_t^{new} represent new observed burrow counts, simulated as:

$$y_t^{new} \sim lognormal\left(log(N_t), \sigma_o^2\right)$$

We then estimated a Bayesian p-value as the proportion of samples for which the observed error was greater than the simulated error (Hobbs and Hooten 2015). The Bayesian p-value was 0.57, indicating no evidence of lack of fit.

We report the medians and 95 % highest posterior density intervals (HPDI) for all model parameters. For ease of interpretation, we also present the annual growth rates (R_t) as the annual % change. For model parameters representing the effect size of each of our covariates, we also report the proportion of samples for which the effect size was greater than or less than zero, which is directly interpreted as the probability that the magnitude of the effect is non-zero.

3. Results

3.1. Colony burrow counts

From 1999 to 2023 the number of burrows in the Red Bluff to Colusa study area varied substantially, with a significant overall declining trend at an average of −1.5 % per year ($F_{(1,22)} = 5.606$, $P = 0.027$, Fig. 3). During this time span the highest count (20,299 burrows) occurred in 2021, and the lowest (7,836 burrows) was recorded in 2023, the last year of our study. The estimated annual growth rates, calculated directly from burrow counts in sequential years, have ranged from a 42 % decline in 2022 to a 52 % increase in 2018. No burrow count data were available in 2006, and thus growth rates in 2006 and 2007 could not be directly estimated.

3.2. Model covariates

From 1999 to 2023, the total annual streamflow (sum of the daily mean streamflow, $flow_t$) ranged from a low of 1.90 million cfs in 2022 (1 October 2021——30 September 2022) to high values of 8.38 million cfs in 2006 and 8.33 million cfs in 2017, with an overall median of 3.37 million cfs (Fig. 4A). We noted that this lowest value in 2022 followed relatively low values in 2020 and 2021 and coincided with the strongest decline in burrow counts observed during this study in 2022, while the high value in 2017 was followed by the largest increase in burrow counts observed in 2018.

Over the same time frame, the breeding season drought index (mean of the monthly Palmer Drought Severity Index values, April–August, $pdsi_t$) ranged from a low of −5.14 in 2021 to a high of 3.41 in 2011, with an overall mean value of −1.02 (Fig. 4B). Only 3 breeding seasons had mean values ≥ 2, the threshold for moist conditions (2005, 2011, and 2019), while 10 years had mean values ≤ -2, the threshold for drought conditions.

3.3. Population model

Examining the marginal posterior distributions of the model parameters representing each of our hypotheses, we found strong evidence supporting effects of prior total annual streamflow ($flow_{t-1}$) and prior burrow count (N_{t-1}) on the population growth rate from year *t-1* to *t*, with 95 % HPDI that do not overlap 0 (Fig. 5). The high probability we found of a positive effect of $flow_{t-1}$ ($P\{\beta_2 > 0\} = 99$ %) supported Hypothesis 2, in which relatively high flows in the winter before the previous breeding season (*t-1*), such as observed in 2011, 2017, and 2019 (Fig. 4), contributed to high annual population growth rates in year *t* (Fig. 6B). Low flow years, such as those that occurred in 2014, 2021 and 2022, produced the opposite result with the lowest annual growth rates occurring in years that immediately followed. The high probability of a negative effect of N_{t-1} ($P\{\beta_4 < 0\} = 99$ %) supported Hypothesis 4, in which large total breeding population sizes on the Sacramento River in year *t-1* lead to lower rates of population growth in year *t*, due to density-

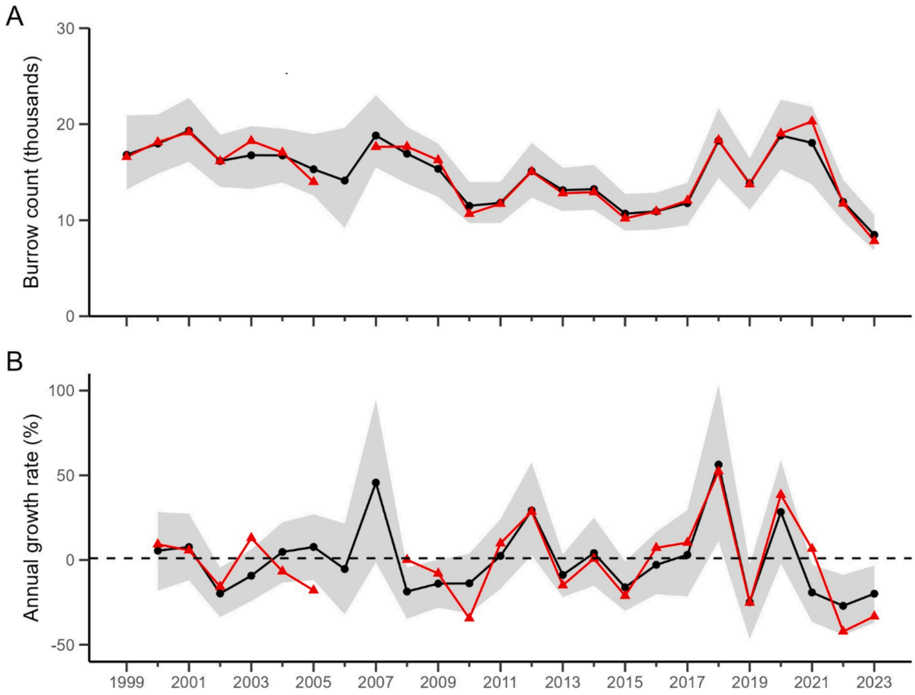

Fig. 3. Annual variation in (A) observed burrow counts (1999–2023) and (B) estimated annual growth rates, 2000–2023 (both in red). Also shown are the median (in black) and 95% highest posterior density intervals (in gray) for the model-estimated burrow counts and annual growth rates in each year, including the missing burrow count in 2006 and missing growth rates in 2006 and 2007. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

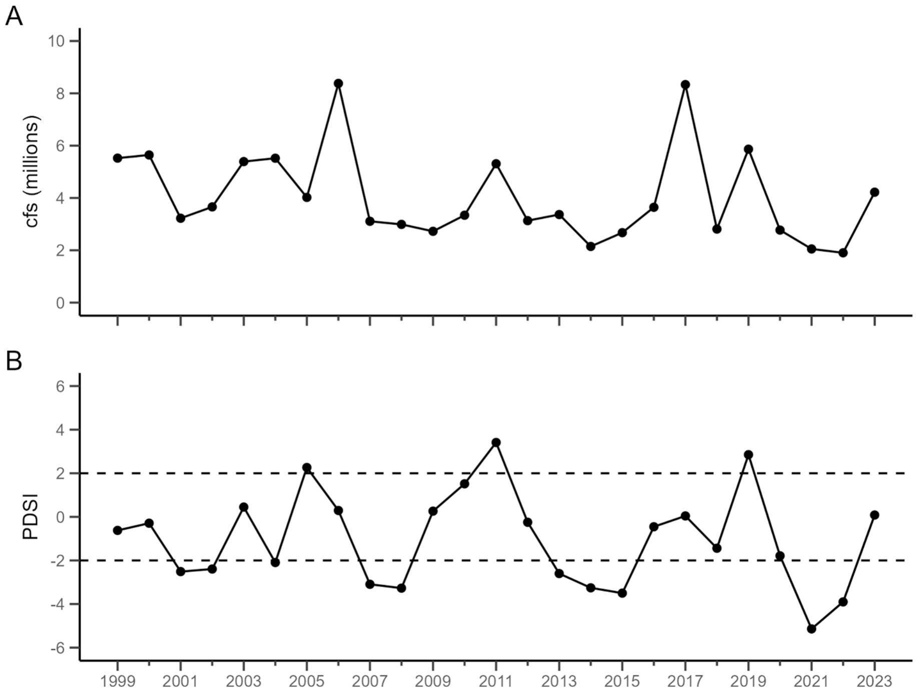

Fig. 4. Annual variation in candidate covariates of population growth. (A) Total annual flow, the total of mean daily streamflow for each water year (October 1 – September 30), calculated as the mean over 4 gauging stations. (B) Mean monthly Palmer Drought Severity Index (PDSI) for the breeding season (April–August), in which values < -2 indicate drought conditions and values > 2 indicate moist conditions.

dependent effects associated with large Bank Swallow colonies (Fig. 6D).

In contrast, we did not detect strong effects of total annual streamflow ($flow_t$), prior breeding season drought ($pdsi_{t-1}$) or water year (t), with 95 % HPDI for the effect sizes overlapping 0 in all cases (Fig. 5). The relatively weak probability of a negative effect of $flow_t$ ($P\{\beta_1 < 0\} = 77$ %) suggests a neutral to negative effect of higher flows in the winter immediately preceding the breeding season (Fig. 6A), in opposition to Hypothesis 1. This could result from birds avoiding breeding if banks are more prone to collapse following high flow winters, fewer burrows persisting from the previous year, and/or fewer burrows being counted

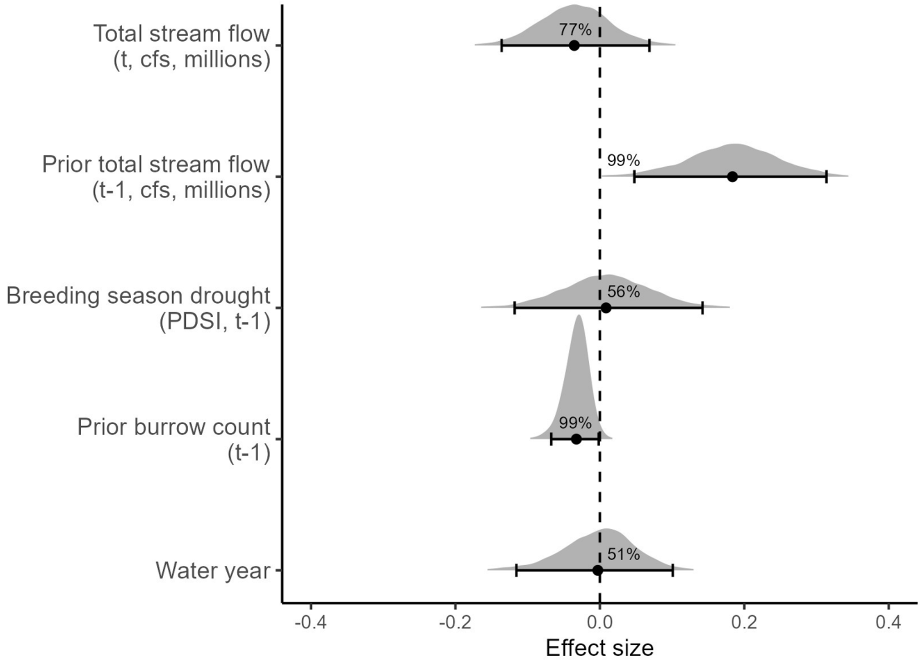

Fig. 5. Posterior distributions for each of the model parameters β, shown with the mean, 95% highest posterior density intervals (HPDI), and the probability that each parameter estimate is greater than or less than 0. Effects of streamflow are on a log-scale, and all but prior burrow count were scaled and centered (mean 0, sd 1). The effect of prior burrow count represents the effect per 1,000 burrows.

due to bank collapses prior to the survey. Similarly, the effect of $pdsi_{t-1}$ was neutral ($P\{\beta_3 > 0\} = 56$ %), indicating no support for Hypothesis 3, in which more severe drought conditions during the breeding season in year *t-1* lead to lower reproductive success and fewer young recruited into the population in year *t* (Fig. 6C). Finally, although not presented as a distinct hypothesis, we also found the effect of *t* was neutral ($P\{\beta_5 > 0\}$ = 51 %), indicating no evidence for any additional long-term trend in the population growth rate that was unaccounted for by the other covariates examined. (Fig. 3B).

In addition to using the model to calculate parameters representing each of our hypotheses, we used it to estimate other parameters, including the unobserved burrow count in 2006 (14,126, 95 % HPDI: 9,208–19,605, Fig. 3A), and the unobserved growth rates in 2006 (−5%, –32–21 %) and 2007 (46 %, −1–94 %) (Fig. 3B). We estimated the marginal posterior distribution for r_{max}, the maximum growth rate of the population when the population is small, as 61 % (95 % HPDI: 0–169 %), and we derived an estimate of the carrying capacity (*K*) for the study period as 14,600 (95 % HPDI: 10,800–18,000, Fig. 6D). Finally, we estimated an annual streamflow threshold for positive Bank Swallow population growth of ~4 million cfs (Fig. 6B).

4. Discussion

In our 25-year study, the Bank Swallow breeding population on the Sacramento River fluctuated widely and declined at an average overall rate of 1.5 % per year. We found strong evidence that periodic high streamflow played an important role in maintaining the population, which has important implications for this state-threatened species. Climate change is increasing the variability of streamflow in California (He et al. 2019, Chen et al. 2022), with more severe droughts and higher magnitude flood events (Diffenbaugh, et al. 2015). This is impacting local ecosystems (Prugh et al. 2018), including our study area on the largest river in California where annual flow tended to decline during our study (Fig. 4A).

Interestingly, we found the effect of streamflow on Bank Swallow breeding population size to be time-lagged, such that the population growth rate did not increase immediately following a winter of high flow, as might be expected if it was simply in response to more birds choosing to breed on the river in years with improved nesting habitat conditions. Rather, it manifested one year later, suggesting that high flow conditions are positively impacting Bank Swallow reproductive success, and potentially survival, leading to increases in the breeding population in the subsequent year. Importantly these results also demonstrate the converse, that low flow conditions are followed by population declines.

Although our analysis was unable to distinguish effects of flow on reproductive success versus juvenile or adult survival (and may impact multiple parameters), we expect chicks to be most sensitive. Variation in juvenile survival has a large influence on population growth rates in short-lived bird species (Sæther and Bakke 2000), and the probability of quasi-extinction in Bank Swallows is especially sensitive to this parameter (Girvetz 2010).

Our finding of density dependence suggests that when there were more breeders across all colonies, the population growth rate in the following year was reduced, as previously reported (Girvetz 2010). This finding, coupled with observations of population decline when bank habitat is destroyed (Schlorff 1997) and rapid colonization when it is created, suggests that the impact of streamflow on the population is mediated via habitat limitation: high flows in year *t-1* increase limited near-vertical bank habitat, improving breeding conditions and population growth rates in year *t*.

4.1. Causal mechanisms

More research is needed to fully define the causal mechanisms responsible for increasing Bank Swallow population growth rates associated with high annual streamflows on the Sacramento River, but available evidence suggests that it is a consequence of increased winter bank erosion leading to better spring breeding conditions. When old nesting burrows are eroded away and fresh steep cutbanks are formed, higher quality breeding habitat is created. This increases nest success, juvenile and possibly adult survival, resulting in more birds returning to breed the subsequent year.

When flows are sufficient to promote significant new erosion, steep

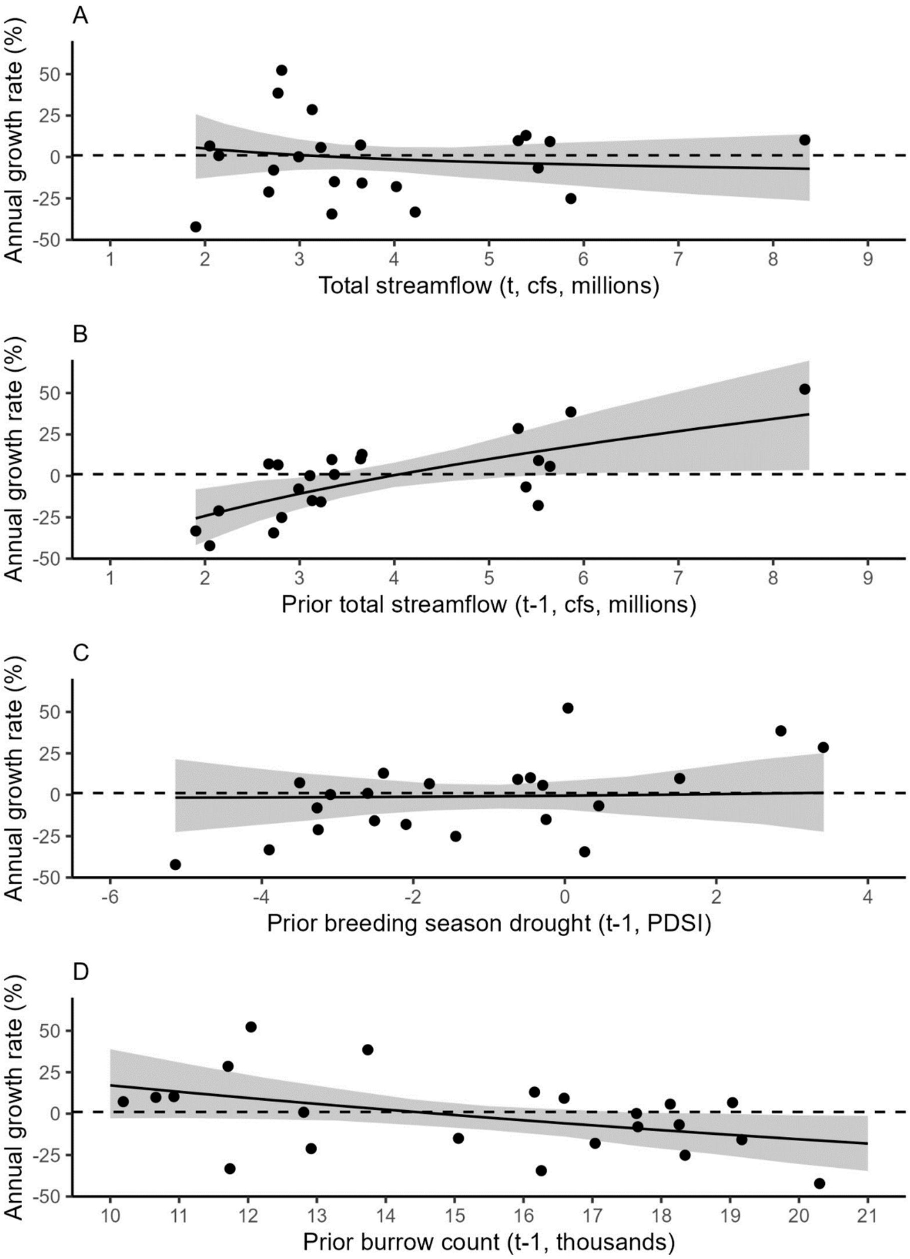

Fig. 6. Partial effects plots for each model covariate: (A) Total annual flow (sum total of mean daily streamflow in the Sacramento River each water year, October 1 – September 30), (B) Prior total annual flow (t-1), (C) Prior breeding season Palmer Drought Severity Index (mean monthly index, April – August, t-1), and (D) Prior burrow count (t-1). Also shown are the observed population growth rates across the range of each model covariate observed in this study. The effect of a long-term trend in annual growth rate was also evaluated (see Fig. 3B, 5).

cutbanks are formed that are difficult to access for nest predators such as gopher snakes (*Pituophis catenifer*) and racoons (*Procyon lotor*). Erosion also reduces parasitic loads in the burrows (Hoogland and Sherman 1976). Colonial breeders have more nest parasites than their non-colonial counterparts (Poulin 1991). Their burrows are dug deeply into the banks; however, if erosion does not eliminate them, then ectoparasites (including blowflies [*Protocalliphora spp*.; Whitworth and Bennett 1992], fleas [*Ceratophyllus spp*. and *Celsus spp*.; Haas et al. 1980], lice [Stoner 1936, Emerson 1972] and mites [Peters 1936]) may persist, and even increase, over time.

Ectoparasites are known to have adverse effects on Bank Swallows. Ticks (*Ixodes lividus*) reduced the reproductive success of adults in Hungary (Szép and Møller 1999). Fleas (*Ceratophyllus styx*) lowered chick growth rates and body mass in Scotland (Alves 1997), and in Utah, blowflies (*Protocalliflora chrysorrhoea*) reduced nestling hematocrit and hemoglobin levels, although not mortality rates (Whitworth and Bennett 1992).

Further suggestion that nest parasites may have impacts on Bank Swallows comes from studies of the Cliff Swallow (*Petrochelidon pyrrhonota*), a colonial species that shares some breeding sites with Bank Swallows on the Sacramento River (G. Golet pers obs). Ectoparasite densities in Cliff Swallow mud nests increased with colony size in Nebraska (Brown et al. 2020) and persisted in unused nests for up to three years, timing their reproduction to coincide with that of their host (Brown et al. 2020). Cliff Swallow ectoparasites lowered adult survivorship during breeding (Brown and Brown 2004), elevated circulating levels of corticosterone (Raouf et al. 2006), increased spleen size (Brown and Brown 2002a), and caused asymmetry in wing, tail, and tarsus lengths (Brown and Brown 2002b).

The effect of density dependence on the population growth rate may manifest in multiple ways. When Bank Swallow breeding populations are larger, reproductive success may decline due to some birds being forced to occupy lower quality colony sites or poorer burrow locations within a colony. Moffatt et al. (2005) found reduced extinction rates for colonies adjoining grasslands, suggesting that Bank Swallows select colony locations near open foraging habitats. Other research has identified that differences in microhabitats within colonies are important. Nest sites lower on the bank faces with less firm soils are more prone to predation and burrow collapse (Sieber 1980), and have lower reproductive success (Hoogland and Sherman 1976). Overcrowding in limited habitat is likely to reduce reproductive success due to increased prevalence of nest parasites, as shown in Cliff Swallows (Brown et al. 2020).

It is possible that the lower population growth rates observed following breeding seasons with more breeders resulted from prey depletion around the colonies. This seems unlikely however, given that depletions are expected to be greater during drought, and we found no evidence of a drought effect.

Previous modeling has shown that reductions in the amount of available nesting habitat lowers mean juvenile and adult survival rates, and increases variation in these parameters, thus reducing the viability of the population beyond the effects of habitat loss alone (Girvetz 2010). It follows then that the continued installation of riprap, which eliminates prime Bank Swallow breeding habitat, and the increased frequency of low flow years (Dettinger et al. 2015), are combining to pose a significant threat to the species.

Ultimately, we cannot say with certainty what specific factors are driving the relationships we discovered between Bank Swallow breeding population annual growth rate and the time-lagged effects of streamflow and density dependence. However, our work provides solid evidence that these factors are critical drivers of Bank Swallow population dynamics on the Sacramento River. Other factors, including drought and food availability during the wintering period, have been shown to be important elsewhere. For a medium- to long-distance migrant with a cosmopolitan distribution, it is expected that population regulation in different regions would be dictated by unique combinations of factors interacting in complex ways over time. Even so, it is fitting that we found that the river's flow regime, a "master variable" for determining physical and biological processes in rivers (Poff et al. 1997, Snelder et al. 2005), to be fundamentally important for a species whose Latin name is *Riparia riparia*.

4.2. *Management implications*

Our research provides strong support for the idea that maintaining environmental flows is pivotal to stemming the loss of biodiversity in freshwater ecosystems (Acreman et al. 2020) and moreover, that it can be particularly effective when coupled with protection and restoration of critical habitats (Tickner et al. 2020). Much of the land along the middle Sacramento River is owned by government wildlife agencies, yet this is not enough to ensure that the habitat needs of its wildlife are being met. Like many other alluvial river systems, the Sacramento has an altered flow regime which is imperfectly matched to the needs of native species.

For the Bank Swallow, river flows appear to be currently supportive of reproduction at a level needed to sustain the population in most years. Storm runoff from the upper watershed is captured behind Shasta Dam; however, there are significant tributary inputs to the mainstem river below the dam, such that in wet years high flow events occur, refreshing bank habitats where swallows breed. High flow is needed for maintaining good breeding habitat, but it can be detrimental if it occurs during breeding when bank sloughing can cause mortality of eggs and chicks (Humphrey and Garrison 1987, Garcia et al. 2008). While tributary inputs cannot be regulated, large volume reservoir releases should be avoided during the nesting season (late April-mid July, Wright et al. 2011). Earlier in the winter, however, managed releases from the dam could be an effective way to ameliorate poor breeding conditions in the coming months for the birds. Our study provides information on the total volume of flow needed to bring about positive annual growth in the population in recent decades. Future work should explore how adjustments in the timing, magnitude and duration of flows in the river can reduce this amount while simultaneously meeting other ecosystem and societal needs. Having a large storage reservoir upstream in the watershed does not necessarily preclude efficiency in delivering balanced water allocation objectives (Null et al. 2024).

Our finding that the Bank Swallow population growth rate is density dependent suggests that a lack of high-quality habitat is limiting the maximum population size of the Sacramento River population. This argues for both restoration of natural bank habitat and avoidance of new riprap, as previously recommended by others. Moffatt et al. (2005) concluded that removal of ~10 % of existing riprap from suitable nesting areas would be an effective way to restore Sacramento River metapopulations, and Girvetz (2010) found that riprap removal would reduce the risk that the population drops below a quasi-extinction threshold of 2000 pairs in the next 50 years from 21 % to less than 10 %.

Although dumping riprap on top of colonies during the breeding season on agency-sanctioned projects was halted in 1989 when the Bank Swallow was listed as a State Threatened species, riprapping projects which remove suitable and occupied habitat still take place during other times of the year (Schlorff 1997). Avoidance and restoration measures for riprap projects have been identified as critical for promoting recovery of Bank Swallows for decades (California Department of Fish and Game CDFG, 1992), yet little progress has been made. In 2002 there was an estimated 81,135 m of riprap on the middle Sacramento River. Over the next 16 years, this increased by 7 % (Fig. 7). Most was installed by private landowners without the necessary permits, simply to halt erosion and not associated with levees for flood control. At only one site within our 161 river-km study reach is there currently any progress towards removing a substantial section (1,585 m) of riprap (California Department of Water Resources (CDWR), 2022; Larsen and Greco, 2002).

4.3. *Sentinel of river health*

Birds are recognized as excellent indicators of ecosystems health (Morrison 1986), and our ability to monitor them over vast spatial scales and long-time frames far exceeds that of other animal groups. California Partners in Flight (Carter et al. 2000), selected the Bank Swallow as one of 16 focal species for characterizing the status of riparian habitats and prioritizing management-oriented conservation actions (Garrison, 1998; Riparian Habitat Joint Venture, 2004). Even among these species, the Bank Swallow stands apart in what it can tell us about riparian biodiversity health. This is because its well-being is so tightly linked to natural riverine processes which shape the entire ecosystem. As our study and the work of others makes clear, for Bank Swallow populations to thrive they need unaltered riverbanks for breeding that are exposed to naturally dynamic erosive flows (Schlorff 1997; Moffatt et al. 2005; Girvetz 2010). Their cutbank breeding habitat is created and maintained by sediment mobilization which drives channel meander migration, a process vital to the wellbeing of a multitude of riparian and riverine aquatic species (Florsheim et al. 2008, Bellmore et al. 2014) that are important from cultural and commercial perspectives (Jakubínský et al. 2020), and have great intrinsic worth. All of this, combined with its cosmopolitan Holarctic distribution, make the Bank Swallow an excellent indicator of river health for lowland alluvial ecosystems, and underscore the importance of working to "keep common birds common" (Berlanga et al. 2010).

CRediT authorship contribution statement

Gregory H. Golet: Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Conceptualization.

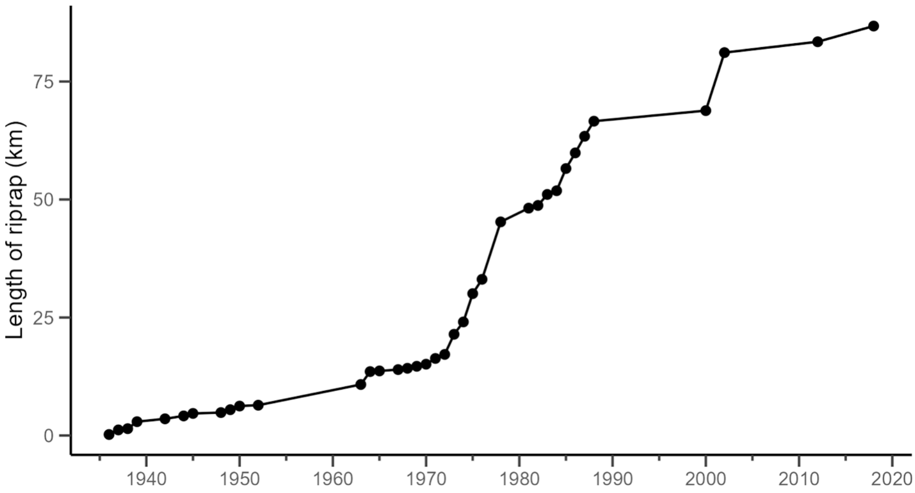

Fig. 7. Riprap extent on the Sacramento River from Red Bluff to Colusa, including all the mapped placements of large rocks and demolition concrete, on and off the current channel.
Source: CDWR Northern District

Kristen E. Dybala: Writing – review & editing, Writing – original draft, Methodology, software, Formal analysis, Data curation, Conceptualization. **Joseph G. Silveira:** Writing – review & editing, Investigation. **Adam Henderson:** Writing – review & editing, Investigation, Data curation. **Jennifer Isola:** Writing – review & editing, Investigation, Data curation. **David H. Wright:** Writing – review & editing. **Ron Melcer Jr:** Writing – review & editing. **Danika Tsao:** Writing – review & editing, Data curation.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113460.

Data availability

The data and R code used to conduct this analysis are available from Zenodo [https://github.com/pointblue/bank_swallow].

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