

Multi-scale demographic analysis reveals range contraction via pseudo-source and sink population structure

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Abstract. Naturally occurring populations of most species are distributed non-uniformly across their ranges. Observed changes in range-wide population size are attributed to local-scale processes such as fecundity and survival and to regional scale demographic processes such as immigration. It is often infeasible to study a species across its entire range, and we frequently make inferences on populations as a whole based on the demographic rates of a more restricted area. Extrapolating inferences about demographic processes from study areas to the entire species' range can lead to erroneous estimations, particularly when permanent emigrants contribute significantly to individual population processes. In this paper, we evaluated demographic processes and population trends at multiple scales for tricolored blackbirds (*Agelaius tricolor*) in California using site-specific banding data and range-wide citizen-science data. First, we found that a previous estimate of statewide decline of 34% is largely driven by an estimated decline of 51.7% for the southern population. Second, we found evidence of a pseudo-source and sink system, with the northern region acting as a sink for individuals moving from the declining southern region. The southern region is a "pseudo-source" since it has lower rates of adult survival and an annual growth rate of $r = -0.099$, while still acting as a source of immigrants for the northern region. In turn, the north fits the traditional definition of a sink by an annual growth rate near zero, in addition to declining at a rate of 2.5% even though it is estimated to receive immigrants from the south at rates ranging from 8.3% to 13.2% per year. Our results suggest that the loss of wetland habitats in Southern California, coupled with increasing severity of droughts driven by changing climatic conditions, has created this pseudo-source and sink system. Long term, tricolored blackbirds are likely to experience range contraction in the south, and the northern region is likely to undergo declines due to a loss of immigrants from the south.

Key words: capture–mark–recapture; emigration; immigration; integrated population model; multistate model; pseudo-source; scale; source–sink.

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INTRODUCTION

Natural populations are often patchily distributed across the landscape (Pulliam 1988, Levin 1992, Runge et al. 2006). However,

studying a species across many sites or its entire range is typically impractical, and we often resort to making inferences on the dynamics of a population based on the results of a more restricted area. When there is a high degree of spatial

heterogeneity within populations, inferences based on a restricted part of the range can lead to erroneous extrapolations about what factors most influence range-wide population dynamics (Johnson et al. 2010). Understanding both the local and the range-wide drivers of population size is also critical for designing effective conservation policy and management for the population as a whole (Akçakaya et al. 2007).

Survival is one of the population-level demographic processes that is often most difficult to estimate at scales that are representative of the variation that exists across the range of a species (but see Saracco et al. 2008, Saracco et al. 2010, Robinson et al. 2014, Ahrestani et al. 2017). Survival is often informed by a limited number of restricted sampling sites, where individuals are likely to permanently emigrate from the sampled area. Therefore, we are largely restricted to estimating *apparent* survival, acknowledging that permanent emigration from the study confounds estimates of *true* survival (Lebreton et al. 1992). Ideally, we would estimate survival probabilities using methods that account for the scale of movements (e.g., Gilroy et al. 2012, Schaub and Royle 2014), but the data required for these types of approaches are challenging to collect for species which are itinerant (Hamilton 1998) or have low site fidelity (Marshall et al. 2004).

Populations of species with these life-history strategies have population processes that are more likely to be influenced by permanent emigrants (Zimmerman et al. 2007). For example, immigration allowed an overwintering population of Greenland white-fronted geese (*Anser albifrons flavirostris*) to maintain stable population size despite declines in recruitment (Weegman et al. 2016). Under these scenarios, not accounting for movement and/or extrapolating the growth rate at one part of the species' range to others could lead to biased inferences about the ability of the population to persist without immigration (Runge et al. 2006, Griffin and Scott Mills 2009). On the other hand, considering only range-wide demographic processes and changes in population size (e.g., Ahrestani et al. 2017, Robinson et al. 2018) may misidentify source-sink dynamics by obfuscating the varying contributions of local or regional populations to these large-scale trends (Johnson et al. 2010). This is especially important when considering conservation actions

across scales, since inferences of local-level demographic processes and population trends will be more accurate when examined in the context of large-scale processes such as movement and range-wide population trajectories.

Here, we explore how to address these challenges by leveraging range-wide information collected using citizen-science efforts on population trends with local-scale information on demographic rates, to better understand spatial variation in demographic processes at multiple scales. We use an example based on research efforts focused on understanding the drivers of population decline for tricolored blackbird (*Agelaius tricolor*), a colonial passerine of high conservation concern in the western United States. Recent work estimated a range-wide population decline of 34% since 2010 in California (Robinson et al. 2018b), where ~99% of the global population is found (Beedy et al. 2020). As the species is a colonial breeder with low site fidelity (Holyoak et al. 2014, Airola et al. 2016), permanent emigration is likely to influence population-level inferences on population decline. In addition, this is an itinerant species during the breeding season (Hamilton 1998) and nomadic during the non-breeding season. Therefore, the effectiveness of conservation actions on the ground could be dampened by potential regional differences in drivers of population declines. To address these challenges, we explored potential regional differences in demographic rates, movement, and the overall population decline for the species. In addition, we examined movement rates among regions and evaluated the extent to which this affects the demographic processes both locally and range-wide.

METHODS

Study system

Tricolored blackbirds are found almost entirely in California and historically nested in the wetlands across the state; however since the 1980s, they have also nested in silage fields and in stands of some invasive plants (Holyoak et al. 2014, Weintraub et al. 2016, Robinson et al. 2018a, Beedy et al. 2020). Tricolored blackbirds have experienced a 63% decline in breeding abundance from 1935 to 1975 and a 34% decline since 2007 (Graves et al. 2013, Robinson et al. 2018). This decline leads to the species being

listed as threatened under the California Endangered Species Act (ESA) in April 2018, and it is currently under consideration for listing under the United States ESA (Beedy et al. 2020). As such, it is imperative that we understand population dynamics across their range to effectively identify and prioritize research needs and conservation actions.

Mark–recapture data

Tricolored blackbirds were uniquely banded at 18 sites throughout central California from 2007 to 2016 (Fig. 1). Trapping occurred during the breeding season (April–July) using traps, typically baited with cracked corn and infrequently supplemented with mealworms (Meese and Simmons 2010, Wilson et al. 2016). Recaptures were recorded each year during the breeding season, and each breeding season was considered a separate recapture occasion. Few individuals were encountered more than once within a particular year; as such, data for within-season recaptures were pooled into a single encounter event for that year. A total of 64,129 tricolored blackbirds were banded (49,668 females and 14,461 males). However, despite quite large samples of newly marked individuals, total adult recaptures were very low (1336 females and 124 males; Appendix S1: Table S1). Preliminary analysis indicated that numerical estimation was not robust for adult males, and as the contribution of males to overall population growth is minimal (Robinson et al. 2018b), we restricted our analysis to adult females only.

Statistical analysis: live-encounter data

Our primary interest was in estimating the pattern(s) of temporal and spatial variation in survival, recruitment, and movement for adult (female) tricolored blackbirds. We approached our analysis of live-encounter data in two stages. First, we applied a time-symmetric, open population mark–recapture model to estimate apparent survival, recruitment, and population growth using data pooled over all sampling locations, analogous to a previous analysis of statewide count index data (Robinson et al. 2018b). Second, we used a multistate mark–encounter approach (Williams et al. 2002; references therein) to separate mortality from permanent emigration, a particularly important consideration for species

with high rates of movement and low site fidelity. In addition, this model can provide additional insights as to how much our estimates of recruitment from the time-symmetric models might reflect movement of adults among sampling regions.

Population growth models

For this analysis, we used a time-symmetric open population mark–recapture modeling approach (Pradel 1996, Nichols et al. 2000, Nichols 2016) in Program MARK v.9 (White and Burnham 1999) to estimate retrospective (realized) annual population growth λ_t from the 10 yr of mark–recapture data. The time-symmetric model allows the decomposition of annual estimates of λ_t into two components representing annual apparent survival (ϕ) and annual recruitment (f_t): $\lambda = \phi + f$. Recruitment refers to the number of new animals in the study area at time t relative to the number of animals present at time $t + 1$. Apparent survival (here, annual survival from breeding season [April–July] in one year to breeding season in the next) reflects overall subtractions from the population, combining both true mortality and permanent emigration. Recruitment rate reflects the per capita additions of new, yearling breeders to the sampling areas, including both those produced within and outside of it. Since there were no individuals banded as juveniles in our sample, and very low numbers of repeat recaptures within season, we were unable to partition variation in recruitment f to contributions of recruits produced in other areas versus in situ recruits (sensu Nichols and Pollock 1990), and thus, our estimates of recruitment refer to net per capita recruitment to the adult female population only. The time-symmetric model accounts for imperfect detection probability (p) in the encounter history, reducing potential bias in the estimates of ϕ , f , and λ (Nichols et al. 2000, Nichols 2016). Since population growth is a linear function of apparent survival and recruitment, all three parameters cannot be simultaneously estimated. Therefore, we jointly modeled the underlying processes ϕ_t and f_t and algebraically derived estimates for λ_t as the sum of the two. This approach directly partitions variation in growth due to differences in survival and recruitment (sensu Nichols et al. 2000; Nichols 2016).

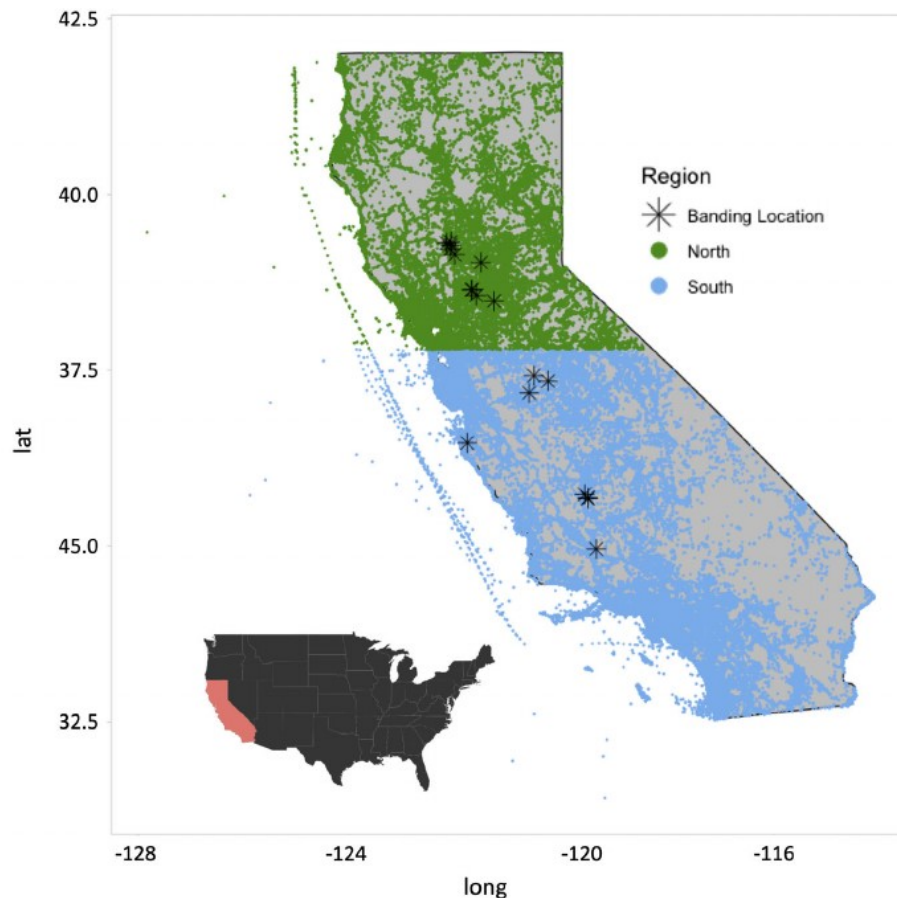


Fig. 1. Map of mark–live release banding locations for adult female tricolored blackbirds, 2007–2016 (black stars), and eBird checklists from the “northern” (green) and “southern” (blue) populations. The division of the “north” and “south” eBird data represents geographic axis of data aggregation into a “northern” and “southern” populations used in the multistate analysis.

To examine the pattern of variation in apparent survival and recruitment and population growth, we first evaluated a candidate set of 49 fixed-effect approximating models, nested within a general omnibus model where all 3 structural parameters (ϕ , f , and p) were allowed to vary randomly over time. Goodness of fit of the general model to the data was confirmed using the Fletcher statistic (Fletcher 2012). The model set also included models where either or both survival and recruitment were constrained to follow a simple linear trend over time. We were concerned about the possible influence of pooling annual capture–live-encounter data over the marking period from April to July, since this ~3-month period would seem to strongly violate the

assumptions of instantaneous mark–release, relative to the interval over which parameters are being estimated. Specifically, we were concerned that comparing fates of individuals marked in (say) April with those marked in July would induce significant heterogeneity in our annual estimates. Because of the sparseness of the encounter data, we were unable to control for this by partitioning the annual cycle into sets of “secondary” (monthly) periods, constructing a model where the differing intervals between periods could be explicitly modeled. As such, we resorted to including different measures of the differences in timing of the mark–encounter events, by including either (1) time elapsed at marking from season start or (2) Julian date, as

individual covariates for survival, ϕ , and recruitment, f , in some models. To facilitate evaluation of the relative importance of different factors and our parameter estimates, the candidate model set was constructed with symmetry in the number of models with and without various effects (time, individual covariates).

Multistate models

Multistate models allow individuals in the population to be distributed across multiple sites and provide robust estimation of transition probabilities (i.e., movement) among sites, under conditions where the probability of observing an individual for a given sampling occasion is <1 . If we assume that survival from time i to $i + 1$ depends only on the location (state) at time i , then separate estimation of survival from movement is possible, where S_i^r is the probability that an animal in state r at time i survives and remains in the study population until period $i + 1$; and Ψ_i^{rs} is the probability that an animal in state r at time i is in state s at time $i + 1$, given that the animal is alive at $i + 1$.

The sparsity of the encounter data (Appendix S1: Table S1) precluded modeling survival and movement by individual banding location, so we pooled the data into two discrete locations (i.e., “north” and “south”; Fig. 1; Appendix S2: Table S1). The demarcation between the two locations was based on a natural clustering of the banding data on either side of the dividing line, as well as clear differences between the two in terms of habitat and proximity to agricultural activities. The candidate model set of approximating models was constructed using a set of reduced parameter models nested within a general omnibus model, where all three structural parameters (S , Ψ , and p) were allowed to vary randomly over time. Goodness of fit of the general model to the data was confirmed using both the median- \hat{c} (White and Burnham 1999) and the JMV model as implemented in program U-CARE (Pradel 2005; Choquet et al. 2009).

Numerical optimization

Consistent with the very low number of total recaptures (1336 out of 49,668 total banded adult females; Appendix S1: Table S1), we used a Markov chain Monte Carlo (MCMC) procedure for parameter estimation for all our models to yield

more stable parameter estimates and more plausible credibility intervals given the sparseness of the dataset. The MCMC procedure was implemented sequentially in MARK using a Metropolis-Hastings sampler (Givens and Hoeting 2005). For each candidate model, we simulated five chains, each consisting of 15,000 tuning samples to obtain an acceptance rate of approximately 45%, followed by a burn-in period of 35,000 samples. We used 150,000 samples from the Markov chain to generate posterior distributions. We assumed prior distributions of $N(0, 1.75)$ variables on a logit scale (for probability parameters on the $[0,1]$ interval) and on a log scale for parameters on the $[0, \infty]$ scale (White et al. 2009). The proposal distribution was $N(0, 0.5)$. Convergence of the sample chains was evaluated following Brooks and Gelman (1998) and graphically through plots of sequential values and histograms of the posterior distributions. In no case, was a lack of convergence suggested, given the length of the chains and burn-in period. We report parameter estimates as the median of the posterior, with associated 95% credibility intervals based on the highest posterior density.

Accounting for temporary emigration

The tricolored blackbird is a mobile species, which when coupled with geographically small sampling regions sampled by mark-recapture suggested that there was significant potential for temporary emigration of marked individuals from the sample sites (where the marked individuals are potentially observable), to areas where the individuals might remain alive, but unobservable. Temporary emigration can present significant challenges for estimating important demographic parameters (e.g., Fujiwara and Caswell 2002, Kendall and Nichols 2002, Schaub et al. 2004, Bailey et al. 2010, Nichols 2016). These problems are exacerbated by sparse data, and lack of a strong determinism in the expected pattern of survival and movement between observable and unobservable states (either natural or imposed as a constraint in model construction) makes it difficult to make strong inference about systematic bias in estimates.

For our analysis, we made the simplifying assumptions that possible temporary emigration was strictly random (i.e., the probability of temporarily emigrating from “observable” at time i

to “unobservable” at time $i + 1$ is the same as the probability of moving from “unobservable” to “observable” over the same time interval) and did not differ as a function of year or sampling location. Under these assumptions, temporary emigration is simply a component of non-detection (Nichols 2016). What is more important is that strictly random temporary emigration does not lead to systematic bias in estimates over the majority of the time series, although it can potentially negatively bias estimates of survival over the final in some cases (e.g., Peñaloza et al. 2014). To assess the degree to which temporary emigration might influence our results, we conducted a series of numerical simulation experiments under varying patterns of temporary emigration, using parameter values we believed plausible given the species, and results of our preliminary analysis of the mark–recapture data. Over a broad range of simulated scenarios (which we do not detail here), we were unable to generate *systematic* bias over time in key parameters over time (or space with respect to the multistate models).

Model selection

We used the Watanabe-Akaike information criterion (WAIC; Watanabe 2013) to rank candidate models fit using MCMC. Heuristically, and in similar fashion to the AIC, the WAIC balances fit with parsimony to improve predictive ability because the uncertainty will increase as the model complexity increases (Hooten and Cooch 2019). Thus, the WAIC is specified as $-2 \log f(\mathbf{y}|\mathbf{y}) + 2p_D$. Using MCMC samples, WAIC can be calculated as

$$-2 \sum_{i=1}^n \log \sum_{t=1}^T f(y_i | \boldsymbol{\beta}^{(t)}) / T + 2p_D$$

where $p_D = \sum_{i=1}^n \text{var}(\log f(\mathbf{y}|\boldsymbol{\beta}))$ and the “var” corresponds to the variance over the posterior distribution for $\boldsymbol{\beta}$. As the posterior variance of the deviance increases, the model is increasingly penalized. We generated normalized WAIC weights using the same procedure as applied to generating AIC weights (sensu Burnham and Anderson 2002, 2004). We derived estimates of annual demographic rates in two ways. First, we averaged parameters over our candidate set of

models (Burnham and Anderson 2002, Fletcher 2019). Model averaging explicitly accounts for model selection uncertainty in inference based on multiple competing models and generally produces a more stable set of parameter estimates (Doherty et al. 2012). In addition, for models where parameters varied randomly over time, we also estimated average parameter values over years by fitting an intercept-only (mean) linear model to a hyperdistribution of the parameters centered on a conceptual mean, ϕ , with some population variation, σ^2 .

Statistical analysis: integrated population model

Because the multistate models suggested movement between the two regions, we revisited the IPM (Robinson et al. 2018b) by analyzing the “north” and “south” regions separately. The eBird checklists from north of our dividing line (Fig. 1) were used in the analysis of the north region, and those checklists from south of the line were included in the analysis of the south region. We used only complete checklists from the years 2007–2016 that reported a count or a zero (we did not include checklists that simply reported the presence of tricolored blackbirds with no count information) and limited to the early pre-breeding period (23 March–25 April). This resulted in 113,501 checklists (43,122 in the north region and 70,379 in the south region). We filtered the data to address class imbalance and spatial and temporal bias according to Robinson et al. (2018a). As filtering removes data available to the analysis, we resampled/re-filtered 1000 times, creating 1000 unique eBird datasets. We followed the same general method as Robinson et al. (2018b) by estimating eBird relative abundance using a zero-inflated generalized additive model for each of the eBird datasets which provided the population count data (the expected number of birds counted by an average eBird user in one-hour traveling one km.; Appendix S4: Table S1) to a two-stage population model based on a pre-breeding census, with submodels linking demographic parameters. However, we split the trend analysis between the two regions and estimated constant immigration (ω) in the population trend submodel to determine how much of the population in each region is gained or lost via dispersal. ω was given a uniform prior with a maximum of the highest total observed

abundance in the time series for the region and a minimum of the negative of that number (i.e., the entire population could be immigrants, or the entire population could be lost to dispersal)

$$N_{1,t} \sim \text{Norm}((F_{t-1} \times \phi_{j,t-1}^{\text{IPM}} \times (0.66667 \times N_{\text{tot},t-1})), \tau_{y_y}),$$

$$N_{2,t} \sim \text{Norm}(N_{\text{tot},t-1} \times ((0.33333 \times \phi_{\text{am},t-1}^{\text{IPM}} + (0.66667 \times \phi_{\text{af},t-1}^{\text{IPM}})), \tau_{y_y}),$$

$$N_{\text{tot},t} = N_{1,t} + N_{2,t} + \omega$$

where ϕ_a^{IPM} is adult annual survival for both males (m) and females (f), juvenile survival from an egg to the next breeding season (ϕ_j^{IPM}). F is fecundity and N_{tot} is relative abundance summed for both age classes (non-adults [1] and adults [2]) at each year (t). τ is the estimated error in the eBird abundance index (i.e., the count data) given an uninformative uniform prior (min = 0 and max = 10,000). F is estimated from the fecundity data in (Robinson et al. 2018b) as

$$J \sim \text{Poisson}(n_t F_t)$$

where J is the number of nestlings counted in n nests each year (t). ϕ is estimated for adults of each sex independently using the multinomial likelihood of the CJS model for the banding data pooled across regions (Appendix S1; Kery and Schaub 2012). Note that N_{tot} is multiplied by 2/3 and ϕ_a^{IPM} is modified by 1/3 for males and 2/3 for females in the first two equations. We were concerned that assuming equal survival for males and females could bias our results if a true difference exists. In a typical tricolored blackbird colony, there are two females for each male, although this ratio could be as high as 4:1 (Beedy et al. 2020). We estimated the annual growth rate (r) for each region during the 10 yr of the study and the overall decline across the entirety of the study from the posterior estimates of relative abundance. We also evaluated the effect of sample size on our ability to detect a trend in the data (Appendix S3).

RESULTS

Variation in λ : influences of survival and recruitment

There was no support in our model fitting to the data for any effect of either (1) time of marking

relative to the start of the season or (2) Julian date, on temporal variation in either survival, ϕ , or recruitment, f . There was also no support for models where either or both survival and recruitment were constrained to follow a simple linear trend. In fact, the most parsimonious model, with >80% of the support in the data (based on normalized WAIC values), was the general omnibus model with unstructured variation in all three model parameters, $\{\phi_t, p_t, f_t\}$. As a result, inference was strongly influenced by this model.

Model-averaged estimates of apparent annual survival varied considerably over years 2008–2014, ranging from ~0.9 to a minimum value of ~0.5 (Fig. 2a). Survival estimates were very close to those from the integrated population model (IPM) reported by Robinson et al. (2018b) (Fig. 2a). Average survival, ϕ , over the period from 2008 to 2014 was 0.711 [0.612, 0.850]. Annual per capita recruitment, f , was generally stable over time, with the notable exception of 2012 and 2013, when there was essentially no detectable recruitment into the adult female population (Fig. 2b). Excluding 2012 and 2013, average annual recruitment was 0.505 [0.395, 0.652]. Confirming our preliminary analysis of the data, annual estimated encounter probability was generally very low (<0.05; Appendix S1), most notably in 2012 and 2013, the two years with extremely low estimated recruitment.

Since $\lambda = \phi + f$, we derived estimates of annual realized growth, by analysis of the posterior distribution of the summed estimates of survival and recruitment calculated at each iteration of the MCMC chains. Realized growth of the adult female population varied annually from 2008 to 2014, but there was no indication of a trend (Fig. 3). Geometric mean stochastic growth rate over this interval was estimated as $\lambda_s = 1.042$ with an estimated process variance of $\hat{\sigma}^2 = 0.171$. The estimated 95% highest posterior credibility interval for λ_s [0.734, 1.515] included 1. This result would appear to indicate that no decline or increase in population size can be detected from 2008 to 2014 for the adult female tricolored blackbird population comprising the sample of marked individuals.

We apportioned annual variation in realized growth by evaluating the proportion of realized growth due to variation in the survival and recruitment sub-processes (sensu Nichols et al.

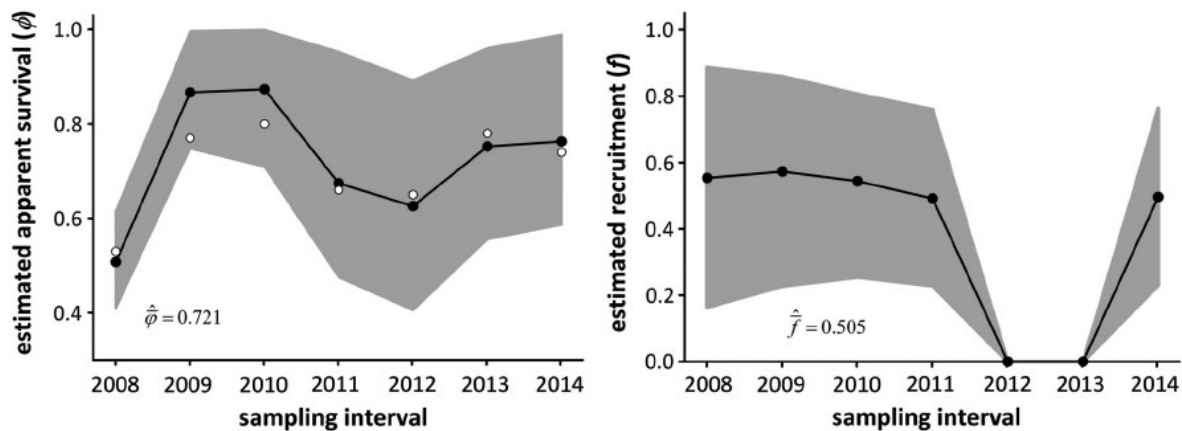


Fig. 2. Solid circles indicate model-averaged estimates of apparent survival (ϕ) and per capita recruitment (f), for adult female tricolored blackbirds, 2008–2014. Estimates for 2007 not shown because of potential bias for estimated recruitment in the first year. Estimates for 2015 not shown because terminal estimates of survival are not separately identifiable from encounter probability in time-specific models. Data pooled over all live mark–release sampling locations (Fig. 1). Shaded areas represent 95% credibility limits to the estimates. Mean per capita recruitment calculated excluding 2012 and 2013. Open circles are estimates of apparent survival based on IPM (Robinson et al. 2018a, 2018b).

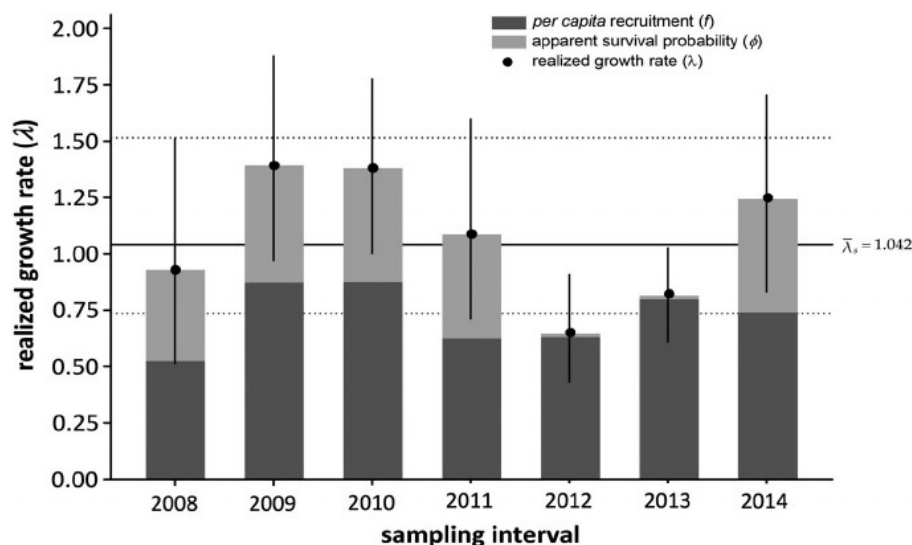


Fig. 3. Annual variation in realized growth rate, λ , for the adult female population of tricolored blackbirds, 2008–2014, showing absolute contributions from apparent survival (ϕ) and per capita recruitment (f). Error bars represent 95% credibility limits to the annual estimates. Mean stochastic growth ($\bar{\lambda}_s$) over the sampling period is indicated by a solid horizontal line. The dashed horizontal lines represent the upper and lower 95% highest posterior density credibility intervals for the mean stochastic growth.

2000). Since recruitment was relatively stable, except for 2012 and 2013, annual variation in realized growth for the adult female population was most strongly influenced by variation in

apparent survival, except for 2012 and 2013, when there was effectively no detectable recruitment to the adult female population (Figs. 2 and 3).

Multistate analysis: regional differences in survival and movement

The lack of apparent trend in population trajectory from our mark–recapture analysis would appear to be inconsistent with the strong negative trend in growth shown in Robinson et al. (2018b), despite the fact that the present mark–recapture data were used as part of the IPM presented therein. Further, our results suggest that in most years, the primary driver of variation in population trajectory is variation in annual survival. With live-encounter data alone, we cannot separate mortality from permanent emigration. Given the itinerant nature of this species, it seemed reasonable to assume that a proportion of the variation in apparent survival reflected permanent movement out of the sampling region. In the absence of radio-marked individuals or recoveries of known dead individuals, it is not practically possible to separate mortality from emigration in our data.

However, we considered the question indirectly in a multistate analysis. We partitioned our data into north and south regions (Fig. 1). Our focus was on testing for differences in survival between birds originally marked in the north or south clusters of banding locations and differences in movement probability between the two locations that were conditioned on survival. As with the preceding mark–recapture analysis using data pooled over all banding sites, we did not find support for any effect of either (1) time of marking relative to the start of the season or (2) Julian date, on temporal variation in either survival, ϕ , or recruitment, f . There was also no support for models where either or both survival and movement were constrained to follow a simple linear trend. As with the preceding analysis, the most parsimonious model, with >80% of the support based on normalized WAIC values, was the general omnibus model with unstructured variation in all three model parameters $\{\phi_t, p_t, \psi_t\}$. There were clear and dramatic differences in both apparent survival and movement between north and south locations (Fig. 4). In most years, apparent survival (meaning, the probability of surviving and remaining in the sample) was higher in the north than in the south. In addition, surviving individuals in the north had a very low probability of moving from north to south, whereas surviving individuals in the south

showed a high probability (>0.90) of moving to the north following an encounter in most years.

Integrated population model: regional differences in population trends and immigration

The IPM analysis of tricolored blackbirds in the north estimated an annual growth rate (r) of

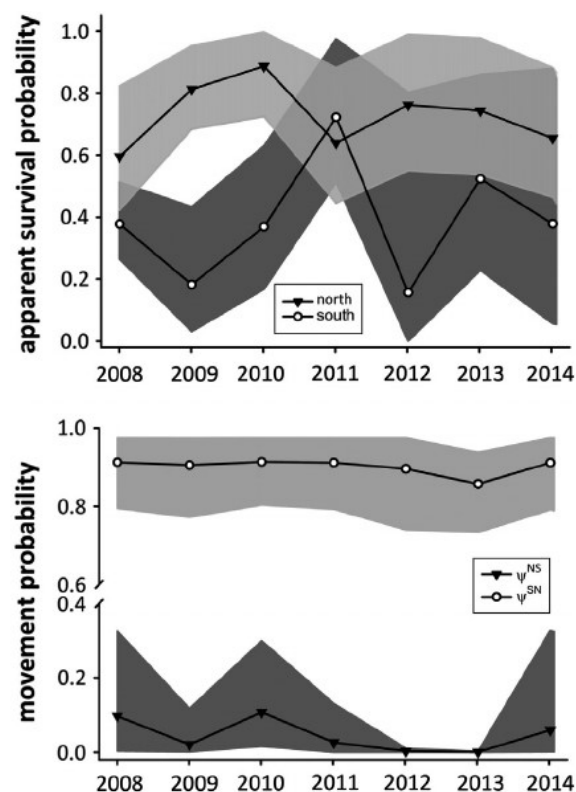


Fig. 4. Model-averaged estimates of location-specific (“north” and “south”) survival (S) and movement conditional on survival (ϕ) for adult female tricolored blackbirds, 2008–2014. Estimates for 2007 not shown because no individuals were captured and released in the “south” in 2007 (Appendix S2: Table S1). Estimates for 2015 not shown because terminal estimates of survival are not separately identifiable from encounter probability in time-specific models. Open circles indicate estimates from individuals encountered in the “south,” while solid triangles represent estimates from individuals encountered in the “north.” Movement estimates represent the probability of moving from one location to the other (i.e., ψ^{NS} —“north to south” and ψ^{SN} —“south to north”). Shaded areas represent 95% credibility limits to the estimates.

0.007 (95% highest posterior density interval $[-0.07, 0.055]$), an estimated decline of -2.49% (HPDI $[-51.8\%, 54.7\%]$) from 2007 to 2016, and a probability of 0.608 that the portion of the population in the north declined at all over the years of the study. eBird data cannot be used to estimate population size or number of individuals added/subtracted by immigration. We were restricted to relative abundance for each yearly population estimate (Fig. 5). The constant immigration from the south to the north was an addition of 6.51 (HPDI $[-13.6, 24.2]$) “relative individuals,” with 77% of model realizations resulting in a net addition of individuals to north. This suggests that 8.35–13.22% of the population observed in the north were immigrants (Fig. 6). The IPM analysis for tricolored blackbirds in the south region estimated an annual growth rate of -0.099 (HPDI $[-0.234, 0.026]$), an estimated decline of -51.7% (HPDI $[-96.5\%, -4.14\%]$) from 2007 to 2016, and a probability of 0.962 that the southern portion of the population declined across the years of the study (Fig. 5). Constant emigration from the south to the north was a loss of 1.89 (HPDI $[-9.04, 4.04]$) “relative individuals,” with 67.2% of model realizations resulting in a net loss of individuals from the south. This suggests that between 7.37% and 13.57% of the population in the south region is lost to emigration each year (Fig. 6).

DISCUSSION

Population-level ecological inferences are often made based on information about demographic processes collected over a restricted sampling region. However, restricting inferences to just one or a few local populations may give an inaccurate picture of the demographic rates and population trends for a species across its occupied range (Cilimburg et al. 2002, Zimmerman et al. 2007). As a result, our knowledge of the factors that most influence demographic rates and trends is likely to vary depending on the level of spatial heterogeneity in population dynamics (Johnson et al. 2010). Here, we evaluated demographic processes and population trends at multiple scales for tricolored blackbirds in California, statewide and regionally, using site-specific banding data and range-wide citizen-science data (Robinson et al. 2018b). Based on our results

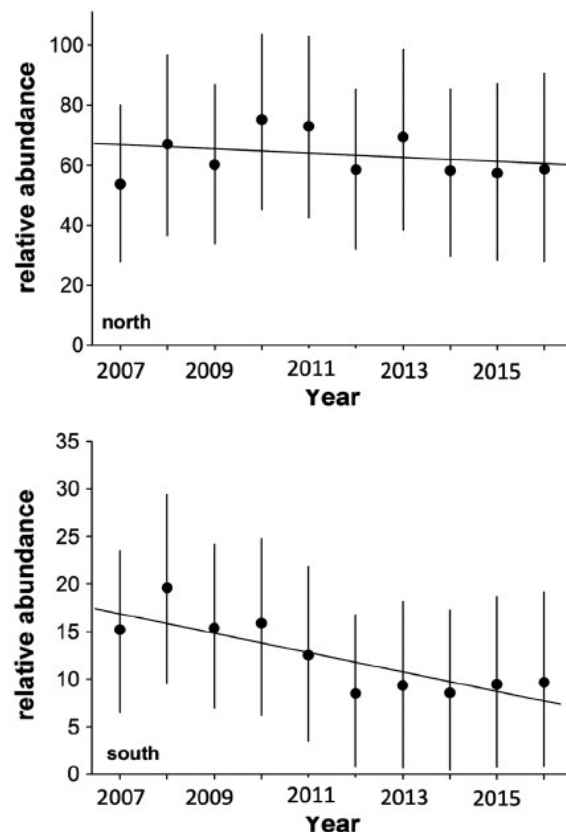


Fig. 5. Population trajectory in terms of relative abundance for the north (top) and south (bottom) populations as estimated by the IPM for each region.

on survival, movement, population growth, and population trends, we could infer that there is a pseudo-source and sink system for northern and southern populations of tricolored blackbirds in California. Here, we define “pseudo-source” as a source (e.g., source of individuals) with growth <1 (Kristan 2003) and undergoing a significant long-term decline. Under this definition, the southern portion of the population is a pseudo-source since it has declined considerably over the ten years of our study and has a large and negative annual growth rate, while still acting as a source of immigrants for the north. In turn, the northern region fits the traditional definition of a sink population (Dias 1996) by having an annual growth rate near zero and has experienced a small decline over the last 10 yr, even though it is estimated to receive immigrants from the southern region. However, some individuals

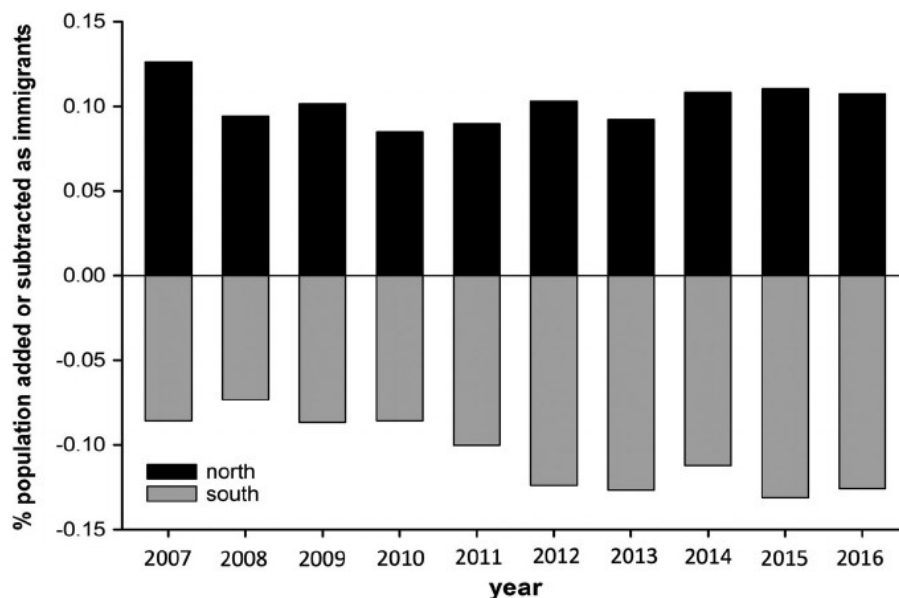


Fig. 6. Average percentage of the observed population at each year in the north (black) and south (gray) that was added or lost to immigration.

were found to move from north to south, suggesting that the regions may have exchanged individuals in the past (e.g., balanced exchange; Doncaster et al. 1997). If this exchange was more balanced in the past (Berg et al. 2010), we could also consider that instead of acting as source and sink for each other, these regions are subject to highly imbalanced movement from south to north. Long term, this imbalance in movement may lead to range contraction in the south, and the northern region is likely to experience increased rates of decline with the loss of immigrants from the south.

These regional differences in trends would not have been evident if we had based our inferences on statewide results from just the banding data. Our range-wide, multistate analysis suggested a stable population ($\lambda_s = 1.042$), although the credible interval was very wide. This seems to be in contrast to previous statewide results based on an IPM, which showed a 0.94 probability of a decline and an average 34% decline in the population across California over the same time period (Robinson et al. 2018b). However, our statewide survival estimates for adult females are similar to those reported in the range-wide IPM (Fig. 2). This is perhaps not surprising, since

the IPM structure was identical to the most strongly supported model in the present analysis. Therefore, the difference in estimates of population decline is likely due to the additional sources of data included in the IPM data on fecundity and range-wide relative abundance from eBird (Sullivan et al. 2014). Jointly modeling multiple datasets using IPMs has been shown to reduce uncertainty in the estimation of demographic parameters (Kéry and Schaub 2012) and likely contributed to the difference in inference in the two analyses.

The availability of range-wide, comprehensive data on relative abundance further allowed us to understand the role of regional differences in movement on population growth. The regional IPM allowed us to determine that a significant portion of the population in the south is lost due to emigration each year, in agreement with our multistate analysis. These results support the idea that the apparent stability of the population in the north is bolstered by a large number of immigrants, likely from the south as almost the entire known tricolored blackbird population is within California (Beedy et al. 2020). This suggests that the decline in the south is in part driven by individuals emigrating north and that our

inability to find a decline in the north is likely due to an influx of individuals from the southern region. The lack of evidence for an increase in individuals in the northern region shows strong support for our conclusion of a pseudo-source and sink system occurring between the two regions.

Our regional partitioning of banding data using multistate models showed lower adult female survival in the south region relative to the north, and that birds initially banded in the south were very likely to be recaptured in subsequent years in the north. One potential driver of these results is the sustained drought in the southern region during the interval studied. While both regions have experienced drought during the years of our study according to the Palmer Drought Index, the southern region has suffered far more severely (NDMC et al. 2019). Southern California suffered an unprecedented drought from 2012 to 2015, including the most severe single-season drought in the instrumental record in 2014 (1895–2014; Robeson, 2015). These droughts have exacerbated the loss of wetlands, tricolored blackbirds' historical preferred nesting sites, that was already occurring across the state throughout the 1900s (Dahl 1990, Chang and Bonnette 2016). The drought conditions may lead to poor productivity or few suitable nest sites; thus, the birds in the south region experiencing these conditions simply move north to escape them (McCreedy and van Riper 2015, Conrey et al. 2016). Another potential source of these results is the increase in nut crops in California, particularly the counties of Merced and Kern in our south region, which together held roughly 51% of California's breeding tricolored blackbirds during a 2017 statewide survey (Meese 2017). California's acreage of walnuts has increased substantially (USDA 2018a), while total walnut production has more than doubled within the timeframe of our study (USDA 2018b). Similarly, the number of acres in almond groves has increased (CDFA 2018). In recent years, pistachios have been the fastest growing nut crop, increasing in acreage and production more than any other (CDFA 2018). The increasing acreage converted to these water intensive crops (Fulton et al. 2012), and to other forms of agriculture, may reduce water available to tricolored blackbirds even further.

These recent trends in land-use change, combined with the habitat loss that occurs from drought and conversion to agriculture, could easily explain why most of the individuals banded in the south moved and were recaptured in the north in subsequent years. These factors could also explain the lower female adult survival in the region, since estimates of apparent survival are often biased low when marked individuals move out of the study area (Cilimburg et al. 2002, Zimmerman et al. 2007, Alonso and Arizaga 2013). Without any direct information on both movement and survival (e.g., tracked individuals), it is difficult to tease apart with certainty how much of the reduced survival in the south is mortality due to the environmental conditions and how much is driven by movement out of areas where individuals are originally banded.

IMPLICATIONS FOR CONSERVATION

Our initial estimation of a population trend for tricolored blackbirds in California (Robinson et al. 2018b) was informative to help provide scientific evidence of the magnitude and drivers of a statewide population decline. This information was valuable for justifying the listing of the species as threatened under the California Endangered Species Act, as this policy decision was made at the state scale (Beedy et al. 2020). However, prioritizing management actions aimed at mitigating the drivers of decline at scales more relevant for management and restoration will require more detailed information. We have shown that statewide results are not detailed enough to guide targeted actions for restoring tricolored blackbird populations, given the regional differences we found in demographic processes and population trends. In addition, looking only at live-encounter data does not provide sufficient information to make range-wide inferences. The integration of all relevant data sources through the application of an IPM provided the most accurate inferences on regional variation. However, the live-encounter information was critical for examining the effect of movement on vital rates.

Our combined results suggest that a focus on the northern region might be beneficial for the species, since this is where individuals from the

south are likely to move (Lehikoinen and Virkкала 2016, Socolar et al. 2017). If actions can be designed to increase in situ recruitment and survival of residents and immigrants in the northern region, success would be evident through a measurable increase in relative abundance and potential increase in distribution. On the other hand, focusing on mitigating the effects of drying conditions and the expansion of croplands into wetlands might change current immigration trends and slow down current rates of decline. The relative contribution of either one of these options needs to be rigorously evaluated by integrating count data with information on movement and survival from tracked individuals, and regional information on reproductive success.

Current suggestions are to prioritize research aimed at collecting information on how individuals move in this system. Improving our understanding on movement across the range will improve our knowledge on survival of both males and females, and allow us to better tease apart the apparent survival estimates into true survival and immigration. This will also provide information on movement for the purposes of multiple breeding attempts which may allow us to fine-tune fecundity parameters in future models and differentiate between movements due to breeding and non-breeding events. We strongly suggest the application of telemetry and/or satellite tracking, as the effort to band individuals has been massive, yet the recapture rates are very low.

CONCLUSIONS

We have shown the importance of exploring the factors that drive demographic processes and population trends at multiple scales, in order to increase the accuracy of inferences needed to document local and range-wide patterns. In addition, inferences will be most accurate if count-based information is available for a large portion of the range of the population, and integrated with other sources of data on marked individuals. In our case study, we show that the conclusions with regard to the population dynamics of the tricolored blackbird in California varied on the scale of the analysis. Our results suggest that tricolored blackbirds in California are likely to undergo a significant contraction in range long term, largely driven by coupled

effects of climate change and agricultural conversion of wetland habitats. Therefore, efforts to secure the long-term persistence of this species should prioritize research and habitat management efforts to address sources of mortality for immigrants from the south, as well as increasing reproductive success and recruitment for the northern portion of the population.

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