

# JOURNAL OF AVIAN BIOLOGY

## Article

### Population decline of a long-distance migratory passerine at the edge of its range: nest predation, nest replacement and immigration

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#### Journal of Avian Biology

2020: e02286

doi: 10.1111/jav.02286

Subject Editor: Wesley Hochachka

Editor-in-Chief: Jan-Åke Nilsson

Accepted 22 March 2020

The relative importance of predators and resources (i.e. food) for the dynamics of migratory bird populations is poorly known. Resource availability may be more likely in resource poor environments, but given that nest failure in most systems is due mainly to predation, predator effects may predominate. We document a rapid decline of an isolated eastern kingbird *Tyrannus tyrannus* population breeding in the Great Basin Desert of eastern Oregon, USA, and evaluate whether it was driven by limited food resources (water availability ~ food), nest predation, or first-year or adult return rate ( $RR_J$  and  $RR_A$ , respectively) that reflect nonbreeding season events. Most nests failed (~68% of nests) due mainly to nest predation (> 90% of failures); nestling starvation was rare. Biowater precipitation (October–April), breeding season precipitation, and river flow all varied widely but none could account for annual variation in either nest success (NS) or fledging success of successful nest (FSSN). Neither  $RR_J$  nor  $RR_A$  varied with year, any measure of water resources, or reproductive success. Annual population growth rate ( $\ln[N_{t+1}/N_t]$ ) was independent of year, all measures of water availability,  $RR_J$  and  $RR_A$ , and NS of replacement nests, but was high following years of high NS of initial nests; FSSN was also higher in years of high NS. High rates of nest predation, due likely to the expansion of the local American crow *Corvus brachyrhynchos* population, appeared to drive the population decline. Empirical data and population simulations indicated that replacement nests contributed little to  $\lambda$ , while simulations revealed that, given site-specific vital rates, the decline would have been even greater without immigration ( $\lambda = 0.812$ ) than the observed ( $\lambda = 0.914$ ). Long distance dispersal may thus be critical for persistence of kingbirds in the naturally highly fragmented habitat that it occupies in the Great Basin Desert.

Keywords: annual fecundity, immigration, lambda, nest predation, population decline, replacement nests



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## Introduction

Populations may be limited by habitat (Rappole et al. 2003, Hemerik et al. 2015), food (Holmes et al. 1986, Benton et al. 2002), competition (Garcia 1983, Dugger et al. 2011), predation/parasitism (Robinson et al. 1995, Smith et al. 2002, Schmidt and Ostfeld 2003), or especially near range edges, extreme weather (Arcese et al. 1992, Mehlman 1997, Garcia and Arroyo 2001). For migratory species, events away from the breeding grounds may also have strong influences (Sanderson et al. 2006, Schaub et al. 2011, Woodworth et al. 2017, Kramer et al. 2018). Of the aforementioned factors, enhanced fecundity in response to natural (Blancher and Robertson 1987, Hussell and Quinney 1987, Grant et al. 2000, Bolger et al. 2005) and experimental (Nagy and Holmes 2005, Preston and Rotenberry 2006) increases in food suggests a key role for food resources. This seems especially so for small relatively short-lived birds in which population growth is most often linked to annual fecundity (Grant et al. 2000, Sæther and Bakke 2000, Murphy 2001, Rodenhouse et al. 2003, Clark and Martin 2007).

Population limitation by food supply in birds may be especially important in resource-limited environments such as arid regions where water limits primary productivity (Dunham 1980, Blancher and Robertson 1987, Smith et al. 1995, Preston and Rotenberry 2006, Lima et al. 2008). Indeed, both observational (Sims and Singh 1978, Sala et al. 1988, Lauenroth and Sala 1992, Haddad et al. 2002) and experimental work (Knapp et al. 2001) have established a direct relationship between water availability and above ground net primary production (ANPP). ANPP directly affects the abundance and diversity of the primary consumers (i.e. arthropods) upon which higher-level consumers depend (Bell 1985, Polis et al. 1997, Bolger et al. 2005, Branson 2008, Wenninger and Inouye 2008, Borer et al. 2012). Strong associations between weather, principally precipitation and population trends of birds from the Mediterranean region (Herrando et al. 2019) and arid to semi-arid grasslands of North America (Gorzo et al. 2016) attest to the importance of water availability for the dynamics of avian populations. Given that climate extremes are often greatest near the edge of a species ranges (above), the dynamics of populations near the edge of a species range may be particularly sensitive to high temporal variation in abiotic factors that influence ANPP, and as a consequence, food resources (Garcia and Arroyo 2001; but see Berl et al. 2014).

However, nest predation is by far the most common cause of nest failure for most birds (Ricklefs 1969, Martin 1993), and thus, nest predators have the potential to heavily influence, if not drive, population dynamics. For instance, declining populations of red-headed woodpeckers *Melanerpes erythrocephalus* at the edge of their northern range has been attributed to low productivity caused mainly by high nest predation (Frei et al. 2015). Similarly, removal of brood parasitic brown-headed cowbirds *Molothrus ater*, which both reduce brood size and destroy nests, caused declining song sparrow

*Melospiza melodia* populations to become stable (Smith et al. 2002). Low nest success driven by the abundance of sciurid nest predators in eastern North America are likely the main contributor to population dynamics of some passerine species (Schmidt and Ostfeld 2003, Sherry et al. 2015). Although data are limited, in arid western North America the relative influence of food resources and nest predators on avian populations may depend on water availability, with nest predators holding sway in wetter years (Rotenberry and Wiens 1989, Morrison and Bolger 2002, Preston and Rotenberry 2006).

It is also possible, however, that local population dynamics are affected more by external forces than local reproductive success and survival. For instance, fluctuations in local population abundance may be a consequence of non-breeding season events for migratory species (above). Moreover, few populations are closed, and studies of a number of species (Schaub et al. 2010, 2013, Rushing et al. 2017), including those with isolated populations (Schaub et al. 2012, Taylor et al. 2018), have shown that population dynamics could not be understood without accounting for immigration.

Here we report on a 10-year study of a population of eastern kingbirds (*Tyrannus tyrannus*; hereafter ‘kingbirds’) breeding at Malheur National Wildlife Refuge (MNWR). MNWR is a high elevation site located in southeastern Oregon, USA, at the northern end of the Great Basin Desert and on the western edge of the kingbird’s geographic range. Our study thus provides data with which to address the relative importance of food limitation and nest predation in limiting populations of birds at the edge of their range. Our goals were to 1) describe population dynamics, and 2) assess the relative influence of resources (as approximated by water availability), nest predators, and weather in generating year-to-year variation in population size. Given that MNWR is an ecological island for kingbirds (below), and site fidelity of juveniles and adults is high (Redmond and Murphy 2012), our a priori expectation was that in situ vital rates (i.e. ‘self-recruitment’; Runge et al. 2006) would account for annual variation in numbers. To test this, but also test for a possible influence of immigration on population dynamics, 3) we develop a model based on site-specific vital rates to evaluate the population’s capacity to replace itself, and through simulation, evaluate the contribution of immigration to local population dynamics.

## Material and methods

### Species and study site

Kingbirds (~ 40 g) are aerial insectivorous Nearctic–Neotropical migratory birds. Males, and older, high quality individuals of both sexes, are the first to return to North America from South America (Cooper et al. 2011). Territories are established beginning by mid- to late May at MNWR (Cooper et al. 2009), and females build open-cup nests in trees and shrubs in open habitats. Socially monogamous pair bonds persist through the season (Murphy 1996). Females

alone incubate eggs (15 days) and brood young, but both sexes feed young at equal rates at MNWR (Chutter et al. 2016). Typical clutch size is 3 or 4 eggs (range=2–5) and young fledge at 16–17 days of age (hatching=1). Only a single brood is raised annually, but nest failure is common and failed initial nesting attempts are often replaced if failure occurs in June, but the likelihood of replacement declines precipitously after June (below).

MNWR (42°49'N, 118°54'W; 1256 m a.s.l.) is located in High Desert habitat dominated by big sagebrush *Artemisia tridentata* and rabbitbrush *Chrysothamnus* spp. Climate of the High Desert is very seasonal, and mean monthly temperature (average of daily low and high) is lowest between December and February (−1° to −4°C) and highest between June and August (14.5–18.8°C). Daily highs in July, the month when most young are fed, regularly reach 30°C and not uncommonly exceed 38°C. By contrast, being high elevation desert, overnight temperatures at any point in the breeding season can drop below 5°C, and we recorded snowfall in early June in several years. Most precipitation falls from December through March (123.5 mm; ~50% of annual total) with little contribution from the months of the kingbird breeding season (June through August; 38.4 mm [14.3% of the annual total; data from the Oregon Climate Service: <<http://www.ocs.oregonstate.edu>>]). Studies of kingbirds elsewhere at roughly equivalent latitudes report a mean date of clutch initiation of initial clutches of 8 June (Murphy 1983, 2001,

Blancher and Robertson 1985); mean clutch initiation date at MNWR is delayed by 10 days compared to the other sites (M. T. Murphy unpubl.). Furthermore, annual variation in first egg date (i.e. date of the first egg of a clutch) at MNWR is strongly and inversely linked to May temperatures (M. T. Murphy, unpubl.). Thus, as an aerial insectivore dependent on flying insects for food, the wide daily fluctuations and often low temperatures at MNWR are challenging for kingbirds compared to most other locations where they breed (see Järvinen and Väisänen 1984 for a similar example in the pied flycatcher *Ficedula hypoleuca*).

Typical sagebrush steppe habitat of the High Desert is unsuitable for kingbirds, but the Donner und Blitzen River, fed by snowmelt from the nearby Steens Mountain, creates nesting and foraging habitat in the willow *Salix* spp. dominated riparian zone and nearby marshes. Kingbirds occasionally nest in sagebrush (<5% of nests), but only if within ~150 m of the river. Thus, breeding populations in the High Desert are widely separated and limited to sites with aquatic habitats (Csuti et al. 2001). Our main study site began at the south end of MNWR where the Donner und Blitzen River enters the refuge, and continued ~20 km upriver to a point located 1.5 km north of the bridge to Krumbo Reservoir (Fig. 1 in Redmond and Murphy 2012). We also included suitable habitat along East Canal, a major tributary of the Donner und Blitzen River forming the eastern boundary of the refuge, the smaller West Canal running west along the south border of the refuge, and small ox-bows

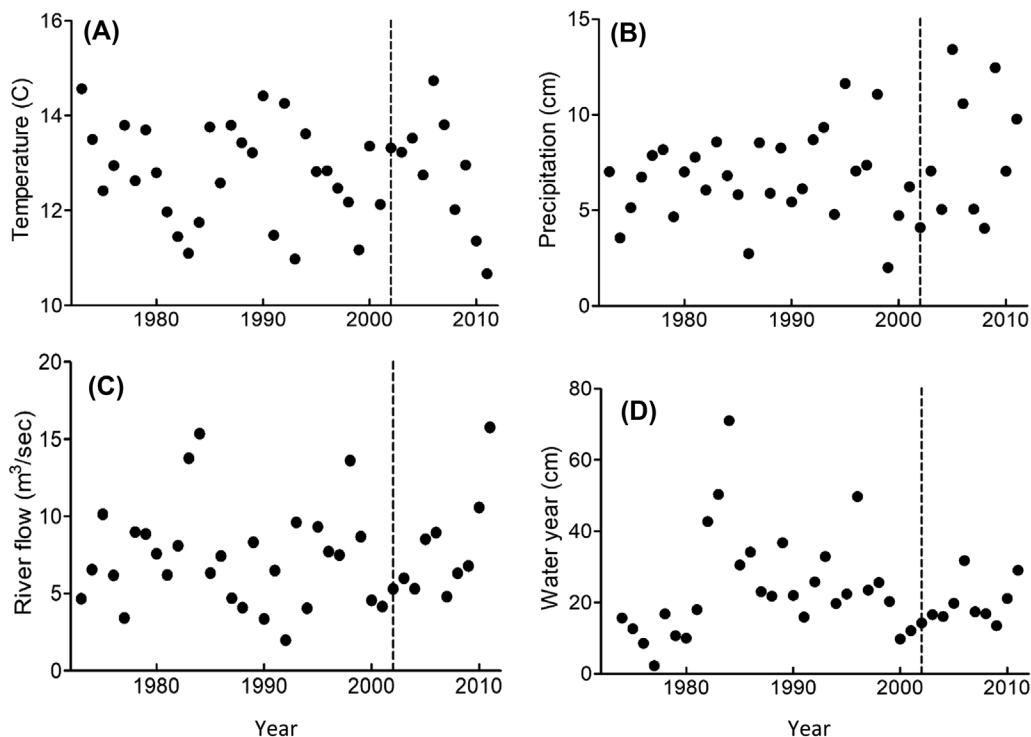


Figure 1. Annual variation (1973–2011) in (A) breeding season temperature, (B) breeding season precipitation (both averaged from April through July), (C) flow of the Donner und Blitzen River upon entry into Malheur Wildlife Refuge (averaged from May through July of breeding season) and (D) precipitation accumulated over the bioyear (October through April). Dashed vertical line at year 2002 marks the beginning of the eastern kingbird population study.

formed by former meanderings of the river. Several roads that closely parallel the waterways provided access to nesting habitat. A second study site (Buena Vista), separated from the main study site by ~6 km of treeless riparian habitat, was not included in the analysis of annual variation in population size because it was not surveyed thoroughly in all years, but it did provide data to assess annual variation in reproductive success and return rate/survival (below). A previous publication (Redmond and Murphy 2012), based on the first seven years of data from the entire study site described here, produced Cormack–Jolly–Seber (CJS) estimates of apparent adult ( $S_A$ ) and juvenile survival ( $S_J$ ). We used the survival estimates from the 2012 publication to compare to annual return rates (RR; proportion of banded birds to return) for the 10-year period of the current study, and to serve as the best available estimate of apparent survival for simulations of annual variation in population size (below).

### Weather and water availability

Weather records from MNWR were incomplete and therefore we used records from Burns Airport located ~80 km north of the center of our study area to describe long-term variation in weather. Although daily weather, especially precipitation, can be very localized, our goal was to describe long-term patterns of weather variation rather than short-term, daily events, and Burns Airport was the closest weather station with a moderately long-term data set (1973 to present) that was also at the same elevation (1267 m a.s.l.) as MNWR. We therefore used mean monthly temperature and total precipitation for April through July to characterize each year's breeding season weather. Our reason for beginning in April was that breeding season phenology is dependent on prior conditions; leaf-out and growth of arthropod populations were likely affected by weather in the 4–6 week period prior to the return of kingbirds from migration in mid-May.

Summer drought characterizes much of western North America, including MNWR, and water supply in mountain regions depends heavily on precipitation accumulated over the 'water-year' (beginning on 1 October of previous year). Our intent was to assess the importance of winter precipitation for summer processes and therefore, like Rotenberry and Wiens (1991), we define the 'bioyear' as starting on 1 October and ending on 30 April. We also used snow accumulated by April in the nearby Steens Mountains at Fish Creek (42°70'N–118°63'W; 2335 m a.s.l.), a major tributary feeding the Donner und Blitzen River, to quantify snowpack (U.S. Department of Agriculture's Natural Resources Conservation Service: <[http://www.nrcs.usda.gov/wps/portal/nrcs/detail/nh/home/?cid=nrcs142p2\\_046215](http://www.nrcs.usda.gov/wps/portal/nrcs/detail/nh/home/?cid=nrcs142p2_046215)>). Data on snowpack were available beginning in 1979. A final source of information on water availability was mean monthly water flow rates for the Donner und Blitzen River collected by the U.S. Geological Survey (42°47'N–118°52'W; 1297 m a.s.l.) at the south end of the refuge <[http://waterdata.usgs.gov/nwis/monthly/?search\\_site\\_no=10396000&agency\\_cd=USGS&referred\\_module=sw&format=sites\\_selection\\_links](http://waterdata.usgs.gov/nwis/monthly/?search_site_no=10396000&agency_cd=USGS&referred_module=sw&format=sites_selection_links)>).

### Population surveys

We surveyed populations from mid-May to early August, 2002 through 2011. Briefer surveys of the population were also conducted from late May to early June of 2012 and from early June to early July of 2015. Kingbirds are easily detected when present because of their loud and frequent vocalizations during territory establishment, and highly visible foraging behaviors that they carry out from conspicuous perches. Population surveys were based on total counts of pairs nesting on the main study area. Beginning in mid-May we spent 10+ hours daily on the study area often with 2 or 3 vehicles slowly driving the roads that parallel the river and its tributaries. We located and mapped each kingbird detected and then used plumage and behavior to determine sex and paired status. Surveys from the river (and tributaries) by canoe and searches of other potential nesting habitat by foot were also conducted weekly. Accurate counts were facilitated by the fact that ≥75% of pairs had at least one member color banded in every year except the first (65% by the end of that year), and the virtual absence of within-season dispersal of pairs to a new territory after failure of a nesting attempt.

### Reproduction and return rate

Kingbird nests are often easily found as they are placed on the periphery of trees and often overhang water (Cancellieri and Murphy 2014). We thus found ≥80% of nests by at least early incubation. We checked nests every 2–3 days to establish first egg dates, clutch size and number of young fledged. Assuming one egg was laid per day and an incubation length of 15 days, first egg date of nests found after completion of laying could often be determined by backdating from known events (e.g. hatching, growth of young). Nests that failed during incubation for which first egg date was unknown could sometimes be dated using changes in shell color. Recently laid eggs have an orange cast due to the yolk's color made visible by the relatively translucent egg shell. However, egg shells begin to become opaque by day 3–4 of incubation, and if found after this date, we could not backdate nests unless they survived to hatching. All dates were standardized (May 1 = day 1). Most nests were not checked after day 13 and we assumed, unless a later nest check showed otherwise, that all young present at day 13 fledged. Kingbirds often re-nest after failed first attempts, and because dispersal following nest failure is rare, we are confident that nearly all replacement nesting attempts were detected; identical reproductive data were collected from replacement nests so that seasonal fecundity was known for all pairs. Adults of both sexes were captured using mist nets, and full description of methods used to handle, sex and color band adults and young are given in Dolan et al. (2007) and Redmond and Murphy (2012). Return rate of adults ( $RR_A$ ) and first-year (i.e. juvenile;  $RR_J$ ) birds were documented by daily monitoring of the population and repeated re-sightings of marked individuals by multiple observers over the full breeding season.

## Statistical analysis

We used data from 1973 to 2011 to describe long-term variation in breeding season temperature and precipitation, precipitation during the bioyear year (1 October to 30 April), snowpack (starting in 1979) and river flow. Linear and polynomial regression were used to test for linear and non-linear patterns of variation, respectively, while linear regression was used to test for trends over our study period (2002–2011). To describe kingbird population trends, we regressed the natural log of population size against year, the slope of which is growth rate ( $\lambda$ ; Akçakaya et al. 1997).

Spatiotemporal variation in water availability directly affects primary plant production and abundance of primary consumers that potentially drive reproduction of vertebrates in arid environments (above; Beatley 1969, Dunham 1980, Rotenberry and Wiens 1991, Schuett et al. 2011). We thus used water availability as a proxy for annual variation in overall quality of food resources in this arid and water limited environment. We likewise use weather and, in particular, breeding season temperature to represent potential abiotic influences on demography. Given that over 90% of kingbird nest failure was due to nest predation ( $91.3 \pm 2.5\%$  SE,  $n = 10$  years), we also used annual variation in nest success (NS; proportion of nests to fledge at least one young) as a direct measure of the potential effect of predators on population dynamics. NS, corrected for exposure time (Mayfield 1961, 1975), was calculated for the entire nest cycle (35 days; 3 days of egg-laying, 15 days of incubation and 17 day nestling period) by raising daily mortality (DMR) rate to the length of the nest cycle. DMR was calculated for initial nests, replacement nests, and the combined sample of initial and replacement nests for each year individually using Hazler's (2004) logistic exposure method. The standard error of DMR was then used to calculate 95% confidence intervals of DMR and NS. All analyses of the driver(s) of annual variation in NS and fledging success per successful nest (FSSN; number of young fledged),  $RR_A$  and  $RR_J$ , and  $\lambda$  were based on annual means.

Although our analysis of annual variation in population size was limited to the main study area, we included reproductive and mark–resight–recapture data for birds from the Buena Vista area in our calculation of annual variation in reproductive success and  $RR_A$  and  $RR_J$ . This was appropriate because all birds, but especially juveniles, moved freely between all of our sub-study sites and thus reproductive success of kingbirds across all of MNWR was likely to affect numbers of potential recruits. Furthermore, virtually all mortality of free-flying individuals occurs away from the breeding grounds (Redmond and Murphy 2012) and thus annual survival reflects mortality in the non-breeding period (as in other passerines; Sillert and Holmes 2002, Rockwell et al. 2017, Rushing et al. 2017). Consequently, the larger sample of all banding records from the entirety of MNWR should ensure more accurate measures of return rate and survival (Runge et al. 2006). Prior analysis of Cormack–Jolly–Seber (CJS) adult male and female survival from a subset

of the data (2002–2008) were virtually identical and averaged 0.65 (95% CI = 0.560–0.732; Redmond and Murphy 2012). Detectability of both sexes was high (males = 0.901, females = 0.847; Redmond and Murphy 2012), and consistent with Martin et al.'s (1995) conclusion that RR should closely approximate true survival at high detectability, average annual RR over the entire study period ( $0.63 \pm 0.026$ , 95% CI = 0.570–0.688,  $n = 9$  years) was within 3% of apparent annual survival. Similarly, CJS estimates of apparent survival of juvenile male ( $0.292 \pm 0.037$  SE) and female ( $0.284 \pm 0.039$  SE) kingbirds did not differ (Redmond and Murphy 2012), and average annual RR from 2002 to 2011 ( $0.226 \pm 0.015$ ,  $n = 9$  years) fell within the 95% confidence interval of apparent survival for both sexes (Redmond and Murphy 2012). We therefore used  $RR_A$  and  $RR_J$  in our analyses to approximate annual differences in adult and juvenile survival. Only one year was available to estimate  $RR_J$  for the 2010 cohort (2010–2011) and it was the lowest of all years (15.4%). All other cohorts had at least two years to estimate survival of juveniles, and of the eight cohorts with two or more years to sight returning juveniles, only 67.0% of the survivors were seen in the year following their fledging. A large proportion of survivors were thus not seen in the first year that they could have been resighted, but by the second year after hatch we detected 93% of the juveniles that were known to have survived. To correct for the underestimate of  $RR_J$  for the 2010 cohort, we therefore divided the observed return rate from 2010 to 2011 by the proportion of returnees seen in the first year after hatching in other cohorts ( $0.154/0.67 = 0.230$ ).

We tested for associations between annual variation in NS, FSSN,  $RR_A$ ,  $RR_J$  and  $\lambda$  in relation to year and weather variables using correlation analysis and linear regression. The analysis of  $\lambda$  also included annual estimates of NS, FSSN,  $RR_A$ ,  $RR_J$  and population size as possible sources of variation.

## Population simulations

To model population growth, and to investigate the relative contribution of reproductive success of initial and replacement nests and immigration to population dynamics, we used STELLA programming language (v. Stella 10.0.3; ISEE systems) to construct a population model that was equivalent to a two-stage, post-breeding census Leslie matrix. The model components included average seasonal fecundity (F) for pairs and  $S_A$  and  $S_J$  from Redmond and Murphy (2012) were used to compute an annual estimate of  $\lambda$  ( $\lambda = S_A + (S_J \times F/2)$ ). We used the CJS estimate of apparent annual survival instead of RR because, although very similar, CJS estimates of survival account for detectability and yield estimates of survival closer to true values. F was discounted by 50% to account for the 50: 50 sex ratio of kingbirds at fledging (Dolan et al. 2009). We simulated a 10-year period in which each annual estimate of  $\lambda$  was multiplied by current population size to generate a decade-long population trajectory. All simulations began with 60 pairs, a number just above the population at the study's start (below).

At the population level,  $F$  was the sum of average productivity from initial ( $F_{\text{initial}}$ ) and replacement ( $F_{\text{replacement}}$ ) nests. Preliminary simulations showed that incorporating a second re-nesting attempt following the failure of a first re-nesting attempt, at rates of nest success and re-nesting observed in our study, never added more than 3% to seasonal productivity and therefore we limited simulations to a single re-nesting attempt. The number of young to fledge from initial nesting attempts was the product of NS and FSSN. Number to fledge from the single replacement nesting attempt that was allowed was the product of the proportion of initial nests that failed ( $= 1 - \text{NS}$ ), the proportion of females to re-nest, NS of replacement nests, and FSSN of replacement nests. Proportion of females to re-nest was dependent on average nest failure date (below). Failure date in the simulation was the sum of the average annual first egg date and number of days to a nest failure. Values for both (and all remaining) variables were chosen from a uniform random distribution. Upper and lower bounds of first egg date and failure date were the earliest and latest mean annual first egg dates and shortest and longest mean annual days to failure observed between 2002 and 2011. Annual values of  $S_A$  and  $S_J$  in the model were selected randomly from between the lower and upper 95% CI of the CJS estimates of  $S_A$  and  $S_J$  reported in Redmond and Murphy (2012). Annual estimates of NS, calculated separately for initial and replacement nests, were also selected randomly from between the lower and upper 95% CI of mean annual estimates of nests success observed between 2002 and 2011. We found that FSSN of initial nests varied directly with NS (below) and therefore annual variation in NS predicted FSSN of initial nests. No such relationship existed for replacement nests and therefore annual FSSN of replacement nests was selected randomly from between the lower and upper 95% CI observed between 2002 and 2011.

Full stochastic models were run to estimate growth rate over a 10-year period to replicate our study duration. To reduce the potential for serial autocorrelation among randomly chosen variables we used every fifth of 500 simulations to calculate average population growth rate (i.e. slope of regression of  $\ln[\text{population size}]$  against year). To assess the contribution of vital rates to  $\lambda$ , and specifically to estimate the contribution of  $F_{\text{initial}}$  and  $F_{\text{replacement}}$ , we calculated correlation coefficients between  $\lambda$  and average vital rates for each of the 100 simulations. We also used the model to explore the extent to which population numbers depended on immigration by running identical stochastic simulations but now with low (1–2 individuals per year; 2–7%), medium (3–4 individuals per year; 5–13%) or high (5–6 immigrants per year; 8–20%) annual immigration rates over a 10-year period. For all immigration scenarios, the above percentages represent the number of immigrants relative to a population size of 60 and 30 pairs, respectively. We again selected every 5th of 500 simulations for all scenario to calculate an average growth rate (above). Model performance was assessed by comparing simulated growth rates to that observed, and by comparing simulated (predictor variable) and observed

(response variable) population sizes for the decade long simulation using linear regression. Perfect fit of the simulated to observed numbers would be indicated by an intercept and slope of 0.0 and 1.0, respectively.

All analyses were conducted with STATISTIX 9.0, and values are reported as mean  $\pm$  SE, and  $n$ . Results are reported as significant ( $p \leq 0.05$ ), marginally non-significant ( $0.10 \leq p < 0.05$ ) or non-significant ( $p > 0.10$ ).

## Results

### Annual variation in weather

Mean breeding season temperature varied considerably between 1973 and 2011 (Fig. 1A). Although generally within the range of other years, our study experienced both the lowest (2011) and highest (2006) mean temperature of the 39-year period, and breeding season temperature declined between 2002 and 2011 ( $r = -0.655$ ,  $p = 0.040$ ; Fig. 1A). Breeding season precipitation did not vary with year over either the long-term (Fig. 1B;  $r = 0.049$ ,  $p = 0.177$ ,  $n = 39$ ) or our 10-year study ( $r = 0.288$ ,  $p = 0.420$ ). Rainfall was especially variable over the years of our study, and the two highest rainfall years (2005 and 2009) produced early breeding season (May) floods. River flow also varied widely, but opposite of temperature, increased between 2002 and 2011 (Fig. 1C;  $r = 0.673$ ,  $p = 0.033$ ); the last two years of our study were the fifth and single highest river flows observed over the period for which weather records were available (Fig. 1C) and both produced additional floods. Bioyear precipitation varied widely, but did not vary predictably with time over our study ( $r = 0.384$ ,  $p = 0.273$ ), and was low to average compared to the long-term (Fig. 1D). High bioyear precipitation was associated with high river flows ( $r = 0.549$ ,  $p < 0.001$ ,  $n = 39$ ), and snowpack in April, a reflection of bioyear precipitation ( $r = 0.908$ ,  $p < 0.001$  for 2002–2011), was a strong predictor of river flow during our study ( $r = 0.807$ ,  $p = 0.005$ ).

### Population size

Population size varied between 50 and 56 pairs for the first three years, but by 2005 a decline began that resulted in an overall 8.6% annual drop in numbers between 2002 and 2011 (Fig. 2;  $\lambda = 0.914$ ). Population size fluctuated between 27 and 31 pairs from 2008 to 2011, roughly half the average of the first three years. Surveys from 2012 and 2015 showed the population's decline appeared to have halted, but without indication of recovery (Fig. 2).

### Annual variation in nest success and offspring production

Roughly one-third of nests fledged young (Mayfield nest success =  $0.320 \pm 0.033$ , range =  $0.203$ – $0.479$ ,  $n = 10$  years), and at a population level, 38% of nests were replaced ( $0.376 \pm 0.0343$ , range =  $0.214$ – $0.580$ ;  $n = 10$  years). In

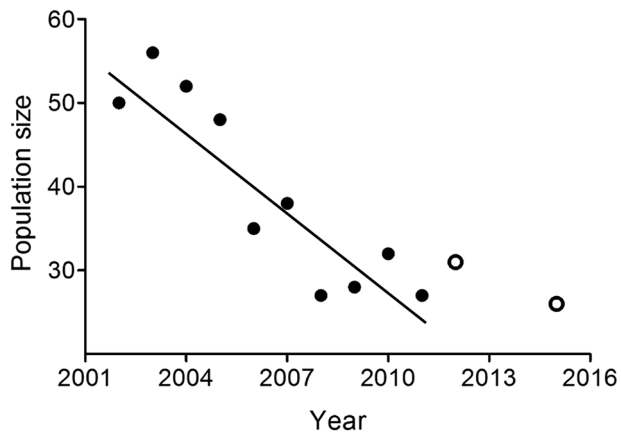


Figure 2. Annual variation in number of eastern kingbird pairs breeding at Malheur National Wildlife Refuge, Oregon, between 2002 and 2011 (solid points). Open circles, which are estimates of number of breeding pairs from surveys conducted in 2012 and 2015, were not included in the analysis of population growth.

comparisons among years, date of nest failure was a better predictor of proportion of nests to be replaced ( $r = -0.682$ ,  $p = 0.030$ ; proportion replaced =  $1.26 - 0.014$  [mean failure date]) than average annual first egg date ( $r = -0.558$ ,  $p = 0.094$ ). Nearly half ( $0.461 \pm 0.035$ ,  $n = 5$  years) of failed nests were replaced when the average date of nest failure was less than 4 July, but replacement dropped to under a third ( $0.290 \pm 0.022$ ,  $n = 5$  years) if average nest failure date was 4 July or later ( $t_8 = 4.15$ ,  $p = 0.003$ ). Nests were never replaced after a failure date of 12 July.

NS of initial ( $0.320 \pm 0.040$ , range = 0.144–0.610,  $n = 10$ ) and replacement nests ( $0.312 \pm 0.064$ ; range = 0.066–0.776,  $n = 10$ ) was nearly identical and, when combined, NS was lowest in the middle years of the study (polynomial regression,  $r^2 = 0.592$ ,  $p = 0.043$ ). Similar tendencies existed for initial ( $r^2 = 0.574$ ,  $p = 0.051$ ) and replacement nests ( $r^2 = 0.535$ ,  $p = 0.068$ ; Fig. 3A), but the low point of NS of initial and replacement nests occurred in the first and second halves of the study, respectively (Fig. 3A). Hence, NS of replacement nests was independent of NS of initial nests in the same year ( $r = -0.063$ ,  $n = 10$ ,  $p = 0.854$ ). NS of initial, replacement, and the combined sample of nests were unrelated to annual differences in breeding season temperature and precipitation, water year, snow pack and river flow with one exception. Success of initial nests tended to be higher when river flow was high (Table 1), but the relationship depended entirely on nest success in 2011 (without 2011,  $r = 0.269$ ,  $p = 0.523$ ). The positive association of NS of replacement nests with population size (Table 1) was a year effect; NS and population size were both high in the first three years of the study (Fig. 1, 3).

FSSN averaged 2.7 young ( $\pm 0.108$  young, range = 2.19–3.43), and did not differ between initial ( $2.8 \pm 0.140$  young, range = 2.15–3.43) and replacement nests ( $2.5 \pm 0.112$  young, range = 2.00–3.00;  $t_{18} = 1.33$ ,  $p = 0.201$ ). None of the measures of FSSN varied either linearly with year (highest

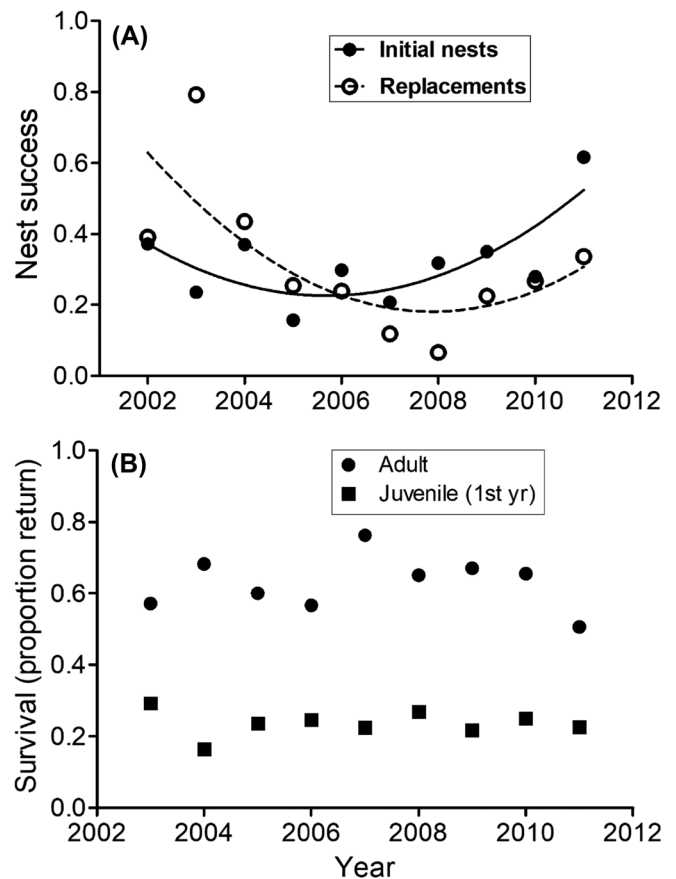


Figure 3. Annual variation in (A) Mayfield nest success for first nests of the season (Initial nests) and all subsequent nests that followed a nest failure (Replacements) and year, and (B) adult and first year (Juvenile) return rate (proportion of marked birds to return) and year for eastern kingbirds breeding at Malheur National Wildlife Refuge between 2002 and 2011. Second-order polynomial relationships between nest success and year was significant for initial nests ( $p = 0.051$ ) and marginally non-significant for replacements ( $p = 0.068$ ). Adult and juvenile return rates were independent of year.

$r^2 = 0.151$ ,  $p = 0.267$  for FSSN of all nests combined), or with the second-order polynomial of year (highest  $r^2 = 0.428$ ,  $p = 0.141$  for FSSN of all nests). Again, with one exception, FSSN was unrelated to breeding season temperature and all measures of water availability (Table 1). FSSN for all nests and initial nests tended to be lower in years when temperature during the breeding season was high, but this was due to the high productivity of 2011, the year of unusually low temperatures (Fig. 1A; without 2011,  $r^2 = 0.088$  and  $0.054$  for all nests and initial nests, respectively; lower  $p = 0.440$ ). By contrast, FSSN of all nests combined ( $r^2 = 0.578$ ,  $\beta = 2.48 \pm 0.750$ ,  $p = 0.011$ ), and likely that of initial nests ( $r^2 = 0.315$ ,  $\beta = 1.60 \pm 0.833$ ,  $p = 0.091$ ), was greater in years when NS was high. Hence, partial loss of eggs and/or nestlings tended to be more common in years of low NS. No relationship existed between FSSN and NS of replacement nests ( $r^2 = 0.000$ ,  $p = 0.986$ ).

Table 1. Pearson-product moment correlation (p in parentheses) between Mayfield nests success and fledging success of eastern kingbirds breeding at Malheur National Wildlife Refuge, Oregon, from 2002 through 2011, in relation to annual differences in breeding season (April through July) temperature and precipitation, bioyear precipitation (1 October to 30 April) over the preceding year, snow pack in the nearby Steen's Mountains (as of April), river flow of the Donner und Blitzen River (May through July) upon entry to the refuge, and number of breeding pairs of eastern kingbirds. Initial nests refer to first nests of the season while replacements are all nests that followed a prior failed nesting attempt. Sample size is 10 (years) for all analyses.

| Variable        | Mayfield nest success (proportion of nests to fledge) |                |                | Fledging success (young fledged/successful nest) |                |                |
|-----------------|---|----------------|----------------|--|----------------|----------------|
|                 | All nests   | Initial nests  | Replacements   | All nests  | Initial nests  | Replacements   |
| Temperature     | -0.445 (0.197)  | -0.494 (0.147) | 0.113 (0.757)  | -0.621 (0.055)                                   | -0.552 (0.098) | -0.541 (0.106) |
| Precipitation   | -0.029 (0.937)  | -0.064 (0.861) | 0.002 (0.997)  | 0.211 (0.559)                                    | 0.262 (0.465)  | -0.190 (0.598) |
| Bioyear         | 0.224 (0.533)   | 0.324 (0.362)  | -0.147 (0.685) | -0.063 (0.862)                                   | -0.158 (0.662) | 0.345 (0.329)  |
| Snow pack       | 0.278 (0.438)   | 0.429 (0.216)  | -0.287 (0.422) | 0.060 (0.870)                                    | -0.063 (0.863) | 0.243 (0.499)  |
| River flow      | 0.529 (0.116)   | 0.595 (0.070)  | -0.088 (0.808) | 0.476 (0.164)                                    | 0.377 (0.283)  | 0.513 (0.129)  |
| Population size | -0.130 (0.721)  | -0.411 (0.238) | 0.768 (0.010)  | -0.198 (0.583)                                   | -0.030 (0.934) | -0.061 (0.867) |

### Annual variation in adult and juvenile return rate

Neither  $RR_A$  nor  $RR_J$  varied with year (Fig. 3B), and RR of age classes were independent of one another ( $r = -0.347$ ,  $p = 0.360$ ). With one possible exception,  $RR_A$  and  $RR_J$  were independent of temperature and all measures of water availability (Table 2). The apparent higher  $RR_A$  following warm breeding seasons was driven by a single year;  $r = 0.439$ ,  $p = 0.276$  without 2006).  $RR_A$  and  $RR_J$  were also independent of population size in the year preceding (Table 2) and year of return (adults:  $r = 0.020$ ,  $p = 0.958$ ; juveniles:  $r = -0.044$ ,  $p = 0.902$ ). Finally,  $RR_A$  and  $RR_J$  were independent of all measures of NS and FSSN (Table 2).

### Population growth rate ( $\lambda$ )

There was no linear ( $r = 0.024$ ,  $p = 0.672$ ) or polynomial ( $r^2 = 0.252$ ,  $p = 0.363$ ) relationship between  $\lambda$  and year, or linear relationship between  $\lambda$  and mean breeding season temperature or measures of water availability in the previous year (Table 2). Similarly,  $\lambda$  was independent of both  $RR_A$  ( $r = 0.378$ ,  $p = 0.315$ ,  $n = 9$ ) and  $RR_J$  ( $r = -0.008$ ,  $p = 0.983$ ,  $n = 9$ ). By contrast,  $\lambda$  increased with NS in the previous year

for both initial nests (Fig. 4) and the combined sample of initial and replacement nests (Table 2), but not with either NS of replacement nests (Table 2) or the proportion of failed nests that were replaced ( $r = -0.191$ ,  $p = 0.597$ ). No relationship existed between  $\lambda$  and FSSN (Table 2).

### Population simulations

Simulating a closed population with stochastic variation in observed vital rates produced a  $\lambda$  (0.821) significantly below that observed (0.914). Without immigration, and at observed rates of annual nest replacement, replacement nests contributed just over 20% of total seasonal offspring production ( $F_{\text{initial}} = 0.97 \pm 0.009$  young/attempt;  $F_{\text{replacement}} = 0.28 \pm 0.003$  young/attempt;  $t_{198} = 73.14$ ,  $p < 0.001$ ). Examination of the strength of relationship between  $\lambda$  and  $S_A$ ,  $S_J$ ,  $F_{\text{initial}}$  and  $F_{\text{replacement}}$  showed that annual variation in  $\lambda$  was most strongly associated with variation in  $S_A$  and  $F_{\text{initial}}$ , followed distantly by  $S_J$  (Fig. 5).  $\lambda$  appeared to be unaffected by variation in  $F_{\text{replacement}}$  (Fig. 5), but after holding the effects of the other three vital rates constant, partial correlation ( $r_p$ ) of  $\lambda$  against  $F_{\text{replacement}}$  was significant ( $r_p = 0.414$ ,  $p < 0.01$ ).

Table 2. Pearson-product moment correlation (p in parentheses) between return rate of adult and 1st year birds, and population growth rate of eastern kingbirds breeding at Malheur National Wildlife Refuge, Oregon, from 2002 through 2011, in relation to annual differences in breeding season (April through July) temperature and precipitation, bioyear precipitation (1 October to 30 April) over the preceding year, snow pack in the nearby Steen's Mountains (as of April), and river flow of the Donner und Blitzen River (May through July) upon entry to the refuge. Return rates and population growth rates are also compared to number of breeding pairs, Mayfield nest success (NS) and fledging success of successful nests (FSSN) of eastern kingbirds in the preceding year. Initial nests refer to first nests of the season while replacements are all nests that followed a prior failed nesting attempt. Sample size is 9 (years) for survival and 10 (years) for growth rate.

| Variable           | Adult return rate | 1st year return rate | Growth rate ( $\lambda$ ) |
|--------------------|-------------------|----------------------|---------------------------|
| Temperature        | 0.670 (0.048)     | 0.142 (0.715)        | -0.155 (0.670)            |
| Precipitation      | 0.123 (0.752)     | -0.080 (0.839)       | 0.038 (0.916)             |
| Water year         | 0.404 (0.280)     | -0.219 (0.571)       | 0.200 (0.580)             |
| Snow pack          | 0.435 (0.242)     | -0.282 (0.463)       | 0.359 (0.309)             |
| River flow         | -0.220 (0.568)    | -0.232 (0.549)       | 0.298 (0.404)             |
| Population size    | -0.172 (0.658)    | -0.113 (0.773)       | -0.350 (0.322)            |
| NS all nests       | -0.026 (0.947)    | -0.040 (0.919)       | 0.755 (0.012)             |
| NS initial nests   | 0.040 (0.918)     | 0.241 (0.533)        | 0.775 (0.008)             |
| NS replacements    | -0.045 (0.909)    | -0.504 (0.166)       | 0.019 (0.959)             |
| FSSN all nests     | -0.285 (0.457)    | -0.009 (0.982)       | 0.380 (0.279)             |
| FSSN initial nests | -0.218 (0.572)    | -0.094 (0.809)       | 0.320 (0.368)             |
| FSSN replacements  | -0.514 (0.157)    | -0.176 (0.651)       | -0.240 (0.504)            |



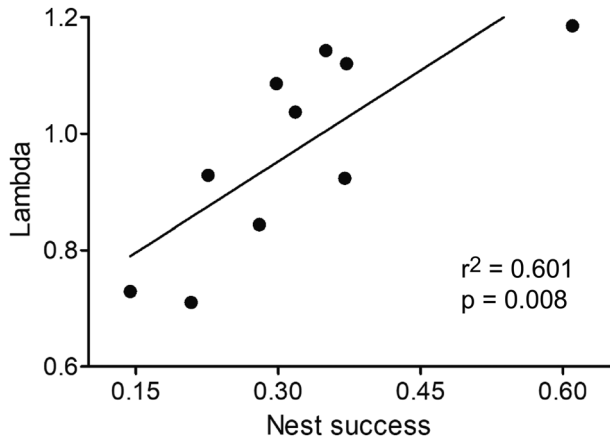


Figure 4. Variation in annual growth rate ( $\lambda = N_{t+1}/N_t$ ) in relation to probability of success of initial nests of the season in year  $t$  for eastern kingbirds breeding at Malheur National Wildlife Refuge, Oregon USA, between 2002 and 2011.

Partial correlation analyses likewise increased the strength of relationship between  $\lambda$  and the other three vital rates ( $r_p$  of  $S_A = 0.846$ ,  $r_p$  of  $F_{\text{initial}} = 0.790$ ,  $r_p$  of  $S_J = 0.525$ ,  $p < 0.001$  for all).

Allowing immigration predictably raised  $\lambda$  at all levels of immigration (Fig. 6), but only when 3–4 individuals entered the population annually (i.e. 5–13% of population

size) did the simulated and observed  $\lambda$  not differ (Fig. 6). Medium levels of immigration likewise produced the closest correspondence between observed and simulated numbers as only this level of immigration produced a slope and intercept from the regression of observed population size against the simulated numbers that did not differ from one and zero, respectively (Fig. 6).

## Discussion

The MNWR population of kingbirds declined precipitously over our 10-year study, and granting that population size may have been slightly underestimated in 2002 due to it being our first year, the decline may have been even steeper than recorded. Although much weaker, Murphy (2001) also recorded a population decline of kingbirds over a 10-year period in New York. The New York population also responded negatively to years of low nest productivity, but Murphy (2001) ascribed the decline mainly to a drop in apparent adult survival that likely reflected undetected long-distance dispersal related to a decline in habitat quality. Unlike New York, our Oregon site is situated near the periphery of the kingbird's range where physical (i.e. abiotic) forces are generally expected to have greater influences on vital rates

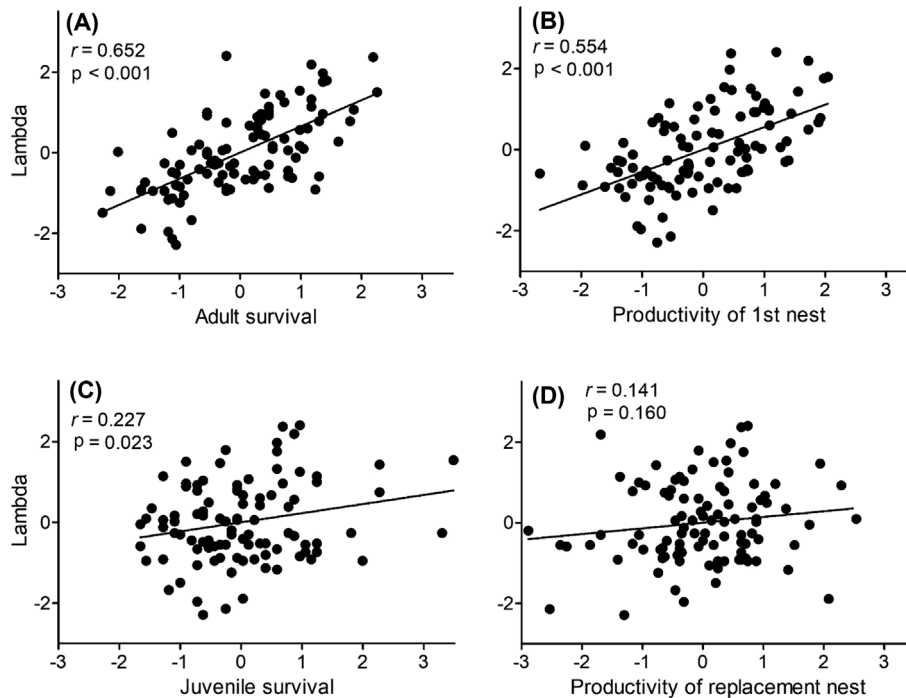


Figure 5. Relationship between population growth rate (lambda), where  $\lambda = S_A + S_J \times F/2$  and (A) adult survival ( $S_A$ ), (B) productivity of initial nests of the season ( $F_{\text{initial}}$  = number of young/nesting attempt), (C) juvenile survival ( $S_J$ ) and (D) productivity of replacement nests ( $F_{\text{replacement}}$ ) that followed the failure of initial nests.  $F$  in the above equation equals  $F_{\text{initial}} + F_{\text{replacement}}$ , and is reduced by 50% to include only female young. Data are from the simulated population growth of eastern kingbirds at Malheur Wildlife Refuge in Oregon that used stochastic variation in the observed vital rates for all variables and in which no immigration was assumed to occur. All variables are represented as Z-scores (i.e. mean of 0.0 and standard deviation of 1.0) to permit direct comparisons of effects.  $r$  in all figures is the Pearson-product moment correlation coefficient between lambda and each vital rate.

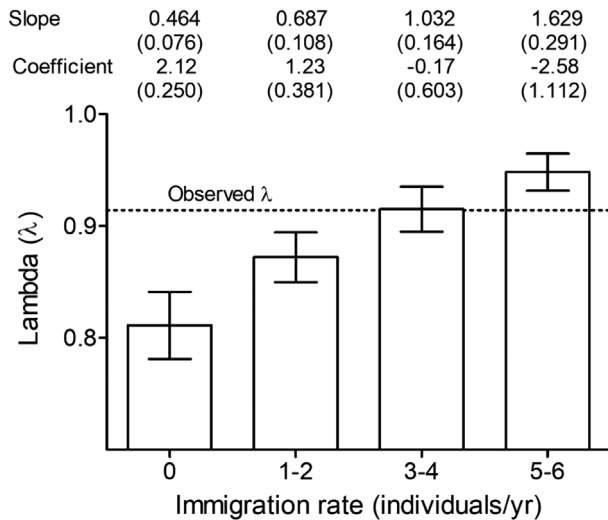


Figure 6. Simulated population growth rate (lambda;  $\lambda$ ) over a 10-year period for eastern kingbirds breeding at Malheur National Wildlife Refuge, Oregon, USA, based on stochastic variation in apparent survival of adults and juveniles and stochastic variation in productivity of initial and replacement nests. Immigration rate was allowed to vary between none (i.e. closed population) to either 1–2 (low immigration), 3–4 (medium immigration) or 5–6 (high immigration) individuals per year. The average ( $\pm$  SD) of 100 iterations is reported and compared to the observed lambda (dashed line). In addition, the slope and coefficient (SE in parentheses) of the regression equation describing the relationship between observed population size (ordinate) and average simulated population size (abscissa) over the 10-year period is reported above the figure. A perfect fit between observed and simulated population size is indicated by a slope = 1.0 and intercept = 0.0, as is shown by the medium immigration rate scenario.

and  $\lambda$  (Sexton et al. 2009). However, this did not appear to be the case. Weather and water availability over our study varied greatly compared to previous decades, but we found no relationship between any physical environmental factors and any measure of reproductive success, return rate or  $\lambda$ . Population decline was linked to low NS, and the latter appears to have been driven almost entirely by heavy nest predation. Below, we further discuss the relative importance of resources and nest predators, assess the value of nest replacement, and highlight the important contribution of immigration to kingbird population dynamics at MNWR.

### Limiting factors

Frequent loss of nests to predators appears to be responsible for the decline of the kingbird population, a conclusion consistent with the dominant role of nest predation for nest failure of birds (Ricklefs 1969, Martin 1993), and the importance of fecundity for population growth of shorter-lived bird species (Sæther and Bakke 2000, Clark and Martin 2007). The absence of any relationship between annual variation in growth rate and FSSN, but strong association between growth rate and NS (Table 2), demonstrates that the success

or failure of entire nests was the driver of seasonal productivity. However, the positive association between FSSN and NS across years also showed that successful nests fledged fewer young when the probability of nest success was low, implicating partial nest loss as a probable contributor to overall low productivity in years of high nest loss.

Many species depredate bird nests, but a meta-analysis indicates that birds and/or mammals are the main predators at higher latitudes (Degregorio et al. 2016). Luginbuhl et al. (2001) also showed, elsewhere in the Pacific Northwest of North America, that corvid abundance was the best predictor of depredation of artificial bird nests. Both are consistent with film evidence from our site from the Pacific Northwest that nearly all nest predation was by corvids (M. T. Murphy unpubl.), principally black-billed magpies *Pica hudsonia*. While black-billed magpies and common ravens *Corvus corax* have been historically common at MNWR, American crows *Corvus brachyrhynchos* have not (Littlefield 1990). Indeed, we did not observe any crows in 2002, but recorded a single crow in 2003 and observed flocks of 30–50 crows in 2004. By 2005 and onward they bred successfully on the main study, and the decline in kingbird numbers began at that point (Fig. 2). The absence of variation in  $RR_A$  or  $RR_J$  (Fig. 3B), a finding consistent with our earlier report of an absence of annual variation in  $S_A$  and  $S_J$  (year treated as a categorical predictor; Redmond and Murphy 2012), suggests strongly that nonbreeding events had no impact on  $\lambda$ . Hence, additive losses to magpies and crows seem the most parsimonious explanation for the population's decline (see Roos and Pärt 2004 for a similar European example).

By contrast, neither weather nor resources appeared to limit the MNWR kingbird population. The high elevation desert of MNWR is an extreme environment at the far western edge of the kingbird's breeding range. In some species, physical challenges at range edges limit demographic processes (Mehlman 1997, Garcia and Arroyo 2001), and ultimately,  $\lambda$  (reviewed by Sexton et al. 2009). Furthermore, abundant water in arid to semi-arid environments is strongly associated with high above ground net primary productivity (Introduction) such that arthropod diversity and/or abundance typically increase with rainfall and/or above ground net primary productivity (Whitford and Creusere 1977, Tanaka and Tanaka 1982, Polis et al. 1997, Wenninger and Inouye 2008, Studds and Marra 2011, Borer et al. 2012). Populations of birds and other vertebrates respond positively to rain and plant productivity in arid environments (Whitford and Creusere 1977, Blancher and Robertson 1987, Grant et al. 2000, Morgan Ernest et al. 2000, Bolger et al. 2005, Schuett et al. 2011). However, despite wide annual variation in every weather variable, that in some cases exceeded patterns seen in decades just prior to our study (Fig. 1; including four flooding events by the Donner und Blitzen River), population size, reproductive success and RR varied independently of weather and water availability. Thus, although we cannot completely eliminate the possibility that weather and/or resources may have been limiting in some years (but masked by high rates of nest

predation), it seems that neither extreme physical conditions nor food limitation can account for the population decline.

### Nest replacement and immigration

In avian populations with high nest failure rates, replacement broods can make important contributions to population productivity (Grzybowksi and Pease 1995, Jones et al. 2005, Murray and Nolan 2007). However, several lines of evidence suggest that young from replacement broods had little influence on kingbird population dynamics. First, annual variation in  $\lambda$  was unrelated to both the rate of re-nesting, and the success of replacement nests. Secondly, our simulations indicated that success of replacement nests was the only vital rate that did not contribute significantly to annual variation in  $\lambda$  (unless other effects were controlled statistically). Moreover, while the simulations assumed equal probability of recruitment of young fledged at any time of the breeding season, abundant evidence (Tarof et al. 2011, Öberg et al. 2014), including kingbirds (Dolan et al. 2009), suggests that young fledged later in the season are less likely to recruit. Hence, the contribution of young from replacement broods to population dynamics was likely overestimated in our simulations. In single-brooded species with restricted breeding seasons (Antzcak et al. 2009, Becker and Zhang 2011), such as kingbirds (Cooper et al. 2011), fitness benefits from replacement broods likely accrue for replacement nesters, but the population-level impact appears limited in the MNWR kingbird population and other single-brooded species with limited breeding seasons (Becker and Zhang 2011).

On the other hand, immigration appeared to play a critical role in explaining annual variation in kingbird population size. Despite the fact that MNWR is an ecological island where recruitment of locally fledged young is unusually high for a migratory passerine (~30% [Redmond and Murphy 2012]; compare to Weatherhead and Forbes' 1994 estimate of 4–5%), self-recruitment (Runge et al. 2006) through local vital rates could not account for observed population dynamics. Only with an assumed immigration rate of at least 5–13% of annual population size did simulated populations mirror local population dynamics. The role of immigration for understanding local population dynamics of birds has become apparent in recent years regardless of whether populations are distributed continuously across landscapes (Schaub et al. 2012, 2013, Rushing et al. 2017) or in isolated units (Ward 2005, Schaub et al. 2012, Hemerik et al. 2015, Taylor et al. 2018), and kingbirds are an example of the latter.

### Viability of kingbird populations in the high desert

Whether kingbirds can persist in the face of such severe nest depredation and low growth rate is unclear, and likely hinges on the role of immigration in population dynamics. Population processes of kingbirds, and possibly other Nearctic–Neotropical migrants of the Great Basin Desert that nest obligately in isolated wetlands (Csuti et al. 2001), can probably only be understood from a broader landscape

perspective. Movement among suitable breeding sites may be far more extensive than could be documented from our relatively limited sample area (Paxton et al. 2007) and, conceivably, permanent emigration arising from long distance dispersal may have led to underestimates of true survival, especially for juveniles returning to breed for the first time. If isolated kingbird populations of the Great Basin Desert (Csuti et al. 2001) function as a source–sink system (Tittler et al. 2006) or as a metapopulation (Runge et al. 2006) in which different local populations rise and fall with asynchronous declines and increases of local nest predator populations, sites and/or years of especially high productivity, followed by dispersal, may be key for maintaining kingbirds and other species in the desert landscape of eastern Oregon. Further work is thus needed to document the potential importance of long-distance dispersal movements. Despite recent miniaturization of wildlife tracking technology, such devices may not be useful in the study of songbird dispersal until the weight and cost of non-archival tags is substantially reduced. In the meantime, the use of stable isotopes (Studds et al. 2012, Rushing et al. 2015) and spatially correlated and demographically linked populations (Tittler et al. 2006, 2009) holds more promise in advancing our knowledge of the role of dispersal in the population dynamics of birds of the Great Basin Desert and other naturally highly fragmented habitats.

### Data availability statement

Data available from the Dryad Digital Repository: <<http://doi.org/10.5061/dryad.sqv9s4n1d>> (Murphy et al. 2020).

*Acknowledgements* – We would like to thank Cal and Alice Elshoff for allowing us to intrude on their lives each summer and to the staff of Malheur National Wildlife Refuge and the Malheur Field Station for their support. Helpful comments on an earlier version were provided by Samantha Gillette.

*Funding* – Our research was supported by a grant from the U.S. National Science Foundation, an NSERC grant from the Canadian Government, and additional student grants provided by the Forbes-Lea Fund of Portland State University, the Frank M. Chapman Fund from the American Museum of Natural History, the American Ornithologists' Union and the Association for the Study of Animal Behaviour.

*Conflict of interest* – There are no conflicts of interests.

*Author contributions* – Sequence of authors, except for MTM, listed by number of years contributed to field work and chronology of start on the project. All authors contributed to field work and writing, while idea for the project and data analysis conducted by MTM.

*Permits* – All capture, handling and banding of birds was conducted under USGS permit number 22230 of MTM, while permission to conduct research at Malheur National Wildlife Refuge were through permits 13570-030117, 13570-060205, and 13570-060008.

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