Impacts of increasing isolation and environmental variation on Florida Scrub-Jay demography

Jeremy Summers[1*], Elissa J. Cosgrove[2], Reed Bowman[3], John W. Fitzpatrick[4,5], Nancy Chen[1]

[1]Department of Biology, University of Rochester, Rochester, NY
[2]Department of Molecular Biology & Genetics, Cornell University, Ithaca, NY
[3]Avian Ecology Program, Archbold Biological Station, Venus, FL
[4]Cornell Lab of Ornithology, Cornell University, Ithaca, NY
[5]Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY
[*]Correspondence: jsummer7@ur.rochester.edu

Abstract

Isolation caused by anthropogenic habitat fragmentation and degradation can destabilize populations. Population demography is shaped by complex interactions among local vital rates, environmental fluctuations, and changing immigration rates. Empirical studies of these interactions are critical for testing theoretical expectations of how populations respond to isolation. We used a 34-year demographic and environmental dataset from a population of Florida Scrub-Jays (*Aphelocoma coerulescens*) that has experienced declining immigration to create mechanistic models linking environmental factors and variation in vital rates to population growth rates over time. We found that the population has remained stable despite declining immigration and increasing inbreeding, owing to a coinciding increase in breeder survival. We find evidence of density-dependent responses of immigration, breeder survival, and fecundity, indicating that interactions between vital rates and local density likely play a role in buffering the population against change. Our study elucidates the interactions between environment and demography that underlie population stability.

Introduction

How populations can remain stable over time despite variable environments is a foundational question in ecology (Cappuccino & Price 1995). Population growth rates are influenced by density-dependent (*i.e.*, resource competition) and independent (*i.e.*, climate) factors that interact in ways that remain poorly understood, resulting in long-term population stability despite short-term variability in population growth (Goswami *et al.* 2011; Oro 2013). One factor of particular interest is immigration, owing to its potential to buffer populations across temporal and spatial heterogeneity (Gurney & Nisbet 1975; Holt & McPeek 1996; Lemel *et al.* 1997; Millon *et al.* 2019; Schaub & Ullrich 2020; Tenan *et al.* 2023; Weegman *et al.* 2016) and even to maintain otherwise declining populations (Pulliam 1988; Schaub & Ullrich 2020). Furthermore, gene flow into populations via immigration may counter the negative demographic effects of inbreeding depression (Hedrick & Garcia-Dorado 2016; Niskanen *et al.* 2020; Whitlock *et al.* 2000), *i.e.*, decreased fitness of inbred individuals (Brown & Kodric-brown 1977; Charlesworth & Charlesworth 1987). Within ecological timescales, the demographic impact of immigration has been shown to vary depending on recent changes in metapopulation structure

(Reichert *et al.* 2021), resource availability (Horswill *et al.* 2022), temporal variation in the environment (Millon *et al.* 2019), and population density (Harman et al. 2020). Empirical studies that integrate the environmental and demographic contexts of immigration are needed to clarify the role of immigration in demographic resilience, *i.e.*, population's capacity to resist and rebound from disturbances (Holling 1973), especially in the face of rapid climate and landscape changes causing declines in global biodiversity (Jaureguiberry *et al.* 2022; Simberloff 1999).

Population dynamic theory predicts that the vital rates with the greatest impact on population growth will be under selection not to vary across environmental conditions (Lewontin & Cohen 1969), yet this pattern is rarely observed empirically when studying survival and reproduction in the wild (Jäkäläniemi *et al.* 2013; Koons *et al.* 2009; Stien *et al.* 2015). Within the context of density-dependent immigration, we would expect a population to remain robust through responses in vital rates with reduced impacts on population growth. In particular, vital rates of non-breeding individuals, when they are present, are expected to buffer a population (Porter & Coulson 1987; Ridley *et al.* 2003). Testing these expectations is difficult because of the need to track all new individuals in a population (Greenwood & Harvey 1982; Hixon *et al.* 2002; Millon *et al.* 2019). While recent advances in population modeling have allowed for the inference of immigration rates in situations where data are limited (Abadi *et al.* 2010), these inferences may overestimate the impact of immigration by failing to account for temporal variation in immigration rates (Paquet *et al.* 2019). Long-term, detailed population and ecological data obviate the need to infer immigration rates, and, while rare, provide the best method to empirically test expectations of the consequences of changing immigration rates.

Long-term studies also permit fitting demographic models trained on females and males. Female-based models are typical owing to the assumption that modeling a single sex is sufficient for describing population-wide dynamics (Caswell 2001), as well as the difficulty inherent in collecting data on both males and females. Yet, sex-specific dispersal rates are common (Greenwood & Harvey 1982; Williams & Rabenold 2005), and individuals of different sexes may compete for different resources, potentially impacting density-dependent vital rates (Matthysen 2012; Millsap *et al.* 2023). Investigating the consequences of immigration change using both female and male models will help evaluate the importance of two-sex models in describing population dynamics.

Large amounts of data available through long-term ecological studies can be analyzed with recently developed transient life table response experiments (hereafter tLTRE) to retrospectively investigate how population trends contribute to observed variation in population growth rate while accounting for variation in vital rates and demographic structure among years (Koons *et al.* 2016, 2017). These methods can be built upon to link environmental factors to vital rates, ultimately linking variation in the environment to variation in population growth rate (Coulson *et al.* 2005, 2008; Dahlgren & Ehrlén 2009; Knape *et al.* 2023; Nater *et al.* 2021). With sufficiently detailed demographic and environmental data, we can now characterize the relative impacts of vital rates, including immigration, on realized trends of population growth, decline, or stability.

Here we empirically test how a natural population of Federally Threatened Florida Scrub-Jays (*Aphelocoma coerulescens*) responds to increasing isolation. Florida Scrub-Jays are facultative cooperative breeders, as most individuals delay dispersal and assist with rearing young on their natal territories (Woolfenden & Fitzpatrick 1984). Females are more likely to

disperse earlier and farther than males, but few other vital rates differ between sexes (Aguillon *et al.* 2017; Suh *et al.* 2020; Woolfenden & Fitzpatrick 1984). Florida Scrub-Jays occupy territories year-round and are restricted to fire-mediated xeric oak scrub habitat (Fitzpatrick & Bowman 2016). Habitat loss and degradation has led to declines across their range (Boughton & Bowman 2011; Coulon *et al.* 2008). One color-banded population of Florida Scrub-Jays at Archbold Biological Station has been monitored for >50 years, providing optimal conditions to elucidate the impact of variation in immigration on population dynamics. This long-term study has accumulated complete life histories for thousands of individuals, territory and burn area maps, climate and acorn abundance data, and a 14-generation population pedigree (Chen *et al.* 2019; Fitzpatrick and Bowman 2016). The focal population has experienced a significant decline in immigration over the past 30 years, which has contributed to increased inbreeding and inbreeding depression (Chen *et al.* 2016). Despite inbreeding and a large expected genetic contribution of immigrants (Chen *et al.* 2019), the population has remained demographically stable over time.

We used both female-specific and male-specific stage-structured matrix population models to investigate the consequences of declining, sex-biased dispersal over a period of 34 years (1989-2021). We performed tLTREs to quantify the impact of variation in vital rates and environmental factors including population density, food availability, and population-wide inbreeding coefficients on population stability. We predicted that density-dependent responses in the vital rates of non-breeders would compensate for declining immigration, given the abundance of resident non-breeders available to fill breeding vacancies (Woolfenden & Fitzpatrick 1984). This study uses a unique combination of long-term ecological data and recent population dynamic modeling approaches designed to test population dynamic theory. We consider this approach to be crucial for understanding how to preserve threatened populations.

Methods

1. Data Collection

1.1 Study Population

We used data from a long-term study of Florida Scrub-Jays at Archbold Biological Station (Woolfenden & Fitzpatrick 1984). The population is censused monthly, and all nests are tracked during the breeding season (March-June), creating continuous location, survival, and detailed breeding records for all individuals within the study area. We limited our study area to 14.8 km^2 of land that has been consistently monitored between 1988-2021. Our dataset includes 4,627 individuals (1,880 female, 1,733 male, and 658 unsexed) from 1,894 territory-years. Please see Supplementary Methods for details on demographic data collection.

1.2 Environmental Data

We considered several covariates that likely impact Florida Scrub-Jay demography: population density, annual acorn abundance, burned area, the equatorial southern oscillation index during the dry (breeding) season (EQSOI), and pedigree-based inbreeding and relatedness coefficients (Supplementary Methods). We calculated population density as the total number of adults per hectare, which is representative of the number of individuals competing for breeding opportunities within the area without conflating our density metric with

fecundity or breeder survival. As a proxy for habitat quality, we calculated the area burned within the past 2-9 years. This burn frequency generates optimal Florida Scrub-Jay habitat (Fitzpatrick & Bowman 2016). We used acorn abundance as a metric of resource availability, as acorns are the most important over-winter food source for the Florida Scrub-Jay and vary greatly in abundance over time (DeGange *et al.* 1989, Pesendorfer et al. 2021). EQSOI is a commonly used climate index that captures atmospheric conditions that influence El Niño events (Shi & Su 2020), which heavily impact precipitation and temperature in Florida. Inbreeding coefficients capture the effect of known inbreeding depression on fecundity and survival in our study population (Chen *et al.* 2016).

2. Impact of Environment on Vital Rates

To determine how environmental variation influences population growth rate, we modeled the underlying vital rates in terms of the environmental factors described above. We also included year as a fixed effect to capture the impact of temporal trends that do not correlate with the other environmental factors. We used generalized linear mixed models (GLMMs) with a binomial distribution to model survival for each social class (juveniles, helpers, and breeders) and transition rates from non-breeding to breeding status. We added sex as a fixed effect in the helper and breeder models but not in the juvenile survival model due to the large number of unsexed juveniles (631). Note that because Florida Scrub-Jays typically disperse as helpers (Suh *et al.* 2022; Woolfenden & Fitzpatrick 1984), helper mortality may be inflated by emigration, but emigration rates from our study population are low. We created one transition rate model for both helpers and juveniles that only included individuals who survived to the next year and added sex and social class (juvenile or helper) as fixed effects. We used a zero-inflated Conway-Maxwell Poisson distribution (Sellers *et al.* 2012) to model fecundity. Random effects for all GLMMs included year and territory identity, as well as individual identity to deal with repeated observations. We modeled immigration as the total number of individuals that arrived in the study tract between breeding seasons using generalized linear models (GLMs) with a Poisson distribution. We modeled immigration separately for males and females to capture the impact of female-biased dispersal (Woolfenden & Fitzpatrick 1984). Please see Supplementary Methods for full details.

3. Contribution of Variation in Vital Rates to Population Growth

3.1 Stage-Structured Matrix Population Model

We constructed matrix population models with four stages (juveniles, helpers, new pairs, and established pairs; Figure 1) and a post-breeding census (Supplementary Methods). We defined juveniles as any individuals between 11 days and 1 year of age, which includes all sexually immature individuals. Helpers are individuals of 1 year of age or older who are not established as a socially dominant breeder. Previous work showed that experienced pairs have higher fecundity compared to newly-formed pairs (Woolfenden & Fitzpatrick 1984); therefore we divided breeding pairs into new and established pairs based on whether the two individuals had previously paired during a breeding season. Extensive population monitoring allowed us to fit both female-only and male-only models. To account for uncertainty caused by unsexed individuals, we randomly assigned these individuals a sex based on a 1:1 sex ratio (Woolfenden

& Fitzpatrick 1984) 100 times for each model and calculated annual vital rates for each iteration to parameterize annual projection matrices (Supplementary Methods).

3.2 Transient Life Table Response Experiment

To quantify how vital rates result in observed variation in population growth rates over time, we performed a tLTRE (Koons *et al.* 2016). We calculated the realized growth rate as the product of the projection matrix (*A(t)*) that is parameterized with the observed vital rates (θ_i, for all vital rates *i*) and the stage distribution vector for each year (*n*). This method does not assume that the population is near its stable stage distribution and allows variation in stage structure to contribute to variation in population growth rate (Koons *et al.* 2016). We calculated the sensitivities of the realized growth rate to the vital rates using the *Deriv* package (Clausen *et al.* 2021). To include time-lagged effects, we considered the contribution of variation in vital rates from the same year (*t*) and from the previous year (*t* - 1) to variation in the growth rate. Please see Supplementary Methods for details.

4. Contribution of Environmental Variation to Population Growth

To quantify the contributions of environmental factors to variation in the population growth rate, we performed a path analysis (Van Tienderen 2000) as an extension of our tLTRE (Knape *et al.* 2023). We decomposed variation in growth caused by each vital rate (quantified in our tLTRE) by the environmental factors associated with these rates. We analytically solved for the sensitivities of the vital rates to each environmental factor using the link functions and estimated β values from our GLMMs. We then used these sensitivities along with the chain rule to convert the sensitivities of the population growth rate to the observed vital rates into the sensitivities of the population growth rate to each environmental factor. We then performed another tLTRE using the environmental factors in place of the vital rates. We summed the contributions to variation in the population growth rate based on both the environmental factors themselves and the vital rates through which the environmental factors impact population growth. Please see Supplementary Methods for details.

Results

1. Demographic and Environmental Trends

We measured temporal trends and correlations across the population growth rate, vital rates, and environmental factors used in our models. The geometric mean of the population growth rate is 0.998 (Table S1, Figure S1), indicating remarkable stability. Year to year growth rates rapidly fluctuated between growth ($\lambda > 1$) and decline ($\lambda < 1$) (Figure S1), and we found no significant temporal trend in the annual growth rate (Mann Kendall tau = -0.024, $p = 0.858$). We did find significant temporal trends in several vital rates: immigration and the proportion of the population in new pairs decreased and the proportion of the population in established pairs increased (Table S2, Figure S2), together leading to a decrease in new breeders over time. The only significant correlations across vital rates were between the same rates across life stages, between breeder survival and fecundity of all pairs (new pair: Spearman's rho = 0.48, established pair: Spearman's rho = 0.36), and the probability of helpers to form new pairs and the fecundity of established pairs (Spearman's rho = 0.50, Figure S3). All vital rates correlated

between our female-only and male-only models except helper survival and the probability of breeders to form new pairs (Figure S4). Female immigration correlated with male breeder survival (Spearman's rho = 0.37) and both male juveniles' (Spearman's rho = 0.47) and male breeders' probability to form new pairs (Spearman's rho = 0.47), with no such correlations between male immigration and other female vital rates. The probability of male helpers to form new pairs correlated with fecundity of new (Spearman's rho = 0.49) and established pairs (Spearman's rho = 0.56, Figure S4). Acorn abundance significantly decreased over time and all inbreeding metrics increased (Table S3, Figure S5), consistent with previous work (Chen *et al.* 2016; Pesendorfer *et al.* 2021). No other significant correlations existed between environmental factors beyond correlations across inbreeding metrics (Figure S6).

2. Impact of Environment on Vital Rates

Greater acorn abundance was associated with increased juvenile (β = 0.276, p = 0.009) and breeder survival (β = 0.166, p = 0.003, Figure 2, Table S3). Greater population density was negatively associated with breeder survival (β = -0.130, p = 0.008, Table S3), female immigration (β = -0.165, p = 0.01, Table S4), and fecundity (conditional: β = -0.036, p = 0.043; zero-inflated: β = 0.382, p < 0.001, Table S5). Increased relatedness between breeders in a pair was associated with decreased fecundity for the conditional portion of our model (β = -0.052, p = 0.017) but not the zero-inflated portion (β = -0.147, p = 0.094), except as an interaction term with pair status (β = 0.413, p < 0.0017), indicating that nest failure was more common for established pairs that were more related than for new pairs (Table S5). We found that time was positively associated with breeder survival (β = 0.184, p < 0.001, Table S3) and negatively associated with both female (β = -0.194, p -0.005) and male immigration (β = -0.400, p < 0.001, Table S4). EQSOI was only associated with greater breeder survival (β = 0.097, p = 0.034, Table S3). We found no significant associations between burned area and any vital rates, or between any of our environmental factors and probability of transitioning to breeder status (Table S6).

3. Contribution of Variation in Vital Rates to Population Growth

We decomposed variation in population growth rate by variation within and covariation across vital rates. Results for our female-only and male-only models were similar, thus we are reporting the results for the female-only model except when noted. When combined, variation in fecundity accounted for most of the variation in population growth rate (49.5%), followed by variation in survival (35.1%, Figure 3). Of these vital rates, established pair fecundity (14.4%) and breeder survival (11.0%) made the largest individual contributions (Figure S7). Immigration accounted for 12.4% of variation in population growth rate in the female-only model and -1.3% in the male-only model due to covariation between immigration and both survival and fecundity (Figure 3). Contributions of each individual vital rate and covariation between vital rates can be found in Figure S7.

4. Contribution of Environmental Variation to Population Growth

4.1 Contribution of environmental factors to variation in growth

We summed the contribution of each environmental factor through their impact on vital rates, including covariation between environmental factors. Variation in population density

contributed the most to variation in population growth rate (13.5%), followed by variation in acorn abundance (7.1%), EQSOI (0.6%), and average relatedness of breeding pairs (0.2%, Figure 4). Temporal trends (variation in time) contributed negatively to variation in population growth (-0.1%) owing to covariation between time and acorn abundance, which represented a decline in acorn abundance over time (Table S2, Figure S5). Variation in burned area did not contribute at all (Figure 4).

4.2 Contribution of environmental factors through vital rates

We performed a path analysis to elucidate how environmental impacts on vital rates contribute to variation in the population growth rate. Variation in population density impacts population growth rate via fecundity (6.5%), survival (3.9%), and, in the female-only model, immigration (female-only: 3.1%, male-only: 0%, Figure 5). In contrast, acorn abundance primarily affects survival (7.1%), with a small negative covariation between acorn abundance and time (-0.2%). Temporal trends contributed negatively to the variation in population growth rate despite the positive contribution of its individual association with survival (2.1%) and immigration (1.9%). These contributions were counteracted by covariation between breeder survival and immigration (-2.7%) and the negative covariation between time and acorn abundance (-1.2%). Variation in EQSOI and inbreeding acted through survival and fecundity, respectively. We found no impact of variation in burned area on population growth rate.

Discussion

We investigated how long-term population stability is maintained in a wild population despite increasing isolation by analyzing interactions among local demography, immigration, and environmental fluctuations. The remarkable stability of our Florida Scrub-Jay population results from a combination of density dependence in female immigration and a coinciding increase in breeder survival. This result contradicts our initial expectation that flexibility in the demography of non-breeders would buffer the population at saturation during changing conditions (Porter & Coulson 1987). The importance of sex-specific density dependence in immigration strongly suggests that demographic models should investigate both female and male vital rates to represent populations accurately (Millsap *et al.* 2023). Finally, evidence of inbreeding depression in fecundity did not contribute importantly to variation in population growth rate, indicating that the increase in relatedness among breeders has not reached a magnitude sufficient to impact population dynamics.

Our results demonstrate the power of long-term ecological studies to provide highly detailed insight into the regulation of populations during changing conditions. Our evidence of density dependent immigration supports the “equal balance” hypothesis (Doncaster *et al.* 1997), whereby context-dependent dispersal tends to equalize emigration and immigration between populations relative to their carrying capacities. In contrast to source-sink dynamics (Pulliam 1988), here smaller, peripheral populations continue to contribute to large, stable populations, but dispersal rates fluctuate in response to environmental change. Metapopulations that meet equal balance expectations are more likely to remain stable through fluctuating dispersal regimes and environmental change (Holt & McPeek 1996; Lemel *et al.* 1997; McPeek & Holt

1992) relative to source-sink populations. Consequently, our focal population may continue to be robust to increasing isolation, unless the effects of inbreeding depression become severe.

The set of vital rates impacted by density (breeder survival, juvenile survival, and fecundity) provides rare insight into the mechanisms of density dependence in a natural population. Within family groups, increased group size is associated with higher breeder survival and reproductive success (Breininger *et al.* 2022; Mumme 1992; Woolfenden & Fitzpatrick 1984), suggesting that territorial interactions *among* family groups are the most likely cause of density dependence in these vital rates. Lack of evidence for density dependence in both helper survival and their probability to form breeding pairs was unexpected, given that breeding vacancies are considered the main limiting resource within our saturated study population (Woolfenden & Fitzpatrick 1984). However, competition for breeding vacancies among resident individuals is influenced by a social hierarchy that is not density-dependent (Suh *et al.* 2020, 2022; Woolfenden & Fitzpatrick 1977). Territorial defense may be the greatest risk associated with increased population density, which primarily impacts breeders and incoming immigrants (Woolfenden & Fitzpatrick 1984).

Density dependence mediated by territorial defense also may explain the increase in breeder survival that, from a population stability standpoint, compensates for declining immigration, although cause and effect are not yet clear. Decreased immigration could result in higher breeder survival by reducing the amount of territorial defense required of breeders. Alternatively, increased breeder survival could decrease effective immigration rates by reducing breeder vacancies and increasing hostility experienced during transience by potential immigrants (Bonte *et al.* 2012). A third possibility is that these trends may reflect factors not included in our analysis, such as lags in demographic synchrony between our focal population and the source populations for immigrants (Kendall *et al.* 2000). However, the evidence of density dependence in both breeder survival and female immigration does support the hypothesis that relationships between immigration and other vital rates likely contribute to population stability in the face of declining immigration.

Our study emphasizes the importance of considering both males and females when modeling population dynamics when – as is often the case – sex-biases exist among demographic processes. For example, we found evidence of density dependence in immigration of females but not males. Similar sex-specific population dynamics have been found in sexually monomorphic species that exhibit some sex differences in vital rates (Kraus *et al.* 2008), and may interact with environmental change (Gianuca *et al.* 2019; Oro *et al.* 2010). Sex-specific density dependence in immigration possibly results from female-biased dispersal in the Florida Scrub-Jay, although density dependence has been found in immigration rates of both sexes for other bird species that also exhibit female-biased dispersal (Wilson *et al.* 2017). For the highly territorial Florida Scrub-Jay, female immigrants likely experience greater competition than males to establish themselves with territorial groups, either as breeders or helpers (Suh *et al.* 2022), owing to the greater number of dispersing females. While the predictions of our female and male models were overall similar, we would have underestimated the impact of population density if we had considered only a male-specific model.

Despite evidence of inbreeding depression (Chen *et al.* 2016), increasing levels of inbreeding in our focal population contributed relatively little to variation in population growth rate, consistent with previous findings that inbreeding depression may not directly translate into

population decline (Johnson *et al.* 2011). Declines in individual fitness associated with inbreeding depression are expected to have little impact when population growth is negatively density-dependent, as decreases in the fitness of inbred individuals can contribute to increased average fitness by reducing density (Bozzuto *et al.* 2019). Future work should test the level of inbreeding required for a significant demographic response to determine the conditions under which the current resistance to inbreeding depression is expected to persist.

Our results showing the importance of breeder survival and environmental fluctuations on population dynamics are largely consistent with previous work on the Florida Scrub-Jay (Breininger *et al.* 2022, 2023; Breininger & Oddy 2004; Woolfenden & Fitzpatrick 1984). The large contributions of variation in fecundity and population density both result from high temporal variation in fecundity, with high fecundity years frequently followed by low fecundity years (Woolfenden & Fitzpatrick 1984). Unlike other studies (Breininger 2009; Breininger *et al.* 2022, 2023; Fitzpatrick & Bowman 2016), we did not find an association between fire history and variation in vital rates at the population-wide scale. This discrepancy is likely due to the low variation in the proportion of burned area observed across our study area during the study period. The current burn regime was started in 1981 (Main & Menges 1997), and the amount of burned scrub across the study area as a whole has been more or less constant. However, post-fire succession and changing climate have caused declines in acorn abundance at Archbold (Pesendorfer *et al.* 2021). Thus, a population-wide interaction between fire and climate has occurred, but is acting through an average decline in acorn abundance.

We note that our GLMM/GLMs cannot specify causation. However, the tLTRE provides direct information on how observed variation in vital rates results in the observed variation in population growth rate. Our analysis would benefit from more precise estimates of emigration from our focal population, as density dependent emigration is another important aspect of equal balance populations (Doncaster *et al.* 1997; Harman *et al.* 2020). Finally, identifying the source populations of immigrants would allow us to perform a metapopulation analysis, capturing regional demographic stability and allowing us to study the impact of dispersal at different geographic scales.

While the theoretical basis of dispersal behavior has been well explored (Holt & McPeek 1996; Johnson & Gaines 1990; Johst & Brandl 1997; Lemel *et al.* 1997; McPeek & Holt 1992), here we provide much needed empirical evidence on the demographic consequences of changes in dispersal in the context of complex social and environmental conditions. Our results support the role of density dependence and context-dependent dispersal in maintaining populations through variable environments, and emphasize the importance of maintaining high quality habitat that is capable of supporting such robust populations. Globally, countless populations are threatened by landscape fragmentation and climate change (Marzluff *et al.* 2001; Simberloff 1999; Young *et al.* 2016), declining due to direct impacts on vital rates, including immigration (Schaub & Ullrich 2020), or as a consequence of inbreeding depression magnified by isolation and small population size (Bozzuto *et al.* 2019; Kardos *et al.* 2023). Our results address how a Threatened population has remained locally stable despite increasing isolation and some degree of inbreeding. Overall, our study demonstrates how path analyses of extensive demographic and environmental data collected from long-term ecological studies can elucidate the mechanisms of population stability.

Data Accessibility

All data and code used in this study area available at github.com/jtsummers53/LTRE_project.

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Figures:

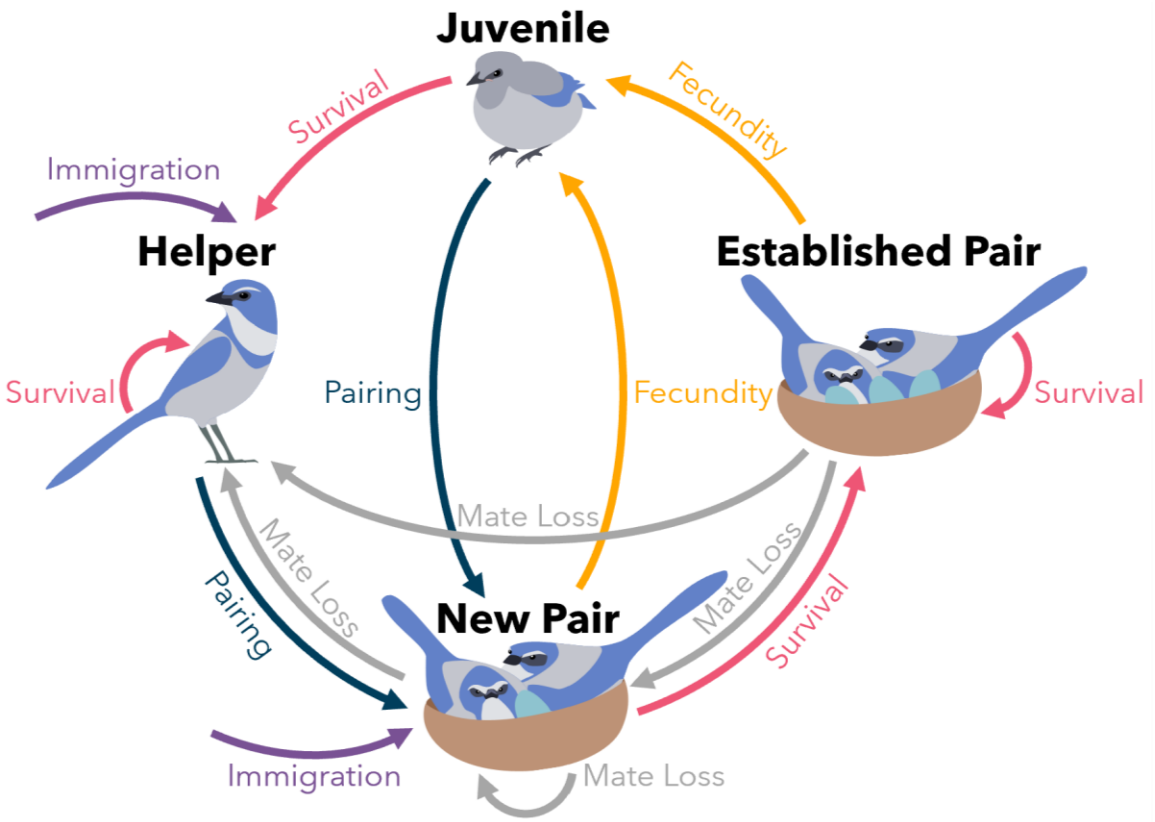

Figure 1. Life cycle diagram for the Florida Scrub Jay. Individuals who survive to the next breeding season may remain in their existing pair status (pink arrows), form new pairs (dark blue arrows), or lose a mate through divorce or death (gray arrows). New individuals enter the population either through reproduction (orange arrows) or immigration (purple arrows).

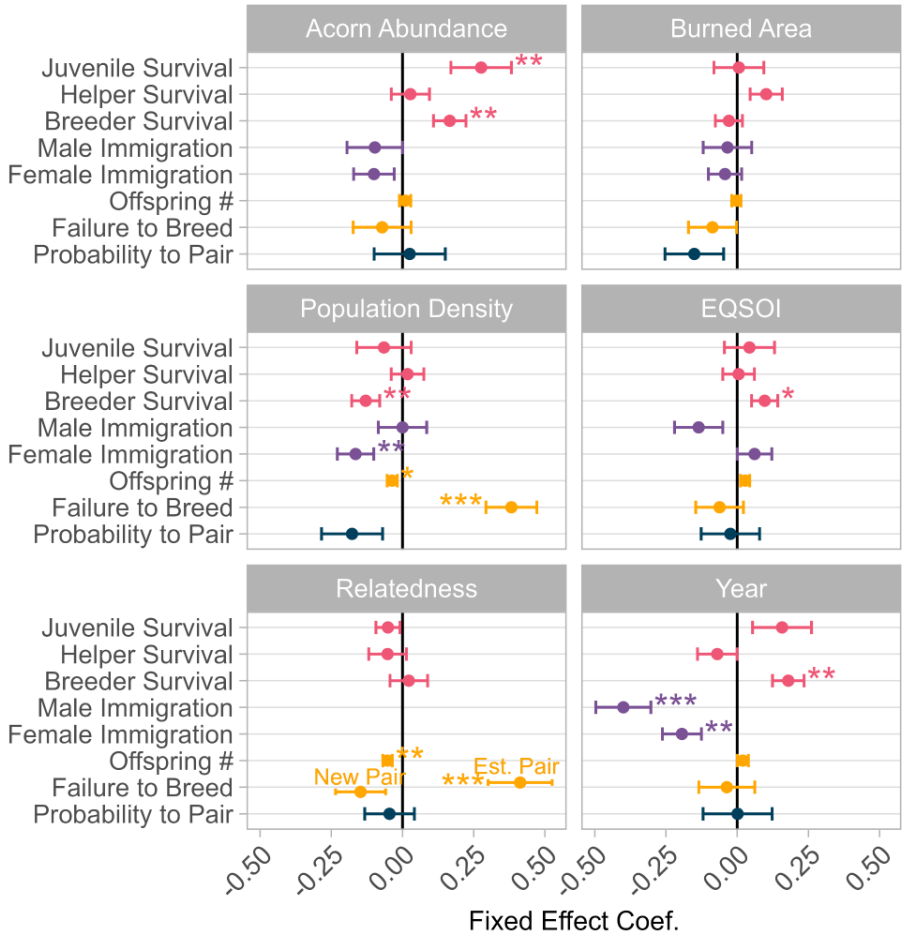

Figure 2. Impact of environmental variables and year on vital rates. Error bars represent the 95% confidence interval. Colors indicate the type of vital rate modeled (pink: survival, purple: immigration, yellow: fecundity, dark blue: probability to pair). Immigration is split into male and female immigration. Fecundity is split into the zero-inflated (Failure to Breed) and conditional (Offspring number) portions of the model. Asterisks indicate significance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Figure 3. Contributions of variation in vital rates to variation in population growth rate for the female-only model (left) and male-only model (right). Bars are colored by the covariance involved (*e.g.*, pink bars in the fecundity column are contributions made by covariance between fecundity and survival). Negative contributions indicate that the covariation between two vital rates diminished the variation in the population growth rate (*i.e.*, one rate promoted growth while the other promoted decline).

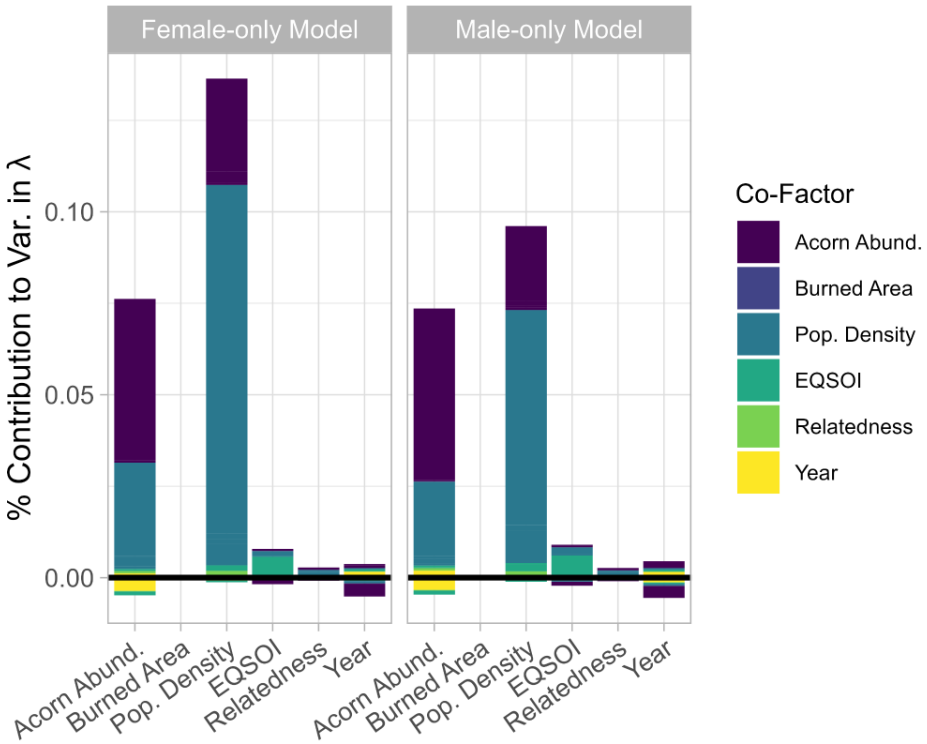

Figure 4. Contributions of variation in environmental factors to variation in population growth rate. Environmental factors contributed to the population growth rate through their association with vital rates. Bars are colored by the covariance involved (*e.g.*, yellow bars in the acorn abundance column are contributions made by covariance between acorn abundance and year). Negative contributions indicate that the covariation between two environmental factors diminished the variation in the population growth rate (*i.e.*, one factor promoted growth while the other promoted decline).

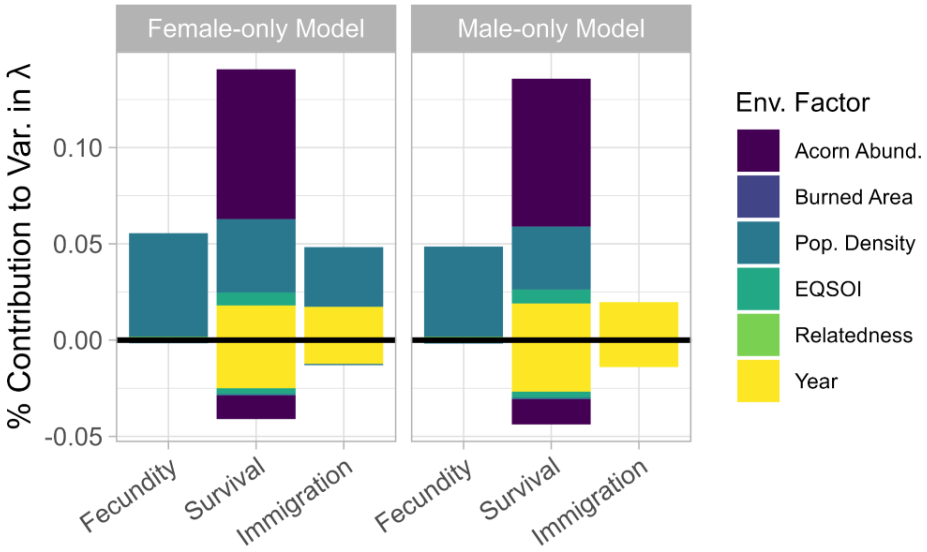

Figure 5. Contributions of variation in environmental factors to variation in population growth due to their impact on vital rates for the female-only model (left) and male-only model (right). Bars are colored by the environmental factor contributing to variance (*e.g.*, yellow bars in the immigration column are contributions made by variation in year due to the impact of time on immigration). Negative contributions indicate that either negative covariation between two environmental factors or opposing impacts of an environmental factor on two vital rates diminished the variation in the population growth rate (*i.e.*, the impact of a factor on one rate promoted growth while the impact of the same factor on another rate promoted decline).