Reduced levels of relatedness indicate that great-tailed grackles disperse further at the edge of their range

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ABSTRACT

It is generally thought that behavioral flexibility, the ability to change behavior when circumstances change, plays an important role in the ability of a species to rapidly expand their geographic range. To expand into new areas, individuals might specifically show flexibility in dispersal behavior, their movement away from their parents to where they themselves reproduce. Great-tailed grackles (*Quiscalus mexicanus*) are a bird species that is rapidly expanding its geographic range and are behaviorally flexible. Here, we infer dispersal rates in wild-caught grackles from two populations across their range (an older population in the middle of the northern expansion front in Arizona nearer the core of their original range versus a young population on the northern edge of the expansion front in California) to investigate whether grackles show flexibility in their dispersal behavior between these two populations. Based on genetic relatedness, we observe no closely related pairs of individuals at the edge, suggesting that individuals of both sexes disperse further from their parents and siblings in this population than in the population nearer the core. Our analyses also suggest that, in both populations, females generally move shorter distances from where they hatched than males. These results elucidate that the rapid geographic range expansion of great-tailed grackles is associated with individuals, in particular females, differentially expressing dispersal behaviors.

INTRODUCTION

Where individuals live, and how this area changes over time, is shaped by the behavior of these individuals (Martin, 1998). It has been argued that behavioral flexibility, the ability to change behavior when circumstances change (see Mikhalevich et al., 2017 for theoretical background on our flexibility definition), plays an important role in the ability of a species to rapidly expand their geographic range (Chow et al., 2016; Griffin & Guez, 2014; e.g., Lefebvre et al., 1997; Sol et al., 2002, 2005, 2007; Sol & Lefebvre, 2003). One specific behavior where flexibility could be crucial at the expanding edge of a population range is dispersal, the movement individuals show from the place they were born to the place they reproduce. At the edge, individuals might have to travel different distances to reach suitable habitat than nearer the core of their range (Simmons & Thomas, 2004) or coordinate to move to a place where they can find a mate (Bocedi et al., 2014). Here, we determine whether we can infer flexible changes in dispersal behavior in a population at the edge of a rapidly expanding avian species.

There are two flexible changes in dispersal behavior that could be expected at the edge of a population's geographic range because they are linked to the expansion rate. First, some individuals might disperse longer distances than they would in more established populations (Trakhtenbrot et al., 2005). Such increased dispersal distances could facilitate movement across uninhabitable environments and bring together a larger number of individuals from different areas within the original range. Second, there might be changes in sex-specific dispersal. In most animal populations, individuals of one sex tend to disperse less than individuals of the opposite sex (Pusey, 1987). This sex bias in dispersal could limit expansion into novel areas, particularly if females do not disperse but remain close to the place they were born (Miller et al., 2011; Santini et al., 2025). Shorter dispersal distances in females would reduce expansion rates because most individuals in a novel area would be male vagrants, whereas females and their offspring would remain in or closer to the range core. Reduced dispersal of females slows the establishment of breeding populations in the range edge, thereby limiting further movements beyond the current range edge. Accordingly, an extension of a range might occur more rapidly in species in which individuals show flexibility in sex specific dispersal biases, with individuals of both sexes dispersing farther at the edge of the range.

In this study, we test whether flexibility in dispersal behavior might have played a role in the rapid geographic range expansion of great-tailed grackles (*Quiscalus mexicanus*). Great-tailed grackles show behavioral flexibility in experimental tasks (Logan, 2016) and continue to rapidly expand their geographic range (Wehtje, 2003), thus offering an opportunity to assess the role of changes in dispersal behavior during the course of their expansion. Great-tailed grackles are seasonal breeders, with most young hatched between April to June, and individuals can begin breeding the year after hatching (Selander & Hauser, 1965). Individuals often forage in larger geographical areas during the winter before moving to the breeding sites, which is also when they might disperse. We previously found in the population nearer the core, with a smaller dataset, that great-tailed grackles show sex biases in dispersal, with females dispersing shorter distances than males (Sevchik et al., 2022). We also found indications of changes in the behavior of great-tailed grackles across their range. Compared to the population nearer to the core, individuals in the population nearer the edge are more persistent, participating in more of the trials they were offered and often returning to a problem even they did not receive a reward, and have a higher variance in behavioral flexibility in a reversal learning task (Logan et al., 2023). We therefore expect flexibility in dispersal behavior between the two populations, with no sex biases in dispersal at the edge of the population expansion.

We compare the dispersal behavior of great-tailed grackles between a recently established edge population (California) and a population that has existed for several generations nearer the core of their original range (Arizona)(Table 1). We examine whether individuals in the edge population are more likely to move away from the location where they hatched than individuals in the population nearer the core, and, in particular, whether we observe less sex bias in dispersal in the edge population. We infer rates of dispersal by determining whether the average relatedness (calculated using single nucleotide polymorphisms, SNPs) between pairs of individuals in each population is lower or higher than what we would expect if individuals move randomly (Sevchik et al., 2022). Genetic approaches are one of the main ways to determine patterns of dispersal in birds because actual dispersal events are rare and difficult to study. In most species, individuals only show limited movement from their place of origin to where they themselves breed, creating patterns of isolation by distance as pairs of individuals are less likely to share genetic variants the further away they are (Manel et al., 2003). We measure this sharing of genetic variants using relatedness (Spong & Creel, 2001), with individuals who show low relatedness to others in the population being assumed to have dispersed further (Aguillon et al., 2017). Though we refer to our two sampling sites as two populations, it is important to note that the distribution of great-tailed grackles appears continuous and connected. Even at the edge, the expansion appears to occur gradually, rather than through the establishment of separate, distanced populations (Wehtje, 2003). Accordingly, our focus is not on the overall levels of genetic diversity or relatedness in our sample of individuals, but how genetic variation at each site is structured according to the sex of individuals and the distances between them to lead to patterns of relatedness. Due to sampling limitations, our inferences are based on a single comparison between two populations. Accordingly, we cannot directly infer the causes of any changes in dispersal behavior. However, we can infer whether there is flexibility in dispersal behavior in this expanding species if we detect differences in relatedness patterns between the two populations.

RESEARCH QUESTION

Our research question is listed as it appeared in the preregistration (Logan et al., 2020). We completed the research and published the results linked to the other research questions in other articles (Logan et al., 2023, 2025; Summers et al., 2023)

Q2 (dispersal behavior: great-tailed grackles): Are there differences in dispersal behavior across the great-tailed grackle's geographic range? (Fig. 1, Table 1)

Prediction 2: We predict **more dispersal at the edge**: a higher proportion of individuals, particularly females, which is the sex that appears to disperse less in the population in the middle of the range expansion (Sevchik et al., 2022), disperse in a more recently established population and, accordingly, fewer individuals are closely related to each other. *This would support the hypothesis* that changes in dispersal behavior are involved in the great-tailed grackle's geographic range expansion.

Prediction 2 alternative 1: We predict that the **proportion of individuals dispersing is not related to when the population established** at a particular site and, accordingly, the average relatedness is similar across populations. *This supports the hypothesis* that the original dispersal behavior was already well adapted in this species to facilitate a range expansion.

Table 1. Population characteristics of the two field sites. The number of generations at a site is based on a generation length of 5.6 years for this species (BirdLife_International, 2018, note that this species starts breeding at age 1), and on the first year in which this species was reported or estimated to breed at each location. Woodland, California: Yolo Audubon Society's newsletter *The Burrowing Owl* (July 2004); Tempe, Arizona: based on 1945 first-sighting report in nearby Phoenix, Arizona (Wehtje, 2004) to which we added 6 years, which is the average time between first-sighting and first-breeding - see Table 3 in (Wehtje, 2003).

Site	Range position	Breeding since	Number of years breeding	Average number of generations
Tempe, Arizona	Middle of expansion	1951	69	12.3
Woodland, California	Northern edge	2004	16	2.9

STATE OF THE DATA AND CHANGES FROM PREREGISTRATION

The preregistration was written (March 2020) prior to collecting any data from the edge population (which began in January 2021), therefore we were blind to these data. However, we were not blind to some of the data from the Arizona population: some of the relatedness data (SNPs used for Hypothesis 2 to quantify relatedness to infer whether individuals disperse away from relatives) from the middle population (Arizona) had already been analyzed for other purposes (n=57 individuals, see Sevchik et al., 2022). Therefore, we consider it secondary data: data that were collected for other investigations. We collected blood samples from 37 more grackles in Arizona, and we repeated the analyses for the Arizona population with the complete sample. This preregistration was submitted in May 2020 to PCI Ecology for pre-study peer review. We received the reviews, and revised and resubmitted in August 2020, and it passed pre-study peer review in October 2020.

While our ideal plan was to include three field sites, due to restrictions around COVID-19 and because we learned about potential risks to the safety of study participants at the initially considered third field site, it was not possible for us to accomplish all of our goals within our current funding period. We therefore compare only two populations.

METHODS

Sample

Q2: Great-tailed grackles were caught in the wild in Tempe, Arizona, and in Woodland and Sacramento, California. Adults were identified from their eye color, which changes from brown to yellow upon reaching adulthood (Johnson & Peer, 2001). We applied colored leg bands in unique combinations for individual identification. Some individuals (~20) were brought temporarily into aviaries for behavioral choice tests, and then were released back to the wild at their point of capture. We caught grackles with a variety of methods (e.g., walk-in traps, mist nets, bow nets), some of which decrease the likelihood of a selection bias for exploratory and bold individuals because grackles cannot see the traps (i.e., mist nets).

We recorded the latitude and longitude at locations where each grackle was caught. We also noted the location where we first resighted the individual after it was released back into the wild. We always attempted to resight the individual the day after its release because this location is less influenced by the food we put at trapping locations. We used the resight location for all individuals, but we used the trapping location if we were unable to find them again after release. For Figure 1, we mapped these locations using QGIS (version 3.4.5) and the Google Satellite basemap obtained through QuickMapServices QGIS plugin (Map data ©2020, Google). We used the Categorize point properties feature to distinguish each individual's point on the map based on whether they were adult or juvenile and male or female.

Sample size rationale

We caught as many great-tailed grackles as we could during the two to three years we spent at each site given that the birds were only brought into the aviaries during the non-breeding season (approximately September through March). We sampled more than the expected 20 grackles per site for the genetic analyses.

Protocols and open materials

DNA was collected from the grackles, processed, and analyzed for pairwise relatedness using ddRADseq and Stacks as in Sevchik et al. (2022) (protocol). Our pre-registration only included a brief summary of the methods, we describe them in detail below for full reproducibility.

We previously generated genotypes for 57 individuals from Arizona in 2018 (Sevchik et al., 2022). For the current analyses, we added genotypes for 37 individuals from Arizona and 35 individuals from California. In brief, we collected 150uL of blood from individual birds by brachial or medial metatarsal venipuncture. Samples were centrifuged at 15x gravity for 10 minutes directly after collection to separate the serum from the cellular fraction. The serum layer was removed and 600uL of lysis buffer was added to the remaining packed cells. Tubes containing packed cells and lysis buffer were stored at room temperature for up to 5 years before DNA extraction. The time gap between sampling and extraction could have reduced the quality of the samples, as we observed that some samples had clotted. This potentially explains the reduced SNP recovery rate for one of the samples we had to exclude (see below). DNA was extracted from the samples using the DNeasy Blood and Tissue kit (Qiagen). Extracted DNA samples were shipped with ice packs to the Cornell Lab of Ornithology for ddRAD sequencing in August 2023. The sequencing to generate single-nucleotide polymorphism (SNP; where at a given position in the genome two different bases, alleles, can occur) genotypes was performed at the Cornell University Lab of Ornithology. Fragments were digested with a combination of two restriction enzymes (SbfI-HF and MspI), cleaned, size-selected, amplified using a low-cycle PCR process, and pooled together for sequencing on an Illumina NextSeq500.

We performed the SNP processing and selection as in Thrasher et al. (2018), processing the samples from the two populations separately. For Arizona, we combined the genotypes of the individuals sequenced in 2018 with the genotypes sequenced in 2023 prior to the processing so that all individuals have the same set of alleles to compare for the relatedness estimation. Occurrences of rare alleles are likely to differ among the two separate populations, therefore combining the data from the two populations could potentially lead to ascertainment biases, where alleles that occur in the population with the larger sample but not in the population with the smaller sample are included as informative whereas alleles that occur only in the population with the smaller sample are excluded. This would bias the relatedness estimation in the smaller population because differences among individuals in this population would be lost. The re-processing means that, for those individuals already included in Sevchik et al. (2022), the genotypes, and the resulting pairwise relatedness estimates, are slightly different compared to those previously estimated. For both populations, loci were considered only if they were present in 95% of the samples (r) and had a minimum minor allele frequency of 0.05 (min maf).

To prepare, check, and describe the genotype data (expected heterozygosity, probability of identity), we used functions in the R packages 'adegenet' (Jombart, 2008), 'pegas' (Paradis, 2010), and 'popgenutils (Tourvas, 2020).

For each population, we calculated the pairwise relatedness among all dyads of adult individuals using the estimator by Queller & Goodnight (1989), which was more robust for our inferences in a subset of the Arizona data (Sevchik et al., 2022), as implemented in the package 'related' (Pew et al., 2015) in R. For the relatedness calculation, we only used the genotypes of individuals in the respective population to derive the allele frequencies that set the baseline chance of sharing alleles. That means that, overall, in both populations average relatedness will be close to zero. Individuals who share fewer alleles than expected have a negative relatedness value, while individuals who share more alleles than expected have a positive value. Our focus is not on comparing the overall levels of genetic diversity in the two populations, but whether there is structure in the sharing of alleles that lead to patterns of relatedness among individuals of the same sex. We identified as potential kin those pairs of individuals whose estimated relatedness was equal to or larger than 0.25 (closer relatives, at the level of half-siblings) or larger than 0.125 (distant relatives, at the level of cousins)(Goudet et al., 2018).

We recorded the longitude and latitude of the first locations where individuals were observed after they had been caught and released, or for those individuals who were not resighted, the location where they were trapped. To calculate the geographic distance among pairs of individuals based on these locations, we used the function 'distm' in the package 'geosphere' (Hijmans, 2022) with the Vincenty ellipsoid great circle function.

Open data

All data for analyses are available at Edmond (Lukas & Logan, 2024). Raw genotype files are available in the Sequence Read Archive of the National Center for Biotechnology Information (NCBI, accession number: PRJNA658480).

Blinding during analysis

Blinding is usually not involved in the final analyses because the experimenters collect the data (and therefore have seen some form of it) and run the analyses. However, when processing the genetic data, the experimenters and the people who conducted the lab work were blind to the relatedness amongst the birds.

ANALYSIS

We did not exclude any data except for instances where missing data made analyses not reliable. Samples with a low DNA quantity and quality produce data for only a small number of SNP loci. Relatedness estimates are only reliable if they are based on several hundred SNP loci (Foroughirad et al., 2019; Wang, 2016), because small numbers of loci can lead to high variances in the estimates. Analyses were conducted in R [current version 4.4.3; R Core Team (2023)] and Stan (version 2.18, Carpenter et al., 2017). We used functions in the package ‘rethinking’ (McElreath, 2020) to construct and summarize the linear models. Following the social convention of this approach, we report the 89% compatibility intervals (89% CI) of the posterior sample.

Our response variable is the average relatedness between all pairs of individuals within one sex. As in Sevchik et al. (2022), we analysed this in two ways: first, as a continuous variable ranging between -1 and +1, reflecting average relatedness as whether individuals share more or less alleles than expected by chance; and second, as a categorical variable coded as yes/no, reflecting whether the average relatedness among a pair of individuals is more or less than the threshold that kin are expected to have (r 0.125 and r 0.25). We had planned to include as explanatory variables the site diameter, the site sample size, and the number of generations at a site. However, because we were able to only obtain samples from two populations, we did not include these variables in the models because it would be impossible to say which of the factors might explain the site differences (see also our Discussion). We did however use the site diameter data to ensure that the two populations were comparable. Permutations (i.e., randomly assigning site ID to individuals) and general linear models estimating average relatedness of each individual to all others at that site (averagerelatedness ~ α[site]) were used to determine whether individuals at one site are more closely related to each other than the individuals at another site.

Comparison of average relatedness between the two populations

We compared the overall levels of average relatedness, as well as the average relatedness among the females and among the males, between the population in Arizona and the population in California using a linear model:

$$
\begin{aligned}
pairwiserelatedness_d &\sim Normal(\mu_d, \theta) \\
\mu_d &= \alpha_{pop[d]} + \beta_{sex[d],pop[d]} \\
\alpha_{pop[d]} &\sim Normal(0,1) \\
\begin{bmatrix} \beta_{d,1} \\ \beta_{d,2} \end{bmatrix} &\sim \text{MVNormal}\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, S_{sex} \right) \\
S = \begin{pmatrix} \sigma_{sex=1} & 0 \\ 0 & \sigma_{sex=2} \end{pmatrix} & R \begin{pmatrix} \sigma_{sex=1} & 0 \\ 0 & \sigma_{sex=2} \end{pmatrix} \\
R &\sim LKJcorr(4) \\
\sigma_{sex} &\sim Exponential(1) \\
\theta &\sim Exponential(1)
\end{aligned}
$$

where the $pairwiserelatedness_d$, the relatedness among all pairs of relatives in the two populations pop of either sex, is assumed to be distributed according to a normal distribution with mean μ and variance θ. We assumed that relatedness overall might be higher in one population than the other, and therefore included an interaction between population and sex, such that the intercepts are defined by a two dimensional Gaussian distribution ($MVNormal$) with means of 0, because we separately include the population means as α_{pop}, and covariance matrices S reflecting the two $sexes$. The covariance matrix, S, is factored into separate standard deviations, σ_{sex}, and a correlation matrix, R. The prior for the correlation matrix is set to come from the Lewandowski-Kurowicka-Joe ($LKJcorr$) distribution, and is set to be weakly informative and skeptical of extreme correlations near -1 or 1.

Comparison of degree of kinship between the two populations

We compared the number of of individuals classified as either close or distant relatives in the two populations using a binomial model:

$$
\begin{aligned}
kin_d &\sim Binomial(1, p_d) \\
logit(p_d) &= \alpha_{pop[d]} + \beta_{sex[d],pop[d]} \\
\alpha_{pop[d]} &\sim Normal(0,1) \\
\begin{bmatrix} \beta_{d,1} \\ \beta_{d,2} \end{bmatrix} &\sim \text{MVNormal}\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, S_{sex} \right) \\
S = \begin{pmatrix} \sigma_{sex=1} & 0 \\ 0 & \sigma_{sex=2} \end{pmatrix} & R \begin{pmatrix} \sigma_{sex=1} & 0 \\ 0 & \sigma_{sex=2} \end{pmatrix} \\
R &\sim LKJcorr(4) \\
\sigma_{sex} &\sim Exponential(1)
\end{aligned}
$$

where the kin_d reflects whether the relatedness of a given pair of individuals is or is not larger than the threshold for either close or distant relatives. All remaining terms as above.

Second, we compared the presence of kin in the two populations using permutations. Average relatedness declines the more individuals are included in the calculation (Lukas et al., 2005). Permutations are a way to account for this by assessing whether any observed differences remain when comparing the same number of individuals. We randomly took 10,000 draws of the same number of individuals we had in the California population, which was a smaller sample, from the genotypes we had in the Arizona population (e.g., randomly drawing 13 of the female genotypes in Arizona and calculating the number of kin observed in this sample, before repeating the random draw another 9999 times, each time calculating the number of kin observed in the sample). We then compared the observed number of kin in California to the numbers obtained in the 10,000 random samples to assess whether the kinship composition in California is similar or different to that observed in Arizona

Sex biases in dispersal in the two populations

To determine whether, in either or both populations, individuals of one sex are more likely to disperse farther than individuals of the opposite sex, we first compared the average relatedness among females to the average relatedness among males in the same population. We performed 10,000 random draws, drawing the same number of individuals from the whole population as there are females or males in that population, to assess whether the relatedness among individuals of one sex is different than that observed in a random sample of individuals of the same size from that population. Next, we determined the geographic distances among those pairs of individuals identified as potential close or distant kin. We again performed 10,000 draws, drawing the same number as there are kin of that sex from all the females or males in that population to assess the expected distance among such a sample of same-sex individuals. If the distances among the 10,000 draws are generally larger than those observed among kin, then we infer that kin of that sex remain closer together than what would be expected by chance. Finally, we performed assessments of spatial autocorrelation to link the pairwise relatedness among individuals of each sex to the geographic distances of their locations.

To test whether males and females show different patterns of genetic isolation by geographic distance, we followed analyses as in Aguillon et al. (2017). In each population, for males and females separately, we assessed the strength of the association between the the matrices of average relatedness and of geographic distance using Mantel correlograms with the function ‘mantel.correlog’ in the ‘vegan’ package (Oksanen et al., 2013) in R. For each of the four associations (two sexes in two populations), we performed 10,000 permutations to assess the strength of the association. The approach involves partitioning the geographic locations into a series of discrete distance classes. We used two methods to create the distance classes. First, we attempted to have about equal numbers of pairs of individuals within each distance class, creating nine distance classes of (0-100m, 100-200m, 200-300m, 300-400m, 400-500m, 500-750m, 750-1000m,1 000-1250m, and 1250-2000m). With the second method, we only created two distance classes to increase the sample size in each class, splitting the distance according to the limit at which most close kin were detected (0-400m and 400-1400m). For each distance class, a normalized Mantel statistic is calculated using permutations of values within that distance class. The permutation statistics, plotted against distance classes, produce a multivariate correlogram. A negative correlation between genetic relatedness and spatial distance indicates that the more closely related individuals are found closer to each other, indicating that these individuals likely disperse shorter distances than those individuals where a positive correlation is found.

RESULTS

Summary statistics

California SNP data

We retained 493 SNPs. Data was missing for 3.3% of all alleles (individuals missing information for either one or both of their chromosomes for that particular position). None of the SNPs showed a particular underrepresentation of information. The missingness was due to the incomplete genotype of one individual (C116RY, adult male), who had missing data at 459 of the 493 SNPs (93%), whereas all other individuals had data missing at four or fewer SNPs. We excluded this individual from the further analyses, because relatedness calculations based on so few SNPs were, as expected, highly stochastic and led to extreme deviations (see code chunk 'kin composition' in the Rmd file for illustration). For the remaining individuals, all SNPs had two alleles and the observed heterozygosity (individuals carrying one copy each of the two bases) was 0.29, identical to the heterozygosity expected in a population with the same allele frequencies and random mating. The probability of identity for siblings, the chance that two siblings will show the same genotypes given the allele frequencies across these 493 SNP loci and random mating among individuals, is less than 10^{-64}. This indicates that any relatedness we detect among individuals is likely to reflect biological relatedness, rather than resulting from limited sampling making individuals more similar.

Arizona SNP data

We retained 462 SNPs. Data was missing for 3.0% of all alleles (individuals missing information for either one or both of their chromosomes for that particular position). None of the SNPs showed a particular underrepresentation of information. There were three individuals whose genotypes were less complete (A072KB, adult female, missing data at 191 (41%) of SNPs; A088YR, adult male, missing data at 174 (38%) of SNPs; A059NB, adult female, at 148 (32%) of SNPs), whereas all other individuals had data missing at less than 10% of SNPs. Here, we did not exclude any individuals because the number of SNPs with information was still sufficiently high for all genotypes to reduce the noise in the relatedness estimation. All SNPs had two alleles and the observed heterozygosity (individuals carrying one copy each of the two bases) was 0.29, similar to the heterozygosity expected in a population with the same allele frequencies and random mating. The probability of identity for siblings, the chance that two siblings will show the same genotypes given the allele frequencies across these 462 SNP loci and random mating among individuals, is less than 10^{-60}.

Sample

In total, we included genotype information for 52 females and 27 males in Arizona, and 13 females and 15 males in California. In Arizona, all birds were found within a maximum of 1,991m from each other (median 669m). In California, birds were found at multiple locations (Figure 1). Twelve females and twelve males were found at a location in Sacramento that spanned about the same range as the population in Arizona (maximum geographic distance 1,592m, median 474m). Three birds (one female, two males) were resighted at a separate location in Sacramento ~7,000m away from the main location. In addition, one male was trapped and resighted at a location ~33,000m away in Woodland. Therefore, the maximum and average geographic distances between the locations of individuals are much higher for the California sample than the Arizona sample. For the set of analyses that include pairwise geographic distances among individuals, we performed the analyses only with the birds found at the single location in Sacramento in order to keep the California population comparable to the Arizona population (i.e., we excluded these four birds).

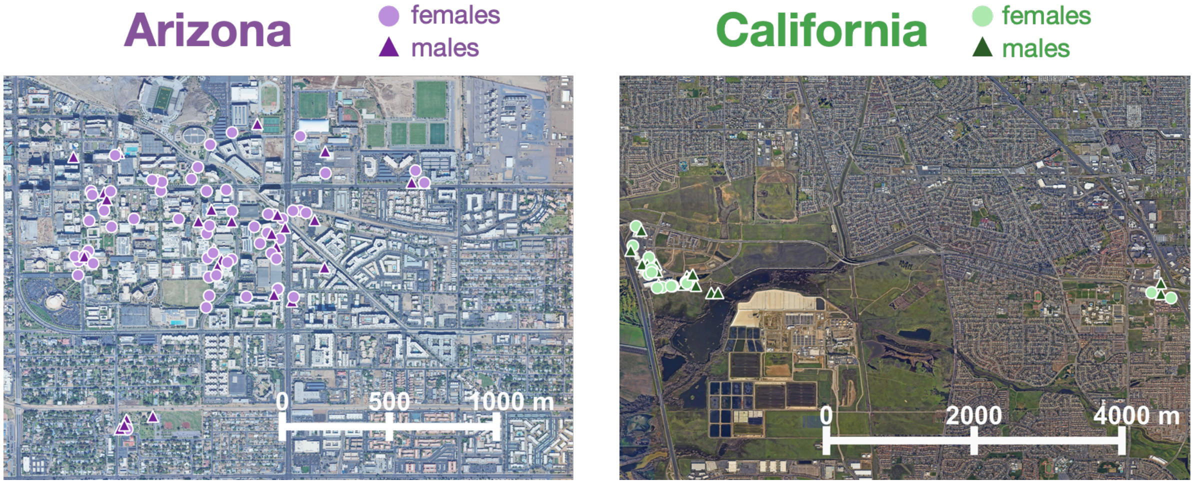

Figure 1: Maps showing where individuals were located in Arizona (left, purple) and in California (right, green). In both populations, most individuals were sampled within 1,500m of each other, with females (lighter color circles) and males (darker color triangles) being found throughout the populations. For the analyses incorporating location data in California, we only used the birds from the cluster on the left and excluded the individuals to the far right and the individuals used in a separate location (Woodland). Excluding these individuals makes the distribution more comparable between the two populations (see also Figure 2). We wanted to show here that individuals in the population in California appear to roam across larger areas - individuals on the far right were sighted together with the individuals on the cluster to the left.

Difference in dispersal behavior between the two populations

Comparison of average relatedness in the two populations

Overall, the average relatedness among individuals in the two populations is slightly negative, which is more pronounced in California (average relatedness: Arizona -0.013, California -0.037). This slight skew toward negative relatedness values suggests that both populations, but particularly the population in California, might contain individuals who have immigrated into these populations and are therefore sharing fewer alleles than would be expected by chance. In Arizona, males (-0.009) have slightly higher average relatedness than females (-0.013). In California, females (-0.024) have higher average relatedness than males (-0.048).

The model comparing levels of pairwise relatedness between the two populations indicates that the values in California are consistently lower than the values in Arizona because their confidence intervals do not cross zero (median of contrast for females -0.003, 89%CI of contrast -0.006 to -0.001, for males median -0.009, 89% CI -0.011 to -0.007).

Comparison of the degree of likely kin in the two populations

Overall, in both populations we identified very low numbers of dyads that are potentially kin (Figure 2). In California, none of the dyads are estimated to be related with r 0.25, and only one opposite sex dyad is estimated to be related with r 0.125 (out of 105 male-male dyads, 78 female-female dyads, and 195 opposite sex dyads). In Arizona, 3 male-male dyads (0.9% of the 351 male-male dyads), 12 opposite sex dyads (0.9% of the 1404 dyads), and 9 female-female dyads (0.7% of 1326 dyads) are estimated to be related with r 0.25. With the lower threshold of r 0.125, 9 (2.5%) of all male-male dyads, 39 (2.9%) of female-female dyads, and 32 (2.3%) of opposite sex dyads in Arizona are classified as related.

A binomial model indicates that the probability that any dyad would be kin at r 0.25 is higher among individuals in Arizona than in California (median posterior estimate of difference in probabilities for close kin r 0.25 0.6%, 89% CI 0.4 to 1.0%, for more distant kin r 0.125 median difference 2.2%, 89% CI 1.6 to 2.9%). The differences in probability hold for both female-female dyads (r 0.25: 0.7, 89% CI 0.3 to 1.0%; r 0.125: 2.5%, 89% CI 1.7 to 3.3%) and for male-male dyads (r 0.25: 0.6%, 89% CI 0.2 to 1.1%; r 0.125: 2.3%, 89% CI 1.2 to 3.2%).

The permutations support that the absence of same-sex individuals related at r 0.125 in the California population is not simply due to the smaller sample of individuals. There are no relatives in only 12% of permutations drawing 13 individuals from among the 52 females in Arizona, and there are no relatives in only 2% of permutations drawing 15 individuals from among the 27 males in Arizona.

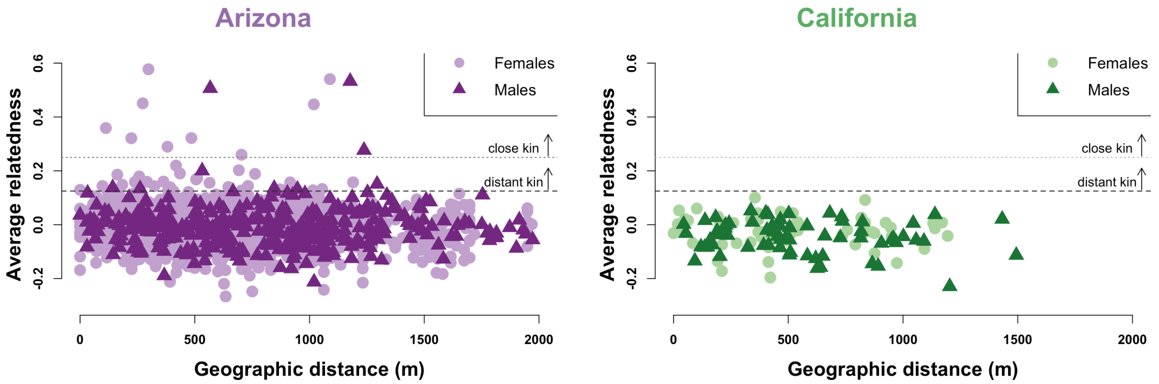

Figure 2: The relatedness and geographic distance observed among grackles in Arizona (left, purple) and in California (right, green). Average relatedness is higher in Arizona than in California. In Arizona, there are several pairs of females (lighter circles) and males (darker triangles) who are related at levels higher than 0.25 (dotted line, close kin of half-sibling or closer) and 0.125 (dashed line, distant kin of cousin or closer), while there are no close or distant same-sex kin in California. In terms of potential sex-biases in dispersal, in Arizona, we observe more females than males related at levels of distant kin and of close kin. Closely related females tend to be found at shorter geographic distances than the average female pair, while closely related males are not found at short geographic distances.

Sex biases in dispersal in the two populations

Average relatedness within the sexes

Average relatedness among both the females and the males in Arizona is not different from what would be expected by chance. Randomly drawing the same number of individuals from the full sample gives an average relatedness that is lower than that observed among the females in 45% of permutations and for males in 29% of permutations. In contrast, the observed average relatedness among females in California is slightly higher than what would be expected by chance, with 90% of the permutations drawing the same number of individuals from the overall population as there are females leading to lower average relatedness than that observed among the females (Figure 3). In contrast, the observed average relatedness among males is slightly less than what would be expected by chance given the relatedness among individuals in this population, with 91% of permutations giving higher levels of average relatedness than that observed among the males (Figure 3).

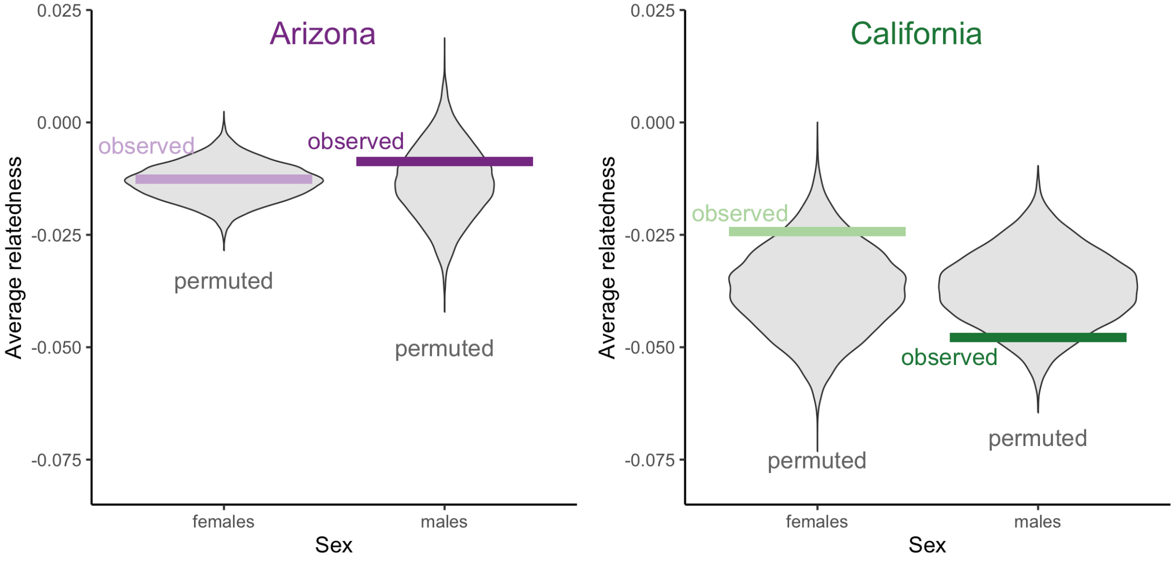

Figure 3: Observed levels of average relatedness among females and males in the two populations compared to expected levels of relatedness based on permutations. Overall, average relatedness is lower in California (right panel, green lines) than in Arizona (left panel, purple lines). In Arizona, the observed average relatedness among females (light purple line, left) and males (dark purple line, right) are similar and fall within the expected levels of average relatedness based on permutations (grey shaded areas). In California, the average relatedness observed among females (light green line, left) is higher than the average relatedness observed in most permutations, while the average relatedness observed among males (dark green line, right) is lower than the relatedness observed in most permutations. 10,000 permutations were performed for each sex in each population, drawing a subset of individuals from the sample of individuals in that population and calculating their average relatedness. The width of the violin plots (grey shaded areas) reflects the number of permutations during which a particular level of average relatedness was observed.

Distances among kin of the different sexes

In Arizona, the only population where our relatedness calculations indicated likely kin, females related at r 0.25 are found a median of 391m from each other, while males related at this level are found 1,177m from each other (Figure 2). Similarly, females related at r 0.125 are found a median of 435m from each other, while males related at this level are found 846m from each other. These differences in distance are not due to females generally being found closer to each other, because in only 2% of permutations drawing from the same number of female and male dyads as those that are related at the respective levels, are the differences in distance as large or larger than those observed (Figure 4). We cannot perform this analysis for California because there are no kin among either sex (Figure 2).

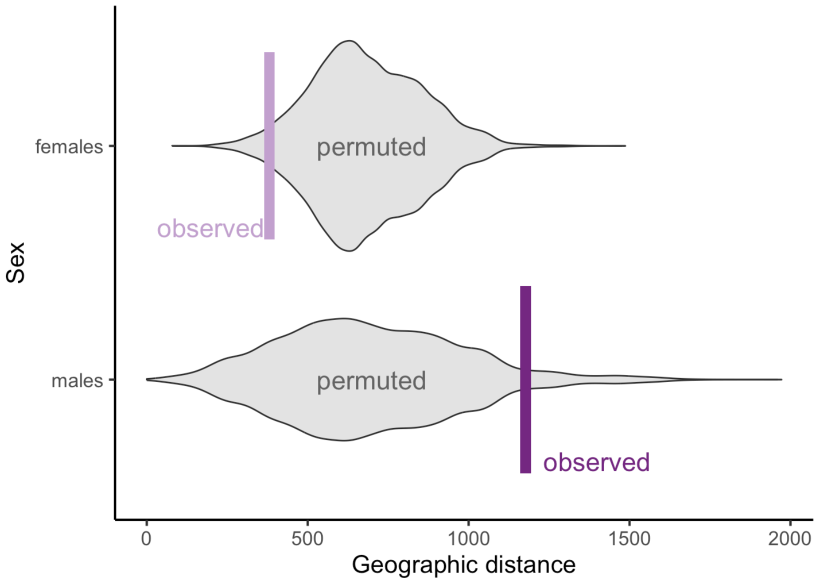

Figure 4: In Arizona, females related at r 0.25 (light purple line, top) are found closer to each other than the average set of females (grey shaded area, top), while males related at r 0.25 (dark purple line, bottom) are found at larger distances from each other than the average set of males (grey shaded area, bottom). We cannot perform this analysis for California, because none of the same-sex dyads are related at r 0.25. 10,000 permutations were performed for each sex, drawing a subset of individuals from the total sample matching the number of close kin and calculating their average geographic distance The width of the violin plot (grey shaded area) reflects the number of permutations during which a particular average distance was observed.

Spatial autocorrelation between geographic distance and relatedness in the two sexes

The spatial autocorrelation analyses indicate that, in both Arizona and California, female relatives likely stay close to each other while male relatives move away from each other (Figure 2). For Arizona, more closely related females are found at shorter distances from each other (negative correlation between relatedness and geographic distance based on a Mantel test when females are close, -0.08, p=0.02; positive correlation when females are far, 0.06, p=0.03). In contrast, at short distances males are not related to each other (0.05, p=0.21), but relatives are found at larger distances (-0.11, p=0.02). The same pattern is found for females in California, though with the smaller sample size, the effects are not significant (females close -0.15, p=0.12, distant 0.15, p=0.12), whereas for males there is no obvious pattern (close 0.04, p=0.38; distant 0.04, p=0.43). These results are similar when using the larger number of distance classes, with correlations switching from negative to positive for females as distance increases, and from positive to negative for males.

DISCUSSION

Our results provide support for our prediction that natal dispersal is higher in great-tailed grackle populations that are closer to the edge of the expansion range. We find that the average levels of relatedness, as well as the number of pairs of same-sex individuals that are closely related are lower in the population in California than in the population in Arizona. Grackles have been breeding since 2004 in California and since 1951 in Arizona. Our analyses suggest that the observed differences between the two populations in the levels of relatedness are unlikely to be simply due to the larger sample of individuals included in the Arizona population. While the results support our main prediction, further assessment of the hypothesis that individuals in edge populations behave differently than those nearer the core of the range is required, because our inferences rely on only a single comparison between two populations that might also differ in other aspects besides the age at which they were established. Independent of the potential aspects involved, our findings do reveal flexibility in dispersal behavior in this species that is rapidly expanding its range. We also find that, in both populations, females are more likely to remain closer to same-sex relatives than males, suggesting that females disperse shorter distances than males. These findings, with our larger sample from this article, confirm our previous inferences for the population in Arizona (Sevchik et al., 2022), that the sex biases in dispersal in great-tailed grackles are the opposite to that observed in most other bird species.

In the population closer to the edge of the range in California, our relatedness analyses indicate that no pair of same-sex individuals is related at the level of cousins (r 0.125) or higher. Our inference is based on a relatively small sample of 13 females and 15 males, which is nevertheless larger than the minimum sample size set in our preregistration. In addition, all analyses suggest that the low relatedness, and in particular the absence of related same sex dyads, is unexpected given the levels of relatedness we observe among the individuals in Arizona. While the permutation analysis suggests that there might be a chance to observe no female relatives in such a sample, this approach is limited because it does not fully take into account the potential contingencies in the observed data (for example, if a mother is present with two daughters, these dyads are not independent). We therefore performed an unregistered post-hoc analysis using a social network approach that accounts for such potential interdependence using functions of the package 'STRAND' in R (Ross et al., 2024). We coded whether a given pair of individuals in either population was likely kin or not (r 0.125) and determined whether the likelihood that individuals are in a kin dyad is different between the two populations. These models also indicate that the likelihood that individuals in California are closely related is substantially lower than that of individuals in Arizona (for all individuals: 89%CI estimate of difference in likelihood 0.94 to 6.81; for females 89% CI -2.36 to 4.79; for males 89% CI -0.04 to 6.16). Our results suggest that beyond the radius that we sampled, California individuals of both sexes disperse further from where they hatched than individuals in Arizona.

Previous theoretical and empirical studies predict such increased dispersal at the edge of a population expansion. Multiple processes could contribute to the higher dispersal at the edge of the population expansion. The higher frequency of dispersers at the edge could result from simple sorting processes, whereby highly dispersive individuals are over-represented in edge populations because they are more likely to end up in these novel areas (Shine et al., 2011; Travis & Dytham, 2002). Alternatively, or in addition, the conditions at the edge could shift the trade-off of the costs and benefits towards dispersing in the edge population (Chuang & Peterson, 2016; Simmons & Thomas, 2004). Such trade-offs linked to expansion have been observed in relation to dispersal of aggressive individuals in bluebirds (Duckworth & Badyaev, 2007) and morphological adaptation for speed in cane toads (Clarke et al., 2019).

In the population in Arizona, we observed a small number of pairs of individuals related at the level of cousins or higher. However, while only 3% of all dyads are related at r 0.125, 60% of females (31 out of the 52) and 56% of males (15 out of the 27) have at least one same-sex relative in the population. The kin composition we observed among great-tailed grackles in Arizona is similar to what has been reported for ravens, where 2.2% of dyads were classified as close kin and 20% of individuals had a close kin in their foraging group (the study used a different approach to estimate relatedness so the category is between our cut-offs of 0.25 and 0.125; Parker et al. (1994)). The raven study also suggested that kinship, besides parent-offspring relations, did not play a major role in structuring social interactions. Both ravens and grackles form foraging groups, where individuals are generally resighted at the same location with the same set of others. However, groups are not closed and cohesive, unlike the stable groups found in cooperatively breeding birds or several social mammals, where levels of kinship are generally higher than what we observed here and kinship plays an important role in social relationships (Pereira et al., 2023).

In both populations, we find indications of a sex bias in dispersal, with females apparently dispersing shorter distances than males. Despite the absence of close relatives in California, the analyses linking relatedness to geographic distance also supports a similar bias in this population. This confirms our previous conclusion with a smaller sample in Arizona (Sevchik et al., 2022). We find more male relatives in Arizona than in our earlier study that used a subset of these Arizona individuals (Sevchik et al., 2022). This indicates that, while males disperse more than females, they apparently do not move much further than the distances involved in our sampling areas (2,000m). With our approach, we cannot track individual movements. Sex biases in dispersal could either arise because, on average, all males move larger distances than all females. Alternatively, differences could arise because a higher frequency of males compared to females disperse, even though, when they disperse, both males and females move similar distances(Sutherland et al., 2000). The male bias in dispersal also matches with observational reports of which individuals are first observed at the edge of the range expansion. An earlier study found that, of the first sightings of a great-tailed grackle in a new location, where the sex of the individual was reported, the pioneer individual was a male in 65% of instances (Dinsmore & Dinsmore, 1993).

The male sex bias in dispersal, and the reduced sex bias in the edge population where females also appear to disperse more, might interact with the ongoing range expansion of the great-tailed grackles. In most sexually reproducing species, the distribution and movement of females determines the range limits (Miller & Compagnoni, 2022). Particularly in species where single males mate with multiple females, as in the great-tailed grackles, we would expect that moderate levels of female-biased dispersal would increase the range expansion speed because this would lead to the sex ratio of multiple females per mating male in the new populations (Miller et al., 2011). Accordingly, the adaptability of dispersal behavior in grackles, with both sexes showing more dispersal at the edge than nearer the core, might contribute to their ability to expand into new areas.

These results elucidate that the rapid geographic range expansion of great-tailed grackles is associated with individuals differentially expressing dispersal behaviors. Additional studies are needed to determine the robustness and potential mechanisms involved in finding different dispersal behavior in an edge population. It is not clear whether these differences reflect the particular conditions of edge populations or other ecological conditions that could also influence dispersal behavior. The differences in dispersal behavior could also be linked to differences in other behavior, rather than directly reflecting a response to whether the individuals are at the edge or nearer the core of the distribution. Our previous comparison of several behaviors indicated higher persistence and interindividual differences in behavioral flexibility in the edge population, but no differences in average exploration, innovativeness, or behavioral flexibility (Logan et al., 2023). We hope that our findings will stimulate additional studies into the traits that characterize individuals and populations at the edge of population range expansions.

ETHICS

This research is carried out in accordance with permits from the:

1) US Fish and Wildlife Service (scientific collecting permit number MB76700A-0,1,2)
2) US Geological Survey Bird Banding Laboratory (federal bird banding permit number 23872)
3) Arizona Game and Fish Department (scientific collecting license number SP594338 [2017], SP606267 [2018], SP639866 [2019], and SP402153 [2020])
4) Institutional Animal Care and Use Committee at Arizona State University (protocol number 17-1594R)
5) California Department of Fish and Wildlife (scientific collecting permit [specific use] number S-192100001-19210-001)
6) Institutional Animal Care and Use Committee at the University of California Santa Barbara (protocol number 958)
7) RegionalSan access permit (number AP 2021-01)

AUTHOR CONTRIBUTIONS

Dieter Lukas: Hypothesis development, data analysis and interpretation, write up, revising/editing
Aaron Blackwell: data collection, data interpretation, revising/editing
Maryam Edrisi: data collection, revising/editing
Kristin Hardy: data collection, revising/editing
Christa LeGrande: data collection, revising/editing
Zara Marfori: data collection, revising/editing
Kelsey McCune: data collection, data interpretation, revising/editing
August Sevchik: data collection, data interpretation, revising/editing
Caroline Smith: data collection, revising/editing
Corina Logan: Hypothesis development, data collection, data interpretation, revising/editing, materials/funding.

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CONFLICT OF INTEREST DISCLOSURE

We, the authors, declare that we have no financial conflicts of interest with the content of this article. CJ Logan and D Lukas are Recommenders at PCI Ecology, and CJ Logan was on the Managing Board at PCI Ecology (2018-2022).

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