

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

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23 ABSTRACT

24 It is generally thought that behavioral flexibility, the ability to change behavior when circum-
25 stances change, plays an important role in the ability of a species to rapidly expand their
26 geographic range. However, it is an alternative non-exclusive possibility that an increase in
27 the amount of available habitat can also facilitate a range expansion. Great-tailed grackles
28 (*Quiscalus mexicanus*) are a social, polygamous species that is rapidly expanding its geographic
29 range and eats a variety of human foods in addition to foraging on insects and on the ground
30 for other natural food items. They are behaviorally flexible and highly associated with human-
31 modified environments, thus offering an opportunity to assess the role of behavior and habitat
32 change over the course of their expansion. Here, we compare behavior in wild-caught grack-
33 les from two populations across their range (a more recent population in the middle of the
34 northern expansion front in Arizona versus a very recent population on the northern edge of
35 the expansion front in California) to investigate whether individuals in a more recently estab-
36 lished population exhibit more dispersal behavior (i.e., individuals are more likely to move
37 away from their parents). We find that levels of relatedness are lower in the population closer
38 to the edge compared to the population nearer the core. In particular, we observe no closely
39 related individuals at the edge, suggesting that individuals of both sexes disperse further in
40 this population than in the population nearer the core. Our analyses also suggest that, in both
41 populations, females generally move shorter distances from where they hatched than males.
42 These results elucidate that the rapid geographic range expansion of great-tailed grackles is
43 associated with individuals differentially expressing dispersal behaviors.

44 INTRODUCTION

45 It is generally thought that behavioral flexibility, the ability to change behavior when cir-
46 cumstances change (see Mikhalevich et al., 2017 for theoretical background on our flexibility
47 definition), plays an important role in the ability of a species to rapidly expand their geo-
48 graphic range (Chow et al., 2016; Griffin & Guez, 2014; e.g., Lefebvre et al., 1997; Sol et al.,
49 2002, 2005, 2007; Sol & Lefebvre, 2003). These ideas predict that flexibility, exploration, and
50 innovation facilitate the expansion of individuals into completely new areas and that their
51 role diminishes after a certain number of generations (Wright et al., 2010). In support of this,
52 experimental studies have shown that latent abilities are primarily expressed in a time of need
53 (Auersperg et al., 2012; Bird & Emery, 2009; Laumer et al., 2018; Manrique & Call, 2011; e.g.,
54 Taylor et al., 2007). Therefore, we do not expect the founding individuals who initially dis-
55 persed out of their original range to have unique behavioral characteristics that are passed on
56 to their offspring. Instead, we expect that the actual act of continuing a range expansion relies
57 on flexibility, exploration, innovation, persistence, and dispersal, and that these behaviors are
58 therefore expressed more on the edge of the expansion range where there have not been many
59 generations to accumulate relevant knowledge about the environment.

60 To determine whether behavior is involved in a rapid geographic range expansion, direct mea-
61 sures of individual behavioral abilities must be collected in populations across the range of
62 the species (see the discussion on the danger of proxies of flexibility in Logan et al., 2018).
63 We tested whether dispersal might have played a role in the rapid geographic range expansion
64 of great-tailed grackles (*Quiscalus mexicanus*). Great-tailed grackles are behaviorally flexible
65 (Logan, 2016), rapidly expanding their geographic range (Wehtje, 2003), and highly associated
66 with human-modified environments (Johnson & Peer, 2001), thus offering an opportunity to
67 assess the role of behavior and habitat change over the course of their expansion. This social,
68 polygamous species eats a variety of human foods in addition to foraging on insects and on
69 the ground for other natural food items (Johnson & Peer, 2001).

70 We here compare behavior in wild-caught great-tailed grackles from two populations across
71 their range (a more recent population in the middle of the northern expansion front in Arizona
72 versus a very recent population on the northern edge of the expansion front in California). We
73 investigate whether certain behaviors are expressed differently in the edge population relative
74 to older populations. There could be multiple mechanisms underpinning the results we find,
75 however our aim is to narrow down the role of changes in behavior and changes in habitats
76 in the range expansion of great-tailed grackles. Results will elucidate whether the rapid ge-
77 ographic range expansion of great-tailed grackles is associated with individuals differentially
78 expressing particular behaviors and/or whether the expansion is facilitated by the alignment
79 of their natural behaviors with an increase in suitable habitat (i.e., human-modified environ-
80 ments). The preregistration associated with our article set out multiple hypotheses for how
81 behavior could be linked to the rapid range expansion of great-tailed grackles. We previ-
82 ously completed the research and published the results linked to the hypotheses on habitat
83 changes (Summers et al., 2023), behavioral flexibility, innovativeness, exploration, and persis-
84 tence across the range of great-tailed grackles (Logan CJ et al., 2023) and species differences
85 between great-tailed and boat-tailed grackles (C. Logan et al., 2024).

86 In this article, we compare the dispersal behavior of great-tailed grackles between a recently
87 established population (California) and a population that has existed for several generations
88 (Arizona)(Table 1). We examine whether individuals in a recently established population
89 (California) are more likely to move away from the location where they hatched by determining
90 whether their average relatedness (calculated using single nucleotide polymorphisms, SNPs) is
91 lower than what we would expect if individuals move randomly (Sevchik et al., 2022). Genetic
92 approaches are one of the main ways to determine patterns of dispersal in birds, because
93 actual dispersal events are rare and difficult to study. In most species, individuals only show
94 limited movement from their place of origin to where they themselves breed, creating patterns
95 of isolation by distance as pairs of individuals are less likely to share genetic variants the
96 further away they are (Manel et al., 2003). We measure this sharing of genetic variants using
97 relatedness (Spong & Creel, 2001), with individuals who show low relatedness to others in the
98 population being assumed to have moved further (Aguillon et al., 2017). Though we refer to
99 our two sampling sites as two populations, it is important to note that the distribution of great-
100 tailed grackles appears continuous and connected. Even at the edge, the expansion appears
101 to occur gradually, rather than through the establishment of separate, distanced populations

102 (Wehtje, 2003). Accordingly, our focus is not on the overall levels of genetic diversity or
 103 relatedness in the full sample, but how genetic variation at each site is structured according
 104 to the sex of individuals and the distances between them to lead to patterns of relatedness.

105 **RESEARCH QUESTION**

106 Our research question is listed as it appeared in the preregistration.

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

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

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

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

Site	Range position	Breeding since	Number of years breeding	Average number of generations	Citation
Tempe, Arizona	Middle of expansion	1951	69	12.3	Wehtje 2003, 2004
Woodland, California	Northern edge	2004	16	2.9	Burrowing Owl July 2004, Pandolfino et al. 2009

127 STATE OF THE DATA AND CHANGES FROM PREREGISTRATION

128 The preregistration was written (March 2020) prior to collecting any data from the edge
129 population, therefore we were blind to these data. However, we were not blind to some of the
130 data from the Arizona population: some of the relatedness data (SNPs used for Hypothesis
131 2 to quantify relatedness to infer whether individuals disperse away from relatives) from the
132 middle population (Arizona) had already been analyzed for other purposes (n=57 individuals,
133 see Sevchik et al., 2022). Therefore, we consider it secondary data: data that were collected
134 for other investigations. We collected blood samples from many more grackles in Arizona,
135 and we repeated the analyses for the Arizona population with the complete sample. This
136 preregistration was submitted in May 2020 to PCI Ecology for pre-study peer review. We
137 received the reviews, and revised and resubmitted in August 2020, and it passed pre-study
138 peer review in October 2020.

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

143 METHODS

144 Sample

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

153 Sample size rationale

154 We tested as many great-tailed grackles as we could during the two to three years we spent
155 at each site given that the birds are only brought into the aviaries during the non-breeding
156 season (approximately September through March). It is time intensive to conduct the aviary
157 test battery (2-6 months per bird at the Arizona field site), therefore we approximated that
158 the minimum sample size at each site will follow the minimum sample sizes in Table 2 with
159 the aim that half of the grackles tested at each site are female. We sampled more than the
160 expected 20 grackles per site for the genetic analyses.

161 **Protocols and open materials**

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

181 We performed the SNP processing and selection as in Thrasher et al. (2018), processing the
182 samples from the two populations separately. For Arizona, we combined the genotypes of the
183 individuals sequenced in 2018 with the genotypes sequenced in 2023 prior to the processing
184 so that all individuals have the same set of alleles to compare for the relatedness estimation.
185 Occurrences of rare alleles are likely to differ among the two separate populations, therefore
186 combining the data from the two populations could potentially lead to ascertainment biases,
187 where alleles that occur in the population with the larger sample but not in the population
188 with the smaller sample are included as informative whereas alleles that occur only in the
189 population with the smaller sample are excluded. This would bias the relatedness estimation
190 in the smaller population because differences among individuals in this population would be
191 lost. The re-processing means that, for those individuals already included in Sevchik et al.
192 (2022), the genotypes, and the resulting pairwise relatedness estimates, are slightly different
193 compared to those previously estimated. For both populations, loci were considered only if
194 they were present in 95% of the samples (r) and had a minimum minor allele frequency of 0.05
195 (min maf).

196 To prepare, check, and describe the genotype data (expected heterozygosity, probability of
197 identity), we used functions in the R packages ‘adegenet’ (Jombart, 2008), ‘pegas’ (Paradis,
198 2010), and ‘popgenutils’ (Tourvas, 2020).

199 For each population, we calculated the pairwise relatedness among all dyads of adult indi-
200 viduals using the estimator by Queller & Goodnight (1989), which was more robust for our
201 inferences in a subset of the Arizona data (Sevchik et al., 2022), as implemented in the package

202 ‘related’ (Pew et al., 2015) in R. For the relatedness calculation, we only used the genotypes
203 of individuals in the respective population to derive the allele frequencies that set the baseline
204 chance of sharing alleles. That means that, overall, in both populations average relatedness
205 will be close to zero. Individuals who share fewer alleles than expected have a negative re-
206 latedness value, while individuals who share more alleles than expected have a positive value.
207 Our focus is not on comparing the overall levels of genetic diversity in the two populations,
208 but whether there is structure in the sharing of alleles that lead to patterns of relatedness
209 among individuals of the same sex. We identified as potential kin those pairs of individuals
210 whose estimated relatedness was equal to or larger than 0.25 (closer relatives, at the level of
211 half-siblings) or larger than 0.125 (distant relatives, at the level of cousins).

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

217 **Open data**

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

221 **Blinding during analysis**

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

226 **ANALYSIS**

227 We did not exclude any data except for instances where missing data made analyses not reliable.
228 Samples with a low DNA quantity and quality produce data for only a small number of SNP
229 loci. Relatedness estimates are only reliable if they are based on several hundred SNP loci
230 [wang2016pedigrees, foroughirad2019quality], because small numbers of loci can lead to high
231 variances in the estimates. Analyses were conducted in R [current version 4.3.3; R Core Team
232 (2023)] and Stan (version 2.18, Carpenter et al., 2017). We used functions in the package
233 ‘rethinking’ (McElreath, 2020) to construct and summarize the linear models. Following the
234 social convention of this approach, we report the 89% compatibility intervals (89% CI) of the
235 posterior sample.

236 **Comparison of average relatedness between the two populations**

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

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

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

250 **Comparison of degree of kinship between the two populations**

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

$$\begin{aligned}
 \text{kin}_d &\sim \text{Binomial}(1, p_d) \\
 \text{logit}(p_d) &= \alpha_{\text{pop}[d]} + \beta_{\text{sex}[d], \text{pop}[d]} \\
 \alpha_{\text{pop}[d]} &\sim \text{Normal}(0, 1) \\
 \begin{bmatrix} \beta_{d,1} \\ \beta_{d,2} \end{bmatrix} &\sim \text{MVNormal} \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, S_{\text{sex}} \right)
 \end{aligned}$$

$$S = \begin{pmatrix} \sigma_{sex=1} & 0 \\ 0 & \sigma_{sex=2} \end{pmatrix} R \begin{pmatrix} \sigma_{sex=1} & 0 \\ 0 & \sigma_{sex=2} \end{pmatrix}$$

$$R \sim LKJcorr(4)$$

$$\sigma_{sex} \sim Exponential(1)$$

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

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

267 **Sex biases in dispersal in the two populations**

268 To determine whether, in either or both populations, individuals of one sex are more likely to
 269 disperse farther than individuals of the opposite sex, we first compared the average relatedness
 270 among females to the average relatedness among males in the same population. We performed
 271 10,000 random draws, drawing the same number of individuals from the whole population
 272 as there are females or males in that population, to assess whether the relatedness among
 273 individuals of one sex is different than that observed in a random sample of individuals of the
 274 same size from that population. Next, we determined the geographic distances among those
 275 pairs of individuals identified as potential close or distant kin. We again performed 10,000
 276 draws, drawing the same number as there are kin of that sex from all the females or males in
 277 that population to assess the expected distance among such a sample of same-sex individuals.
 278 If the distances among the 10,000 draws are generally larger than those observed among kin,
 279 then we infer that kin of that sex remain closer together than what would be expected by
 280 chance. Finally, we performed assessments of spatial autocorrelation to link the pairwise
 281 relatedness among individuals of each sex to the geographic distances of their locations.

282 To test whether males and females show different patterns of genetic isolation by geographic
 283 distance, we followed analyses as in Aguillon et al. (2017). In each population, for males and
 284 females separately, we assessed the strength of the association between the the matrices of
 285 average relatedness and of geographic distance using Mantel correlograms with the function
 286 ‘mantel.correlog’ in the ‘vegan’ package (Oksanen et al., 2013) in R. For each of the four

287 associations (two sexes in two populations), we performed 10,000 permutations to assess the
288 strength of the association. The approach involves partitioning the geographic locations into
289 a series of discrete distance classes. We used two methods to create the distance classes.
290 First, we attempted to have about equal numbers of pairs of individuals within each distance
291 class, creating nine distance classes of (0-100m, 100-200m, 200-300m, 300-400m, 400-500m,
292 500-750m, 750-1000m, 1 000-1250m, and 1250-2000m). With the second method, we only
293 created two distance classes to increase the sample size in each class, splitting the distance
294 according to the limit at which most close kin were detected (0-400m and 400-1400m). For each
295 distance class, a normalized Mantel statistic is calculated using permutations of values within
296 that distance class. The permutation statistics, plotted against distance classes, produce
297 a multivariate correlogram. A negative correlation between genetic relatedness and spatial
298 distance indicates that the more closely related individuals are found closer to each other,
299 indicating that these individuals likely disperse shorter distances than those individuals where
300 a positive correlation is found.

301 RESULTS

302 Summary statistics

303 *California SNP data*

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

319 *Arizona SNP data*

320 We retained 462 SNPs. Data was missing for 3.0% of all alleles (individuals missing information
321 for either one or both of their chromosomes for that particular position). None of the SNPs
322 showed a particular underrepresentation of information. There were three individuals whose
323 genotypes were less complete (A072KB, adult female, missing data at 191 (41%) of SNPs;
324 A088YR, adult male, missing data at 174 (38%) of SNPs; A059NB, adult female, at 148 (32%)
325 of SNPs), whereas all other individuals had data missing at less than 10% of SNPs. Here,

326 we did not exclude any individuals because the number of SNPs with information was still
327 sufficiently high for all genotypes to reduce the noise in the relatedness estimation. All SNPs
328 had two alleles and the observed heterozygosity (individuals carrying one copy each of the two
329 bases) was 0.29, similar to the heterozygosity expected in a population with the same allele
330 frequencies and random mating. The probability of identity for siblings, the chance that two
331 siblings will show the same genotypes given the allele frequencies across these 462 SNP loci
332 and random mating among individuals, is less than 10^{-60} .

333 *Sample*

334 In total, we included genotype information for 52 females and 27 males in Arizona, and 13
335 females and 15 males in California. In Arizona, all birds were found within a maximum of
336 1,991m from each other (median 669m). In California, birds were found at multiple locations.
337 Twelve females and twelve males were found at a location in Sacramento that spanned about
338 the same range as the population in Arizona (maximum geographic distance 1,592m, median
339 474m). Three birds (one female, two males) were resighted at a separate location in Sacramento
340 ~7,000m away from the main location. In addition, one male was trapped and resighted at
341 a location ~33,000m away in Woodland. Therefore, the maximum and average geographic
342 distances between the locations of individuals are much higher for the California sample than
343 the Arizona sample. For the set of analyses that include pairwise geographic distances among
344 individuals, we performed the analyses only with the birds found at the single location in
345 Sacramento in order to keep the California population comparable to the Arizona population
346 (i.e., we excluded these four birds).

347 **Difference in dispersal behavior between the two populations**

348 *Comparison of average relatedness in the two populations*

349 Overall, the average relatedness among individuals in the two populations is slightly negative,
350 which is more pronounced in California (average relatedness: Arizona -0.013, California -
351 0.037). This slight skew toward negative relatedness values suggests that both populations,
352 but particularly the population in California, might contain individuals who have immigrated
353 into these populations and are therefore sharing fewer alleles than would be expected by chance.
354 In Arizona, males (-0.009) have slightly higher average relatedness than females (-0.013). In
355 California, females (-0.024) have higher average relatedness than males (-0.048).

356 The model comparing levels of pairwise relatedness between the two populations indicates
357 that the values in California are consistently lower than the values in Arizona because their
358 confidence intervals do not cross zero (median of contrast for females -0.003, 89%CI of contrast
359 -0.006 to -0.001, for males median -0.009, 89% CI -0.011 to -0.007).

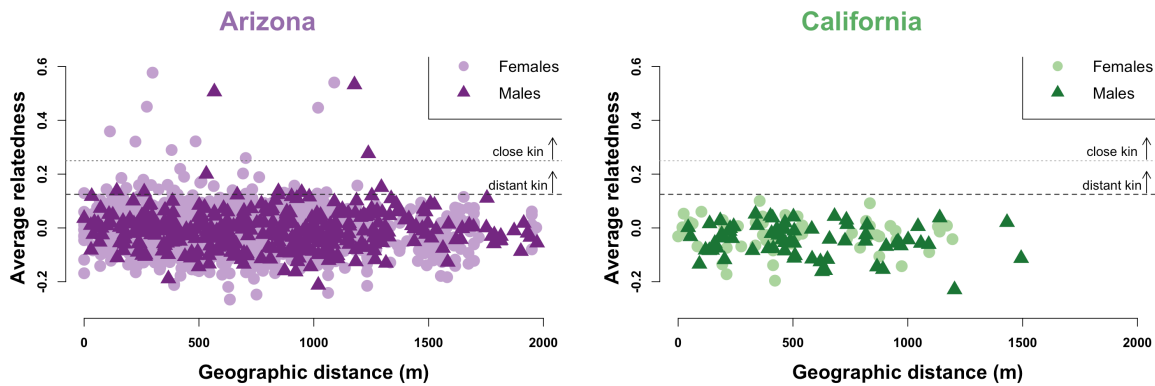
360 *Comparison of the degree of likely kin in the two populations*

361 Overall, in both populations we identified very low numbers of dyads that are potentially kin
362 (Figure 1). In California, none of the dyads are estimated to be related with $r > 0.25$, and only
363 one opposite sex dyad is estimated to be related with $r > 0.125$ (out of 105 male-male dyads, 78
364 female-female dyads, and 195 opposite sex dyads). In Arizona, 3 male-male dyads (0.9% of the

365 351 male-male dyads), 12 opposite sex dyads (0.9% of the 1404 dyads), and 9 female-female
 366 dyads (0.7% of 1326 dyads) are estimated to be related with $r \geq 0.25$. With the lower threshold
 367 of $r \geq 0.125$, 9 (2.5%) of all male-male dyads, 39 (2.9%) of female-female dyads, and 32 (2.3%)
 368 of opposite sex dyads in Arizona are classified as related.

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

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



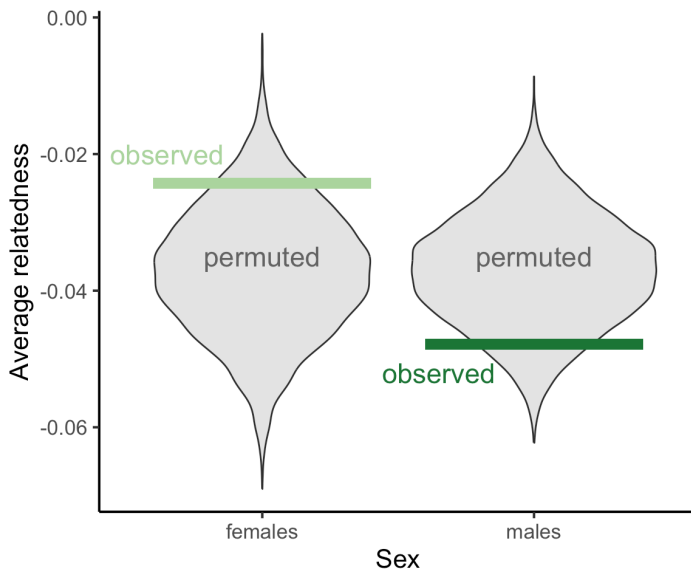
380
 381 Figure 1: The relatedness and geographic distance observed among grackles in Arizona (left,
 382 purple) and in California (right, green). Average relatedness is higher in Arizona than in
 383 California. In Arizona, there are several pairs of females (lighter circles) and males (darker
 384 triangles) who are related at levels higher than 0.25 (dotted line, close kin of half-sibling or
 385 closer) and 0.125 (dashed line, distant kin of cousin or closer), while there are no close or
 386 distant same-sex kin in California. In terms of potential sex-biases in dispersal, in Arizona,
 387 we observe more females than males related at levels of distant kin and of close kin. Closely
 388 related females tend to be found at shorter geographic distances than the average female pair,
 389 while closely related males are not found at short geographic distances.

390 Sex biases in dispersal in the two populations

391 *Average relatedness within the sexes*

392 Average relatedness among both the females and the males in Arizona is not different from what

393 would be expected by chance. Randomly drawing the same number of individuals from the
 394 full sample gives an average relatedness that is lower than that observed among the females in
 395 45% of permutations and for males in 29% of permutations. In contrast, the observed average
 396 relatedness among females in California is slightly higher than what would be expected by
 397 chance, with 90% of the permutations drawing the same number of individuals from the
 398 overall population as there are females leading to lower average relatedness than that observed
 399 among the females (Figure 2). In contrast, the observed average relatedness among males is
 400 slightly less than what would be expected by chance given the relatedness among individuals
 401 in this population, with 91% of permutations giving higher levels of average relatedness than
 402 that observed among the males (Figure 2).



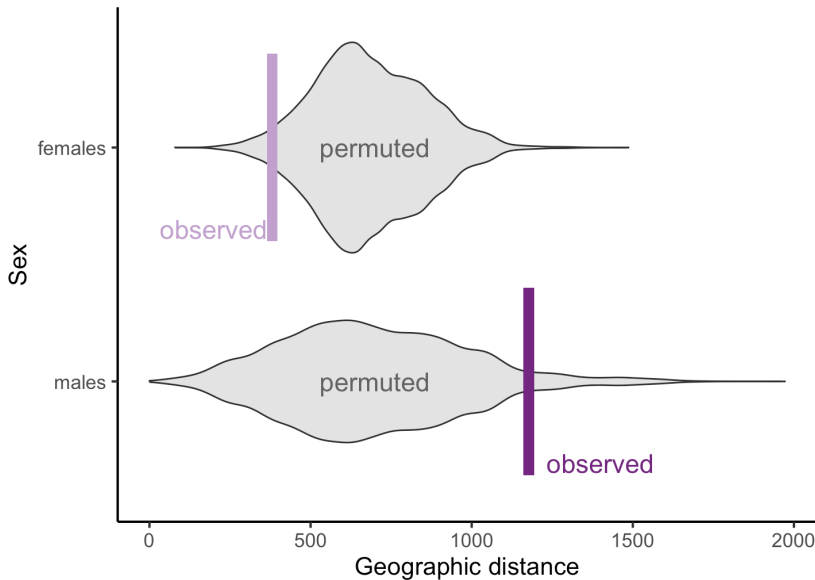
403

404 Figure 2: In California, the average relatedness observed among females (light green line,
 405 left) is higher than the average relatedness observed in most permutations, while the average
 406 relatedness observed among males (dark green line, right) is lower than the relatedness observed
 407 in most permutations. 10,000 permutations were performed for each sex, drawing a subset of
 408 individuals from the total sample and calculating their average relatedness. The width of the
 409 violin plot (grey shaded area) reflects the number of permutations during which a particular
 410 level of average relatedness was observed.

411 *Distances among kin of the different sexes*

412 In Arizona, the only population where our relatedness calculations indicated likely kin, females
 413 related at r 0.25 are found a median of 391m from each other, while males related at this level
 414 are found 1,177m from each other (Figure 1). Similarly, females related at r 0.125 are found a
 415 median of 435m from each other, while males related at this level are found 846m from each
 416 other. These differences in distance are not due to females generally being found closer to
 417 each other, because in only 2% of permutations drawing from the same number of female and

418 male dyads as those that are related at the respective levels, are the differences in distance as
 419 large or larger than those observed (Figure 3). We cannot perform this analysis for California
 420 because there are no kin among either sex (Figure 1).



421

422 Figure 3: In Arizona, females related at r 0.25 (light purple line, top) are found closer to each
 423 other than the average set of females (grey shaded area, top), while males related at r 0.25
 424 (dark purple line, bottom) are found at larger distances from each other than the average set of
 425 males (grey shaded area, bottom). 10,000 permutations were performed for each sex, drawing
 426 a subset of individuals from the total sample matching the number of close kin and calculating
 427 their average geographic distance. The width of the violin plot (grey shaded area) reflects the
 428 number of permutations during which a particular average distance was observed.

429 *Spatial autocorrelation between geographic distance and relatedness in the two sexes*

430 The spatial autocorrelation analyses indicate that, in both Arizona and California, female
 431 relatives likely stay close to each other while male relatives move away from each other (Figure
 432 1). For Arizona, more closely related females are found at shorter distances from each other
 433 (negative correlation between relatedness and geographic distance based on a Mantel test when
 434 females are close, -0.08 , $p=0.02$; positive correlation when females are far, 0.06 , $p=0.03$). In
 435 contrast, at short distances males are not related to each other (0.05 , $p=0.21$), but relatives are
 436 found at larger distances (-0.11 , $p=0.02$). The same pattern is found for females in California,
 437 though with the smaller sample size, the effects are not significant (females close -0.15 , $p=0.12$,
 438 distant 0.15 , $p=0.12$), whereas for males there is no obvious pattern (close 0.04 , $p=0.38$; distant
 439 0.04 , $p=0.43$). These results are similar when using the larger number of distance classes, with
 440 correlations switching from negative to positive for females as distance increases, and from
 441 positive to negative for males.

442 **DISCUSSION**

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

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

478 Previous theoretical and empirical studies predict such increased dispersal at the edge of a
479 population expansion. Multiple processes could contribute to the higher dispersal at the edge
480 of the population expansion. The higher frequency of dispersers at the edge could result from
481 simple sorting processes, whereby highly dispersive individuals are over-represented in edge

482 populations because they are more likely to end up in these novel areas Travis & Dytham
483 (2002). Alternatively, or in addition, the conditions at the edge could shift the trade-off of
484 the costs and benefits towards dispersing in the edge population Chuang & Peterson (2016).
485 Such trade-offs linked to expansion have been observed in relation to dispersal of aggressive
486 individuals in bluebirds (Duckworth & Badyaev, 2007) and morphological adaptation for speed
487 in cane toads (Clarke et al., 2019). Great-tailed grackle females, who show more of a change
488 in their dispersal patterns at the edge, are likely to have changes in their trade-offs of the costs
489 and benefits of dispersal. At the edge, females might gain increased benefits from dispersing
490 via reduced resource competition by moving into new areas. In contrast, nearer the core,
491 females might benefit from local knowledge and potential kin tolerance when remaining, but
492 would face competition even if they move because all areas are already occupied.

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

507 In both populations, we find indications of a sex bias in dispersal, with females apparently
508 dispersing shorter distances than males. Despite the absence of close relatives in California,
509 the analyses linking relatedness to geographic distance also supports a similar bias in this
510 population. This confirms our previous conclusion with a smaller sample in Arizona (Sevchik
511 et al., 2022). We find more male relatives in Arizona than in our earlier study that used a
512 subset of these Arizona individuals (Sevchik et al., 2022). This indicates that, while males
513 disperse more than females, they apparently do not move much further than the distances
514 involved in our sampling areas (2,000m). With our approach, we cannot track individual
515 movements. Sex biases in dispersal could either arise because, on average, all males move larger
516 distances than all females. Alternatively, differences could arise because a higher frequency of
517 males compared to females disperse, even though, when they disperse, both males and females
518 move similar distances (Sutherland et al., 2000). The male bias in dispersal also matches with
519 observational reports of which individuals are first observed at the edge of the range expansion.
520 An earlier study found that, of the first sightings of a great-tailed grackle in a new location,
521 where the sex of the individual was reported, the pioneer individual was a male in 65% of
522 instances (Dinsmore & Dinsmore, 1993). The male sex bias in great-tailed grackle dispersal
523 is the opposite of that found in most other bird species (Greenwood, 1980) where single pairs

524 of males and females breed monogamously, and males remain where they were hatched and
525 females disperse. This contrast in the great-tailed grackle sex bias in dispersal matches their
526 social and mating system of polygamous breeding in larger groups (Wehtje, 2003), which is
527 more similar to that of mammals where males generally disperse further than females (Trochet
528 et al., 2016).

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

539 Our study on dispersal supports the role of variability in behavior for the ability of great-
540 tailed grackles to rapidly expand their range, in line with our other findings resulting from
541 this preregistration. Additional studies are needed to determine the robustness and potential
542 mechanisms involved in finding different dispersal behavior in an edge population. It is not
543 clear whether these differences reflect the particular conditions of edge populations or other
544 ecological conditions that could also influence dispersal behavior. The differences in dispersal
545 behavior could also be linked to differences in other behavior, rather than directly reflecting
546 a response to whether the individuals are at the edge or nearer the core of the distribution.
547 Our previous comparison of several behaviors indicated higher persistence and interindivid-
548 ual differences in behavioral flexibility in the edge population, but no differences in average
549 exploration, innovativeness, or behavioral flexibility (Logan CJ et al., 2023). In addition,
550 these analyses can not unravel whether the differences in dispersal behavior reflect population
551 level differences in the expression of individual behavior. Alternatively, individuals with high
552 dispersal tendencies might occur across the range, but, at the edge, those dispersing the fur-
553 thest might accumulate because of the lag in arrival of individuals with lower dispersal ability.
554 We hope that our findings will stimulate additional studies into the traits that characterize
555 individuals and populations at the edge of population range expansions.

556 **ETHICS**

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

- 558 1) US Fish and Wildlife Service (scientific collecting permit number MB76700A-0,1,2)
- 559 2) US Geological Survey Bird Banding Laboratory (federal bird banding permit number
560 23872)
- 561 3) Arizona Game and Fish Department (scientific collecting license number SP594338 [2017],
562 SP606267 [2018], SP639866 [2019], and SP402153 [2020])
- 563 4) Institutional Animal Care and Use Committee at Arizona State University (protocol
564 number 17-1594R)
- 565 5) California Department of Fish and Wildlife (scientific collecting permit [specific use]
566 number S-192100001-19210-001)
- 567 6) Institutional Animal Care and Use Committee at the University of California Santa
568 Barbara (protocol number 958)
- 569 7) RegionalSan access permit (number AP 2021-01)

570 **AUTHOR CONTRIBUTIONS**

571 **Dieter Lukas:** Hypothesis development, data analysis and interpretation, write up, revis-
572 ing/editing

573 **Aaron Blackwell:** data collection, data interpretation, revising/editing

574 **Maryam Edrisi:** data collection, revising/editing

575 **Kristin Hardy:** data collection, revising/editing

576 **Zara Marfori:** data collection, revising/editing

577 **Kelsey McCune:** data collection, data interpretation, revising/editing

578 **August Sevchik:** data collection, data interpretation, revising/editing

579 **Caroline Smith:** data collection, revising/editing

580 **Corina Logan:** Hypothesis development, data collection, data interpretation, revis-
581 ing/editing, materials/funding.

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585 **CONFLICT OF INTEREST DISCLOSURE**

586 We, the authors, declare that we have no financial conflicts of interest with the content of this
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602 **REFERENCES**

- 603 Aguilon, S. M., Fitzpatrick, J. W., Bowman, R., Schoech, S. J., Clark, A. G., Coop, G.,
604 & Chen, N. (2017). Deconstructing isolation-by-distance: The genomic consequences of
605 limited dispersal. *PLoS Genetics*, *13*(8), e1006911. [https://doi.org/10.1371/journal.pgen.
606 1006911](https://doi.org/10.1371/journal.pgen.1006911)
- 607 Auersperg, A., Szabo, B., Von Bayern, A. M., & Kacelnik, A. (2012). Spontaneous innovation
608 in tool manufacture and use in a goffin's cockatoo. *Current Biology*, *22*(21), R903–R904.
609 <https://doi.org/10.1016/j.cub.2012.09.002>
- 610 Bird, C. D., & Emery, N. J. (2009). Insightful problem solving and creative tool modification
611 by captive nontool-using rooks. *Proceedings of the National Academy of Sciences*, *106*(25),
612 10370–10375. <https://doi.org/10.1073/pnas.0901008106>
- 613 Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker,
614 M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language.
615 *Journal of Statistical Software*, *76*(1). <https://doi.org/10.18637/jss.v076.i01>
- 616 Chow, P. K. Y., Lea, S. E., & Leaver, L. A. (2016). How practice makes perfect: The role of
617 persistence, flexibility and learning in problem-solving efficiency. *Animal Behaviour*, *112*,
618 273–283. <https://doi.org/10.1016/j.anbehav.2015.11.014>
- 619 Chuang, A., & Peterson, C. R. (2016). Expanding population edges: Theories, traits, and
620 trade-offs. *Global Change Biology*, *22*(2), 494–512. <https://doi.org/10.1111/gcb.13107>
- 621 Clarke, G. S., Shine, R., & Phillips, B. L. (2019). May the (selective) force be with you: Spatial
622 sorting and natural selection exert opposing forces on limb length in an invasive amphibian.
623 *Journal of Evolutionary Biology*, *32*(9), 994–1001. <https://doi.org/10.1111/jeb.13504>
- 624 Dinsmore, J. J., & Dinsmore, S. J. (1993). Range expansion of the great-tailed grackle in the
625 1900s. *Journal of the Iowa Academy of Science: JIAS*, *100*(2), 54–59.

- 626 Duckworth, R. A., & Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates
627 the rapid range expansion of a passerine bird. *Proceedings of the National Academy of*
628 *Sciences*, 104(38), 15017–15022. <https://doi.org/10.1073/pnas.0706174104>
- 629 Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals.
630 *Animal Behaviour*, 28(4), 1140–1162. [https://doi.org/10.1016/S0003-3472\(80\)80103-5](https://doi.org/10.1016/S0003-3472(80)80103-5)
- 631 Griffin, A. S., & Guez, D. (2014). Innovation and problem solving: A review of common
632 mechanisms. *Behavioural Processes*, 109, 121–134. [https://doi.org/10.1016/j.beproc.2014.](https://doi.org/10.1016/j.beproc.2014.08.027)
633 [08.027](https://doi.org/10.1016/j.beproc.2014.08.027)
- 634 Hijmans, R. J. (2022). *Geosphere: Spherical trigonometry*. [https://CRAN.R-project.org/](https://CRAN.R-project.org/package=geosphere)
635 [package=geosphere](https://CRAN.R-project.org/package=geosphere)
- 636 International, B. (2018). *Quiscalus mexicanus*. *The IUCN Red List of Threatened*
637 *Species 2018*, e.T22724308A132174807. [http://dx.doi.org/10.2305/IUCN.UK.2018-](http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22724308A132174807.en)
638 [2.RLTS.T22724308A132174807.en](http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22724308A132174807.en)
- 639 Johnson, K., & Peer, B. D. (2001). Great-tailed grackle: *Quiscalus mexicanus*. In A. Poole &
640 F. Gill (Eds.), *The birds of north america*. Cornell Lab of Ornithology, Ithaca, NY, USA.
641 <https://doi.org/10.2173/BNA.GRTGRA.02>
- 642 Jombart, T. (2008). Adegnet: A r package for the multivariate analysis of genetic markers.
643 *Bioinformatics*, 24, 1403–1405. <https://doi.org/10.1093/bioinformatics/btn129>
- 644 Laumer, I., Call, J., Bugnyar, T., & Auersperg, A. (2018). Spontaneous innovation of hook-
645 bending and unbending in orangutans (*Pongo abelii*). *Scientific Reports*, 8(1), 1–13. <https://doi.org/10.1038/s41598-018-34607-0>
- 646 Lefebvre, L., Whittle, P., Lascaris, E., & Finkelstein, A. (1997). Feeding innovations and
647 forebrain size in birds. *Animal Behaviour*, 53(3), 549–560. [https://doi.org/10.1006/anbe.](https://doi.org/10.1006/anbe.1996.0330)
648 [1996.0330](https://doi.org/10.1006/anbe.1996.0330)
- 649 Logan, C. J. (2016). Behavioral flexibility and problem solving in an invasive bird. *PeerJ*, 4,
650 e1975. <https://doi.org/10.7717/peerj.1975>
- 651 Logan, C. J., Avin, S., Boogert, N., Buskell, A., Cross, F. R., Currie, A., Jelbert, S., Lukas,
652 D., Mares, R., Navarrete, A. F., et al. (2018). Beyond brain size: Uncovering the neural
653 correlates of behavioral and cognitive specialization. *Comparative Cognition & Behavior*
654 *Reviews*. <https://doi.org/10.3819/CCBR.2018.130008>
- 655 Logan, CJ, McCune, KB, LeGrande-Rolls C, Marfori Z, Hubbard J, & Lukas, D. (2023).
656 Implementing a rapid geographic range expansion - the role of behavior changes. *Peer*
657 *Community Journal*. <https://doi.org/10.24072/pcjournal.320>
- 658 Logan, C., McCune, K., Rowney, C., & Lukas, D. (2024). Behavioral flexibility is similar
659 in two closely related species where only one is rapidly expanding its geographic range.
660 *EcoEvoRxiv*. <https://doi.org/10.32942/X2Q038>
- 661 Lukas, D., & Logan, C. (2024). Data and code associated with "reduced levels of relatedness
662 indicate that great-tailed grackles disperse further at the edge of their range". *Edmond,*
663 *Data package*. <https://doi.org/10.17617/3.Z1VCPT>
- 664 Lukas, D., Reynolds, V., Boesch, C., & Vigilant, L. (2005). To what extent does living in
665 a group mean living with kin? *Molecular Ecology*, 14(7), 2181–2196. [https://doi.org/10.](https://doi.org/10.1111/j.1365-294X.2005.02560.x)
666 [1111/j.1365-294X.2005.02560.x](https://doi.org/10.1111/j.1365-294X.2005.02560.x)
- 667 Manel, S., Schwartz, M. K., Luikart, G., & Taberlet, P. (2003). Landscape genetics: Com-
668

669 bining landscape ecology and population genetics. *Trends in Ecology & Evolution*, 18(4),
670 189–197. [https://doi.org/10.1016/S0169-5347\(03\)00008-9](https://doi.org/10.1016/S0169-5347(03)00008-9)

671 Manrique, H. M., & Call, J. (2011). Spontaneous use of tools as straws in great apes. *Animal*
672 *Cognition*, 14(2), 213–226. <https://doi.org/10.1007/s10071-010-0355-4>

673 McElreath, R. (2020). *Statistical rethinking: A bayesian course with examples in r and stan*.
674 Chapman; Hall/CRC, Boca Raton, FL. <https://doi.org/10.1201/9780429029608>

675 Mikhalevich, I., Powell, R., & Logan, C. (2017). Is behavioural flexibility evidence of cogni-
676 tive complexity? How evolution can inform comparative cognition. *Interface Focus*, 7(3),
677 20160121. <https://doi.org/10.1098/rsfs.2016.0121>

678 Miller, T. E., & Compagnoni, A. (2022). Two-sex demography, sexual niche differentiation, and
679 the geographic range limits of texas bluegrass (*poa arachnifera*). *The American Naturalist*,
680 200(1), 17–31. <https://doi.org/10.1086/719668>

681 Miller, T. E., Shaw, A. K., Inouye, B. D., & Neubert, M. G. (2011). Sex-biased dispersal
682 and the speed of two-sex invasions. *The American Naturalist*, 177(5), 549–561. <https://doi.org/10.1086/659628>

683

684 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O’hara, R., Simpson, G.
685 L., Solymos, P., Stevens, M. H. H., Wagner, H., et al. (2013). Package “vegan.” *Community*
686 *Ecology Package, Version*, 2(9), 1–295.

687 Paradis, E. (2010). Pegas: An R package for population genetics with an integrated–modular
688 approach. *Bioinformatics*, 26, 419–420. <https://doi.org/10.1093/bioinformatics/btp696>

689 Parker, P. G., Waite, T. A., Heinrich, B., & Marzluff, J. M. (1994). Do common ravens share
690 ephemeral food resources with kin? DNA fingerprinting evidence. *Animal Behaviour*, 48(5),
691 1085–1093. <https://doi.org/10.1006/anbe.1994.1342>

692 Pereira, A. S., De Moor, D., Casanova, C., & Brent, L. J. (2023). Kinship composition
693 in mammals. *Royal Society Open Science*, 10(7), 230486. <https://doi.org/10.1098/rsos.230486>

694

695 Pew, J., Muir, P. H., Wang, J., & Frasier, T. R. (2015). Related: An R package for analysing
696 pairwise relatedness from codominant molecular markers. *Molecular Ecology Resources*,
697 15(3), 557–561. <https://doi.org/10.1111/1755-0998.12323>

698 R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation
699 for Statistical Computing. <https://www.R-project.org>

700 Ross, C. T., McElreath, R., & Redhead, D. (2024). Modelling animal network data in R
701 using STRAND. *Journal of Animal Ecology*, 93(3), 254–266. <https://doi.org/10.1111/1365-2656.14021>

702

703 Sevchik, A., Logan, C. J., McCune, K., Blackwell, A. D., Rowney, C., & Lukas, D. (2022).
704 *Investigating sex differences in genetic relatedness in great-tailed grackles in tempe, arizona*
705 *to infer potential sex biases in dispersal*. 9, 37–52. <https://doi.org/10.26451/abc.09.01.04.2022>

706

707 Shine, R., Brown, G. P., & Phillips, B. L. (2011). An evolutionary process that assembles
708 phenotypes through space rather than through time. *Proceedings of the National Academy*
709 *of Sciences*, 108(14), 5708–5711. <https://doi.org/10.1073/pnas.1018989108>

710 Simmons, A. D., & Thomas, C. D. (2004). Changes in dispersal during species’ range expan-
711 sions. *The American Naturalist*, 164(3), 378–395. <https://doi.org/10.1086/423430>

- 712 Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005). Big brains,
713 enhanced cognition, and response of birds to novel environments. *Proceedings of the Na-*
714 *tional Academy of Sciences of the United States of America*, *102*(15), 5460–5465. <https://doi.org/10.1073/pnas.0408145102>
715
- 716 Sol, D., & Lefebvre, L. (2003). Behavioural flexibility predicts invasion success in birds intro-
717 duced to new zealand. *Oikos*, *90*(3), 599–605. [https://doi.org/10.1034/j.1600-0706.2000.](https://doi.org/10.1034/j.1600-0706.2000.900317.x)
718 [900317.x](https://doi.org/10.1034/j.1600-0706.2000.900317.x)
- 719 Sol, D., Székely, T., Liker, A., & Lefebvre, L. (2007). Big-brained birds survive better in
720 nature. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*(1611),
721 763–769. <https://doi.org/10.1098/rspb.2006.3765>
- 722 Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success
723 in birds. *Animal Behaviour*, *63*(3), 495–502. <https://doi.org/10.1006/anbe.2001.1953>
- 724 Spong, G., & Creel, S. (2001). Deriving dispersal distances from genetic data. *Proceedings of*
725 *the Royal Society of London. Series B: Biological Sciences*, *268*(1485), 2571–2574. <https://doi.org/10.1098/rspb.2001.1835>
726
- 727 Summers, J., Lukas, D., Logan, C., & Chen, N. (2023). The role of climate change and niche
728 shifts in divergent range dynamics of a sister-species pair. *Peer Community Journal*, *3*.
729 <https://doi.org/10.24072/pcjournal.248>
- 730 Sutherland, G. D., Harestad, A. S., Price, K., & Lertzman, K. P. (2000). Scaling of natal
731 dispersal distances in terrestrial birds and mammals. *Conservation Ecology*, *4*(1).
- 732 Taylor, A. H., Hunt, G. R., Holzhaider, J. C., & Gray, R. D. (2007). Spontaneous metatool use
733 by new caledonian crows. *Current Biology*, *17*(17), 1504–1507. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.cub.2007.07.057)
734 [cub.2007.07.057](https://doi.org/10.1016/j.cub.2007.07.057)
- 735 Thrasher, D. J., Butcher, B. G., Campagna, L., Webster, M. S., & Lovette, I. J. (2018).
736 Double-digest RAD sequencing outperforms microsatellite loci at assigning paternity and
737 estimating relatedness: A proof of concept in a highly promiscuous bird. *Molecular Ecology*
738 *Resources*, *18*(5), 953–965. <https://doi.org/10.1111/1755-0998.12771>
- 739 Tourvas, N. (2020). PopGenUtils: An R package of helper functions for the analysis of popu-
740 lation genetics data. <https://github.com/Nikostourvas/PopGenUtils/>.
- 741 Travis, J. M., & Dytham, C. (2002). Dispersal evolution during invasions. *Evolutionary*
742 *Ecology Research*, *4*(8), 1119–1129.
- 743 Trochet, A., Courtois, E. A., Stevens, V. M., Baguette, M., Chaine, A., Schmeller, D. S.,
744 Clobert, J., & Wiens, J. J. (2016). Evolution of sex-biased dispersal. *The Quarterly*
745 *Review of Biology*, *91*(3), 297–320. <https://doi.org/10.1086/688097>
- 746 Wehtje, W. (2003). The range expansion of the great-tailed grackle (*quiscalus mexicanus*
747 *gmelin*) in north america since 1880. *Journal of Biogeography*, *30*(10), 1593–1607. <https://doi.org/10.1046/j.1365-2699.2003.00970.x>
748
- 749 Wehtje, W. (2004). *The great-tailed grackle (Quiscalus mexicanus Gmelin) in the Western*
750 *United States of America: Range expansion and secondary contact between subspecies*. Uni-
751 versity of California, Riverside.
- 752 Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L., & Russello, M. A. (2010).
753 Behavioral flexibility and species invasions: The adaptive flexibility hypothesis. *Ethology*
754 *Ecology & Evolution*, *22*(4), 393–404. <https://doi.org/10.1080/03949370.2010.505580>