

# Behavioral flexibility is similar in two closely related species where only one is rapidly expanding its geographic range

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## Abstract

Human modified environments are rapidly increasing, which puts other species in the precarious position of either adapting to a new area or, if they are not able to adapt, shifting their range to a more suitable environment. 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 determine whether species differences in range expansion propensity are linked to differences in behavioral flexibility, we compared two closely related species, great-tailed grackles (*Quiscalus mexicanus*; GTGR) and boat-tailed grackles (*Quiscalus major*; BTGR). The former is rapidly expanding their geographic range by settling in new areas, whereas the latter is not. We previously found that GTGR are behaviorally flexible, however not much is known about BTGR behavior, which provides an ideal way to test the hypothesis that behavioral flexibility plays a key role in the GTGR rapid range expansion using the comparative method. We compared behavioral flexibility of GTGR from two populations across their range (an older population in the middle of the northern expansion front: Tempe, Arizona, and a more recent population on the northern edge of the expansion front: Woodland, California) with BTGR from Venus, Florida, to investigate whether the rapidly expanding GTGR are more flexible. We found that both species, and both GTGR populations, have similar levels of flexibility (measured as food type switching rates during focal follows). Our results elucidate that, while GTGR are highly flexible, flexibility may not be the primary factor involved in their successful range expansion. If this were the case, we would expect to see a rapid range expansion in BTGR as well. This comparative perspective adds further support to our previous intraspecific findings that persistence and flexibility variance play a larger role in the edge GTGR population than in the GTGR population away from the edge. Our research indicates that the hypothesis that flexibility is the primary facilitator of rapid geographic range expansions into new areas needs to be revisited.

**Keywords:** behavioral flexibility, boat-tailed grackle, *Quiscalus major*, great-tailed grackle, *Quiscalus mexicanus*, focal follow, food type, range expansion, comparative approach

## 40 Introduction

41 Human modified environments are rapidly increasing (Goldewijk, 2001; Wu et al., 2011; Liu et al., 2020),  
42 which puts other species in the precarious position of either requiring the ability to adapt to a new area  
43 or, if they are not able to adapt, moving to a different area if they are able to (Sol et al., 2014, 2017).  
44 Behavioral flexibility (hereafter, ‘flexibility’), the ability to change behavior when circumstances change via  
45 processing information that becomes available to other cognitive processes (see Mikhalevich et al., 2017 for  
46 theoretical background), is hypothesized to play an important role in the ability of a species to adjust to new  
47 areas and rapidly expand its geographic range (Lefebvre et al., 1997; Sol et al., 2002; Wright et al., 2010;  
48 Griffin & Guez, 2014; Chow et al., 2016). The prediction is that flexibility, along with behaviors such as  
49 exploration, and innovation, facilitate the expansion of individuals into completely new areas, and that the  
50 role of these behaviors diminishes after an initial adjustment stage (Wright et al., 2010). This prediction is  
51 supported by experimental studies that have shown that latent abilities are primarily expressed when needed  
52 (e.g., Taylor et al., 2007; Bird & Emery, 2009; Manrique & Call, 2011; Auersperg et al., 2012; Laumer et  
53 al., 2018). Therefore, the founding individuals who initially dispersed out of their original range should  
54 not have unique behavioral characteristics that are passed on to their offspring. Instead, the continuation  
55 of a range expansion should rely on flexibility, and potentially behaviors such as exploration, innovation,  
56 and persistence. These behaviors should therefore be expressed more on the edge of the expansion range  
57 where there have not been many generations to accumulate relevant knowledge about the environment, and  
58 expressed more in species that are rapidly expanding their range relative to species that are not.

59 Whether and how flexibility relates to a rapid range expansion is still an open question (Wright et al., 2010).  
60 To determine whether behaviors are involved, they must be directly measured in individuals in populations  
61 across the range of the species, and, ideally, also include cross-species comparisons using the same methods  
62 Logan et al. (2024). There is only a small amount of direct evidence that is beginning to answer this question  
63 and it suggests that populations on the range edge express certain behaviors more than populations away  
64 from the edge. Cohen et al. (2020) showed that common mynas (*Acridotheres tristis*) in populations on  
65 the edge were more innovative and less neophobic with food than individuals in populations away from the  
66 edge, while there were no differences in object neophobia. Logan et al. (2023b) found that edge great-tailed  
67 grackles (*Quiscalus mexicanus*) were more persistent and had a higher flexibility variance than individuals  
68 in a more central population, while there were no differences in average flexibility, innovation, or exploration.  
69 Evidence also shows that individuals on the edge or in newer populations were faster to eat new foods  
70 (house sparrows, *Passer domesticus*) (Martin & Fitzgerald, 2005; Liebl & Martin, 2014) and were more risk  
71 averse (bank voles *Myodes glareolus*) (Eccard et al., 2022) than individuals away from the edge or in older  
72 populations. In contrast, spiders (*Cyrtophora citricola*) at newer sites were less exploratory and less bold  
73 than spiders at older sites (Chuang & Riechert, 2021). Such differences can also vary seasonally: Liebl &  
74 Martin (2012) found that house sparrows closer to the edge were more exploratory than those away from the  
75 edge, but only during the breeding season. This suggests that behavior is differentially involved in expanding  
76 a range, however flexibility may not play the primary role and the relative expression of the behaviors might  
77 be contrary to predictions.

78 While some intra-species comparisons of behaviors in edge and non-edge populations exist, we were not able  
79 to find inter-species investigations that directly measure flexibility or similar behaviors in closely related  
80 species that differ in their range expansion rates. This comparative method is a useful approach because it  
81 can serve as a type of natural experiment when testing closely related species that are known to differ in  
82 one of the two traits of interest (Davies et al., 2012). Here, we investigate flexibility in two closely related  
83 species, great-tailed grackles (hereafter GTGR) and boat-tailed grackles (*Quiscalus major*, hereafter BTGR),  
84 that differ in their range expansion rates: GTGR are rapidly expanding, while BTGR are not (Wehtje, 2003;  
85 DaCosta et al., 2008). GTGR are highly flexible (Logan, 2016; Logan et al., 2023a), but no flexibility data  
86 exist for BTGR. Both species are associated with human-modified environments, are social and polygynous,  
87 and eat a variety of human foods in addition to foraging on insects and on the ground for other natural food  
88 items (Post, 1992; Johnson & Peer, 2001; Post et al., 2020). We aimed to compare flexibility, measured as  
89 food type switches during focal follows, in two populations of GTGR (an older population in the middle of  
90 the northern expansion front, Tempe, Arizona, and a very recent population on the northern edge of the  
91 expansion front: Woodland, California) with one population of BTGR in the center of their range (Venus,

92 Florida). We investigated whether the GTGR edge population has higher flexibility averages and variances  
93 relative to BTGR and to the older GTGR population. Determining whether GTGR are more flexible will  
94 allow us to accumulate more evidence to determine whether there is support for the hypothesis that flexibility  
95 might play a key role in the GTGR rapid geographic range expansion. Alternatively, if BTGR and GTGR  
96 perform similarly, this would suggest that other abilities, either behavioral or physiological, may play a larger  
97 role in restricting the BTGR range expansion.

## 98 PREREGISTERED RESEARCH QUESTION

99 **Are there differences in behavioral traits (flexibility, innovation, exploration, and persistence)**  
100 **between boat-tailed and great-tailed grackles?**

101 **Prediction:** If behavior modifications are needed to adapt to new locations, then great-tailed grackles,  
102 which are rapidly expanding their geographic range, will have higher averages and/or larger variances than  
103 boat-tailed grackles, which are not rapidly expanding their range (Wehtje, 2003), in at least some behavioral  
104 traits (behavioral flexibility: speed at reversing a previously learned color preference, innovativeness: number  
105 of options solved on a puzzle box, exploration: latency to approach/touch a novel object, and persistence:  
106 proportion of trials participated in). Higher averages in behavioral traits indicate that each individual can  
107 exhibit more of that trait. If resources are regularly distributed in time and space, perhaps boat-tailed  
108 grackles require less flexibility when visiting these resources and attend less to their temporal availability  
109 or the individual's food preferences. Perhaps the problems BTGR solve do not require much exploration  
110 or persistence. Lower variances in behavioral traits indicate that there is less diversity of individuals in the  
111 population, which means that there is a lower chance that some individuals in the population would innovate  
112 new foraging techniques and be more flexible, exploratory, and persistent.

113 **Prediction alternative 1:** Human-modified environments are suitable habitat for GTGR and BTGR and  
114 the amount of human-modified environments has and is increasing. If the original behaviors exhibited by  
115 these species happen to be suited to the uniformity of human-modified landscapes, then averages and/or  
116 variances of these traits will be similar in the great-tailed and boat-tailed grackles sampled. This supports  
117 the hypothesis that, because these species are closely associated with human-modified environments (Wehtje,  
118 2003), which may be similar across the geographic range, individuals in new areas may not need to learn  
119 very much about their new environment: they can eat familiar foods and access these foods in similar ways  
120 across their range (e.g., fast food restaurant chains likely make the same food and package it in the same  
121 packaging in Central and North America, outdoor cafes and garbage cans also look the same across their  
122 range).

123 **Prediction alternative 2:** If BTGR have higher averages and/or larger variances in the behavioral traits  
124 measured, this could indicate that perhaps these traits are not the primary facilitators of the great-tailed  
125 grackle's rapid geographic range expansion. Alternatively, perhaps these species differ in a life history variable  
126 that restricts the BTGR from expanding, or there is some geographic feature that prevents the BTGR from  
127 rapidly expanding its range.

## 128 Methods

### 129 Updates and changes to the preregistration

130 This study began as a preregistration, which received in principle acceptance at PCI Ecology in 2021: [https://](https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/gxpopbehaviorhabitatPassedPreStudyPeerReview16D.pdf)  
131 [github.com/corinalogan/grackles/blob/master/Files/Preregistrations/gxpopbehaviorhabitatPassedPreStudyPeerReview16D](https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/gxpopbehaviorhabitatPassedPreStudyPeerReview16D.pdf)  
132 [pdf](https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/gxpopbehaviorhabitatPassedPreStudyPeerReview16D.pdf). The preregistration contains the pre-planned analyses. Here, we report the rationale for the ways in  
133 which we conducted the study differently from the plan, and then describe the methods we used to obtain  
134 the results.

### 135 Changes made in the middle of data collection

- 136 1) After the first BTGR field season in 2022, we **stopped the aviary experiments and switched to**  
137 **measuring reversal learning in the wild**. We received permission to make the change in Feb 2023  
138 from the PCI Ecology Managing Board and from the recommender, Esther Sebastián González, who  
139 incorporated it into our in principle acceptance. The reason for stopping the aviary experiments is that  
140 we discovered that BTGR are very different from GTGR. BTGR seem to be having health issues as  
141 indicated by multiple deaths in the wild (including two that we witnessed), which unfortunately also  
142 carried over to the aviaries where two of the six aviary birds died. This meant that we were not able  
143 to obtain measures for three of the four variables we planned on investigating: innovation, exploration,  
144 and persistence. These three variables would have required aviary testing to conduct a comparison  
145 between the two species because this is the setting in which the GTGR were tested. We planned to  
146 measure reversal learning in the wild using an automated feeder experiment that we were planning on  
147 running in GTGR (as in Logan et al., 2022). After data collection started in November 2023, and after  
148 extensive work trying to get the automated feeders to function, we discovered in January 2024 that  
149 the feeders were not usable. Therefore, we have no data on reversal learning in BTGR.
- 150 2) We previously measured flexibility in the wild in GTGR using behavioral observations (Logan et al.,  
151 2024), and found a variable that correlates with reversal learning performance: switching between food  
152 types during focal follows. This provided us with a way to collect comparable data in BTGR in the  
153 wild. Therefore, we **added this measure of flexibility**. Before we started collecting this data using  
154 focal follows, we received permission to make the addition in Sep 2023 from the recommender, Esther  
155 Sebastián González, who incorporated it into our in principle acceptance.

## 156 Sample

157 GTGR were caught in the wild in Woodland and Sacramento, California and Tempe, Arizona; and BTGR  
158 were caught in the wild in Venus and Lake Placid, Florida. We aimed to bring adult grackles, rather  
159 than juveniles, temporarily into the aviaries for behavioral choice tests to avoid the potential confound of  
160 variation in cognitive development due to age, as well as potential variation in fine motor-skill development  
161 (e.g., holding/grasping objects; early-life experience plays a role in the development of both of these behaviors;  
162 e.g., Collias & Collias (1964), Rutz et al. (2016)) with variation in our target variables of interest. After  
163 switching away from the aviary tests in BTGR (see above), we continued to focus our study on adult  
164 individuals, however, it was not usually possible to discern female adults from juveniles. Adult GTGR were  
165 identified from their eye color, which changes from brown to yellow upon reaching adulthood (Johnson and  
166 Peer 2001). Juvenile male BTGR were identified by their dark brown feathers (rather than shiny black as  
167 in the adult males), and we were not able to distinguish between adult and juvenile females because they  
168 both have light brown feathers and brown eyes. We applied colored leg bands in unique combinations for  
169 individual identification. For some BTGR individuals, one leg band contained an RFID/PIT tag (Eccel  
170 Technology Ltd, <https://eccel.co.uk/>). GTGR were trapped in the wild using mist nets, walk-in traps, and  
171 bownets, and BTGR were trapped using walk-in traps. The bird was then processed by collecting biometric  
172 measurements, and, in the case of GTGR, also feathers and blood. After processing, the bird was released  
173 back to the wild either immediately (all BTGR and many GTGR), or after participating in behavioral tests  
174 in aviaries (many GTGR; these data are reported in other publications).

## 175 Focal follow protocol

176 We used the focal follow protocol described in a previous study (see Logan et al., 2024) for the data collection  
177 for both GTGR and BTGR, where we measured flexibility as the probability of switching between food types  
178 (see Altmann, 1974 for a general description of the focal follow method). 10 min focal follows were conducted  
179 in which all food types were recorded (both species), as well as the foraging bout start and end times (BTGR;  
180 Table 1). BTGR and most GTGR data were collected using a voice recorder (Voice Memos app on an iPhone)  
181 and later transcribed into the datasheet in Google Sheets (<https://www.google.com/sheets/about/>). Some  
182 GTGR data were first entered into the program Prim8 Software (<https://www.prim8software.com/>), and  
183 then transcribed into the Google Sheet. The GTGR focal follow protocol was modified in three ways to

184 accommodate that we were only interested in collecting foraging behavior in BTGR, whereas in GTGR, we  
185 collected data on other behaviors as well. The BTGR protocol differed in the following ways:

- 186 • End each focal when the bird goes out of view and start a new focal when they come back in view  
187 (rather than allow “out of view” for up to 5 min per focal). This omits the problem of trying to account  
188 for what might have happened in the time out of view when running the analysis.
- 189 • No minimum of 3 weeks between separate focal follows because we are only looking at food type switch  
190 rates and these are, by definition, less autocorrelated with time because a switch could only occur  
191 within the same focal follow. This will still match what occurred with the GTGR data because, while  
192 the aim was to conduct a 10 min focal follow, many ended early because the bird went out of view and  
193 was not findable again that day. In these cases, the observer would continue to seek the bird out on  
194 consecutive days to obtain the rest of the 10 min and finish this one focal follow. A study on dolphins  
195 (*Tursiops cf. aduncus*) found that focal follow data that was separated by 10.5 min was functionally  
196 independent (Karniski et al., 2015). Therefore, changing the 3 week spacing minimum to 1 day (until  
197 4 focal follows were reached and then spacing them 1 week apart after) should be enough temporal  
198 distance to assume independence of the data points.
- 199 • Collect data only on the How (how did the bird obtain the food, e.g., dunk, dig, gape) and What (what  
200 did the bird eat, e.g., fries, grains, insect) categories that were found in the GTGR and add more food  
201 types (the What category) and/or foraging techniques (the How category) for the BTGR as needed.  
202 We also recorded the location as in the GTGR protocol.

203 We set the BTGR minimum sample size to the average number of focal follows obtained from GTGR in  
204 Logan et al. (2024): we aimed for a minimum of 4 focal follows per bird (conducted on separate days  
205 between 09:00 and 16:00, attempting to counterbalance mornings and afternoons). We set the minimum  
206 sample size at 6 BTGR with an average of 3.2 focal follows per individual, which was the number of GTGR  
207 in the flexibility manipulated condition in Logan et al. (2024) and their average number of focals per bird.  
208 Using this sample size, we were able to detect differences between the manipulated and control conditions in  
209 GTGR (Logan et al., 2024). The full experimental protocol is online at: [https://docs.google.com/document/  
210 d/1WK6oR04LR1Q2CGXgICvUNN28MWIM-3o2U66lanDv-lc/edit?usp=sharing](https://docs.google.com/document/d/1WK6oR04LR1Q2CGXgICvUNN28MWIM-3o2U66lanDv-lc/edit?usp=sharing).

211 While methods for BTGR focal follows used the same protocol as for GTGR, there were 8 BTGR focal  
212 follows that were exceptions: they either occurred less than a week after the last focal follow (for those birds  
213 who had at least 4 focal follows, focal follow numbers 5+ should have been spaced apart by at least 1 week),  
214 or occurred on a day when another focal follow was also conducted at the same location. Across all of these  
215 8 exceptions, only 1 food item was taken and no food type switches occurred. The data from these 8 focal  
216 follows therefore did not match the filter criteria, and are not part of the analyses.

217 Only those focal follows that contained data on food types, including unknown food types, were included  
218 in the analyses. This made it so focal durations were balanced between the species. In BTGR, focals only  
219 started if a bird was foraging, whereas in GTGR, focals could start as soon as the bird was found (because  
220 social data as well as foraging data were collected on this species).

221 **Table 1.** The foraging section of the GTGR ethogram that was used for (and added to) BTGR data  
 222 collection.

Foraging behavior	Behavior	Description
HOW is the bird searching for food? (foraging technique)	Flip	Flipping over objects
	Lift / nudge	Lifting or nudging objects with bill
	Pick up	Pick up object
	Dig	Digging in ground with bill or feet
	Sweep	Sweeping head back and forth (i.e., actually sweeping the bill across the substrate)
	Gape	Using gaping bill to search through substrate
	Extract	Extracting from a substrate ( <i>didn't show up in the <u>GTGR</u> techniques, but was on their ethogram</i> )
	Stalk / catch	Lowers body posture to be parallel to ground to stalk/catch prey from air, from ground, from tree, etc.
	Share	Food is shared with the focal bird by another bird
	Break	Break object into pieces
	Dunk	Dunk object in water or other liquid substance
	Theft	Steal object from another bird's bill/feet or near its body
	NEW for BTGR: Drink	When the item they are foraging on is liquid (e.g., oil water, soda, etc.)
NEW for BTGR: Pull	Pull on an item until it breaks off or is otherwise obtained (e.g., a leaf off of a branch)	
WHAT are they eating?	23 categories (add more if needed)	Fry, lizard, unknown, grains (pizza, noodles, bread, rice, chips, rice krispies, crackers, pretzel, muffin, cookie, popcorn), insect, rock, cat food, worm, seed, food crumbs, vegetation (leaf, grass, branch, flower, moss), fruit (flesh, peel), bird poop, candy, vomit, misc. trash (paper, condiment packet), soil (clay, dirt), condiment, carcass, chicken (bone, skin), peanut, mulch. New for BTGR: oil, cheese
FORAGING (state)	Record the start and stop times for each foraging bout	When the bird is searching for food (have to be touching what they are searching through), pecking in the ground, and/or eating food. If the bird pauses foraging behavior for up to 10s, keep this state going. If it pauses for >10s, end the foraging state

223

## 224 Open data

225 The data are published in the Knowledge Network for Biocomplexity’s data repository (Logan & McCune,  
226 2024).

## 227 Analyses

228 We did not exclude any data. When there were missing data (e.g. if a bird did not have any food type  
229 data), then it was not included in the analyses. Following procedures in McElreath (2020), we constructed  
230 a hypothesis-appropriate mathematical model for the response variable that examines differences in the  
231 response variable between sites. The single population of BTGR in Venus, Florida, were considered a site  
232 and we examined differences between them and each of the two GTGR sites. For each focal follow, we  
233 calculated the number of switches between food types that occurred and the total amount of time that the  
234 bird was observed. We summed both measures across focal follows to have one data point per bird. This  
235 model takes the form of:

$$236 \text{switches}_i \sim \text{Binomial}(\text{totaltime}_i, p),$$

$$237 \text{logit}(p) \sim a_i[\text{site}],$$

238 where  $\text{switches}_i$  is the sum of the number of times individual,  $i$ , changed food types within focal follows  
239 that contained food type data,  $\text{totaltime}_i$  is the number of seconds individual,  $i$ , was observed across all of  
240 its focal follows that contained food type data,  $p$  is the probability of switching to a different food type per  
241 second, and  $a_i$  is the intercept (one per level of  $\text{site}$ : GTGR Arizona, GTGR California, and BTGR).

242 The model was the same for analyzing the variance in switch rates except  $b[\text{individual}]$  and an extra prior  
243 were added as follows:

$$244 \text{logit}(p) \sim a_i[\text{site}] + b[\text{individual}],$$

245 which gives the probability of switching food types per bird. We specified the priors for this as:

$$246 d[\text{individual}] \sim \text{Normal}(0, \sigma[\text{site}]),$$

$$247 \sigma[\text{site}] \sim \text{Exponential}(1),$$

248 where  $\sigma[\text{site}]$  gives the average variance across individuals per site.

249 We then performed pairwise contrasts to determine whether there were differences between sites, concluding  
250 that there is a difference if 89% of the difference between two sites is on the same side of zero (following  
251 McElreath, 2020). We ran these analyses in R (current version 4.0.3; R Core Team (2017)) and used  
252 the following R packages: rethinking (McElreath, 2020), cmdstanr (Gabry & Češnovar, 2021), and dplyr  
253 (Wickham et al., 2021).

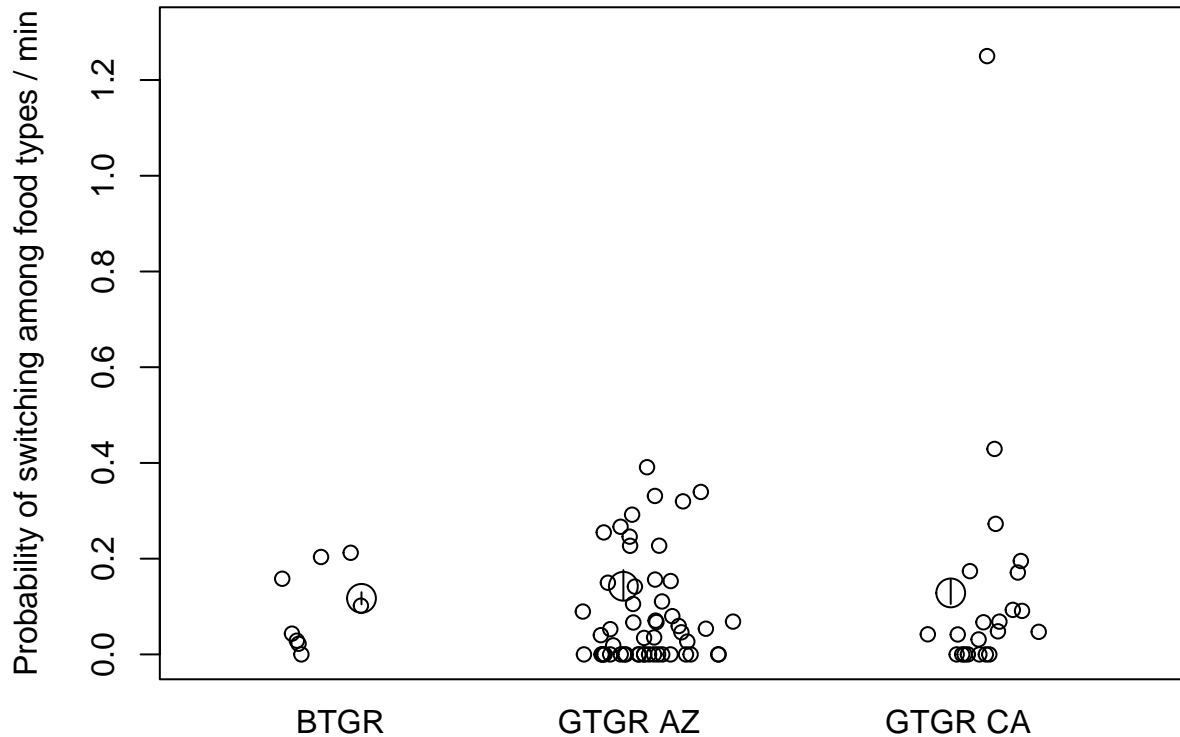
## 254 Results

255 The dataset consisted of 8 BTGR and 76 GTGR (54 in Arizona, 22 in California) who had data that involved  
256 eating at least one food type. A total of 36 food types across all sites were documented. The BTGR took a  
257 total of 14 food types, including cheese and oil, which the GTGR did not have. The Arizona GTGR took 20  
258 food types, including lizard, bird poop, candy, vomit, condiment, and carcass, which the other populations  
259 did not have. The California GTGR took 15 food types, including mulch, which the other populations did  
260 not have.

261 There were **no strong differences in the AVERAGE probability of switching** among food types per  
262 second between BTGR and either population of GTGR, nor between the two GTGR populations (Figure  
263 1; contrasts: GTGR AZ-BTGR: mean difference per second=-0.0004, sd=0.0003, 89%CI=-0.001-0.0001;

264 GTGR CA-BTGR: mean=-0.0002, sd=0.0004, 89%CI=-0.001-0.0004; GTGR AZ-GTGR CA: mean=-0.0002,  
265 sd=0.0003, 89%CI=-0.0007-0.0002). This supports Prediction 6 alternative 1.

266 There were also **no strong differences in the VARIANCE of the probability of switching** among food  
267 types per second between BTGR and either population of GTGR, nor between the two GTGR populations  
268 (Figure 1; contrasts: GTGR AZ-BTGR: mean difference per second=-0.16, sd=0.61, 89%CI=-0.99-0.76;  
269 GTGR CA-BTGR: mean=0.13, sd=0.73, 89%CI=-0.94-1.28; GTGR AZ-GTGR CA: mean=-0.29, sd=0.45,  
270 89%CI=-0.97-0.37). The variances from the raw data for food switches per minute for each site were 0.01  
271 for BTGR, 0.12 for GTGR Arizona, and 0.14 for GTGR California. This supports Prediction 6 alternative  
272 1.



273  
274 **Figure 1.** The probability of switching among food types per minute for the BTGR (n=8), and GTGR in  
275 Arizona (n=54) and California (n=22). The small circles are the data points per individual and the large  
276 circles are the estimated means with their 89% compatibility intervals represented by the vertical lines.

## 277 Discussion

278 There were no strong differences in flexibility (averages or variances), measured as food type switching during  
279 focal follows, between BTGR and GTGR. This converges with the small amount of evidence we were able  
280 to obtain from the reversal learning tests in the aviary from two BTGR individuals: their reversal learning  
281 speeds were well within the range of the GTGR reversal learning speeds (Logan et al., 2023b). We know that  
282 GTGR are highly flexible relative to other species (Logan, 2016), therefore the similar levels of flexibility  
283 between the two species indicates that BTGR are also highly flexible.

284 That there was no strong difference in flexibility between the two GTGR populations further validates the  
285 use of food type switching as a measure of flexibility because there was also no difference in the average  
286 flexibility based on reversal learning (Logan et al., 2024). Logan et al. (2024) did find a difference in the  
287 reversal learning flexibility variance and, while we found no strong difference in the variance when using food  
288 type switching probabilities, the California population, which is closer to the edge, had higher variances,  
289 which is in the same direction as what Logan et al. (2023b) found.



290 Unfortunately, we were not able to obtain comparable exploration, innovativeness, and persistence data  
291 on the BTGR to understand whether one or more of these behaviors could relate to species differences in  
292 range expansion rates. The few data we were able to obtain from BTGR in the aviaries were analyzed in  
293 Logan et al. (2023b) and suggest that BTGR are less innovative (n=4) and less persistent (n=5) than both  
294 GTGR populations, while having similar levels of exploration (n=5) as the California GTGR and being less  
295 exploratory than the Arizona GTGR. Indeed, the California GTGR on the northern edge of their range are  
296 more persistent than the Arizona GTGR population, with no strong differences in innovation or exploration.  
297 This lends more support to persistence as the behavior that might play a larger role in the range expansion  
298 of the already highly flexible GTGR. However, this is speculative due to the small BTGR aviary sample sizes.  
299 More research is needed to make robust comparisons between the two species on these other behaviors.

300 The lack of a difference in flexibility between the two species suggests that the original behaviors exhibited  
301 by these species happen to be suited to the uniformity of human-modified landscapes where both species are  
302 found. This supports the hypothesis that, because these species are closely associated with human-modified  
303 environments (Post, 1992; Wehtje, 2003; Post et al., 2020; Summers et al., 2023), which may be similar across  
304 the geographic range, individuals in new areas may not need to learn much about their new environment.  
305 They can eat familiar foods and access these foods in similar ways across their range. For example, fast food  
306 restaurant chains likely make the same food and package it in the same packaging across North America,  
307 and outdoor cafes and garbage cans also look similar across their range. It is possible that environmental,  
308 rather than behavioral, variables play a larger role in restricting the BTGR range expansion. Summers et  
309 al. (2023) found that, between 1979 and 2019, BTGR were present in primarily warm, wet, coastal habitats  
310 and this did not change over time. The range they expanded into during this time was made suitable to  
311 them likely due to climate change. In contrast, GTGR shifted to using more urban, arid habitats over this  
312 time, which suggests that behavior could be a key facilitator involved in their range expansion. Because  
313 urban environments represent a rapidly increasing category of environmental change (Goldewijk, 2001; Wu  
314 et al., 2011; Liu et al., 2020), our observations highlight the importance of differentiating between whether a  
315 behavior might be linked to the ability to live in urban environments versus the ability to expand into new  
316 habitats. Flexibility is potentially linked to living in urban environments, but not necessarily to the ability  
317 to expand into novel habitats.

318 In conclusion, the evidence that two closely related species with similar levels of flexibility, but different range  
319 expansion rates does not support the hypothesis that flexibility is the primary facilitator of rapid geographic  
320 range expansions into new areas. This does not rule out that flexibility might be a needed variable to  
321 rapidly expand a range, as shown by GTGR who have high average levels of flexibility on and away from  
322 the edge. However, it appears that other behaviors, such as persistence (Logan et al., 2023b), innovation,  
323 food neophobia (Martin & Fitzgerald, 2005; Liebl & Martin, 2014; Cohen et al., 2020), exploration (Chuang  
324 & Riechert, 2021), and risk aversion (Eccard et al., 2022) may play a more primary role in expanding the  
325 edge of the range further. This indicates the importance of investigating multiple behaviors in each species  
326 of interest to determine what, if any, role they play and in what direction.

## 327 **Data, script, and code availability**

328 Data, scripts, and code are available online at the Knowledge Network for Biocomplexity's data repository  
329 (Logan & McCune, 2024). The scripts and code are in the Rmd file, which is also available at <https://github.com/corinalogan/grackles/blob/master/Files/Preregistrations/gxpopbehaviorhabitatq1.Rmd>  
330

## 331 **Ethics**

332 This research was carried out in accordance with permits from the:

- 333 1) US Fish and Wildlife Service (scientific collecting permit number MB76700A-0,1,2)
- 334 2) US Geological Survey Bird Banding Laboratory (federal bird banding permit number 23872)

- 335 3) Arizona Game and Fish Department (scientific collecting license number SP594338 [2017], SP606267  
336 [2018], SP639866 [2019], and SP402153 [2020])  
337 4) Institutional Animal Care and Use Committee at Arizona State University (protocol number 17-1594R)  
338 5) Institutional Animal Care and Use Committee at the University of California Santa Barbara (protocol  
339 number 958)  
340 6) Institutional Animal Care and Use Committee at Archbold Biological Station (protocol number ABS-  
341 AUP-033-R)  
342 7) California Department of Fish and Wildlife (scientific collecting permit [specific use] number  
343 S-192100001-19210-001)  
344 8) RegionalSan (access permit number AP 2021-01)  
345 9) Florida Fish and Wildlife Conservation Commission (scientific collecting permit number LSSC-21-  
346 00050)

## 347 **Author contributions**

348 **Logan:** Hypothesis development, data collection (BTGR focal follows and field work), data analysis and  
349 interpretation, write up, revising/editing, materials/funding.

350 **McCune:** Method development, data collection (Arizona and California focal follows and field work), revis-  
351 ing/editing.

352 **Rowney:** Data collection (Arizona field work), revising/editing.

353 **Lukas:** Hypothesis development, data collection (BTGR field work), data analysis and interpretation, write  
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## 358 **Conflict of interest disclosure**

359 We, the authors, declare that we have no financial conflicts of interest with the content of this article. CJ  
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