Implementing a rapid geographic range expansion - the role of behavior and habitat changes

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ABSTRACT

It is generally thought that behavioral flexibility, the ability to change behavior when circumstances change, plays an important role in the ability of a species to rapidly expand their geographic range (e.g., Lefebvre et al. (1997), Griffin and Guez (2014), Chow et al. (2016), Sol and Lefebvre (2000), Sol et al. (2002), Sol et al. (2005), Sol et al. (2007)). However, it is alternatively possible that an increase in the amount of suitable habitat can be the primary facilitator for a range expansion. Great-tailed grackles (*Quiscalus mexicanus*) are a social, polygamous species that is rapidly expanding its geographic range (Wehtje (2003)) and eats a variety of human foods in addition to foraging on insects and on the ground for other natural food items (Johnson and Peer (2001)). They are behaviorally flexible (C. Logan (2016)) and highly associated with human-modified environments (Johnson and Peer (2001)), thus offering an opportunity to assess the role of behavior and habitat change over the course of their expansion. We first aim to compare behavior in wild-caught grackled from three populations across their range (core, middle of the expansion front, northern edge) to investigate whether: 1) certain behaviors (flexibility, innovativeness, exploration, and persistence) have higher averages and variances in some populations relative to others, and 2) individuals in a more recently established population exhibit more dispersal behavior (i.e., individuals are more likely to move away from their parents). Secondly, we aim to investigate whether habitat availability, not necessarily inherent species differences, can explain why great-tailed grackles are able to much more rapidly expand their range than their closest relative, boat-tailed grackles (*Q. major*) (Post et al. (1996), Wehtje (2003)). We will examine temporal habitat changes over the past few decades using existing databases on

presence/absence of both grackle species and compare habitat variables to determine whether: 3) these species use different habitats, habitat availability and connectivity has increased across their range, and what proportion of suitable habitat both species occupy. Results will elucidate whether the rapid geographic range expansion of great-tailed grackles is associated with individuals differentially expressing particular behaviors or whether the expansion is facilitated by the alignment of their natural behaviors with an increase in suitable habitat (i.e., human-modified environments).

A. STATE OF THE DATA

This preregistration was written (Mar 2020) prior to collecting any data from the edge and core populations. Some of the relatedness data from the middle population (Arizona) has already been analyzed for other purposes (n=57 individuals, see Sevchik et al. (2019)), therefore it will be considered secondary data: data that are in the process of being collected for other investigations. However, we have now collected blood samples from many more grackles in Arizona, therefore we will redo the analyses from the Arizona population in the analyses involved in the current preregistration. In May 2020, we completed data collection for other variables at the Arizona field site: flexibility and innovation (Logan et al. 2019), and exploration (McCune KB et al. 2019), and we will soon analyze this data, therefore it will also be considered secondary data. This preregistration was submitted in May 2020 to PCI Ecology for pre-study peer review.

Level of data blindness: Logan, McCune, and MacPherson collect the behavioral data (H1) and therefore have seen this data for the Arizona population. Lukas has access to the Arizona data and has seen some of the summaries in presentations. Chen has not seen any data.

B. PARTITIONING THE RESULTS

We may decide to present the results from different hypotheses in separate articles. We may also decide to test these hypotheses in additional species.

C. HYPOTHESES

Note: There could be multiple mechanisms underpinning the results we find, however our aim here is to narrow down the relative roles of changes in behavior and changes in habitats in the range expansion of great-tailed grackles.

H1 (4 behaviors): Changes in behavioral traits (flexibility, innovation, exploration, and persistence) facilitate the great-tailed grackle's geographic range expansion (Fig. 1 & 2).

Prediction 1: If behavior modifications are needed to adapt to new locations, then there will be a higher average and/or larger variance of at least some traits thought to be involved in range expansions (behavioral flexibility: speed at reversing a previously learned color preference; innovativeness: number of options solved on a puzzle box; exploration: latency to approach/touch a novel object; and persistence: proportion of trials participated in with higher numbers indicating a more persistent individual) in the grackles sampled from the recently established population relative to the individuals sampled in the older populations (Table 1). Higher averages in behavioral traits indicate that each individual can exhibit more of that trait (e.g., they are more flexible/innovative/exploratory/persistent). Perhaps in newly established populations, individuals need to learn about and innovate new foraging techniques or find

Commenté [CN1]: What habitat variables ? This is tricky because:
- the needs of the species need to be known (food sources, habitat type(s) for shelter and nest,…)
- where do the data come from? this type of habitat information is not available through GIS / satellite / remote sensing ?

At the very end of the file I have found the list of specific habitat variables that you intend to map and compare to the occurrence data of the birds, but it would be a useful improvement to specify why/how these variables are important to the ecology of the species. So far it seems that you collect these habitat variables because they are available and they are not necessarily relevant to explain the species distribution. This is my major concern.

Commenté [CN2]: Which means ? Please specify

Commenté [CN3]: Relevant for this study ? Are you going to use relatedness/ genetic data ? Relevance unclear based on abstract above. It is clear later in the description of the protocole but it may be useful to be more explicit earlier about the type of data (snp) and that these data have been proven useful to quantify a range of relatedness in different populations of this species?

Commenté [CN4]: I have not seen this data

Commenté [CN5]: I think that this is not what is expected as an answer : behavioural studies may be biased mostly by knowing which outcome is expected for the animal at the time the data is collected. So we rather expect that the scientist who collected the behavioural observations is not aware of the population origin of the animals, and that animals from different populations (as far as possible) are randomized during successive observations. I understand that this may not be feasible for a study of such large geographical scale (as you write late in the protocols).

Commenté [CN6]: For food items ?

Commenté [CN7]: Link to natural selection in the wild is unclear ?

new food sources. Perhaps grackles require flexibility to visit these resources according to their temporal availability and the individual's food preferences. Perhaps solving such problems requires more exploration and persistence. Higher variances in behavioral traits indicate that there is a larger diversity of individuals in the population, which means that there is a higher chance that at least some individuals in the population could innovate foraging techniques and be more flexible, exploratory, and persistent, which could be learned by conspecifics and/or future generations.

Prediction 1 alternative 1: Human-modified environments are suitable habitat for grackles (e.g., Selander and Giller (1961), Johnson and Peer (2001), Wehtje (2003)), and the amount of human-modified environments has and is increasing (e.g., Liu et al. (2020)). If the original behaviors exhibited by this species happen to be suited to the uniformity of human-modified landscapes (e.g., urban, agricultural, etc. environments are modified in similar ways across Central and North America), then the averages and/or variances of these traits will be similar in the grackles sampled from populations across their range (Table 1). This supports the hypothesis that, because this species is closely associated with human-modified environments, which may be similar across the geographic range of this species, individuals in new areas may not need to learn very much about their new environment: they can eat familiar foods and access these foods in similar ways across their range (e.g., fast food restaurant chains likely make the same food and package it in the same packaging in Central and North America, outdoor cafes and garbage cans also look the same across their range). Alternatively, it is possible that 2.9 generations at the edge site is too long after their original establishment date to detect differences in the averages and/or variances. If the sampled individuals had already been living at this location for long enough (or for their whole lives) to have learned what they need about this particular environment (e.g., there may no longer be evidence of increased flexibility/innovativeness/exploration/persisence), there may be no reason to maintain population diversity in these traits to continue to learn about this environment. We will not be able to distinguish between these two alternatives within alternative 1 because populations closer to the northern edge of this species' range were too small for us to establish such a field site.

Commenté [CN8]: Relevant but then better link your experimental tests to ecologically relevant hypotheses. For example why test for learning of colour change, if not for food? Or puzzle tests while localization /exploration of new / scattered food item is perhaps more relevant?

In general, this becomes more clear after one has read the protocols below, but this is my second and last real concern about this project: can you link better the expected ecological needs (for finding food) and the type of tests that you conduct here? To give you an example, in butterflies we test the specific host plant that females use to oviposit, and the test is about the time they need to find, and remember, the location of the host plant. The link to the demography and on selection in the field is more immediate.

Commenté [CN9]: The expectations about variance in addition to means are highly relevant.

Commenté [CN10]: This result may also occur if irrelevant behaviour have been tested, hence my comments above about ecological relevance of behavioural tests. Hence my concern about the ecological relevance of your experimental behavioural tests.

Commenté [CN11]: It would be relevant to backup this by evidence from experimental evolution on learning skills in vertebrates (like mouse,…). I doubt that populations would get back to ancestral averages in cognition within 3 generations.

Commenté [CN12]: Relevant : then focus on juveniles individuals in sampling, if possible

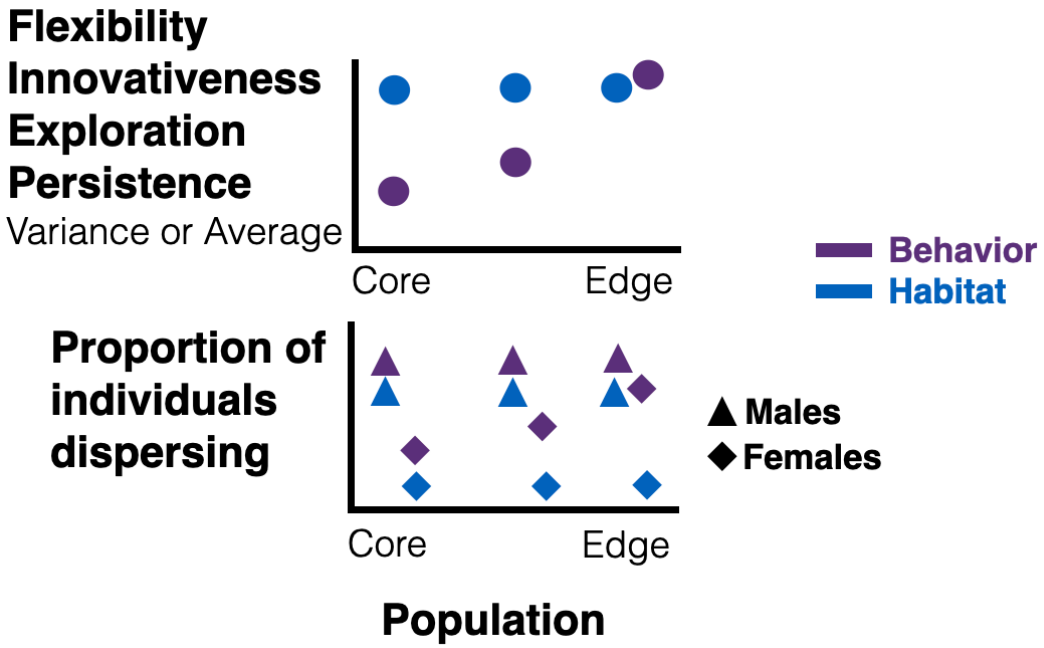

Figure 1. What plays a larger role in a rapid range expansion: behavior changes or suitable habitat changes? A visual representation of H1 (top) and H2 (bottom).

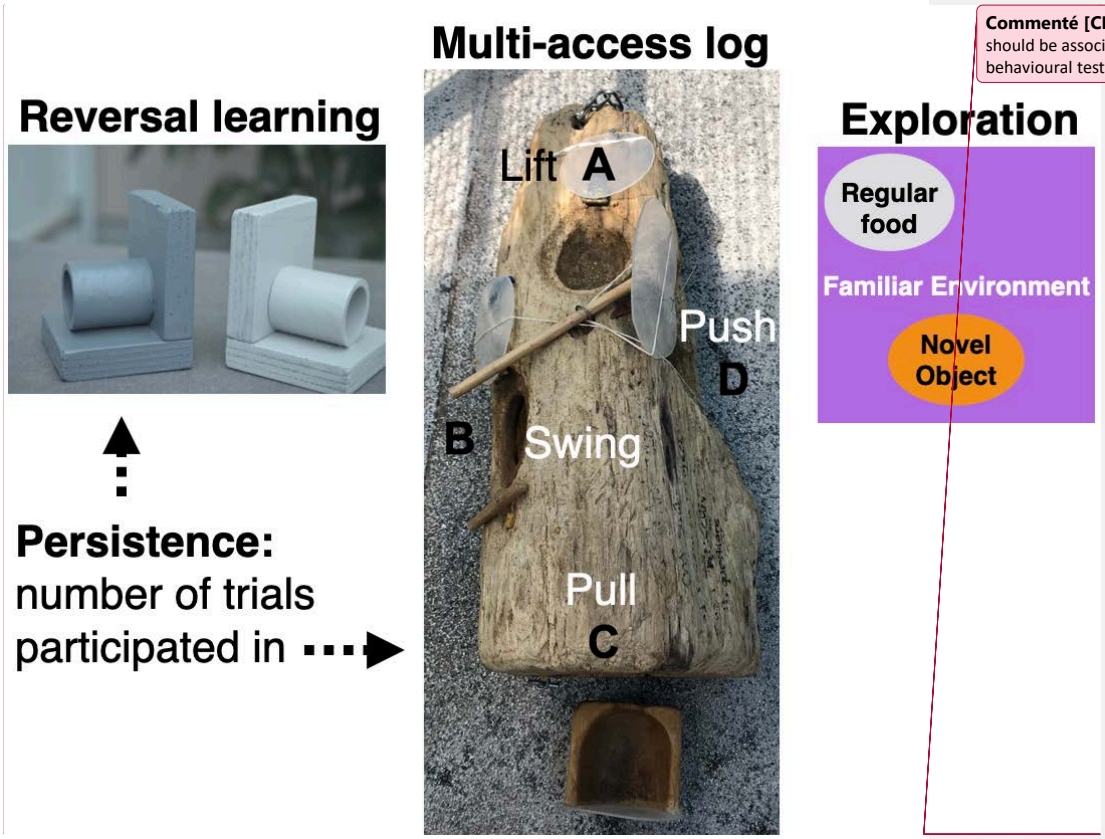

Figure 2. Measuring flexibility (reversal learning), innovation (multi-access log), exploration, and persistence.

H2 (dispersal behavior): Changes in dispersal behavior, particularly for females, which is the sex that appears to be philopatric in the middle of the range expansion, facilitate the great-tailed grackle's geographic range expansion (Fig. 1, Table 1).

Prediction 2: If a change in dispersal behavior is facilitating the expansion, then we predict more dispersal at the edge: a higher proportion of individuals disperse in a more recently established population and, accordingly, fewer individuals are closely related to each other.

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

Table 1. Population characteristics for each of the three field sites in H1 and H2. The number of generations at a site is based on a generation length of 5.6 years for this species (International (2018)) and on the first year in which this species was reported to breed at the

Commenté [CN13]: For non-bird experts these pictures should be associated to explanations to justify the choice of behavioural tests.

Commenté [CN14]: Not clear to me why focus on females. Males is the usual dispersing sex. Females as the limiting factor (without females no nests)? Please clarify.

Commenté [CN15]: This appears to be true in many species, but it may be necessary but not sufficient to colonize new areas. Innovation may be needed in addition to increased dispersal at distribution edges.

Commenté [CN16]: This explains that relatedness measures are collected. However do you have evidence that your markers for quantifying relatedness (microsat? → I got it is snp later on) will be variable enough to detect such limited changes in relatedness? Would another behavioural test perhaps be a better estimate of dispersal (perhaps, propensity to leave a cage for another in large field enclosures, perhaps?)?

Commenté [CN17]: At what age do they start to breed ?

location (Wehtje (2003) for Arizona, Steve Hampton's pers. comm. reported in Pandolfino et al. (2009) for Woodland, California). The first confirmed nest sighting in Woodland, California was reported in the Yolo Audubon Society's newsletter *The Burrowing Owl* (July 2004), which Steve Hampton shared with Logan. For Central America, there is no data on the first year in which they started breeding because this species originates in this region, therefore we used the age of the species: 800,000 years (Johnson and Cicero (2004)).

Central America
Core
Unknown
800000
142857.1
Johnson & Cicero 2004
Tempe, Arizona
Middle of expansion
1936
66
11.8
Wehtje 2003
Woodland, California
Northern edge
2004
16
2.9
Burrowing Owl July 2004, Pandolfino et al. 2009
Loading...

Commenté [CN18]: Nice contrasted population sites

H3 (suitable habitat GTGR & BTGR): The availability of habitat, not inherent species differences, explains why great-tailed grackles (GTGR) are able to much more rapidly expand their range than boat-tailed grackles (BTGR) (Fig. 3; Wehtje (2003), Selander and Giller (1961)).

Prediction 3: GTGR and BTGR use different habitats, and the habitat of GTGR, but not that of BTGR, has increased in availability and connectivity over the past few decades.

Prediction 4: Over the past few decades, GTGR has increased the habitat breadth that they can occupy, whereas BTGR continues to use the same limited habitat types.

Commenté [CN19]: Which are ?

Prediction 5: Some inherent trait allows GTGR to expand even though both species have unused habitat available to them.

Commenté [CN20]: It would be relevant to quantify behavioural traits in the sister species as well.

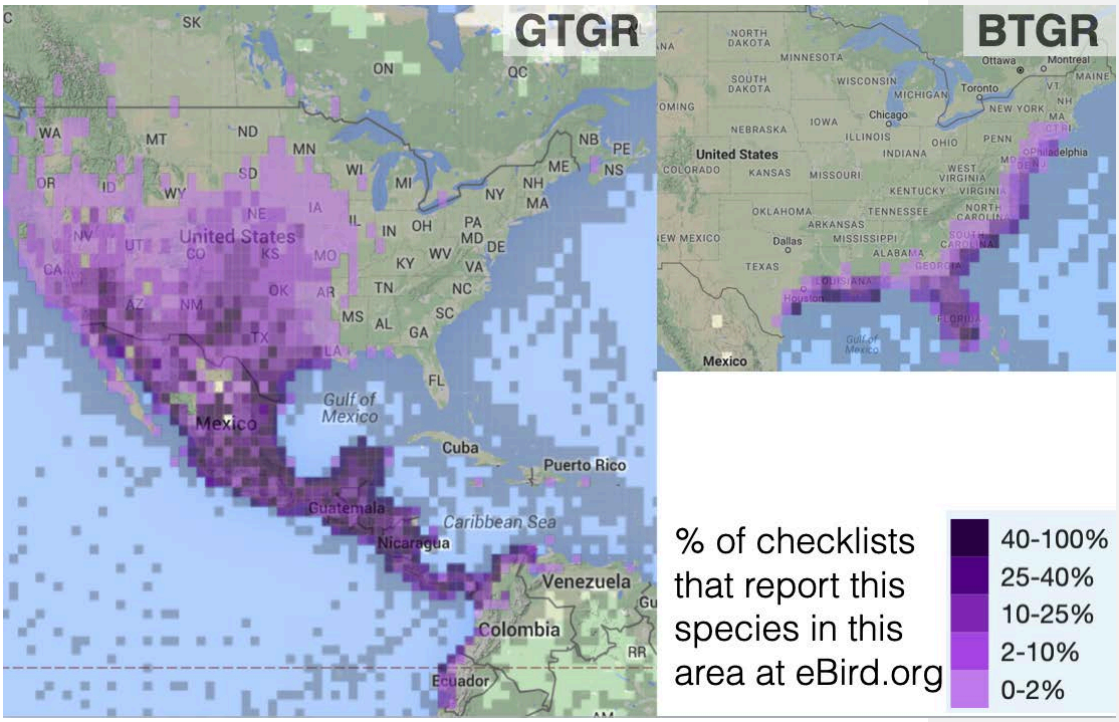

Figure 3. What plays a larger role in a rapid range expansion: behavior changes or suitable habitat changes? Comparing the availability of suitable habitat between great-tailed grackles (GTGR), which are rapidly expanding their geographic range, and boat-tailed grackles (BTGR), which are not. Map credit: eBird.org.

Commenté [CN21]: They certainly have different habitat requirements given that their distribution ranges do not overlap. It will be hard to make a useful comparison between the two species without quantifying behavioural traits in the sister, not expanding, species.

D. METHODS

Planned Sample (H1 & H2)

Great-tailed grackles are caught in the wild in Woodland, California and at a site to be determined in Central America. We apply colored leg bands in unique combinations for individual identification. Some individuals (~20) are brought temporarily into aviaries for behavioral choice tests, and then are released back to the wild at their point of capture. We catch grackles with a variety of methods (e.g., walk-in traps, mist nets, bow nets), some of which decrease the likelihood of a selection bias for exploratory and bold individuals because grackles cannot see the traps (i.e., mist nets). Grackles are individually housed in an aviary (each 244cm long by 122cm wide by 213cm tall) for a maximum of six months where they have *ad lib* access to water at all times and are fed Mazuri Small Bird maintenance diet *ad lib* during non-testing hours (minimum 20h per day), and various other food items (e.g., peanuts, bread) during testing (up to 4h per day per bird). Individuals are given three to four days to habituate to the aviaries and then their test battery begins on the fourth or fifth day (birds are usually tested six days per week, therefore if their fourth day occurs on a day off, they are tested on the fifth day instead).

Commenté [CN22]: Focus on juveniles (as suggested above)?

Commenté [CN23]: good

While the above is our ideal plan, due to restrictions around COVID-19, it may not be possible for us to accomplish all of our goals within our current funding period. We think it will be possible to collect data at one more site (which would be the second of three planned sites) and we will attempt to also include a third field site.

Sample size rationale (H1 & H2)

We test as many birds as we can during the approximately one year we spend at each site given that the birds are only brought into the aviaries during the non-breeding season (approximately September through March). It is time intensive to conduct the aviary test battery (2-6 months per bird at the Arizona field site), therefore we approximate that the minimum sample size at each site will be 20 grackles with the aim that half of the grackles tested at each site are female.

Data collection stopping rule (H1 & H2)

We will stop collecting data on wild-caught grackles in H1 and H2 (data for H3 are collected from the literature) once we have completed one year at each of the California and Central America sites (likely complete in summer 2022), which coincides with the period in which we currently have funding (until early 2023). If we are not able to collect data at a third site, we will attempt to collect more data during a second year at the second site (Woodland, CA).

Commenté [CN24]: this is very surprising : what type of data ? please specify.

Protocols and open materials

- Experimental protocols for H1 are online here.
- **Flexibility** protocol (from Logan et al. (2019)) using reversal learning with color tubes. A light gray tube and a dark gray tube are placed on the table or floor: one color always contains a food reward (not visible by the bird) while the other color never contains a reward. The bird is allowed to choose one tube per trial. An individual is considered to have a preference if it chose the rewarded option at least 17 out of the most recent 20 trials (with a minimum of 8 or 9 correct choices out of 10 on the two most recent sets of 10 trials). We use a sliding window to look at the most recent 10 trials for a bird, regardless of when the testing sessions occurred. Once a bird learns to prefer one color, the contingency is reversed: food is always in the other color and never in the previously rewarded color. The flexibility measure is how many trials it takes them to reverse their color preference using the same passing criterion. Note: we may modify this protocol by moving the passing criterion sliding window in 1-trial increments, rather than 10-trial increments (i.e., a bird could pass criterion at trial 36 rather than only at trials 20, 30, 40, etc.).
- **Innovativeness** protocol (from Logan et al. (2019)) using a multi-access log. A log that has four ways of accessing food (pull drawer, push door, lift door up, swing door out) is placed on the ground and grackles are allowed to attempt to solve or successfully solve one option per trial. Once a bird has successfully solved an option three times, it becomes non-functional (the door is locked open and there is no food at that locus). The experiment ends when all four loci become non-functional, if a bird does not come to the ground within 10 min in three consecutive test sessions, or if a bird does not obtain the food within 10 min (or 15 min if the bird was on the ground at 10 min) in three consecutive test sessions.
- **Exploration** protocol (from McCune KB et al. (2019)) for exploration of a novel object. A familiar object (that contains no food) is placed in the center of the bird's

aviary, while maintenance diet is available at a far end of the aviary away from the object, for 45 min. This is immediately followed by the same set up with a novel object instead of a familiar object. Test sessions are video recorded and experimenters are out of view of the bird during the sessions. This assay is conducted at Time 1 (3-6 days after the bird arrives in the aviary) and Time 2 (1 week after Time 1) with the same novel object (to control for potential differences in perceived threat or attraction between objects) to determine whether measures are repeatable across individuals. Note: we might make two modifications to this protocol as a result of analyzing the results from the Arizona population: 1) we may reduce the session time from 45 min to something shorter if all grackles who came to the ground did so in <45 min in Arizona, and 2) we may replace the novel object with a novel environment - we will choose the one that correlates with boldness measures in Arizona. If both correlate with boldness, we will choose the novel object because it is a simpler test.

- **Persistence** is measured as the proportion of trials participated in during the flexibility and innovativeness experiments. The higher the number, the more persistent they are. We generally offer a grackle the chance to participate in a trial for 5 min. If they don't participate within that time, we record -1 in the data sheet, the apparatus is removed and the trial is re-attempted later.
- **Dispersal:** DNA is collected from the grackles, processed, and analyzed for pairwise relatedness using ddRADseq and Stacks as in Sevchik et al. (2019) (protocol).
- **Suitable habitat:** We will conduct ecological niche modeling to investigate grackle presence as it overlaps with suitable habitat across their range. Grackles will be considered as present or absent in a particular geographic area based on sightings reported at eBird.org. We identified suitable habitat variables from Selander and Giller (1961), Johnson and Peer (2001), and Post et al. (1996), and we added additional variables relevant to our hypotheses. A suitable habitat map will be generated across the Americas using GIS.

Commenté [CN25]: This is central to explain because it is not straightforward to see the relevance and feasability

Open data (H1 & H2)

When the study is complete, the data will be published in the Knowledge Network for Biocomplexity's data repository.

Randomization and counterbalancing (H1 & H2)

Experimental order: The order of experiments, reversal learning or multiaccess log, will be counterbalanced across birds within a site.

Reversal learning: The first rewarded color in reversal learning is counterbalanced across birds at each site. The rewarded option is pseudorandomized for side (and the option on the left is always placed first). Pseudorandomization consists of alternating location for the first two trials of a session and then keeping the same color on the same side for at most two consecutive trials thereafter. A list of all 88 unique trial sequences for a 10-trial session, following the pseudorandomization rules, will be generated in advance for experimenters to use during testing (e.g., a randomized trial sequence might look like: LRLLRRLRLR, where L and R refer to the location, left or right, of the rewarded tube). Randomized trial sequences will be assigned randomly to any given 10-trial session using a random number generator (random.org) to generate a number from 1-88.

Blinding during analysis

No blinding is involved in this investigation.

E. ANALYSIS PLAN

Commenté [CN26]: This seems very well done but I have not read with total attention

We use **simulations** and design customized **models** to determine what sample sizes allow us to detect differences between sites (see chapter 5.3 in Bolker (2008) for why simulations perform more powerful power analyses). We do not plan to **exclude** any data and if there are **missing** data (e.g. if a bird participated in one of the two experiments, then it will only be included in those analyses for which it has data). Analyses will be conducted in R (current version 3.6.3; R Core Team (2017)) and Stan (version 2.18, Carpenter et al. (2017)).

H1: behavior across the range

Response variables

1. Flexibility: number of trials to reverse a color preference.
2. Innovativeness: total number of loci solved on the multiaccess log (maximum=4)
3. Exploration: Latency to approach up to 20cm of an object (novel or familiar, that does not contain food) in a familiar environment (that contains maintenance diet away from the object) - OR - closest approach distance to the object (choose the variable with the most data for the analysis).
4. Persistence: proportion of trials participated in during the flexibility and innovativeness experiments

One model will be run for each response variable

Explanatory variable

There is no explanatory variable: we will conduct pairwise comparisons across sites as described in the next section.

Hypothesis-specific mathematical model

Following procedures in McElreath (2016), we constructed a **hypothesis-appropriate mathematical model** for each of the response variables that examines differences in the response variable between sites. These models take the form of:

$y \sim \alpha$

[site]

y is the response variable (flexibility, innovation, exploration, or persistence). There will be one intercept, α

, per site and we will estimate the site's average and standard deviation of the response variable.

We will then perform pairwise contrasts to determine at what point we will be able to detect differences between sites by manipulating sample size, and α

means and standard deviations. Before running the simulations, we decided that a model would detect an effect if 89% of the difference between the two posterior distributions was on the same side of zero (following McElreath (2016)). We ran these analyses in R (current version 3.6.3; R Core Team (2017)) and used the following R packages: rethinking (McElreath (2020)), rstan (Stan Development Team (2020)), and Rcpp (Eddelbuettel and François (2011)).

Flexibility analysis

Model and simulation

Expected values for reversal learning using color tubes (mean, standard deviation, and range of number of trials to reverse a color preference) were based on previously published data on great-tailed grackles (C.J. Logan (2016)). This data indicates that the average number of trials to reverse a preference is 91 and the standard deviation is 21 (n=7 grackles). The σ

prior is set to produce only positive values that encompass the range of values shown by the Santa Barbara grackles (reversing in 70-130 trials, 130 trials-91 mean is about 40 trials).

y ~ α

[site] *[the model]*

α

[site] ~ Normal(μ,σ) *[α_1*

prior]

μ

~ Normal(91,21) *[μ*

prior]

σ

~ Uniform(0,40) *[σ*

prior]

We then ran the **mathematical model** and performed pairwise contrasts and determined that we will be able to detect differences between sites with a sample size of 15 at each site if the average number of trials to reverse a preference differs by >13 trials, and the standard deviation is a maximum of 21 at each site (Table 2). For a sample size of 20 at each site, which is more like what we expect, we will be able to detect site differences if the average number of trials to reverse a preference differs by >11 trials, and the standard deviation is a maximum of 23 at each site (Table 2).

Table 2. Simulation outputs from varying sample size (n), and α

means and standard deviations. From the pairwise contrasts, if the difference between the distributions crosses zero (yes), then we are not able to detect differences between the two sites. If they do not cross zero (no), then we are able to detect differences between the two sites. Note that for latency, there is no mu_sd, but rather one phi that is the same for all sites.

trials to reverse
60
91
101
81
21
21
21
Yes
No
No
trials to reverse
60
91
115
81
21
21
21
Yes
No
No
trials to reverse
60
91
120
81
21
21
21
No
Yes
No
trials to reverse
60
91
120
79
21
21
21
No
No

No
trials to reverse
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120
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22
22
22
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trials to reverse
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79
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Yes
No
trials to reverse
45
91
120
79
21
21
21
No
Yes
No
trials to reverse
45
91
120
77

21
21
21
No
No
No
trials to reverse
45
91
120
77
24
22
23
No
Yes
No
1-10 of 104 rows
...
Loading...

Results (using our actual data)

We will analyze our data using the above model once all of the data have been collected.

Innovation analysis

Model and simulation

Expected values for the number of options solved on the multiaccess log were set to 0-4 (out of 4 options maximum) because this apparatus had been used on two species of jays who exhibited individual variation in the number of loci solved between 0-4 (California scrub-jays and Mexican jays: McCune (2018), Kelsey B McCune et al. (2019)).

locisolved ~ Binomial(4, p) *[likelihood]*

logit(p) ~ α

[site] *[model]*

locisolved is the number of loci solved on the multiaccess box, 4 is the total number of loci on the multiaccess box, p is the probability of solving any one locus across the whole experiment, α

is the intercept, and each site gets its own intercept. After running simulations, we identified the following distribution to be the most likely priors for our expected data:

α

~ Normal(0,1) *[*α

prior]

We used a normal distribution for α

because it is a sum (see Figure 10.6 in McElreath (2016)) and a logit link to ensure the values are between 0 and 1. We set the mean to 0 on a logit scale, which means an individual solves 2 loci on average on the actual scale at a probability of 0.5.

We then ran the **mathematical model** and performed pairwise contrasts and determined that we will be able to detect differences between sites with a sample size of 15 at each site if the average number of loci solved differs by 1.2 loci or more and the standard deviation is generally a maximum of 0.9 at each site (Table 2). For a sample size of 20 at each site, we will be able to detect site differences if the average number of loci solved differs by 0.7 of a locus or more and the standard deviation is generally a maximum of 1 at each site (Table 2). Note: the Arizona sample size is 11 for the multiaccess log and 17 on a similar multiaccess box.

Results (using our actual data)

We will analyze our data using the above model once all of the data have been collected.

Exploration analysis

Model and simulation

We modeled the average latency to approach an object and compared these between sites. We simulated data and set the model as follows:

latency ~ gamma-Poisson(λ_i

, ϕ

) *[likelihood]*

log(λ_i

) ~ α

[site] *[the model]*

latency is the average latency to approach an object, λ_i

is the rate (probability of approaching the object in each second) per bird (and we take the log of it to make sure it is always positive; birds with a higher rate have a smaller latency), ϕ is the dispersion of the rates across birds, and α

is the intercept for the rate per site.

Expected values for the latency to approach a novel object range from 0-2700 sec, which encompasses the time period during which they are exposed to the object (sessions last up to 45 min). However, we do not provide an upper limit for the model because those birds that do not approach within 2700 sec would eventually have had to approach the object to access their food (it is just that sessions did not run that long). After running simulations, we identified the following distribution and priors to be the most likely for our expected data:

ϕ

~ 1/(Exponential(1)) *[*ϕ

prior]

α

~ Normal(1350,500) *[*α

prior]

We used a gamma-Poisson distribution for latency because it constrains the values to be positive. For ϕ

, we used an exponential distribution because it is standard for this paramter. We used a normal distribution for α because it is a sum with a large mean (see Figure 10.6 in McElreath (2016)). We estimate that the grackles might approach the object at any time in the session, therefore we held the α mean of 1350 sec in mind as we conducted the modeling. We set the α

standard deviation to 500 because this puts the range of seconds for the distribution in the possible range.

We then ran the **mathematical model** and performed pairwise contrasts and determined that we will be able to detect differences between sites with a sample size of 15 at each site or 20 at each site if the average latency to approach the object differs by at least 450 sec at each site (Table 2). We kept the shape of the curve (which can be thought of as similar to a standard deviation) the same across sites because we do not think this assumption will change across populations (i.e., there will be lots of variation at each site with some individuals approaching almost immediately, others in the middle of the session, and others near the end).

Results (using our actual data)

We will analyze our data using the above model once all of the data have been collected.

Persistence analysis

Model and simulation

Expected values for the number of trials not participated in could range from 0-125 (likely maxima: 300 trials reversal learning [70 trials initial discrimination, 130 trials reversal, ~100 non-participation trials], 50 trials multiaccess log [~25 non-participation trials]). After running simulations, we identified the following distribution and priors most likely for our expected data:

participated ~ Binomial(totaltrials, p) *[likelihood]*

logit(p) ~ α

[site] *[model]*

participated indicates whether the bird participated or not in a given trial, total trials is the total number of trials offered to the individual (those participated in plus those not participated in), p is the probability of participating in a trial, α

is the intercept, and each site gets its own intercept. We used a logit link to constrain the output to between 0 and 1. After running simulations, we identified the following distribution and priors most likely for our expected data:

α

~ Normal(0,0.5) *[*α

prior]

We used a normal distribution for α

because it is a sum (see Figure 10.6 in McElreath (2016)). We set the mean to 0 (on a logit scale, which is a probability of 0.5 that a bird will participate in every other trial on average on the actual scale).

We then ran the **mathematical model** and performed pairwise contrasts and determined that we will be able to detect differences between sites with a sample size of 15 per site or 20 per site if the average proportion of trials participated in differs by at least 0.08 and the standard deviation is generally a maximum of 0.25 at each site (Table 2).

Results (using our actual data)

We will analyze our data using the above model once all of the data have been collected.

Repeatability of exploration and persistence

Analysis: We will obtain repeatability estimates that account for the observed and latent scales, and then compare them with the raw repeatability estimate from the null model. The repeatability estimate indicates how much of the total variance, after accounting for fixed and random effects, is explained by individual differences (bird ID). We will run this GLMM using the MCMCglmm function in the MCMCglmm package ((Hadfield 2010)) with a Poisson distribution and log link using 13,000 iterations with a thinning interval of 10, a

burnin of 3,000, and minimal priors (V=1, nu=0) (Hadfield 2014). We will ensure the GLMM shows acceptable convergence (i.e., lag time autocorrelation values <0.01; (Hadfield 2010)), and adjust parameters if necessary.

H2: dispersal

Response variable

1. Average relatedness between all pairs of individuals within one sex

Explanatory variables

1. Site diameter (meters)
2. Site sample size
3. Number of generations at a site

One model will be run per sex

The data will be analyzed as in Sevchik et al. (2019). To summarize, blood is collected from the bird, DNA is extracted (by Aaron Blackwell at Washington State University), size selected (between 400-700 base pairs), and sequenced using ddRADseq (at Cornell University Lab of Ornithology) on an Illumina NextSeq500 machine using the mid-output setting for 150 base pair single end reads. Data are post processed to generate single nucleotide polymorphisms (SNPs) as in Thrasher et al. (2018). Genetic relatedness between all pairs of individuals is calculated using the package "related" (Pew et al. (2015)) in R (as in Thrasher et al. (2018)). Permutations (i.e., randomly assigning site ID to individuals) and general linear models estimating average relatedness of each individual to all others at that site will be used to determine whether individuals at one site are more closely related to each other than the individuals at another site.

Model and simulation

Expected values for average relatedness per bird were based on the fact that average relatedness with these estimators has to range between -1 and 1 and because it is an average we expect a normal distribution.

averagerelatedness ~ α

[site] *[the model]*

α

[site] ~ Normal(μ,σ) *[α_1*

prior]

μ

~ Normal(0,1) *[μ*

prior]

σ

~ Uniform(0,1) *[*σ

prior]

H3: suitable habitat

P3: GTGR & BTGR use different habitats and GTGR's habitat has increased over time and P4: GTGR increased habitat breadth over time, but BTGR did not

Response variable: Presence/absence of GTGR and BTGR

Explanatory variable

1. Land cover (e.g., forest, urban, crop land, coastal marsh, coastal prairie, coastal plain, grassland, brush, mangrove, distance from road/water body/wetland/water treatment plant)
2. Elevation
3. Climate (e.g., daily/annual temperature range)
4. Predator density
5. Distance to the next suitable habitat patch weighted by nearest mountain range/forest
6. Distance to the nearest conspecific population 10 years previous to the point in time being investigated

Commenté [CN27]: Here are the variables for habitat comparison. It would be useful to specify what range of values for these variables are relevant for each of the two species (is it known?)

One model will be run for GTGR and a separate model will be run for BTGR

Analysis

1. Download and preprocess eBird data. Conduct spatial filtering to account for sampling bias
2. Clean the species occurrence data: remove any uncertain records or geographic outliers
3. Import climactic variables from WorldClim and landscape data from MODIS and crop to region of interest
4. Match environmental data to grackle occurrence records
5. Fit models with maxent to get predicted distributions and estimate importance/contribution of each environmental variable

We will refer to Strimas-Mackey et al. (2016) best practices for using eBird data when extracting data on grackle presence in a region from eBird.org. We will gather environmental data from databases, including a database that maps global urban change from 1985-2015 to a high (30 m) resolution (Liu et al. (2020)). We will use a variety of R packages, including auk (Strimas-Mackey et al. (2018)), dismo (Hijmans et al. (2017)), raster (Hijmans (2020)), maptools (Bivand and Lewin-Koh (2019)), tidyverse (Wickham et al. (2019)), rgdal (Bivand et al. (2019)), rJava (Urbanek (2020)), and elevatr (Hollister and Tarak Shah (2017)).

F. ETHICS

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

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

G. AUTHOR CONTRIBUTIONS

Logan: Hypothesis development, data collection (H1 & H2), data analysis and interpretation, write up, revising/editing, materials/funding.

McCune: Method development, data collection (H1 & H2), data analysis and interpretation, revising/editing.

Chen (H3): Hypothesis development, data collection, ecological niche modeling, data interpretation, revising/editing.

Lukas: Hypothesis development, data analysis and interpretation, write up, revising/editing.

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I. CONFLICT OF INTEREST DISCLOSURE

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

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