Does great-tailed grackle space use behavior relate to individual differences in exploration?

McCune KB (University of California Santa Barbara, UCSB, kelseybmccune@gmail.com), Ross C (MPI EVA), Folsom M (Max Planck Institute for Evolutionary Anthropology, MPI EVA), Bergeron L (UCSB), Logan CJ (MPI EVA)

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Code

```
#Make code wrap text so it doesn't go off the page when Knitting to PDF
library(knitr)
opts_chunk$set(tidy.opts=list(width.cutoff=60),tidy=TRUE)
```

Click here to navigate to the version-tracked reproducible manuscript (.Rmd file)

ABSTRACT

Great-tailed grackles (*Quiscalus mexicanus*) are rapidly expanding their geographic range (Wehtje (2003)) and it is generally thought that they must rely on behavioral flexibility to achieve this feat Logan et al. 2019. However, it is alternatively possible that the individuals on the range edge are more exploratory and exhibit distinct movement behaviors in space (e.g. have larger home ranges and are less predictable about which locations they visit daily), facilitating the range expansion. There is evidence for a relationship between exploratory traits and dispersal (the movement of young and/or adults into new territories; Cote et al. (2010)), but it is still unknown whether individual differences in exploration relate to daily movement patterns. Grackles are strongly associated with human-modified landscapes and eat a variety of human foods (e.g crops, at outdoor cafes, and out of garbage cans) in addition to foraging on insects and on the ground for natural food items (Johnson and Peer (2001)). Distinct daily movement behaviors (i.e. "space use") might facilitate range expansion above and beyond dispersal if the ability and motivation to encounter novel foods and food sources is the limiting factor in grackles' expansion (Spiegel and Crofoot (2016)), rather than their ability to flexibly choose among a variety of options (e.g., to keep track of which restaurants serve lunch at outdoor cafes, when the busiest times are and potentially choose among them according to preferred food type). We aim to understand whether measures of exploration in captivity are associated with space use behavior in the wild in great-tailed grackles from three populations that span the current range: Central America (their original range), Arizona (middle of the northern expanding edge), and northern California (near the northern edge of their range). Additionally, we aim to describe whether samples of grackles from the three populations systematically vary in space use behavior; this will allow us to overall infer a potential relationship between exploration, space use and range expansion. Exploration, measured here following McCune et al. 2019, is interpreted as an individual's response to novelty, such as novel environments or novel objects (Réale et al. (2007)), to gather

information that does not satisfy immediate needs (Mettke-Hofmann, Winkler, and Leisler (2002)). We will subsequently measure the space use behavior of wild, adult grackles on which exploration measures have been obtained in captivity, using radio telemetry to find color-banded grackles and record spatial locations across time using GPS units. Traditional studies of animal space use require spatial and temporal independence of data points for statistical analysis (Swihart and Slade (1985)). However, spatial and temporal autocorrelation (where individuals are found in the same locations across time, such that subsequent relocations are predictable based on previous space use) is an intrinsic component of animal behavior and eliminating it can reduce biological relevance (Dray, Royer-Carenzi, and Calenge (2010), e.g. animal movement behavior is influenced by intrinsic factors as well as the available habitat and resources which are distributed non-randomly across the landscape). Therefore, in addition to using a typical measure of space use that controls for autocorrelation (i.e. home range size), we propose two new methods for analyzing wild grackle space use behaviors. The first will describe individual differences in movement behavior by analyzing the autocorrelation of step length (distance between two sequential observations) and turning angle for each individual over time (Pacheco-Cobos et al. (2019)), while the second will describe individual differences in spatial preferences by analyzing the repeatability of each individual's occurrence in particular geographic locations. These results will inform whether individual differences in space use behavior are associated with consistent individual differences in exploration, which could be subject to selection and influence this species' range expansion within populations. Furthermore, if space use behavior correlates with ~~experimental~~ measures of exploration, then space use data could be used to inform conservation management strategies (e.g. which individuals are likely to remain in new or restored habitat after a translocation (May, Page, and Fleming (2016))) in species where it is not logistically feasible to a priori~~experimentally~~ measure exploration in captivity.

Commentaire [B1]: is this relevant for an abstract ? maybe delete this part here

Commentaire [B2]: to me this is not experimental in the sense that it does not aim at manipulating exploration but is only a way to measure the basic level if this trait (a bit like measuring tarsus length requires catching the bird and using a caliper, but this is not an experiment). I would delete the word here.

Commentaire [B3]: same as above

A. STATE OF THE DATA

This preregistration uses secondary data: data that are already being collected for other purposes (GPS points in hypothesis 3 and home range sizes in prediction 3 in the flexibility and foraging preregistration). This preregistration was written in June 2019, while at the same time increasing the number of GPS points taken per time per bird to provide enough data for the analyses here, and submitted in September 2019 to PCI Ecology for pre-study peer review. Reviews were received in December 2019 and we revised and resbumitted in March 2020.

Commentaire [B4]: ? unit of time ?

B. HYPOTHESES

H1: Individual differences in measures of exploration using novel environment and novel object tasks (see separate preregistration for methods) are related to variation in space use (measured via home range size, autocorrelation of step lengths and turning angles, or whether individuals are predictably found in the same locations) across the breeding and non-breeding seasons. Previous studies on birds have found a relationship between movement behavior in the wild and exploration measured in captivity using novel environment (Minderman et al. (2010), Dingemanse et al. (2003)) and novel object (Mettke-Hofmann, Winkler, and Leisler (2002)) tests, therefore the measures we are investigating have the potential to be relevant to grackles. We expect space use

to vary within an individual across breeding seasons because during the non-breeding season this species forages in smaller groups and communally roosts in larger groups (Johnson and Peer 2001). During the breeding season, one or more males defend a territory and females place their nests within territories to raise the young [johnson2000male]. Roaming males are also present and can obtain extra-pair copulations with females on other male's territories [johnson2000male].

Prediction 1: ~~The m~~More exploratory grackles, i.e. individuals that get closer or make more touches to the novel object and novel environment will be found in a larger expanse (larger home range size), use less predictable movement patterns (low autocorrelation of step lengths and turning angles), and occupy a greater variety of spatial locations. This would suggest~~s~~ that exploratory individuals ~~may be~~are more willing to move into novel areas in the wild.

Commentaire [B5]: more touches to the novel environment ? This may require reformulation

Prediction 1 alternative 1: ~~The m~~More exploratory grackles that get closer or make more touches to the novel object and novel environment will use a smaller amount of space (smaller home range size), use more predictable movement patterns (high autocorrelation of step lengths and turning angles), and consistently occupy the same spatial locations. This would suggest~~s~~ that more exploratory individuals may be able to more efficiently use the habitat within their home range. For example, in great tits, the slow-exploring phenotype relates to more in-depth investigatory behaviors to changes in the local environment (Verbeek, Drent, and Wiepkema 1994), switching to utilization of different resources in the same area (Overveld and Matthysen 2009), and better problem-solving abilities (Cole and Quinn 2011). Therefore it may not be necessary for these individuals to move into new areas for resources such as food or mating opportunities.

Commentaire [B6]: repetition not needed I think ?

Commentaire [B7]: maybe use here the same words as above

Prediction 1 alternative 2: Only performance on the novel environment task will correlate positively with space use behavior in the wild. This would suggest~~s~~ that perception of, and behavioral interactions with, novel environments (spatial information) differs from that used for novel objects (Mettke-Hofmann et al. 2009).

Prediction 1 alternative 3: Only performance on the novel object task will correlate positively with space use behavior in the wild. This would suggest~~s~~ that, in these populations located in human-modified environments, space use may primarily be driven by grackles searching for novel objects that represent human-provided sources of food. Much of the food grackles consume is contained within human-made packaging (e.g. grackles search inside take out bags from restaurants) or enclosed in human-made containers (e.g. garbage cans), therefore they should have a reason to approach and explore new objects to determine whether they could be a new food source.

Prediction 1 alternative 4: There will be no correlation between an individual's proximity or touches to the novel object or novel environment and their space use behavior. This would suggest~~s~~ that the ~~experimental~~ measures of exploration in captivity either are not relevant enough to how grackles use space in the wild to be able to measure the same trait, or they are independent of space use behavior potentially because the individuals tracked are primarily adults and are already familiar with their home range and surrounding areas and thus do not need to further use the space as if it were novel.

Commentaire [B8]: same comment as above

H2: Space use behavior will vary among grackles from our three study populations located along different points in the geographic range of this species (core, middle of expansion, and range edge; Table 1).

Prediction 2: Home range size~~s~~ will increase, autocorrelation of step lengths and turning angles will decrease (i.e. grackle movement behavior will be less predictable), and grackles will use a greater variety of spatial locations as the geographic distance from the original center of the range increases. Specifically, the grackles sampled from our site on the edge of the range (northern California), will have larger overall home range sizes, exhibit more variety in step lengths and turning angles, and use a greater variety of spatial locations than the sample of grackles in the core of the range (Central America). Grackles in the sample from the middle of the expanding range will be intermediate in space use (Arizona). ~~This~~ Such population differences in space use behaviour may relate to range expansion because some of the individuals on the leading edge of the range may use more space and move longer distances (Duckworth and Badyaev 2007). However, larger-scale sampling of grackle groups across the strata of the expansion front and core range would be needed to more robustly validate the hypothesis that our cross-site differences are indicative of a broader pattern driven by the location of the expansion front.

Prediction 2 alternative 1: Grackles sampled on the edge of the range will have smaller overall home range sizes, high autocorrelation in step length and turning angle (i.e. movement behavior will be more predictable), and consistently use the same spatial locations compared to grackles sampled in the middle or core of the current range. This would suggest~~s~~ that suitable habitat may be distributed in small patches, that novel habitats at the edge of the range may have high predation on grackles that use more space, and/or that individual grackles specialize on certain novel habitat types that are patchily distributed.

Prediction 2 alternative 2: ~~There is~~We will find no difference across the geographic range in the space use behavior of the grackles sampled. This would suggest~~s~~ that, on average, all grackles may use the same amount of space, or that there is a similar distribution of individual differences in space use in each population. Alternatively, grackles sampled in different populations may converge on similar space use behavior during development, however we will not be able to distinguish between these two options with our data, which is primarily from adults.

Table 1. Population characteristics for each of the three field sites. Generation length = 5.6 years as estimated by (International 2018).

C. METHODS

Planned Sample

Great-tailed grackles are caught in the wild, given colored leg bands in unique combinations for individual identification, and released at their point of capture. The color-marked grackles in this study have one of two different backgrounds: those that do not have radio tags and those that do. First, we opportunistically track color-marked grackles that do not have a radio tag (and thus have not spent time in the aviaries) to compare whether time spent in the aviaries is related to space use behavior. When a color-marked bird is encountered, researchers track it for 20-90 minutes, recording the spatial location every one minute. If the bird goes out of view, researchers attempt to find it again for 15-30 minutes before moving on. Because these data are opportunistic, we do not attempt to balance for sex, but we aim to follow at least 20 non-tagged individuals in each population.

Second, those that do have radio tags (estimated 20 individuals per population) are primarily adults who we attempt to balance for sex, and who spent up to six months in an aviary while they participated in behavioral choice tests (see Logan et al. 2019 for details) and individual differences assays, including measures of exploration in captivity (see McCune et al. 2019 for details), as part of other research projects by this lab. Note that we aim to bring only adults in to the aviaries for the cognitive test battery so that we are able to understand what this species is capable of, rather than testing juveniles who might still be developing their cognitive skills. The radio tags were originally applied to all aviary-tested birds to ensure that we could find their nest sites and track measures of reproductive success for these individuals for which we have an extensive amount of data. Now we additionally use the radio tags to collect data for this space use preregistration, which was later developed to address additional questions based on data we were already collecting. For details about the captive environment, please refer to the preregistration associated with this part of the research: McCune et al. 2019. Before the aviary grackles are released, they are fitted with VHF radio tags (Lotek PipLL (model Ag386), Advanced Telemetry Systems (model A2455) or Holohil Systems Ltd. (model BD-2)) so we can track space use behavior using radio telemetry. Radio tags were initially attached to the grackles by gluing them to their backs (Johnson and Peer (2001), Mong and Sandercock (2007)), however these did not stay on for very long. Therefore, we now use a leg loop harness (methods as in Rappole and Tipton (1991)) made from sutures and secured with crimp beads (Vicryl undyed 36in sutures, item number D9389 at eSutures.com; 0.5mm diameter, absorbable so they fall off after one to four months).

Commentaire [B9]: what type of data : space use data and/or exploration measures in captivity ?

After release, an experimenter tracks each tagged grackle for approximately 1.5 hours on a given day, recording a GPS point approximately every one minute, regardless of whether the bird moved (Cushman, Chase, and Griffin 2005). We aim to follow each tagged grackle at least four times per week to obtain as much data on space use as possible. Additionally, we aim to track all grackles equally during morning and afternoon time periods. Researchers maintain a distance of at least 30 m and observe the bird with binoculars so the grackle's behavior is not influenced or artificially changed. If the grackle alarm calls while oriented towards the researcher (indicating the researcher's presence affected the grackle's behavior), all tracking on that individual is stopped for the day. To ensure we capture all locations the individual visits and not just those where they are most easily seen and followed, tagged grackles that move out of sight during tracking are searched for with telemetry until they are found again.

To account for alternative variables that may relate to space use behavior in wild grackles, we will also include covariates in our models that measure energetic condition (described in Berens et al. 2019), and habitat characteristics such as human food sources and available breeding habitat (described in Logan et al. 2019).

Conspecific density has also been shown to affect home range size in other bird species (Flockhart et al. (2016); Garabedian et al. (2018)). To control for the possibility that home range size may vary among our populations due to conspecific density rather than exploratory traits, we will use point count surveys to measure grackle population density. We will place 225 point count stations across the landscape encompassing each population (Tempe, AZ; Woodland, CA; Gamboa, Panama). For each study population, the first central point will be randomly placed within 500 m of the center of the study area. The remaining points are placed in a 500 m grid pattern extending out from this central point. In total, the sample area will cover an area that is 7 km by 7 km. Each point will be visited once during the non-breeding season (Sep-Mar). During the survey, researchers will record all grackles visually and aurally detected for six minutes.

Sample size rationale

We test as many birds as we can during the approximate five years of this study 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 for captive subjects will be 57 across the three sites (approximately 20 birds per site with the aim that half of the grackles tested at each site are females). We catch grackles with a variety of methods, 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). Once released, we will primarily track the space use behavior of these ~57 grackles that have radio tags. We will also opportunistically collect GPS point locations on all occasions that we see any color-marked grackle to determine whether grackles that were previously in the aviary have different space use behavior from non-aviary-held grackles after their release. We will attempt to match the sample size of aviary birds, and in our Arizona population we currently have over 20 points (the minimum number for reliably calculating home range size: Noonan et al. (2019)) for 31 individuals that have never had radio tags. We aim to acquire more than 20 points on at least 20 non-tagged grackles in the other two populations as well. Additionally, we attach radio tags to birds that do not participate in aviary tests (currently 3 individuals) and are released early to determine whether space use behavior differs between participatory and non-participatory grackles.

Data collection stopping rule

We will stop collecting GPS location data on tagged and non-tagged birds when home ranges are fully revealed for data collected in both breeding and non-breeding seasons. To determine at what point home ranges have been fully revealed, we will calculate the asymptotic convergence of home range area as in Leo et al. (2016). We will test home range asymptotic convergence for breeding season and non-breeding season movements separately (breeding season: Apr - Aug, non-breeding season: Sep - Mar).

Open materials

Protocols:

- Exploration protocol for exploration of new environments and objects, boldness, persistence, and motor diversity.
- Radio tracking protocol for attaching radio tags and collecting GPS points using radio telemetry.
- Point count protocol for measuring grackle population density in the study area.

Open data

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

Randomization and counterbalancing

There is no randomization in this investigation. The order of the exploration tasks is counterbalanced across birds (see the separate preregistration for details). The time of day that we collect GPS point locations is counterbalanced within and across birds to account for potential variation in movement behavior arising from daily circadian rhythms.

Blinding of conditions during analysis

No blinding is involved in this investigation.

Summary of methods for measuring exploration McCune et al. 2019

Exploration assays for the grackles that are temporarily held in aviaries occur twice for each bird: once near the beginning of their aviary time and once again approximately 6 weeks later. We will analyze whether behavioral responses during assays are repeatable within individuals. The order of assays (exploration novel environment, exploration novel object, and boldness) is counterbalanced across individuals. If the two exploration measures are consistent within individuals and correlate with each other, we will choose the variable with the most data. If the two measures do not correlate, we will include both as independent variables.

Dependent variables

P1-P2

1. Home range size (square meters): an estimate calculated using the autocorrelated-Gaussian reference function kernel density estimate (AKDE), which is the only estimate of home range that accounts for autocorrelation due to the small time period between each of our GPS locations (Noonan et al. 2019). This estimate consists of the area enclosing the GPS location points for an individual grackle during its normal activities.
2. Autocorrelation of step length (meters): measured as the standard deviation of step lengths (the distance between two sequential GPS points)
3. Autocorrelation of turning angle (degrees): measured as the standard deviation of turning angles
4. Spatial location preference: measured as the repeatability of grackle occurrence in a given cell of a 5 x 5 m grid array across the landscape

One model will be run for each dependent variable

Independent variables

P1 and P1 alternatives 1-4

1. Exploration of novel environment: Latency to approach up to 20cm of a novel environment (that does not contain food) set inside a familiar environment (that contains maintenance diet away from the object) - OR - closest approach distance to the novel environment (choose the variable with the most data)
2. Exploration of novel object: 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)
3. Sex: Male or female
4. History: the number of days the individual was temporarily held in the aviaries before data collection on space use began (0 indicates the grackle was only ever in the wild)
5. The number of known breeding sites (shade trees, date palms, marsh vegetation (Johnson and Peer 2001)) within the home range of each individual (data collected as part of Logan et al. 2019)
6. The number of human food source areas (dumpsters, cat food bowls, outdoor restaurant seating areas and parking lots) within the home range of each individual (data collected as part of Logan et al. 2019)
7. Scaled mass index (Peig and Green 2009) as a measure of energetic condition
8. Maximum group size observed across each individual's focal follows (data collected as part of Logan et al. 2019)

P2

1. Site: Whether the grackle was from our study population located on the edge of the range (Northern California), the center of the original range (Central America), or the center of the current expanding edge (Arizona).
2. Sex: Male or female
3. History: the number of days the individual was temporarily held in the aviaries before data collection on space use began (0 indicates the grackle was only ever in the wild)
4. Population density (number of grackles per square meter in each study area: Arizona, California, Central America)

D. ANALYSIS PLAN

We do not plan to **exclude** any data and if there are **missing** data (e.g. if a bird had to be released before collecting their data at time 2) these birds will be excluded from analyses requiring data from times 1 and 2. Analyses will be conducted in R (current version 3.5.2; R Core Team (2017)) and Stan (version 2.18, Carpenter et al. (2017)).

We will first verify that the GPS point locations for each bird result in asymptotic convergence as in Leo et al. (2016). To calculate our dependent variable we will use the autocorrelated kernel density estimate method for quantifying home range size (in square meters) using the akde function in the R packages ctmm (Calabrese, Fleming, and Gurarie 2016) and sf (Pebesma 2018). Autocorrelated kernel density estimates (AKDE) of home range size are the most accurate when data are collected close together in time and space (Noonan et al. 2019). We are interested in all movements by grackles, therefore we will not exclude any outlier relocations collected during "normal daily activities" (C. Calenge 2011). "Normal daily activities" indicate that grackles are not engaging in behaviors that would artificially skew their space use, for example mobbing a predator or the experimenter, or behavior before sunrise or after sunset when they are at the roost. Outside of these circumstances, we will include all data to detect space use movements.

Second, we will determine whether our space use variables vary by season (breeding or non-breeding). If season has no significant effect, all data will be included in our subsequent analyses. If there is a significant effect of season, we will run models separately for each dependent variable and each season.

From the GPS point locations collected on each individual, we will use a Bayesian model (detailed below) to estimate the following parameters: mean and dispersion (variance) of step lengths and turning angles for each bird on each daily track (Pacheco-Cobos et al. (2019)). We will determine whether these parameters governing movement are stable or variable within individuals across days. A small variance would indicate there is low variability (high repeatability) in the daily movement behaviors of the individual.

Moreover, we will determine whether grackles show individual differences in consistent use of habitat by overlaying a grid array across the landscape. We will then create matrices describing the number of times a grackle was observed in each cell on each day. High autocorrelation among daily matrices indicates an individual that frequents the same spatial locations across days.

We will then model the relationship between bird-specific data on performance in the exploration tasks (and other covariates), and bird-specific movement parameters (e.g. step-size, turning angle, autocorrelation in space use).

Ability to detect actual effects

To understand what effect sizes we will be able to detect given our sample size limitations and the number of explanatory variables, we used G*Power (v.3.1, Faul et al. (2007), Faul et al. (2009)) to conduct power analyses based on confidence intervals. G*Power uses pre-set drop down menus and we chose the options that were as close to our analysis methods as possible (listed in each analysis below). We realize that these power analyses are not fully aligned with our study design, however we are unaware of better options at this time. Additionally, it is difficult to run power analyses because it is unclear what kinds of effect sizes we should expect due to the lack of data on this species for these measures.

Calculating home range size

Code to create functions for analyzing movement behaviors

All scripts and code are available at https://github.com/ctross/grackleator.

Modeling bird movement behaviors: step length, turning angle, spatial location preference

H1: P1 - Exploration measured in captivity relates to space use behavior

To roughly estimate our ability to detect actual effects, we ran a power analysis in G*Power with the following settings: test family=F tests, statistical test=linear multiple regression:

Fixed model (R^2 deviation from zero), type of power analysis=a priori, alpha error probability=0.05. We reduced the power to 0.70 and increased the effect size until the total sample size in the output matched our projected sample size (n=57). The number of predictor variables was restricted to only the fixed effects because this test was not designed for mixed models. The protocol of the power analysis is here:

Input:

Effect size f^2 = 0,26

α err prob = 0,05

Power (1-β err prob) = 0,7

Number of predictors = 8

Output:

Noncentrality parameter λ = 14,5600000

Critical F = 2,1426580

Numerator df = 8

Denominator df = 47

Total sample size = 56

Actual power = 0,7034441

This means that, with our minimum sample size of 57, we have a 70% chance of detecting a small effect (approximated at f^2=0.20 by Cohen (1988)).

Code

```
data <- read.csv("Space_use.csv", header = T)

# Home range
m1 = lm(log(area) ~ ExpObj + ExpEnv + Sex + History + Breeding + Feeding +
Condition + Group, data = data)
hist(m1$resid)
summary(m1)

# Step length
m2 = lm(log(std_step)) ~ ExpObj + ExpEnv + Sex + History + Breeding +
Feeding + Condition + Group, data = data)
hist(m2$resid)
summary(m2)

# Turning angle
m3 = lm(log(std_angle)) ~ ExpObj + ExpEnv + Sex + History + Breeding +
Feeding + Condition + Group, data = data)
hist(H3$resid)
summary(m3)
```

```
# Spatial preferences
m4 = lm(log(loc_pref)) ~ ExpObj + ExpEnv + Sex + History + Breeding +
Feeding + Condition + Group, data = data)
hist(H4$resid)
summary(m4)
```

H2: P2 - Space use behaviors vary among populations across the range

To roughly estimate our ability to detect actual effects, we ran a power analysis in G*Power in the same way as for Hypothesis 1. The protocol of the power analysis is here:

Input:

Effect size f^2 = 0,19

α err prob = 0,05

Power (1-β err prob) = 0,7

Number of predictors = 4

Output:

Noncentrality parameter λ = 10,6400000

Critical F = 2,5533954

Numerator df = 4

Denominator df = 51

Total sample size = 56

Actual power = 0,7009879

This means that, with our minimum sample size of 57, we have a 70% chance of detecting a small effect (approximated at f^2=0.20 by Cohen (1988)).

Code

```
data <- read.csv("Space_use.csv", header = T)

# Home range
m1 = lm(log(area) ~ Site + Sex + History, data = data)
hist(m1$resid)
summary(m1)

# Step length
m2 = lm(log(std_step)) ~ Site + Sex + History, data = data)
hist(m2$resid)
summary(m2)

# Turning angle
m3 = lm(log(std_angle)) ~ Site + Sex + History, data = data)
```

```
hist(m3$resid)
summary(m3)

# Spatial preference
m4 = lm(log(loc_pref)) ~ Site + Sex + History, data = data)
hist(m4$resid)
summary(m4)
```

E. 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)

F. AUTHOR CONTRIBUTIONS

McCune: Hypothesis development, data collection (trapping, GPS tracking), data analysis and interpretation, write up, revising/editing.

Folsom: Data collection (trapping, GPS tracking), revising/editing.

Ross: Model development, data analysis and interpretation, revising/editing.

Bergeron: Data collection (trapping, GPS tracking), revising/editing.

Logan: Hypothesis development, data interpretation, write up, revising/editing, materials/funding.

G. FUNDING

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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. Corina Logan is a Recommender and on the Managing Board at PCI Ecology.

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