Comparing space use behavior and aviary-based exploration measures in a species rapidly expanding its geographic range

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Abstract— Species range expansions could be facilitated by consistent behavioral differences between individuals on the range edge relative to those in other parts of the range. Movement behaviors in particular are thought to be important for expanding and invasive species. There is evidence for a relationship between consistent individual differences in exploratory behavior and dispersal (the permanent movement an individual makes from its birth site to the place where it reproduces), but it is still unknown whether individual differences in exploration propensity relate to daily adult movement patterns within the home range ("space use"). Evidence suggests that daily space use behavior can vary consistently among individuals, but no studies have examined the relationship between empirical space use behavior and aviary-based measures of exploration, or space use behavior in different populations along an expanding range. Here, we studied a range-middle and range-edge population of great-tailed grackles (*Quiscalus mexicanus*), a species that is rapidly expanding its geographic range. We evaluated whether performance on an exploration task in captivity related to subsequent space use behavior in the wild, measured using home-range size, mean and variation in log movement velocity (step length per time), and spatial location preferences. We found that exploration performance was related to space use in the wild for the range-middle (Arizona) population but not the range-edge (California) population. The movement behavior of Arizona grackles was also related to the number of breeding and food sites within their home ranges. Moreover, we found that California grackles had significantly larger home-range sizes, but lower average movement velocities than Arizona grackles. Our results indicate that individual differences in exploration, measured in captivity, do seem to be a contributing mechanism explaining variation in space use in the wild. However, context dependent environmental factors, such as the presence of important resources or population proximity to the edge of the range can have a large impact on some aspects of daily space use patterns. To further clarify how behavior influences invasion success, future studies are needed to investigate additional edge–middle population pairs for daily space use and alternative personality traits, like activity or aggression.

Keywords— space use, great-tailed grackle, invasion syndrome, exploration, range expansion, movement

Introduction

Problematic range expansions of invasive species are occurring across the globe. However, not all species that invade novel areas outside of their traditional range become established [1, 2] and it is still unclear what characteristics facilitate successful invasions [3]. These characteristics are important for predicting potential invasions, especially since invasive species are implicated as a leading cause of biodiversity loss [4, 5]. One hypothesis is that the specific behavioral types of individuals at the invasion front facilitates geographic range expansion [6]. Traits such as exploration propensity and aggressiveness may make some individuals more likely to succeed when venturing into new habitats and competing with heterospecifics [7]. Evidence linking consistent individual differences in behavioral types to invasion success is accumulating. For example, Duckworth and Badyaev [8] found that western bluebird males on the range edge expressed more aggressive behavior, suggesting that range expansion was facilitated by aggressive males dispersing further and displacing less aggressive mountain bluebirds. Additionally, invasive cane toads on the invasion front in Australia spent longer in the dispersal movement mode and moved greater distances than other toads tracked several years later in the same location [9].

Within-species variation in the ability (movement) and motivation (exploratory tendency) to encounter conspecifics, novel foods, and novel food sources could be a limiting factor in successful species range expansions [10]. In novel areas, these resources and other environmental factors may not be as easily detectable or recognizable, and may be distributed differently across the landscape than in core areas of the range. Although individuals with exploratory phenotypes may be more successful at colonizing new habitat, more exploratory individuals may also face higher predation risk [11], and could be less likely to find local food sources [12]. Consequently, new areas may only become colonized by invaders if individuals exhibit a range of exploratory behaviors. Additionally, while

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dispersal—the permanent movement of an individual from its place of birth to the place where it reproduces [13]—is necessary to initially invade a novel habitat, subsequent daily space use patterns could determine establishment success. There is likely to be a dependence between space use preferences (e.g., in terms of movement patterns, and temporal consistency of revisiting known areas) and exploration propensity (e.g., in terms of investigating new locations and objects in the landscape). Moreover, as is evident from the cane toad invasion into Australia [@lindstrom2013rapid], space use patterns could also vary based on location along the invasion front. For example, on the range edge, conspecific density might be lower and individuals may be able to maintain larger home-range sizes or may use space differently due to differences in resource distribution [14]. However, current research on invasion success and movement behavior focuses most heavily on dispersal. While dispersal and exploration propensity have been shown to be associated [7], we still do not know how exploration tendency influences space use patterns in the daily lives of individuals expanding their ranges.

Space use behavior is expected to be influenced by internal states like exploratory tendency and hunger, as well as by the non-random distribution of available habitat and resources [15]. Space use can also consistently differ among individuals [16], which indicates that each individual has distinct preferences for how, when, and where to move within their home range. Traditional analyses of animal space use required spatial and temporal independence of data points for statistical analysis [17], yet movement data are unlikely to meet these criteria. Spatial and temporal autocorrelation occurs when the position of an individual at a given time is tightly linked to its position both before and after, including cases where individuals are repeatedly found in the same locations across time. This autocorrelation is an intrinsic component of space use behavior and eliminating it can reduce biological relevance and obscure relationships with behavioral types [18]. Using new models [19], we can draw more information from movement data to better illuminate the relationship between individual differences in exploratory tendency, space use behavior, and invasion success.

Study species

Great-tailed grackles (*Quiscalus mexicanus*, hereafter "grackles") are rapidly expanding their geographic range [20]. They are "invasive" because they meet the criteria for the establishment and spread stages of invasion [21], and they are considered a pest in some areas where they reduce crop yields [22]. However, the nature and level of ecological and social factors that grackles experience may vary in importance between populations in different parts of the range. Generally, this species is strongly associated with human-modified landscapes and is able to take advantage of a variety of human foods (e.g., crops, leftovers at outdoor cafes, or even scraps from garbage cans) in addition to foraging on insects and natural food items [23]. Furthermore, they exhibit variation in territorial social behavior in both the breeding and non-breeding seasons. During the non-breeding season, this species forages in smaller groups and communally roosts in larger groups [23]. During the breeding season, one or more males defend a territory where multiple females place their nests to raise the young [24]. Roaming males are also present and can obtain extra-pair copulations with females on other males' territories [24].

In this investigation, we aimed to understand whether exploratory tendency, measured in captivity, is associated with space use behavior, measured in the wild. We draw on individual-level data populations of grackles across the current range (see Table 1): Central America (core of the original range), Arizona (middle of the northern expanding edge) and northern California (near the northern limit of the expanding edge). Exploration propensity—measured following the protocol described in McCune et al. [25]—is interpreted as an individual's response to novelty, such as novel environments or novel objects [26], to gather information that does not satisfy immediate needs [27]. Previous studies on birds have found a relationship between some movement behaviors (home-range size and natal dispersal) in the wild and exploration propensity measured in captivity using novel environment [28, 29] and novel object [27] tests. As such, these measures have the potential to be relevant to grackles as well.

After measuring exploratory tendency in captivity, we used radio telemetry to measure space use behavior in the wild. We quantified a standard measure of space use that controls for autocorrelation (i.e., we defined a home range size for each bird), but we also investigated the behavioral relevance of autocorrelation in space use with two relatively new methods. The first method describes individual differences in path-level movement behavior by analyzing the mean and variation (standard deviation) of log step-length (i.e., the log distance between two sequential observations) and turning angle for each individual over time [33, 16], while the second method describes individual differences in spatial location preferences by analyzing whether each individual predictably returns to particular grid-cells (i.e., geographic locations) across successive weeks [34, 35], above and beyond what is expected given the general suitability of each grid-cell (e.g., in terms of food locations and breeding sites).

With these data, we tested two separate hypotheses. First, we tested whether grackle performance on exploration tasks in captivity is related to the space use metrics of the same individuals in the wild. Second, we tested the hypothesis that the space use behavior of wild grackles systematically varies with respect to the location of the population in the expanding range. This research has implications for invasive species management [6], but could also be used to inform the conservation of threatened and endangered species [e.g., to identify which individuals are likely to remain in new or restored habitat after a translocation; 36]. In particular, linking space use and exploratory tendency will be important for identifying variation in behavioral phenotypes in species where it is not logistically feasible *a priori* to measure exploration in captivity.

Table 1: Population characteristics for each field site. The number of generations at a site is based on a generation length of 5.6 years for this grackle species [30] and on the first year in which this species was reported to breed at the location—1936 for Tempe, Arizona [20] and 2000 for Woodland, California [Steve Hampton's reports in: 31]. 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 C.J. 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 [32].

Site	Range position	Breeding since	Years of breeding	Mean number of generations	Kilometers to nearest field site	Nearest field site	Citation
Central America	Core	Unknown	800000	142857.1	5594	Tempe	[32]
Tempe, AZ	Middle of expansion	1936	66	11.8	1259	Woodland	[20]
Woodland, CA	Edge of expansion	2000	20	3.6	1259	Tempe	[31]

Preregistration details

This manuscript is the post-study article resulting from a preregistration that received an in-principle recommendation. The proposed hypotheses, methods, and analysis plan were described in detail in the peer-reviewed preregistration (see Supplementary Materials). The preregistration was written in June 2019. At the same time, GPS points were already being collected during daily telemetry tracking sessions for other purposes [37]. To collect enough data for the hypotheses tested here, we increased the duration of tracking sessions and the number of GPS points collected per unit-time. We submitted the preregistration in September 2019 to *Peer Community in Ecology* for pre-study peer review. After four rounds of revisions, the preregistration received an in-principal recommendation at *Peer Community in Ecology* in September, 2020.

Specific hypotheses and predictions

Note that the hypotheses and predictions listed below are reproduced from the preregistration and do not reflect the deviations mentioned in the sub-section that follows.

Hypothesis 1:

Individual differences in measures of exploration using novel environment and novel object tasks [see: 25, 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 [28, 29] and novel object [27] 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 [23]. During the breeding season, one or more males defend a territory and females place their nests within territories to raise the young [24]. Roaming males are also present and can obtain extra-pair copulations with females on other male's' territories [24].

To investigate the first hypothesis, we derived the following main prediction (P1), and four alternate predictions (P1.a1–P1.a4):

P1 More exploratory grackles, i.e., individuals that get closer to the novel object and novel environment, will be found in larger expanses (larger home range sizes), use less predictable movement patterns (low autocorrelation of step lengths and turning angles), and occupy a greater variety of spatial locations. This would suggest that more exploratory individuals are more willing to move into novel areas in the wild.

P1.a1 The more exploratory grackles will be found in a smaller expanse (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 that the more exploratory individuals may dedicate more time to investigating a smaller area within their home range, rather than moving into new areas for resources such as food or mating opportunities.

P1.a2 Only performance on the novel environment task will correlate positively with space use behavior in the wild. This would suggest that perception of, and behavioral interactions with, novel environments (spatial information) differs from that used for novel objects [38].

P1.a3 Only performance on the novel object task will correlate positively with space use behavior in the wild. This would suggest 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.

P1.a4 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 that the measures of exploration in captivity are 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. Such independence could arise due to the tracked individuals being primarily adults who may already be familiar with their home range and surrounding areas, and thus do not need to further use the space as if it were novel.

Hypothesis 2:

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). These populations are theoretically connected; however, actually moving between any two of our field sites within a few grackle lifespans is unlikely due to the large distances between field sites and geographic barriers (e.g., the Sierra Nevada and Sierra Madre mountain ranges, and the high elevation areas of Mexico).

To investigate the second hypothesis, we derived the following main prediction (P2), and two alternate predictions (P2.a1–P2.a2):

P2 Home-range size will be larger, 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 the 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 (Arizona) will be intermediate in space use. Such population differences in space use behavior 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 [8]. 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 cross-site differences are indicative of a broader pattern driven by the location of the expansion front.

P2.a1 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 that suitable habitat may be distributed in small patches, that novel habitats at the edge of the range may have high predation risk which discourages grackles from using novel space, and/or that individual grackles specialize on certain novel habitat types that are patchily distributed.

P2.a2 We will find no difference across the geographic range in the space use behavior of the grackles sampled. This would suggest 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, it could indicate that we did not detect differences because we measured adults rather than juveniles. Grackles sampled in different populations may converge on similar space use behavior during development, or juvenile grackles may disperse further on the edge of the range. However, we are not able to detect these differences with our data, which are primarily from adults.

Deviations from the preregistration

In the course of the research process, a number of deviations from the preregistration were necessitated either by exigent circumstances or by scientific rational:

D1: Due to the COVID-19 pandemic and credible safety concerns at the planned study site research station, we did not travel to Central America to measure the space use and exploratory propensity of grackles in the endemic portion of the range.

D2: We modeled only step length—rather than both step length and turning angle—as a dependent variable for assessing space use behavior. The preregistered model of search dynamics introduced in Ross et al. [39] and tested in Pacheco-Cobos et al. [33] as well as Ross and Winterhalder [40] relies on food-encounter-annotated, equal-interval GPS points over short time-steps. Due to constraints in the field, GPS data could not be collected using equal-interval track points, nor annotated with food item encounters. We instead have unannotated GPS data taken at short time-steps with fairly uniform, though not exactly equal, intervals. As such, we are unable to measure variation in turning angle, but we are still able to model variation in step length as planned by normalizing the distance between GPS points by the time between GPS points, to yield a movement velocity.

D3: We discovered in our investigation of grackle personality traits [see: 25] that exploration of a novel object was not repeatable. This indicates that this particular test was not a good measure of the personality trait we refer to as “exploration”. As such, here we only use each grackle’s exploratory tendency as measured by their performance on the novel environment test which was repeatable.

D4: Because the population density of California grackles was significantly less than the density of grackles in Arizona (see Results, Hypothesis 2, Population density), we could not include population density in the models for H2, when the categorical variable for site was already included. This is because these two correlated variables account for the same variance.

D5: We preregistered that we would follow color-marked individuals for 20-90 minutes and radio-tagged individuals for 90 minutes to collect GPS points for the

grackle's location at one-minute intervals. However, we were not always able to achieve this goal because the grackles sometimes flew, or moved out of view for extended periods of time. Similarly, although we preregistered that we would search for grackles 4 times per week, personnel constraints and difficulty of finding focal individuals made it difficult to achieve this goal for all individuals.

Methods

Subjects

Great-tailed grackles were caught from the wild using a variety of methods (e.g., mist nets, walk-in traps, and bow nets), given colored leg bands in unique combinations for individual identification, and brought into large aviaries at each site. We prioritized capturing adult individuals (older than 1 year), because cognitive and behavioral traits are often not fully developed in hatch-year birds [41]. We identified grackles as adults using eye color, where hatch year birds have brown eyes, but second year and older birds have yellow to white eyes. While it is possible that cognitive traits continue to develop in second year and older birds, it is impossible to distinguish grackle age after the bird's first year [23]. We also attempted to balance subjects by sex. Subjects spent up to six months in an aviary while they participated in behavioral choice tests and individual differences assays, including measures of exploration in captivity (see below), as part of other research projects by this lab. We preregistered that we would need a sample size of 20 grackles per population to have a 70% chance of detecting a small effect (see Analysis Plan in Supplementary Materials) and our actual sample was very close to this number ($n = 19$ in Arizona, $n = 24$ in California).

Space use

Before the grackles were released from the aviaries, they were fitted with VHF radio tags (Lotek PipLL model Ag386, Advanced Telemetry Systems model A2455, or Holohil Systems model BD-2) attached to a leg loop harness [methods as in: 42] so that we could track space use behavior in the wild. We searched for each tagged grackle multiple times per week. Once found, the experimenter followed the focal individual for approximately 20–90 minutes, using the iPhone application *GPX Tracker* [43] to record a GPS point at the bird's location every one minute, regardless of whether the bird moved [44]. Researchers only approached to a distance that did not affect the grackle's behavior (approximately 30m away) and observed the grackle's behavior with binoculars. If the grackle alarm called or oriented towards the researcher (indicating that the researcher's presence affected the grackle's behavior), all tracking on that individual was stopped for the day. To ensure we captured 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 were searched for with telemetry until they were found again. However, we excluded GPS points collected outside of "normal daily activities" [45], for example mobbing a predator, or points before sunrise or after sunset when grackles are at the roost. Additionally, as noted below, we excluded a small number of points for methodological reasons (e.g., implausibly high velocities suggesting GPS resolution errors). Outside of these circumstances, we included all GPS points in our analysis of space use behavior.

We attempted to balance the collection of space-use data across morning and afternoon time periods for all grackles. We hoped to track the same individuals across the breeding and non-breeding seasons. However, the leg loop harnesses often degraded and fell off after 1–4 months. Therefore, we have few data points on the same individuals in both seasons, but we can compare space use in different individuals across seasons.

Dependent variables for space use models

We quantified grackle space use behavior with four metrics: home-range size, mean and variation of log movement velocity (log step length per time), and spatial location preference.

Home range size

First, we used a traditional measure of space use that controls for spatial and temporal autocorrelation in relocations: home range size. For each grackle that had more than 20 GPS point locations [46], we calculated home range size in km^2 using the *akde* function in the R packages *ctmm* [47] and *sf* [48].

Mean and variation in log movement velocity

Second, we quantified small-scale movement decisions by extracting step length (the geographic distance between two sequential GPS points, ideally taken at 1-minute intervals) from the tracking data. We were interested in both the distance moved, as well as the variation in distance moved. As detailed in the deviation from the preregistration, GPS points were not captured at exact 1-minute intervals, so we calculated the mean and standard deviation of step length per unit time for each bird. The total number of GPS points used to calculate the mean and standard deviation varied across birds. Step length per time was log-transformed, and we dropped a small number of estimates that were implausibly high (i.e., $>$ 200 m/min), presumably resulting from GPS resolution errors.

Temporal correlation in spatial location preferences

To better understand spatial location preferences, we determined the rectangles of the smallest area that would enclose the maximum number of data points (see Figure 1). At the California site, this is a 2.04×1.94 km rectangle, and at the Arizona site, this is a 2.38×1.79 km rectangle. The best rectangle for the Arizona site let us capture 16,873 out of 17,000 GPS points (99.25%) within our sample area. The best rectangle for the California site let us capture 19,534 out of 21,361 GPS points (91.44%) within our sample area (see Figure 1). The slightly lower fraction of data inclusion in the California site was due to a few individuals that were tracked at two distant study sites, leading to GPS tracks falling substantially outside of the central study area. We

Figure 1: Space use data processing pipeline. We visualize the raw data on grackle space use in Arizona and California in sub-figures (a) and (d), respectively. We then highlight the in-sample region (containing the bulk of observations) in sub-figures (b) and (e). Finally, in sub-figures (c) and (f), we highlight the overall frequency of grid-cell space use (aggregating over birds and weeks) using two-dimensional heat-maps. Similar gridded frequency data, computed per bird, per week, constitute the final data that are fed into the space use model in Stan.

excluded these points because, for computational reasons, it was impossible to extend the boundaries of our study area to capture all such points, while maintaining a reasonable grid-cell resolution. By focusing on the site where the bulk of GPS points were observed, we are able to maintain computational tractability, fine-scale grid-cell resolution, and comparability with the Arizona site.

Once geographic boundaries were selected, we divided the geographic sample space into a list of G grid-cells, so that each cell was approximately equal in area for each site. For the California site, the space is divided into a 66×66 array of grid-cells, which leads to an average grid-cell size of about 29×30 m and a grid-cell density of 1,100 grid-cells per km^2. For the Arizona site, the sample space is divided into a 71×71 array of grid cells, which leads to an average grid-cell size of about 25×33 m and a grid-cell density of 1,183 grid cells per km^2. By choosing the number of subdivisions to be 66 and 71 respectively, we equalize the scale of inference at both sites. We then used 2-dimensional binning with the *ash* package [49] in R to quantify the number of recorded GPS points inside each of the grid-cells for each bird on each day.

We model temporal autocorrelation in spatial location preference by studying the bird-specific time-series of movement behavior. Let $F_{[b,w,g]}$ be the count of times that bird b was observed in grid-cell g on week w. For any week after the first week of continuous observations, we can model the entire G-vector, $F_{[b,w,1:G]}$, using a multinomial regression [34] of the form:

$$F_{[b,w,1:G]} \sim \text{Multinomial}(\Theta_{[b,w,1:G]}) \quad (1)$$

where:

$$\Theta_{[b,w,1:G]} = (1-\alpha_{[b]})\theta_{[1:G]} + \alpha_{[b]}\hat{F}_{[b,w-1,1:G]} \quad (2)$$

where:

$$\alpha_{[b]} = \text{logistic}(\beta_{[0]} + \beta_{[1]}Z_{[1,b]} + ... + \phi_{[b]}) \quad (3)$$

and where:

$$\beta_{[p]} \sim \text{Normal}(0, 2.5) \quad (4)$$

$$\phi_{[b]} \sim \text{Normal}(0, \sigma) \quad (5)$$

$$\sigma \sim \text{Exponential}(1) \quad (6)$$

$$\theta \sim \text{Dirichlet}(1, \ldots, 1) \quad (7)$$

Eq. 1 shows that we model the distribution of space use as a multinomial outcome with probability vector $\Theta_{[b,w,1:G]}$. Eq. 2 then shows how $\Theta_{[b,w,1:G]}$ is constructed. The G-vector $\Theta_{[b,w,1:G]}$ is generated as a convex combination of two other G-vectors, $\theta_{[1:G]}$—a vector giving the "suitability" or "attractiveness" of each grid-cell to grackles in general—and $\hat{F}_{[b,w-1,1:G]}$, a vector giving the fraction of time bird b spent in each and every grid-cell on week $w-1$ ($\hat{F}$ is just a normalized version of F). The mixing rate of these two components—the suitability component and the 1-week lag component—is controlled by a bird-specific

parameter, $\alpha_{[b]}$. Eq. 3 shows that $\alpha_{[b]}$ is constructed using a simple logistic regression model, with an intercept parameter, $\beta_{[0]}$, slope parameters, $\beta_{[p]}$, bird-specific covariates, $Z_{[p,b]}$, and finally, a bird specific random effect, $\phi_{[b]}$. This regression equation allows us to study how exploratory different birds are as indicated by the predictabilty of space use: birds with a large $\alpha_{[b]}$ are less exploratory in that their space use in week w is well predicted by their space use in week $w-1$. While birds with a small $\alpha_{[b]}$ are more exploratory in that they are more likely to visit all grid-cells (in proportion to their suitability) regardless of their space use distribution in the previous week. Eqs. 4–7 show that we use weak priors.

Models were fit using R [50] and Stan [51] through the *cmdstanr* package [52]. Model fit was assessed using the effective sample size and $\hat{r}$ statistics. Models were also quality-checked by creating simulated data under the data generating process described by Eqs. 1-7 in R, and then using the Stan model to recover the generative parameters: see `https://github.com/ctross/grackleator` for details. In our Supplementary Materials, we also provide an example of a forward simulation showing the differing space-use distributions across successive time-steps for a hypothetical bird with $\alpha = 0.1$ versus a hypothetical bird with $\alpha = 0.9$.

Predictor variables

Exploration

We used data collected as part of another investigation [see: 25] to quantify the personality trait "exploration". In that investigation, we adapted commonly used methods to test exploratory tendency of grackles that were temporarily held in aviaries. Exploratory tendency was measured as the *latency to approach* and the *duration spent in proximity* (within 20 cm) of a novel environment set within the familiar environment of their aviary (Figure 2). Exploration assays occur twice for each bird: once near the beginning of their aviary time and once again approximately 6 weeks later. In our previous investigation [25], we also validated that performance on the exploration assays reflected exploration rather than boldness, and that performance was repeatable across time.

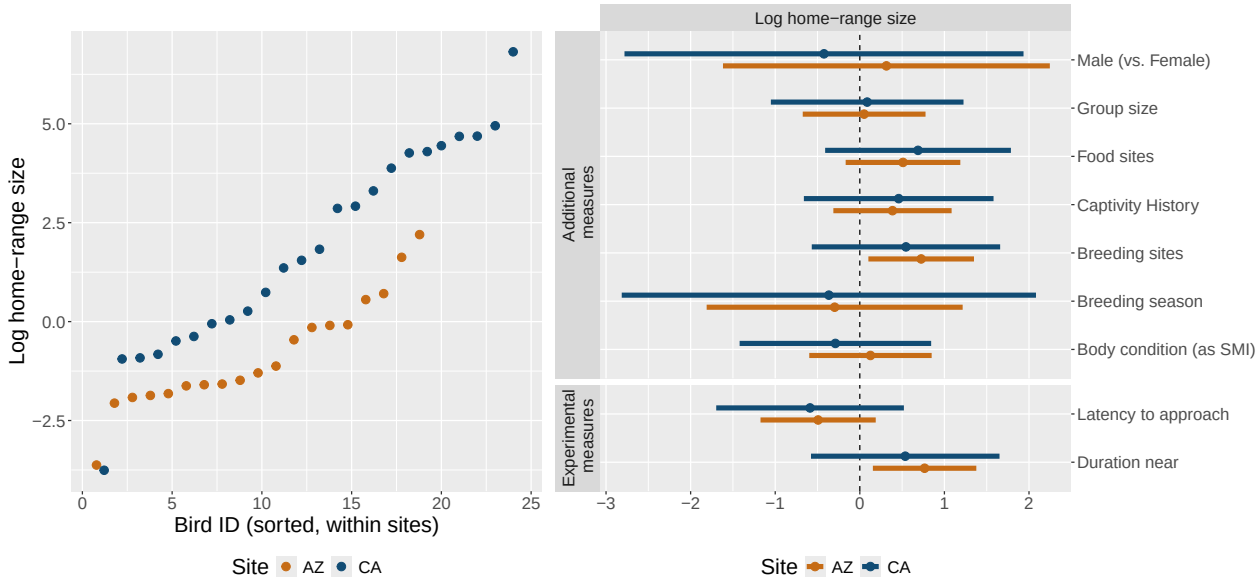
Other predictor variables

We recorded the sex of each bird and whether the data were collected in the breeding or non-breeding season. We also measured energetic condition using a scaled mass index [53, 54] to investigate whether differences in the energetic or physiological mobility may limit an individual's space use behaviors [15]. We measured captivity history as the number of days each individual spent in the aviaries to assess the impact of captivity on subsequent movement in the wild. Moreover, we recorded the maximum group size that the focal grackle was observed with, as well as habitat characteristics—such as human food sources and available breeding habitat—using data collected as part of a separate investigation [see: 37]. These factors of the external environment could potentially affect how grackles choose to move or where they spend time [15]. We also tested whether time spent in captivity altered the social behavior of grackles when they were subsequently released into the wild by investigating if the maximum group size observed across each individual's focal follows varied as a function of each individual's captivity history.

Figure 2: Depiction of the novel environment assay. After grackles habituated to their aviaries, we introduced a novel environment, a small pop-up tent. We measured the latency to approach the tent and the duration spent in proximity to the tent during 2-hour trials. Grackles did not need to approach the tent to acquire food and water (visible at the back of the aviary).

Lastly, conspecific density (the number of individuals per square meter) has also been shown to affect home range size in other bird species [55, 56]. To assess whether home range size may vary between our populations due to conspecific density, rather than exploratory traits, we conducted point count surveys to measure grackle population density. We placed 225 point count stations across the geographic boundaries encompassing each population (Tempe, AZ; Sacramento, CA). For each study population, the first central point was randomly placed within 500 m of the center of the study area. The remaining points were placed in a 500 m grid pattern extending out from this central point. In total, the grid covered an area that was 7 x 7 km. Each point was visited once during the non-breeding season (September–March). During the survey, researchers recorded all grackles that were visually and aurally detected for six minutes. We quantified region-specific grackle density by fitting a hierarchical model that accounts for imperfect detection. Specifically, we used the model developed by Amundson et al. [57], which integrates data on time of detection and distance estimates to account for the probability a bird is available to be detected (p_a), and the probability it is detected given that it is available (p_d), respectively [58]. All parameters (density, p_a, and p_d) were modeled as a function of the study site. Because we expected vocalization rates to be greater for males than females, we also modeled p_a as a function of sex.

Figure 3: Log home range size results. In the left frame, we plot bird-specific log home-range size (with birds sorted within sites). In the right frame, we plot the effects of predictors on the outcome of log home-range size. Predictor variables are plotted as rows and colored by site. Each dot indicates the posterior mean relationship between the predictor variable and outcome in a univariate model, and the horizontal line through each dot shows the 95% credible region. Reliable relationships are indicated by a lack of overlap of the credible interval with zero (the vertical dashed line).



Results

Hypothesis 1: Are individual differences in exploration related to variation in space use?

We collected an average of 838 GPS points (range: 21–1,781) during an average of 26 (range: 2–78) tracking sessions on each Arizona grackle (n: 19). For California grackles (n: 24), we averaged 1,178 GPS points (range: 47–1,968) during an average of 18 (range: 1–38) tracking sessions per grackle. Overall, we found mixed evidence that exploration measured in captivity was related to space use in the wild.

Home range size

Neither latency to approach, nor duration near, the novel environment were related to variation in home range size in California (Figure 3). In contrast, more exploratory grackles in Arizona did have larger home range sizes. There was a reliably positive relationship between duration near the novel environment and log home range size of Arizona grackles. Similarly, though the credible region crosses zero, there was a nearly reliable negative relationship between latency to approach the novel environment and log home range size. In California, no other predictor variables were reliably related to home range size. In Arizona the number of both breeding sites and food sites were positively associated with log home range size (Figure 3).

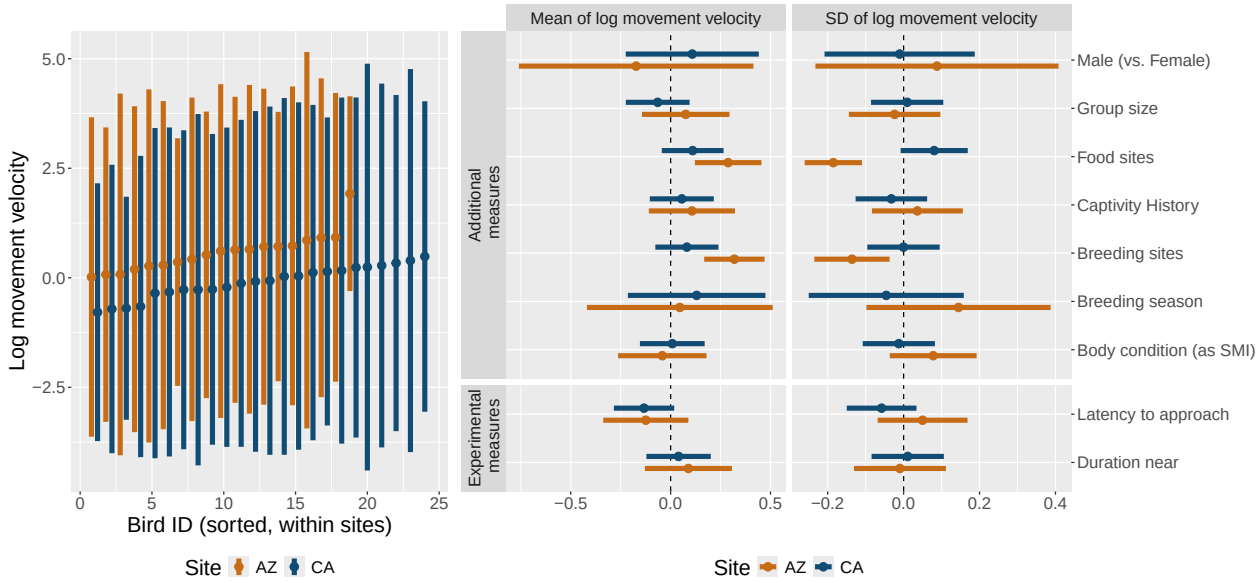
Mean and variation in log movement velocity

The relationships between log movement velocity (i.e., log step length per unit time) and some predictor variables differed based on the study site (see Figure 4). However, there was no evidence that either measure of exploration was related to either the average or standard deviation of log movement velocity for either population. In California, birds with a larger number of food sites had more variable log movement velocities, indicating that more variable food locations led to more Lévy-like foraging behavior. However, in Arizona, it appears that a greater number of food or breeding sites leads to generally faster, but less variable movement dynamics. No other effects are reliably non-zero.

Temporal correlation in spatial location preferences

We investigated which predictor variables were related to temporal autocorrelation (i.e., predictability) of grackle spatial location preferences. In Arizona, the exploration measures were indeed related to temporal autocorrelation in space use in the predicted direction (Figure 5). Birds who waited longer to approach a novel environment in their aviaries showed elevated temporal autocorrelation (i.e., less exploration) and birds who spent more time near the novel environment in their aviaries showed lowered temporal autocorrelation (i.e, more exploration). There was also a negative effect of the number of food sites and breeding sites on autocorrelation at the Arizona site (see Figure 5), indicating that grackles that had a higher number of human food source areas (e.g, dumpsters, cat food bowls, outdoor restaurant seating areas, etc.) within their home ranges were less predictable, week to week, in space use. At the California site, the credible regions of all variables (except group size) overlapped zero, indicating that none were reliably related to spatial-location preferences. More generally, there was substantial between-individual variation in autocorrelation at both the California and Arizona sites, indicating that individuals differ in how likely they were to be found in the same spatial locations across weeks (i.e., some were consistently predictable with high autocorrelation values and others were unpredictable with low autocorrelation values). In sum, we note evidence for

Figure 4: Log movement velocity results. In the left frame, we plot bird-specific log movement velocity distributions (summarized as a mean ±2 SDs; birds sorted within sites). In the right frame, we plot the effects of predictors on the outcomes of average log movement velocity (left sub-panel) and standard deviation in log movement velocity (right sub-panel). Predictor variables are plotted as rows and colored by site. Each dot indicates the posterior mean relationship between the predictor variable and outcome in a univariate model, and the horizontal line through each dot shows the 95% credible region. Reliable relationships are indicated by a lack of overlap of the credible interval with zero (the vertical dashed line).



P1 at the Arizona site, in that more exploratory grackles were more dynamic in their space use, showing reduced autocorrelation across a 1-week time gap. At the California site, the data were most consistent with P1.a4, showing no association between the temporal consistency of space use and aviary-measured exploratory tendency.

Hypothesis 2: Does space-use behavior vary between two study populations located at different points in the geographic range?

Population density

We conducted point count surveys at 214 point-count sites, rather than the planned 225 at our Tempe, Arizona site due to access issues (e.g., when a point count site was located in an inaccessible construction site or wetland) or scheduling oversights (i.e., points 196–202 were missed due to scheduling conflicts). We conducted point count surveys at all 225 planned sites in Sacramento, California. We estimated the great-tailed grackle population density in Tempe, Arizona at 0.073 birds/ha (CI: 0.057, 0.093) and in Woodland, California at 0.016 birds/ha (CI: 0.012, 0.021). Population density was significantly higher at our Arizona site relative to the California site (β: -1.54, CI: -1.91, -1.17).

Home range size

California grackles exhibited significantly larger home range sizes, measured in square kilometers using autocorrelated kernel density estimates, relative to Arizona grackles (Table 2). No other predictor variables were significantly related to home range size. This provides partial support for prediction P2. It is also notable that although California grackles had larger average home range sizes, most of the home ranges were highly overlapping compared to the discrete, smaller home ranges in Arizona (Figure S1).

Mean and variation in log movement velocity

Grackles in California showed slightly smaller mean log movement velocity (i.e., step length per unit time), but no difference in variation (standard deviation) of log movement velocity, relative to grackles in Arizona (left panel of Figure 4).

Temporal correlation in spatial location preferences

As stated above regarding P1, we did find evidence of a linkage between exploratory tendency and autocorrelation in space use at the Arizona, but not the California site. However, there were no large differences in the average level of autocorrelation in space use between sites. The left panel of Figure 5 shows that the variation across birds in temporal autocorrelation level within either field site is much larger than the variation between sites, but on a rank-matched basis, there is slightly less autocorrelation in the California site, which is consistent with P2. The credible interval for this comparison encompasses zero, so the evidence here is weak and should be seen as suggestive not confirmatory (Table 2).

Impact of captivity on social behavior

The amount of time that grackles spent in captivity did not affect their maximum social group size after release back to the wild (β: -0.00; CI: -0.01, 0.00; p: 0.56) for either the Arizona or California study sites (β: 0.37; CI: -0.48, 1.25; p: 0.51).

Figure 5: Spatial location preference results. In the left frame, we plot sorted posterior estimates of $\alpha_{[b]}$, the bird-specific parameter defining the level of temporal autocorrelation in space use, where higher scores represent *less* exploratory behavior, across weeks, on average. Since we have approximately the same number of birds in each sample, these sorted individual-level estimates are suggestive of rank-matched differences in temporal autocorrelation, with Arizona birds showing slightly higher levels of temporal autocorrelation for their rank, especially at higher ranks. In the right frame, we plot the effects of predictor variables on bird-specific temporal autocorrelation (positive effects here represent lower exploratory tendency and more autocorrelation). Predictor variables are plotted as rows and colored by site. Credible regions are plotted as 95% intervals. Note that we have 20 CA birds in this analysis, since this analysis required observations over several weeks in succession.

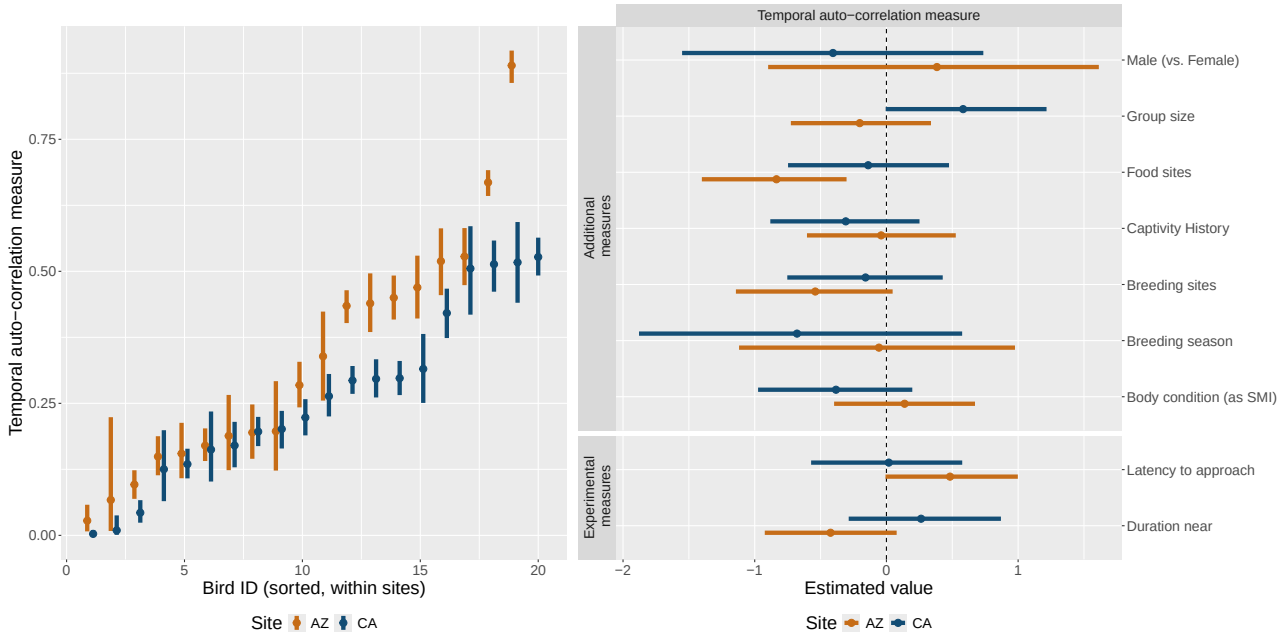


Table 2: Effects of field site location on each of the considered outcome variables. Here, we include all predictors using a multivariate regression. There is some evidence that California birds have larger home ranges and slower average movement velocities. All other effects, for all other outcomes, include the value of zero within the credible region.

	Log home-range size			**Log movement velocity (mean)**			**Log movement velocity (SD)**			**Autocorrelation in space-use**		
	Mean	**2.50%**	**97.50%**	**Mean**	**2.50%**	**97.50%**	**Mean**	**2.50%**	**97.50%**	**Mean**	**2.50%**	**97.50%**
(Intercept)	-0.092	-1.907	1.723	0.564	0.218	0.909	1.725	1.527	1.923	0.277	0.1	0.455
CA (vs. AZ)	**2.255**	**0.768**	**3.741**	**-0.671**	**-0.953**	**-0.388**	0.129	-0.034	0.291	-0.063	-0.212	0.086
Male (vs. Female)	0.153	-1.471	1.778	0.015	-0.294	0.324	0.004	-0.174	0.181	0.104	-0.055	0.263
Captivity History	0.753	-0.065	1.572	0.079	-0.077	0.235	-0.018	-0.107	0.071	-0.008	-0.09	0.074
Breeding Season	-1.261	-3.075	0.554	-0.005	-0.35	0.34	0.061	-0.138	0.259	-0.05	-0.233	0.134

Discussion

Movement and space use behavior are theoretically motivated by internal states such as personality traits, hunger, reproductive drive, and risk perception [15]. Variation in movement can significantly impact the rate and longevity of species invasions [59]. Research testing internal states like behavioral and cognitive traits via assays in captivity often assumes that laboratory performance reflects fitness-relevant behavior in the wild. However, few studies have experimentally tested the relationship between personality traits - like exploratory tendency - and natural movement behavior in the wild. Here, we found that the relationship between movement behavior and exploration, measured as the latency to approach or the duration in proximity to a novel environment, was dependent on which movement variables were considered and the proximity of the focal population to the range edge.

Exploration was related to home range size and temporal autocorrelation in space use only in the range-middle population (Arizona), providing partial support for prediction P1. In contrast, exploration was not related to movement velocity (step length per unit time) in either site. Thus, variation in individual decisions at the step level (a fine-grained measure of movement behavior) is not well explained by the exploration personality trait as we measured it, although larger-scale measures of space use like total space explored (i.e., home range size) or spatial location preference at approximately 30m square resolution were. We also found that some movement variables differed between the range-edge and range-middle populations: home range was larger among range-edge grackles, providing partial support for our prediction P2 that range-edge grackles would use a great amount of space less predictably. However, average movement velocity was lower among range-edge grackles, which instead supports P2 alternative 1, while temporal autocorrelation was similar between populations, which supports P2 alternative 2. These inconsistent results could indicate that different types of movement behavior are motivated by distinct internal states

that influence fitness or range expansion in different ways.

Classic models in optimal foraging theory, like the marginal value theorem [60, 61] and its extension to models of movement dynamics in patchy environments [33], suggest that both average search velocity and variation in search velocity will be tightly coupled to the distribution of resources on the landscape. We did find a reliable relationship between ecological factors like food and breeding site availability and movement behavior of Arizona grackles. As such, movement patterns in the wild were broadly affected by the distribution of key resources in addition to internal personality states, although we lack information on step-level food encounter rates. When individuals encounter food items, they reduce velocity to process and consume those items. If food items are clustered, foragers should continue to deploy slower and more tortuous area-restricted search to remain in a patch where subsequent encounters are likely, until some threshold "giving-up time" is reached and they resume a faster between-patch search mode [33]. As such, future work investigating linkages between step-level movement dynamics and the personality trait of exploration should minimally account for environmental richness and patchiness—as variation in these variables may explain some of the between-site differences we found here, independent of the proximity to the range edge. At a more nuanced level, it may be that exploration propensity regulates the "giving-up time" for encounter-conditional area-restricted search, with more exploratory individuals moving on to new patches at faster rates, holding all else constant. However, such an association would only be detectable if GPS tracks are annotated with food-item encounters. In the absence of encounter-annotated GPS, it is impossible to tell if differences in movement velocity are due to differences in individual preferences (i.e., different "giving up times") or differences in environmental richness (e.g., due to different arrival rates of human food-scraps in different areas).

Although the relationship between environmental factors, movement dynamics, space use, and exploratory tendency differed for grackles at the two sites, we found limited evidence for an "invasion syndrome": i.e., consistent differences in the behavior or physiology of pioneer individuals pushing the geographic range boundaries into new areas relative to individuals in the middle of the range [59, 7, 62]. Pioneers are often shown to be more exploratory [63], bolder [64], and more aggressive [8], as well as more likely to move further in a single lifespan [9, 65], and disperse away from areas that are densely populated with conspecifics [3]. Grackles on the edge of the range do appear to be using space differently than grackles in the middle of the range. However, our current study does not provide consistent support that this population difference is attributable to exploration. Previously, we found that grackles on the range-edge were not different in overall exploration propensity or average behavioral flexibility relative to grackles in the middle of the expanding range. However, they had greater flexibility variance (measured by reversal learning), higher average persistence (they participated in a larger proportion of trials) [66], and they dispersed further from their parents and siblings [67]. Here, we found that grackles on the invasion front had larger home range sizes, but moved slightly smaller distances per unit time. Similar to our focal species, exploratory and range-edge individuals from other native and invasive species show larger home range sizes [28, 65]. However, we cannot exclude the possibility that the larger home range size of the range-edge population was due to the significantly lower population density relative to the range-middle population [55, 56].

Our finding that range-edge grackles showed smaller average step lengths per unit time does stand in contrast to much of the other research on movement and invasion success. For example, invasive cane toads and mynas on the range-edge in Australia showed greater distances moved per time than those in the range-middle [9, 65] and invasive signal crayfish moved twice as far per unit time compared to sympatric native crayfish [14]. Thus, population differences existed in our study, but did not conform to what is empirically and theoretically expected for an "invasion syndrome". However, as we eluded to above, such a difference might be expected if the California site were characterized by higher food-item richness (in calories available per hectare, per day, per bird) due to reduced scramble competition (owing to the lower density of conspecifics), reducing the need for grackles there to engage in active search. Sit-and-wait or slow velocity search is energetically preferable to high-velocity search, as long as the renewal rate of food items (e.g., due to humans littering) is sufficiently high [68]. With few exceptions, all California grackles spent the majority of their time around the parking lots of a single large shopping center with numerous fast food restaurants, even though there were abundant nearby natural resources (e.g., fallow agricultural fields and ponds). Consequently, the daily space use of all California grackles occurred in a similar location and centered on a similar, high-yield food source. In such a context, simply waiting near a high-yield location may be fitness maximizing relative to more energetically costly high-velocity active search, as long as the density of competitors is low. As such, additional research is needed to disentangle the complicated interaction between individual-level features (e.g., exploratory tendency) and site-level features (e.g., conspecific density and environmental richness and patchiness) that should jointly determine movement dynamics and space use.

Future research may also need to more purposefully balance inclusion of multiple range-middle and range-edge sites relative to key environmental variables to draw conclusions about between-group differences in outcomes that are not confounded by differences in ecology. We hesitate to make broad conclusions about the role of home range size or step length on invasion success from our study because we focused on only one edge and one middle population. Moreover, both of our focal populations were located in the non-native portion of the great-tailed grackle range. It is possible that exploration and movement behavior of grackles in the endemic portion of the range in Central America would differ in ways that could clarify the mechanisms influencing grackle invasion success into North America. More generally, movement decisions of pioneer individuals might also be linked to other personality traits

like activity or sociability [3], or state-conditional risk preferences [69]. We believe that exploratory tendency likely does have direct causal influence on real-world space use, movement and invasion success, but future empirical work must collect more granular data to permit adjustment for important confounds that we could not account for here.

There is currently limited research that measures performance on assays in captivity and fitness-relevant behavior of the same individuals across multiple populations in the wild. Our study contributes important information on the ecological validity of a personality assay in captivity, the factors that affect the predictability of movement behavior in the wild, and the variation in specific types of movement that could influence invasion success. These results can help inform conservation and invasive species management strategies by highlighting that populations can vary in multiple behavioral traits, and in potentially counterintuitive ways. However, further research is needed on additional populations and personality traits to make more general conclusions about the relationship between animal personality, movement behavior and invasion success.

Ethics

This research was 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)

Author contributions

McCune: Hypothesis development, methodology, data collection (trapping, GPS tracking), data analysis and interpretation, write up, revising/editing.
Ross: Methodology, model development, data analysis and interpretation, write up, revising/editing.
LeGrande: Methodology, data collection (trapping, GPS tracking, point count surveys), data interpretation.
Logan: Hypothesis development, methodology, data interpretation, write up, revising/editing, materials/funding.

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Conflict of interest disclosure

We, the authors, declare that we have no financial conflicts of interest with the content of this article. Corina Logan is a Recommender and on the Managing Board at PCI Ecology.

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References

[1] D. G. Chapple, S. M. Simmonds, and B. B. Wong, "Can behavioral and personality traits influence the success of unintentional species introductions?" *Trends in ecology & evolution*, vol. 27, no. 1, pp. 57–64, 2012.

[2] K. R. Hayes and S. C. Barry, "Are there any consistent predictors of invasion success?" *Biological invasions*, vol. 10, no. 4, pp. 483–506, 2008.

[3] S. Fogarty, J. Cote, and A. Sih, "Social personality polymorphism and the spread of invasive species: a model," *The American Naturalist*, vol. 177, no. 3, pp. 273–287, 2011.

[4] S. H. Butchart, M. Walpole, B. Collen, A. Van Strien, J. P. Scharlemann, R. E. Almond, J. E. Baillie, B. Bomhard, C. Brown, J. Bruno *et al.*, "Global biodiversity: indicators of recent declines," *Science*, vol. 328, no. 5982, pp. 1164–1168, 2010.

[5] M. Clavero and E. García-Berthou, "Invasive species are a leading cause of animal extinctions," *Trends in ecology & evolution*, vol. 20, no. 3, p. 110, 2005.

[6] C. Carere and F. Gherardi, "Animal personalities matter for biological invasions," *Trends in ecology & evolution*, vol. 1, no. 28, pp. 5–6, 2013.

[7] J. Cote, J. Clobert, T. Brodin, S. Fogarty, and A. Sih, "Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 365, no. 1560, pp. 4065–4076, 2010.

[8] R. A. Duckworth and A. V. Badyaev, "Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird," *Proceedings of the National Academy of Sciences*, vol. 104, no. 38, pp. 15 017–15 022, 2007.

[9] T. Lindström, G. P. Brown, S. A. Sisson, B. L. Phillips, and R. Shine, "Rapid shifts in dispersal behavior on an expanding range edge," *Proceedings of the National Academy of Sciences*, vol. 110, no. 33, pp. 13 452–13 456, 2013.

[10] O. Spiegel and M. C. Crofoot, "The feedback between where we go and what we know—information shapes movement, but movement also impacts information acquisition," *Current opinion in behavioral sciences*, vol. 12, pp. 90–96, 2016.

[11] E. F. Stuber, Y. G. Araya-Ajoy, K. J. Mathot, A. Mutzel, M. Nicolaus, J. J. Wijmenga, J. C. Mueller, and N. J. Dingemanse, "Slow explorers take less risk: a problem of sampling bias in ecological studies," *Behavioral Ecology*, vol. 24, no. 5, pp. 1092–1098, 2013.

[12] T. van Overveld and E. Matthysen, "Personality predicts spatial responses to food manipulations in free-ranging great tits (parus major)," *Biology letters*, vol. 6, no. 2, pp. 187–190, 2009.

[13] P. J. Greenwood and P. H. Harvey, "The natal and breeding dispersal of birds," *Annual review of ecology and systematics*, vol. 13, no. 1, pp. 1–21, 1982.

[14] D. H. Bubb, T. J. Thom, and M. C. Lucas, "Movement, dispersal and refuge use of co-occurring introduced and native crayfish," *Freshwater Biology*, vol. 51, no. 7, pp. 1359–1368, 2006.

[15] R. Nathan, W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse, "A movement ecology paradigm for unifying organismal movement research," *Proceedings of the National Academy of Sciences*, vol. 105, no. 49, pp. 19 052–19 059, 2008.

[16] A. G. Hertel, P. T. Niemelä, N. J. Dingemanse, and T. Mueller, "A guide for studying among-individual behavioral variation from movement data in the wild," *Movement Ecology*, vol. 8, no. 1, pp. 1–18, 2020.

[17] R. K. Swihart and N. A. Slade, "Testing for independence of observations in animal movements," *Ecology*, vol. 66, no. 4, pp. 1176–1184, 1985.

[18] S. Dray, M. Royer-Carenzi, and C. Calenge, "The exploratory analysis of autocorrelation in animal-movement studies," *Ecological Research*, vol. 25, no. 3, pp. 673–681, 2010.

[19] K. R. Janmaat, M. de Guinea, J. Collet, R. W. Byrne, B. Robira, E. van Loon, H. Jang, D. Biro, G. Ramos-Fernandez, C. Ross *et al.*, "Using natural travel paths to infer and compare primate cognition in the wild," *Iscience*, vol. 24, no. 4, 2021.

[20] W. Wehtje, "The range expansion of the great-tailed grackle (*Quiscalus mexicanus* gmelin) in north america since 1880," *Journal of Biogeography*, vol. 30, no. 10, pp. 1593–1607, 2003.

[21] T. M. Blackburn, P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. Wilson, and D. M. Richardson, "A proposed unified framework for biological invasions," *Trends in ecology & evolution*, vol. 26, no. 7, pp. 333–339, 2011.

[22] J. F. Glahn, J. D. Palacios, and M. Garrison, "Controlling great-tailed grackle damage to citrus in the lower rio grande valley, texas," 1997.

[23] K. Johnson and B. D. Peer, "Great-tailed grackle: *Quiscalus mexicanus*," in *The Birds of North America*, A. Poole and F. Gill, Eds. Cornell Lab of Ornithology, Ithaca, NY, USA, 2001.

[24] K. Johnson, E. DuVal, M. Kielt, and C. Hughes, "Male mating strategies and the mating system of great-tailed grackles," *Behavioral Ecology*, vol. 11, no. 2, pp. 132–141, 2000.

[25] K. B. McCune, D. Lukas, M. P. MacPherson, and C. J. Logan, "Behavioral flexibility is related to exploration, but not boldness, persistence or motor diversity," *Peer Community Journal*, vol. 5, 2025.

[26] D. Réale, S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse, "Integrating animal temperament within ecology and evolution," *Biological reviews*, vol. 82, no. 2, pp. 291–318, 2007.

[27] C. Mettke-Hofmann, H. Winkler, and B. Leisler, "The significance of ecological factors for exploration and neophobia in parrots," *Ethology*, vol. 108, no. 3, pp. 249–272, 2002.

[28] J. Minderman, J. M. Reid, M. Hughes, M. J. Denny, S. Hogg, P. G. Evans, and M. J. Whittingham, "Novel environment exploration and home range size in starlings sturnus vulgaris," *Behavioral Ecology*, vol. 21, no. 6, pp. 1321–1329, 2010.

[29] N. J. Dingemanse, C. Both, A. J. Van Noordwijk, A. L. Rutten, and P. J. Drent, "Natal dispersal and personalities in great tits (parus major)," *Proceedings of the Royal Society of London. Series B: Biological Sciences*, vol. 270, no. 1516, pp. 741–747, 2003.

[30] B. International, "*Quiscalus mexicanus*," *The IUCN Red List of Threatened Species 2018*, p. e.T22724308A132174807, 2018.

[31] E. Pandolfino, B. Deuel, and L. Young, "Colonization of the California's central valley by the great-tailed grackle," *Central Valley Bird Club Bulletin*, vol. 12, pp. 77–95, 2009.

[32] N. K. Johnson and C. Cicero, "New mitochondrial dna data affirm the importance of pleistocene speciation in north american birds," *Evolution*, vol. 58, no. 5, pp. 1122–1130, 2004.

[33] L. Pacheco-Cobos, B. Winterhalder, C. Cuatianquiz-Lima, M. F. Rosetti, R. Hudson, and C. T. Ross, "Nahua mushroom gatherers use area-restricted search strategies that conform to marginal value theorem predictions," *Proceedings of the National Academy of Sciences*, vol. 116, no. 21, pp. 10 339–10 347, 2019.

[34] P. De Valpine and A. N. Harmon-Threatt, "General models for resource use or other compositional count data using the dirichlet-multinomial distribution," *Ecology*, vol. 94, no. 12, pp. 2678–2687, 2013.

[35] G. Wang, "Bayesian and frequentist approaches to multinomial count models in ecology," *Ecological Informatics*, vol. 61, p. 101209, 2021.

[36] T. M. May, M. J. Page, and P. A. Fleming, "Predicting survivors: animal temperament and translocation," *Behavioral Ecology*, vol. 27, no. 4, pp. 969–977, 2016.

[37] C. J. Logan, D. Lukas, X. Geng, C. LeGrande, Z. Marfori, M. MacPherson, C. Rowney, C. Smith, and K. B. McCune, "Behavioral flexibility is related to foraging, but not social or habitat use behaviors in a species that is rapidly expanding its range," *Peer Community Journal*, 2025.

[38] C. Mettke-Hofmann, S. Lorentzen, E. Schlicht, J. Schneider, and F. Werner, "Spatial neophilia and spatial neophobia in resident and migratory warblers (sylvia)," *Ethology*, vol. 115, no. 5, pp. 482–492, 2009.

[39] C. Ross, L. Pacheco-Cobos, and B. Winterhalder, "A general model of forager search: Adaptive encounter-conditional heuristics outperform lévy flights in the search for patchily distributed prey," *Journal of theoretical biology*, vol. 455, pp. 357–369, 2018.

[40] C. T. Ross and B. Winterhalder, "Evidence for encounter-conditional, area-restricted search in a preliminary study of colombian blowgun hunters," *PloS one*, vol. 13, no. 12, p. e0207633, 2018.

[41] P. Zucca, N. Milos, and G. Vallortigara, "Piagetian object permanence and its development in eurasian jays (garrulus glandarius)," *Animal Cognition*, vol. 10, no. 2, pp. 243–258, 2007.

[42] J. H. Rappole and A. R. Tipton, "New harness design for attachment of radio transmitters to small passerines (nuevo diseño de arnés para atar transmisores a passeriformes pequeños)," *Journal of field Ornithology*, pp. 335–337, 1991. [Online]. Available: https://www.holohil.com/wp-content/uploads/2017/10/Rappole-Tipton-1991.pdf

[43] J. M. Merlos, "Merlos/ios-open-gpx-tracker: Gps tracker app for ios + watchos. log your tracks without limits and share them; open source gpx tracker app written in swift," 2014. [Online]. Available: https://github.com/merlos/iOS-Open-GPX-Tracker

[44] S. A. Cushman, M. Chase, and C. Griffin, "Elephants in space and time," *Oikos*, vol. 109, no. 2, pp. 331–341, 2005.

[45] C. Calenge, "Home range estimation in r: the adehabitathr package," *Office national de la classe et de la faune sauvage: Saint Benoist, Auffargis, France*, 2011.

[46] M. J. Noonan, M. A. Tucker, C. H. Fleming, T. S. Akre, S. C. Alberts, A. H. Ali, J. Altmann, P. C. Antunes, J. L. Belant, D. Beyer *et al.*, "A comprehensive analysis of autocorrelation and bias in home range estimation," *Ecological Monographs*, vol. 89, no. 2, p. e01344, 2019.

[47] J. M. Calabrese, C. H. Fleming, and E. Gurarie, "ctmm: An r package for analyzing animal relocation data as a continuous-time stochastic process," *Methods in Ecology and Evolution*, vol. 7, no. 9, pp. 1124–1132, 2016.

[48] E. Pebesma, "Simple features for r: standardized support for spatial vector data," *The R Journal*, vol. 10, no. 1, pp. 439–446, 2018.

[49] D. Scott, "ash: David scott's ash routines. r package version 1.0-15," 2015.

[50] R Core Team, *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria, 2022. [Online]. Available: https://www.R-project.org/

[51] B. Carpenter, A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, and A. Riddell, "Stan: A probabilistic programming language," *Journal of Statistical Software*, vol. 76, no. 1, pp. 1–32, 2017.

[52] J. Gabry, R. Češnovar, A. Johnson, and S. Bronder, *cmdstanr: R Interface to 'CmdStan'*, 2025, r package version 0.9.0, https://discourse.mc-stan.org. [Online]. Available: https://mc-stan.org/cmdstanr/

[53] J. Berens, C. Logan, M. Folsom, L. Bergeron, and K. McCune, "Validating morphological condition indices and their relationship with reproductive success in great-tailed grackles," *In principle acceptance by PCI Ecology of the version on 8 Nov 2019*, 2019. [Online]. Available: http://corinalogan.com/Preregistrations/gcondition.html

[54] J. Peig and A. J. Green, "New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method," *Oikos*, vol. 118, no. 12, pp. 1883–1891, 2009.

[55] D. Flockhart, G. Mitchell, R. Krikun, and E. Bayne, "Factors driving territory size and breeding success in a threatened migratory songbird, the canada warbler," *Avian Conservation and Ecology*, vol. 11, no. 2, 2016.

[56] J. E. Garabedian, C. E. Moorman, M. N. Peterson, and J. C. Kilgo, "Relative importance of social factors, conspecific density, and forest structure on space use by the endangered red-cockaded woodpecker: A new consideration for habitat restoration," *The Condor: Ornithological Applications*, vol. 120, no. 2, pp. 305–318, 2018.

[57] C. L. Amundson, J. A. Royle, and C. M. Handel, "A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts," *The Auk: Ornithological Advances*, vol. 131, no. 4, pp. 476–494, 2014.

[58] J. D. Nichols, L. Thomas, and P. B. Conn, "Inferences about landbird abundance from count data: recent advances and future directions," in *Modeling demographic processes in marked populations*. Springer, 2009, pp. 201–235.

[59] R. Shine, G. P. Brown, and B. L. Phillips, "An evolutionary process that assembles phenotypes through space rather than through time," *Proceedings of the National Academy of Sciences*, vol. 108, no. 14, pp. 5708–5711, 2011.

[60] E. L. Charnov, "Optimal foraging, the marginal value theorem," *Theoretical population biology*, vol. 9, no. 2, pp. 129–136, 1976.

[61] E. Wajnberg, X. Fauvergue, and O. Pons, "Patch leaving decision rules and the marginal value theorem: an experimental analysis and a simulation model," *Behavioral Ecology*, vol. 11, no. 6, pp. 577–586, 2000.

[62] O. Spiegel, S. T. Leu, C. M. Bull, and A. Sih, "What's your move? movement as a link between personality and spatial dynamics in animal populations," *Ecology letters*, vol. 20, no. 1, pp. 3–18, 2017.

[63] D. G. Chapple, A. C. Naimo, J. A. Brand, M. Michelangeli, J. M. Martin, C. T. Goulet, D. H. Brunton, A. Sih, and B. B. Wong, "Biological invasions as a selective filter driving behavioral divergence," *Nature Communications*, vol. 13, no. 1, p. 5996, 2022.

[64] P. A. Biro, M. V. Abrahams, J. R. Post, and E. A. Parkinson, "Predators select against high growth rates and risk–taking behaviour in domestic trout populations," *Proceedings of the Royal Society of London. Series B: Biological Sciences*, vol. 271, no. 1554, pp. 2233–2237, 2004.

[65] B. Josephine, S. Clulow, K. Colyvas, K. Salit, and A. S. Griffin, "Radiotracking invasive spread: are common mynas more active and exploratory on the invasion front?" *Biological Invasions*, vol. 22, no. 8, pp. 2525–2543, 2020.

[66] C. J. Logan, K. B. McCune, C. LeGrande, Z. Marfori, J. Hubbard, and D. Lukas, "Implementing a rapid geographic range expansion - the role of behavior changes," *Peer Community Journal*, 2023. [Online]. Available: https://doi.org/10.24072/pcjournal.320

[67] D. Lukas, A. D. Blackwell, M. Edrisi, K. Hardy, Z. Marfori, K. B. McCune, A. Sevchik, C. Smith, and C. J. Logan, "Reduced levels of relatedness indicate that great-tailed grackles disperse further at the edge of their range," *EcoEvoRxiv*, 2024.

[68] C. T. Ross and B. Winterhalder, "Sit-and-wait versus active-search hunting: A behavioral ecological model of optimal search mode," *Journal of Theoretical Biology*, vol. 387, pp. 76–87, 2015.

[69] D. W. Stephens and E. L. Charnov, "Optimal foraging: some simple stochastic models," *Behavioral Ecology and Sociobiology*, vol. 10, no. 4, pp. 251–263, 1982.