

Investigating sex differences in learning in a range-expanding bird

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Abstract

How might differences in dispersal and learning interact in range expansion dynamics? To begin to answer this question, in this preregistration we detail the background, hypothesis plus associated predictions, and methods of our proposed study, including the development and validation of a mechanistic reinforcement learning model, which we aim to use to assay colour-reward reinforcement learning (and the influence of two candidate latent parameters—speed and sampling rate—on this learning) in great-tailed grackles—a species undergoing rapid range expansion, where males disperse.

Introduction

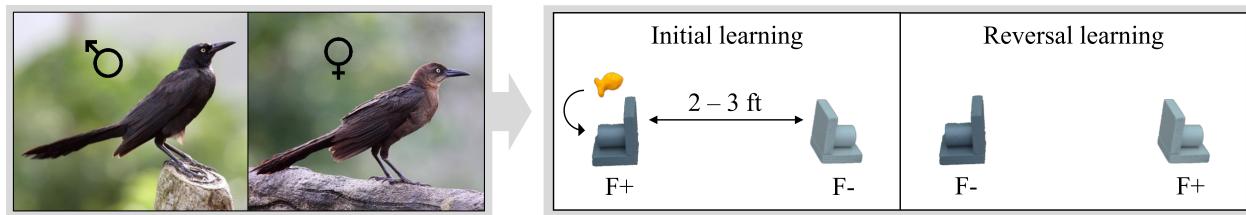
Dispersal and range expansion go ‘hand in hand’; movement by individuals away from a population’s core is a pivotal precondition of witnessed growth in species’ geographic limits (Chuang & Peterson, 2016; Ronce, 2007). Because ‘who’ disperses—in terms of sex—varies both within and across taxa (for example, male-biased dispersal is dominant among fish and mammals, whereas female-biased dispersal is dominant among birds; see Table 1 in Trochet et al., 2016), skewed sex ratios are apt to arise at expanding range fronts, and, in turn, differentially drive invasion dynamics. Female-biased dispersal, for instance, can ‘speed up’ staged invertebrate invasions by increasing offspring production (Miller & Inouye, 2013). Alongside sex-biased dispersal, learning ability is also argued to contribute to species’ colonisation capacity, as novel environments inevitably present novel (foraging, predation, shelter, and social) challenges that newcomers need to surmount in order to settle successfully (Sol et al., 2013; Wright et al., 2010). Indeed, a growing number of studies show support for this supposition (as recently reviewed in Lee & Thornton, 2021). Carefully controlled choice tests, for example, show that urban-dwelling individuals—that is, the ‘invaders’—will both learn and unlearn novel reward-stimulus pairings more rapidly than their rural-dwelling counterparts (Batabyal & Thaker, 2019), suggesting that range expansion selects for enhanced learning ability at the dispersal and/or settlement stage(s). Given the independent influence of sex-biased dispersal and learning ability on range expansion, it is perhaps surprising, then, that their potential interactive influence on this aspect of movement ecology remains unexamined, particularly as interactive links between dispersal and other behavioural traits such as aggression are documented within the range expansion literature (Duckworth, 2006; Gutowsky & Fox, 2011).

That learning ability can covary with, for example, exploration (e.g., Auersperg et al., 2011; Guillette et

al., 2011) and neophobia (e.g., Verbeek et al., 1994), two behaviours which may likewise play a role in range expansion (Griffin et al., 2017; Lee & Thornton, 2021), is one potential reason for the knowledge gap introduced above. Such correlations stand to mask what contribution, if any, learning ability lends to range expansion—an undoubtedly daunting research prospect. A second (and not mutually exclusive) reason is that, for many species, a detailed diary of their range expansion is lacking (Blackburn et al., 2009; Udvardy & Papp, 1969). And patchy population records inevitably introduce interpretive ‘noise,’ imaginably impeding population comparisons of learning ability (or the like).

In range-expanding great-tailed grackles (*Quiscalus mexicanus*), however, learning ability appears to represent a unique source of individual variation; more specifically, temporarily-captive great-tailed grackles’ speed to solve colour-reward reinforcement learning tests does not correlate with measures of their exploration (time spent moving within a novel environment), inhibition (time to reverse a colour-reward preference), motor diversity (number of distinct bill and/or feet movements used in behavioural tests), neophobia (latency to approach a novel object), risk aversion (time spent stationary within a ‘safe spot’ in a novel environment), persistence (number of attempts to engage in behavioural tests), or problem solving (number of test-relevant functional and non-functional object-choices) (Logan, 2016a, 2016b). Moreover, careful combing by researchers of public records, such as regional bird reports and museum collections, means that great-tailed grackle range-expansion data is both comprehensive and readily available (Dinsmore & Dinsmore, 1993; Pandolfino et al., 2009; Wehtje, 2003). Thus, great-tailed grackles offer behavioural ecologists a useful study system to investigate the interplay between life-history strategies, learning ability, and range expansion.

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Figure 1 Left panel: images showing a male and female great-tailed grackle (credit: Wikimedia Commons). Right panel: schematic of the colour-reward reinforcement learning experimental protocol. In the *initial learning* phase, great-tailed grackles are presented with two colour-distinct tubes; however, only one coloured tube (e.g., dark grey) contains a food reward (F+ versus F-). In the *reversal learning* phase, the colour-reward tube-pairings are swapped. The passing criterion was identical in both phases (see main text for details).

63

Here, for the first time (to our knowledge), we propose to investigate potential differences in colour-reward reinforcement learning performance between male and female great-tailed grackles (Figure 1), to test the hypothesis that sex differences in learning ability are related to sex differences in dispersal. Since the late nineteenth century, great-tailed grackles have been expanding their range at an unprecedented rate, moving northward from their native range in Central America into the United States (breeding in at least 20 states), with several first-sightings spanning as far north as Canada (Dinsmore & Dinsmore, 1993; Wehtje, 2003). Notably, the record of this range expansion in great-tailed grackles is heavily peppered with first-sightings involving a single or multiple male(s) (Dinsmore & Dinsmore, 1993; Kingery, 1972; Littlefield, 1983; Stepney, 1975; Wehtje, 2003). Moreover, recent genetic data show that, when comparing great-tailed grackles within a population, average relatedness: (i) is higher among females than among males; and (ii) decreases with increasing geographic distance among females; but (iii) is unrelated to geographic distance among males; hence, confirming a role for male-biased dispersal in great-tailed grackles (Sevchik et al., in press). Considering these natural history and genetic data, then, we expect male and female great-tailed grackles to differ across at least two colour-reward reinforcement learning parameters: speed and sampling rate (here, sampling is defined as switching between choice-options). Specifically, we expect male—versus female—great-tailed grackles: (prediction 1 & 2) to be faster to, firstly, learn a novel colour-reward pairing, and secondly, reverse their colour preference when the colour-reward pairing is swapped; and (prediction 3) to be more deterministic—that is, sample less often—in their colour-reward learning; if learning ability and dispersal relate. Indeed, since invading great-tailed grackles face agribusiness-led wildlife management

88 strategies, including the use of chemical crop repellents (Werner et al., 2011, 2015), range expansion should
89 disfavour slow, error-prone learning strategies, resulting in a spatial sorting of learning ability in great-
90 tailed grackles (Wright et al., 2010). Related to this final point, we further expect (prediction 4) such sex
91 differences in learning ability to be more pronounced in great-tailed grackles living at the edge, rather than
92 the intermediate and/or core, region of their range (e.g., Duckworth, 2006).

93 Methods

94 Data

95 This preregistration aims to use colour-reward reinforcement learning data collected (or being collected)
96 in great-tailed grackles across three study sites that differ in their range-expansion demographics; that is,
97 belonging to a core, intermediate, or edge population (based on time-since-settlement population growth
98 dynamics, as outlined in Chuang & Peterson, 2016). Specifically, data will be utilised from: (i) Tempe,
99 Arizona—hereafter, the core population (estimated—by adding the average time between first sighting and
100 first breeding to the year first sighted—to be breeding since 1951) (Walter, 2004; Wehtje, 2003); (ii) Santa
101 Barbara, California—hereafter, the intermediate population (known to be breeding since 1996) (Lehman,
102 2020); and (iii) Woodland, California—hereafter, the edge population (known to be breeding since 2004)
103 (Hampton, 2001). Data collection at both the Tempe, Arizona and Santa Barbara, California study sites has
104 been completed prior to the submission of this preregistration (total sample size across sites: nine females
105 and 25 males); however, data collection at the Woodland, California study site is ongoing (current sample
106 size: three females and nine males; anticipated minimum total sample size: five females and ten males).
107 Thus, the final data set should contain colour-reward reinforcement learning data from at least 14 female
108 and 35 male great-tailed grackles.

109 Experimental protocol

110 General

111 A step-by-step description of the experimental protocol is reported elsewhere (e.g., Blaisdell et al., 2021). As
112 such, below we detail only the protocol for the colour-reward reinforcement learning tests that we propose
113 to analyse herein.

114 Colour-reward reinforcement learning tests

115 The reinforcement learning tests consist of two phases (Figure 1, right panel): (i) colour-reward learning
116 (hereafter, initial learning) and (ii) colour-reward reversal learning (hereafter, reversal learning). In both
117 phases, two different coloured tubes are used: for Santa Barbara great-tailed grackles, gold and grey (Logan,
118 2016b, 2016a); for all other great-tailed grackles: light and dark grey (Blaisdell et al., 2021). Each tube
119 consists of an outer and inner diameter of 26 mm and 19 mm, respectively; and each is mounted to two
120 pieces of plywood attached at a right angle (entire apparatus: 50 mm wide × 50 mm tall × 67 mm deep);
121 thus resulting in only one end of each coloured tube being accessible (Figure 1, right panel).

122 In the *initial learning phase*, great-tailed grackles are required to learn that only one of the two coloured
123 tubes contains a food reward (e.g., dark grey; this colour-reward pairing is counterbalanced across great-tailed
124 grackles within each study site). Specifically, the rewarded and unrewarded coloured tubes are placed—either
125 on a table or on the floor—in the centre of the aviary run (distance apart: table, 2 ft; floor, 3 ft), with the
126 open tube-ends facing, and perpendicular to, their respective aviary side-wall. Which coloured tube is
127 placed on which side of the aviary run (left or right) is pseudorandomised across trials. A trial begins at
128 tube-placement, and ends when a great-tailed grackle has either made a tube-choice or the maximum trial
129 time has elapsed (eight minutes). A tube-choice is defined as a great-tailed grackle bending down to examine
130 the contents (or lack thereof) of a tube. If the chosen tube contains food, the great-tailed grackle is allowed
131 to retrieve and eat the food, before both tubes are removed and the rewarded coloured tube is rebaited out
132 of sight (for the great-tailed grackle). If a chosen tube does not contain food, both tubes are immediately
133 removed. Each great-tailed grackle is given, first, up to three minutes to make a tube-choice (after which
134 a piece of food is placed equidistant between the tubes to entice participation); and then, if no choice has
135 been made, an additional five minutes maximum, before both tubes are removed. All trials are recorded
136 as either correct (choosing the rewarded colour tube), incorrect (choosing the unrewarded colour tube), or

137 incomplete (no choice made); and are presented in 10-trial blocks. To pass initial learning, a great-tailed
138 grackle must make a correct choice in at least 17 out of the most recent 20 trials, with a minimum of eight
139 and nine correct choices across the last two blocks.

140 In the *reversal learning phase*, great-tailed grackles are required to learn that the colour-reward pairing
141 has been switched; that is, the previously unrewarded coloured tube (e.g., light grey) now contains a food
142 reward. The protocol for this second and final learning phase is identical to that, described above, of the
143 initial learning phase.

144 Analysis plan

145 General

146 Here, we will analyse, process, and visually present our data using, respectively, the ‘rstan’ (Stan Development
147 Team, 2020), ‘rethinking’ (McElreath, 2018), and ‘tidyverse’ (Wickham et al., 2019) packages in R (R
148 Core Team, 2021). Our reproducible code is available on GitHub (<https://github.com/alexisbreen/Sex-differences-in-grackles-learning>).

150 Reinforcement learning model

151 In this preregistration, we propose to employ an adapted (from Deffner et al., 2020) Bayesian reinforcement
152 learning model, to examine the influence of sex on great-tailed grackles’ initial and reversal learning perfor-
153 mance. The reinforcement learning model, defined below, allows us to link observed coloured tube-choices to
154 latent individual-level knowledge-updating (of attractions towards, learning about, and sampling of, either
155 coloured tube) based on recent tube-choice reward-payoffs, and to translate such latent knowledge-updating
156 into individual tube-choice probabilities; in other words, we can reverse engineer the probability that our
157 parameters of interest (speed and sampling rate) produce great-tailed grackles’ observed tube-choice behaviour
158 by formulating our scientific model as a statistical model (McElreath, 2018, p. 537). This method can there-
159 fore capture whether, and, if so, how multiple latent learning strategies simultaneously guide great-tailed
160 grackles’ decision making—an analytical advantage over more traditional methods (e.g., comparing trials to
161 passing criterion) that ignore the potential for equifinality (Barrett, 2019; Kandler & Powell, 2018).

162 Our reinforcement learning model consists of two equations:

$$A_{i,j,t+1} = (1 - \phi_{k,l})A_{i,j,t} + \phi_{k,l}\pi_{i,j,t}, \quad (1)$$

$$P(i)_{t+1} = \frac{\exp(\lambda_{k,l}A_{i,j,t})}{\sum_{m=1}^2 \exp(\lambda_{k,l}A_{m,j,t})}. \quad (2)$$

163 Equation 1 expresses how attraction (A) to a choice-option (i) changes for an individual (j) across time
164 ($t + 1$) based on their prior attraction to that choice-option ($A_{i,j,t}$) plus their recently experienced choice-
165 payoff ($\pi_{i,j,t}$), whilst accounting for the weight given to recent payoffs ($\phi_{k,l}$). As $\phi_{k,l}$ increases in value,
166 so, too, does the rate of individual attraction-updating; thus, $\phi_{k,l}$ represents the individual learning rate.
167 We highlight that the k, l indexing denotes that we estimate separate ϕ parameters for each phase of the
168 experiment ($k = 1$ for initial, $k = 2$ for reversal) and each sex ($l = 1$ for females, $l = 2$ for males).

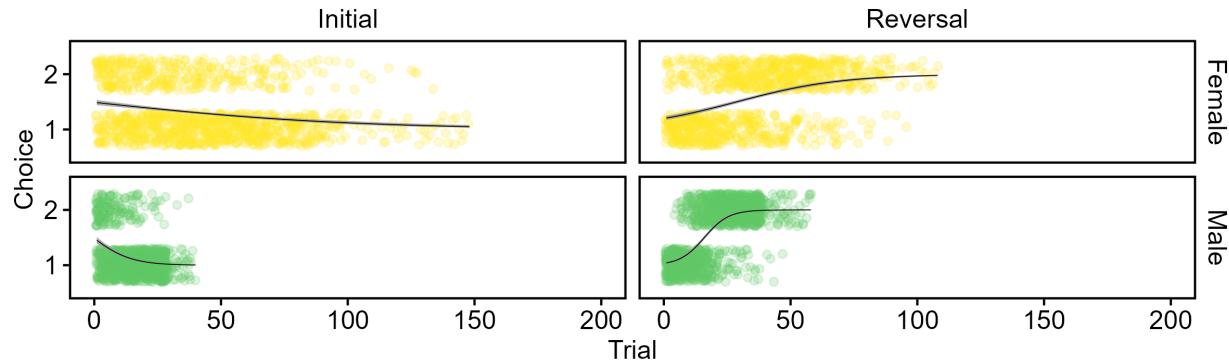
169 Equation 2 is a softmax function that expresses the probability (P) that option (i) is selected in the next
170 choice-round ($t + 1$) as a function of the attractions and a parameter ($\lambda_{k,l}$) that governs how much relative
171 differences in attraction scores guide individual choice-behaviour. The higher the value of $\lambda_{k,l}$, the more
172 deterministic (less option-switching) the choice-behaviour of an individual becomes (note $\lambda_{k,l} = 0$ generates
173 random choice); thus, $\lambda_{k,l}$ represents the individual sampling rate for phase k and sex l .

174 From the above reinforcement learning model, then, we will generate inferences about the effect of sex on $\phi_{k,l}$
175 and $\lambda_{k,l}$ from at least 1000 effective samples of the posterior distribution (see our model validation below).
176 We note that our reinforcement learning model also includes both individual bird and study site as random
177 effects (to account for repeated measures within both individuals and populations); however, for clarity,

178 these parameters are omitted from our equations (but not our code: <https://github.com/alexisbreen/Sex-differences-in-grackles-learning>). Regarding our study site random effect, we further note that, as introduced above, we will also explore population-mediated sex-effects on ϕ and λ , by comparing these learning parameters both within and between sexes at each study site. Finally, our reinforcement learning model excludes trials where a great-tailed grackle did not make a tube-choice, as this measure cannot clearly speak to individual learning ability—for example, satiation rather than any learning of ‘appropriate’ colour tube-choice could be invoked as an explanation in such cases. Indeed, there are, admittedly, a number of intrinsic and extrinsic factors (e.g., temperament and temperature, respectively) that might bias great-tailed grackles’ tube-choice behaviour, and, in turn, the output from our reinforcement learning model (Webster & Rutz, 2020). Nonetheless, our reinforcement learning model serves as a useful first step towards addressing if learning ability and dispersal relate in great-tailed grackles (for a similar rationale, see McElreath & Smaldino, 2015).

190 Model validation

191 We validated our reinforcement learning model in three steps. First, we performed agent-based simulations. Specifically, we followed the tube-choice behaviour of simulated great-tailed grackles—that is, 14 females 192 and 35 males from one of three populations (where population membership matched known study site sex 193 distributions)—across the described initial learning and reversal learning phases. The tube-choice behaviour 194 of the simulated great-tailed grackles was governed by a set of rules identical to those defined by our mathematical 195 equations—for example, coloured tube attractions were independently updated based on the reward 196 outcome of tube choices. Because we assigned higher average ϕ and λ values to simulated male (versus 197 female) great-tailed grackles, the resulting data set should show males outperform females on initial and 198 reversal learning, at both the group and individual-level; it did (Figure 2 & S1, respectively).

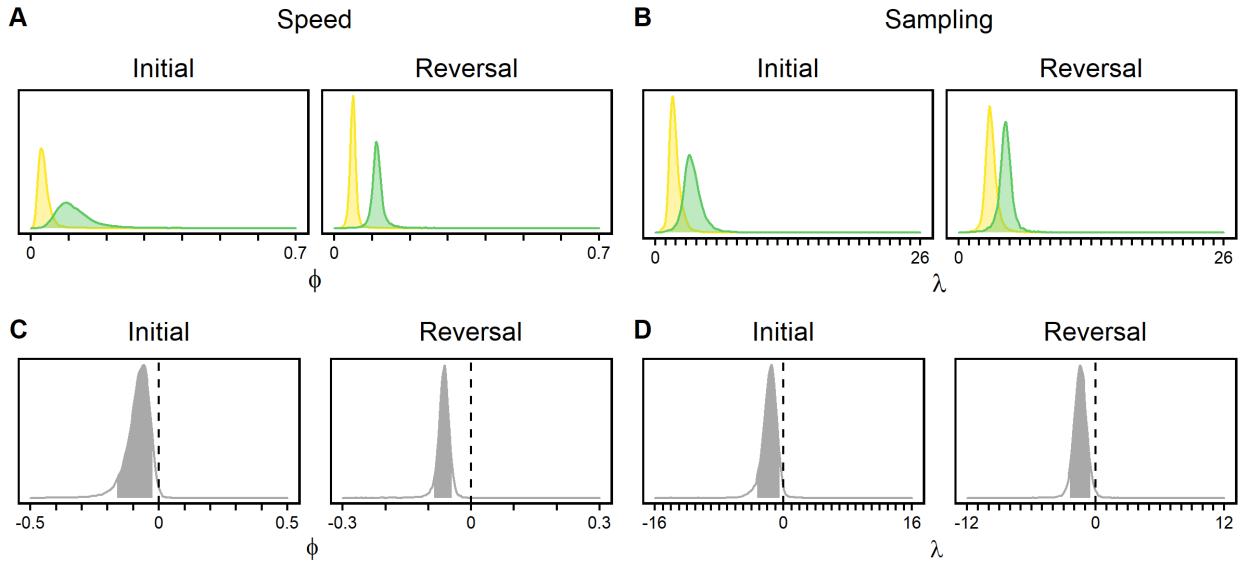


200
 201 **Figure 2** Group-level tube-choice behaviour of simulated great-tailed grackles across colour-reward reinforcement learning trials (females: yellow, $n = 14$; males: green, $n = 35$), following model validation step 202 one. Tube option 1 (e.g., dark grey) was the rewarded option in the initial learning phase; conversely, tube 203 option 2 (e.g., light grey) contained the food reward in the reversal learning phase. Each open circle represents 204 an individual tube-choice; black lines indicate binomial smoothed conditional means fitted with grey 205 89% compatibility intervals.

206 Next, we ran our simulated data set on our reinforcement learning model. Here, we endeavored to determine 207 whether our reinforcement learning model: (i) recovered our assigned $\phi_{k,l}$ and $\lambda_{k,l}$ values (it did; Table 1); 208 and (ii) produced ‘correct’ qualitative inferences—that is, detected the simulated sex differences in great- 209 tailed grackles’ initial and reversal learning (it did; Figure 3).

Table 1: Comparison of assigned and recovered ϕ and λ values, following model validation step two. Eighty-nine percent highest posterior density intervals (HPDI) are shown for recovered values.

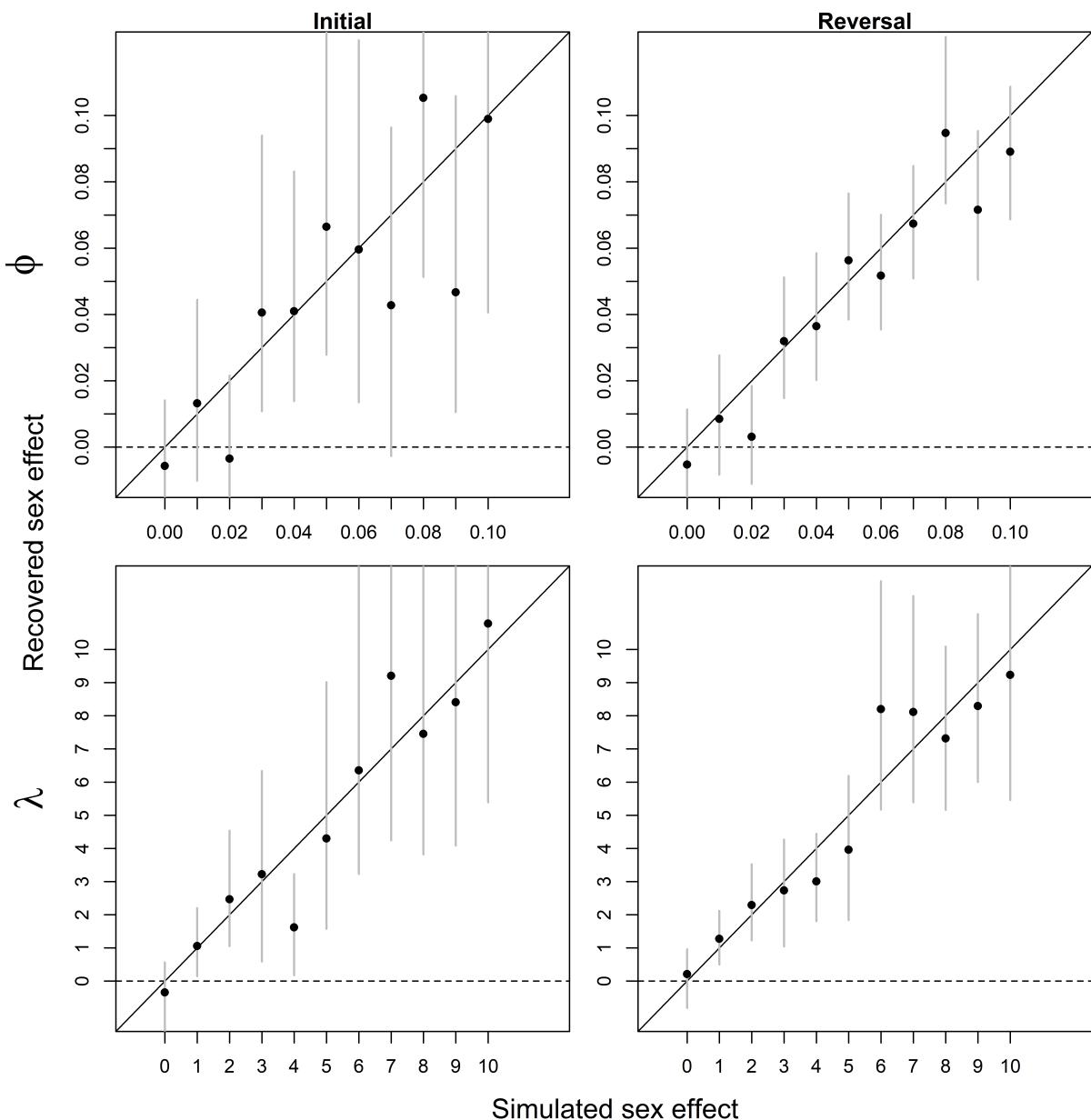
	ϕ				λ			
	Female		Male		Female		Male	
	Initial	Reversal	Initial	Reversal	Initial	Reversal	Initial	Reversal
Assigned	0.03	0.05	0.09	0.11	2.00	3.00	4.00	5.00
Recovered	0.03	0.05	0.07	0.10	2.16	2.82	4.31	5.68
89% HPDI	0.01 - 0.04	0.04 - 0.06	0.03 - 0.11	0.08 - 0.12	1.29 - 2.99	2.05 - 3.58	2.65 - 6.00	4.41 - 6.97



211

212 **Figure 3** Comparison of learning ability in simulated female (yellow; $n = 14$) and male (green; $n = 35$) great-
213 tailed grackles across initial and reversal colour-reward reinforcement learning, following model validation
214 step two. (A) ϕ , the rate of learning i.e., speed. (B) λ , the rate of sampling i.e., switching between choice-
215 options. (C) and (D) show posterior distributions for respective contrasts between female and male learning.
216 Eighty-nine percent highest posterior density intervals are shaded in grey; that this interval does not cross
217 zero evidences a simulated effect of sex on learning ability.

218 Finally, we repeated step one and step two, using a range of realistically plausible ϕ and λ sex differences
219 (note that values for female great-tailed grackles were left unchanged from Table 1), to determine whether
220 our reinforcement learning model could detect different effect sizes of sex on our target learning parameters.
221 This final step confirmed that, for our anticipated minimum sample size, our reinforcement learning model:
222 (i) detects sex differences in ϕ values ≥ 0.03 and λ values ≥ 1 ; and (ii) infers a null effect for ϕ values
223 < 0.03 and λ values < 1 i.e., very weak simulated sex differences (Figure 4). Both of these points together
224 highlight how our reinforcement learning model allows us to say that null results are not just due to small
225 sample size. Additionally, estimates obtained from step three were more precise in the reversal learning phase
226 compared to the initial learning phase (Figure 4), and we can expect to detect even smaller sex differences if
227 we analyse learning across both phases—an approach we will apply if we detect no effect of phase. In sum,
228 model validation steps one through three confirm that our reinforcement learning model is reasonably fit.



229
230 **Figure 4** Parameter recovery test for different sizes of simulated sex differences. Plots show posterior
231 estimates of the effect of sex (contrasts between simulated male and female great-tailed grackles; $n =$
232 14 and 35, respectively) on speed (ϕ) and sampling (λ) learning parameters, following model validation
233 step three. Black circles represent the mean recovered sex effect estimates with grey eighty-nine percent
234 highest posterior density intervals (HPDIs); black solid diagonal lines represent a ‘perfect’ match between
235 assigned and recovered parameter estimates (note that we would not expect a perfect correspondence due
236 to stochasticity of agent-based simulations); and black dashed horizontal lines represent a recovered null
237 sex effect.

238 **Bias**

239 AJB and DD are (at the time of submitting this preregistration) blind with respect to all but two aspects
240 of the target data: the sex and population membership of each grackle that has, thus far, completed, or is
241 expected to complete, the colour-reward reinforcement learning tests (because these parameters were used
242 in model validation simulations—see above).

243 **Open materials**

244 <https://github.com/alexisbreen/Sex-differences-in-grackles-learning>

245 **Acknowledgements**

246 We thank all members, past and present, of the Grackle Project for collecting and sharing the data that we
247 propose to analyse herein. We further thank Richard McElreath for study support.

248 **Ethics**

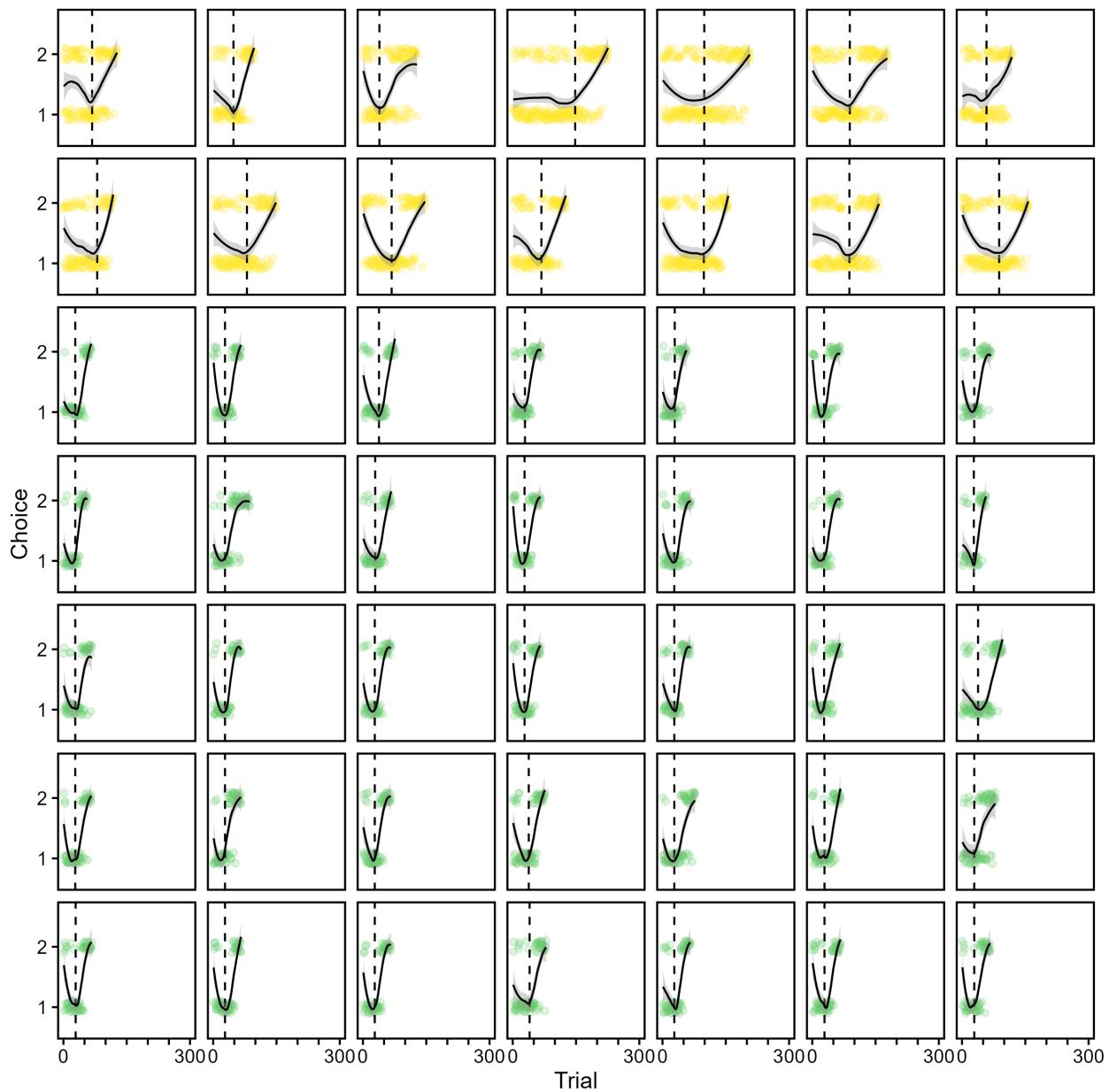
249 All data utilised herein were collected with ethical approval.

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344 **Supplementary material**



345

346 **Figure S1** Individual-level tube-choice behaviour of simulated great-tailed grackles across colour-reward
 347 reinforcement learning trials (females: yellow, $n = 14$; males: green, $n = 35$). Tube option 1 (e.g., dark grey)
 348 was the rewarded option in the initial learning phase; conversely, tube option 2 (e.g., light grey) contained
 349 the food reward in the reversal learning phase. Each open circle shows an individual tube-choice; black solid
 350 lines show loess smoothed conditional means fitted with grey 89% compatibility intervals; and dashed black
 351 lines show individual-unique transitions between learning phases.

Table S1 Peer Community in Registered Reports required study design table.

Question	Hypothesis	Sampling plan	Analysis Plan	Rationale for deciding the sensitivity of the test for confirming or disconfirming the hypothesis	Interpretation given different outcomes	Theory that could be shown wrong by the outcomes
Do learning ability and dispersal relate?	Sex differences in learning ability are related to sex differences in dispersal.	Use colour-reward reinforcement data from three study sites in great-tailed grackles—a species undergoing rapid range expansion, where males disperse.	Bayesian experience weighted attraction (EWA) model; modelling the influence of sex on two parameters of grackles' colour-reward reinforcement learning: speed and sampling rate (where sampling is defined as switching between choice-options).	This method can* capture whether, and, if so, how multiple latent learning strategies simultaneously guide grackles' decision making—an analytical advantage over more traditional methods (e.g., comparing trials to passing criterion) that ignore the potential for equifinality. *We performed agent-based simulations to ensure our reasonable model-fit/effect detection <i>a priori</i> .	Hypothesis confirmed in full or in part: Males are speedier and sample less than females <i>because range expansion disfavours slow, error-prone learning strategies in range expansion</i> . Males are speedier than females <i>because range expansion disfavours slow learning strategies in range expansion</i> . Males sample less than females <i>because range expansion disfavours error-prone learning strategies in range expansion</i> . Between and/or within population differences exist with respect to any of the above cases	N/A

					<p><i>because range expansion results in a spatial sorting of learning ability</i></p> <p>Hypothesis not confirmed:</p> <p>Males and females do not differ in their colour-reward reinforcement learning; and, consequently, between or within population differences not detected because (not mutually exclusive) such sex-mediated differences never existed; too much time has passed since settlement and differences are no longer detectable as females 'catch up' (e.g., via assortative mating) and/or males 'lose' their learning 'edge' (e.g., via shifts in favourable post-establishment phenotypes) over successive breeding generations; our measure of learning ability does not capture this dynamic.</p>	
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					Females are faster and/or sample less than males <i>because (not mutually exclusive) range expansion disfavours slow, error-prone learning strategies in females as they provide the bulk of parental care; females have 'overtaken' (e.g., via shifts in favourable post-establishment phenotypes) males across successive breeding generations.</i>	
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