

Range-expanding male birds buffer environmental change by strategising risk-sensitive learning

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Abstract

How might differences in dispersal and learning interact in range expansion dynamics? Here, we employ tailored computational and simulation methods to assay stimulus-reward initial and reversal reinforcement learning across a core, middle, and edge population of great-tailed grackles—a bird species undergoing rapid range expansion, where males disperse. We show that—irrespective of population membership—male and female great-tailed grackles initially learn at comparable pace, but, when reward contingencies reverse, males recover their learning faster via pronounced reward-payoff sensitivity, catalysing adaptive recalibration of choice-behaviour. Together, these robust sex-difference data demonstrate, in a changing world, learners strategising risk-sensitivity can swiftly succeed, implying the interplay between life history and cognition is a dynamic demographic driver of organismal geographic and phenotypic distributions in the Anthropocene.

Main text

Understanding how links between life history and cognition allow species to thrive—that is, expand into—human-modified environments is of urgent research importance (Goumas et al., 2020; Lee and Thornton, 2021; Pirotta et al., 2018; Tuomainen and Candolin, 2011). 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 and 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

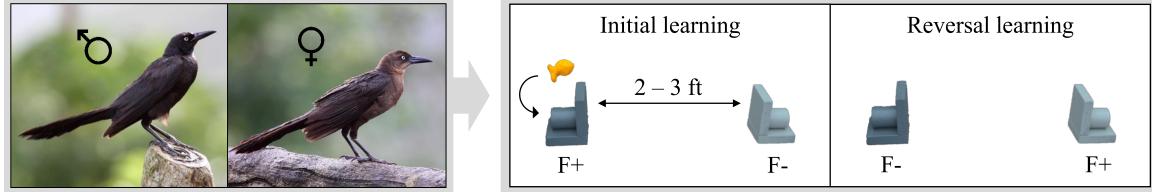


Figure 1: Subjects and experimental protocol. Left panel: images showing a male and female great-tailed grackle (credit: Wikimedia Commons). Right panel: schematic of the stimulus-reward reinforcement paradigm. In initial learning, great-tailed grackles are presented with two colour-distinct tubes; however, only one coloured tube (e.g., dark grey) contains a food reward (F+ versus F-). In reversal learning, the stimulus-reward tube-pairings are swapped. The passing criterion is identical in both learning phases: a minimum of eight and nine F+ choices across the last two blocks of 10 trials—for details, see *Methods*.

20 dynamics. Female-biased dispersal, for instance, can ‘speed up’ staged invertebrate invasions by increasing
 21 offspring production (Miller and Inouye, 2013). Alongside sex-biased dispersal, learning is also argued
 22 to contribute to species’ colonisation capacity, as novel environments inevitably present novel (foraging,
 23 predation, shelter, and social) challenges that newcomers need to surmount in order to settle successfully
 24 (Sol et al., 2013; Wright et al., 2010). Indeed, a growing number of studies show support for this supposition
 25 (as recently reviewed in Lee and Thornton 2021). Carefully controlled choice tests, for example, show
 26 that urban-dwelling individuals—that is, the ‘invaders’—will learn novel reward-stimulus pairings faster
 27 than rural-dwelling counterparts (Batabyal and Thaker, 2019), suggesting range expansion selects for rapid
 28 learning at the dispersal and/or settlement stage(s). Given the independent influence of sex-biased dispersal
 29 and learning on range expansion, it is perhaps surprising, then, that their potential interactive influence on
 30 movement ecology remains unexamined.

31 Great-tailed grackles (*Quiscalus mexicanus*; henceforth, grackles) are an excellent model for empirical
 32 examination of the interplay between sex-biased dispersal, learning, and ongoing rapid range expansion:
 33 over the past \sim 150 years, they have (seemingly) utilised human-modified environments to move out from
 34 their native range in Central America into much of the United States (Summers et al., 2022), with several
 35 first-sightings spanning as far north as Canada (Dinsmore and Dinsmore, 1993; Wehtje, 2003). Notably, the
 36 record of this range expansion is heavily peppered with first-sightings involving a single or multiple male(s)
 37 (Littlefield, 1983; Stepney, 1975; Kingery, 1972; Dinsmore and Dinsmore, 1993; Wehtje, 2003). Moreover,
 38 recent genetic data show, when comparing grackles within a population, average relatedness: (i) is higher
 39 among females than among males; and (ii) decreases with increasing geographic distance among females; but
 40 (iii) is unrelated to geographic distance among males; hence, confirming a role for male-biased dispersal in
 41 this species (Sevchik et al., 2022). Considering these life history and genetic data in conjunction with data on
 42 agribusiness-led grackle ‘deterrent’ efforts (e.g., chemical crop repellents; Werner et al. 2015, 2011), we expect

43 range expansion to disfavour slow, error-prone learning in male grackles, potentially resulting in a spatial
44 sorting—in terms of the magnitude of any such sex difference—with respect to population establishment age
45 (i.e., sex effect: newer > older; Wright et al. 2010). Collating, cleaning, and curating existing reinforcement
46 learning data—wherein novel stimulus-reward pairings are presented (i.e., *initial learning*), and, once learned,
47 these reward contingencies are reversed (i.e., *reversal learning*)—we examine, for the first time (to our
48 knowledge), whether, and, if so, how sex differentially mediates learning across 32 male and 17 female
49 grackles either inhabiting a core (17 males, 5 females), middle (4 males, 4 females) or edge (11 males,
50 8 females) population (based on year-since-first-breeding: 1951, 1996, 2004, respectively; for definitional
51 background, see: Chuang and Peterson 2016; Figure 1).

52 Across all three populations, we observe robust reinforcement learning dynamics (Figure 2; Figure S1,
53 S2). Specifically, male and female grackles start out as similarly speedy learners (mean \pm standard error (SE)
54 number of trials in initial learning: males_n = 32, 40 \pm 2.81; females_n = 17, 41 \pm 2.43; Figure 2A, left plot;
55 total-trial Poisson regression female-male posterior contrast widely overlaps zero: -5.17 - 7.44), but, once
56 reward contingencies reverse, male grackles outpace female counterparts considerably (mean \pm SE number
57 of trials in reversal learning: males_n = 29, 72 \pm 4.45; females_n = 17, 85 \pm 6.69; Figure 2A, right plot; total-
58 trial Poisson regression female-male posterior contrast lies appreciably above zero: 6.39 - 29.95). During
59 this reinforcement learning, male and female grackles initially sample—by switching between—the rewarded
60 and unrewarded choice-option at similar frequency (mean \pm SE cumulative proportion of choice-option
61 switches across initial learning: males_n = 32, 0.38 \pm 0.01; females_n = 17, 0.40 \pm 0.01; Figure 2B, left plot;
62 total-switches Poisson regression female-male posterior contrast broadly bounds zero: -2.59 - 5.18); however,
63 in reversal learning males make markedly fewer choice-option switches, compared to female counterparts
64 (mean \pm SE cumulative proportion of choice-option switches across reversal learning: males_n = 29, 0.34
65 \pm 0.01; females_n = 17, 0.39 \pm 0.01; Figure 2B, right plot; total-switches Poisson regression female-male
66 posterior contrast sits distinctly above zero: 6.48 - 22.62). That population membership appears (see inserts
67 in Figure 2A, B; and Table S1, S2) unimportant to grackles' reinforcement learning suggests a number
68 of nonexclusive possibilities, including the potential for selection to operate on learning pre- and/or post-
69 dispersal at powerful 'equalising' pace (empirical examples supporting such adaptive avian trait evolution:
70 Duckworth 2006; Bonnet et al. 2022), but our utilised data cannot inform any such hypothesis—for this,
71 spatial replicates and a study design targeting causal inference are required (Blackburn et al., 2009; Pearl,
72 2009; Glymour et al., 2016). Environmental change and not novelty alone, then, dependably directs disparate
73 reinforcement learning trajectories between male and female grackles (perhaps unsurprisingly given their
74 neophilic nature e.g., Fronimos et al. 2011), supporting our overall expectation of sex-mediated differential
75 learning in range-expanding grackles.

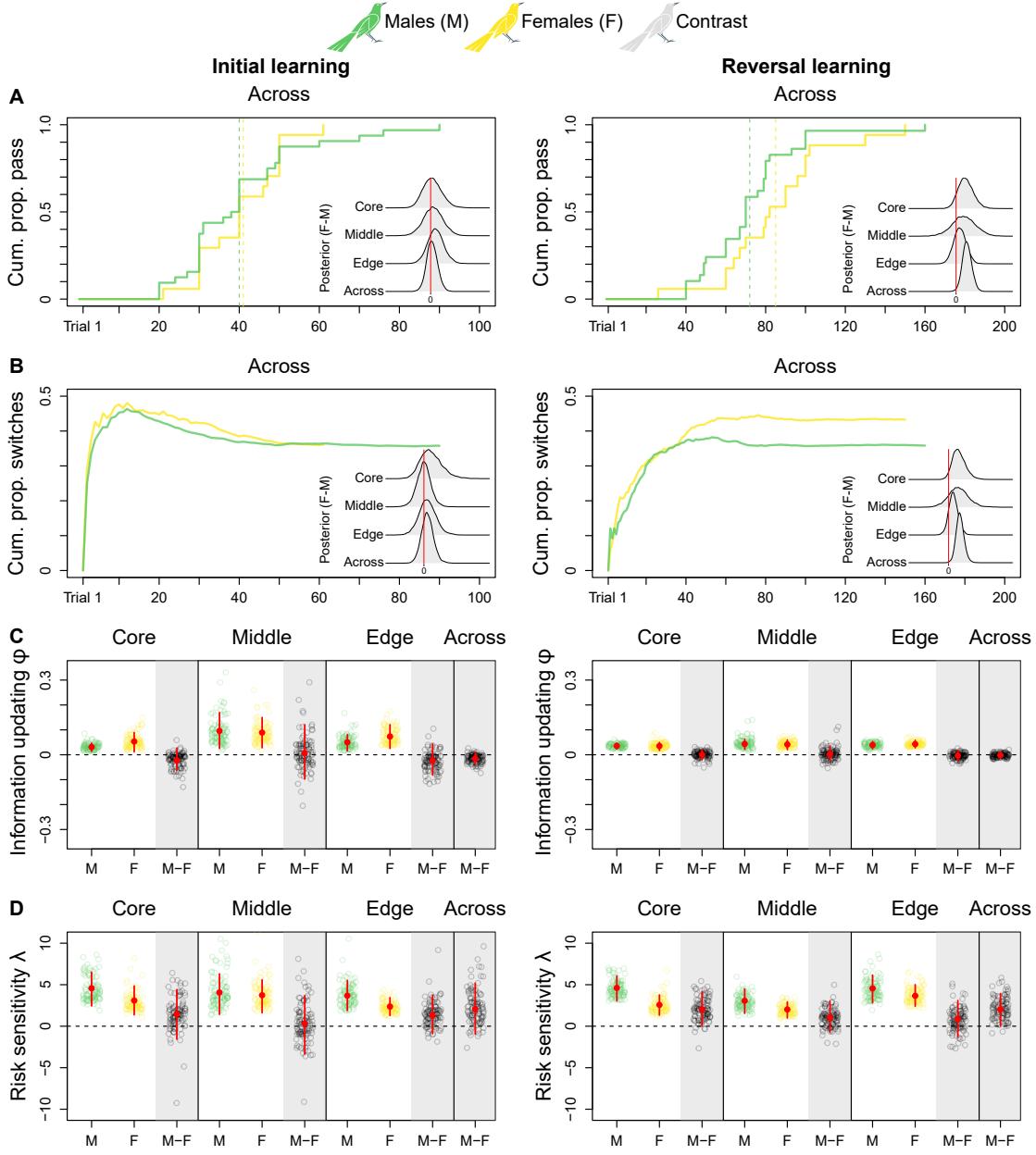


Figure 2: Behavioural and mechanistic reinforcement learning results. (A) The cumulative proportion of male and female grackles passing initial and reversal learning across populations. In both plots, dashed vertical lines indicate means (reported in main text); a ‘step’ represents a grackle passing; the steeper the slope of the line the faster the finish. (B) The cumulative proportion of choice-option switches made by male and female grackles in initial and reversal learning across populations. For (A) and (B), inserts show Poisson regression posterior density female-male contrasts, at both population and across-population level; the further the distribution falls from zero—solid vertical red lines—the stronger the sex difference. (C) and (D) show the influence in initial and reversal learning of core latent learning parameters—that is, the information-updating rate ϕ and the risk-sensitivity rate λ —between male and female grackles inhabiting a core, middle or edge population; as well as between and across population posterior male-female contrasts. As $\phi_{0 \rightarrow 1}$, information-updating increases; as $\lambda_{0 \rightarrow \infty}$, risk-sensitivity strengthens. For (C) and (D), open circles correspond to 100 draws from the posterior; red filled circles and red vertical lines correspond to posterior means and 89% highest posterior density intervals, respectively. See Table S1 - S4 for full model outputs.

Because (dis)similar behaviour can result from multiple latent processes—an often overlooked phenomenon termed equifinality (Kandler and Powell, 2018; Barrett, 2019)—we next employ computational methods to delimit mechanism(s). Specifically, we use an adapted (from Deffner et al., 2020) multi-level Bayesian reinforcement learning model, which we vet *a priori* via agent-based simulation (see *Supplementary material*), to estimate the contribution of two core latent learning parameters to grackles’ reinforcement learning: the *information-updating rate* and the *risk-sensitivity rate* (ϕ and λ , respectively). Both latent learning parameters capture individual-level internal response to incurred reward-payoffs (full mathematical details in *Methods*); that is, as $\phi_{0 \rightarrow 1}$, information-updating increases; as $\lambda_{0 \rightarrow \infty}$, risk-sensitivity strengthens. Looking between populations to determine replicability (Figure 2C, D), our computations show: in initial learning, the information-updating rate ϕ of core- and edge-inhabiting male grackles is noticeably lower than that of female counterparts (denoted by the bulk of the male-female posterior contrasts being below zero; Figure 1C, left plot; Table S3), with the middle population’s wider, mostly overlapping male and female posteriors reflecting this group’s relatively smaller sample size (all computations use the full data set—see *Statistical analyses*); while in reversal learning, the information-updating rate ϕ of male and female grackles is nearly identical irrespective of population membership (denoted by the centering of the male-female posterior contrasts around zero; Figure 1C, right plot; Table S3). Therefore, the information-updating rate ϕ in male and female grackles is initially opposed but converges across reinforcement learning phases.

These primary computational findings are, at first glance, perplexing: if male grackles are faster than female grackles in reversal learning (Figure 2A, right plot), why do all grackles ultimately update information at matched pace? This apparent conundrum, however, in fact highlights the potential for multiple latent learning processes to direct choice-behaviour (Kandler and Powell, 2018; Barrett, 2019). Case in point: in line with the choice-switch behavioural data, reported above, the risk-sensitivity rate λ is distinctly higher in male grackles, compared to female counterparts, regardless of whether the comparison occurred within individuals inhabiting a core, middle or edge population in *both* initial and reversal learning (denoted by the bulk of the male-female posterior contrasts being above zero; Figure 1D, both plots; Table S4); in other words, male grackles favour the choice-option with higher expected payoffs. Thus, these combined computational data demonstrate, when reward contingencies reverse, male—versus female—grackles recover their learning faster via pronounced reward-payoff sensitivity—a risk-sensitive learning strategy spotlighted in full by across-population male-female computational contrasts (Figure 2C, D; Table S3, S4; for similar findings in a social learning context, see Bono et al. 2018).

To better understand the adaptive consequences of strategising risk-sensitive learning, we simulate new reinforcement learning trajectories informed by grackles in our study; more specifically, we simulate new ‘birds’ from random draws of the varying-effects multivariate normal distribution of sex- and phase-specific

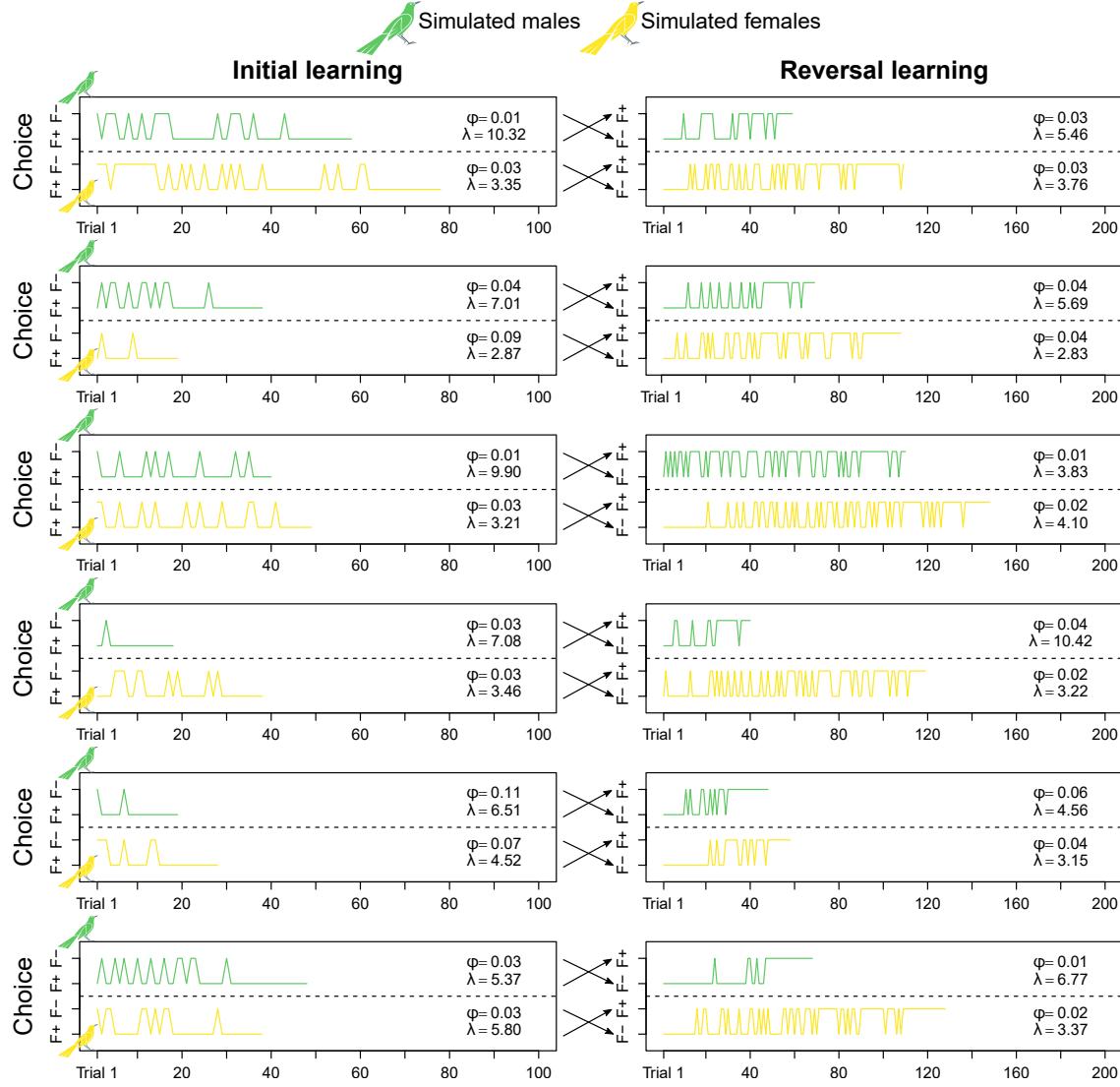


Figure 3: Adaptive consequences of strategising risk-sensitive learning. Stimulus-reward reinforcement learning trajectories by six simulated males and six simulated females (one simulated male-female pair per row), based on random draws (from the multivariate normal posterior distribution of our across-population computations) of latent learning parameter pairings; that is, the information-updating rate ϕ and the risk-sensitivity rate λ . As $\phi_{0 \rightarrow 1}$, information-updating increases; as $\lambda_{0 \rightarrow \infty}$, risk-sensitivity strengthens. As a rule: the stronger the risk-sensitivity rate λ , the more advantaged is initial and reversal learning. In all plots, F+ = the rewarded choice-option; F- = the unrewarded choice-option.

109 information-updating rate ϕ and risk-sensitivity rate λ estimates generated by our across-population com-
110 putations (*sensu* Deffner et al., 2020). Reassuringly, our simulations matched for actual sample size reliably
111 track our behavioural data (Figure S3). But a random draw of six simulated males and six simulated females
112 is sufficient to view the consequences of variation in latent learning parameter pairings (Figure 3). The overall
113 pattern that presents is: no ‘winning’ pairing exists. As a rule, however, reinforcement learning *is* advan-
114 taged when the risk-sensitivity rate λ is of intermediate to high value: because ‘birds’ can catalyse adaptive
115 recalibration of choice-behaviour by sticking steadily to ‘safe’—that is, recently profitable—choice-options.
116 For perspective, despite exhibiting a very low information-updating rate ϕ (0.01), the sixth simulated male
117 (Figure 3, bottom row) is among those ‘birds’ fastest in reversal learning—finishing in front of all but three
118 simulants—since his relatively high risk-sensitivity rate λ (6.77) facilitates fine-tuning of choice-option focus
119 in response to foraging returns. When profitable foraging returns change, then, and information-updating
120 retards (Figure 2C), learners strategising risk-sensitivity can swiftly succeed, such as male—versus female—
121 grackles in the current study.

122 In conclusion, mapping a full pathway from behaviour to mechanism through to adaptation, our study re-
123 veals range-expanding male grackles are pronounced payoff-sensitive learners, which buffers them to ‘bounce-
124 back-better’ when confronting environmental change, compared to female counterparts. By revealing robust
125 interactive links between the dispersing sex and strategic learning in a species rapidly expanding its range,
126 our study implies success in the Anthropocene is simultaneously shaped, in part, by life history and cogni-
127 tion. Our modelling methods, which we document in-depth and make freely available (Breen and Deffner,
128 2022), can now be comparatively applied, establishing a novel analytical approach for much-needed (Goumas
129 et al., 2020; Lee and Thornton, 2021; Pirotta et al., 2018; Tuomainen and Candolin, 2011; Breen et al., 2021;
130 Breen, 2021; Deffner et al., 2021) constructive cross-taxonomic study on candidate characteristics considered
131 demographic drivers of organismal geographic and/or phenotypic distributions.

132 Methods

133 Data

134 The current study used published (Logan et al., 2022; Logan, 2016) and unpublished (see Acknowledgements)
135 colour-reward reinforcement learning data from 32 male and 17 female grackles across three study sites that
136 differ in their range-expansion demographics; that is, belonging to a core, intermediate or edge population
137 (based on time-since-settlement population growth dynamics, as outlined in Chuang and Peterson 2016).
138 Specifically, we focused on colour-reward reinforcement learning data from the following populations: (i)
139 Tempe, Arizona (17 males and five females)—herein, the core population (estimated—by adding the average

140 time between first sighting and first breeding to the year first sighted—to be breeding since 1951; Wehtje 2003,
141 2004); (*ii*) Santa Barbara, California (four males and four females)—herein, the intermediate population
142 (known to be breeding since 1996; Lehman 2020); and (*iii*) Greater Sacramento, California (eleven males
143 and eight females)—herein, the edge population (known to be breeding since 2004; Hampton 2004). All
144 utilised data were collected with ethical approval. A full record of our collating and cleaning of these curated
145 data is available at our GitHub repository (Breen and Deffner, 2022).

146 *Experimental protocol*

147 A step-by-step description of the experimental protocol is reported elsewhere (e.g., Blaisdell et al., 2021). As
148 such, below we detail only the protocol for the colour-reward reinforcement learning tests that we analysed
149 herein.

150 *Colour-reward reinforcement learning tests*

151 The reinforcement learning tests consist of two experimental phases (Figure 1): (*i*) colour-reward learning
152 (that is, initial learning) and (*ii*) colour-reward reversal learning (that is, reversal learning). In both ex-
153 perimental phases, two different coloured tubes are used: for Santa Barbara grackles, gold and grey; for all
154 other grackles: light and dark grey. Each tube consists of an outer and inner diameter of 26 mm and 19 mm,
155 respectively; and each is mounted to two pieces of plywood attached at a right angle (entire apparatus: 50
156 mm wide × 50 mm tall × 67 mm deep); thus resulting in only one end of each coloured tube being accessible
157 (Figure 1).

158 In initial learning, grackles are required to learn that only one of the two coloured tubes contains a food
159 reward (e.g., dark grey; this colour-reward pairing is counterbalanced across grackles within each study site).
160 Specifically, the rewarded and unrewarded coloured tubes are placed—either on a table or on the floor—in
161 the centre of the aviary run (distance apart: table, 2 feet; floor, 3 feet), with the open tube-ends facing, and
162 perpendicular to, their respective aviary side-wall. Which coloured tube is placed on which side of the aviary
163 run (left or right) is pseudorandomised across trials. A trial begins at tube-placement, and ends when a
164 grackle has either made a tube-choice or the maximum trial time has elapsed (eight minutes). A tube-choice
165 is defined as a grackle bending down to examine the contents (or lack thereof) of a tube. If the chosen tube
166 contains food, the grackle is allowed to retrieve and eat the food, before both tubes are removed and the
167 rewarded coloured tube is rebaited out of sight (for the grackle). If a chosen tube does not contain food,
168 both tubes are immediately removed. Each grackle is given, first, up to three minutes to make a tube-choice
169 (after which a piece of food is placed equidistant between the tubes to entice participation); and then, if no
170 choice has been made, an additional five minutes maximum, before both tubes are removed. All trials are

171 recorded as either correct (choosing the rewarded colour tube), incorrect (choosing the unrewarded colour
172 tube), or incomplete (no choice made); and are presented in 10-trial blocks. To pass initial learning, a grackle
173 must make a correct choice in at least 17 out of the most recent 20 trials, with a minimum of eight and nine
174 correct choices across the last two blocks.

175 In the reversal learning, grackles are required to learn that the colour-reward pairing has been swapped;
176 that is, the previously unrewarded coloured tube (e.g., light grey) now contains a food reward. The protocol
177 for this second and final experimental phase is identical to that, described above, of initial learning.

178 *Statistical analyses*

179 We analysed, processed, and visually present our data using, respectively, the ‘rstan’ (Team, 2020), ‘rethink-
180 ing’ (McElreath, 2018), and ‘tidyverse’ (Wickham et al., 2019) packages in R (Team, 2021). We note our
181 reproducible code is available at our GitHub repository (Breen and Deffner, 2022). We further note all re-
182 ported (in the main text) posterior contrasts are 89% highest posterior density intervals (McElreath, 2018).
183 Finally, we note that our computational model, defined below, does not exclude cases—two males in the core,
184 and one male in the middle population—where a grackle was dropped (subjectively by experimenters due
185 to time constraints) early on from reversal learning: because individual-level ϕ and λ estimates can still be
186 generated irrespective of trial number; the certainty around the estimates will simply be wider (McElreath,
187 2018, Ch. 15). Our Poisson models, however, do exclude these three cases for our modelling of reversal
188 learning, to conserve estimation.

189 *Poisson models*

190 For our behavioural analyses, we used multi-level Bayesian Poisson regressions to quantify the effect(s) of
191 sex and learning phase (initial versus reversal) on grackles’ recorded: (i) number of trials to pass learning
192 criterion; and (ii) number of switches between tube-choice options; these models were performed at both
193 the population and across-population level, and accounted for individual differences among birds through
194 the inclusion of individual-specific varying (i.e., random) effects.

195 *Computational model*

196 We employed an adapted (from Deffner et al., 2020) multi-level Bayesian reinforcement learning model, to
197 examine the influence of sex on grackles’ initial and reversal reinforcement learning. Our computational
198 reinforcement learning model, defined below, allows us to link observed coloured tube-choices to latent
199 individual-level attraction updating, and to translate the influence of latent attractions (i.e., expected pay-
200 offs) into individual tube-choice probabilities; in other words, we can reverse engineer which values of our two

201 latent learning parameters—that is, the information-updating rate ϕ and the risk-sensitivity rate λ —most
 202 likely produce grackles' choice-behaviour by formulating our scientific model as a statistical model (McEl-
 203 reath, 2018, p. 537). Therefore, this computational method facilitates mechanistic insight into how multiple
 204 latent learning parameters simultaneously guide grackles' reinforcement learning—an analytical advantage
 205 over more traditional methods that omit mechanism and ignore equifinality (Kandler and Powell, 2018; Bar-
 206 rett, 2019). Our computational model consists of two main equations:

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

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

207 Equation 1 expresses how attraction A to choice-option i changes for an individual j across time ($t+1$) based
 208 on their prior attraction to that choice-option ($A_{i,j,t}$) plus their recently experienced choice reward-payoffs
 209 ($\pi_{i,j,t}$), whilst accounting for the weight given to incurred reward-payoffs ($\phi_{k,l}$). As $\phi_{k,l}$ increases in value, so,
 210 too, does the rate of individual-level attraction updating based on reward-payoffs; here then, $\phi_{k,l}$ represents
 211 the information-updating rate. We highlight that the k, l indexing (here and elsewhere) denotes that we
 212 estimate separate ϕ parameters for each population ($k = 1$ for core; $k = 2$ for middle; $k = 3$ for edge) and
 213 for each experimental treatment ($l = 1$ for females/initial, $l = 2$ for females/reversal; $l = 3$ for males/initial;
 214 $l = 4$ for males/reversal).

215 Equation 2 is a *softmax* function that expresses the probability P that choice-option i is selected in the
 216 next choice-round ($t+1$) as a function of the attractions A and the parameter $\lambda_{k,l}$, which governs how much
 217 relative differences in attraction scores guide individual choice-behaviour. In the reinforcement learning
 218 literature, the λ parameter is known by several names—for example, ‘inverse temperature’ or ‘exploration’
 219 (Sutton and Barto, 2018)—since the higher its value the more deterministic (less option-switching) the
 220 choice-behaviour of an individual becomes (note $\lambda = 0$ generates random choice). Following Chimento et al.
 221 (2021), we call λ the risk-sensitivity rate, where higher values of λ imply that agents are more sensitive to risk,
 222 seeking higher expected payoffs based on their prior experience, instead of randomly sampling alternative
 223 options.

224 From the above computational model, then, we generate inferences about the effect of sex on $\phi_{k,l}$ and
 225 $\lambda_{k,l}$ from at least 1000 effective samples of the posterior distribution, at both the population- and across-
 226 population-level. We note that our computational model also includes bird as a random effect (to account

227 for repeated measures within individuals); however, for clarity, this parameter is omitted from our equations
228 (but not our code—see Breen and Deffner 2022). Our computational model does not, on the other hand,
229 include trials where a grackle did not make a tube-choice, as this measure cannot clearly speak to individual
230 learning—for example, satiation rather than any learning of ‘appropriate’ colour tube-choice could be invoked
231 as an explanation in such cases. Indeed, there are, admittedly, a number of intrinsic and extrinsic factors
232 (e.g., temperament and temperature, respectively) that might bias grackles’ tube-choice behaviour, and, in
233 turn, the output from our computational model (Webster and Rutz, 2020). But the aim of computational
234 models is not to replicate the entire study system (Fogarty et al., 2022).

235 *Pre- and post-study computational model validation*

236 As detailed in-depth in our pre-registration (see *Supplementary material*), we used agent-based modelling
237 to validate our computational model prior to analysing our data. When simulating ‘new’ birds from the
238 estimated population of varying effects (see main text), we performed additional (affirming) post-study
239 validation checks of our computational approach—see Figure S3.

240 *Open materials*

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

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249 *Author contributions*

250 A.J.B. conceived of the study; collated, cleaned, and curated all target data; D.D. led model and simulation
251 building, with input from A.J.B.; A.J.B and D.D. contributed equally to data modelling and pre/post-study
252 simulations; A.J.B. prepared figures and tables, with input from D.D.; A.J.B. and D.D. annotated together
253 all open source material; A.J.B. wrote the manuscript, with constructive contributions and revisions by D.D.;
254 A.J.B. and D.D. agree over and approve the final draft of the manuscript.

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Supplementary material for
Range-expanding male birds buffer environmental change by strategising risk-sensitive learning

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This PDF includes:

Table S1 - S4 containing full model outputs

Figure S1 showing reinforcement learning speed by population and sex

Figure S2 showing reinforcement learning sampling by population and sex

Figure S3 showing post-study simulations further validating our computational model approach

Study pre-registration, including computational model validation

Table S1: Between and across-population total-trials-in-test Poisson regression model estimates and female-male contrasts with corresponding 89% highest-posterior density intervals in parentheses.

| Population | Speed | | | | | |
|------------|---------------------|---------------------|---------------------|----------------------|----------------------|----------------------|
| | Initial | | | Reversal | | |
| | Male | Female | Contrast | Male | Female | Contrast |
| Core | 42.19 (36.80-47.47) | 43.54 (33.82-52.62) | 1.34 (-9.72-11.87) | 69.06 (60.31-77.57) | 84.80 (67.33-101.88) | 15.75 (-3.85-34.64) |
| Middle | 30.90 (23.26-38.91) | 32.73 (24.42-40.75) | 1.83 (-10.11-13.16) | 83.57 (63.45-104.34) | 96.11 (75.33-119.22) | 12.54 (-18.20-42.85) |
| Edge | 37.09 (31.37-42.90) | 40.78 (33.26-47.80) | 3.69 (-5.79-13.16) | 68.13 (58.15-78.40) | 74.40 (62.04-87.00) | 6.27 (-10.18-22.44) |
| Across | 38.44 (34.75-42.26) | 39.48 (34.29-44.46) | 1.03 (-5.17-7.44) | 64.64 (58.35-70.52) | 82.47 (72.48-92.36) | 17.83 (6.39-29.95) |

Table S2: Between and across-population total-choice-option-switches-in-test Poisson regression model estimates and female-male contrasts with corresponding 89% highest-posterior density intervals in parentheses.

| Population | Sampling | | | | | |
|------------|---------------------|---------------------|--------------------|---------------------|---------------------|---------------------|
| | Initial | | | Reversal | | |
| | Male | Female | Contrast | Male | Female | Contrast |
| Core | 14.57 (11.59-17.51) | 17.54 (11.09-23.30) | 2.97 (-4.17-9.55) | 23.59 (18.71-28.20) | 37.22 (24.49-49.00) | 13.63 (-0.11-26.57) |
| Middle | 7.09 (3.97-10.25) | 7.02 (3.87-9.94) | -0.07 (-4.49-4.51) | 31.55 (18.92-43.89) | 44.32 (27.30-59.29) | 12.77 (-9.24-32.77) |
| Edge | 13.25 (9.79-16.65) | 14.68 (10.31-18.78) | 1.43 (-4.34-6.78) | 21.74 (16.35-26.98) | 27.96 (20.10-35.52) | 6.22 (-2.96-16.16) |
| Across | 13.88 (11.68-16.03) | 15.30 (12.16-18.39) | 1.42 (-2.59-5.18) | 22.84 (19.38-26.20) | 37.74 (30.35-44.80) | 14.90 (6.48-22.62) |

Table S3: Between and across-population computational model ϕ estimates and male-female contrasts. The information-updating rate ϕ values are posterior means with corresponding 89% highest-posterior density intervals in parentheses.

| Population | ϕ | | | | | |
|------------|------------------|------------------|--------------------|------------------|------------------|-------------------|
| | Initial | | | Reversal | | |
| | Male | Female | Contrast | Male | Female | Contrast |
| Core | 0.03 (0.01-0.05) | 0.05 (0.01-0.09) | -0.02 (-0.07-0.03) | 0.04 (0.02-0.05) | 0.04 (0.02-0.05) | 0.00 (-0.02-0.02) |
| Middle | 0.10 (0.01-0.17) | 0.09 (0.02-0.15) | 0.01 (-0.11-0.13) | 0.04 (0.02-0.06) | 0.04 (0.02-0.06) | 0.00 (-0.03-0.03) |
| Edge | 0.05 (0.02-0.08) | 0.07 (0.02-0.12) | -0.02 (-0.09-0.04) | 0.04 (0.02-0.05) | 0.04 (0.03-0.06) | 0.00 (-0.02-0.02) |
| Across | 0.02 (0.01-0.04) | 0.04 (0.02-0.06) | -0.01 (-0.04-0.01) | 0.03 (0.02-0.04) | 0.03 (0.02-0.04) | 0.00 (-0.01-0.01) |

Table S4: Between and across-population computational model λ estimates and male-female contrasts. The risk-sensitivity rate λ values are posterior means with corresponding 89% highest-posterior density intervals in parentheses.

| Population | λ | | | | | |
|------------|------------------|------------------|-------------------|------------------|------------------|-------------------|
| | Initial | | | Reversal | | |
| | Male | Female | Contrast | Male | Female | Contrast |
| Core | 4.54 (2.47-6.28) | 3.08 (1.37-4.78) | 1.47 (-1.20-4.57) | 4.64 (3.11-6.08) | 2.56 (1.31-3.75) | 2.08 (0.10-4.12) |
| Middle | 4.12 (1.56-6.53) | 3.74 (1.66-5.76) | 0.38 (-3.23-4.06) | 3.05 (1.58-4.38) | 2.01 (1.01-2.94) | 1.04 (-0.90-2.70) |
| Edge | 3.71 (1.77-5.52) | 2.36 (1.27-3.39) | 1.35 (-0.93-3.57) | 4.59 (2.75-6.12) | 3.66 (2.40-4.94) | 0.93 (-1.12-3.12) |
| Across | 5.87 (3.46-8.10) | 3.88 (2.17-5.55) | 1.99 (-0.88-5.18) | 5.42 (3.80-6.80) | 3.47 (2.18-5.55) | 1.95 (0.11-3.75) |

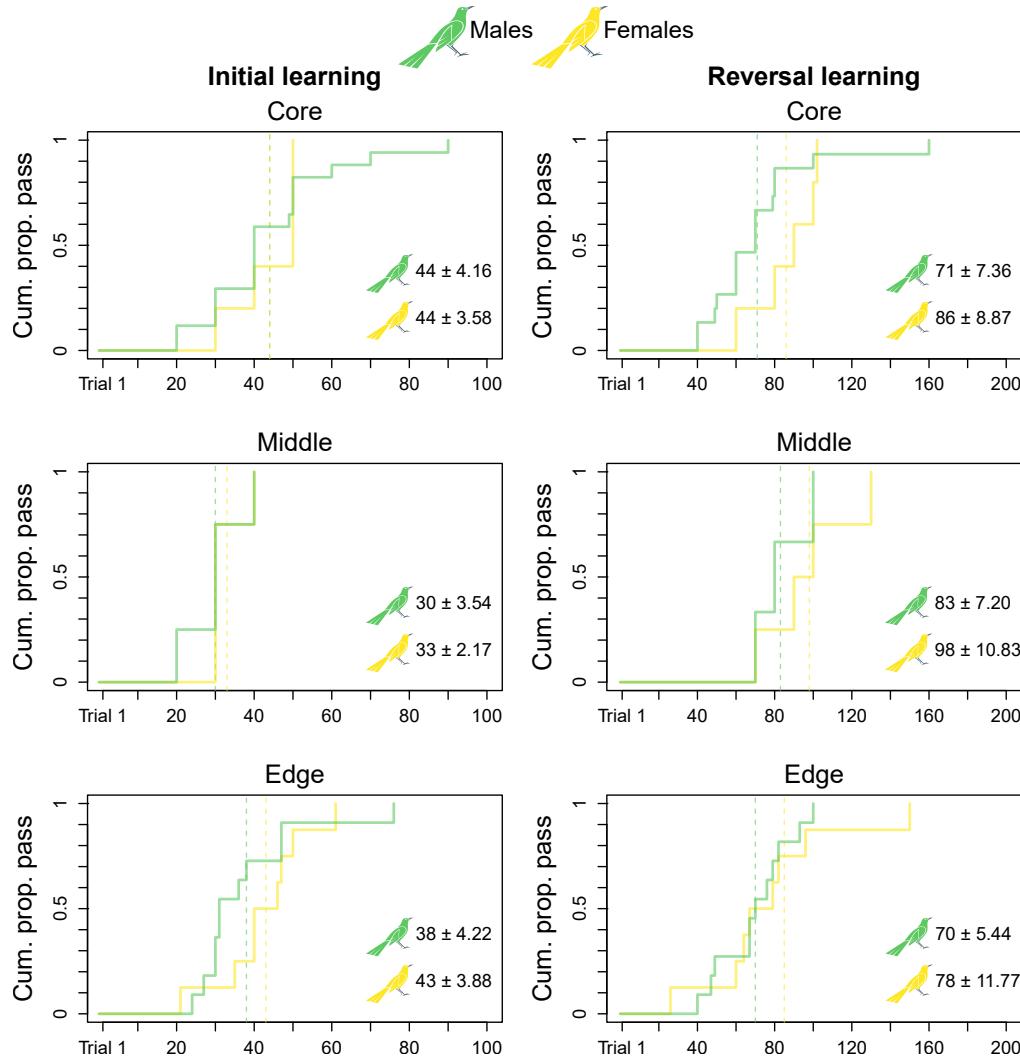


Figure S1: Reinforcement learning speed. The cumulative proportion of core-, middle-, and edge-inhabiting male and female grackles passing initial and reversal learning. For all plots: each ‘step’ represents a grackle passing their respective learning phase; the steeper the slope of the line the faster the finish; and means \pm standard errors are reported. Table S1 and S2 contain Poisson regression model estimates of these reinforcement learning dynamics.

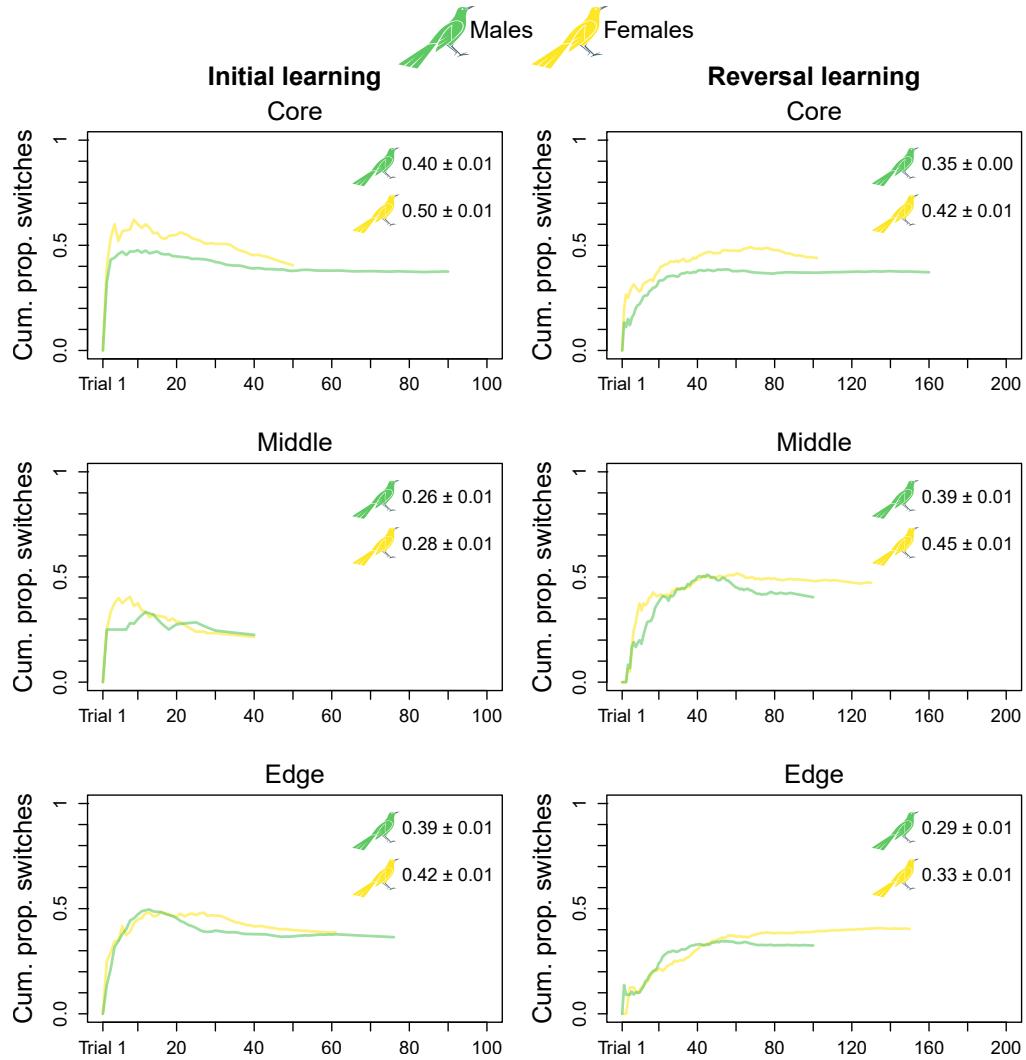


Figure S2: Reinforcement learning sampling. The cumulative proportion of choice-option switches between male and female grackles inhabiting a core, middle or edge population across initial and reversal learning. For all plots, means \pm standard errors are reported. Table S1 and S2 contain Poisson regression model estimates of these reinforcement learning dynamics.

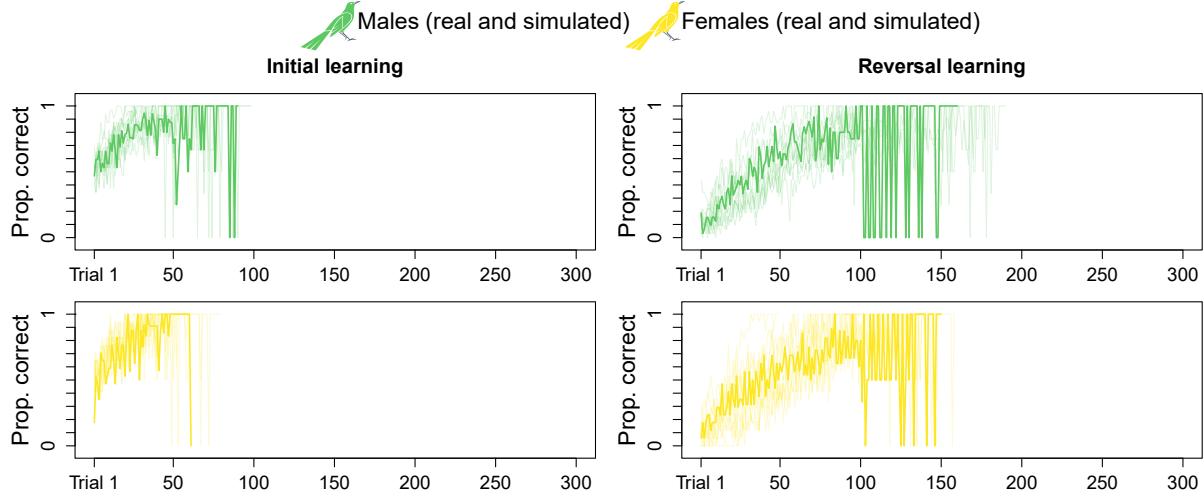


Figure S3: Post-study simulations. The proportion of correct (i.e., rewarded) choices per trial in initial and reversal reinforcement learning by male and female great-tailed grackles in the current study (thick/dark lines), compared to simulated—10 independent times—‘birds’ (thin/transparent lines). The degree of fluctuation across trials for both real and simulated learning trajectories is inversely related to the number of birds remaining in-test (i.e., fluctuation amount: few birds > many birds). Each simulation is matched for sample size to our full data set (males, $n = 32$; females, $n = 17$); and is generated from random draws of the estimated population of varying effects from our across-population computational model (full code available at our GitHub repository—see *Open materials*). That the 10 simulations for each sex and each learning phase reliably track real learning slopes—note ‘perfect’ tracking is not expected—provides post-study assurance for the validity of our computational approach (for pre-study validation checks, see our below pre-registration). Note the reversal learning trajectory sample size of real males is 29, as detailed in *Statistical analyses*.

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

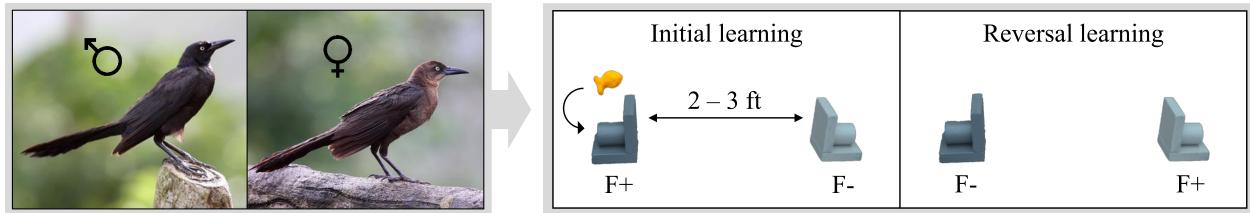
Dispersal and range expansion go ‘hand in hand’; movement by individuals away from a population’s core is a pivotal precondition of witnessed growth in species’ geographic limits (Chuang & Peterson, 2016; Ronce, 2007). Because ‘who’ disperses—in terms of sex—varies both within and across taxa (for example, 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.

61



62

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).

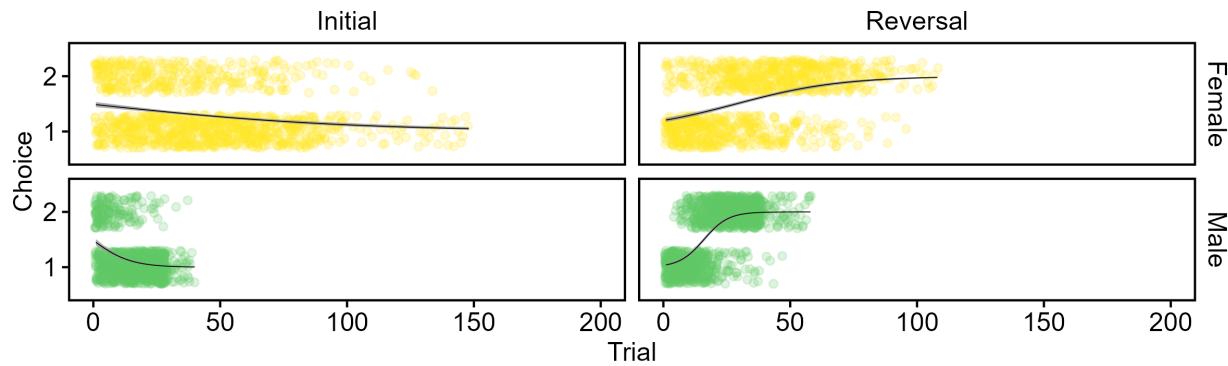
169 Equation 2 is a softmax function that expresses the probability (P) that option (i) is selected in the next
170 choice-round ($t + 1$) as a function of the attractions and a parameter ($\lambda_{k,l}$) that governs how much relative
171 differences in attraction scores guide individual choice-behaviour. 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 193 and 35 males from one of three populations (where population membership matched known study site sex 194 distributions)—across the described initial learning and reversal learning phases. The tube-choice behaviour 195 of the simulated great-tailed grackles was governed by a set of rules identical to those defined by our mathematical 196 equations—for example, coloured tube attractions were independently updated based on the reward 197 outcome of tube choices. Because we assigned higher average ϕ and λ values to simulated male (versus 198 female) great-tailed grackles, the resulting data set should show males outperform females on initial and 199 reversal learning, at both the group and individual-level; it did (Figure 2 & S1, respectively).

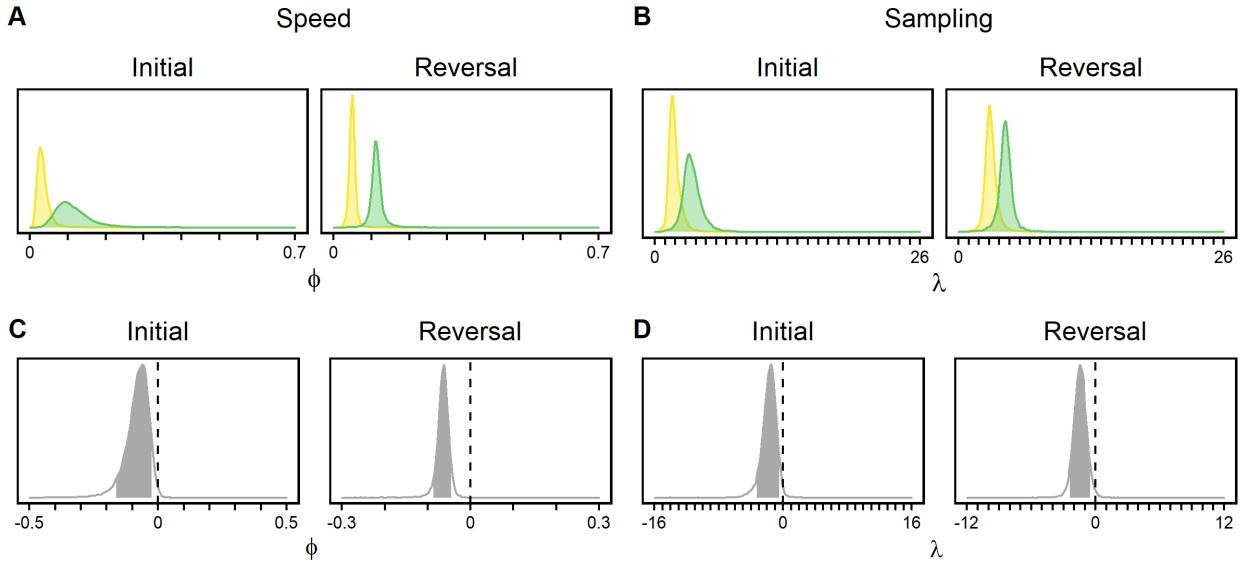


200 **Figure 2** Group-level tube-choice behaviour of simulated great-tailed grackles across colour-reward reinforcement learning trials (females: yellow, $n = 14$; males: green, $n = 35$), following model validation step 202 one. Tube option 1 (e.g., dark grey) was the rewarded option in the initial 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.

207 Next, we ran our simulated data set on our reinforcement learning model. Here, we endeavored to determine 208 whether our reinforcement learning model: (i) recovered our assigned $\phi_{k,l}$ and $\lambda_{k,l}$ values (it did; Table 1); 209 and (ii) produced ‘correct’ qualitative inferences—that is, detected the simulated sex differences in great- 210 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.

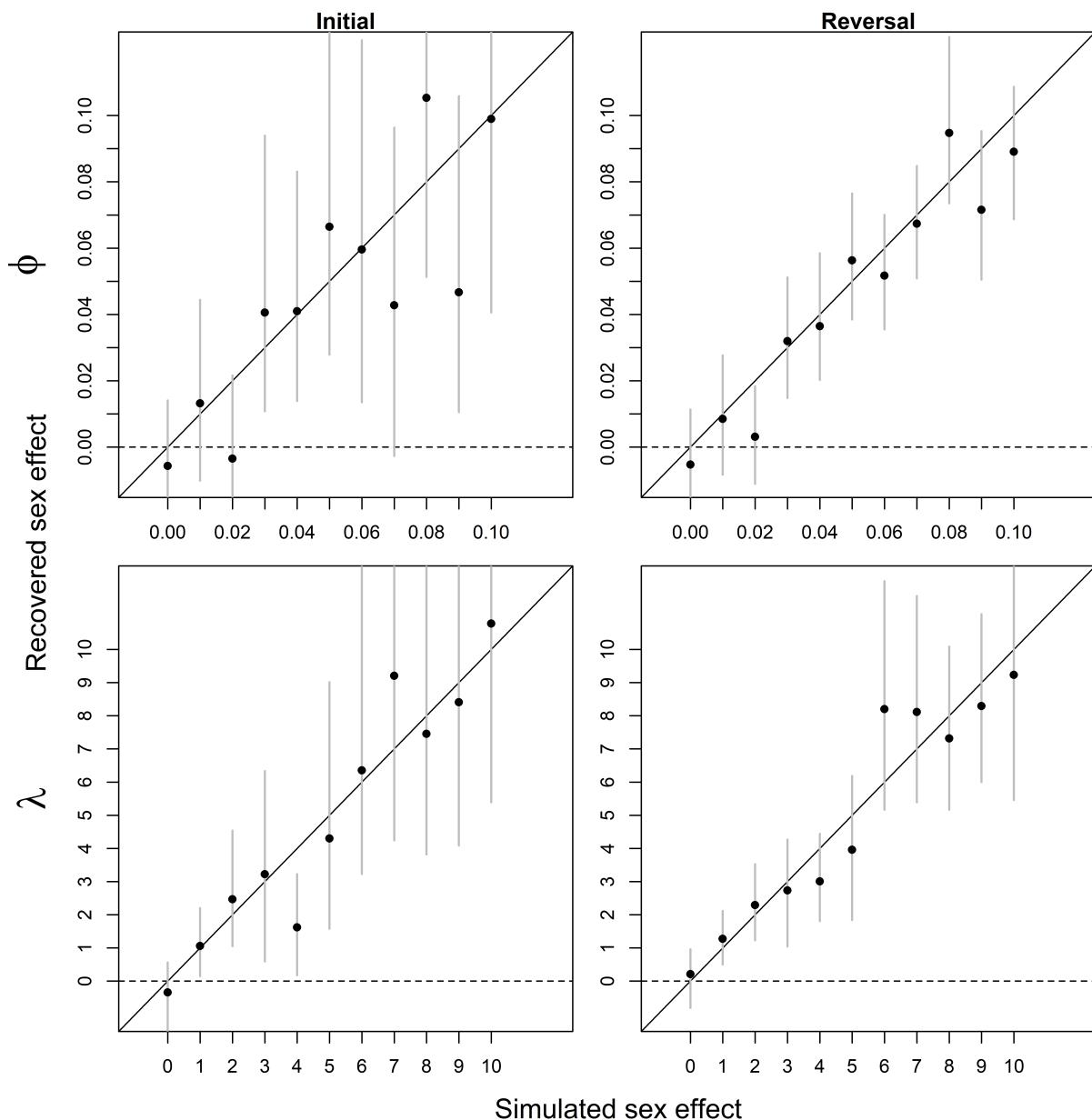
| | ϕ | | | | λ | | | |
|-----------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | Female | | Male | | Female | | Male | |
| | Initial | Reversal | Initial | Reversal | Initial | Reversal | Initial | Reversal |
| Assigned | 0.03 | 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**

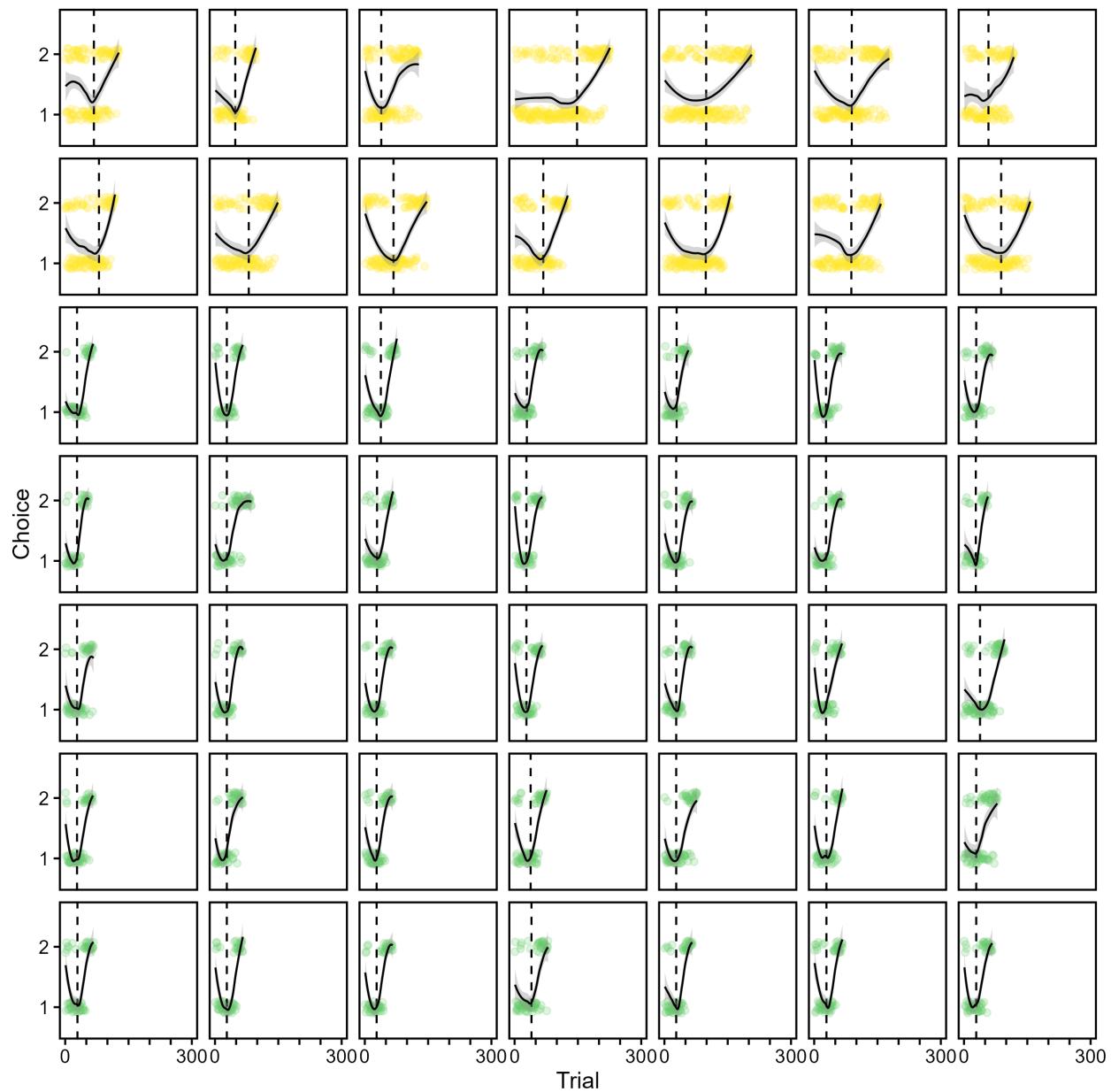
249 All data utilised herein were collected with ethical approval.

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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.