

Investigating sex differences in learning in a range-expanding bird

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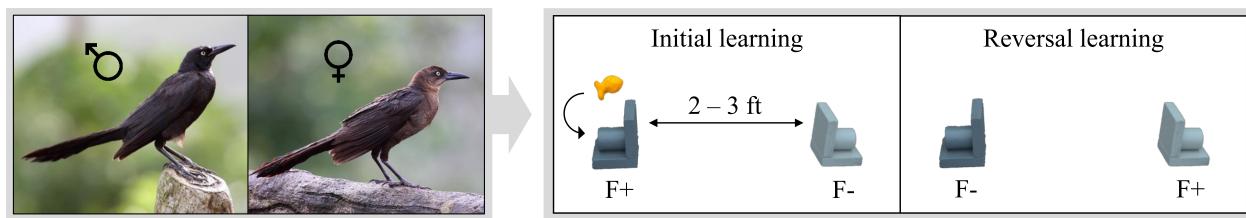
Abstract

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’; individuals must move away from a population’s core to catalyse growth in their species’ geographic distribution (Ronce 2007; Chuang and Peterson 2016). 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 and 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 (Wright et al. 2010; Sol et al. 2013). Indeed, a growing number of studies show support for this supposition (as recently reviewed in Lee and 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 and Thaker 2019), suggesting that range expansion selects for enhanced learning ability at the dispersal and/or settlement stage(s). Given the influence of sex-biased dispersal and learning ability on range expansion, it is perhaps surprising, then, that their potential joint impact on this aspect of movement ecology remains unexamined, particularly as links between dispersal and other behavioural traits such as aggression are documented within the range expansion literature (Duckworth 2006; Gutowsky and Fox 2011).

40 That learning ability can covary with, for example, exploration (e.g., Auersperg et al. 2011; Guillette et al.
 41 2011) and neophobia (e.g., Verbeek et al. 1994), two behaviours which may likewise play a role in range
 42 expansion (Griffin et al. 2017; Lee and Thornton 2021), is one potential reason for the knowledge gap
 43 introduced above. Such correlations stand to mask what contribution, if any, learning ability lends to range
 44 expansion—an undoubtedly daunting research prospect. In range-expanding great-tailed grackles (*Quiscalus*
 45 *mexicanus*), however, learning ability appears to represent a unique source of individual variation; more
 46 specifically, temporarily-captive great-tailed grackles' speed to solve colour-reward reinforcement learning
 47 tests does not correlate with measures of their exploration (time spent moving within a novel environment),
 48 inhibition (time to reverse a colour-reward preference), motor diversity (number of distinct bill and/or feet
 49 movements used in behavioural tests), neophobia (latency to approach a novel object), risk aversion (time
 50 spent stationary within a 'safe spot' in a novel environment), persistence (number of attempts to engage in
 51 behavioural tests), or problem solving (number of test-relevant functional and non-functional object-choices;
 52 Logan 2016a; Logan 2016b). Thus, great-tailed grackles offer behavioural ecologists a useful study
 53 system to investigate the interplay between life-history strategies, learning ability, and range expansion.
 54



55 **Figure 1** Left panel: images showing a male and female great-tailed grackle (credit: Wikimedia Commons).
 56 Right panel: schematic of the colour-reward reinforcement learning experimental protocol. In the *initial*
 57 *learning* phase, grackles are presented with two colour-distinct tubes; however, only one coloured tube
 58 (e.g., dark grey) contains a food reward (F+ versus F-). In the *reversal learning* phase, the colour-reward
 59 tube-pairings are swapped. The passing criterion was identical in both phases (see main text for details).
 60

61 Here, we propose to investigate potential differences in colour-reward reinforcement learning performance
 62 between male and female great-tailed grackles (Figure 1), to test the hypothesis that sex differences in learning
 63 ability are related to sex differences in dispersal. Since the late nineteenth century, great-tailed grackles have
 64 been expanding their range at an unprecedented rate, moving northward from Central America into the
 65 United States (breeding in at least 20 states), with several first-sightings spanning as far north as Canada
 66 (Dinsmore and Dinsmore 1993; Wehtje 2003). Notably, the record of this range expansion in great-tailed
 67 grackles is heavily peppered with first-sightings involving a single or multiple male(s) (Kingery 1972; Stepney
 68 1975; Littlefield 1983; Dinsmore and Dinsmore 1993; Wehtje 2003). Moreover, recent genetic data show that,
 69 when comparing great-tailed grackles within a population, average relatedness: (i) is higher among females
 70 than among males; and (ii) decreases with increasing spatial proximity among females; but (iii) increases with
 71 increasing spatial proximity among males; hence, confirming a role for male-biased dispersal in great-tailed
 72 grackles (Sevchik et al.). Considering these natural history and genetic data, then, we expect male and female
 73 great-tailed grackles to differ across at least two colour-reward reinforcement learning parameters: speed
 74 and sampling rate (here, sampling is defined as switching between choice-options). Specifically, we expect
 75 male—versus female—great-tailed grackles: (prediction 1 & 2) to be faster to, firstly, learn a novel colour-
 76 reward pairing, and secondly, reverse their colour preference when the colour-reward pairing is swapped;
 77 and (prediction 3) to be more deterministic—that is, sample less often—in their colour-reward learning;
 78 if learning ability and dispersal relate. Indeed, since invading great-tailed grackles face agribusiness-led
 79 wildlife management strategies, including the use of chemical crop repellents (Werner et al. 2011; Werner
 80 et al. 2015), natural selection should disfavour slow, error-prone learning strategies in great-tailed grackle
 81 range expansion.
 82

83 **Methods**

84 **Data**

85 This pre-registration aims to use colour-reward reinforcement learning data collected (or being collected) in
86 great-tailed grackles across three study sites: (*i*) Santa Barbara, California (breeding since: 1996; Lehman
87 2020) (*ii*) Tempe, Arizona (estimated—by adding the average time between first sighting and first breeding to
88 the year first sighted—to be breeding since: 1951; Wehtje 2003; Walter 2004); and (*iii*) Woodland, California
89 (breeding since: 2004; Hampton 2001). Specifically, data collection at both the Santa Barbara, California and
90 Tempe, Arizona study sites has been completed prior to the submission of this pre-registration (total sample
91 size across sites: nine females and 25 males); however, data collection at the Woodland, California study site
92 is ongoing (current sample size: three females and nine males; anticipated minimum total sample size: five
93 females and ten males). Thus, the final data set should contain colour-reward reinforcement learning data
94 from at least 14 female and 35 male great-tailed grackles.

95 **Experimental protocol**

96 *General*

97 A step-by-step description of the experimental protocol is reported elsewhere (Logan 2016a; Logan 2016b;
98 Logan et al.). As such, below we detail only the protocol for the colour-reward reinforcement learning tests
99 that we propose to analyse herein.

100 *Colour-reward reinforcement learning tests*

101 The reinforcement learning tests consist of two phases (Figure 1, right panel): (*i*) colour-reward learning
102 (hereafter, initial learning) and (*ii*) colour-reward reversal learning (hereafter, reversal learning). In both
103 phases, two different coloured tubes are used (for Santa Barbara grackles: gold and grey; Logan 2016b;
104 Logan 2016a; for all other grackles: light and dark grey; Logan et al.), each measuring an outer and inner
105 diameter of 26 mm and 19 mm, respectively; and each being mounted to two pieces of plywood attached at
106 a right angle (entire apparatus: 50 mm wide × 50 mm tall × 67 mm deep); thus resulting in only one end
107 of each coloured tube being accessible (Figure 1, right panel).

108 In the *initial learning phase*, grackles are required to learn that only one of the two coloured tubes contains
109 a food reward (e.g., dark grey; this colour-reward pairing is counterbalanced across grackles within each
110 study site). Specifically, the rewarded and unrewarded coloured tubes are placed—either on a table or on
111 the floor—in the centre of the aviary run (distance apart: table, 2 ft; floor, 3 ft), with the open tube-ends
112 facing, and perpendicular to, their respective aviary side-wall. Which coloured tube is placed on which side
113 of the aviary run (left or right) is pseudorandomised across trials. A trial begins at tube-placement, and
114 ends when a grackle has either made a tube-choice or the maximum trial time has elapsed (eight minutes).
115 A tube-choice is defined as a grackle bending down to examine the contents (or lack thereof) of a tube. If the
116 chosen tube contains food, the grackle is allowed to retrieve and eat the food, before both tubes are removed
117 and the rewarded coloured tube is rebaited out of sight (for the grackle). If a chosen tube does not contain
118 food, both tubes are immediately removed. Each grackle is given, first, up to three minutes to make a
119 tube-choice (after which a piece of food is placed equidistant between the tubes to entice participation); and
120 then, if no choice has been made, an additional five minutes maximum, before both tubes are removed. All
121 trials are recorded as either correct (choosing the rewarded colour tube), incorrect (choosing the unrewarded
122 colour tube), or incomplete (no choice made); and are presented in 10-trial blocks. To pass initial learning,
123 a grackle must make a correct choice in at least 17 out of the most recent 20 trials, with a minimum of eight
124 and nine correct choices across the last two blocks.

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

128 **Analysis plan**

129 *General*

¹³⁰ Here, we will analyse and visually present our data using, respectively, the ‘rethinking’ (McElreath 2018)
¹³¹ and ‘ggplot2’ (Wickham 2016) packages in R (Team 2021). Our reproducible code is available on GitHub
¹³² (<https://github.com/alexisbreen/Sex-differences-in-grackles-learning>).

¹³³ *Reinforcement learning model*

¹³⁴ In this pre-registration, we propose to employ an adapted (from Deffner et al. 2020) Bayesian reinforce-
¹³⁵ ment learning model, to examine the influence of sex on grackles’ initial and reversal learning performance.
¹³⁶ The reinforcement learning model, defined below, allows us to link observed coloured tube-choices to latent
¹³⁷ individual-level knowledge-updating (of attractions towards, learning about, and sampling of, either coloured
¹³⁸ tube) based on recent tube-choice reward-payoffs, and to translate such latent knowledge-updating into indi-
¹³⁹ vidual tube-choice probabilities; in other words, we can reverse engineer the probability that our parameters
¹⁴⁰ of interest (speed and sampling rate) produce grackles’ observed tube-choice behaviour by formulating our
¹⁴¹ scientific model as a statistical model (McElreath 2018: 537). This method can therefore capture whether,
¹⁴² and, if so, how multiple latent learning strategies simultaneously guide grackles’ decision making—an ana-
¹⁴³ lytical advantage over more traditional methods (e.g., comparing trials to passing criterion) that ignore the
¹⁴⁴ potential for equifinality (Kandler and Powell 2018; Barrett 2019).

¹⁴⁵ Our reinforcement learning model consists of two equations:

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

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

¹⁴⁶ Equation 1 expresses how attraction (A) to a choice-option (i) changes for an individual (j) across time
¹⁴⁷ ($t + 1$) based on their prior attraction to that choice-option ($A_{i,j,t}$) plus their recently experienced choice-
¹⁴⁸ payoff ($\pi_{i,j,t}$), whilst accounting for the weight given to recent payoffs ($\varphi_{k,l}$). As $\varphi_{k,l}$ increases in value,
¹⁴⁹ so, too, does the rate of individual attraction-updating; thus, $\varphi_{k,l}$ represents the individual learning rate.
¹⁵⁰ We highlight that the k, l indexing denotes that we estimate separate φ parameters for each phase of the
¹⁵¹ experiment ($k = 1$ for initial, $k = 2$ for reversal) and each sex ($l = 1$ for females, $l = 2$ for males).

¹⁵² Equation 2 is a softmax function that expresses the probability (P) that option (i) is selected in the next
¹⁵³ choice-round ($t + 1$) as a function of how much relative differences in attraction scores guide individual
¹⁵⁴ choice-behaviour ($\lambda_{k,l}$). The higher the value of $\lambda_{k,l}$, the more deterministic (less option-switching) the
¹⁵⁵ choice-behaviour of an individual becomes; thus, $\lambda_{k,l}$ represents the individual sampling rate for phase k and
¹⁵⁶ sex l .

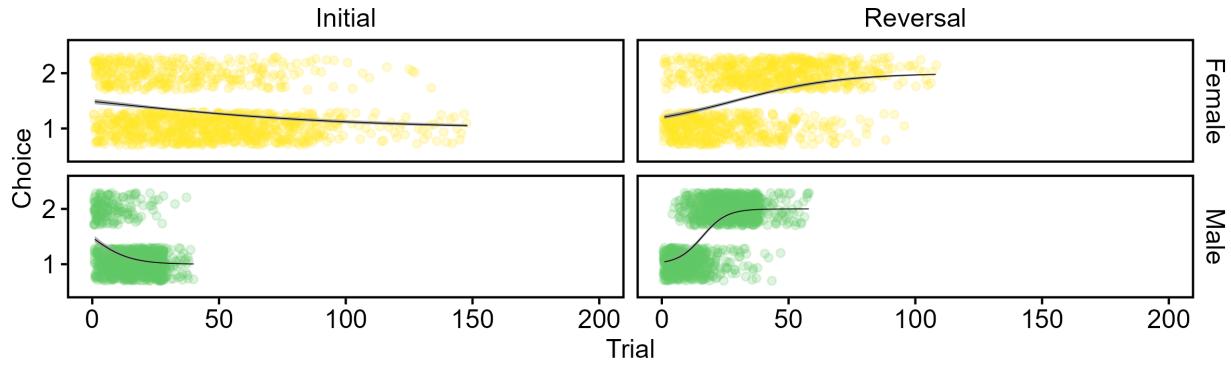
¹⁵⁷ From the above reinforcement learning model, then, we will generate inferences about the effect of sex on
¹⁵⁸ $\varphi_{k,l}$ and $\lambda_{k,l}$ from at least 1000 effective samples of the posterior distribution (see our model validation
¹⁵⁹ below). We note that our reinforcement learning model also includes both individual bird and study site
¹⁶⁰ as random effects (to account for repeated measures within both individuals and populations); however, for
¹⁶¹ clarity, 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 an
¹⁶² analytical extension, we may also explore population-mediated sex-effects on φ and λ , to test the hypothesis
¹⁶³ that such behavioural differences are more pronounced at range fronts (e.g., Duckworth 2006); if so, we will
¹⁶⁴ revise our Introduction accordingly.

¹⁶⁵ *Model validation*

¹⁶⁶ We validated our reinforcement learning model in two steps. First, we performed agent-based simulations.
¹⁶⁷ Specifically, we followed the tube-choice behaviour of simulated great-tailed grackles—that is, 14 females
¹⁶⁸ and 35 males from one of three populations (where population membership matched known study site sex
¹⁶⁹ distributions)—across the described initial learning and reversal learning phases. The tube-choice behaviour

171 of the simulated great-tailed grackles was governed by a set of rules identical to those defined by our mathematical equations—for example, coloured tube attractions were independently updated based on the reward outcome of tube choices. Because we assigned higher average φ and λ values to simulated male (versus female) great-tailed grackles, the resulting data set should show males outperform females on initial and reversal learning, at both the group and individual-level; it did (Figure 2 & S1, respectively).

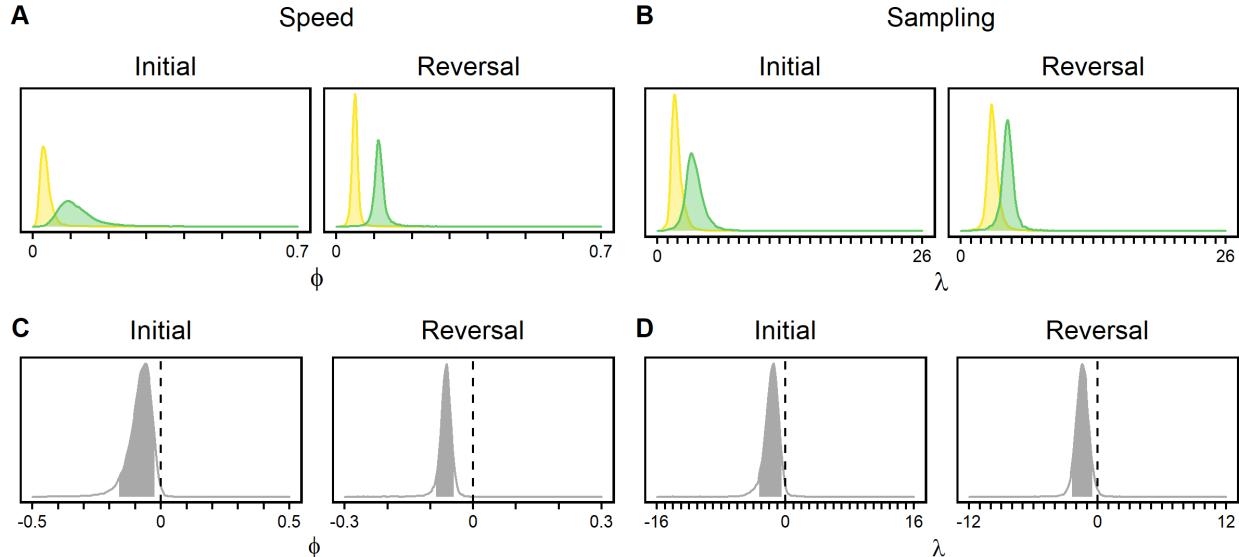
176 Next, we ran our simulated data set on our reinforcement learning model. Here, we endeavoured to determine if our reinforcement learning model: (i) recovered our assigned $\varphi_{k,l}$ and $\lambda_{k,l}$ values (it did; Table 1); and (ii) produced ‘correct’ qualitative inferences—that is, detected the simulated sex differences in grackles’ initial and reversal learning (it did; Figure 3). Our reinforcement learning model, then, is reasonably fit.



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

Table 1: Comparison of assigned and recovered φ and λ values. 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



186

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

193 Bias

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

198 Open materials

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

200 Acknowledgements

201 We thank all members, past and present, of the Grackle Project for collecting the data we propose to analyse
202 herein. We further thank Richard McElreath for research funding.

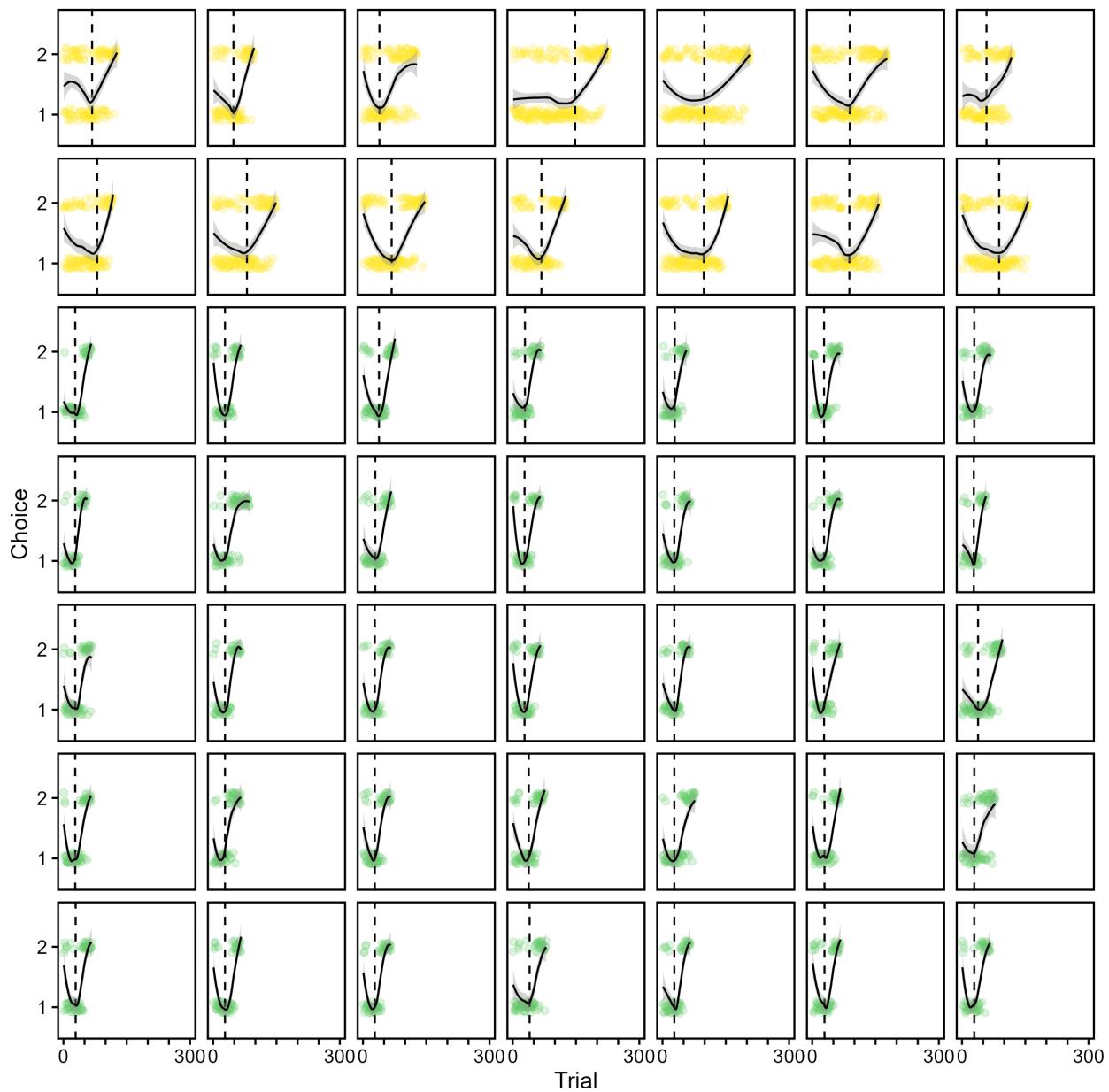
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277 **Supplementary material**



278

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