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Adjusting foraging strategies: a comparison of rural and urban common mynas

(*Acridotheres tristis*)

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Abstract Establishment in urbanized environments is associated with changes in physiology, behaviour, and problem solving. We compared the speed of learning in urban and rural female common mynas, *Acridotheres tristis*, using a standard visual discrimination task followed by a reversal learning phase. We also examined how quickly each bird progressed through different stages of learning, including sampling and acquisition within both initial and reversal learning, and persistence following reversal. Based on their reliance on very different food resources, we expected urban mynas to learn and reversal learn more quickly but to sample new contingencies for proportionately longer before learning them. When quantified from first presentation to criterion achievement, urban mynas took more 20-trial blocks to learn the initial discrimination, as well as the reversed contingency, than rural mynas. More detailed analyses at the level of stage revealed that this was because urban mynas explored the novel cue-outcome contingencies for longer and, despite transitioning faster through subsequent acquisition, remained overall slower than rural females. Our findings draw attention to fine adjustments in learning strategies in response to urbanization and caution against interpreting the speed to learn a task as a reflection of cognitive ability.

Keywords Behavioural flexibility, reversal learning, discrimination learning, urbanisation, rural birds, Indian mynah

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1 **Introduction**

2 Conversion of natural habitats to cities is currently one of the fastest sources of global environmental
3 change. Life in urbanized environments is associated with changes in morphology, physiology and
4 behaviour of animals, which include effects such as altered body condition, modified communication
5 signals and changes in personality (e.g. Slabbekoorn and Peet 2003; Yeh and Price 2004; Partecke et
6 al. 2006; Yeh et al. 2007). These changes have been most often identified through comparisons of
7 urbanized and non-urbanised populations of the same species (Miranda et al. 2013).

8 It is now well established that urban environments are characterised by a substantial loss in
9 avian species richness, coupled with significant increases in avian biomass (Shochat 2004; Evans
10 2010). The ecological processes that underpin these paradoxical demographic alterations remain
11 unclear. While it has been suggested that greater predictability of urban food sources coupled with
12 lower predation pressure might be implicated (Shochat 2004; Anderies et al. 2007), empirical support
13 for these ideas remains scant and mixed (López-Flores et al. 2009; Bókony et al. 2010; Seress et al.
14 2011). In birds, increased predictability of urban food sources often makes reference to bird feeders
15 and food dumps (Oro et al. 2013). However, for those avian species that forage primarily on
16 anthropogenic waste found around fast food outlets, supermarkets, and school playgrounds, food
17 resources that come and go with the activity of humans, we suggest that food might constitute a more
18 variable resource than in natural habitats. Together with other proposed challenges associated with
19 feeding in cities, such as coping with novel foods and overcoming fear of humans to access those
20 foods, urban animals might well need to be more flexible in their foraging strategies than do animals
21 living in non-urban habitats.

22 Variation in behavioural flexibility in foraging has most often been measured using variation
23 in the frequency of anecdotal reports of novel feeding behaviours (reviewed by Lefebvre and Sol
24 2008; Lefebvre 2013) and variation in the propensity to solve novel foraging problems (reviewed by
25 Griffin and Guez 2014). Within these contexts, behavioural flexibility has often been viewed as the
26 phenotypical expression of a cognitive ability to adjust behaviour when ecological conditions change
27 (reviewed by Lefebvre and Sol 2008; Lefebvre 2013). Another means of measuring behavioural
28 flexibility experimentally, therefore, is discrimination reversal learning, a standard psychology

29 learning task used to measure the propensity to change behaviour when the environment changes
30 (Schusterman 1966; Gossette and Hood 1967; Gossette 1969; Gossette and Hombach 1969; Tebbich et
31 al. 2010; Guillette et al. 2011; Logan 2016). In the initial phase, an instrumental conditioning task is
32 presented, which requires the individual to choose a rewarded cue (CS+) over a non-rewarded one
33 (CS-). As soon as this discrimination has been acquired, the contingencies are then reversed. The
34 speed at which the new environmental contingency is acquired provides a proxy for an individual's
35 propensity to adjust behaviour to changes in the environment. Hence, discrimination reversal learning
36 tasks provide both a measure of initial acquisition speed (initial discrimination learning phase) and
37 behavioural adjustments in response to new environmental information (reversal phase), two key
38 components of behavioural flexibility. While the reversal-learning paradigm itself has been applied to
39 a broad range of taxa, it has only begun to be used more recently to explore behavioural flexibility in
40 an ecological context. Specifically, it is only recently that it has begun to be used to determine
41 whether populations that live in different environments differ in their propensity to respond to
42 previously learned contingencies (Guillette et al. 2011; Audet et al. 2015).

43 The common (Indian) myna (*Acridotheres tristis*; recently proposed to be reclassified as
44 *Sturnus tristis*, see Christidis and Boles 2008), a social, omnivorous songbird and close relative of
45 starlings, is native to Asia. Highly adaptable, the species was introduced to the Australian continent in
46 the late 19th century where mynas are primarily urbanized (Sol et al. 2012). Small populations of
47 mynas can, however, be found in rural areas (Martin 1996; McGiffin et al. 2013). The occurrence of
48 mynas in both urban and rural environments in Australia means that it is a useful species with which to
49 examine some of the predictions regarding the ways in which the cognitive abilities of urban birds
50 might be affected by life in human-dominated environments.

51 Mynas inhabiting areas with high concrete cover forage primarily on sealed surfaces (Crisp
52 and Lill 2006), where they rely upon anthropogenic waste found around fast food outlets,
53 supermarkets, and school playgrounds (Sol et al. 2012). Accordingly, these urban mynas respond to
54 human provisioning more readily than a range of other sympatric species (Sol et al. 2012). These
55 foraging habits contrast with those of mynas in their original native range where the species is
56 primarily a consumer of crop insects (Sengupta 1976). Foraging habits of urban mynas also contrast

57 with those of rural mynas in Australia. In the areas where the present study was conducted, rural
58 mynas, which are most often found in association with horses, typically forage on the insect larvae in
59 horse dung (Griffin pers. obs.). Whereas horse dung is consistently present all year round in horse stud
60 farms and riding schools, food sources in urban areas come and go with the activity of humans.
61 Therefore, we hypothesised that urban mynas might experience greater variability in food availability
62 than rural mynas. Under this assumption, we predicted that coping with such differences in food
63 variability might lead to differences in behavioural flexibility in the foraging context between urban
64 and rural mynas. This is the possibility we addressed in the present study.

65 We used a discrimination-reversal learning task to compare the behavioural flexibility of
66 urban and rural mynas. We compared trials to reach criterion on each of the two phases of the learning
67 task (initial learning, reversal learning) (Audet et al. 2015). If urban mynas deal with more variable
68 food resources, they should be faster to learn a task and faster to reverse the discrimination on that task
69 than would rural mynas. This is because greater variability should raise the value (and salience) of the
70 food (an unconditioned stimulus), a parameter well known to increase the speed of associative
71 learning (Pearce 1997).

72 Here, then, we examined in detail how the behaviour of each individual progressed during
73 initial learning from sampling of new environmental contingencies (i.e. equal levels of response to the
74 CS+ and CS-) to acquisition of the new environmental contingencies (i.e. greater responsiveness to the
75 CS+ than to the CS-), and then, following reversal, from persistence (i.e. maintaining a previously
76 correct response to an old CS+), to, once again, sampling and acquisition (Jones and Mishkin 1972;
77 note that different authors use different names for these three stages). Drawing upon a family of
78 theoretical models of associative learning, in which it is assumed that conditioned responding to a
79 predictor cue (e.g. light) only occurs when animals have accumulated enough evidence for a given CS-
80 US (unconditioned stimulus; e.g. food) contingency (Gallistel and Gibbon 2000; Gallistel and Gibbon
81 2001), we reasoned that the more an individual is accustomed to experiencing variable food sources
82 the more it might be inclined to accumulate evidence that a new predictive cue reliably signals food
83 before beginning to respond to it preferentially. We, therefore, predicted that urban birds should
84 sample cue contingencies for longer before shifting to acquisition during both initial learning and

85 reversal learning than should rural mynas. Put differently, given the different foraging habits of urban
86 and rural mynas, urban mynas should sample for proportionally longer than should rural ones.

87

88 **Methods**

89

90 *Subjects*

91

92 Subjects were 34 wild-caught common mynas. Rural mynas were captured in two different rural
93 locations (four traps in proximity of GPS locations -32.816429, 151.818322 and two traps around -
94 32.794276, 151.910855). Urban mynas were captured in three different urban locations across
95 Newcastle (in proximity of -32.906238, 151.735669; -32.902575, 151.690831; -32.892223,
96 151.729433, respectively), the second largest urban development in New South Wales, Australia.
97 Rural capture sites were located near and in horse farms, approximately 30 km from downtown
98 Newcastle, and surrounded by rural land. Urban sites were located in heavily-built, residential areas
99 with a high density of streets and/or close to shopping centres. We refer loosely to mynas from these
100 geographically distinct areas as ‘populations’ without any reference to whether they constitute
101 genetically isolated populations. Genetic connectivity between birds in these different areas is
102 currently under investigation, but its extent is not known at the current point in time.

103 Our sample of 34 birds included 17 females from urbanised areas and 8 males and 9 females
104 from rural areas. These 34 birds constituted a subset of a much larger sample of mynas ($N = 62$)
105 trapped to take part in an overarching project on urban-rural behavioural differences. Each of the 34
106 birds was caught using a hand-held net from within group aviaries containing the larger sample of
107 birds (separated by rural and urban origin). Although we intended the netting process to be random
108 with respect to sex (male and female mynas cannot be distinguished on the basis of plumage), for
109 some unknown reason, all the urban birds turned out to be female when they were dissected at a later
110 point in time. Following an exploratory data analysis, we elected to include females only in the study
111 (see *Data Analysis*).

112 Birds were captured using walk-in traps (1 x 1 m, 2 m high) specifically designed to trap this
113 species (Tidemann 2006) and baited with dog pellets. The bottom cage could be accessed from outside
114 through two openings. Birds could then enter the top cage could via the bottom cage through two one-
115 way channels. The top cage was equipped with an opaque roof, and its sides were covered in shade
116 cloth. Both cages contained several perches, dog pellets, a preferred food of mynas, and ad libitum
117 water. The design of the trap is based on the ethological observation that mynas are likely to fly up
118 through a small opening after they have picked up food from the ground (Tidemann 2006). Individuals
119 thus accumulate in the top cage where they continue to eat the available food and remain calm because
120 of their natural tendency to flock. The opaque roof and shaded sides help by providing birds with sun
121 protection and cover (see Griffin 2008). The trap was checked and emptied daily.

122 Upon capture, birds were transported to the Central Animal House at the University of
123 Newcastle, where they were measured, weighed and individually marked by plastic coloured leg
124 bands. They were then released into an outdoor group aviary (4.4 x 1.25 m, 2.25 m high) equipped
125 with perches, shelters and water baths and placed on a 10-day treatment for internal parasites
126 (coccidian). They were left undisturbed in order to allow them to acclimatize to captivity. Dog pellets
127 and water were available ad libitum. At the end of testing, mynas were returned to the flight aviaries to
128 take part in other ongoing studies in the lab. Because mynas are classified as a pest species in
129 Australia, it is illegal to release them back into the wild after capturing them. Hence, at the end of the
130 study, in accordance with the Australian and New Zealand Council for the Care of Animals in
131 Research and Training and the University of Newcastle Animal Care and Ethics Committee, birds
132 were euthanized using a CO₂ overdose (Reilly 2001) (for details, see Griffin 2008). They were then
133 sexed by post-mortem analysis of sexual organs. Procedures were conducted in line with the
134 University of Newcastle Animal Ethics Committee's protocol A-2011-154. No other licence is needed
135 to trap or hold mynas in Australia.

136

137 *Test apparatus*

138

139 For the discrimination reversal learning task, mynas were transferred to individual operant
140 conditioning cages (60 x 30 cm, 60 cm high) where they were housed for the duration of the
141 experiment. Conditioning cages were partially visually (birds could see each other, but not each
142 other's conditioning apparatus, when sitting on the top perch of their cage), but not acoustically,
143 separated from one another. Each cage was equipped with perches, a dripper bottle filled with water,
144 and a pecking key attached to a food hopper filled with dog pellets. The pellets could be accessed
145 when the hopper was engaged, e.g. after a correct response to the pecking key. The pecking key could
146 be backlit with either a white, blue or red light. A 'request' perch was located 15 cm in front of the
147 food hopper. When landing on the perch, the bird interrupted an infra-red beam and caused the
148 pecking key to light up. In this way, the bird self-initiated a trial (i.e. the presentation of one pecking
149 key). Equipment and stimulus presentations were controlled automatically by 'Med Associates PC-IV'
150 software program on a computer in an adjacent room, and the birds' performance was monitored
151 continuously by the computer-controlled software.

152

153 *Procedure*

154

155 Each bird underwent preliminary shaping before it transitioned to initial discrimination learning,
156 followed by reversal learning.

157

158 *Shaping* Following transfer to the cages, birds were left undisturbed for a minimum of two
159 days with food freely available from the food hopper so they could acclimatise to their new
160 surroundings and the location of food. Each bird then began a three-stage shaping procedure in which
161 it was gradually trained to use the request perch to activate the pecking key, as well as to peck the
162 backlit key to engage the food hopper and gain access to food. Each pecking key presentation
163 constituted a trial. Performance was calculated automatically at the end of each 20-trial block by the
164 control computer and the subject was provided automatically with ad libitum access to food when it
165 reached criterion. Mynas transitioned through these training stages at variable rates but due to technical

166 challenges (computer crashes, electrical interruptions, weekend breaks), training conditions were not
167 sufficiently standardized across birds to allow an analysis of learning rates during shaping.

168 During the first stage of shaping, each bird was trained to peck the pecking key using a
169 standard autoshaping procedure in which the pecking key was backlit with a white light for a period of
170 10 s before the feeder engaged for 5 s. In this situation, birds spontaneously began to peck the key.
171 During this stage of shaping, trials in which the feeder was activated automatically and trials on which
172 the bird had to peck the key to engage the feeder were intermixed with more of the former than the
173 latter.

174 Once the bird reliably pecked the pecking key (i.e., more than 70% of backlit key
175 presentations were pecked), it was moved to the second stage of shaping. Here, trials on which the
176 feeder was automatically activated following the pecking key presentation ceased, such that the bird
177 only gained access to the feeder if it pecked the backlit key.

178 During both previous stages, landing on the request perch activated the pecking key;
179 however, the pecking key was also presented in the absence of a perch landing. In the third and final
180 stage of shaping, the pecking key was no longer activated automatically, such that the bird had to land
181 on the request perch to activate it. Shaping was complete when the bird pecked the white backlit key
182 on 18 of 20 pecking key presentations on two consecutive 20-trial blocks. Once this criterion was met,
183 each bird was manually switched to Discrimination training (see below).

184 During the entire shaping procedure and all subsequent phases, a food-fail, safe check was in
185 place: If a bird failed to feed for 4 h, the feeder engaged and provided the bird with free access to food
186 for 8 h. In addition, each bird was weighed on a regular basis. If a bird lost more than 10 % of its ad
187 libitum food body weight (i.e. its weight when first moved from the group aviary into an instrumental
188 conditioning cage), it received free food until it regained the lost weight.

189

190 *Phase 1: Discrimination training* During this first phase of the learning task, birds were trained
191 on a red-blue colour discrimination task. The two colours are highly discriminable for various avian
192 species, such as budgerigars (*Melopsittacus undulates*), domestic chickens (*Gallus gallus*), Japanese
193 quail (*Coturnix japonica*), pigeons (*Columba livia*) and zebra finches (*Taeniopygia guttata*)

194 (Bowmaker et al. 1997). Each bird was allocated either blue or red as a CS+ and the second colour as a
195 CS-, and colour was counterbalanced within and across rural and urban birds. Upon activation of the
196 request perch, the pecking key lit up with either the CS+ or the CS- colour. The CS+ and CS- order
197 was random but no more than two presentations of the same stimulus occurred in a row. Pecking the
198 CS+ was rewarded by a 5-s feeder presentation. In contrast, pecking the CS- resulted in the pecking
199 key switching off and the bird having to return to the perch to request another trial. CS+ and CS- were
200 presented for a maximum of 10 s. The frequency and total number of key presentations was entirely
201 under the bird's control as it depended entirely upon the frequency with which they used the request
202 perch. The control computer calculated performance automatically when a bird completed a block of
203 20 trials. As soon as a bird reached a criterion of 80% correct responses (pecking the CS+ and
204 withholding from pecking the CS-) on two consecutive blocks of 20 trials, the computer automatically
205 progressed the bird to the next phase (reversal learning).

206

207 *Phase 2: Reversal learning* At the start of this second phase of the learning task, the control
208 computer automatically reversed the predictive value of the CS+ and CS-. Now the birds needed to
209 learn to withhold from pecking the stimulus they had previously pecked and to peck the stimulus to
210 which they had previously withheld their pecking response. As in the initial discrimination phase,
211 performance in the reversal phase was calculated automatically by the computer at the end of each
212 block of 20 key presentations and the birds continued to undergo the task until they had reached a
213 criterion of 80% correct responses (pecking the new CS+ and withholding from pecking the new CS-)
214 on two consecutive blocks of 20 trials.

215

216 *Data analysis*

217

218 We recorded the number of correct responses for each of the 20-trial blocks until the bird reached
219 criterion on the initial CS+/CS- discrimination (initial learning), as well as on the reversed cue
220 contingencies (reversal learning). To test for an effect of sex on learning performance, we modelled
221 the number of correct responses of the rural sample alone using a GLMM with a Poisson error and a

222 log link, including sex as an explanatory variable and bird identity as a random factor. This model
223 revealed a marginal effect of sex on number of correct responses (mean (+/- SE) number of correct
224 responses: females: 14.87 +/- 0.30; males: 13.75 +/-0.29; $\chi^2(1) = 3.011$; $p = 0.083$). Hence, for all
225 further analyses, we used females only. Number of correct trials (out of 20) was modelled using a
226 Generalized Linear Mixed Model with a Poisson error structure and a log link function. Population
227 (urban, rural) was included as fixed explanatory variables, as well as phase (initial learning, reversal
228 learning) and block (1-25) as an ordered fixed explanatory variable. We capped the number of blocks
229 at 25 because blocks beyond this point (and up to a maximum of 74) had mostly very small sample
230 sizes (e.g. 1-3 birds). Sample sizes for each successive block are provided in Table S1. Furthermore,
231 including a factor with 74 levels lead to rank deficiency in the model. Bird identity was included in the
232 GLMM as a random factor.

233 To determine whether urban and rural birds differed in their allocation to persistence, sampling
234 and acquisition, each block of 20 trials was allocated to one of three behavioural patterns. Specifically,
235 we distinguished between blocks with primarily incorrect choices (0-5 correct choices out of 20), a
236 random distribution of correct and incorrect responses (6-14 correct choices out of 20) and blocks with
237 predominantly correct choices (15-20 correct choices out of 20). These categories are linked to the
238 detection limit of a binomial test ($N = 20$ trials per block; 0-5 significantly less than 50%; 15-20
239 significantly more than 50%). In the context of reversal learning, blocks with primarily incorrect
240 responses (i.e. pecking the *previously* rewarded CS+) provided a measure of perseverance and were
241 referred to as ‘persistence’ blocks. Blocks with a random number of correct and incorrect responses
242 provided a measure of sampling of new (initial learning) and altered (reversal learning) cue-outcome
243 contingencies and were referred to as ‘sampling’ blocks. Finally, blocks with more correct responses
244 than incorrect responses provided a measure of acquisition of cue-outcome contingencies (during both
245 initial and reversal learning) and were referred to as ‘acquisition’ blocks.

246 For each bird and the initial learning phase, we calculated for each bird the ratio between the
247 number of sampling blocks and the total number of blocks to reach criterion. We repeated this
248 calculation for the reversal phase. That is, for each bird and the reversal learning phase, we calculated
249 the ratio between the number of sampling blocks and the total number of blocks to reach criterion.

250 Using ratios rather than absolute numbers of blocks allowed us to take into account that birds reached
251 criterion in different numbers of blocks. We repeated the same calculations for the acquisition blocks
252 to yield an acquisition ratio for each of the two phases of learning (initial learning, reversal learning)
253 for each myna.

254 We then fitted a MANOVA to the ratio data with population (urban, rural), phase (initial
255 learning, reversal learning), and the interaction between population and phase as explanatory
256 variables. The MANOVA allowed us to include both sampling ratios and acquisition ratios as
257 response variables reducing the likelihood of Type 1 errors. We included bird identity as a repeated
258 measure. We followed up the MANOVA with univariate repeated measures ANOVAs on each of the
259 two response variables. Although comparing the ratios of persistence blocks across populations would
260 have been theoretically interesting, the ratios of persistence, sampling and acquisition during reversal
261 sum to one. Hence, it would have been statistically incorrect to include this ratio in the multivariate
262 MANOVA along side the sampling and acquisition ratios. Hence, for this component of the reversal
263 learning curve, we only report means and confidence intervals for each of the populations.

264

265 **Results**

266

267 Figure 1 depicts the learning curves of rural and urban female mynas during initial and reversal
268 learning. The number of correct trials increased significantly across blocks (GLMM: $\chi^2(24) = 295.939$;
269 $p < 0.001$; Fig. 1). The GLMM also revealed a significant effect of phase whereby mynas displayed
270 lower numbers of correct trials during reversal learning than during initial learning ($\chi^2(1) = 63.940$; p
271 < 0.001 ; Fig. 1). Finally, across both phases, urban mynas showed significantly fewer correct trials
272 than rural mynas ($\chi^2(1) = 6.543$; $p < 0.011$; Fig. 1). The interaction between population and phase was
273 non significant ($\chi^2(1) = 0.064$; $p < 0.801$; Fig. 1).

274

275

----- Insert Figure 1 -----

276

277 A multivariate MANOVA model fitted to the ratios of sampling and acquisition blocks revealed
278 a significant effect of population ($F(2,47) = 3.440, p = 0.040$) and a highly significant effect of phase
279 ($F(2,47) = 11.303, p < 0.001$). The interaction between population and phase was non significant
280 ($F(2,47) = 0.608, p = 0.549$). These effects were followed up using two repeated measures ANOVAs,
281 one for each response variable. Significant effects are depicted in Figure 2. Urban female mynas
282 allocated proportionally more blocks to sampling than rural birds ($F(1,48) = 6.538, p = 0.014$; Fig. 2A)
283 and less blocks to acquisition than rural birds ($F(1,48) = 5.313, p = 0.026$; Fig. 2B). Across
284 populations, sampling during reversal learning was proportionally longer than sampling during initial
285 acquisition, but this effect fell just short of significance ($F(1,48) = 3.670, p = 0.061$; Fig. 2C). In
286 addition, acquisition was proportionally shorter during initial learning than during reversal learning
287 ($F(1,48) = 8.678, p = 0.005$; Fig. 2D). During reversal, rural mynas displayed an average of 7.1% (CI:
288 3.2-11.0%) persistence blocks, whereas urban birds displayed an average of 5.1% (CI: 2.8- 7.5%). In
289 absolute numbers of blocks, this corresponded to an average of 1.1 (CI: 0.3-1.8) persistence blocks for
290 rural birds and 1.1 (CI: 0.2-2.1) for urban birds.

291 ----- Insert Figure 2 -----
292

293

294 **Discussion**

295

296 Taking into account the potentially greater variability of food sources exploited by urban mynas
297 relative to rural mynas, we had expected urban mynas to learn a cue discrimination and a cue reversal
298 faster, but to sample cue-outcome contingencies for proportionally longer than would rural mynas.

299 Our comparative analysis of their learning performances showed that urban female mynas took more
300 20-trial blocks to reach criterion starting from first cue-outcome presentation than rural female mynas
301 across both the initial learning phase and the reversal learning phase of the task. Examining the
302 different stages of learning in detail revealed why urban mynas were overall slower: urban individuals
303 spent more time sampling the significance of new predictor cues (initial learning) and reversed
304 predictor cues (reversal learning) than did the rural individuals. Although urban individuals also then

305 acquired the significance of predictor cues significantly more quickly than rural birds, this faster
306 acquisition was not sufficient to compensate for their longer sampling. Hence, urban birds reached
307 criterion from first cue presentation more slowly than did rural birds in both learning phases of the
308 task. These results do not support the prediction that more variable food sources should raise the value
309 of food and lead to faster learning of cue-outcome contingencies in urban mynas. In contrast, they are
310 in line with our hypothesis that urban birds experience more variable food resources and should
311 therefore accumulate more evidence that novel predictor cues reliably predict the availability of food
312 before learning them.

313 Although our rural sample contained both male and female mynas, our urban sample
314 contained only females. For this reason, we focused our analysis of learning performance and
315 strategies on a comparison of urban and rural female mynas to avoid confounding sex and population
316 of origin. As a consequence, we cannot speak to whether similar behavioural differences in learning
317 and sampling occur in male mynas. In extensive previous work on problem solving, we have not found
318 any sex effects on performance (Griffin et al. 2013b; Griffin et al. 2014; Griffin and Diquelou 2015).
319 In a previous study on discrimination learning in mynas (Griffin et al. 2013a), we did not examine sex
320 effects as we were interested in cross-task correlations. In the present study, an exploratory analysis
321 with the smaller rural sample suggested that females tended to learn more quickly than did male
322 mynas. We can only speculate that male mynas would show the same behavioural differences between
323 urban and rural mynas in terms of their learning speeds and strategies relative to rural male mynas.
324 Given that both sexes exploit the same resources in their respective environments, it would seem
325 surprising that only females should adjust their foraging strategies.

326 Urban mynas sampled new cue-outcome contingencies for longer, but then transitioned
327 through the acquisition phase more quickly than did the rural mynas. Overall, these behavioural
328 patterns resulted in urban mynas taking more trials to learn when performance was measured from
329 first stimulus encounter to criterion achievement. Learning speed is one of the measures that is often
330 assumed to reflect the limits of an animal's cognitive ability. Accordingly, it is often used as an inter-
331 and intra-species comparative proxy (Galsworthy et al. 2005; Roth et al. 2010; Roth et al. 2012; Audet
332 et al. 2015). Within this framework, the slower overall learning of urban mynas might be interpreted

333 as a reduced learning ability, presumably linked to relaxed demands for experience-dependent
334 behavioural adjustments. The present findings suggest that caution is needed when interpreting
335 learning curves. It is possible that differences in overall learning speed reflect finer adjustments to the
336 dynamics of learning that arise as a consequence of conditions experienced by the animal in the past.
337 Alternatively, finer adjustments might occur despite a lack of overall differences. More generally, we
338 suggest that the use of learning speed as a measure of cognitive ability without consideration of the
339 types of strategies animals might employ given their past experiences and the conditions at test might
340 lead to erroneous conclusions (Girvan and Braithwaite 1998; Chittka et al. 2009; Ducatez et al. 2014).
341 As well established in basic associative learning research, there is not always a direct correspondence
342 between what animals know (their learning) and how they behave (their performance) (Pearce 1997).

343 Overall, neither urban nor rural mynas persisted for long immediately after cue reversal.
344 Indeed, many birds moved from perseverating with a previously successful response (systematically
345 pecking the previously rewarded CS+) to a sampling strategy (pecking both the new CS+ (previously
346 the CS-) and the old CS+ (now the CS-)) at approximately equal levels within the first 20 trials
347 following reversal (i.e. within the first block after cue reversal). This suggests that mynas can rapidly
348 adjust to new and altered cue contingencies and shift to sampling them when a change is detected.
349 Further, this tendency might be a characteristic of this highly successful ecological invader, which is
350 not influenced by urbanization.

351 Past research has indicated that within species differences in operant learning speed can arise
352 relatively independently from experience. Black-capped chickadees (*Parus atricapillus*) from
353 environments that undergo harsh winter environments learn a new foraging behaviour significantly
354 faster than birds from environments that undergo less harsh winters (Roth et al. 2010). A common
355 garden design provided robust evidence that this behavioural difference emerges relatively
356 independently from the environment in which the birds are raised. The genetic structure of urban and
357 rural populations of mynas is currently under investigation, but at the current time, the amount of
358 genetic flow between the populations is not known. In contrast to learning differences in black-capped
359 chickadees, we predict that changes in learning strategies are likely to emerge as a consequence of
360 experience-dependence exposure to different foraging conditions. Population specific, experience-

361 dependent shifts in behaviour are in line with the growing body of work demonstrating the
362 extraordinary behavioural flexibility of mynas (Griffin 2008; Dhimi and Nagle 2009; Griffin and
363 Boyce 2009; Feare 2010; Griffin and Haythorpe 2011; McGiffin et al. 2013) and the central role of
364 behavioural plasticity in adjustments to urban environments (Sol et al. 2013), and new environments
365 more generally (Sol et al. 2005; Sol et al. 2008; Mason et al. 2013).

366 In contrast to a lack of differences in learning in urban and rural Barbados bullfinches
367 (*Loxigilla barbadensis*) (Audet et al. 2015), we found both differences in overall learning speed and
368 differences in the dynamics of learning. Previous research in our lab has revealed faster problem
369 solvers in urban mynas relative to suburban mynas (Sol et al. 2011), as well as positive correlations
370 between problem solving and classical conditioning, where faster problem solvers also learn a colour
371 cue discrimination faster (Griffin et al. 2013a). Together, these findings lead to the prediction that
372 rural mynas should outperform urban mynas on problem solving. Future research will aim to test this
373 prediction.

374 We hypothesized that differences in overall learning speed and differences in the dynamics of
375 learning might arise as a consequence of exposure of the urban mynas to greater variability in food
376 resources. It is also possible, however, that such differences might arise as a consequence of
377 differences in fearfulness between urban and rural mynas. It is now well established that animals from
378 urbanised environments, including mynas, are more tolerant of nearby humans relative to individuals
379 from non urbanized environments (Møller 2008; McGiffin et al. 2013; Uchida et al. 2016; Vincze et
380 al. 2016). Although both groups of birds in our study experienced very similar conditions following
381 capture and during testing (capture, transport, housing, handling, daily cleaning, time held in captivity
382 prior to testing), a reasonable alternative hypothesis is that rural mynas are generally less accustomed
383 to humans and, as a consequence, sample new cue-outcome contingencies in stressful conditions less.
384 Determining whether such adjustments are specific to urbanization, or whether they occur more
385 generally under conditions in which animals have experienced resource variability and/or stressful
386 conditions, coupled with an experimental approach in which food variability and safety are
387 manipulated, will provide fruitful avenues for future research. Lastly, it is perhaps also possible that
388 rural mynas find colour cues easier to learn than urban mynas, perhaps due to more fruit in their diet,

389 and therefore sample for less long and learn colour-cue discriminations more quickly. Given that our
390 predictions relate to variability in where and when food is available in urban and rural environments,
391 comparing the ability of rural and urban mynas to learn about space and time more specifically, rather
392 than cue-outcome contingencies, will provide a very useful extension of the present hypotheses and
393 study outcomes.

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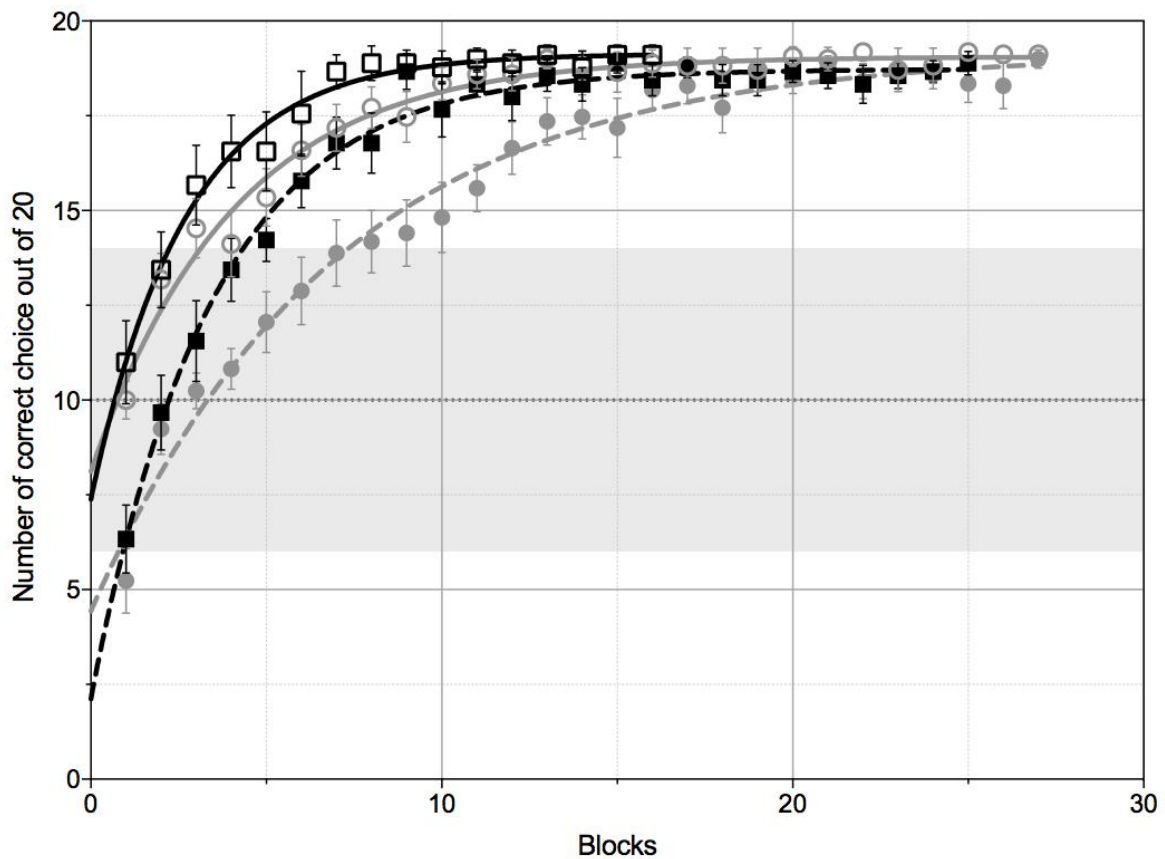
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503 **Figure 1. Initial (full lines) and reversal (dashed lines) learning curves of urban (grey) and rural**
504 **(black) female mynas.** The mean (± 1 SE) number of correct responses (peck at a CS+; withhold
505 from pecking a CS-) for each 20-trial block is depicted as a function of block number. As birds
506 progressed at different speeds through the task, sample sizes changed across blocks. The fitted curves
507 indicated in this figure assumed that birds that reached criterion would have maintained criterion
508 performance. Specifically, we artificially allocated criterion-level performances to early completers for
509 all post-criterion blocks including performances up to block 29 only. The functional form for curve
510 fitting is $y=a+b(1-\exp(-Kx))$ and the parameters specific to each curve (a, b and K) were obtained
511 using non linear curve fitting. Grey is the area of random choice. See text for more details.

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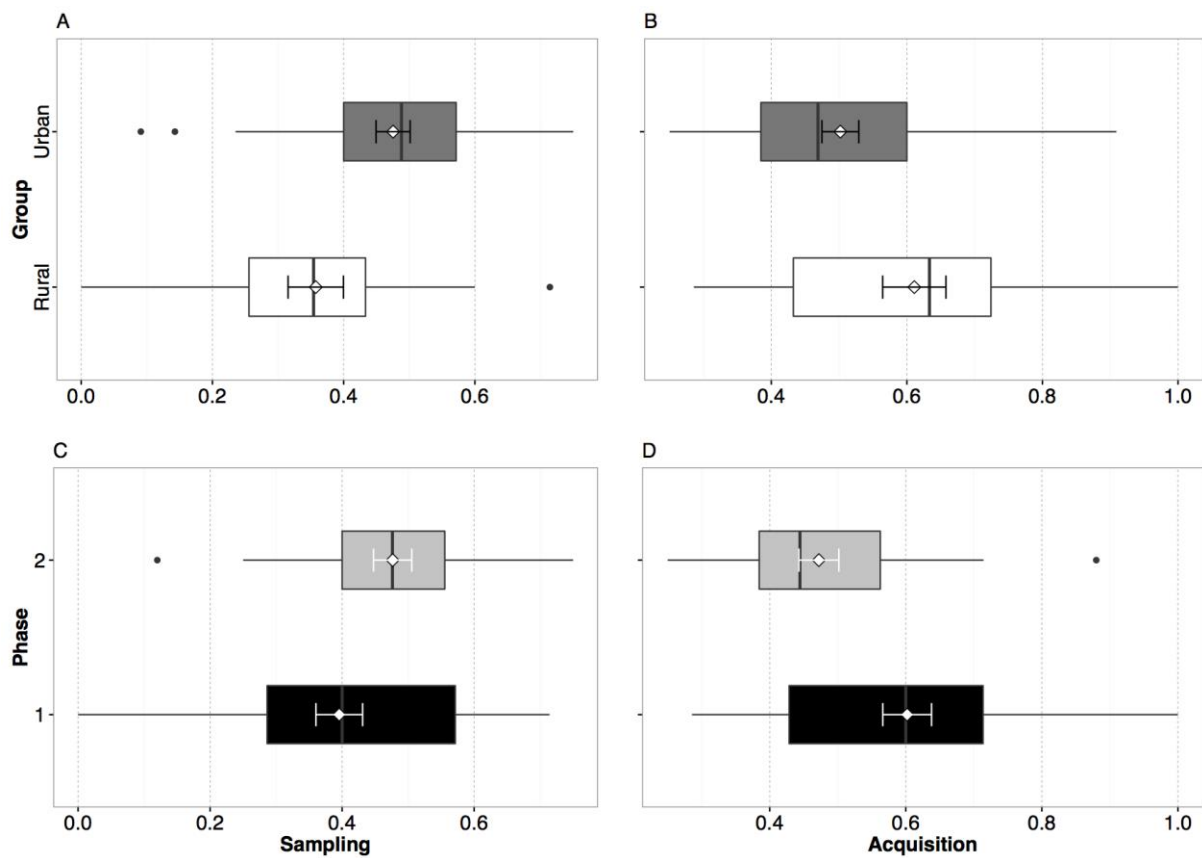
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515 **Figure 2. Population and phase effects on sampling and acquisition ratios.** Panel A depicts the
 516 effect of population (urban vs. rural) on mean proportion of sampling blocks, whereas panel B depicts
 517 the effect of population on the mean proportion of acquisition blocks. Panel C depicts the effect of
 518 phase (one/initial discrimination vs. two/reversal learning) on mean proportion of sampling blocks,
 519 while panel D depicts the effect of phase on the mean proportion of acquisition blocks. The mean (+/-
 520 1 SE) proportion of sampling (panels A and C) blocks is the proportion of 20-trial blocks with
 521 approximately 50% correct responses (6-14 correct choices out of 20). The mean (+/- 1 SE) proportion
 522 of acquisition blocks (panels B and D) is the proportion of 20-trial blocks with greater numbers of
 523 correct responses than incorrect responses (>14 correct responses out of 20). For more details, see text.

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