

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 myna

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Introduction

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

It is now well established that urban environments are characterized by a substantial loss in avian species richness, coupled with significant increases in avian biomass (Shochat 2004; Evans 2010). The ecological processes that underpin these paradoxical demographic alterations remain unclear. While it has been suggested that greater predictability of urban food sources coupled with lower

predation pressure might be implicated (Shochat 2004; Anderies et al. 2007), empirical support for these ideas remains scant and mixed (López-Flores et al. 2009; Bókony et al. 2010; Seress et al. 2011). In birds, increased predictability of urban food sources often makes reference to bird feeders and food dumps (Oro et al. 2013). However, for those avian species that forage primarily on anthropogenic waste found around fast food outlets, supermarkets, and school playgrounds, food resources that come and go with the activity of humans, we suggest that food might constitute a more variable resource than in natural habitats. Together with other proposed challenges associated with feeding in cities, such as coping with novel foods and overcoming fear of humans to access those foods, urban animals might well need to be more flexible in their foraging strategies than do animals living in non-urban habitats.

Variation in behavioural flexibility in foraging has most often been measured using variation in the frequency of anecdotal reports of novel feeding behaviours (reviewed by Lefebvre and Sol 2008; Lefebvre 2013) and variation in the propensity to solve novel foraging problems (reviewed by Griffin and Guez 2014). Within these contexts, behavioural flexibility has often been viewed as the phenotypical expression of a cognitive ability to adjust behaviour when ecological conditions change (reviewed by Lefebvre and Sol 2008; Lefebvre 2013). Another means of measuring behavioural flexibility experimentally, therefore, is discrimination-reversal learning, a standard psychology learning task used to measure the propensity to change behaviour when the environment changes (Schusterman 1966; Gossette and Hood 1967; Gossette 1969; Gossette and Hombach 1969; Tebbich et al. 2010; Guillette et al. 2011; Logan 2016). In the initial phase, an instrumental conditioning task is presented, which requires the individual to choose a rewarded cue (CS+) over a non-rewarded one (CS−). As soon as this discrimination has been acquired, the contingencies are then reversed. The speed at which the new environmental contingency is acquired provides a proxy for an individual's propensity to adjust behaviour to changes in the environment. Hence, discrimination-reversal learning tasks provide both a measure of initial acquisition speed (initial discrimination learning phase) and behavioural adjustments in response to new environmental information (reversal phase), two key components of behavioural flexibility. While the reversal learning paradigm itself has been applied to a broad range of taxa, it has only more recently begun to be used to explore behavioural flexibility in an ecological context. Specifically, it is only recently that it has begun to be used to determine whether populations that live in different environments differ in their propensity to respond to previously learned contingencies (Guillette et al. 2011; Griffin et al. 2013a; Audet et al. 2016).

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

Mynas inhabiting areas with high concrete cover forage primarily on sealed surfaces (Crisp and Lill 2006), where they rely upon anthropogenic waste found around fast food outlets, supermarkets, and school playgrounds (Sol et al. 2012). Accordingly, these urban mynas respond to human provisioning more readily than a range of other sympatric species (Sol et al. 2012). These foraging habits contrast with those of mynas in their original native range where the species is primarily a consumer of crop insects (Sengupta 1976). Foraging habits of urban mynas also contrast with those of rural mynas in Australia. In the areas where the present study was conducted, rural mynas, which are most often found in association with horses, typically forage on the insect larvae in horse dung (Griffin pers. obs.). Whereas horse dung is consistently present all year round in horse stud farms and riding schools, food sources in urban areas come and go with the activity of humans. Therefore, we hypothesized that urban mynas might experience greater variability in food availability than rural mynas. Under this assumption, we predicted that coping with such differences in food variability might lead to differences in behavioural flexibility in the foraging context between urban and rural mynas. This is the possibility we addressed in the present study.

We used a discrimination-reversal learning task to compare the behavioural flexibility of urban and rural mynas. We compared trials to reach criterion on each of the two phases of the learning task (initial learning, reversal learning) (Audet et al. 2016). If urban mynas deal with more variable food resources, they should be faster to learn a task and faster to reverse the discrimination on that task than would rural mynas. This is because greater variability should raise the value (and salience) of the food (an unconditioned stimulus), a parameter well known to increase the speed of associative learning (Pearce 1997).

Here, then, we examined in detail how the behaviour of each individual progressed during initial learning from sampling of new environmental contingencies (i.e. equal levels of response to the CS+ and CS−) to acquisition of the new environmental contingencies (i.e. greater responsiveness to the CS+ than to the CS−), and then, following

reversal, from persistence (i.e. maintaining a previously correct response to an old CS+), to, once again, sampling and acquisition (Jones and Mishkin 1972; note that different authors use different names for these three stages). Drawing upon a family of theoretical models of associative learning, in which it is assumed that conditioned responding to a predictor cue (e.g. light) only occurs when animals have accumulated enough evidence for a given CS– US (unconditioned stimulus; e.g. food) contingency (Gallistel and Gibbon 2000, 2001), we reasoned that the more an individual is accustomed to experiencing variable food sources, the more it might be inclined to accumulate evidence that a new predictive cue reliably signals food before beginning to respond to it preferentially. We, therefore, predicted that urban birds should sample cue contingencies for longer before shifting to acquisition during both initial learning and reversal learning than should rural mynas. Put differently, given the different foraging habits of urban and rural mynas, urban mynas should sample for proportionally longer than should rural ones.

Methods

Subjects

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

Our sample of 34 birds included 17 females from urbanized areas and eight males and nine females from rural areas. These 34 birds constituted a subset of a much larger sample of mynas ($N = 62$) trapped to take part in an overarching project on urban–rural behavioural

differences. Each of the 34 birds was caught using a hand-held net from within group aviaries containing the larger sample of birds (separated by rural and urban origin). Although we intended the netting process to be random with respect to sex (male and female mynas cannot be distinguished on the basis of plumage), for some unknown reason, all the urban birds turned out to be female when they were dissected at a later point in time. Following an exploratory data analysis, we elected to include females only in the study (see “Data Analysis”).

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

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

Test apparatus

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

Procedure

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

Shaping

Following transfer to the cages, birds were left undisturbed for a minimum of two days with food freely available from the food hopper, so they could acclimatize to their new surroundings and the location of food. Each bird then began a three-stage shaping procedure in which it was gradually trained to use the request perch to activate the pecking key, as well as to peck the backlit key to engage the food hopper and gain access to food. Each pecking key presentation constituted a trial. Performance was calculated automatically at the end of each 20-trial block by the control computer, and the subject was provided automatically with ad libitum access to food when it reached criterion. Mynas transitioned through these training stages at variable rates, but due to technical challenges (computer crashes, electrical interruptions, and weekend breaks), training conditions were not sufficiently standardized across birds to allow an analysis of learning rates during shaping.

During the first stage of shaping, each bird was trained to peck the pecking key using a standard autoshaping

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

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

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

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

Phase 1: discrimination training

During this first phase of the learning task, birds were trained on a red–blue colour discrimination task. The two colours are highly discriminable for various avian species, such as budgerigars (*Melopsittacus undulatus*), domestic chickens (*Gallus gallus*), Japanese quail (*Coturnix japonica*), pigeons (*Columba livia*), and zebra finches (*Taeniopygia guttata*) (Bowmaker et al. 1997). Each bird was allocated either blue or red as a CS+ and the second colour as a CS–, and colour was counterbalanced within and across rural and urban birds. Upon activation of the request perch, the pecking key lit up with either the CS+ or the CS– colour. The CS+ and CS– order was random, but no more than two presentations of the same stimulus occurred in a row. Pecking the CS+ was rewarded by a 5-s feeder presentation. In contrast, pecking the CS– resulted in the pecking key switching off and the bird having to return to the perch to request another trial. CS+ and CS– were presented for a maximum of 10 s. The frequency and total

number of key presentations were under the bird's control as it depended entirely upon the frequency with which they used the request perch. The control computer calculated performance automatically when a bird completed a block of 20 trials. As soon as a bird reached a criterion of 80 % correct responses (pecking the CS+ and withholding from pecking the CS-) on two consecutive blocks of 20 trials, the computer automatically progressed the bird to the next phase (reversal learning).

Phase 2: reversal learning

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

Data analysis

We recorded the number of correct responses for each of the 20-trial blocks until the bird reached criterion on the initial CS+/CS- discrimination (initial learning), as well as on the reversed cue contingencies (reversal learning). To test for an effect of sex on learning performance, we modelled the number of correct responses of the rural sample alone using a GLMM with a Poisson error and a log link, including sex as an explanatory variable and bird identity as a random factor. This model revealed a marginal effect of sex on number of correct responses (mean (\pm SE) number of correct responses: females: 14.87 ± 0.30 ; males: 13.75 ± 0.29 ; $\chi^2(1) = 3.011$; $P = 0.083$). Hence, given that we had no males in the urban sample, for all further analyses, we used females only. Number of correct trials (out of 20) was modelled using a Generalized Linear Mixed Model with a Poisson error structure and a log link function. Population (urban, rural) was included as a fixed explanatory variable, along with phase (initial learning, reversal learning) and block (1–25) as an ordered fixed explanatory variable. We capped the number of blocks at 25 because blocks beyond this point (and up to a maximum of 74) had mostly very small sample sizes (e.g. 1–3 birds). Sample sizes for each successive block are provided in Table S1. Furthermore, including a factor with 74 levels led to rank deficiency in the model. Bird identity was included in the GLMM as a random factor.

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

For each bird and the initial learning phase, we calculated for each bird the ratio between the number of sampling blocks and the total number of blocks to reach criterion. We repeated this calculation for the reversal phase. That is, for each bird and the reversal learning phase, we calculated the ratio between the number of sampling blocks and the total number of blocks to reach criterion. Using ratios rather than absolute numbers of blocks allowed us to take into account that birds reached criterion in different numbers of blocks. We repeated the same calculations for the acquisition blocks to yield an acquisition ratio for each of the two phases of learning (initial learning, reversal learning) for each myna.

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

Results

Figure 1 depicts the learning curves of rural and urban female mynas during initial and reversal learning. The number of correct trials increased significantly across blocks (GLMM: $\chi^2(24) = 295.939$; $P < 0.001$; Fig. 1). The GLMM also revealed a significant effect of phase whereby mynas displayed lower numbers of correct trials during reversal learning than during initial learning ($\chi^2(1) = 63.940$; $P < 0.001$; Fig. 1). Finally, across both phases, urban mynas showed significantly fewer correct trials than rural mynas ($\chi^2(1) = 6.543$; $P < 0.011$; Fig. 1). The interaction between population and phase was not significant ($\chi^2(1) = 0.064$; $P < 0.801$; Fig. 1).

A multivariate MANOVA model fitted to the ratios of sampling and acquisition blocks revealed a significant effect of population ($F(2,47) = 3.440$, $P = 0.040$) and a highly significant effect of phase ($F(2,47) = 11.303$, $P < 0.001$). The interaction between population and phase was not significant ($F(2,47) = 0.608$, $P = 0.549$). These effects were followed up using two repeated measures ANOVAs, one for each response variable. Significant effects are depicted in Fig. 2. Urban female mynas allocated proportionally more blocks to sampling than rural birds ($F(1,48) = 6.538$, $P = 0.014$; Fig. 2a) and fewer

blocks to acquisition than rural birds ($F(1,48) = 5.313$, $P = 0.026$; Fig. 2b). Across populations, sampling during reversal learning was proportionally longer than sampling during initial acquisition, but this effect fell just short of significance ($F(1,48) = 3.670$, $P = 0.061$; Fig. 2c). In addition, acquisition was proportionally shorter during initial learning than during reversal learning ($F(1,48) = 8.678$, $P = 0.005$; Fig. 2d). During reversal, rural mynas displayed an average of 7.1 % (CI 3.2–11.0 %) persistence blocks, whereas urban birds displayed an average of 5.1 % (CI 2.8–7.5 %). In absolute numbers of blocks, this corresponded to an average of 1.1 (CI 0.3–1.8) persistence blocks for rural birds and 1.1 (CI 0.2–2.1) for urban birds.

Discussion

Taking into account the potentially greater variability of food sources exploited by urban mynas relative to rural mynas, we had expected urban mynas to learn a cue discrimination and a cue reversal faster, but to sample cue-outcome contingencies for proportionally longer than would rural mynas. Our comparative analysis of their learning performances showed that urban female mynas

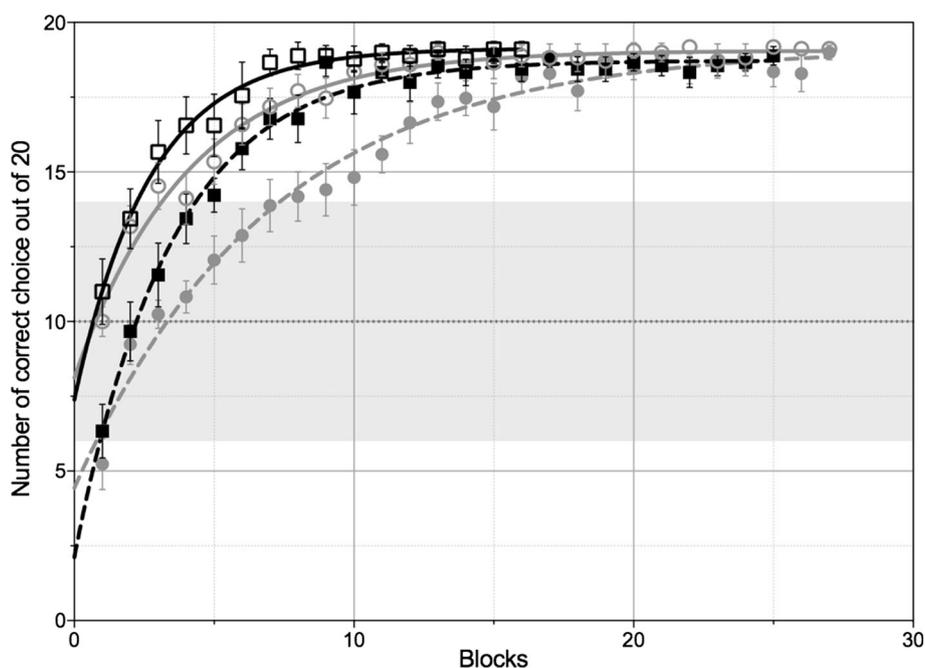


Fig. 1 Initial (full lines) and reversal (dashed lines) learning curves of urban (grey) and rural (black) female mynas. The mean (± 1 SE) number of correct responses (peck at a CS+; withhold from pecking a CS-) for each 20-trial block is depicted as a function of block number. As birds progressed at different speeds through the task, sample sizes changed across blocks. The fitted curves indicated in this figure assumed that birds that reached criterion would have

maintained criterion performance. Specifically, we artificially allocated criterion-level performances to early completers for all post-criterion blocks including performances up to block 29 only. The functional form for curve fitting is $y = a + b(1 - \exp(-Kx))$, and the parameters specific to each curve (a , b and K) were obtained using nonlinear curve fitting. Grey is the area of random choice. See text for more details

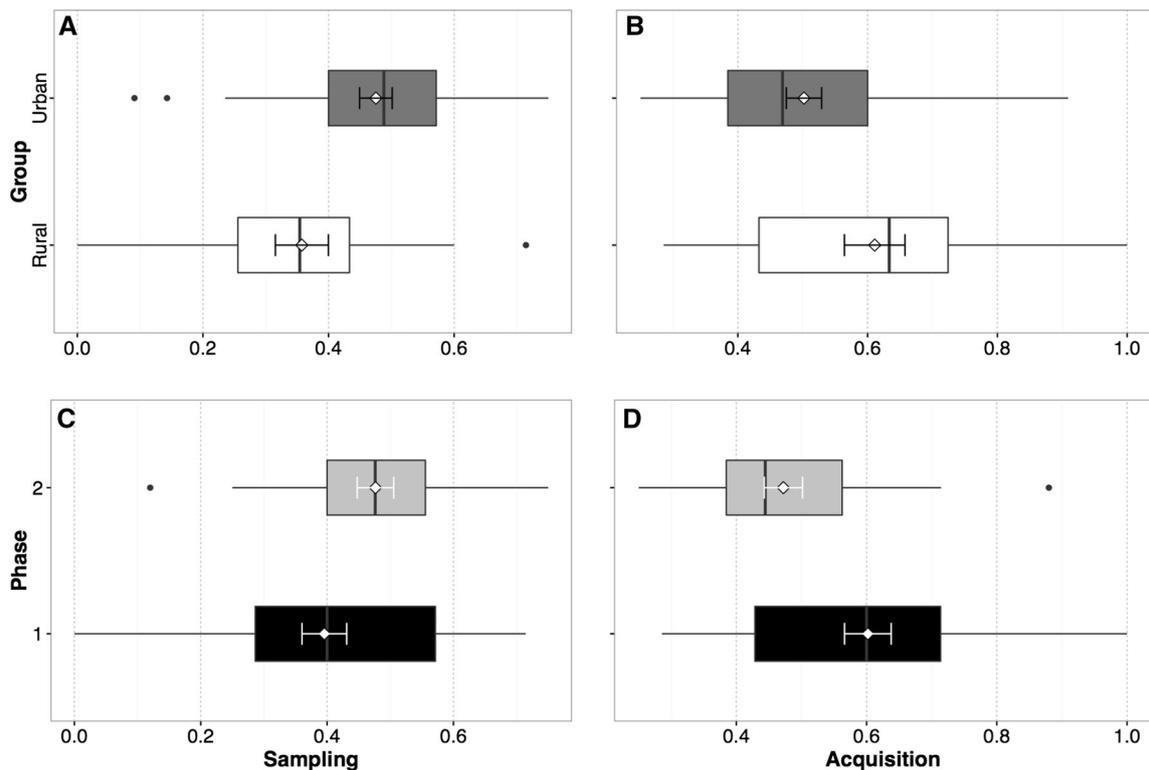


Fig. 2 Population and phase effects on sampling and acquisition ratios. **a** Depicts the effect of population (urban vs. rural) on the mean proportion of sampling blocks, whereas **b** depicts the effect of population on the mean proportion of acquisition blocks. **c** Depicts the effect of phase (one/initial discrimination vs. two/reversal learning) on mean proportion of sampling blocks, while **d** depicts the effect of phase on the mean proportion of acquisition blocks. The mean (± 1 SE)

proportion of sampling (**a, c**) blocks is the proportion of 20-trial blocks with approximately 50 % correct responses (6–14 correct choices out of 20). The mean (± 1 SE) proportion of acquisition blocks (**b, d**) is the proportion of 20-trial blocks with greater numbers of correct responses than incorrect responses (>14 correct responses out of 20). Minimum and maximum values, as well as outliers (values greater than 1.5 times the interquartile range) are depicted. For more details, see text

took more 20-trial blocks to reach criterion starting from first cue-outcome presentation than rural female mynas across both the initial learning phase and the reversal learning phase of the task. Examining the different stages of learning in detail revealed why urban mynas were slower overall: urban individuals spent more time sampling the significance of new predictor cues (initial learning) and reversed predictor cues (reversal learning) than did the rural individuals. Although urban individuals also then acquired the significance of predictor cues significantly more quickly than rural birds, this faster acquisition was not sufficient to compensate for their longer sampling. Hence, urban birds reached criterion from first cue presentation more slowly than did rural birds in both learning phases of the task. These results do not support the prediction that more variable food sources should raise the value of food and lead to faster learning of cue-outcome contingencies in urban mynas. In contrast, they are in line with our hypothesis that urban birds experience more variable food resources and should therefore accumulate more evidence that novel predictor cues reliably predict the availability of food before learning them.

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

Urban mynas sampled new cue-outcome contingencies for longer, but then transitioned through the acquisition phase more quickly than did the rural mynas. Overall, these behavioural patterns resulted in urban mynas taking more trials to learn when performance was measured from first stimulus encounter to criterion achievement. Learning speed is one of the measures that is often assumed to reflect the limits of an animal's cognitive ability. Accordingly, it is often used as an inter- and intra-species comparative proxy (Galsworthy et al. 2005; Roth et al. 2010, 2012; Audet et al. 2016). Within this framework, the slower overall learning of urban mynas might be interpreted as a reduced learning ability, presumably linked to relaxed demands for experience-dependent behavioural adjustments. The present findings suggest that caution is needed when interpreting learning curves. It is possible that differences in overall learning speed reflect finer adjustments to the dynamics of learning that arise as a consequence of conditions experienced by the animal in the past. Alternatively, finer adjustments might occur despite a lack of overall differences. More generally, we suggest that the use of learning speed as a measure of cognitive ability without consideration of the types of strategies animals might employ given their past experiences and the conditions at test might lead to erroneous conclusions (Girvan and Braithwaite 1998; Chittka et al. 2009; Ducatez et al. 2014). As well established in basic associative learning research, there is not always a direct correspondence between what animals know (their learning) and how they behave (their performance) (Pearce 1997).

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

Past research has indicated that within species differences in operant learning speed can arise relatively independently from experience. Black-capped chickadees (*Parus atricapillus*) from environments that undergo harsh winter environments learn a new foraging behaviour significantly faster than birds from environments that undergo less harsh winters (Roth et al. 2010). A common garden design provided robust evidence that this behavioural difference emerges relatively independently from the environment in which the birds are raised. The genetic structure

of urban and rural populations of mynas is currently under investigation, but at the current time, the amount of genetic flow between the populations is not known. In contrast to learning differences in black-capped chickadees, we predict that changes in learning strategies are likely to emerge as a consequence of experience-dependent exposure to different foraging conditions. Population specific, experience-dependent shifts in behaviour are in line with the growing body of work demonstrating the extraordinary behavioural flexibility of mynas (Griffin 2008; Dhama and Nagle 2009; Griffin and Boyce 2009; Feare 2010; Griffin and Haythorpe 2011; McGiffin et al. 2013) and the central role of behavioural plasticity in adjustments to urban environments (Sol et al. 2013), and new environments more generally (Sol et al. 2005, 2008; Mason et al. 2013).

In contrast to a lack of differences in learning in urban and rural Barbados bullfinches (*Loxigilla barbadensis*) (Audet et al. 2016), we found both differences in overall learning speed and differences in the dynamics of learning. Previous research in our laboratory has revealed faster problem solvers in urban mynas relative to suburban mynas (Sol et al. 2011), as well as positive correlations between problem solving and classical conditioning, where faster problem solvers also learn a colour cue discrimination faster (Griffin et al. 2013a). Together, these findings lead to the prediction that rural mynas should outperform urban mynas on problem solving. Future research will aim to test this prediction.

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

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

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