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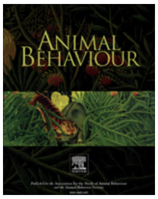

Consumer and motor innovation in the common myna: the role of motivation and emotional responses

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Behavioural innovation is believed to be an important way in which animals devise solutions to new problems, yet the factors underpinning individual differences in innovation remain unclear. Here, we asked how motivational states and emotional responses to novelty shape the innovation process with a series of experiments in common mynas, *Sturnus tristis*. To this aim, we measured experimentally the willingness of adult individuals to eat a new food (consumer innovation) and to develop a new foraging technique (motor innovation), as well as their degree of neophobia, exploration, shyness, motivation and activity levels. Common mynas showed some propensity for consumer and motor innovations, with 55% and 22% of individuals solving the respective tasks. Moreover, individuals that solved the task significantly decreased their latency to solve it subsequently, indicating that learning had occurred. Differences in problem-solving performance were not related to sex, and individuals that solved the consumer task did not solve the motor innovation task faster. The likelihood of solving the motor task increased with propensity of the individual to explore the test apparatus, suggesting that the task was solved by trial and error. Exploration increased with the motivation to feed and decreased with the degree of neophobia. Thus, while differences in innovation propensity between individuals may result from cognitive differences, our results highlight that they may also reflect particular motivational states or emotional responses of individuals to novel situations.

Behavioural innovation, defined as the process that results in new or modified learned behaviours (Reader & Laland 2003), is an important way in which animals devise solutions to new problems (Lefebvre et al. 1997; Ramsey et al. 2007). Thus, innovations are theoretically expected to have important consequences for species when confronted with changes in their environment (Lefebvre et al. 1997; Sol et al. 2005). Although there is little doubt that species differ in their propensity to innovate (Köster & Köster 1983; Lefebvre et al. 1997; Webster & Lefebvre 2001; Day et al. 2003; Lefebvre & Bolhuis 2003), demonstrating interindividual differences in innovativeness within species and explaining their causes have proven challenging (Reader 2003). For example, observations and experiments in fish and primates suggest that particular classes of individuals (e.g. females or low-ranking individuals) may be more inclined to solve novel problems (Laland & Plotkin 1990; Laland & Reader 1999; Reader & Laland 2003), yet it remains unclear whether these differences reflect cognitive abilities, a particular motivational state or emotional variation in the way in which novel situations are dealt with (Laland & Reader 1999).

Motivational factors have typically been regarded as a state-dependent determinant of innovation (e.g. when it is driven by hunger or the need to feed offspring), and findings have led to the widely held view that 'necessity is the mother of innovation' (Laland & Reader 1999). However, motivation may include a stable individual component (i.e. some individuals may be consistently more motivated throughout their lifetimes than other individuals), and its influence on the innovation process may be either direct or indirect via its influence on emotional responses (Sol et al. 2011). The emotional responses that may act as a gateway to innovation include neophobia (i.e. fear of novelty), shyness (avoidance of risky situations) or general levels of activity (Greenberg 2003; Sih et al. 2003; Reale et al. 2007; Coppens et al. 2010). For example, if an animal consistently avoids approaching unfamiliar feeding

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opportunities, then it is less likely to devise innovative behaviours to exploit these new opportunities (Greenberg 2003). Emotional responses of an individual are often consistent over time and/or across situations, and hence may be viewed as temperament or personality traits (Reale et al. 2007). It is therefore important to consider motivational and emotional influences if we are to understand the processes that lead to the emergence of novel behaviours fully.

Attempts to quantify individual performance in innovative behaviour have tended to overlook the distinction between innovative behaviours that involve an unusual motor action and those that involve the use of new food types, despite the finding that these forms of innovation may have different causes and consequences (Greenberg 2003; Overington et al. 2009). In fact, motor innovations are more closely associated with brain size, relative to body size, suggesting that they require a greater information-processing capacity than nontechnical innovations (Greenberg 2003; Overington et al. 2009). However, whether consumer and motor innovations are qualitatively different processes or reflect a 'unitary phenomenon' is unknown (Reader & Laland 2003). One way to address this question is to examine whether both types of innovation are underpinned by similar emotional and motivational processes, and furthermore, whether performance on one kind of innovation predicts performance on the other. Stable individual differences across both motor and food type innovations and similar intervening variables would lend support to the idea that they form a unitary phenomenon, while lack of either or both of these effects would point towards a dissociation of the two kinds of innovation in line with that suggested by macroecological analyses of technical and nontechnical innovations (Overington et al. 2009).

In the present study, we investigated the factors underpinning individual differences in innovation in the common myna, *Sturnus tristis* (alias Indian mynah, formerly *Acridotheres tristis*; Christidis & Boles 2008). We studied two populations introduced to New South Wales, Australia, as part of a more general project aimed at understanding the role of innovative behaviours in the success of invasive species (Sol et al. 2005, 2008, 2011). The ecological context favouring innovative behaviours during the invasion process of the species was examined in a previous paper (Sol et al. 2011). In the present study, we focused on the mechanisms that facilitate or inhibit innovations. Our main goal was to evaluate the extent to which innovation performance could be explained by differences in motivation and/or emotional behaviour, including neophobia, exploration, motivation, shyness and activity. We designed experiments to quantify the willingness of captive adult mynas to eat a new food (consumer innovation test) and to develop a new foraging technique (motor innovation test), problems that mynas are likely to confront when introduced into novel environments, as well as an experiment to quantify the degree of neophobia (neophobia test). We measured exploration, motivational state, shyness and activity level during each of these three experimental tasks. The integration of all this information using structural equation models allowed us to assess whether consumer and motor innovations reflect a 'unitary phenomenon' or are affected by different processes.

METHODS

Subjects and Apparatus

The common myna is naturally distributed throughout southeastern Asia and has been introduced to Australia, New Zealand, Hawaii, Europe and Mauritius (Lever 2006). We trapped 36 adult common mynas in Canberra (population established in 1960–1970) and 24 in Newcastle (population established in 1970–1975) using a species-specific walk-in baited trap (Tideman 2006) and a trapping protocol described in detail elsewhere (Griffin 2008; Griffin & Boyce 2009; Griffin et al. 2010). Although pilot tests were not done for this specific protocol, extensive prior behavioural work on mechanisms of learning and behaviour in this species in the second author's laboratory (Griffin 2008; Griffin & Boyce 2009; Griffin et al. 2010) has demonstrated repeatedly that the sample size used here is adequate to reveal how behaviour is simultaneously affected by a variety of factors (see details in Analyses of experiments below).

After capture, birds were transported by vehicle over short distances in small individual cotton bird bags, or in large cages with ca. 10 birds per cage for longer transport times. We banded individuals with unique colour ring combinations and placed them in groups of up to 25 birds in large outdoor flight aviaries (4.5 × 1.25 m and 2.25 m high) equipped with numerous perches, nestboxes, and bathing tubs, and partly covered to provide shelter against rain for at least 7 days to acclimatize to captivity. All birds had access to food (dog pellets) and water ad libitum. Two individuals became sick during the tests and, despite being isolated and treated with antibiotics, did not recover; hence, the sample size varied from 58 to 60 depending on the behavioural test. Because the common myna is considered a pest in Australia and the government does not allow them to be released once captured, all individuals were euthanized via a CO_2 overdose at the end of the experiments using the same procedure as described elsewhere (Griffin 2008; Griffin et al. 2010). Sex was determined by post mortem examination of the reproductive organs, yielding 34 males and 26 females. All animal care, husbandry, and experimental procedures were in accordance with the Australian code of practice for the care and use of animals for scientific purposes and were approved by the University of Newcastle Animal Ethics Committee (protocol 1058).

General Procedure

Although mynas are highly social, we measured individual performance during temporary separation from the group (Boogert et al. 2006, 2008). This is justified as, even in social animals, one animal will typically initiate the diffusion of a novel behaviour (Laland & Plotkin 1990). Once a week, from June to September 2007, we randomly chose either four or six common mynas from the group aviaries and placed them in individual cages (0.6. × 0.6 m, and 0.6 m high) located in an outdoor fenced-off area with a roof and two walls. These cages allowed acoustic but not visual contact between individuals, and all contained a nestbox, a watering/bathing bowl and a small (4 × 4 cm and 2 cm high) feeding dish. Each weekly cohort included individuals from the same population (Canberra or Newcastle), the identity of which was alternated each week. All birds were left for 2 days to acclimatize to their new environment and the experimental sessions took place on each of the following 3 consecutive days, early in the morning. Birds may gradually habituate to novel stimuli, implying that performance in a novel test may be affected by experience with a novel object in the previous test. Consequently, we chose to conduct the three experimental sessions in a fixed order (Bouchard et al. 2007), beginning with the session during which birds underwent the easiest test to solve (i.e. neophobia test) and ending with the session during which birds underwent the most difficult test (i.e. motor innovation test).

During experimental sessions, birds were observed from behind a blind to avoid disturbance by the observer. All experiments were videotaped and behaviour was scored using Jwatcher (Blumstein & Daniel 2010). This software allows the user to score a suite of user-defined behaviours in real time, making it straightforward to calculate durations of behavioural states and frequencies of behavioural events. To prevent any observer biases, all observations were made blind by the same researcher (I.B.) who ignored the population origin of each cohort during the recording. Individuals had access ad libitum to food (dog pellets) and to water, except overnight when they were food deprived in preparation for morning tests, and during experimental sessions when the experimenter controlled food access.

Wild-caught caged mynas show little tolerance of close human proximity, particularly if they are stared at. Consequently, during times when the observer was visible to the subject myna (i.e. while setting up the blind and the video camcorder and preparing to run the experimental session), subjects always sought refuge in their nestbox. As a measure of shyness, we used the time interval between the moment the observer finished setting up the experimental test and settled quietly behind the screen to begin the experimental session and the moment the myna exited its nestbox. All other behavioural variables (see below) were always recorded from the moment the focal myna exited its nestbox.

All experimental sessions included four successive phases: a 2 min baseline period, followed immediately by a 10 min initial control phase, a 20 min test phase, which encompassed the neophobia, the consumer innovation or the motor innovation test, and a 10 min final control phase.

During the baseline period, each focal myna was videotaped for 2 min. The number of times the bird moved between the different sections of the cage (floor, perch, cage and nestbox) per minute was used as a baseline measure of activity (hereafter activity). Activity was measured during both control phases (initial and final), as well as during the test phase, for each experimental session. In this context activity may reflect both general activity patterns and nervous activity caused by stress.

During the initial and final control phases, the observer waited until the subject had moved away from the feeder and then reached his/her hand into the cage through a small hole in the blind and placed two dog pellets in the subject's empty feeding dish. Latency to approach the food dish and to begin feeding during initial and final control phases was used as a measure of motivation. To avoid birds determining from a distance whether food was available or not, all food dishes were made deep enough to ensure that approach was necessary to detect the presence of food. Methodological details for the neophobia, consumer innovation and motor innovation tests are presented next.

Neophobia Test

Neophobia, defined as the aversion to approach novel objects (Greenberg 2003), was measured using the classical approach of placing an unfamiliar object next to the animal's usual feeding spot (Reale et al. 2007). Here, we used a role of yellow tape and a green hairbrush, which are objects that mynas are unlikely to have encountered in the wild. Half the mynas received the yellow tape, while the other half received the green hairbrush.

The neophobia test was initiated immediately after the myna had consumed the food from the initial control phase. The observer waited until the myna had moved away from the feeder, and then reached through the small hole in the blind to hang a novel object on a hook next to the bird's feeder, and then place two dog pellets in the feeder.

The performance in the task was measured in three ways (see details in Table 1). First, we measured success by scoring individuals that ate the food in the presence of the novel object within the 20 min time period as successful, and those that did not as unsuccessful. Second, we measured the total latency (s) to begin eating. Third, we decomposed this latter measure into two: the latency to approach the feeder and the latency to begin feeding after first approach (Table 1).

Consumer Innovation Test

While innovation is the process that results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire (Reader & Laland 2003), consumer innovation refers to the acquisition of a novel food using pre-established foraging techniques. To measure consumer innovation in mynas, we used cooked rice, coloured either blue or green, as a novel food. The consumer innovation test was initiated immediately after the myna had consumed the food from the initial control phase. The observer waited until the myna moved away from the feeder, and then reached through the small hole in the blind to place the novel food in the myna's feeder.

Table 1
Names, abbreviations and description of the variables used in the SEM

Variable	Description
Neophobia test	
Latency (s) to approach (LA)	Latency to first approach to the novel object. Individual moved to within 20 cm (two bird lengths) of the feeder*
Latency (s) to eat after first approach (LEA)	Latency from first approach to eating in the presence of the novel object
Consumer innovation test	
Latency (s) to eat novel food (LEC)	Latency from first visual contact to eating the novel food
Time (s) exploring (TEX)	Time allocated to visual exploration of the novel food. Individual was within 20 cm of the feeder and its head was facing it*
Food items eaten (FIE)	Number of rice grains eaten during the test
Motor innovation test	
Latency (s) to approach (LAM)	Latency to first approach to the apparatus*
Latency (s) to the first peck (LEP)	Latency from first approach to first peck (bill contact) with the lid
Latency (s) to open the lid (LEM)	Latency from first bill contact to opening the lid and eating the food
Bill contacts (BIC)	Number of pecks to the apparatus
Intervening variables	
Movements (1/min) (MOV)†,‡	Number of movements/min between the different sections of the cage (floor, perch, cage and nestbox)
Time (s) in the nestbox (NES)†	Time spent in the nestbox, starting from the moment the experimenter was out of sight (see text for more details)
Latency (s) to eat during controls (EAT)†	Latency to feed on the pellets during the controls*

* These time periods began as soon as the subject myna exited its nestbox after the experimenter had placed food (initial control trial), the novel object (neophobia test) or the dog pellets and lid (motor innovation test) in the subject's cage (see text for details).

† Measured in the initial control (IC), test phase (PS) and final control (FC) of each experiment.

‡ Also measured in the baseline period (BP).

To estimate performance in problem solving, we used four different variables (Table 1), the first of which was success. Successful individuals were defined as those that ate the novel food and unsuccessful individuals those that did not. Second, we measured the latency from first visual contact, defined as the first time the myna faced the feeder when located within 20 cm of it to the time the myna ate the food. Third, we measured the time each myna allocated to exploring the novel food (Table 1). Finally, we quantified the number of rice grains eaten.

Motor Innovation Test

Motor innovation refers to the acquisition of a novel food or a previously used food via the use of a new foraging technique (Reader & Laland 2003). Hence, motor innovation is generally considered more cognitively demanding than consumer innovation (Greenberg 2003). To measure motor innovation in mynas, we placed two dog pellets in a wooden well (20 mm diameter and 15 mm deep) and covered it with an opaque lid. The pellets were placed out of sight of the individual to avoid some birds seeing the food and hence being more motivated to solve the task. The lid was fitted with a small (10 mm diameter) metal eye to facilitate manipulation. As for the consumer innovation test, the motor innovation test began immediately after the myna had consumed the food from the initial control phase and moved away from it, and was initiated by reaching through the small hole in the blind and putting the dog pellets and lid into place.

To estimate performance in problem solving, we used four different measures (Table 1). First, we measured the success by scoring individuals that opened the well and ate the food within the 20 min of the test as successful and those that did not as unsuccessful. Second, we measured the total latency to eat the first pellet. Third, we decomposed this total latency into three periods: latency to approach the wooden well, latency from first approach to first peck on the lid, and latency from first peck to opening the lid and eating the food. Finally, we counted pecks to the well.

For those mynas that successfully opened the well and consumed at least one food pellet (innovation), subsequent learning was quantified by presenting the covered wooden well to those birds once again immediately after the first successful trial and determining whether the latency from first peck to opening the lid (Table 1) using the same opening technique decreased upon second presentation.

Following Boogert et al. (2006), we habituated individuals to the experimental apparatus (wooden well) prior to the motor innovation test. This was achieved by presenting two dog pellets beside the well during the initial control phase, rather than in the feeding dish, as during all other initial controls. Thus, we partially reduced the neophobic response to the experimental apparatus per se. We took care to place the pellets beside the hole, rather than inside it, however, so as to avoid facilitating the innovation task.

Analyses of Experiments

We modelled the problem-solving performance in consumer innovation and motor innovation as a function of emotional responses (neophobia, shyness and activity) and motivation using structural equation modelling (SEM). SEM allows the testing of complex models including latent variables (variables that are not directly observed, but rather inferred from several measured variables), as well as the errors associated with all exogenous variables (latent and observable; Dingemanse et al. 2011). We built structural equation models using AMOS 16.0 (Arbuckle 2007), which we fitted using maximum likelihood with the multinormal errors method (Fox 2006). The path coefficients and model fits were estimated based on information from all individuals, with means and intercepts estimated to deal with missing values (Arbuckle 2007). The model fits were evaluated using a chi-square test to compare the observed and predicted covariance matrices (Grace 2006).

Not all individuals solved the task during the 20 min left for each test, making these exogenous variables right censored. Although in animal behaviour studies these types of variables are usually analysed with ordinary regressions or ANOVAs, these approaches are inappropriate because censored variables are unlikely to meet the assumption of normality. In addition, regressions and ANOVAs give the same response value to all individuals that failed to complete the task; however, it is likely that the individual values would have differed had individuals been given more time to solve the task. AMOS 16.0 allows the modelling of censored data within a Bayesian framework. Unfortunately, our models did not converge when using this approach. Hence we opted to run the general models with uncensored data and then confirm the significant paths using censored survival analyses. Specifically, we used the Cox proportional hazard models, a nonparametric approach that requires few assumptions and allows the inclusion of covariables in the model (Crawley 2002). In addition to the above approaches, we adopted other methods for more specific analyses. First, to assess the repeatability of some of our behavioural traits, we used either a Pearson correlation (when we compared two variables) or a variance component analysis (when there were several variables; Crawley 2002). Second, to model exploration in the motor innovation test, we used a generalized linear model approach. The response variable was the number of pecks on the test apparatus, and hence we defined a Poisson structure of errors and a log-link (Crawley 2002). All the analyses were performed using R software (R Development Core Team 2009).

RESULTS

Are Common Mynas Innovative?

A substantial proportion of common mynas displayed behavioural innovations. In the consumer innovation test, 55% individuals tasted the novel food. Moreover, 31 of the 33 individuals that ate the novel food returned to it to continue feeding, and all 31 reduced their latency to eat the second time round, indicating that the new food was acknowledged as profitable. The latency to eat the food was unaffected by the colour of the rice (Cox model: $z = 0.91$, $P = 0.36$), the sex of individuals ($z = 0.131$, $P = 0.89$) or the population of origin ($z = -0.52$, $P = 0.64$). Consequently, we pooled all data for subsequent analyses.

The motor innovation test was solved by 22% of mynas. Although individuals developed a variety of methods to lift the lid, each bird was consistent in the use of one or other technique over the two trials: eight birds always solved the tasks by pecking and rotating the lid on to its edge within the hole; four solved it by snatching the eye on the lid in their beak and throwing the lid away; and finally, one individual solved it by accidentally knocking the feeder over with its wing, a technique it repeated in its second exposure to the apparatus. Moreover, 11 of the 13 individuals that solved the task significantly decreased their latency from first pecking the test apparatus to solving it the second time round, indicating that learning had occurred (Wilcoxon paired test: $V = 80$, $P = 0.013$). The latency to eat the food was unaffected by the sex of individuals (Cox model: $z = -1.35$, $P = 0.18$) or the population of origin ($z = 1.25$, $P = 0.21$), and hence all data were pooled for subsequent analyses.

Only eight individuals solved both tests. For the rest, 25 individuals solved the consumer innovation test, but failed to solve the motor innovation test, while five succeeded in the motor innovation test, but had previously failed to solve the consumer innovation test. The individuals that solved the consumer innovation task faster did not solve the motor innovation task faster (Cox model: $z = -0.194$, $P = 0.84$).

Why do Individuals Differ in Innovation Performance?

The structural equation models for consumer and motor innovation incorporating motivation, shyness and activity consistently suggested that the principal factor underlying myna performance was motivation (Figs 1, 2, respectively). Neither shyness nor activity affected performance significantly. Thus, differential success in solving the task may in part be explained by interindividual differences in motivation, a finding that was confirmed via a survival analysis on the motor innovation test (Cox model: $z = -2.20$, $P = 0.02$), but not the consumer innovation task ($z = -1.25$, $P = 0.21$). To explore the stability components of our innovation measures, we tested whether motivation was a stable individual feature or whether it varied from one test to another. A variance component analysis with latency to feed in the initial control of the consumer, motor and neophobia tests as response variable and including individual as a random factor revealed that only 16% of the variance in motivation was explained by individual differences. Although the explained variance is highly significant ($P < 0.001$) and points towards there being a small stable component of our motivation measure, this result also indicates that each individual varied substantially in motivation to feed across tests.

Do Individuals Differ in Neophobia?

In the neophobia test, mynas perceived the novel objects as a risk, as suggested by the increase in latency to start feeding in the presence of the objects compared to the latency to start feeding during the initial control phase (Wilcoxon paired test: $T = 2428$, $P < 0.0001$). As for innovation, structural equations evaluating the concurrent effects of motivation, shyness and activity revealed that motivation was the main factor underlying differences in myna performance during the neophobia test (Fig. 3): Individuals that ate faster during the initial and final controls showed shorter latencies to feed in presence of a novel object than those that were less motivated to feed.

We tested whether neophobia was a stable individual trait or whether it varied from one test to another. The latency to feed in presence of a novel object in the neophobia experiment was positively correlated with the latency to feed from the test apparatus in the initial control of the motor innovation experiment (Pearson correlation: $r = 0.45$, $P = 0.001$). Thus, some individuals showed a tendency to be more neophobic than others, at least on a short-term basis.

Do Neophobia and Motivation Underpin Differences in Innovation?

We evaluated the concurrent effect of neophobia and motivation on innovation using SEM (Figs 4, 5). In the consumer innovation test, individuals perceived the new food as a risk, as suggested by the increase in latency to start feeding on a novel food relative to the latency to start feeding on a familiar food presented during the control phase (Wilcoxon paired test: $T = 1675$, $P < 0.0001$). Although the SEM fitted the data well (Fig. 4), neither motivation (Cox model: $z = -1.06$, $P = 0.29$) nor neophobia (Cox model: $z = 0.73$, $P = 0.47$) had a significant effect on consumer innovation performance when tested with the survival analysis approach.

The model for motor innovation also fitted the data well, and in this case some of the main paths were significant (Fig. 5). The model

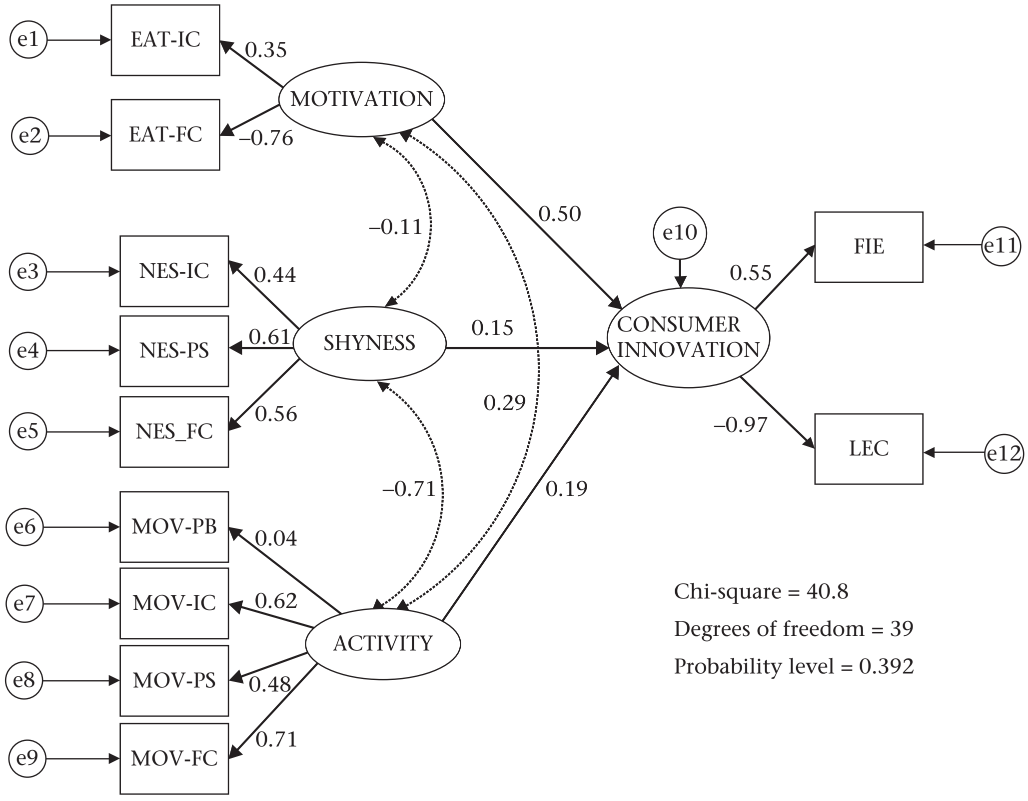

Figure 1. SEM deconstructing the effects of motivation, activity and shyness on consumer innovation performance. Consumer performance is a latent variable that gives higher scores to individuals that started eating the novel food faster and consumed more food items. See Table 1 for abbreviations. The model fits the data, yet none of the main paths are significant when tested using survival analyses.

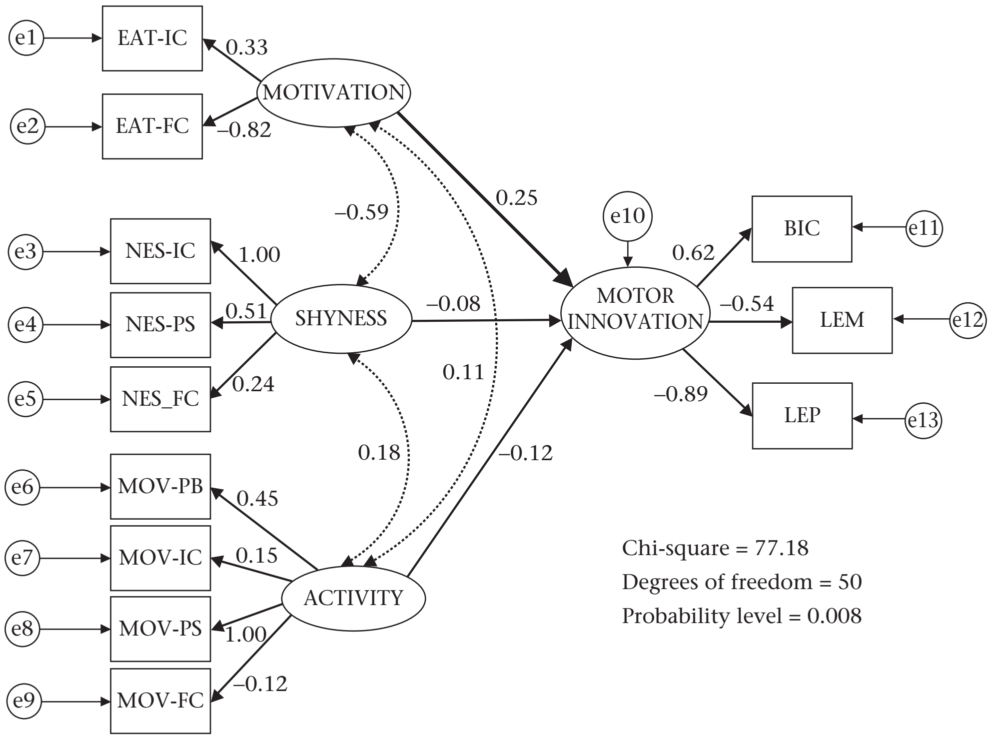

Figure 2. SEM deconstructing the effects of motivation, activity and shyness on motor innovation performance. Performance in motor innovation is higher for individuals that took less time to approach, explore and open the lid, and that pecked more frequently at the test apparatus. See Table 1 for abbreviations. The model does not fit the data, yet one of the main paths (bold arrow) is still significant when tested using survival analyses.

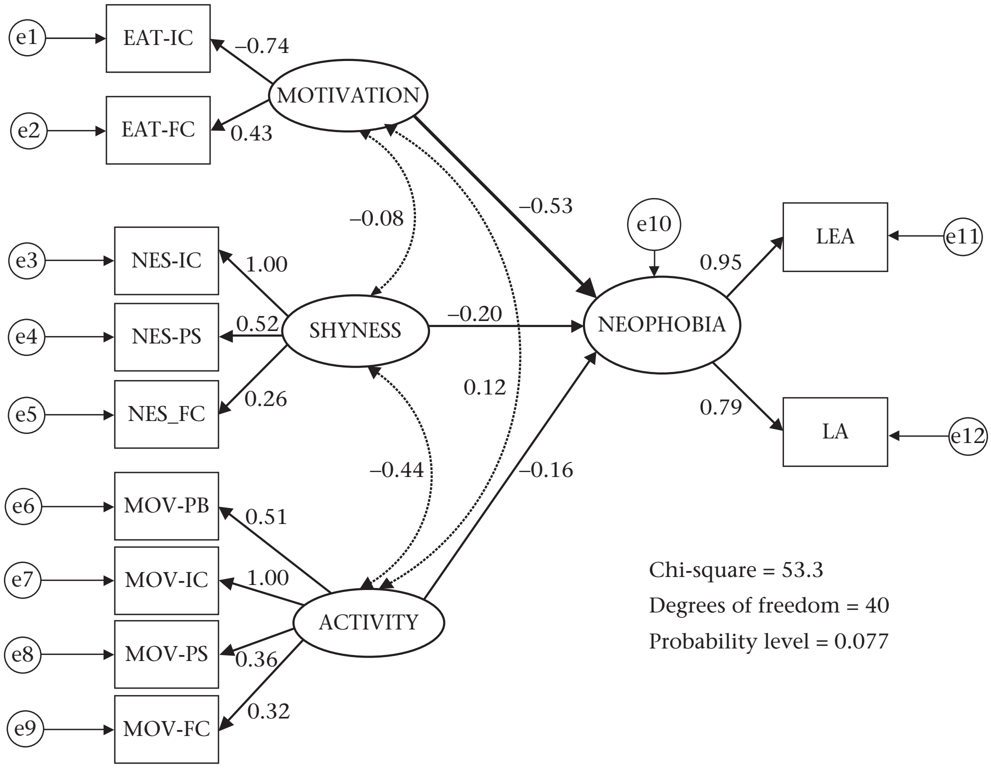

Figure 3. SEM deconstructing the effects of motivation, activity and shyness on neophobia. Neophobia attains higher scores for individuals that took longer to approach and start eating in the presence of the novel object, which explains why its relationship with motivation (i.e. the latency to eat in the initial and final controls) is negative rather than positive. See Table 1 for abbreviations. The paths that are significant using survival analyses are shown in bold.

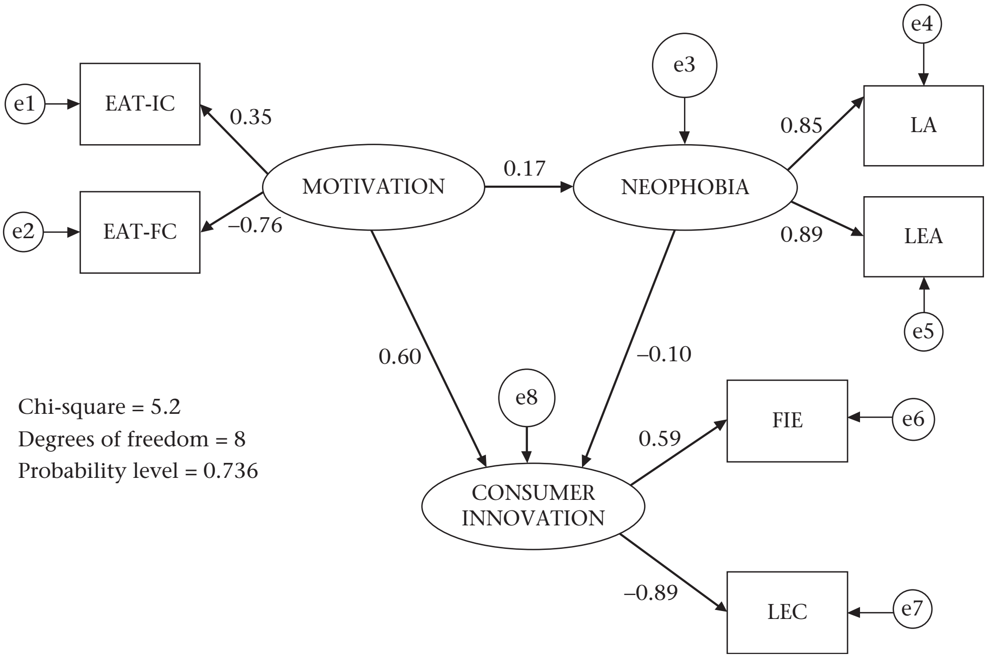

Figure 4. SEM deconstructing direct and indirect effects of motivation and neophobia on consumer innovation performance. See Table 1 for abbreviations. Although the model fits the data, none of the paths are significant when tested using survival analyses.

suggests that motivation significantly affected motor innovation performance: the higher the latency to eat in the initial control test, the shorter the time needed to open the lid (Cox model: $z = -2.37$, $P = 0.01$). The model also suggests that neophobia significantly affected motor innovation performance, with the more neophobic individual needing more time to open the lid (Cox model: $z = -2.63$, $P = 0.009$). One reason is that the likelihood of the individual lifting the lid increased with the number of pecks to the apparatus (Cox model: $z = 2.53$, $P = 0.011$), which was in turn positively associated with motivation (GLM: $z = -3.49$, $P = 0.005$) and negatively associated with neophobia (GLM: $z = -2.65$, $P = 0.008$; after removing an outlier: $z = -3.29$, $P = 0.001$; Fig. 6). Consumer innovation did not predict either performance in motor innovation (Cox model: $z = -0.65$, $P = 0.519$) or the frequency of exploration of the test apparatus (GLM: $z = -1.36$, $P = 0.171$), even when motivation and neophobia were included as covariates in the models.

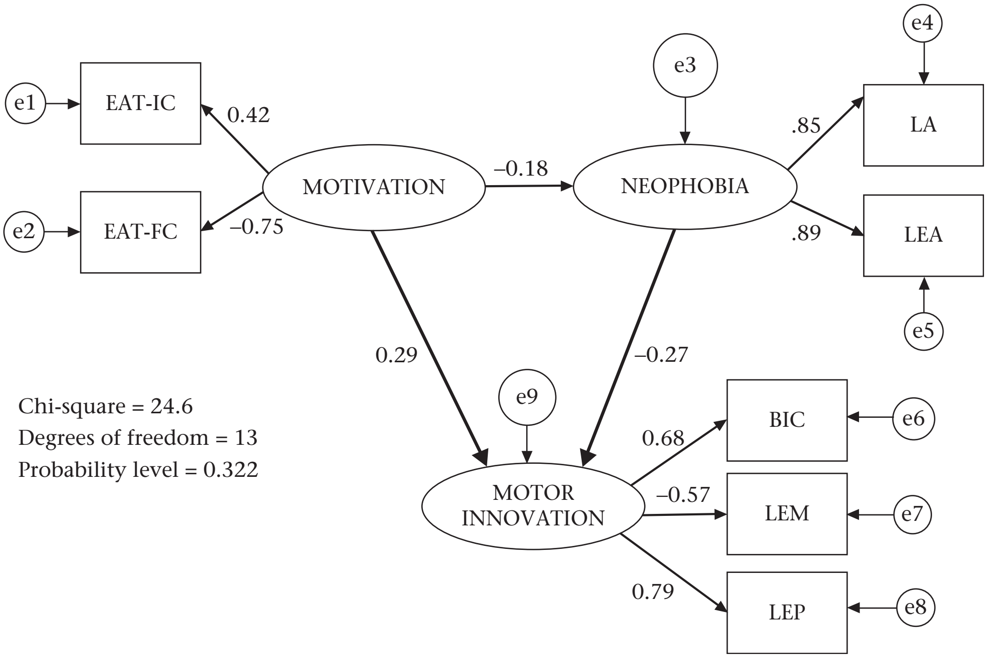

Figure 5. SEM deconstructing direct and indirect effects of motivation and neophobia on motor innovation performance. See Table 1 for abbreviations. The model fits the data and two main paths (in bold) are significant when tested with survival analyses.

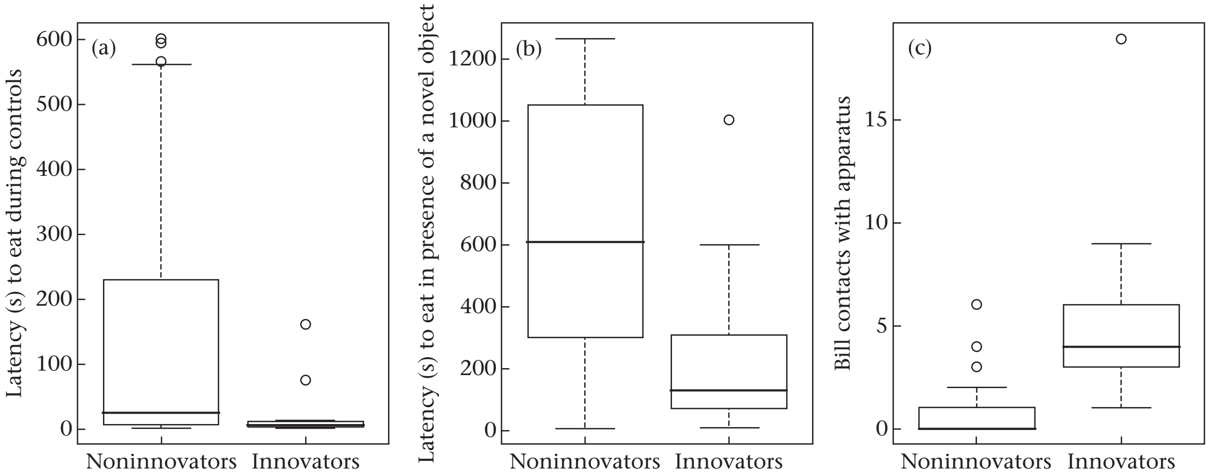

Figure 6. Differences in (a) motivation (latency to eat during the initial control phase), (b) neophobia (latency to eat in presence of a novel object) and (c) exploration (number of pecks to the apparatus during the experimental phase) between mynas that solved and did not solve the motor innovation task. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

DISCUSSION

The propensity for behavioural innovation has been identified as an important feature of many successful invaders (Sol et al. 2005, 2008). Consistent with this, a substantial proportion of mynas displayed the ability to innovate, with 55% and 22% solving a consumer and motor task, respectively. In our study area, common mynas show an important dependence on food derived from human activities (Sol et al. 2011), and hence a high propensity to explore and adopt novel resources may provide substantial fitness benefits for individuals.

The emotional responses of mynas to novelty played a decisive role in their ability to solve a motor innovation task, but not in their ability to solve a consumer innovation task. However, only neophobic emotional responses were important, while shyness and activity played no role in either. The most unexpected finding is the lack of association between shyness and innovation propensity. Growing evidence suggests that proactive coping styles are characterized by low behavioural flexibility (Coppens et al. 2010), but we found no evidence for this to be the case in common mynas. Shyness was also dissociated from exploration and neophobia, two of the main factors underpinning innovation propensity (see below).

Our results also highlight the importance of neophobia in the innovation process. Past work has been contradictory in this regard. Neophobia correlated negatively with innovation propensity in five opportunistic avian species on Barbados (Webster & Lefebvre 2001) and in both feral pigeons, *Columba livia*, and Zenaida doves, *Zenaida aurita* (Seferta et al. 2001; Bouchard et al. 2007). Biondi et al. (2010) also found a similar negative correlation in Chimango caracaras, *Milvago chimango*, although only in juveniles but not in adults. Finally, Boogert et al. (2006) and Liker & Bókony (2009) did not find evidence that object neophobia correlates with innovation performance in starlings, *Sturnus vulgaris*, and house sparrows, *Passer domesticus*, respectively. These contrasting findings could arise at least in part from methodological differences. In protocols in which subjects are not habituated to the test apparatus prior to attempting to solve it, neophobia is likely to play a greater role (e.g. Webster & Lefebvre 2001). Repeatedly exposing subjects to novel objects may facilitate habituation to novelty, and thereby reduce the effects of neophobia on subsequent innovation performance (Boogert et al. 2006).

However, habituation does not seem to be the only explanation. In our study, mynas were provided with the opportunity to consume a food item from the test apparatus before attempting to solve it, partially reducing neophobic responses. In addition, performance was assessed by analysing the latency to lift the lid separately from the latency to approach the apparatus. Nevertheless, neophobia remained a significant determinant of motor innovation performance: individuals that solved the motor innovation task earlier were those least hesitant to feed next to novel objects in the neophobia test. The role of neophobia in the propensity for motor innovation seems in our case also mediated by exploration intensity. The probability of solving the technical innovation task increased with the number of pecks to the test apparatus, suggesting that the problem was solved by trial and error, and the number of pecks to the apparatus was higher for the less neophobic individuals. These findings again contradict the view that proactive coping styles, here measured in terms of lower neophobic responses, are characterized by low behavioural flexibility (Coppens et al. 2010).

Mynas showed consistency in their neophobic responses across both the neophobia test and the motor innovation task, a finding that is consistent with the view that neophobia is an underpinning emotional mechanism for the temperament trait exploration–avoidance (Reale et al. 2007). It seems therefore that the propensity to motor innovate is at least in part driven by a relatively stable individual trait in mynas. In a highly invasive species, such as the common myna, in which innovativeness may be crucial for survival, neophobia could hence provide a platform upon which selection could operate to enhance innovativeness. Further research examining the heritability of neophobia in this species will be needed to ascertain this.

While the influence of neophobia was restricted to performance on the motor innovation task, and did not extend to the consumer innovation test, the influence of motivation was apparent in all three tasks (consumer innovation, motor innovation and neophobia). Indeed, in each test, the individuals that ate the food during an initial control phase faster were then more likely to complete the subsequent test phase than individuals that took longer to eat the control food, even though this effect was nonsignificant in the consumer innovation test when assessed using survival analyses. In the case of the motor innovation task, motivation influenced performance in part through its effect in exploration, in so far that the number of pecks to the apparatus was highest for the most motivated individuals. Even though motivation is typically defined as a state-dependent process (e.g. Laland & Reader), we found that motivation measured in the present study showed a small stable individual component. Although our measure of motivation should capture most of the state-dependent variation (e.g. caused by hunger), the latency to eat during the control phases could also have been influenced by other more stable factors, such as differences in metabolism rates or capacity to deal with stress. Motivation may hence provide another platform for the evolution of enhanced innovativeness in the myna.

Our analyses reveal no evidence that consumer innovators were also motor innovators, suggesting a dissociation between consumer and motor innovation. This is in line with the finding that motor innovation was influenced by an emotional trait, neophobia, while variation in consumer innovation was explained primarily by state-dependent motivation. The dissociation is also in line with that found in the macroecological literature (Overington et al. 2009). In their comprehensive analysis of innovation in birds, Overington et al. (2009) reported that the most common type of innovation in field observations was the consumption of novel food. Thus, our finding that motor innovation occurs less frequently than consumer innovation may be a general pattern. Overington et al. (2009) further reported that the number of both consumer and motor innovations was significantly associated with brain size (relative to body size), but that the relationship with motor innovation was far stronger than that with consumer innovation. Although it is possible that the high failure rate on the motor innovation task reduced variation in latency to solve the task, which in turn may have reduced our ability to resolve the actual strength of the association between consumer and motor innovation performance, our results and those from cross-species comparisons suggest that the processes involved in consumer and motor innovation tasks are qualitatively different (Greenberg 2003; Overington et al. 2009).

Because new or modified behaviours are often developed by one or a few individuals, social learning is critical to spreading the fitness benefits of novel behavioural patterns to other members of the population (Lefebvre 2000). Mynas are very social birds and are capable of transmitting a variety of behaviours via social learning (Griffin 2008). It is thus expected that innovations can be easily transmitted to other members of the group, as has been shown in a taxonomically closely related species, the European starling (Boogert et al. 2008; Griffin & Boyce 2009). Living in groups may also increase innovation performance, whether by chance (e.g. because of the presence of some skilled individuals) or by increasing motivation and exploration and reducing neophobia and time allocated to vigilance (Reader 2003; Liker & Bókony 2009). Thus, we predict that the social context will further facilitate the production of innovations in common mynas, a possibility that awaits empirical confirmation.

By experimentally showing in common mynas that the proximate factors that favour or inhibit innovation include both stable emotional traits, such as neophobia, and more state-dependent variable effects, such as motivation, we support the idea that some individual factors may provide a platform for the evolution of enhanced innovativeness under uncertain environments. Yet, further conclusions about the proximate factors that influence innovation, including those explored here, will require a multipronged approach. To establish beyond doubt the stability of neophobia and the state dependence of motivation, and to establish the extent of their role, it will be necessary first to manipulate these factors experimentally, second, to assess them using alternative personality tests, and third, to measure them over longer periods of time. There is clearly an exciting path ahead to understand the mechanisms of innovative behaviour fully.

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