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To innovate or not: contrasting effects of social groupings on safe and risky foraging in Indian mynahs

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Foraging innovations are increasingly recognized as an important source of phenotypic plasticity, evolutionary change and adaptation to environmental challenges. One line of research has successfully demonstrated that innovation can represent a stable individual trait, but by the same token has shown strong contextual effects on innovation. We examined the effects of social context on innovative foraging behaviour. Across two separate experiments, we measured the individual propensity of Indian mynahs, *Acridotheres tristis*, to innovate when alone, in pairs, or in groups of five birds. Although innovators remained consistent in their relative innovation performance ranking (high, medium, low), the presence of one or more conspecifics reduced the likelihood of innovating, and increased innovation latencies, significantly relative to when individuals were tested alone. A neophobia test in which latency to forage was compared in both the absence and the presence of a novel object, in each of two social contexts (solitary versus social), showed that the presence of conspecifics caused mynahs to forage significantly faster in a safe situation (object absent) relative to when alone, but to delay foraging in a risky situation (object present). Together, these findings suggest that sociality can have contrasting effects on foraging in safe and risky situations, and, in some species at least, effects of sociality on innovative foraging may hence be more akin to those observed in the presence of risk. Negotiation over engaging with risks inherent to innovative foraging offered the most likely explanation for socially inhibited innovation behaviour, and may act to constrain the diffusion of innovations under some conditions.

There is increasing evidence that foraging innovations are a rich source of phenotypic plasticity and evolutionary change (Nicolakakis et al. 2003; Sol et al. 2005b; Lefebvre 2011). A large body of macrocomparative work relating the number of anecdotal reports of novel feeding behaviours across a broad range of avian taxa to a variety of ecological variables and evolutionary processes suggests that innovative foraging behaviour can facilitate access to new ecological niches and accelerate morphological diversification and speciation (Wyles et al. 1983; Sol et al. 2002, 2008; Nicolakakis et al. 2003). Correlational analyses have also revealed that anecdotal reports of novel feeding behaviours are more prevalent in avian and primate taxa with larger relative brain volume, a finding that has fuelled the idea that innovative behaviours are underpinned by enhanced cognitive capacity (Lefebvre et al. 1997, 1998, 2001; Overington et al. 2009a; but see Healy & Rowe 2007; Thornton & Samson 2012). With such important macroecological and evolutionary consequences, the capacity to innovate, and its presumed associated cognition, may provide an important adaptive mechanism to adjust to rampant environmental change including urbanization and habitat degradation (Sol et al. 2005a; Shultz et al. 2005; Møller 2009). As such, it is important that we understand how innovations arise and the circumstances that promote and inhibit the expression of innovation (Lefebvre & Sol 2008).

One line of investigation has involved examining to what extent 'innovativeness' represents a stable attribute of individuals, whereby some individuals are consistently more innovative than others (e.g. Laland & Reader 1999; Cole et al. 2011; Morand-Ferron et al. 2011). Overall, evidence for consistent repeatable individual differences in innovation propensity remains relatively rare (Laland & Reader 1999; Cole et al. 2011; Morand-Ferron et al. 2011). Most strikingly, even in the handful of systems in which stable individual differences have been clearly established within contexts, animals show an apparent lack of consistency across contexts. For example, great tits, *Parus major*, show high repeatability of innovation performance both in captivity and in the wild, but innovation in captivity does not predict innovation in the wild, pointing to important contextual influences on the expression of innovation (Morand-Ferron et al. 2011).

Whether the opportunity to innovate is encountered alone or in the presence of other individuals is one such contextual effect. Depending on the costs and benefits associated with innovating,

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predictions about how social context should affect innovation performance may vary. If the presence of other individuals allows for antipredator vigilance to be shared, and increases scramble competition, as is well established for noninnovative foraging, then innovations should be more frequent in the presence of other individuals (Elgar 1989; Beauchamp & Livoreil 1997; Beauchamp 1998; Lima & Bednekoff 1999; Beauchamp & Ruxton 2003; Bednekoff & Lima 2004). A similar outcome is predicted by the 'pool of competence' hypothesis, whereby social gatherings group together individuals with differing skills to bring to bear on a novel problem, thus facilitating problem solving (Hong & Page 2004; Liker & Bókony 2009; Morand-Ferron & Quinn 2011). In contrast, if the expression of innovative behaviour is vulnerable to interference competition, then the frequency of innovation should decrease in the presence of other individuals when compared with solitary conditions, as has been found for food processing behaviours (Overington et al. 2009b). Decreased innovation rates should be furthermore accompanied by increasing aggression. Determining first whether innovation performance increases or decreases in the presence of conspecifics, and second, examining how secondary variables vary, such as individual food intake rates, vigilance levels and aggression, are key to teasing apart these hypotheses (Liker & Bókony 2009).

One important difference between noninnovative foraging and innovative foraging is that the latter is thought to be associated with increased and/or novel risks (Vas et al. 2011; Soler et al. 2012). For example, innovation may expose individuals to a greater abundance or variety of endoparasites (Garamszegi et al. 2007; Soler et al. 2012; Vas et al. 2011) and/or to novel predators (Overington et al. 2011). Consequently, effects of sociality on innovation may be very different to the well-established effects of sociality on noninnovative foraging. In fact, they may be more akin to social effects on responses to novelty, whereby 'negotiation over risk' can cause individuals to be slower to approach a novel foraging opportunity in the presence of conspecifics than alone (Stöwe et al. 2006b; Overington et al. 2009b). Negotiation over risk may also decrease expression of innovative behaviour (Greenberg 2003). On the other hand, if the presence of other individuals socially facilitates approach and exploration, behaviours proposed to be key determinants of innovative behaviour (Greenberg 2003; Sol et al. 2012), then innovation should be more frequent in social than solitary contexts (Coleman & Mellgren 1994; Visalberghi et al. 1998; Visalberghi & Addessi 2000). Examining whether social effects on innovation parallel those observed in other risky and nonrisky situations provides insight into the costs of innovation.

Predictions about the effects of sociality on innovative foraging are further complicated by potential interactions between sociality and foraging in the presence of increased and/or novel risks, whereby facilitatory effects are observed in some social settings and inhibitory effects are observed under others. Different group sizes and group compositions may be some such variables (Van Oers 2005; Stöwe et al. 2006a; Stöwe & Kotrschal 2007).

The purpose of the present study was to examine the effect of sociality on innovative foraging behaviour, while simultaneously exploring the mechanisms underpinning the observed effect, and its consistency across two different social settings. Using Indian mynahs, *Acridotheres tristis*, a gregarious passerine, which is highly commensal with humans, we conducted two experiments in which each individual's propensity to innovate was quantified both alone and in the presence of one (experiment 1), or several (experiment 2), conspecifics. In experiment 1, we also measured willingness to forage in the absence versus presence of a novel object, both when alone and in a social context in order to determine whether social effects on innovation were apparent in an alternative foraging context involving risks associated with novelty.

EXPERIMENT 1

Study Aim

The aim of experiment 1 was to determine whether the presence of a conspecific modified a mynah's propensity to innovate, while simultaneously exploring underpinning mechanisms of behavioural change (aggression, motivation, neophobia) and cross-contextual stability in performance. Our experimental design differs from previous work examining social effects on innovation, which has typically involved creating social groups with randomly selected individuals (Liker & Bókony 2009; Overington et al. 2009b). By contrast, we were specifically interested in determining whether a mynah with a high innovation propensity would increase innovation in a mynah with a low innovation propensity. Consequently, we first measured each individual's innovation propensity and then created pairs of mynahs in which an individual with a low individual innovation propensity (i.e. a low-rank innovator) was paired with a mynah of high innovation propensity (i.e. a high-rank innovator). In this way, we could be certain that groupings contained birds that were known to be capable of foraging innovatively. We hypothesized that this procedure would maximize our likelihood of observing socially enhanced innovative foraging behaviour in those individuals less inclined to forage that way.

Methods

Subjects and husbandry

Subjects were 34 wild-caught Indian mynahs. As Indian mynahs are not sexually dimorphic, no attempt was made to control for sex. Birds were captured in the Newcastle (NSW, Australia) region using a walk-in baited trap specifically designed to trap this species (Tidemann 2006). A detailed description of the trap can be found in Griffin (2008). Dog pellets were used as bait. Upon capture, mynahs were transported to the Central Animal House at the University of Newcastle. Before release into an outdoor group aviary (4.4×1.25 m and 2.25 m high), each individual was individually identified using plastic coloured leg bands. Group aviaries were equipped with many perches, several shelters and a large water bath. Mynahs were left undisturbed for a period of 7 days to acclimatize to captivity. Birds had access to water and dog pellets ad libitum throughout their stay in captivity, except during tests that required short periods of food deprivation. All tests involved the use of dog pellets.

As mynahs are classified as an introduced pest species in Australia, they are the target of ongoing pest management strategies, and it is illegal to release them. Consequently, mynahs from experiment 1 were euthanized at the end of testing using a procedure described elsewhere (Griffin & Boyce 2009). Sex was determined by post mortem examination of reproductive organs.

All animal care 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 (protocols A-2008-128 and A-2011-154).

General procedure

Each mynah underwent two phases of testing, an individual test phase and a social test phase. The first phase was designed to assess the level of neophobia of each individual mynah alone, as well as its innovation performance. The second phase was designed to assess neophobia and innovation performance of each individual mynah in the presence of a conspecific. For all tests, birds were transferred from the group aviary to test aviaries 2×1 m and 2 m high either

alone (individual phase) or in pairs (social phase) and allowed 2 days to acclimatize. Test aviaries were equipped with perches, a nestbox and a water bath. When housed alone, mynahs had access to one food dish. When housed in pairs, mynahs had access to three feeding dishes to avoid the chances of food monopolization by one bird. Mynahs were food-deprived overnight prior to all tests. For all tests, mynahs were observed from behind an observation hide placed 6 m away from the aviary. All trials were filmed.

Individual phase

On the third morning after transfer to the test aviaries, each mynah underwent a neophobia test. Neophobia, defined as the aversion to approach novel objects (Greenberg 2003), was evaluated by measuring the latency (test latency) of the focal bird to approach its familiar food dish in the presence of a novel object mynahs are unlikely to have encountered in the wild (green plastic hair brush), and comparing it with the latency (baseline latency) to approach the familiar food dish in the absence of any novel object. To obtain a baseline approach latency, the experimenter approached the aviary from behind a hide and placed a food item in the mynah's familiar food dish, and then returned to the hide. Latency to consume the food item was then measured. If the bird failed to approach within 20 min, the test was aborted and the mynah was given access to food. The test was then attempted once again the following day following overnight food deprivation. As soon as the bird had consumed the food item and moved away from the dish, the experimenter approached the dish once again, placed a food item in the dish and a novel object next to it, before returning to the hide. Latency to consume the food was measured once again, and was capped at 1201 s if the bird failed to approach within 20 min.

On the fourth morning after transfer to the test aviaries, each mynah underwent an innovation test. The procedure for the innovation test was designed to measure each bird's innovation propensity and allocate it an innovation rank. Each bird was ranked using its innovation success (see below), attempt rate (the number of beak-to-task contacts per min) and motor diversity (the total number of different motor techniques such as grab, lever, peck used while attempting to solve an innovation task; M. Diquelou & A. S. Griffin, unpublished data). Attempt rate and motor diversity are key determinants of innovation in mynahs, with higher attempt rates and higher motor diversity significant predictors of innovation performance (Sol et al. 2012; M. Diquelou & A. S. Griffin, unpublished data). The expression of motor diversity is dependent upon the particular task used and not all tasks allow the expression of all actions. Specifically, if there is nothing to be leveraged upwards in a particular task, then birds will not express this technique. The innovation task was hence designed to enable the expression of the largest range possible of motor actions in those mynahs that were highly motor flexible. Hence, the measurement of motor diversity precluded us from counterbalancing the task used in the individual versus the subsequent social phase (see below), and all mynahs underwent the same innovation task in order to obtain a measure of motor diversity comparable across individuals.

The innovation task consisted of a Plexiglas box (25 × 10 cm and 6 cm high) with two drawers and two petri dishes attached to the top (Fig. 1a). One of the petri dishes was the right way up so the lid could be removed by either levering the lid upwards or by grabbing a small piece of tape attached to the edge and pulling, whereas the other dish was inverted, so the only way to remove the lid was to grab a small hook on the top. One of the drawers could be pushed open, whereas the other could be moved only by grabbing a piece of string attached to the front. To reduce the neophobic response to the innovation task, each mynah was presented with the task on the day before innovation testing. The task was presented with all containers open and filled with food, and was left in place until all the food was consumed.

An innovation trial started with a food item being placed on top of the puzzle box to ensure the bird was motivated to feed. Once the mynah had consumed the food, the experimenter approached, placed a few food items inside each container of the puzzle box, closed them, and withdrew once again to the hide. Latency to solve the first container on the puzzle as well as any further containers was measured. Mynahs were observed for 30 min, and any containers that were not solved were attributed a capped latency of 1801 s. At the end of testing, each mynah was transferred back into the large group aviary.

Once all 34 mynahs had been tested individually, the number of containers opened, the mean solving latency, the attempt rate and the motor diversity were used to rank the 34 mynahs from highest to lowest innovation performance. These ranks were used to create pairs for the subsequent social phase.

Social phase

During the social phase, neophobia and innovation performance of each mynah were assessed once again in the presence of a conspecific. We created mixed pairs, which included a high-rank innovator and a low-rank innovator, and homogeneous pairs, which consisted of two medium-rank innovators. Specifically, for mixed pairs, the highest ranked innovator mynah (rank 1) was paired with the mynah ranked 26th, the second highest innovator was paired with the mynah ranked 27th, etc. For the homogeneous pairs, each mynah from rank 10 downwards was paired with the closest ranked individual, such that the mynah ranked 10th was paired with the mynah ranked 11th, etc. Pairs of mynahs were moved from group housing into test aviaries and allowed 2 days to acclimatize.

On the second and third morning after transfer, each pair underwent a neophobia test. Baseline and test latencies were obtained on two consecutive mornings, and the order was counterbalanced across subjects. To obtain baseline approach latencies, the experimenter approached the aviary from behind a hide and placed two of the familiar food dishes containing two food items each in two spatially distant locations in the aviary. Using two dishes rather than one ensured that both birds had equal opportunity to approach a food dish, while placing them far apart avoided one bird monopolizing both dishes. Latency to consume the food was measured for both birds. The same procedure was used to obtain test latencies, except that one of two identical novel objects (a plastic brush of similar size to that used during the individual phase but a different colour, blue) was placed beside each food dish. We have previously shown that neophobia responses do not differ significantly across the small range of objects used in our laboratory to measure neophobia in mynahs (Sol et al. 2011; Lermite 2012). Consequently, we considered it unnecessary to counterbalance the use of the two objects across the individual and social phases. Birds were observed for a total of 20 min during each test. During baseline trials, all mynahs fed within the 20 min time period. Mynahs that failed to feed in the presence of a novel object were attributed a capped feeding latency of 1201 s.

On the fourth morning, each pair of mynahs underwent an innovation test. The puzzle box used in the social phase was designed to minimize the carryover of any experience with the task from the individual phase to the social phase, but nevertheless encourage the birds to express a diverse range of motor actions, just like the task in the individual phase. Each pair was presented with two identical tasks each consisting of four opaque Styrofoam cups glued to a plank of wood (Fig. 1b). Each cup was covered with a petri dish lid, enabling the birds to see the food reward inside the cup, and had one hole in the side; on three cups, the hole was fitted

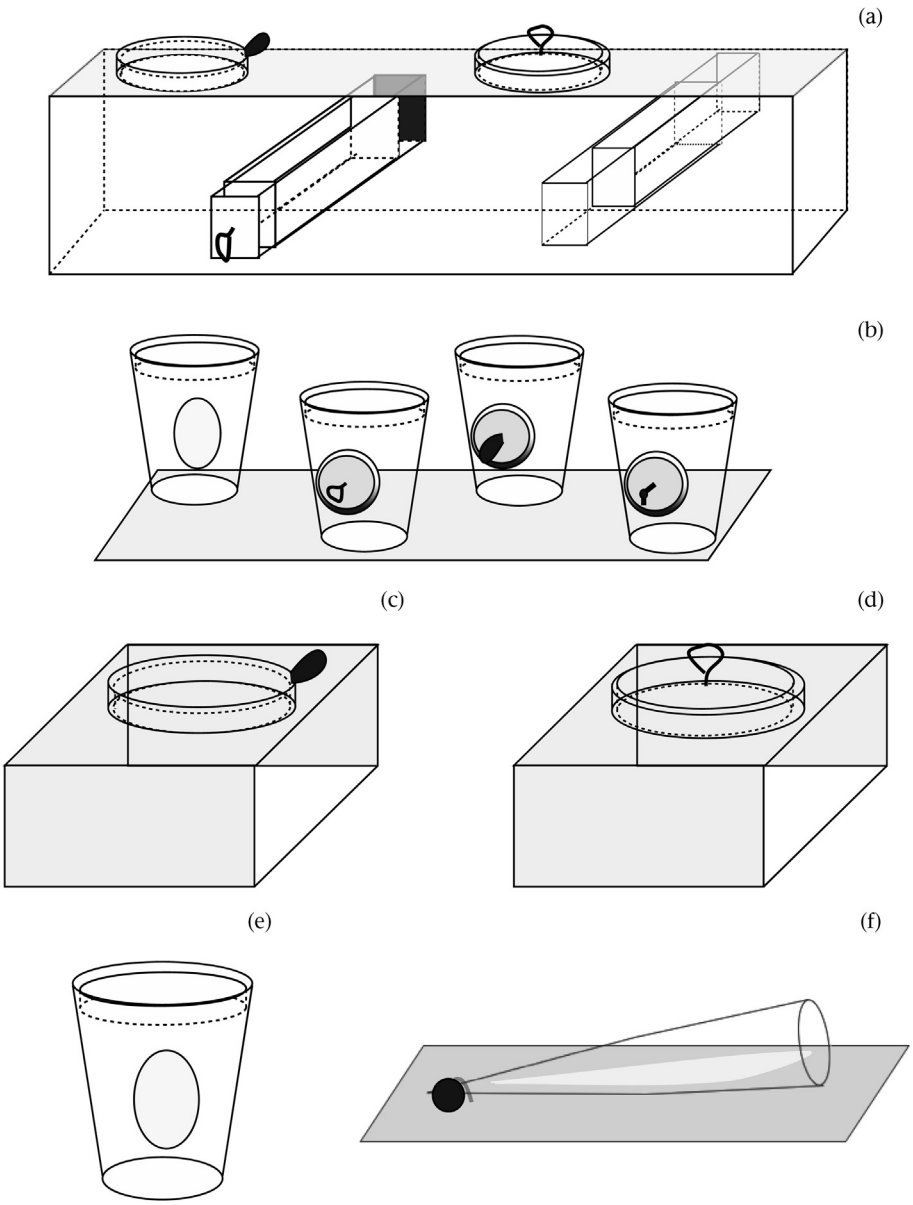

Figure 1. Schematic of innovation tasks used during (a) the individual phase of experiment 1, (b) the social phase of experiment 1, (c), (d), (e) and (f) experiment 2. To hold constant the per capita number of containers during the social phase of experiment 1, two replicates of tasks (b) were placed in the test aviary in the social phase of experiment 1. For the same reason, five replicates of tasks (c–f) were placed in the test aviary during the social phase of experiment 2. See text for more details.

with a bottle lid, which had to be pulled out to reach the food, whereas on the fourth cup, the hole was covered with a thin film of plastic, which had to be pierced. One bottle lid could be removed by pulling a hook, the second by pulling a string, and the third by pulling a piece of tape. The trial started with a food item being placed on top of the cup to measure initial latency to approach and ensure that each bird was motivated to feed. As soon as both birds had consumed a food item, the experimenter approached, placed a food item inside each of the cups and withdrew once again to the observation hide. Latency to solve the first container on the puzzle as well as any further containers was recorded, as well as the identity of the bird that solved the task. Each pair was watched for a 30 min observation period, and any containers that were not solved were attributed a capped latency of 1801 s for each of the birds in the pair.

To measure the effects of dominance on innovation, we scored all displacements within two bird lengths of the innovation task. A displacement was scored each time a bird caused another bird to move away from the feeder by rapidly approaching it and/or pecking at it (Lehner 1998; Tuchscherer et al. 1998). Pecking and fights were rare and no bird was injured during the trials.

Data analysis

All trials were filmed and behaviour scored from video recordings using JWatcher 1.0 (Blumstein et al. 2006). An innovation attempt was scored as any beak-to-task contact. Attempt rate was calculated by dividing the total number of attempts by the total observation time, which was either the solving latency for birds that solved a task or the capped solving latency for birds that did not. Each attempt was defined as one of nine motor actions (M. Diquelou & A. S. Griffin, unpublished data), and for each bird, motor diversity was the total number of actions used (M. Diquelou & A. S. Griffin, unpublished data). Motor diversity was only measured for the individual phase for the purpose of ranking the innovation propensity of mynahs, whereas attempt rates were quantified for

both individual and social phases in order to examine how sociality affected motivation to solve the task.

To quantify the change in innovation performance from the individual to the social phase, we modelled the proportion of containers opened by each individual using a binomial generalized linear mixed model (GLMM) with a logit link and the binomial response variable encoded as the total number of containers opened (successes) relative to total number of containers available to be solved (four in the individual phase; eight in the social phase). Phase (individual versus social) was entered as the predictor variable. This approach enabled us to account for the fact that we doubled the number of containers available when mynahs were in pairs relative to when they were tested alone, in order to retain the per capita number of containers. To compare the change between individual and social phases in the number of containers opened by high-, medium- and low-rank innovators, we calculated the difference between the proportion opened during the individual phase and the social phase for each category of innovator and used nonparametric Mann–Whitney tests for subsequent pairwise comparisons.

We complemented analysis of innovation success with an analysis of solving latencies. To this end, we analysed the latency to solve the first container from first contact to solving, using Cox proportion hazard models (Crawley 2002) with phase (individual, social) as a categorical variable. We conducted an identical analysis on mean latency to solve the task calculated for each bird across all the containers the individual opened.

To examine the effects of phase (individual versus social) and trial (baseline versus novel object) on willingness to feed, feeding latencies from the neophobia tests were analysed using a Cox proportion hazard model with phase and trial, as well as their interaction, as covariates. Significant effects were followed up using parametric paired *t* tests after log transforming the original latency variables. Baseline feeding latencies were compared across phases directly, while neophobia latencies were compared across phases using the difference between the novel object latency and the baseline latency for each bird.

To explore mechanisms underpinning changes in innovation performance, we examined the effects of phase on motivation by modelling attempt rate using a GLMM with a normal distribution and an identity link. We also incorporated the attempt rate and neophobia latency for each individual and each phase as additional explanatory variables into the GLMM for proportion of containers opened.

All analyses were conducted using SPSS version 20 (SPSS Inc., Chicago, IL, U.S.A.). Significance thresholds were set at 0.05.

Results and Discussion

Innovation

Innovation performance declined significantly when mynahs were tested in pairs relative to when they were tested alone. When alone, 29 of 34 (85%) individuals solved at least one container; when in pairs, this number dropped to 15 (44%; Fisher exact test: $P < 0.01$). Overall, the proportion of containers opened per individual decreased (proportion opened when alone: 0.55 ± 0.06; in pairs: 0.12 ± 0.03). A GLMM comparing proportion of containers solved during the individual phase with proportion solved during the social phase indicated that this drop in performance was highly significant (coefficient = 2.153; $t = 8.935$, $P < 0.001$).

Drops in performance affected high-rank and medium-rank innovators similarly (two-tailed Mann–Whitney *U* test: $U = 82.0$, $N_1 = 8$, $N_2 = 18$, $P = 0.605$), but not low-rank innovators, which exhibited a floor effect and decreased performance from the individual to the social phase significantly less than all other innovators (two-tailed Mann–Whitney *U* tests: high versus low: $U = 58.5$, $N_1 = N_2 = 8$, $P < 0.001$; medium versus low: $U = 3.0$, $N_1 = 18$, $N_2 = 8$, $P < 0.001$; Fig. 2). Hence, being paired with a high-rank innovator failed to facilitate innovation in low-rank innovators, despite high-rank innovators remaining consistent and continuing to perform significantly better than the low-rank innovators with which they were paired (proportion of containers opened: high-rank innovators: 0.50 ± 0.12; low-rank innovators: 0.08 ± 0.05; two-tailed Mann–Whitney *U* test: $U = 8.0$, $N_1 = N_2 = 8$, $P = 0.010$).

A reduction of innovation performance in the presence of a social companion was also apparent in an analysis of solving latencies. Mynahs took significantly longer to open their first container during the social phase relative to the individual phase (Cox regression: $W = 18.07$, $P < 0.001$; Fig. 3). Mean latencies averaged across all opened containers also increased significantly when in pairs relative to when individuals were alone (Cox regression: $W = 21.51$, $P < 0.001$).

Neophobia

Feeding latencies during the neophobia trials are depicted in Fig. 4. A survival analysis on latency to feed during neophobia tests revealed a significant effect of test (baseline versus novel object: $W = 25.186$, $P < 0.001$), indicating that individuals took longer to feed in the presence of a novel object than in its absence whether alone or not. The effect of phase was only marginally significant ($W = 3.629$, $P = 0.057$). The Cox regression revealed a significant test * phase interaction ($W = 5.595$, $P = 0.018$). Following up this effect, paired *t* tests revealed that latency to approach and consume food during the baseline trial, when no novel object was present, decreased significantly in the presence of a social companion relative to when mynahs were alone (mean latency: alone: 265.3 s; in pairs: 9.8 s; $t_{33} = 5.800$, $P < 0.001$; Fig. 4). In contrast, latency to approach food in the presence of a novel object relative to when no novel object was present (i.e. test minus baseline latency difference) increased significantly in the presence of a social companion (mean test minus baseline: alone = 235 s; in pairs = 263 s; paired *t* test: $t_{33} = -2.254$, $P = 0.031$; Fig. 4).

Motivation

The presence of a social companion significantly reduced motivation during the problem-solving task (mean attempt rate:

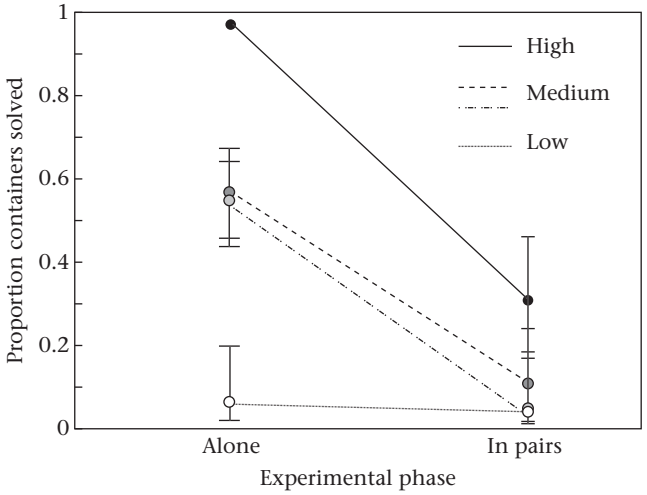

Figure 2. Mean ± SE proportion of containers solved by each of three categories of innovators defined according to a ranking of their innovation performance when tested alone (high, medium, low), and then tested once again in the presence of a conspecific in experiment 1. High-rank innovators were paired with a low-rank innovator, while medium-rank innovators were paired with another medium-rank innovator. See text for more details.

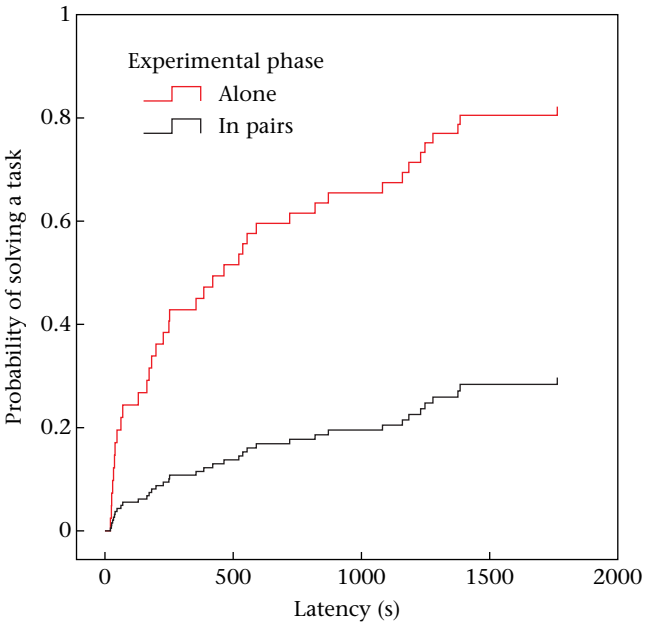

Figure 3. Probability of solving a task as a function of time since first contact by mynahs tested alone and in the presence of a conspecific in experiment 1.

alone: 9.9 attempts/min; in pairs: 3.0 attempts/min; GLMM: coefficient = 6.238; $t = 3.507$, $P = 0.002$). The decrease in attempt rate remained significant when each individual's phase-specific neophobia response (novel object latency minus baseline latency) and the neophobia * phase interaction were introduced into the model as covariates, indicating that neither neophobia nor any changes in neophobia between the individual and the social phase fully mediated the decline in motivation (Table 1).

Role of motivation and neophobia in innovation

Next, we examined whether the observed increases in neophobia and decreases in motivation from individual to social setting explained the drop in innovation performance. Each individual's phase-specific neophobia response and attempt rate, as well as the interaction of these variables with phase, were introduced into a GLMM for proportion of containers solved. Phase and attempt rate were the only significant explanatory variables, indicating that neither neophobia nor changes in neophobia mediated decreased innovation performance (Table 2).

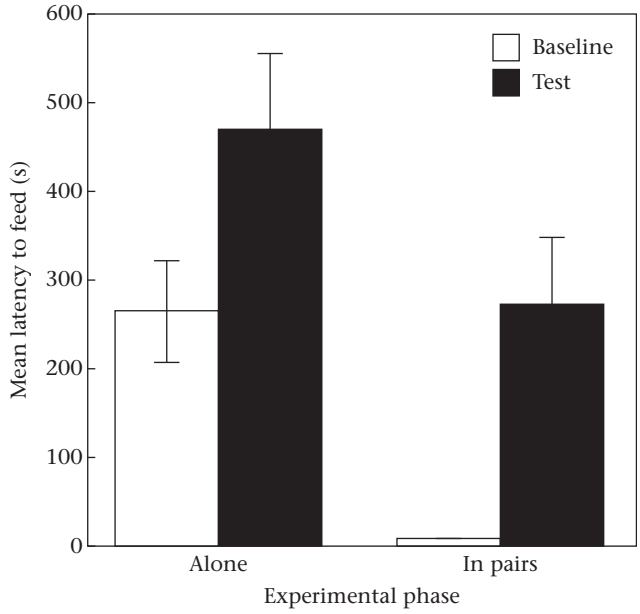

Figure 4. Mean latency to feed ± SE in the absence (baseline) and presence of a novel object by mynahs when tested alone versus in the presence of a conspecific in experiment 1.

Table 1
Attempt rate modelled as a function of phase (individual, social), neophobia and the interaction between phase and neophobia (GLMM)

	Coefficient	SE	t	P
Intercept	3.484	0.881	3.956	<0.001
Phase (social)	5.203	1.889	2.755	0.011*
Neophobia	−0.001	0.002	−0.966	0.338
Neophobia by phase	0.005	0.003	1.791	0.078

The comparisons are relative to a reference level indicated in parentheses.
*$P < 0.05$.

Role of aggression in innovation

Finally, we examined the role of aggression in innovation performance. We reduced the likelihood of resource monopolization influencing individuals' innovation propensity during the social phase by holding constant the per capita number of containers during the individual and social phases of the experiment, and by spacing the tasks out in the aviary. In general aggression was very low in mynah pairs during the innovation tests (mean number of aggressive acts per pair during the 30 min innovation trial = 3.9 ± 1.4; median = 0.0), with 64.7% of mynahs, and 35.3% of pairs, showing no evidence of any aggression. Males were significantly more aggressive than females (Kruskal–Wallis test: $P < 0.001$), whether paired with other males or other females (mean number of aggressive acts during the 30 min innovation trial: males: 6.5 ± 2.4; females: 0.67 ± 0.4; median males = median females = 0.0). The number of aggressive displacements was positively correlated with attempt rate (Spearman rank correlation: $r_S = 0.599$, $P < 0.001$; Fig. 5), indicating that more motivated individuals were also more aggressive. Aggression did not correlate with solving success (Spearman rank correlation: $r_S = 0.294$, $P = 0.91$), however, and individuals in aggressive pairs did not decrease innovation performance more than individuals in pairs in which there was no aggression (change in percentage of containers opened: mynahs in pairs with aggression: −57.8 ± 8.1%; mynahs in pairs with no aggression: −52.0 ± 7.8%; two-tailed Mann–Whitney U test: $U = 144.5$, $N_1 = 22$, $N_2 = 12$, $P = 0.657$), suggesting that changes in performance in a social setting were not systematically associated with higher aggression.

Behavioural consistency

Innovation performance was correlated across the two phases, indicating that the relative performance of individuals remained

Table 2
Innovation success modelled as a function of phase (individual, social), attempt rate, neophobia and the interactions between phase and neophobia, and phase and attempt rate (GLMM)

	Coefficient	SE	t	P
Intercept	−2.489	0.297	−8.389	<0.001*
Phase (social)	1.814	0.307	5.914	<0.001*
Neophobia	−0.001	0.001	−0.850	0.407
Attempt rate	0.163	0.032	5.172	<0.001*
Neophobia by phase	−0.001	0.001	0.908	0.375
Attempt rate by phase	−0.046	0.043	−1.074	0.287

The comparisons are relative to a reference level indicated in parentheses.
*$P < 0.05$.

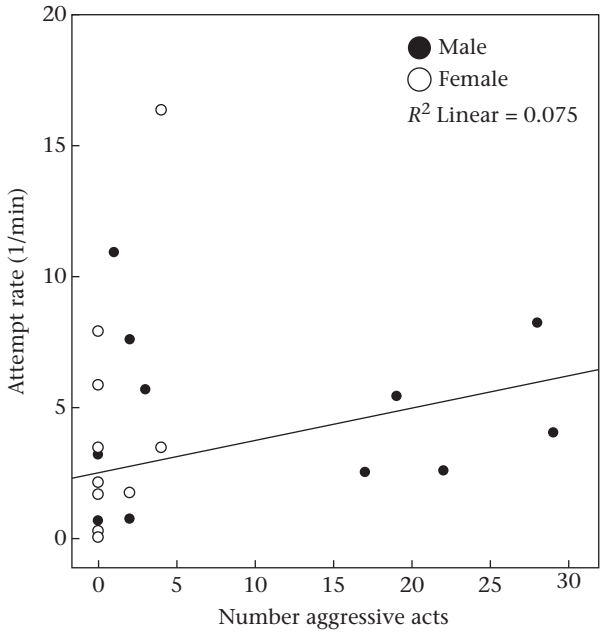

Figure 5. Correlation between the number of displacements/aggressive acts performed by an individual mynah and the number of attempts to solve the innovation task per min during the social phase of experiment 1.

consistent across the two phases despite the overall decline (percentage of containers opened: Spearman rank correlation: $r_S = 0.544$, $P = 0.001$).

Our findings strongly suggest that a social situation inhibits innovation performance with mynahs both opening a smaller proportion of available containers and taking longer to do so. Furthermore, even though high-rank innovator mynahs, which had a high propensity to innovate alone, also innovated in pairs, their innovative behaviour did not facilitate innovation in low-rank innovators. Drops in performance were not confined to aggressive pairs suggesting that socially mediated inhibition of innovative behaviour was not systematically attributable to aggressive competition. Significant decreases in motivation from individual to social phases indicate rather that mynahs refrained from engaging with the task in a social setting. As decreases in motivation did not fully explain reduced innovation performance in a social setting, it appears that mynahs not only attempted the task less, they were also less effective when they did try.

Baseline neophobia tests in which birds were required to forage in the absence of any risk revealed significantly shorter feeding latencies when in pairs than when alone, while in contrast, novel object tests, in which birds were required to forage in the presence of a risk, revealed significantly longer feeding latencies when in pairs than when alone. This difference suggests that the presence of a conspecific facilitates foraging in safe situations, but inhibits foraging under risk.

Rather than social context inhibiting innovation performance, one possible alternative explanation is that the task used in the social phase was more difficult than the task used in the individual phase. We suggest this is unlikely for two reasons. First, both the individual and social task offered a variety of different opening mechanisms (lid that needed to be pulled, plastic film that needed to be pierced, drawer that needed to be pulled, drawer that needed to be pushed, etc. Fig. 1). Increased latencies during the social phase were apparent on the very first container opened. Consequently, for the social task to have been more difficult than the individual task, one would need to assume that all the opening mechanisms on the social task were more difficult than all those on the individual task, which is unlikely. In fact, some of the opening mechanisms experienced during the first phase could have transferred to the second phase (e.g. pulling the hook on the drawer in the individual phase and pulling the hook on the lid in the social phase; Fig. 1), which should have contributed to decreasing opening latencies during the social phase relative to the individual phase. Yet, we found increased solving latencies. Second, in previous work, we have tested similar versions of both these tasks using a fully counterbalanced repeated-measures design in which each mynah attempted all of the available tasks. Results revealed no significant differences in innovation performance across tasks (Diquelou 2010; Lermite 2012). Nevertheless, we designed experiment 2 with this caveat in mind.

AIM OF EXPERIMENT 2

The aim of experiment 2 was to examine the possibility that socially mediated inhibition of innovative behaviour was particular to mynahs held in pairs. We envisaged the possibility that in larger groups, scramble competition might override the effects of inhibition. In experiment 1, birds were allocated to pairs without controlling for sex, creating a mix of same- and mixed-sex pairs, making it difficult to explore the effects of sex on socially mediated inhibition of innovation. Consequently, in experiment 2, birds were sexed genetically before being allocated to single-sex groups of five mynahs to examine whether socially induced inhibition operated in larger groups and similarly across both sexes. Finally, we addressed the possibility that decreased innovation in a social setting was attributable to task difficulty rather than social setting, as well as the possibility that socially induced inhibition of innovation might decrease if birds were given two, rather than just one, innovation tests.

Methods

Subjects and husbandry

Thirty-five wild-caught Indian mynahs took part in experiment 2, none of which had participated in experiment 1. Two feathers of each bird were collected for a DNA analysis of each bird's sex. Birds were captured and held as in experiment 1. Following 10 days of acclimatization to captivity, birds were selected to make four groups of five males and three groups of five females. At the end of testing, mynahs were placed back into large group aviaries to take part in other studies.

General procedure

Each group of birds underwent the same 3-week test procedure. During week 1, five preselected birds were captured in the large group aviary and moved to a flight aviary (1×1 m and 2 m high) with ad libitum access to food and water and were left for 1 week to adjust to their new environment. In week 2, each group underwent two innovation trials. In week 3, birds were separated into individual aviaries and given 2 days to acclimatize to individual housing, after which each bird underwent two individual innovation trials on 2 successive days. Over the course of the four innovation trials, birds were presented with four different innovation tasks in an order that was counterbalanced across birds and phases (individual, social), such that mynahs in groups always experienced different tasks to those they experienced individually. The first two options consisted of a petri dish with either an upright or an inverted lid (Fig. 1c, d). The upright lid could be removed by leveraging it upwards or grabbing a piece of tape attached to its edge. The inverted lid could be lifted only by grabbing a hook attached to its centre. The additional two options consisted of a

Styrofoam cup with a hole in the side covered with plastic film, which needed to be pierced to get access to the food, while the final task consisted of a piece of paper that needed to be pulled out of a plastic champagne flute to get access to the food (Fig. 1e, f).

Social phase: innovation

Each group of mynahs was presented on two successive mornings with two different innovation tasks selected from the four possible options. To reduce any neophobic response, the innovation tasks were presented to the birds with food readily accessible for 2 days during week 1 and on the evening before the test. Following overnight food deprivation, each mynah group was presented with the task with one dog pellet readily available to ensure that birds were motivated to feed, after which the experimenter withdrew to the observation hide. Once the food has been consumed, the innovation task was presented once again with food in each closed container. To avoid any one bird monopolizing the task, and to hold constant the per capita number of containers across individual and social phases, five exact replicates of the innovation task were spaced out on the aviary's floor. Behaviour of all individuals within the group was recorded for 30 min.

Individual phase

To assess each bird's propensity to innovate when alone, individually held mynahs received the two remaining innovation tasks on two successive mornings following a night of food deprivation. As in experiment 1, neophobia responses to the tasks were reduced by presenting the task to the birds on the evening before the test with readily available food. The innovation trial started with a food item being placed on top of the container to ensure that the bird was motivated to feed. Once the focal subject had consumed the baseline food item, the task was presented a second time with food within the container. Mynahs were watched for 30 min. Latency to solve the task was recorded, and trials for which no solving occurred were attributed a capped latency of 1801 s.

Results and Discussion

Despite being tested in the presence of four social companions, rather than only one, innovation performance dropped significantly from individual to social phases, replicating the social inhibition effect found in experiment 1. When alone, 15 of 35 mynahs (43%) solved at least one of the innovation tasks within the total 30 min observation period. Of these, just over half (53%) solved both innovation tasks. In contrast, in a group setting no bird solved either task. The difference in solving success was significant (Fisher exact test: $P < 0.01$). The social suppression effect was identical in both male and female groups.

GENERAL DISCUSSION

This study aimed to test the effects of sociality on innovation propensity by measuring innovation performance in Indian mynahs both when alone and in the presence of either one or four conspecifics. Independent of how many conspecifics were present, we found a robust decrease in innovation performance pointing towards a systematic social inhibition effect on innovation. Birds attempted to solve the problem less often, solved it less frequently and took longer to solve it. In experiment 2, this inhibition occurred regardless of the type of task the birds were attempting to solve in the individual and social phases, indicating that decreased innovation was not attributable to task difficulty. A social inhibition effect was also observed when mynahs were required to forage in a risky context. Mynahs delayed foraging next to an unfamiliar object in the presence of a social companion relative to when they were alone. The presence of conspecifics had the opposite effect on a baseline test, in which latency to feed from a familiar food dish was compared in an individual and social setting. Here, mynahs were faster to feed in the presence of a conspecific than alone. Taken together, these findings suggest that sociality facilitates foraging in safe situations and inhibits foraging in risky ones. This conclusion is in line with several other studies that have found delayed foraging in the presence of others in risky situations (Pfeffer et al. 2002; Van Oers 2005; Stöwe et al. 2006a; Overington et al. 2009b).

Interference competition offers a potential explanation for why mynahs delayed foraging in the presence of conspecifics relative to when alone. Innovators incur the risk of being attacked and/or having the food stolen by a bystander, leading individuals to withhold from innovating when potential thieves are present. Consistent with this idea, carib grackles, *Quiscalus lugubris*, suppress food dunking, which is known to be prone to theft, in the presence of conspecifics, and dunk in water located further away from onlookers (Overington et al. 2009b). We suggest that interference is unlikely to explain the social inhibition effect found here. First, suppression was no more likely to occur in aggressive pairs than in nonaggressive pairs. Second, even though we observed food stealing from an innovator on a few occasions, mynahs also delayed foraging in the presence of a novel object even though there was no risk of food being stolen in that context.

An alternative explanation for delayed foraging in the presence of others involves a social negotiation over engaging in the risks inherent to innovating. There is some evidence suggesting that innovators are more likely to carry parasites (Vas et al. 2011; Soler et al. 2012), but such negative consequences of innovative foraging are more likely to be associated with tasting novel foods than technical innovations of the type measured here (Overington et al. 2009a). Alternatively, it is possible that the act of innovating increases individual predation risk, perhaps because it requires sustained attention to the task and decreases the capacity of individuals to engage simultaneously in antipredator vigilance (Lima & Bednekoff 1999; Bugnyar & Kotrschal 2002; Coolen & Giraldeau 2003; Mathot & Giraldeau 2007). This idea is consistent with the reasoning behind theoretical producer–scrounger models. These models predict that producers should be less common than scroungers under increased predation risk, as long as scroungers have the advantage over producers that they can simultaneously scan the environment for foraging conspecifics and predators (Ranta et al. 1998; Barta & Giraldeau 2000). This idea is supported by empirical data (Bugnyar & Kotrschal 2002).

The idea that sociality induces a negotiation over risk is also consistent with several other studies, which have found increases in foraging latencies in the presence of social companions under risky conditions (Pfeffer et al. 2002; Van Oers 2005; Stöwe et al. 2006a; Overington et al. 2009b). For example, Pfeffer et al. (2002) showed that of 18 greylag geese, *Anser anser*, able to solve a task when alone, only four exhibited this behaviour in a group setting. Similarly, carib grackles, female and slow-exploring male great tits, as well as fast-exploring ravens, *Corvus corax*, all delay foraging in risky situations when others are present, suggesting that social inhibition of foraging under risky conditions may be a widespread phenomenon.

Nevertheless, our findings contrast with those from two recent studies in house sparrows, *Passer domesticus*, and great tits, respectively, which both found that individual innovation rates increased in larger, relative to smaller, groups (Liker & Bókony 2009; Morand-Ferron & Quinn 2011). Having ruled out alternative explanations, the authors of both studies attributed this effect to the 'pool of competency effect', whereby larger social groupings include a greater diversity of individual skills, which in turn leads to greater solving probabilities (Liker & Bókony 2009; Morand-Ferron

& Quinn 2011). As one study was conducted in captivity and the other in the wild, the discrepancy between these studies and ours are unlikely to be an artefact of captivity. We suggest rather that there may be species' differences in the way individuals respond to sociality in the presence of risky foraging opportunities. Free-ranging mynahs behave very cautiously under risky foraging conditions (Sol et al. 2012), more cautiously than other common Australian species (M. Diquelou & A. S. Griffin, unpublished data). Ravens are also well known for their high neophobia (Stöwe et al. 2006a). Such species may be more inclined to attempt to offset risk in the presence of others.

Our study revealed that even though mynahs were less likely to innovate in the presence of conspecifics than alone, individual innovation performance was correlated across individual and social phases. Higher-rank innovators in a solitary setting continued to innovate more often in a social setting than lower-rank innovators, as did medium-rank innovators. To our knowledge, this is the first study to show cross-contextual stability of innovation performance across solitary and social settings. This finding extends the conclusions from several other studies, which have shown individual consistency in innovation performance across time and different innovation tasks, and consolidates the idea that innovation propensity can be a stable individual attribute (Laland & Reader 1999; Morand-Ferron et al. 2011).

In conclusion, our study showed that social groupings facilitated noninnovative foraging, but inhibited innovative foraging and foraging in the presence of an unfamiliar object. Our results suggest that group members engage in a negotiation over risk and leave the act of innovating to other individuals when possible. If innovating does indeed expose individuals to greater predation risk, then predation pressure could act to constrain the diffusion of innovations. Future research examining whether innovations are more common in geographical areas where predation pressure is low, such as on predator-free islands, may offer a comparative approach to testing this idea. It is noteworthy that Overington et al. (2011) failed to find a relationship between the cross-taxa distribution of foraging innovations and exposure to predators, but an analysis focusing on technical innovations, rather than innovations involving tasting novel foods, may reveal a different outcome (Overington et al. 2009a).

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