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Social learning about places: observers may need to detect both social alarm and its cause to learn

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It is widely established that social alarm signals trigger learning about discrete stimuli present at the same time. Such learning facilitates, for example, acquisition of responses to novel predators and has the functional advantage that individuals avoid exposing themselves to a potentially risky situation. Avoidance of potential danger might equally apply to learning about risky places, but would require social alarm signals to trigger learning about contextual cues, rather than discrete stimuli. Here, we tested this hypothesis by analysing the behaviour of experimental observer Indian mynahs, *Acridotheres tristis*, both before and after they had watched demonstrator mynahs showing alarm behaviour at a foraging site where observers were accustomed to feeding. To isolate changes specifically attributable to the behaviour of demonstrators, we compared this group's post-training behaviour with that of a control group, which watched social companions foraging at the feeding site. Unexpectedly, we found no evidence that experimental observers became more wary of the feeding site after observational training relative to control observers, suggesting that social alarm signals do not trigger learning about the location in which an alarmed individual is observed. In light of previous work in our laboratory showing that Indian mynahs become more wary in a place in which they have observed a predator attack on a social companion, we suggest that social learning about places may require observation of both social alarm and its cause.

Functional theories of learning predict that learners should rely more on social information and less on private information as the potential cost of individual assessment increases (Laland 2004; Kendal et al. 2005). Consequently, social learning should be most evident when learning about stimuli that pose threats and thus must be avoided. Such reasoning should equally apply to place learning. Although place learning through direct exposure to danger (e.g. a predator) is well established, such learning carries a potentially high cost to the individual. Risks may be minimized by remembering the location in which a social companion has signalled the presence of a predator and either avoiding that location or engaging in greater risk assessment within that location in the future. Hence, consideration of function suggests that social learning about places should be possible.

Social learning about predators is a taxonomically widespread learning phenomenon, in which animals become more wary of a previously unfamiliar predator after they have experienced it together with conspecific alarm signals (reviewed by Griffin 2004). It is generally accepted that such learning occurs via a classical conditioning mechanism in which social alarm signals play the role of a biologically significant event, the unconditioned stimulus (US), and trigger learning about a novel predator, the initially neutral event or conditioned stimulus (CS), when presented at the same time (Suboski 1990; Heyes 1994). It seems reasonable to suggest that this heuristic could equally apply to social learning about places whereby social alarm signals (US) trigger learning of co-occurring contextual cues (CS), rather than a discrete external stimulus. Indeed, extensive work on individual place learning has shown repeatedly that contextual information can play the role of a CS and become associated with an aversive US (Siegfried & Frischkencht 1989; Dolman et al. 1996; Blanchard et al. 2001; Dunlop et al. 2006). For example, goldfish, *Carassius auratus*, that receive a spatially cued electric shock (US) consequently avoid that area (CS). Similarly, detection of cat odour (US) causes rats to increase defensive behaviours (crouch/freeze with sniff/head movements) significantly when later returned to the test environment (CS) (Blanchard et al. 2001), whereas exposure to a live cat triggers acquired hiding (Blanchard et al. 2005). Furthermore, contextual cues (CS) can be learnt about via social information (US).

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Indeed, work on appetitive learning in various avian species has revealed that individuals show significantly enhanced preferences for areas (CS) in which they have been given the opportunity to observe conspecifics foraging (US) (McQuoid & Galef 1992; Bednekoff & Balda 1996). In sum, a proximate analysis supports the functional prediction that social alarm signals indicating the presence of a predator might well trigger learning about a place.

The Indian mynah, *Acridotheres tristis*, is a highly opportunistic species of passerine that has invaded large areas of the east coast of Australia since it was introduced in the 1800s. Indian mynahs are highly social and can be found foraging in groups of two to 20 individuals throughout the day (Pell & Tideman 1997). At night, birds form communal roosts sometimes containing thousands of individuals. The social and highly adaptable lifestyle of Indian mynahs, together with their propensity to produce a variety of antipredator signals, makes this species an ideal system to study the mechanism and content of social learning about danger (Pell & Tideman 1997; Pizzey & Knight 1998; Tideman 2006; Griffin 2008, 2009; Griffin & Boyce 2009).

We have previously shown that Indian mynahs become more wary in a location in which they are accustomed to foraging after they have observed a human surrogate 'predator' chase, catch, and remove a social companion from that location (Griffin & Boyce 2009). In that study, a control group that watched a human perform the same capture gestures at the feeding site, but with no conspecific present, became less wary in the feeding location during a subsequent foraging trip. Differences in acquired behaviour between experimental and control observers indicate that social alarm stimuli are important for triggering place learning. The aim of this study differed slightly from our earlier work in that we wished to examine to what extent the alarm behaviour of a social companion per se can trigger contextual learning. The aim was hence to test whether the heuristic underpinning social learning about predators can support social learning about places.

Food-deprived mynahs were trained to move between a holding site and a feeding site through a small pipe. Mynahs allocated to an experimental observer group were then provided with the opportunity to watch a demonstrator mynah located at the feeding site expressing high levels of alarm in response to a predator (cat, *Felis catus*), which observer mynahs were unable to see (observational training). In contrast, mynahs assigned to a control observer group watched a demonstrator mynah foraging at the feeding site. To quantify the effects of learning, we measured latency to access the feeding site, behaviour once there, and willingness to remain there, both before and after observational training in both groups of observer mynahs. Comparisons between experimental and control observers allowed changes in behaviour that were specifically attributable to associative learning to be isolated from those caused by nonassociative effects (Shettleworth 1998).

METHODS

Subjects and Husbandry

Fifty Indian mynahs were captured in an urban location in Newcastle, on the eastern coast of Australia, using a walk-in baited trap specifically designed to trap this species and widely used for population control (Tideman 2006). This trap, which is described in detail elsewhere (Griffin 2008), works by allowing mynahs to enter a bottom cage ($1 \times 1 \times 1$ m), collect a bait, fly up through two small (0.1 m diameter), one-way channels into a top cage ($1 \times 1 \times 1$ m), and rest on perches while consuming the food item. Given the natural tendency of this species to aggregate, surrounding mynahs approach and enter the trap, attracted in particular by the contact calls of trapped birds. As a consequence, mynahs accumulate in the top cage. The trap is equipped with an opaque roof and shaded sides, which provide the birds with sun protection and cover. Small dog food pellets, a preferred food of Indian mynahs, were provided ad libitum in both top and bottom cages, together with water ad libitum (for more details, see Griffin 2008).

The trapping and transport procedures were identical to those used in earlier work (Griffin 2008, 2009; Griffin & Boyce 2009), so we provide only a brief description here. The trap was placed in a fenced-off schoolyard and was emptied once a day. Each bird was weighed, measured, and individually identified with a lightweight coloured plastic leg band. Male Indian mynahs are typically heavier than females. However, the extent of this size dimorphism is population specific, so no attempt was made to control for sex during subsequent experiments. Birds were then transported in an air-conditioned vehicle to the Central Animal House at the University of Newcastle and released into a large outdoor group flight aviary ($2.25 \times 1.25 \times 4.4$ m). Birds were left undisturbed for a minimum of 3 weeks to acclimatize to captivity. All captive mynahs had access ad libitum to water and a mixture of dog food pellets, fresh fruit, and vegetables.

Twenty-five randomly selected mynahs were assigned to act as observers and 25 were assigned to act as demonstrators. Of the 25 demonstrators, 13 served as alarmed demonstrators and 12 served as foraging demonstrators (see below). Of the 25 observers, 13 were assigned to watch an alarmed demonstrator during observational training (experimental observers) and 12 were assigned to watch a foraging demonstrator (control observers). Sample sizes were determined on the basis of extensive previous work on predator recognition and predator avoidance learning by the first author (Griffin et al. 2001; Griffin 2003, 2008; Griffin & Galef 2005; Griffin & Boyce 2009).

Each individual was held using a procedure identical to that used in earlier work on place learning in Indian mynahs (Griffin & Boyce 2009). For testing, each subject was transferred from the outdoor flight aviary to an indoor individual home cage ($0.6 \times 0.6 \times 0.6$ m). Cages containing demonstrators were in visual and acoustic contact, whereas those containing observers were only in acoustic contact. Observers were maintained in visual isolation to avoid any observational experience acquired in home cages interfering with that acquired during experiments (see below). Each home cage was equipped with a perch, a food bowl, a water bowl, and an opaque nestbox ($0.3 \times 0.2 \times 0.18$ m), the entrance of which was fitted with a sliding door. Birds were kept on a 12:12 h light:dark cycle with dark onset beginning at 1800 hours. After transfer from group to individual housing, the birds were left undisturbed for 2 days to acclimatize to their new environment.

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 Research Ethics Committee (protocol 9950108). Animal care was identical to procedures in related work (see Griffin & Boyce 2009). As previously, all work was undertaken during the nonbreeding season of Indian mynahs (March–August; Griffin & Boyce 2009).

Apparatus

The experiment took place in a room adjacent to that containing the home cages. The apparatus was identical to the one used in our earlier study on place learning in Indian mynahs (Griffin & Boyce 2009). It consisted of one long table divided into halves by a vertical wooden screen, which could be raised or lowered by the experimenter from behind a curtain (Fig. 1). On the table were two cages ($0.7 \times 0.7 \times 0.7$ m) referred to hereafter as the holding cage and the feeding cage. Both cages were equipped with a perch. In addition,

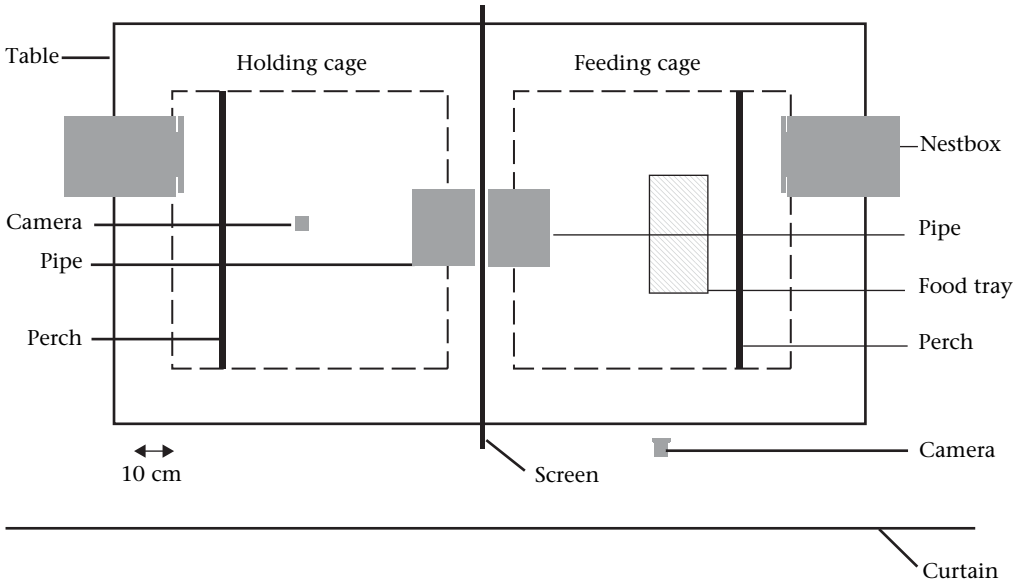

Figure 1. Aerial view of the experimental apparatus. An opaque screen located between the holding cage and the feeding cage could be raised and lowered by an experimenter (not shown) from behind the curtain. One camera providing an aerial view of the holding cage and another providing a lateral view of the feeding cage were connected to a PC computer (not shown) located behind the curtain. Observer mynahs were released from their nestbox into a holding cage and were trained to move through an opaque pipe located at ground height to obtain mealworms from the food tray in the feeding cage. During observational training trials, the pipe was blocked and observers confined to the holding cage watched either an alarmed demonstrator or a foraging demonstrator in the feeding cage. For more details, see text.

a food tray ($0.3 \times 0.15 \times 0.02$ m) containing a layer of paper bedding material (0.01 m depth) was located on the floor of the feeding cage. The cages were connected by one horizontal opaque pipe (8.5 cm diameter, 30 cm long) split down the middle. The half pieces of pipe were placed at ground height and met on either side of the screen, such that the subject could cross through the pipe and enter the second cage while the screen was lifted, but was unable to do so when the divider was lowered. The apparatus was fitted with two small security cameras ($0.03 \times 0.03 \times 0.01$ m; CCD mini B&W 380TVL; Samsung), one providing an aerial view of the holding cage, the second providing a lateral view of the feeding cage. Both cameras were connected to a PC computer running security software (PICO2000; UCL Technologies, Inc., North York, ON, Canada) that was used to record the behaviour of the birds during experiments. A curtain hanging alongside the apparatus hid the experimenter and the computer from the subjects' sight during tests. During all experiments, white noise was played back through two loudspeakers at a mean volume of 70 dB to mask the vocalizations of mynahs in the adjacent home cage room, as well as any noise produced accidentally by the experimenter or other humans in a corridor outside the experimental room.

Initial Training

As in Griffin & Boyce (2009), we began the experiment by training each observer mynah to cross from the holding cage to the feeding cage via the pipe and to forage in the food tray (Fig. 1). In addition, we trained mynahs that were to serve as foraging demonstrators to feed from the tray in the feeding cage. During this phase of initial training, mynahs assigned to act as alarmed demonstrators were left undisturbed in their home cages.

Observer mynahs

On the evening of the third day after transfer from the flight aviary to individual home cages, observers were food-deprived overnight (see Ethical Note for more details regarding food deprivation). The next morning, 40 mealworms cut in two were placed in the food dish in the feeding cage of the experimental apparatus and several others were placed inside the pipe (Fig. 1). The screen between the holding cage and the feeding cage was lowered (Fig. 1). Each observer mynah was then coaxed into the nestbox of its home cage, after which the door was closed and the bird transported to the test room and released into the holding cage of the test apparatus. After lifting the dividing screen, we waited until the subject had crossed into the feeding cage and 10 min had passed. The subject was then removed from the test apparatus by coaxing it into a nestbox attached to the feeding cage and returned to its home cage where it was immediately provided with food. That evening, observers were food deprived once again, and the procedure was repeated the next morning, except that no food was placed in the pipe. By the end of the second training session, all observers had learnt to cross the pipe to access the food in the feeding cage. The above procedure was identical to that used in our earlier study on social learning about dangerous places (Griffin & Boyce 2009).

Foraging demonstrators

Each mynah assigned to act as a foraging demonstrator was treated in the exact same way as an observer, except that it was released directly into the feeding cage and allowed enough time to feed on the mealworms in the tray. Similar to the observer training, the screen between the two cages was raised and lowered during demonstrator training. This ensured that demonstrators were accustomed to movements of the screen and that these did not interrupt foraging during subsequent observational training trials (see below). Demonstrator training was repeated on three consecutive mornings, rather than on only two as for observers. By the end of the third training session, all demonstrators had learnt to forage undisturbed from the food tray immediately after release into the feeding cage.

Testing

Each observer mynah first received a pretest during which it was released into the holding cage and given access by lifting the

dividing screen to the feeding cage where 40 mealworms cut in half were available in the food tray. The next morning, we conducted two observational training trials, separated by 60–90 min, during which each observer was confined to the holding cage and given the opportunity to watch a demonstrator showing either alarm (experimental observers) or foraging behaviour (control observers) in the feeding cage. The morning after the two observational training sessions, each mynah underwent a post-test, the procedure of which was identical to that of the pretest. For pretests and post-tests mynahs were food deprived overnight using the same deprivation schedule as during initial training.

During observational training trials, passage between the holding cage and the feeding cage was blocked by filling the connecting pipe with a cloth (Fig. 1). Each observer was released into the holding cage with the dividing screen lowered. A demonstrator mynah was then placed in the feeding cage where mealworms were available in the food tray. The dividing screen was then raised and the observer given the opportunity to view either an alarmed demonstrator (experimental observers) or a foraging demonstrator (control observers). Alarmed demonstrators tended to show a high level of locomotion simply because they had not undergone any initial training and had therefore never been placed in the test apparatus previously. In addition, to ensure that alarmed demonstrators performed behaviours indicative of the presence of a predator, we evoked a full-blown alarm response, involving high levels of locomotion and high-amplitude broadband alarm calls (Pizzey & Knight 1998; Griffin 2008), by moving a taxidermically prepared mount of a cat alongside the demonstrator's cage. The predator was moved in such a way that it was in full view of the demonstrator, but could not be seen by the observer mynah.

As foraging demonstrators had been trained to forage from the food tray (see initial training) and had been food deprived overnight, they typically foraged on mealworms as soon as they were released into the feeding cage. Foraging demonstrators were not exposed to the predator stimulus (cat). Each demonstration lasted 2 min, after which the dividing screen was lowered and the observer and demonstrator mynahs were returned to their home cages. We elected to conduct two observational training trials to increase the amount of social experience observers received relative to their individual experience of the feeding cage (initial training and pretest). Consequently, each observer mynah received a second observational training trial, identical to the first, between 60 and 90 min after the end of the first. A different taxidermic cat mount was used for each of the two observational training sessions to reduce the likelihood of habituation in alarmed demonstrators.

It is important to note that the observers in the experimental and the control groups had identical total exposure to the feeding cage. The only difference between these treatments was that the experimental observer mynahs observed an alarmed demonstrator, whereas the control observer mynahs watched a foraging demonstrator during social training sessions. Planned comparisons between the two groups' post-training behaviour thus allowed us to detect changes specifically attributable to the behaviour of the demonstrators. This design effectively separates socially acquired behaviour from other effects that might be a consequence of shared experiences, such as confinement in the test apparatus or repeated exposure to the test conditions (Shettleworth 1998).

It is also important to note that we purposefully designed the test apparatus such that the holding cage and the feeding cage were close (i.e. connected by a short pipe) and of identical size. We presumed therefore that observer mynahs would perceive the feeding cage as a nearby area in space (place) rather than an object, as they might have had they been able to fly around a large test room and examine the feeding cage from afar. Consequently, as in earlier work on social learning of places in this species (Griffin & Boyce 2009), we assumed our experiment to be a test of place learning, rather than object learning.

Pretests and post-tests were conducted between 800 and 1000 hours. Observational training sessions were conducted the morning after the pretest between 800 and 1300 hours. Post-tests were conducted the morning after the observational training trials.

Data Analysis

The behaviour of both demonstrators and observers was recorded on videotape. With the exception of latency to enter the feeding cage, which was obtained during experiments, all bird behaviour was scored from video recordings played back at half speed using JWatcher 1.0 (Blumstein et al. 2006) by one experimenter who was unaware of which treatment the subjects had undergone.

Overall, we expected observers to become more wary at the feeding site if they had watched a demonstrator signal the presence of a predator and less wary if they had watched a demonstrator foraging. To measure the effects of observational training, we analysed the behaviour of observers using four dependent measures during pretests and compared results with those obtained for post-tests. First, we measured the latency of each observer to enter the feeding cage both before and after observational training. Second, to ensure that we detected changes in behaviour that might have occurred after observers had reached the feeding site, we also quantified each observer's behaviour whilst it was inside the feeding cage. Earlier research has shown that captive mynahs respond to dangerous situations (e.g. a perched raptor; a place in which a predator attack on a social companion has been observed) by increasing locomotion including walk and flight (Griffin 2008; Griffin & Boyce 2009). Consequently, we calculated the percentage of time allocated to locomotion (walk and flight) during a 90 s interval after the observer had crossed into the feeding cage for the first time. As observers were free to move between the holding cage and the feeding cage during pre- and post-tests, we anticipated that increased wariness in the location in which a demonstrator had signalled the presence of a predator might be reflected by a decrease in total time spent there. Consequently, we calculated the proportion of time spent inside the feeding cage relative to the 90 s total observation time. Finally, as increases in vigilance are commonly associated with decreases in foraging behaviour (Krebs & Davies 1997), we measured peck rates during a 90 s period after observers had entered the feeding cage for the first time.

For each behaviour and each observer, we calculated the difference between the value obtained in the post-test and the value obtained in the pretest (pre/post difference). Kolmogorov–Smirnov tests revealed that the distribution of all dependent variables deviated significantly from normality. Consequently, we used nonparametric, Mann–Whitney *U* tests to compare the probability distribution of the pre/post differences of experimental observers with the probability distribution of the pre/post differences of control observers for each behaviour.

In addition to analysing the behaviour of observers during pre- and post-tests, we scored the behaviour of both observers and demonstrators during each of the observational training sessions. This allowed us to (1) ensure that demonstrator mynahs performed demonstrations that were representative of their group membership (i.e. alarmed or foraging) and (2) determine whether qualitatively different demonstrations (i.e. alarmed or foraging) evoked quantitatively different responses in observers (i.e. experimental versus control). For both observational training sessions, observer and demonstrator behaviour was scored during a 2 min period that

began as soon as the dividing screen between observer and demonstrator was raised. The percentage of time allocated to locomotion was determined for each mynah for each of the two 2-min training sessions. We also determined peck rates, but for demonstrators only, as observers did not have access to any food during demonstrations. For each behaviour and each mynah, we then calculated the mean of the two training sessions. Kolmogorov-Smirnov tests revealed that the distribution of dependent variables deviated significantly from normality. For each behaviour, we therefore used nonparametric Mann–Whitney *U* tests to compare the probability distribution of the percentages of time allocated to locomotion and the peck rates of alarmed demonstrators with the probability distribution of the percentages of time allocated to locomotion and the peck rates of foraging demonstrators. The same approach was used to compare the percentages of time allocated to locomotion by experimental observers with the percentages of time allocated to locomotion by control observers. Finally, we quantified the occurrence of a high-amplitude broadband alarm call, which is produced by free-flight Indian mynahs and which can be evoked experimentally by presenting captive subjects with a model predator (Pizzey & Knight 1998; Griffin 2008). We tested the relationship between the probability of alarm calling and demonstrator treatment (alarmed, foraging) using a Fisher exact test.

All analyses were conducted using SPSS 15.0 (SPSS, Inc., Chicago, IL, U.S.A.). All tests were two tailed and significance thresholds were set at 0.05.

Ethical Note

To increase the motivation of subjects to feed during trials, it was necessary to restrict food access prior to initial training sessions, pretests, and post-tests (observers) and initial and observational training sessions (foraging demonstrators). Food was removed from each bird's home cage at dark onset (1800 hours) and made available again as soon as the mynah returned from its morning trial, with the exception of foraging demonstrators participating in observational training sessions, which received food only when both observational training sessions were completed. Food deprivation was shortened, however, by the fact that all mynahs had access ad libitum to mealworms, a rich fatty food, during trials. Consequently, total deprivation time included a 12 h night-time period, during which birds naturally do not feed, and a 1–3 h daytime period depending on the order in which the birds participated in morning trials. At all other times, birds had access ad libitum to dog food pellets, vegetables, or mealworms. Overall, subjects experienced a 2–15% weight increase during their stay in captivity, indicating that their dietary intake was greater under captive conditions than in the wild, even with a maximum of 4 days of restricted access to food.

RESULTS

Mean differences between pre- and post-test behaviour of experimental and control observers for each of the four behavioural measures are given in Table 1. Contrary to our hypothesis, experimental observer mynahs that watched a conspecific express an alarm response at the feeding site did not take longer to access the site after observational training than before, relative to control observer mynahs that watched a conspecific foraging at the feeding site (Table 1). In addition, experimental observers showed no significant change in the amount of time they spent at the feeding site after observational training relative to before, compared with control observers (Table 1). Furthermore, analyses of pre-/post-response differences revealed no significant differences in the probability distribution of the time allocated to locomotion at the feeding site between experimental observers and control observers after observational training relative to before (Table 1). Finally, analyses of foraging behaviour revealed no significant differences in the probability distribution of the peck rates of experimental observers across observational training relative to control observers (Table 1).

Table 1
Mean ±SE change in observer behaviour after having watched an alarmed demonstrator (experimental observers) or a foraging demonstrator (control observers) in the feeding cage

Behaviour	Experimental observers (N=13)	Control observers (N=12)	U	P
Latency to enter feeding cage (s)	−0.5±0.2	−1.4±1.0	73	0.81
Time in feeding cage (%)	5.7±7.1	0.4±6.2	73	0.81
Total locomotion (%)	1.3±3.2	−4.7±2.5	66	0.54
Peck rate (no./min)	5.4±2.9	8.3±2.2	63.5	0.30

All behaviours were measured during a 90 s interval after the observers accessed the feeding site from a holding cage for the first time in the pretest and the post-test. Means were calculated using the difference between the pretest and the post-test for each subject.

To ensure that the absence of an effect of observational training on observer behaviour was not attributable to a failure of the demonstrators to perform either alarmed or foraging demonstrations, we scored the behaviour of the demonstrators during the two 2-min observational training sessions. This analysis confirmed that alarmed demonstrators spent significantly more time in locomotion than foraging demonstrators (Mann–Whitney *U* test: locomotion, $U = 0.0$, $N_1 = 13$, $N_2 = 12$, $P < 0.001$; Fig. 2) and pecked at the food tray at significantly slower rates than foraging demonstrators (Mann–Whitney *U* test: $U = 8.0$, $N_1 = 13$, $N_2 = 12$, $P < 0.01$; Fig. 2). Finally, five demonstrators exposed to a model cat (alarmed demonstrators) gave at least one alarm call during one of the two social training trials, whereas no foraging demonstrators called. This difference was supported by a significant effect of treatment on probability of alarm calling (Fisher's exact test: $P = 0.039$). These findings confirmed that demonstrators performed demonstrations that were representative of their treatment membership.

Finally, to determine whether observers were affected by the behaviour of their demonstrators, we analysed the behaviour of observers during the two 2-min observational training sessions. Analyses revealed that there were no significant differences between the probability distribution of the percentages of time experimental observers and control observers spent in locomotion (Mann–Whitney *U* test: locomotion, $U = 64$, $N_1 = 13$, $N_2 = 12$, $P = 0.470$; Fig. 2). Together these findings suggest that although alarmed demonstrators behaved significantly more fearfully than foraging demonstrators, the behaviour of observers was unaffected by this difference in demonstration.

DISCUSSION

The aim of this study was to determine whether Indian mynahs became more wary in an area in which they were accustomed to foraging after they had watched a social companion signalling the presence of a predator at that location. Based on both proximate and functional considerations, we had predicted that such learning should occur. To test this hypothesis, we compared the behaviour of observers that watched demonstrators signalling the presence of a predator at the foraging site with that of a control group that observed demonstrators foraging, both before and after observational training. Contrary to our expectations, we found no evidence that experimental observer mynahs became more wary of the

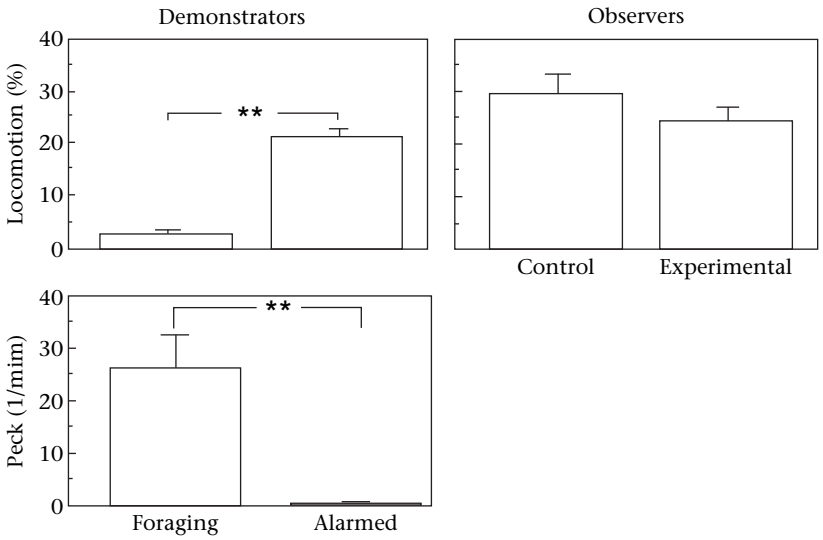

Figure 2. Behaviour of demonstrators (left column) and observers (right column) during observational training sessions. Mean (+SE) percentage of time allocated to locomotion and mean (+SE) peck rate were measured during two 2-min observational training sessions. Observers were not provided with food during demonstrations, so foraging behaviour of this group was not measured. Behaviour of alarmed demonstrators was evoked by moving a taxidermic mount of a cat alongside the demonstrator's cage, in such a way that the model was in full view of the demonstrator, but out of sight of the observer. Foraging demonstrators had been accustomed to obtaining food at the foraging site during initial training sessions and were food deprived overnight before acting as demonstrators. For more details, see text. $^{**}P < 0.01$.

feeding site after observational training relative to before, compared to control observers.

Yet, alarmed demonstrators showed high levels of locomotion and emitted alarm calls at the feeding site, whereas relaxed demonstrators remained immobile and foraged (Fig. 2). Analysis of observer behaviour during observational training revealed, however, that observers were unaffected by this difference in demonstration. This pattern contrasts with abundant work on social learning of predators both in Indian mynahs and in several other systems, which has typically found that observer responses during and after training are positively correlated with those of demonstrators during training and that observer responses during training correlate positively with acquired responses after training (Curio et al. 1978; Mineka & Cook 1993; Chivers & Smith 1994; Griffin & Evans 2003; Griffin 2009). For example, Indian mynahs that show greater responsiveness to social alarm signals (distress calls) when these are presented simultaneously with a novel predator stimulus later show greater acquired responses to the novel predator after training (Griffin 2009). In this study, failure of alarmed demonstrators to influence observer behaviour strongly suggests that observers did not perceive the behaviour of their demonstrator as alarming, which is consistent with the lack of acquired response after training. Yet, we know from several studies in our laboratory that Indian mynahs respond to the alarm signals of social companions and, furthermore, that these stimuli can trigger social learning of external stimuli present at the same time (Griffin 2008, 2009).

Even more surprisingly, we have previously shown in the same experimental apparatus that the alarm behaviour of social companions in response to a human surrogate 'predator' is important for place learning in Indian mynahs (Griffin & Boyce 2009). That finding, together with evidence that social alarm signals trigger learning of discrete stimuli in Indian mynahs (Griffin 2008, 2009), led us to expect that learning would occur in this study. Although cross-study comparisons must be made with caution, comparison between our earlier work and this study might suggest some routes for future exploration into mechanisms of observational place learning. The present design, including the amount of individual (two initial training sessions, one pretest) and observational (two observational training sessions) experience of each observer mynah at the foraging site, was matched to that of our previous study. The only difference between this and past work was the content of the observational experience for both groups of observers. Whereas in this study, observers watched a demonstrator express a high-level alarm response at the foraging site, in our previous study, we used a human as a surrogate predator, and observers watched a conspecific be chased, captured, and removed by the human from the foraging site. Furthermore, in our previous study, no captured demonstrator alarm-called because caged mynahs do not alarm call to humans, suggesting that lack of learning in the present study is not simply attributable to low levels of alarm calling in demonstrators (five of 13 alarmed demonstrators alarm-called). Finally, differences in learning between the two studies emerged despite using a sample size here ($N = 25$) almost identical to that used previously ($N = 23$) and an identical statistical approach (i.e. nonparametric, Mann–Whitney U tests identifying between-group pre/post differences in behaviour).

We suggest that the key difference between our earlier study in which we found evidence for place learning and this one, in which we did not, is that previously, observers had access to both social alarm cues (demonstrator behaviour) and the cause of the demonstrator's alarm (i.e. threatening human), whereas in the present study, observers could see the alarmed companion, but not the cause of its alarm (cat). This hypothesis is consistent with evidence that observational learners integrate not only the behaviour their demonstrators, but also the causes and the consequences of those behaviours (Heyes 1994; Coolen et al. 2005). Indeed, studies of observational learning of food-related cues have consistently revealed that acquisition is impaired if observers are given visual access to an individual demonstrating a foraging technique, but not to the consequence of that behaviour (food consumption; Groesbeck & Duerfeldt 1971; Akins & Zentall 1998). Similar results have been found using a social avoidance learning paradigm (Bunch & Zentall 1980). Rats learn to avoid a candle flame more quickly after they have watched a conspecific approach the flame and singe its whiskers, but not if visual access to the rat's contact with the candle (cause of conspecific behaviour) is blocked (Bunch & Zentall 1980).

It seems therefore plausible that social alarm signals per se may not be sufficient to trigger learning of contextual cues. In contrast to

global cues, discrete stimuli, such as novel predators, provide information about a 'cause' of demonstrator alarm, which may in turn explain why associations between social alarm signals and discrete stimuli have been shown time and time again (reviewed by Griffin 2004). Just like temporal limitations on social learning that ensure that only discrete stimuli that share some temporal overlap with alarm signals are learnt (Griffin 2009), absence of alarm signal–place observational learning may protect against making erroneous associations. Earlier work in fish has revealed that fathead minnows, *Pimephales promelas*, learn to recognize waters from particular habitats after water samples from those habitats have been presented together with chemical alarm substances (Chivers & Smith 1995b). Furthermore, acquired avoidance can be socially transmitted by jointly exposing naïve fish to the fright responses of individuals and habitat-specific chemical cues (Chivers & Smith 1995a). Habitat-specific chemical cues may function more like discrete stimuli than place cues, as such learning seems to rely solely on joint exposure to water cues and chemical alarm substance. Future work is clearly needed to ascertain the extent to which observational learning of contextual cues requires concurrent access to social signals derived from an alarmed companion and information about the cause of that companion's alarm.

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