Indian mynahs, Acridotheres tristis, learn about dangerous places by observing the fate of others

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Studies of learning have consistently shown that animals form strong associations between aversive events, such as a predatory attack, and the environments in which those events are experienced. Place learning through direct exposure to threat puts the individual at a risk that may be avoided, however, by remembering the location in which encounters between conspecifics and dangerous events are observed. Despite much theoretical work predicting that individuals should rely less on private information and more on public information as the risk of individual assessment increases, there have been no tests of observational spatial memory for potentially dangerous places. We investigated whether Indian mynahs learn about an area in which they observe another individual experience an aversive event, namely capture by a human. Experimental observers watched a human chase, catch and remove a conspecific from a feeding site in which observers were accustomed to feeding. A control group watched a human perform the same capture gestures, but with no mynah present. Analysis of observer behaviour at the feeding site both before and after observational training revealed that experimental observers locomoted more after training than before, relative to control observers, suggesting that mynahs acquired a fear response after watching a predatory attack on a conspecific. It appears that, in addition to learning about the location in which aversive events are experienced directly, animals learn about an environment in which they observe others encounter dangerous events.
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A substantial body of empirical work on place learning has demonstrated repeatedly that animals learn readily about a spatial location in which they experience an aversive event. For example, goldfish, Carassius auratus, spend less time in an area in which they have received an electric shock than in an area in which they have not (Dunlop et al. 2006). Similarly, mice, Mus musculus, learn to avoid a location in which they have been bitten by an aggressive conspecific (Siegfried & Frischkencht 1989). In these cases, learning is reflected by acquired place avoidance, but site-specific increases in risk assessment behaviour may also be indicative of learning (Fanselow 1990; Blanchard et al. 2001, 2005; Hubbard et al. 2004). Changes in behaviour acquired as a consequence of experience probably function to reduce the probability of a subsequent encounter with a given environmental threat.

Aversive events that trigger place learning include exposure to predators. For instance, detection of cat, Felis catus, odour causes rats, Rattus norvegicus, to increase defensive behaviours (crouch/freeze with sniff/head movements) significantly when later returned to the test environment (Blanchard et al. 2001), while exposure to a live cat triggers acquired hiding (Blanchard et al. 2005). Learning about dangerous places through direct exposure to the threat carries the downside that it puts the individual in a potentially lethal situation. Perhaps a less risky way of learning about dangerous places is to remember the area in which an encounter between a predator and a conspecific was observed. In situations where an individual is attracted to a predation site from nearby, observations may be made from a distance, such that the location of the observer is relatively distinct from that of the attack. Just as individuals may benefit from remembering a location in which they themselves were threatened, they may equally benefit from remembering the place in which they observed a predator attack on a conspecific. Learning would require associating place information remote from the learner's own location with potential triggers to learning, such as the distress signals of captured conspecifics and/or cues from predators. Contrary to direct learning of place, observational spatial memory has received surprisingly little attention. Although numerous studies have shown that travelling or foraging with conspecifics leads to acquired route and site preferences (Avery 1994; Lachlan et al. 1998; Midford et al. 2000; Day et al. 2001; Reader et al. 2003), only a handful have tested whether animals learn about a place from which they themselves

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are remote, and all have used paradigms in which appetitive stimuli trigger acquired place preferences, rather than situations in which aversive stimuli trigger place avoidance (McQuoid & Galef 1992; Bednekoff & Balda 1996). Specifically, we know of no attempt to determine whether animals avoid, or become more wary in, a location in which they have observed a conspecific experience an aversive event, such as capture by a predator. Observational spatial memory would provide the important benefit that information could be acquired without putting the learner at risk, and would be consistent with theoretical predictions that individuals should rely more on public information and less on private information as the potential costs of individual assessment increase (Laland 2004; Kendal et al. 2005).

The Indian mynah is a highly commensal passerine that lives in close association with humans and can be found in large roosts along the eastern coast of Australia (Tidemann 2006). Indian mynahs are particularly suited to a study of observational place learning for two reasons. First, its highly social and adaptable lifestyle, together with its ability to produce a variety of antipredator vocalizations, makes mynahs particularly well suited to empirical studies of learning (Griffin 2008, 2009). Second, the Indian mynah is a highly successful invasive species that has expanded its range so quickly in the last few decades that it now poses a threat to several native Australian bird species and is the target of ongoing pest control efforts. Observational spatial memory has the potential to reduce the effectiveness of labour-intensive and costly trapping programmes. More specifically, observing a distressed conspecific be caught and removed from a trapping device might later reduce an observer's willingness to approach the vicinity of the trap, which might in turn reduce trapping success. Field observations showing that surrounding Indian mynahs produce alarm calls while observing a human remove conspecifics from a trap support the idea that such situations create learning opportunities (A. S. Griffin, personal observation). Even though this ability has never been explored empirically, the potential for observational learning about traps has led to suggestions that mynah traps should not be approached during daylight and are better emptied after dark (http://fennerschool-associated.anu.edu.au/myna/trapping-show/trap1.html; http://www.indianmynaeradication.com/mynaX.html).

The aim of the present study was to determine whether Indian mynahs learn to avoid, or become more wary in, a location in which they have seen another mynah captured by a predator. We elected to use a human as a surrogate 'predator' for several reasons. First, exposure of captive animals to live predators raises serious ethical concerns that we wished to avoid. Second, both field and laboratory work have revealed that many animals, including birds, behave towards humans as if they were predators (Frid & Dill 2002; Blumstein et al. 2005), with the additional benefit, however, that behaviour can be closely controlled, thus ensuring that all subjects receive a standardized learning experience (Blanchard & Blanchard 2003; Griffin & Evans 2003). Finally, we were interested in exploring the scope for trap avoidance learning in Indian mynahs, in which humans play the role of a predator when birds are removed from trapping devices.

Food-deprived mynahs were trained to move between a holding site and a feeding site. Mynahs allocated to an experimental observer group were then given the opportunity to watch a target mynah being chased with a net, caught and removed by a human from the feeding site. A control group watched a human simulating a capture, but with no mynah present. 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 groups allowed us to isolate changes in behaviour that were attributable to

observation of conspecific capture from those attributable to exposure to a potentially threatening human per se.

METHODS

Subjects and Husbandry

Subjects were 36 wild-caught Indian mynahs. Birds were captured in central Newcastle, Australia, 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. The trap was monitored twice daily and emptied each evening. 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. As Indian mynahs are not sexually dimorphic, no attempt was made to control for sex during subsequent experiments. Mynahs were left undisturbed for at least 4 weeks to acclimatize to captivity. Birds had access to water and a mixture of fresh vegetables and dog pellets ad libitum throughout their stay in captivity.

Twenty-four randomly selected mynahs were assigned to act as observers and 12 were assigned to act as targets. Of 24 observers, 12 were assigned to watch a real capture of a target mynah (experimental observers) and 12 were assigned to watch a simulated capture with no target mynah present (control observers). Sample sizes were determined on the basis of previous work on avian learning by A.S.G. (Griffin & Galef 2005; Griffin 2008, 2009).

For the experiment, each subject was transferred to an indoor individual home cage (0.6 × 0.6 m and 0.6 m high), and left for 2 days (Days 1 and 2) to acclimatize. While cages containing target mynahs were in visual and acoustic contact, observers were maintained in visual isolation to avoid any observational experience in home cages interfering with experience during tests. Each cage was equipped with a nestbox, which was used to transport birds between their home cage and the test apparatus. Birds were kept on an 18:6 h light:dark schedule at 21 °C. Upon request by the University of Newcastle Animal Care and Ethics Committee, mynahs were euthanized at the end of the experiments. Release was not considered because it was thought that captive mynahs would be unable to integrate into a flock or a breeding territory. As recommended by the Australian and New Zealand Council for the Care of Animals in Research and Training (Reilly 2001) and the University of Newcastle Animal Care and Ethics Committee, euthanasia was performed by a qualified veterinarian and was achieved by exposing each bird to a lethal dose of CO_2. In agreement with the most recent recommendations on best-practice procedures in animal research (Hawkins et al. 2006), birds were placed inside a closed container and exposed to a rising concentration of 100% CO_2.

Apparatus

The apparatus was located in a room adjacent to the one containing the home cages. It consisted of a table divided in half by a vertical screen, which could be raised and lowered (Fig. 1). On the table were two cages (0.7 × 0.7 m and 0.7 m high), referred to hereafter as the holding cage and the feeding cage. A food tray was located on the floor of the feeding cage. The cages were connected via a horizontal pipe (8.5 cm diameter × 30 cm long). Passage through the pipe was possible when the screen was raised, but not when it was lowered (Fig. 1). Each cage was fitted with a small security camera. Both cameras were connected to a computer, which recorded behaviour during experiments. A curtain hanging
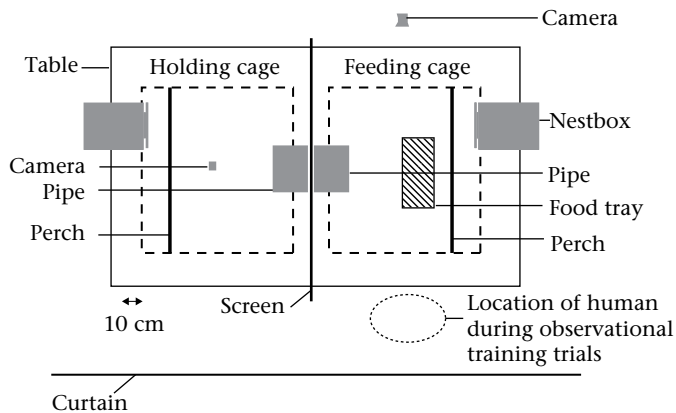
Figure 1. Aerial view of the experimental apparatus. The opaque screen between holding and feeding cages could be raised and lowered by an experimenter (not shown) from behind the curtain. One camera providing an aerial view of the holding cage and another providing a lateral view of the feeding cage were connected to a computer (not shown) located behind the curtain. A pipe located at ground height allowed observer mynahs to move between the two cages in pretests and post-tests.

alongside the apparatus hid the experimenter and computer from the subjects' view. During experiments, white noise was played back through two loudspeakers to mask the sound of mynahs and humans in adjacent rooms.

Experimental Protocol

Initial training

On Days 3 and 4, each observer mynah underwent an initial training session in which it learnt to cross through the pipe from the holding cage into the feeding cage, and to forage in the food tray. On Day 3, following a 12–14 h overnight food deprivation period, each observer was released into the holding cage with the screen lowered. The screen was then raised and the subject allowed to cross into the feeding cage and forage for 10 min on mealworms in the food dish. It was then removed from the test apparatus by coaxing it into its nestbox and returned to its home cage. The same procedure was repeated on Day 4, except that on Day 3 food was available in the food tray and in the pipe to entice subjects to enter it, while on Day 4, food was only available in the food tray. By the end of the second session, all observers crossed into the feeding cage within 60 s of the screen being raised. During this initial training phase, target mynahs were left undisturbed in their home cages.

Pre- and post-tests

On Day 5, each observer mynah received a pretest, during which it was released into the holding cage following a 12–14 h overnight food deprivation period, and given access by raising the screen to the feeding cage where 40 mealworms cut in half were available in the food dish. Pretests were followed on Day 6 by two observational training trials, the procedure of which is described below. On Day 7, each mynah underwent a post-test, the procedure of which was identical to that of the pretest.

Observational training

During observational training, passage between holding and feeding cages was obstructed by filling the pipe with a cloth (Fig. 1). Each observer was released into the holding cage with the screen lowered. Experimental observers were then given the opportunity to watch a human removing a target mynah from the feeding cage. To this end, a target mynah was released into the feeding cage and the screen was raised, immediately after which

the experimenter appeared from behind the curtain, stood between the curtain and the long side of the rectangular table (Fig. 1), and began to chase the target mynah with a net through a door in the side of the feeding cage. As we did not want observers to perceive the capture event as directed towards them, but only towards the target mynah, the position of the experimenter during capture was selected to ensure that she did not make visual contact with the observer mynah. At the end of a 2 min period, the target mynah was caught and removed, immediately after which the screen was lowered and the observer returned to its home cage. In contrast to experimental observers that watched a real capture, control observers were exposed to a simulated capture event, in which the experimenter performed the same body movements as during a real capture except that the feeding cage was empty. To increase the amount of observational experience with the feeding cage relative to the amount of individual experience (initial training and pretest) of each observer, we conducted a second, identical observational training trial between 60 and 90 min after the first.

We purposely designed the test apparatus in such a way that the holding and feeding cages were located within close proximity and were of identical size. We assumed that this arrangement would ensure that mynahs in the holding cage would perceive the feeding cage as a nearby location in space rather than an object, as might have been the case if observers were allowed to observe a small cage from within a large environment. Consequently, we considered our test to be a test of place learning and not object learning. Although the experiment was conducted on a relatively small scale, spatial memory is commonly tested using similar or smaller-scale environments, such as testing arenas and water mazes, demonstrating that animals perform well at such spatial scales (e.g. Balda & Kamil 1989; Bednekoff et al. 1997; Griffin & Etienne 1998; Maurer & Derivaz 2000). For this reason, we do not think that spatial scale had any significant effect on our results. Nevertheless, an investigation of how our findings generalize to larger spatial scales provides scope for future work.

It is important to note that observers in experimental and control groups had identical total exposure to the feeding cage. These treatments differed only in so far that experimental observers watched a human pursuing and capturing a conspecific, whereas controls watched a human moving a net as if to pursue and capture a mynah, but with no mynah present. Consequently, between-group differences after training are necessarily attributable to differential observational training experience. Between-group comparisons are the critical parameter demonstrating observational learning, and not within-group comparisons of behaviour before and after training (Shettleworth 1998; Griffin et al. 2000).

To ensure that post-training differences between the two treatments were not due to differences in the behaviour of the human, the experimenter was instructed to imagine that she was capturing a bird during simulated captures, so that she would not appear less threatening during simulated captures than during real captures, for example by making fewer net moves in the absence of a mynah than in the presence of a mynah. Number of net movements performed by the experimenter was measured to assess any potential differences between treatments. Planned comparisons between the two groups' post-training behaviour thus allowed us to detect acquired changes in behaviour attributable to the behaviour of the mynah undergoing capture, or an interaction between the target mynah and cues from the human.

Pretests and post-tests were conducted between 0800 and 1000. Observational training sessions were conducted on the morning after pretests between 0800 and 1300. Post-tests were conducted the morning after observational training trials.

Data Analysis

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

Four behavioural measures were collected during pretests and post-tests. First, we measured the latency of each observer to enter the feeding cage after the screen was raised. Second, earlier research has shown that antipredator responses of captive Indian mynahs are reflected by increases in locomotion including walk and flight (Griffin 2008). Consequently, we measured the percentage of time allocated to total locomotion (walk and flight) during a 90 s interval that began as soon as observers entered the feeding cage for the first time (observation time). Third, as observers were free to move between holding and feeding cages during pre- and post-tests, we measured the proportion of time spent inside the feeding cage relative to the 90 s observation time. Finally, we measured peck rates directed to the floor during the 90 s observation time, under the assumption that these were always food driven.

For each dependent variable and each subject, we calculated the difference between the value obtained in the pretest and that scored for the post-test (pre/post difference). As none of the behavioural variables were normally distributed, we used nonparametric Mann–Whitney U tests to compare the probability distribution of the pre/post difference of experimental observers with the probability distribution of the pre/post difference of control observers. We hypothesized that an acquired fear response to the feeding cage would be reflected by a longer latency to enter it, an increase in time allocated to locomotion and a decrease in pecking rate while there, and a decrease in the time spent inside the feeding cage. In contrast, habituation to the feeding cage would be reflected by a shorter latency to enter it, a decrease in time allocated to locomotion and an increase in pecking rate while there, and an increase in the time spent inside the foraging cage.

One experimental observer, which took only 33 s to enter the feeding cage before observational training, failed to enter the cage after watching a capture event. While this subject's behaviour is consistent with the hypothesis that mynahs associate a predator attack on a conspecific with the environment in which the event is observed, we excluded this mynah from analyses as it provided no post-test behavioural data.

All statistical analyses were carried out on untransformed data using SPSS 16.0 (SPSS Inc., Chicago, IL, U.S.A.). Two-tailed tests were used throughout and alpha levels were set at 0.05.

RESULTS

Mean differences between pre- and post-test behaviour of experimental and control observers for each of the four behavioural measures are reported in Table 1. Statistical analyses revealed no evidence that experimental observers took significantly longer to enter the feeding cage after observational training than before relative to the control group, or that they spent less time there (Table 1). There was also no evidence that experimental observers significantly decreased their foraging rates across observational training relative to the control group (Table 1).

There was, however, a strong effect of observational training on total time allocated to locomotion (Fig. 2). Experimental observers that had watched the capture of a conspecific mynah in the feeding cage allocated significantly more time to locomotion after observational training than before, relative to control observers that had

Table 1
Mean difference ± SE between pretest and post-test behaviour of experimental and control observers

Behaviour	Experimental observers (N=11)	Control observers (N=12)	U	P
Latency to enter feeding cage (s)	0.4±0.6	1.2±1.2	65	0.976
Time in feeding cage (%)	−4±3.2	−1.3±2.9	44.5	0.19
Total locomotion (%)	6.5±2.4	−5.0±3.9	21	0.004*
Peck rate (1/min)	−2.4±3	0.5±0.6	62	0.833

*$P < 0.05$.

watched a simulated capture (Table 1). To ensure that the between-group differential change was not attributable to differences between the groups' initial levels of locomotion, we compared the probability distribution of the time allocated to locomotion of the experimental group during the pretest with that of the control group. This comparison revealed no significant differences between the two groups before training (Mann–Whitney U test: $U = 49$, $N_1 = 11$, $N_2 = 12$, $P = 0.316$; Fig. 2). Furthermore, to determine whether the behaviour of the human was comparable in both groups, we compared the total number of times the experimenter moved the net during simulated and real captures. Although all other aspects of her behaviour were identical (body position, eye direction gaze), in attempting to follow instructions and to ensure that she did not make fewer net moves, and perhaps appear less threatening, during simulated captures than during real captures, the experimenter inadvertently made significantly more net moves during simulated captures ($\overline{X} \pm SE = 162 \pm 18$) than during real captures (103 ± 22; unpaired t test: $t_{44} = 9.886$, $P < 0.001$). This finding strongly suggests that learning in mynahs that watched a real capture of a conspecific (experimental group) was not triggered by net swipes per se.
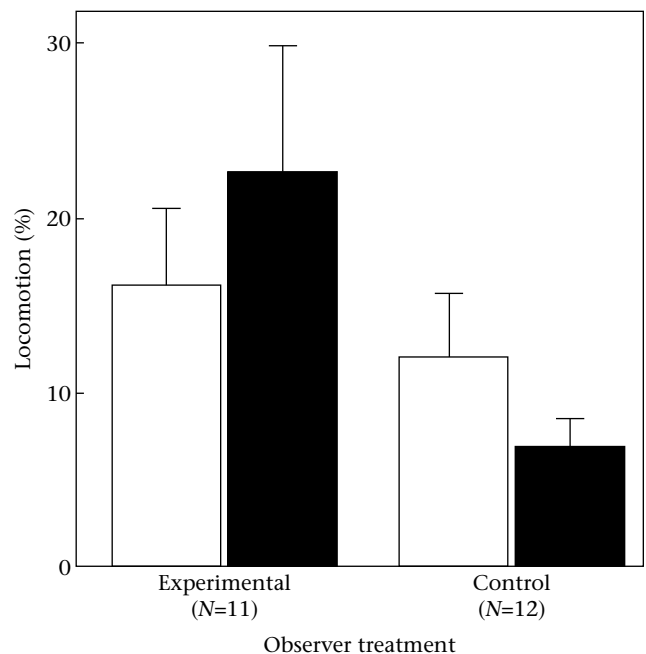

Figure 2. Locomotion expressed in the feeding cage by experimental observer mynahs that viewed the capture of a conspecific by a human during observational training, and control observer mynahs that watched a human wave a net with no mynah present, both before (pretest, open bars) and after (post-test, black bars) observational training. The mean + SE percentage of time allocated to locomotion is indicated for a 90 s period after entering the feeding cage. See text for further details.

DISCUSSION

The purpose of the present study was to determine whether mynahs that observe a predator attack on a conspecific learn to avoid, or become more wary in, the area in which the attack was observed. The present results are consistent with this hypothesis. We used capture by a human to simulate the effects of an attack by a predator. Mynahs feeding in a location in which they had observed the capture of a conspecific by a human allocated a significantly greater proportion of time to locomotion after that observation than before. In contrast, control mynahs, which had watched a simulated capture event with no conspecific present, decreased the time they allocated to locomotion (Fig. 2). In the light of earlier work demonstrating that captive Indian mynahs increase locomotion in threatening situations (Griffin 2008), these results strongly suggest that experimental mynahs became more wary in the location in which they observed an attack on a conspecific, while control observers became less wary in the location in which they had observed a simulated capture. Between-group differences in post-training behaviour demonstrate that behavioural adjustments in the location in which the observations were made were a consequence of observational learning.

Comparable directional changes in behaviour of experimental and control groups have been found during work on social learning in Indian mynahs (Griffin 2008, 2009) and a broad range of other species (reviewed in Griffin 2004). For example, experimental mynahs that receive a novel stimulus simultaneously with a conspecific alarm signal increase their responses to the novel stimulus after training, while control birds that receive novel stimulus and signal separately decrease their responses (Griffin 2008). Here, mynahs became more wary after observing an attack, and less wary after observing a human, suggesting that exposure to a human waving a net as if to catch a bird does not constitute an aversive event. Post-training behaviour of the control group shows importantly that in the absence of an aversive observational experience, mynahs tended to become less wary of the feeding cage on their fourth exposure to it (post-test) than on their third (pretest). The key point is that between-group comparisons of pre/post changes in behaviour, and not within-group comparisons of pre- and post-test behaviour, are critical for demonstrating that changes in behaviour are attributable to learning (Shettleworth 1998; Griffin et al. 2000). Overall, our work provides evidence that mynahs attend to conspecifics and adjust their behaviour accordingly.

Our experimental design catered for a very conservative test of learning. Indeed, observers were food deprived overnight prior to both pretests and post-tests. Parallel work on predator recognition in this system has demonstrated that overnight food deprivation ensures that mynahs are highly motivated to feed (A.S. Griffin, unpublished data). There is a huge literature demonstrating that animals trade off the benefits of foraging opportunities against costs of increased predation risk (e.g. Lima et al. 1985; Fraser & Huntingford 1986). A trade-off in favour of foraging in the present study would have made place learning more difficult to detect. Second, observer mynahs received three sessions, during which they had the opportunity to learn through their own experience that the feeding site was safe (initial training and pretest), before they were exposed to two observational events informing them that the site was dangerous. Potentially greater reliance on early individual experience than on later observational experience would also have reduced our ability to detect learning. Despite such stringent test conditions, we were able to demonstrate that observational place learning occurred. Under less stringent conditions, it is possible that learning might have been reflected by additional changes in behaviour, such as avoidance of the feeding cage. Our findings are consistent with results from work on individual learning of place, which has reliably shown that exposure to an aversive stimulus, such as a predator, causes animals to increase defensive behaviours and hiding when later returned to the test environment (R. J. Blanchard et al. 2001; D. C Blanchard et al. 2005). Furthermore, the present demonstration of observational spatial memory invites further exploration of the ways in which behavioural trade-offs and social/asocial learning interactions affect the expression of observationally learned behaviour.

The finding that mynahs become more wary in a location in which an attack on a conspecific was observed is consistent with results from work on observational place learning in other bird species. McQuoid & Galef (1992) found that observing the pecking behaviour of a conspecific increased the probability that an observer Burmese fowl would later direct its feeding behaviour towards the location in which it had observed the foraging conspecific. The authors attributed acquisition to a process of stimulus enhancement (Spence 1937), in which conspecific feeding behaviour triggered learning of associated place information. Similarly, stimulus enhancement of place information can explain acquired changes in behaviour of observers in the present study, but the stimuli that trigger learning are more difficult to identify. Our experimental design ensured that post-training differences between experimental and control observers were at least in part determined by the behaviour of target mynahs, which displayed high flight rates and made obvious attempts to avoid the hand-held net. Post-training behaviour of control observers showed that these birds became less wary of the feeding cage (habituation; Fig. 2). This finding demonstrates that exposure to a human per se, even if the human waves a net at high rates, was not the cause of the change in behaviour of the experimental birds, suggesting by the same token that the capture of a conspecific was not experienced as a personal encounter with a predator by experimental observers.

It is possible that learning was triggered by exposure to a fearful conspecific on its own, or an interaction between stimuli derived from the target mynah and stimuli derived from the human. Although we cannot exclude that exposure to a fearful conspecific is sufficient to trigger learning, several lines of evidence suggest that observational learners integrate not only the behaviour of other individuals, but also the causes and consequences of those behaviours (Heyes 1994; Coolen et al. 2005). For example, work on observational learning of food-related cues has 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 the behaviour (food consumption; Groesbeck & Duerfeldt 1971; Akins & Zentall 1998). Similarly, rats learn to avoid a candle flame more quickly after they have watched a conspecific approach the flame and singe its whiskers (Bunch & Zentall 1980), but not if visual access to the rat's contact with the candle (cause of conspecific behaviour) is blocked. In the light of these findings, we suggest that place learning in the present study was facilitated by an interaction between the behaviour of the target mynah and the cause of the conspecific's distress (capture by a human; Zentall 2006), rather than exposure to the fearful conspecific alone. Further empirical work is needed to test this hypothesis.

It is of applied interest to evaluate the significance of the present results for mynah trapping programmes. Current recommended practice is to avoid approaching or emptying traps during daylight because onlookers might acquire an avoidance response after watching humans handle conspecifics, which might in turn reduce trapping success (http://fennerschool-associated.anu.edu.au/myna/trapping-show/trap1.html; http://www.indianmynaeradication.com/mynaX.html). The occurrence of observational spatial memory in Indian mynahs has the potential to reduce trapping

success. Indeed, even though only one experimental observer failed to enter the feeding cage after observational training, trade-offs between foraging benefits and predation risk may affect how learning is expressed in the wild, in the same way as they do in the laboratory. For example, if foraging benefits are low (e.g. other food sources are available, or bait is not a preferred food), learning might be expressed by complete trap avoidance. Fieldwork in which success of traps emptied during daylight and after dark is compared would provide an interesting complement to the present study.

Acknowledgments

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