Learning from watching alarmed demonstrators: does the cause of alarm matter?

Andrea S. Griffin [a,*], Kathryn Haythorpe [b]

[a] School of Psychology, University of Newcastle
[b] School of Environmental and Life Sciences, University of Newcastle

ARTICLE INFO

Many social-learning opportunities expose animals to the behaviour of conspecifics, but also to causes and consequences of those behaviours. Attending to information over and above social behaviour per se may provide a strategy by which the reliability of social information is ensured. Earlier work in Indian mynahs, *Sturnus tristis*, has demonstrated that observers become more wary in a location in which they are accustomed to foraging after they have viewed a conspecific undergo a 'predator' attack at that site. We determined whether observation of both an alarmed demonstrator and the cause of the conspecific's alarm (capture by a human) were critical to such observational learning. Experimental observers watched a demonstrator mynah display high levels of alarm in response to pursuit and capture by a human, while control mynahs watched a demonstrator express a similar level of alarm to a threatening nearby human, but visual access to the human by observers was blocked. Analysis of observer behaviour at the feeding site both before and after observational training revealed that experimental observers remained wary at the feeding site after training relative to before, relative to control observers that became far less wary, strongly suggesting that both social and causal information were important for observational learning. This result contributes to the growing body of empirical evidence that use of social learning is modulated by a rich variety of contextual information that may help ensure that its use is adaptive.

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Observational learning is a form of social learning in which animals acquire information about the world by observing the behaviour of other individuals, typically conspecifics (Mason & Reidinger 1981, 1982; Mason 1988; Zentall & Galef 1988; Mineka & Cook 1993; Heyes 1994; Olsson et al. 2007). For example, animals may acquire an alarm response to a novel predator after watching the alarm responses of other individuals to the predator (Mineka & Cook 1993; Blanchard et al. 2001; Griffin & Evans 2003). Observation of social companions creates opportunities to view not only the behaviour of others, but also the causes and consequences of those behaviours. Theoretical analyses, supported by a handful of empirical studies, have revealed that there are a variety of conditions under which using social information may be maladaptive (Laland & Williams 1998; Pongrácz et al. 2003). Consequently, it has been predicted that the use of social learning should be governed by a collection of strategies that define the circumstances under which its use is adaptive (Laland 2004). In addition to strategies such as copying more experienced individuals, and only copying when individual learning is unsuccessful, only copying social

behaviours with causes and consequences may help, under some circumstances, to ensure that learning is worthwhile. For example, copying an alarm response that has no apparent cause, or a foraging technique that fails to produce food, is unlikely to yield an adaptive advantage.

Although observational learning is a well-studied phenomenon, there have been surprisingly few attempts to determine to what extent information other than that provided by demonstrator behaviour per se is necessary for learning to occur. The only systematic work in this area has been in the context of the social transmission of food-finding techniques. Careful behavioural analyses have revealed that visual access to both demonstration of a novel foraging technique (e.g. lid opening) and subsequent food consumption by the demonstrator (consequence) facilitates acquisition of the novel foraging technique in observers, strongly suggesting that observers attend to both the behaviour of the demonstrator and the consequence of that behaviour on the environment (Groesbeck & Duerfeldt 1971; Palameta & Lefebvre 1985; Heyes 1994; Akins & Zentall 1998; Coolen et al. 2005).

To our knowledge, only one study has attempted to examine whether observing the cause of a social companion's behaviour affects the likelihood of observational learning. Observer rats, *Rattus norvegicus*, given the opportunity to watch a demonstrator rat express a fear response after touching a candle with its nose,

* Correspondence: A. S. Griffin, School of Psychology, University of Newcastle, Callaghan, NSW 2308, Australia.
  E-mail address: andrea.griffin@newcastle.edu.au (A. S. Griffin).

and singeing its whiskers, subsequently made fewer nose contacts with a candle than rats that were exposed to a candle and a fearful demonstrator that could not make nose contacts with the candle (Lore et al. 1971). A subsequent analysis indicated that observation of demonstrator contact with the flame played a critical role in observer learning. Indeed, learning was impaired if visual access to the point of contact between the rat's nose and the candle was blocked, suggesting that learning required not only observation of a fearful demonstrator and an external stimulus present at the same time (candle), but also information that allowed one to be related to the other (Bunch & Zentall 1980; Zentall 2006).

Social learning about predators is commonly used to explore mechanisms of social transmission of fear (Griffin 2004). The typical experimental paradigm involves measuring whether the responses of observers to a novel predator increase after they have undergone 'training' sessions in which they view the novel predator in conjunction with social alarm signals. As is, the training protocol combines presentation of social alarm signals and their cause (i.e. the novel predator), making it effective for demonstrating that animals can learn about the cause of a companion's alarm, but, by the same token, making it impossible to examine whether observing the cause of social alarm is necessary for learning. The present study overcame this problem by employing a place-learning paradigm to explore whether observation of the cause of a social companion's alarm plays a determining role in social learning about danger.

The Indian mynah, *Sturnus tristis* (formerly classified as *Acridotheres tristis*, Christidis & Boles 2008; also referred to as the common myna), 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 opportunistic lifestyle of Indian mynahs makes them an ideal system to study mechanisms of social learning about danger (Pell & Tideman 1997; Pizzey & Knight 1998; Tideman 2006; Griffin 2008b, 2009; Griffin & Boyce 2009; Griffin et al. 2010).

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 'predator' chase, catch and remove a social companion from that location, relative to control mynahs that become less wary in the feeding site after they have watched a human perform the same capture gestures at the feeding site, but in the absence of any conspecific mynah (Griffin & Boyce 2009). In that study, the control group became less place-wary after training, suggesting that increased place wariness in experimental birds was not due to observation of a threatening human per se, but rather to social alarm, or alternatively, an interaction between cues from the human and cues from the alarmed demonstrator (Griffin & Boyce 2009). In a parallel study, observer mynahs that watched a demonstrator express a high-level alarm response triggered by a cat that observers could not see subsequently failed to become more place-wary relative to control mynahs that watched a companion mynah feeding at the foraging site; this result pointed to the hypothesis that learning relied upon an interaction, rather than social alarm alone (Griffin et al. 2010). The aim of the present study was to extend this earlier work by specifically testing to what extent place learning is dependent upon viewing both an alarmed demonstrator and capture of the demonstrator by a human, the cause of alarm.

Building on previous work, we used once again capture by a human to trigger place learning. Capture by a human provides the unique opportunity to examine the effects of presenting social alarm with or without an external event (human performing capture gestures), which plays the role of a cause, but at the same time remains neutral in the sense that it does not trigger place learning on its own (Griffin & Boyce 2009). Any acquired place wariness in response to watching a demonstrator be caught is therefore necessarily a consequence of an interaction between human cues and social alarm, or social alarm alone, hypotheses the present experiment was designed to tease apart.

Food-deprived mynahs were trained to move between a holding site and a feeding site through a small pipe. Mynahs allocated to a human-present observer group were then provided with the opportunity to watch a demonstrator mynah located at the feeding site being chased and caught by a human (observational training). Mynahs assigned to a human-absent observer group also watched a demonstrator mynah expressing a high-level alarm response to a nearby threatening human, but visual access to the human by observers was blocked. Consequently, they viewed only the alarmed demonstrator mynah without any information about what was causing the demonstrator's alarm response. As in previous work in our laboratory, and consistent with work on individual learning about dangerous places, we quantified place learning by measuring levels of risk assessment behaviour both before and after observational training in both groups of observer mynahs at the foraging site (Fanselow 1990; Blanchard et al. 2001, 2005; Hubbard et al. 2004; Griffin & Boyce 2009; Griffin et al. 2010). Comparisons between human-present and human-absent observers allowed changes in behaviour that were specifically attributable to differential observational experience (human present versus human absent) to be isolated from those caused by nonassociative learning processes, such as sensitization (Griffin & Evans 2003; Griffin 2009; Griffin & Boyce 2009).

METHODS

Subjects and Husbandry

Fifty-eight Indian mynahs were captured in an urban location in Newcastle, a medium-sized city on the eastern coast of Australia, using a walk-in baited trap designed specifically to trap this species and widely used for population control (Tideman 2006; see Griffin 2008b for a detailed description of the trap). Trapping and transport were identical to earlier work (Griffin 2008b, 2009; Griffin & Boyce 2009). Each bird was weighed, measured and individually identified with a light-weight coloured plastic leg band. Birds were then transported to the Central Animal House at the University of Newcastle and released into a large outdoor group flight aviary (2.25 × 1.25 m and 4.4 m high). Birds were left undisturbed for a minimum of 3 weeks to acclimatize to captivity. All captive mynahs had ad libitum access to water and a mixture of dog pellets, fresh fruit and vegetables.

Twenty-nine randomly selected mynahs were assigned to act as observers and 29 were assigned to act as demonstrators. Of the 29 observers, 15 were assigned to watch a demonstrator undergo capture by a human (human-present observers) and 14 were assigned to watch an alarmed demonstrator in the absence of a human (human-absent observers; see below for more details). Each of the 29 demonstrators was randomly assigned to one of the 29 observers. No attempt was made to control for sex during experiments, as Indian mynahs are not sexually dimorphic. Sample sizes were determined on the basis of extensive previous work on predator recognition and predator avoidance learning by the first author (Griffin 2003, 2008b, 2009; Griffin & Galef 2005; Griffin & Boyce 2009; Griffin et al. 2010).

For testing, each subject was transferred from the outdoor flight aviary to an individual home cage (0.6. × 0.6 × 0.6 m). Cages containing demonstrators were in visual and acoustic contact, while

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 (0.3×0.2 m and 0.18 m high) that was used to move individuals between their home cage and the test apparatus. Individual home cages were held in a room with complete access to natural light. Following transfer from group to individual housing, birds were left undisturbed for 2 days to acclimatize to their new environment.

All animal care, husbandry and experimental procedures were approved by the University of Newcastle Animal Research Ethics Committee. Indian mynahs are classified as a pest species in Australia and neither the government nor the Animal Care and Ethics Committee allows for release after capture. Consequently, all birds were euthanized by a qualified veterinarian at the end of the experiment using an overdose of CO_2. As previously, the study was undertaken during the nonbreeding season of Indian mynahs (March–May; Griffin & Boyce 2009).
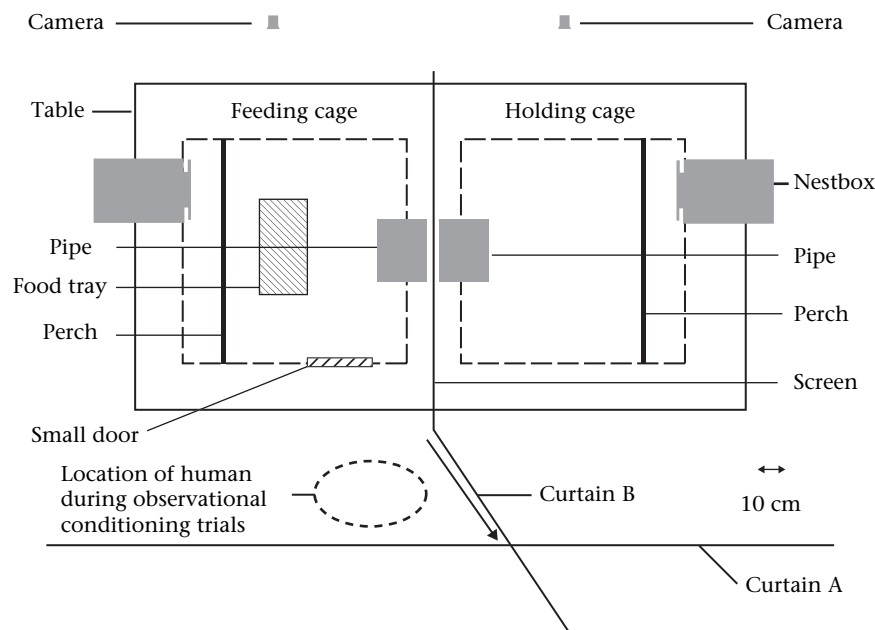
Apparatus

The experiment took place in a separate room to that containing the home cages. The apparatus was identical to the one used in our earlier work on place learning in Indian mynahs with the mere addition of several strategically placed curtains around it (Fig. 1; Griffin & Boyce 2009; Griffin et al. 2010). The apparatus consisted of a long table divided in half by a vertical wooden screen, which could be raised or lowered by the experimenter from behind a curtain (Fig. 1). A cage ($0.7 \times 0.7 \times 0.7$ m) was located on each side of the screen. The two cages were connected by a horizontal opaque pipe (8.5 cm diameter, 30 cm long) located at ground height. When the screen was raised, visual contact between the two cages and passage between them through the pipe was possible; lowering the screen blocked visual contact and passage through the pipe.

One cage was referred to as the holding cage, while the other was referred to as the feeding cage. Both cages were equipped with a perch. In addition, a food tray was located on the floor of the feeding cage. Each cage was fitted with a small security camera ($0.03 \times 0.03 \times 0.01$ m, camera CCD mini B&W 380TVL Samsung), which was connected to a PC computer running security software (PICO2000 UCL Technologies Inc., http://www.ucltech.com). The set-up was used to view and record the behaviour of the birds during experiments. A curtain hanging alongside the wooden screen and perpendicular to the table could be either opened or closed during observational trials depending on the treatment (Fig. 1; see below). 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.

Experimental Protocol

Initial training

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). The procedure was identical to that used in previous work on place learning in Indian mynahs (Griffin & Boyce 2009; Griffin et al. 2010). On the evening of the third day after transfer from the flight aviary to individual home cages, observers were food deprived overnight. The next morning, meal-worms 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 released into 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 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

Figure 1. Aerial view of the experimental apparatus. Cameras were connected to a computer (not shown) located behind curtain A. Curtain B was either open (i.e. drawn in the direction of the arrow) to reveal a human chasing and capturing a demonstrator through a small door on the side of the cage to observers in the holding cage (human-present observers) or closed (i.e. drawn in the opposite direction to the arrow) to hide a nearby threatening human from observers (human-absent observers) during observational training. During both types of trial, the human stood within the indicated zone. See text for further details.

the second training session, all observers had learnt to cross through the pipe to access the food in the feeding cage. During this phase of initial training, mynahs assigned to act as demonstrators were left undisturbed in their home cages.

Pre- and post-tests

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 several mealworms cut in half were available in the food tray. The following day, we conducted two observational training trials during which observers were confined to the holding cage and given the opportunity to watch either a demonstrator express a high-level alarm response to a hidden human (human-absent observers; see below) or a demonstrator undergo capture by a visible human (human-present observers; see below). The day after the two observational training sessions, each observer 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.

Observational 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 then released into the holding cage with the screen lowered. Observers in the human-present group were then given the opportunity to watch a human chase, capture and remove a demonstrator from the feeding cage. To this end, a demonstrator was released into the feeding cage and the screen was raised. A human then appeared from behind a black opaque curtain and began to chase the demonstrator with a net through a small door on the side of the cage (Fig. 1). As in previous work, the human stood alongside the rectangular table to avoid making eye contact with the observer mynah, thus reducing the likelihood that it would perceive the capture event as self-directed (Griffin & Boyce 2009). The capture event lasted 2 min, the last 30 s of which involved the actual capture and removal of the demonstrator from the cage, immediately after which the screen was lowered and the observer returned to its home cage.

Observers in the human-absent group also watched a demonstrator express a high-level alarm response to a nearby threatening human for 2 min, but visual access to the human was blocked by closing a black opaque curtain that hung alongside the screen and perpendicular to the table (Fig. 1). Hiding the human behind the curtain allowed us to expose observers in the human-absent group to an alarmed demonstrator, without allowing them to see the event to which the demonstrator was responding. Wild-caught, caged Indian mynahs naturally show high levels of alarm in response to a human standing next to their cage, particularly if they are stared at. However, to ensure that demonstrators in the human-absent group exhibited alarm responses of similar amplitude to demonstrators undergoing pursuit and capture, the nearby human fixated on the demonstrator and made jerky movements towards it to simulate sudden approach. Alarm responses in both groups of demonstrators involved very high levels of locomotion and obvious attempts to escape from the cage (pushing beak between bars), but no alarm calls as caged Indian mynahs do not alarm call to humans (A. S. Griffin, unpublished data).

As in previous work, we conducted two observational training trials to increase the amount of observational 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.

Our design incorporated the comparison of learning in a group of observers exposed to an alarmed conspecific experiencing pursuit and capture by a human and another group of observers exposed to an alarmed demonstrator on its own. The experience of both groups of observers with the feeding cage was in all other respects identical. Consequently, differences between the two groups' behaviour after observational training are necessarily attributable to differential observational experience. Between-group comparisons of this kind are the critical parameter demonstrating observational learning, and not within-group comparisons between behaviour before and after training, which might be attributable to nonassociative effects, such as sensitization to the experimental setting (Shettleworth 1998; Griffin 2003).

Data Analysis

All trials were video recorded and behaviour was scored from tape played back at half speed using JWatcher 1.0 (Blumstein et al. 2006) by an experimenter who was unaware of which treatment subjects had undergone.

Earlier work on socially acquired predator recognition, as well as observational place learning, in this system has reliably shown that Indian mynahs respond to danger by increasing locomotion (Griffin 2008b; Griffin & Boyce 2009), while, in the literature, changes in foraging patterns are reliably associated with perceived risk (Krebs & Davies 1997). Consequently, we analysed both of these behavioural variables. Specifically, we quantified the percentage of time allocated to locomotion (walk and flight) and peck rates during a 2 min observation period that began immediately after each observer had entered the feeding cage for the first time during both pre- and post-tests. As in our earlier work on place learning in Indian mynahs (Griffin & Boyce 2009; Griffin et al. 2010), we also measured for both pre- and post-tests the latency of each observer to enter the feeding cage after the screen was raised, as well as the proportion of time spent inside the feeding cage relative to the total observation period. As in previous work, neither of these variables was affected by exposure to a treatment; consequently, results are not included here.

Each dependent variable was either logged or square-root transformed to meet the requirements of normality. We then tested for differential changes in behaviour between observer treatments using a repeated measures ANOVA with time (pretest, post-test) as a within-subject variable and observer treatment (human present, human absent) as a factor. We expected that observationally acquired wariness of the feeding cage would be reflected by an increase in the percentage of time allocated to locomotion and a decrease in peck rates once there during post-tests relative to pretests. In contrast, habituation to the feeding cage would be reflected by a decrease in the percentage of time allocated to locomotion and an increase in peck rate once there.

All statistical analyses were carried out using PASW Statistics 18.0 (SPSS Inc., Chicago, IL, U.S.A.). Two-tailed tests were used throughout and alpha levels were fixed at 0.05.

RESULTS

A two-way repeated measures ANOVA on the percentage of time allocated to locomotion by observers revealed a significant main effect of time ($F_{1,27} = 9.403$, $P = 0.005$) and a significant time*treatment interaction ($F_{1,27} = 12.230$, $P = 0.002$). The main effect of treatment was not significant ($F_{1,27} = 0.126$, $P = 0.726$). An identical analysis on pecking rate revealed a time*treatment interaction that fell just short of significance ($F_{1,27} = 3.888$, $P = 0.059$) and no main effect of time ($F_{1,27} = 2.150$, $P = 0.154$) or treatment ($F_{1,27} = 2.103$, $P = 0.159$). Overall, observers that watched a demonstrator mynah

display high levels of alarm in response to being pursued, captured in a net and removed from the feeding site by a human maintained their pretest levels of locomotion after training relative to before, relative to control observers, which watched a highly alarmed demonstrator with no apparent cause, and which decreased locomotion at the feeding site after observational training relative to before (Fig. 2). Together, these results suggest that observation of an alarmed demonstrator being chased, caught and removed from the feeding site inhibited a decrease in wariness at the feeding site that occurred in observers that watched a demonstrator express alarm without cause.

To ensure that between-group differences in acquired locomotion were not attributable to differences in the two groups' initial behaviour, we compared the two treatments' initial levels of locomotion using an independent t test. This analysis revealed no treatment effect indicating that there were no differences in behaviour between the two treatments before observational training ($t_{27} = 1.636$, $P = 0.113$).

Finally, to examine the role of demonstrator alarm in observer learning, we calculated the mean proportion of time allocated to locomotion, as well as the mean locomotion rate, of each demonstrator across the two observational training sessions. As in previous work (see Methods), very high locomotion was the most obvious behavioural response to nearby human presence in both demonstrator treatments. For each demonstrator, locomotion was scored during a 90 s time period that began as soon as the screen between holding and feeding cages was lifted. These analyses revealed no significant differences in either the total time allocated to locomotion (mean + SE; human present: $69.1 + 6.2\%$; human absent: $76.8 + 3.5\%$; independent t test: $t_{27} = 1.062$, $P = 0.298$), or locomotion rate (mean + SE; human present: $0.28 + 0.06$ [1/s]; human absent: $0.41 + 0.08$ [1/s]; independent t test: $t_{27} = 1.950$, $P = 0.062$) by the two demonstrator treatments. The effect of demonstrator locomotion on observer learning was further explored by introducing these descriptors of locomotion as covariates into the overall 2 by 2 time by treatment repeated measures ANOVA on observer locomotion. Proportion of time allocated to locomotion and
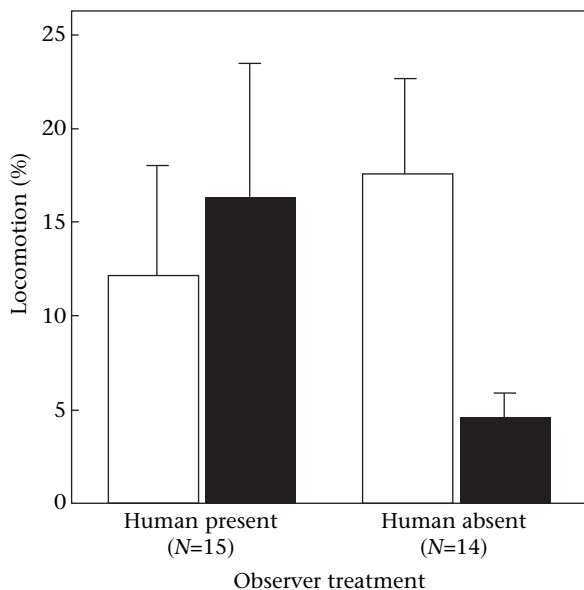

Figure 2. Locomotion expressed in the feeding cage by human-present and human-absent observer mynahs both before (pretest, open bars) and after (post-test, black bars) observational training. The mean + SE percentage of time allocated to locomotion is indicated for a 120 s time period after entering the feeding cage. See text for further details.

locomotion rate were highly negatively correlated (Pearson correlation coefficient: $r = -0.722$, $P < 0.001$), so each variable was introduced into the overall model separately. These analyses revealed no significant effect of either of the two demonstrator locomotion variables on differential changes in locomotion of observer treatments (locomotion rate: $F_{1,26} = 0.02$, $P = 0.888$; percentage locomotion: $F_{1,26} = 0.004$, $P = 0.951$). Furthermore, the significant time*treatment interaction on observer locomotion remained significant in each case indicating that demonstrator locomotion during observational training did not explain treatment differences in observer behaviour after training.

DISCUSSION

In the present study, we examined to what extent observational place learning was dependent upon observing both the alarm behaviour of a conspecific and its cause. Results revealed that observers that had visual access to the capture of a companion by a human remained cautious during a subsequent trip to the foraging site, while observers that had watched a demonstrator exhibit an alarm response without any apparent cause became less wary after training relative to before. These findings suggest that visual access to an interaction between cues from the human and cues from the demonstrator played a key role in triggering acquired changes in behaviour.

Rather than enhancing risk assessment behaviour, it might be argued that observing capture of a companion inhibited a decline in risk assessment behaviour that occurred in mynahs that observed an alarmed companion alone (Fig. 2). Reduced wariness in control mynahs is likely to have been mediated by habituation to the feeding cage, but further research will be needed to ascertain this. Comparable directional changes in behaviour of experimental and control groups have been found during earlier work on observational place learning and social learning of predators in Indian mynahs. For example, presenting a novel predator together with social alarm calls inhibits a reduction in visual attention that occurs in mynahs that receive novel predator and alarm calls separately (Griffin 2009). The key point is that between-group comparisons of behavioural changes across observational training are critical to isolating the effects of a specific between-group manipulation and not within-group comparisons of behaviour before and after training. Although it would be of theoretical interest to habituate observers to the feeding cage fully prior to observational learning, and to show that observation of social alarm and human inculcates a significant increase in wariness in human-present mynahs relative to an absence of change in human-absent mynahs, this approach would require providing mynahs with extensive nonaversive individual experience with the feeding cage prior to observational training. Two aversive social-learning experiences may then be insufficient to modify extended previous individual experience (Galef & Whiskin 2001).

The present findings replicate and extend results from our earlier studies of observational place learning in so far that we consistently find that observing a human chase and catch a demonstrator mynah in a net in an area in which observers are accustomed to feeding heightens risk assessment behaviour on a later trip to the foraging site relative to a control treatment (Fig. 3a, b), while observing an alarmed conspecific per se does not (Fig. 3a, c), and, based on earlier work, neither does a human waving a net in an empty feeding site as if to catch a mynah (Fig. 3b). Consequently, we must assume that some interaction between cues from the human and cues from the demonstrator mynah is necessary for alarm behaviour to be copied. Further work will be needed to isolate exactly what it is about the interaction that produces learning. Given that locomotion behaviour of demonstrators did not explain acquired changes in locomotion of
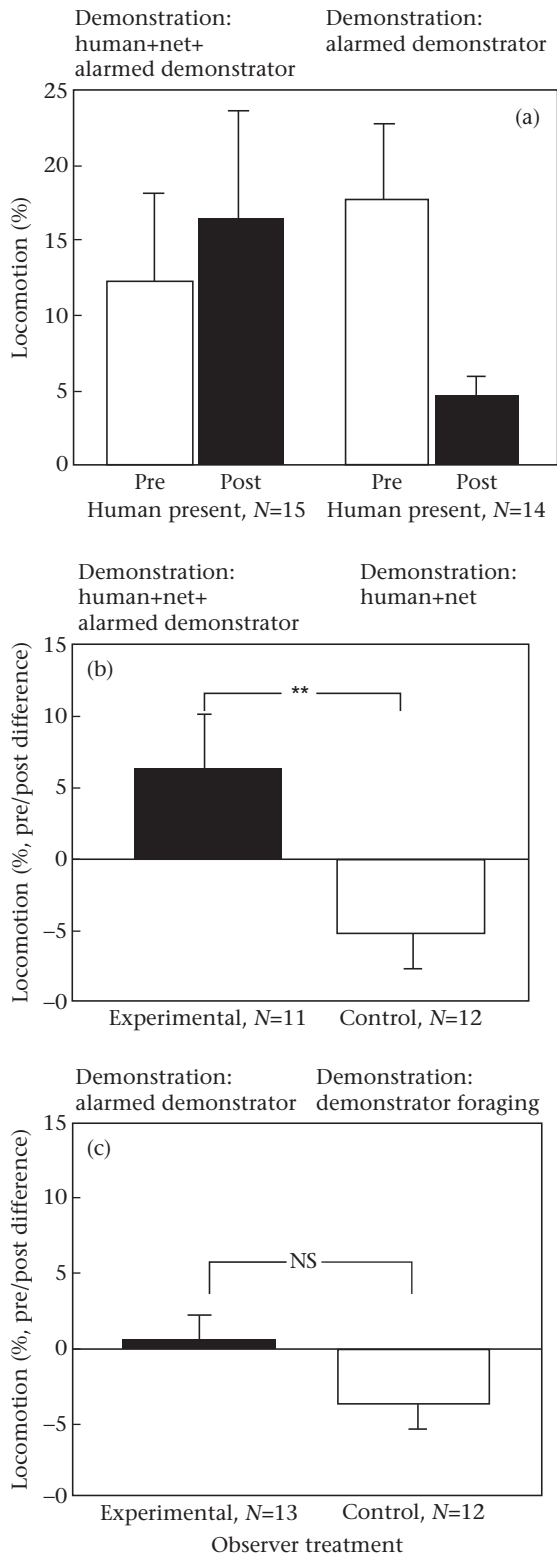
Figure 3. Changes in observer locomotion obtained in (a) the present study, and each of our previous studies on place learning in Indian mynahs: (b) Griffin & Boyce 2009; (c) Griffin et al. 2010. (a) Mean + SE percentage of time allocated to locomotion during pre- and post-tests. (b) and (c) Mean + SE pre/post-test change in locomotion. **$P < 0.01$, nonparametric Mann–Whitney test. To facilitate comparisons, the content of the observational experience of each observer treatment is indicated. (b, c) Reproduced with permission from Elsevier Press.

observers, it is possible that capture by a human is key, rather than merely the presence of both human and demonstrator. As well as providing causal information, capture of a conspecific also encodes predator success, both of which could facilitate learning. Spatial contact between the human and the demonstrator mynah may be sufficient. This hypothesis would be in line with work in rats showing that the presence of a fearful demonstrator and a candle is not sufficient to inculcate candle avoidance. Learning requires observation of the point of contact between the demonstrator's nose and the candle (Bunch & Zentall 1980; Zentall 2006).

However, the interaction effect of human and social alarm may not necessarily be supported by a causal relationship. Human and social alarm cues may interact in such a way that the aversive effect of their combination on observers is greater than that of each of the cues presented alone. These hypotheses could be teased apart by comparing the effect of manipulating the contingent relationship between the two components of the aversive experience (human and social alarm) with the effect of enhancing the intensity of the social alarm demonstration. The former could be achieved by comparing learning in treatments that repeatedly received the two stimuli together with learning in a treatment that repeatedly received the two stimuli separately, while the latter could be achieved by using several demonstrators, for example. In the light of over two decades of learning research showing that animals attend to contingent relationships between physical events (e.g. a light signalling food delivery; Rescorla 1988), it seems reasonable to suggest that they should also have the ability to do so in their social world.

Our results are consistent with detailed work on social transmission of foraging behaviour in pigeons, *Columba livia*, and rats, indicating that observers attend to both the behaviour of social companions and the consequences of those behaviours (Groesbeck & Duerfeldt 1971; Palameta & Lefebvre 1985; Heyes 1994; Akins & Zentall 1998; Coolen et al. 2005). The findings contribute to a growing body of empirical evidence pointing to the fact that social learning is not indiscriminate; animals employ a number of strategies to determine the context in which they should learn from others (Laland 2004). Integration of events over and above social behaviour per se, such as the causes and consequences of the observed behaviour, may assist in ensuring that only reliable social sources are copied. Although field research will be needed to explore the conditions under which causal and outcome information could be used under free-ranging conditions, it will be interesting for future investigations in social learning to entertain the possibility that observational learning may require more complex cognitive integration than proposed by current thinking (Olsson & Phelps 2007; Griffin 2008a).

Acknowledgments

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