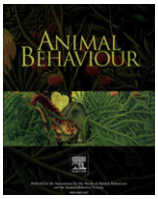
Animal Behaviour 79 (2010) 459–465

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



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

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ARTICLE INFO

Article history:
Received 29 June 2009
Initial acceptance 25 September 2009
Final acceptance 6 November 2009
Available online 11 December 2009
MS. number: 09-00458R1

Keywords:
Acridotheres tristis
common myna
Indian mynah
observational conditioning
predation risk
predator avoidance
social learning
Sturnus tristis

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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doi:10.1016/j.anbehav.2009.11.029

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 × 1 × 1 m), collect a bait, fly up through two small (0.1 m diameter), one-way channels into a top cage (1 × 1 × 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 × 1.25 × 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 × 0.6 × 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 × 0.2 × 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 × 0.7 × 0.7 m) referred to hereafter as the holding cage and the feeding cage. Both cages were equipped with a perch. In addition,