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Social learning in Indian mynahs, *Acridotheres tristis*: the role of distress calls

ANDREA S. GRIFFIN

School of Psychology, University of Newcastle

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Socially acquired predator avoidance is a phenomenon in which individuals acquire an avoidance response towards an initially neutral stimulus after they have experienced it together with the antipredator signals of social companions. Earlier research has established that alarm calls used for intraspecific communication are effective stimuli for triggering acquisition. However, animals produce a large range of other antipredator responses that might engage antipredator learning. Here, I examine the effects of conspecific distress calls, a signal that is produced by birds when restrained by a predator, and that appears to be directed towards predators, rather than conspecifics, on predator avoidance learning in Indian mynahs, *Acridotheres tristis*. Distress calls reflect high levels of alarm in the caller and should, therefore, mediate robust learning. Experiment 1 revealed that subjects performed higher rates of head movements in response to a previously unfamiliar avian mount after it had been presented simultaneously with playbacks of conspecific distress vocalizations. Experiment 2 revealed that increased rates of head saccades resembled the spontaneous response evoked by a novel stimulus more closely than it resembled the response evoked by a perched raptor, suggesting that distress calls inculcated a visual exploratory response, rather than an antipredator response. While it is usually thought that the level of acquisition in learners follows a simple relationship with the level of alarm shown by demonstrators, the present results suggest that this relationship may be more complex. Antipredator signals with different functions may have differential effects on learners.

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Keywords: *Acridotheres tristis*; distress vocalizations; head saccades; Indian mynah; predator avoidance learning; social learning

Social learning is a taxonomically widespread means of acquiring information about the environment. For example, individuals that attend to the feeding behaviours of others may learn where or what to eat (McQuoid & Galef 1992; Lefebvre et al. 1996). Similarly, individuals that attend to the alarm behaviours of others may learn to recognize novel predatory threats (Mathis et al. 1996; Berger et al. 2001). The key to social learning is that one individual performs a behaviour that draws the attention of another individual to some aspect of the environment. With this in mind, behaviours that have the potential to trigger learning in bystanders could range from cues that are produced haphazardly as animals go about their daily

activities, to signals specifically designed for information transfer.

Over two decades of extensive work on social influences on foraging behaviour has revealed that most instances of social learning of where, what and how to forage are not reliant upon specialized signals, but rather on 'information-bearing cues' (Markl 1985) or 'signs' (Hauser 1996; reviewed in Galef & Giraldeau 2001). For example, in rats, *Rattus norvegicus*, food preferences can be acquired through the association of food and conspecific faeces, simply because rats prefer to forage at a location at which conspecifics have foraged, and which is therefore scattered with excretory deposits (Laland & Plotkin 1991, 1993).

In contrast, research on social learning about predators has provided evidence that learning can involve specific signals that are used to transfer information about danger to nearby conspecifics (Curio 1988). For example, the characteristic mobbing behaviour of many bird species is

Correspondence: A. S. Griffin, School of Psychology, University of Newcastle, University Drive, Callaghan, 2308, NSW, Australia (email: andrea.griffin@newcastle.edu.au).

an alarm signal, which is primarily directed towards conspecifics, and which triggers the acquisition of an avoidance response to stimuli with which it is associated (Curio et al. 1978; Vieth et al. 1980; Curio 1993). However, animals produce a range of other responses to predatory threats. These include behaviours that convey information about predation risk, but have no obvious communicative function, such as hiding, freezing, or running away (Morse 1980), as well as a variety of antipredator signals designed for interspecific rather than intraspecific communication (Caro 1986; Ristau 1991; Evans 1997). While all these behaviours may provide a survival benefit to those producing them, they also have the potential to engage learning in those who observe them. Socially acquired predator avoidance, contrary to social learning about food, offers the exciting possibility of exploring not only the effects of information-bearing antipredator behaviours, but also a wide variety of antipredator signals with varying functions, on learning in bystanders. Findings will improve our understanding of the range of social phenomena that can lead to the spread of predator avoidance in a population. Furthermore, the broader the range of antipredator behaviours that facilitate predator avoidance learning, the wider the scope for social learning in a population will be. An individual that is able to associate a large number of demonstrator antipredator behaviours with predation risk has more opportunities to learn about novel threats than an individual that is only able to associate a few.

The response of small birds to seizure by a predator, including by a human, varies greatly both across and within species. In most species of Passerine, however, some individuals produce high amplitude, broad-band vocalizations, referred to as distress calls (Norris & Stamm 1965). Several hypotheses have been proposed to explain why birds produce these vocalizations when they are restrained. One idea is that they function to attract secondary predators that disrupt the predation event and afford the prey an opportunity to escape (Driver & Humphries 1969; Curio 1976). In support of this hypothesis over those suggesting that distress calls serve to warn kin (Rohwer et al. 1976), Perrone (1980) found that distress call playbacks attracted raptors, but not conspecifics, in several species of Passerine. Later work (Högestedt 1983; Wise et al. 1999) confirmed that these calls are highly attractive to predators. Another line of evidence suggesting that distress calls may be used as an interspecific communication signal is the recent finding that these vocalizations may convey information about the quality of the sender to predators (Laiolo et al. 2004).

Even though distress calls may be directed primarily towards predators, these vocalizations are nevertheless associated with elevated predation risk. Indeed, just like the alarm calls of free-flight birds, they reliably signal the presence of a predator. As such, these antipredator signals should trigger robust socially acquired predator avoidance in conspecific receivers if an opportunity arose to associate them with a previously unfamiliar stimulus. For example, there is evidence that chemical alarm substances released by injured fish not only function to attract secondary predators, which interfere with the primary predator and

create escape opportunities for prey (Mathis et al. 1995; Chivers et al. 1996), but also trigger robust predator avoidance learning of novel stimuli with which they are associated in both conspecific and heterospecific prey species (Mathis et al. 1996). Learning triggered by distress calls should be all the more robust given that birds producing these vocalizations are exhibiting extreme levels of alarm, and that research on social learning of predators has reliably shown a close correlation of learning in observers and alarm levels expressed by demonstrators during training (for a review, see Griffin 2004). In birds, work on the role of distress calls in predator avoidance learning has provided ambiguous results. One study found that the distress calls of New Zealand robins, *Petroica australis*, triggered learning about an unfamiliar model predator in conspecifics, albeit at lower levels than alarm calls (Maloney & McLean 1995), while another in European starlings, *Sturnus vulgaris*, found no evidence of an acquired avoidance response following paired presentations of distress calls and a predator mount (Conover & Perito 1981).

The Indian mynah, *Acridotheres tristis*, is a highly commensal species of Passerine that has invaded large areas of the east coast of Australia since its introduction in the 1800s. Indian mynahs compete with native bird species for food and nesting sites and are the target of several ongoing eradication programmes (Pell & Tidemann 1997a; Lowe et al. 2000). Indian mynahs are highly social and can be found foraging in groups of two to 20 individuals throughout the day (Pell & Tidemann 1997b). At night, birds form communal roosts containing sometimes thousands of individuals (Pell & Tidemann 1997b). While there have been no studies of social learning in Indian mynahs, European starlings, which are phylogenetically closely related and have a very similar lifestyle to Indian mynahs, are known to learn socially about novel predatory threats (Conover & Perito 1981).

About one-third of wild-caught Indian mynahs, including juveniles and adults, give high amplitude broad-band distress calls in response to seizure by a human (A. S. Griffin, unpublished data). These calls are acoustically distinct from the lower amplitude broad-band alarm call, which free-flight mynahs give when alarmed (Pizzey & Knight 1998), and which can be evoked experimentally by presenting mynahs with a taxidermically prepared cat (*Felis catus*; A. S. Griffin, unpublished data). The social and highly adaptable lifestyle of Indian mynahs, together with their propensity to produce a variety of antipredator signals, make this species an ideal system for studying the mechanisms of socially acquired predator avoidance.

The aim of the present study was to test whether Indian mynahs can acquire an antipredator response to a novel stimulus after they have associated it with the sound of conspecific distress calls. Subjects in an experimental treatment (paired group) were presented with paired presentations of an unfamiliar live-size avian model and a playback of conspecific distress calls. A control treatment (unpaired group) received identical presentations of both avian mount and playback, but the two events were widely separated in time, and presented in a random order. Comparisons between paired and unpaired groups

allow changes in behaviour that are specifically attributable to associative learning to be isolated from those caused by nonassociative effects (Shettleworth 1998). Results revealed that distress calls triggered an acquired response to the avian mount, the nature of which was unclear. To elucidate this question, I conducted a second experiment in which I measured spontaneous responses evoked by a raptor and a novel visual stimulus, and compared them to responses elicited by a blank control trial, in which no visual stimulus was presented. Results from experiment 2 allowed me to determine whether response acquired in experiment 1 resembled an antipredator response to a perched aerial predator, or a more general visual exploratory response.

METHODS

Subjects and Husbandry

Indian mynahs were caught in urban locations along the Eastern coast of Australia, using a walk-in baited trap specifically designed to trap this species (Tidemann 2006) and widely used for population control. The trap consisted of two cages (1×1 m and 1 m) placed one on top of the other. Birds could access the bottom cage from outside through two openings. The top cage could be accessed from the bottom cage through two one-way channels. The top cage was equipped with an opaque roof and its sides were covered in shade cloth. Both cages were equipped with several perches. Small dog pellets, a preferred food of Indian mynahs, were used as bait and were provided ad libitum in both top and bottom cages, together with ad libitum water. The design of the trap is based on the ethological observation that Indian mynahs fly willingly up through a small opening after they have picked up food from the ground (Tidemann 2006). Consequently, the trap works by allowing mynahs to enter the bottom cage, pick up a bait and fly up into the top cage where they sit on perches and consume the food. Individuals accumulate in the top cage where they continue to eat the available food and remain calm because of their natural tendency to flock. The opaque roof and shaded sides help by providing birds with sun protection and cover. To obtain subjects for the present work, I made nine trapping excursions of 1–3 days, during which a total of 57 individuals were caught. Birds that did not participate in the present experiments were allocated to other ongoing behavioural projects.

I placed the Indian mynah trap in fenced off areas (back gardens and school yards), where it could not be approached by domestic dogs, *Canis lupus familiaris*. No other predator was ever sighted near or around the trap. The trap was monitored closely and birds were removed as soon as there were more than seven in the top cage, but at least once a day in the evening. Each bird was weighed, measured, individually identified with a lightweight coloured plastic leg band, and placed in a small (0.25×0.20 m) individual cotton holding bag, purchased from the Australian Bird Study Association. Birds were then transported in an air-conditioned station wagon 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), which was equipped with abundant perches, several plastic boxes (0.30×0.3 m and 0.6 m) for cover, a large plastic container with water for drinking and bathing, and several suspended feeding dishes. Transport duration varied from 15 to 75 min. No bird was injured during transport, and no bird showed any sign of distress once released into the flight aviary. Birds were left undisturbed for a minimum of 4 weeks to acclimatize to captivity. Mynahs were observed daily during feeding, watering and cleaning sessions, but no systematic behavioural measurements were made. It was thought that the birds were best left alone while they acclimatized to their new surroundings.

For testing, subjects were transferred to one of two individual outdoor test aviaries (1.95×2.2 m and 1.0 m). These were approximately 6 m apart and spatially arranged in such a way that subjects were in visual and acoustic contact. It was assumed that this would help this highly social avian species adjust to individual holding conditions. Each aviary was equipped with several perches and a nestbox. All captive mynahs had access ad libitum to water and a mixture of dog pellets and fresh fruit and vegetables. Although male Indian mynahs are typically larger and heavier than females, the extent of this size dimorphism is population specific (C. R. Tideman, unpublished data). In addition, male and female plumages are identical. Therefore, no attempt was made to control for sex and mynahs were allocated randomly to treatments. Sample sizes were determined on the basis of extensive previous work on predator recognition and predator avoidance learning by the author (Griffin et al. 2001; Griffin 2003; Griffin & Galef 2005).

Upon request by the University of Newcastle Animal Care and Ethics Committee, all individuals were euthanized after participation in the experiments. The ethics committee rejected the possibility of releasing subjects back into the wild because it was thought that they would be unable to reintegrate their breeding territory or a flock after time spent in captivity. 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 (protocol 962 1006), euthanasia was achieved by exposing each bird to a lethal dose of CO₂. In agreement with the most recent recommendations on best-practice procedures in animal research (Hawkins et al. 2006), the birds were placed inside a closed container and exposed to a rising concentration of 100% CO₂. All work was undertaken during the nonbreeding season of Indian mynahs.

All husbandry and experimental procedures used here were approved by the University of Newcastle Animal Care and Ethics Committee (approval no. 962 1006).

EXPERIMENT 1

I undertook experiment 1 to determine whether Indian mynahs acquire an antipredator response to an unfamiliar

stimulus, towards which they show initially little or no response, after it has been presented together with the sound of conspecific distress calls.

Methods

Subjects

Sixteen adult Indian mynahs served as subjects.

Visual and acoustic stimuli

Familiarity with a stimulus can interfere with subsequent acquisition of responses to that stimulus. To quantify learning, I therefore selected a stimulus that had no resemblance to a predator or to a nonpredator species that Indian mynahs would probably encounter naturally, namely a taxidermically prepared mount of a Reeve's pheasant, *Syrnaticus reevesii*. This species is native to central China. In Australia, it only exists in captivity, where it is bred by a few bird fanciers. Similarly, all other introduced Phasianidae are primarily bred in captivity, despite a few small isolated semiferall mainland (e.g. Indian peafowl, *Pavo cristatus*), or offshore island (e.g. common pheasant, *Phasianus colchichus*) populations (Pizzey & Knight 1998). The only free-living Phasianidae native to Australia are typical quails and do not resemble pheasants (Pizzey & Knight 1998). It is therefore highly unlikely that the Indian mynahs used in this study, which were trapped in urban locations, had any evolutionary or ontogenetical experience of Reeve's pheasants or any other pheasant-like birds.

To create the distress call playback sequences, I made recordings of eight individual Indian mynahs. Distress calls were collected opportunistically while birds were being handled for the purposes of banding. Vocalizations were recorded using a Sennheiser directional microphone connected to a Marantz analogue tape deck (model PMD222). Recordings were digitized using a G3 iBook computer (Amadeus sound software, sample rate 44.1 kHz, 16-bit amplitude encoding). I then edited the recordings to make eight distinct 120 s distress call playback sequences to sample natural variation in the acoustic structure of these vocalizations (Fig. 1). Each distress call sequence was only used once during the course of the experiment, so a total of eight distress call sequences were used per treatment (see below).

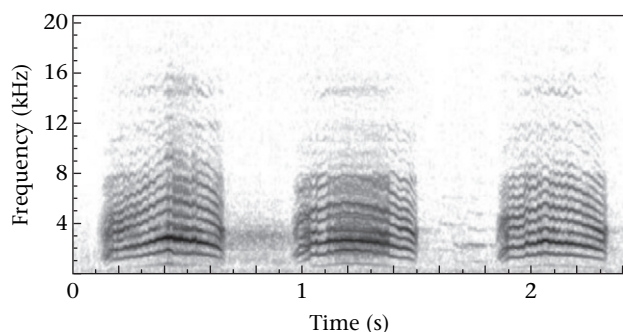


Figure 1. Spectrograms of representative distress calls of Indian mynahs played back in experiment 1. Sampling rate was 44.1 kHz, 512 point FFT, grey scale represents an amplitude range of 80 dB.

To avoid startling the birds, each chorus began with a 4-s fade in (0–88 dB) and ended with a 4-s fade out (88–0 dB). Mean distress call rate was 67.3 ± 1.2 SE) calls per min, which approximated that observed naturally. Acoustic stimuli were then saved to type II analogue tapes and played back from a Marantz analogue tape deck (model no. PMD222) through two Clarion loudspeakers (model SRR1028; frequency response 45–30 000 Hz), one placed 1 m from an aviary containing a paired experimental mynah (see below), the other placed 1 m from an aviary containing an unpaired control bird (see below). The amplitude of all stimuli was matched at the output using a digital sound level meter (Radioshack, model no. 33-2085) and played back at a mean amplitude of 88 dB (± 1 dB measured 1 m in front of each speaker) roughly equivalent to the birds' own output volume measured at a distance of 1 m.

Procedure

For experiments, mynahs were caught in pairs in the flight aviary. One randomly selected bird was allocated to the paired experimental group (see below) and placed in one individual test aviary, while the other was allocated to the unpaired control group (see below) and placed in a second individual test aviary. Birds were then left undisturbed for 48–72 h before testing began.

During trials, the mynah that was not being tested was visually isolated from its entire surroundings. This was achieved by covering each meshed side of the aviary in which the nonfocal bird was housed with curtains. I thus ensured that the focal subject's response was caused by the visual stimulus and not by the behaviour of a nearby conspecific. The Reeve's pheasant was then placed on a platform (0.45×0.45 m) located approximately 4 m away from the focal test aviary and 2 m above the ground. A 0.5-m high plastic screen surrounding the platform could be moved up and down via a pulley system operated by the experimenter from a hide located approximately 8 m from the aviary. The stimulus was hidden when the screen was raised and visible when it was lowered. After placing the stimulus on the platform, the experimenter entered the hide and waited for 15 min before the trial began.

Each mynah first received a pretraining trial during which I determined its initial response to a 60-s presentation of the Reeve's pheasant. I then conducted one training trial in which each subject received either paired (experimental group) or explicitly unpaired (control group) exposure to both the pheasant and a randomly selected distress call playback. After training, each mynah underwent a post-training trial in which it was again presented with the pheasant for 60 s.

For training trials, each paired experimental individual was presented with the pheasant for 120 s simultaneously with a randomly selected 120-s mynah distress call playback sequence. Each mynah's matched unpaired control bird also received a 120-s pheasant presentation and the same 120-s distress call stimulus exemplar, but these two events were separated by a minimum of 30 min and a maximum of 1.5 h, and their order of

presentation was balanced across birds. As each distress call sequence was only used once, each pair of birds (made up of one paired experimental mynah and the matched unpaired control mynah) received a different distress call sequence to any other pair of birds participating in the experiment. Comparisons between post-training responses of paired and unpaired groups allow the experimenter to isolate changes in behaviour that are the consequence of associative learning, and to separate these from changes in behaviour attributable to nonassociative effects, such as increases in responsiveness caused by exposure to each of the training stimuli alone (Shettleworth 1998).

Given that playbacks to one test aviary could be heard at the second aviary, paired presentation of pheasant and distress calls to experimental subjects was conducted simultaneously with unpaired presentation of the acoustic stimulus to control subjects. This was achieved by playing back the distress call sequence through two loudspeakers. One speaker was placed beside the aviary containing the paired experimental mynah; the second loudspeaker was placed beside the aviary containing the matched unpaired control bird. While the paired individual was given simultaneous visual access to the pheasant during the playback, the curtains on the unpaired individual's cage were closed so that the unpaired mynah was visually isolated. In this way, I ensured that both paired experimental, and unpaired control individuals, only heard the distress call playback once.

Pretraining trials were conducted early in the morning, and training trials were run 1 h 30 min to 3 h after the pretraining trials. Post-training trials were conducted the following morning.

Data analysis

I videorecorded all trials, but scored and analysed only pre- and post-training trials. I videorecorded mynahs for 60 s immediately prior to pheasant presentation (baseline), and 60 s during pheasant presentation. A 5-s time interval between the 60-s baseline and the 60-s presentation period, during which the screen was moving down to reveal the stimulus, was not analysed. Bird behaviour was scored from video recordings using JWatcher 1.0 (Blumstein et al. 2006).

If the focal subject moved to a location where it could not be observed (e.g. behind a metal support structure in the aviary), it was scored as 'out-of-sight'. Time out-of-sight was subtracted from the 60-s baseline and the 60-s presentation time to obtain total time 'in-sight' for each time period. In practice, out-of-sight only occurred very rarely because care had been taken to place the perches in locations that avoided blind spots.

To quantify responses to the stimulus, I measured changes in locomotion from prestimulus baseline. Flight included any movement between perches, between a perch and the floor, or between a perch and the wire mesh of the aviary. Flight length ranged, therefore, from 0.15–1.3 m. Walking was defined as any lateral movement along a perch, or forward movement along the floor. I scored the number of times each mynah flew and walked

during the 60-s prestimulus baseline and the 60-s pheasant presentation period. For each behaviour, I calculated the change in frequency between baseline and the 60-s presentation time periods.

In addition to measuring changes in behaviour from prestimulus baseline, I measured absolute rates of head movement during the first 30 s after the stimulus had appeared. Birds have well-developed visual systems including colour vision and good visual acuity. However, they have limited eye movements (Pratt 1982). Consequently, rather than moving their eyes to scan a visual scene or follow a moving stimulus, they move their heads (Nye 1969). Many birds also have two or more high acuity areas on their retina. These spatially distinct foveas may allow birds to derive different kinds, or quality, of information from a visual stimulus (Maldonado et al. 1988; Lima & Bednekoff 1999; Land 1999a, b). Head movements may also facilitate depth perception (Wallace 1959; Ellard et al. 1984). On the basis of these findings, I reasoned that an acquired antipredator response to the pheasant might not only involve changes in body movement, but also changes in the rate of head movements. A head saccade was defined as any detectable movement of the head that occurred during periods of time when the bird was not walking or flying. Head saccade frequencies were calculated by dividing the number of head movements by the total time the bird was not walking or flying. As successive head saccades can occur extremely rapidly, head movements were scored from video recordings played back at one-quarter normal speed.

Finally, I scored all instances of a high amplitude broadband call, which is produced by free-flight mynahs when they are alarmed (Pizzey & Knight 1998), and which can be evoked experimentally by presenting mynahs with a taxidermically prepared cat (A. S. Griffin, unpublished data).

To identify the effects of training, I compared the mean change from baseline frequency of flight and walk in the pretraining trials with that of post-training trials using a two-way, repeated measures ANOVA with factors for group (paired, unpaired) and trial (pretraining trial, post-training trial). The head saccades of two individuals in the paired experimental group could not be measured because they moved to a location where their heads were out-of-sight. The pretraining head movement frequencies of the remaining 14 individuals were compared with those obtained after training by using a two-way repeated measures ANOVA with factors for group (paired, unpaired) and trial (pretraining trial, post-training trial). To ensure that changes in head saccade rate were attributable to pheasant presentation and did not reflect a change in the general state of arousal of the birds after training relative to before training, I calculated head movement rates during a 30-s time period before pheasant presentation for pretraining trials, and compared them with head movement rates during a 30-s prestimulus time period for post-training trials using a two-way repeated measures ANOVA with factors for group (paired, unpaired) and trial (pretraining trial, post-training trial). One individual in the paired group moved to a location where its head was out-of-sight, so head movements were not quantified for

this bird. I used an alpha level of 0.05 throughout. All analyses were carried out on untransformed data using Statview 5.2 (SAS Institute 1998) and SPSS 11 (SPSS Incorporated 2005).

Results and Discussion

Indian mynahs that had undergone paired presentations of pheasant and conspecific distress calls did not alter their patterns of locomotion in response to the pheasant after training relative to control mynahs that had experienced pheasant and distress call playbacks separately. Analyses of variance revealed no significant group*trial interactions on flight rate or walk rate (flight: $F_{1,14} = 0.184$, $P = 0.675$; walk: $F_{1,14} = 1.643$, $P = 0.221$). There were also no significant main effects of group or trial on either flight rate or walk rate (flight: main effect group: $F_{1,14} = 1.912$, $P = 0.188$; main effect trial: $F_{1,14} = 0.005$, $P = 0.945$; walk: main effect group: $F_{1,14} = 112$, $P = 0.742$; main effect trial: $F_{1,14} = 0.258$, $P = 0.619$). Nor did mynahs change the rates with which they produced alarm vocalizations in response to the novel stimulus after training relative to before training. No mynah alarm-called in response to pheasant presentation either before, or after, training.

Training caused a differential change in head saccade rate in paired mynahs relative to unpaired mynahs, however. Mynahs that had experienced pheasant simultaneously with the sound of conspecific distress calls increased the rate at which they moved their heads in response to the pheasant after training, while control mynahs that had experienced pheasant separately from distress calls decreased head movement rate (Fig. 2). This difference was reflected by a significant group*trial interaction on head movement rate (ANOVA: $F_{1,12} = 7.917$, $P = 0.016$). Main effects of group and trial on head saccade rate were not significant (main effect group: $F_{1,12} = 0.900$, $P = 0.361$; main effect trial: $F_{1,12} = 0.600$, $P = 0.453$). Comparisons between

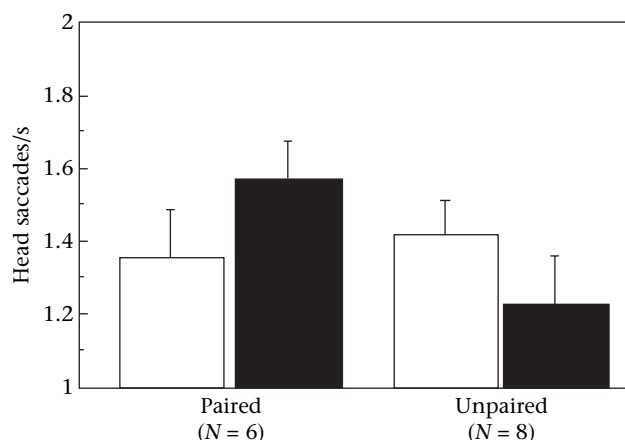


Figure 2. Head movements evoked by a model pheasant both before (□: pretraining trial) and after (■: post-training trial) training by mynahs that had received paired presentations of pheasant and distress calls and mynahs that had received unpaired presentations of pheasant and distress calls. The mean ± SE head saccade rate is indicated for a 30-s time period after stimulus onset. See text for more details.

prestimulus head movement rates of pretraining trials and those of post-training trials revealed no significant effects, indicating that neither paired, nor unpaired, presentations of pheasant and distress calls caused a general change in arousal (ANOVA: main effect group: $F_{1,13} = 0.001$, $P = 0.976$; main effect trial: $F_{1,13} = 0.794$, $P = 0.389$; group*trial interaction: $F_{1,13} = 0.168$, $P = 0.688$). Differences in head saccade rates between paired and unpaired groups after training relative to before training were hence evoked by pheasant presentation per se, and did not reflect a change in the general state of the birds.

When disturbed by a cat, captive mynahs increase head saccade and flight rates, and alarm call (A. S. Griffin, unpublished data). Furthermore, several earlier studies have shown that predator avoidance learning is typically reflected by increases in antipredator responses to the novel stimulus for which training is undertaken, including increases in movement and alarm calling (Vieth et al. 1980; Curio 1988; Maloney & McLean 1995). For these reasons, I assumed predator avoidance learning would be reflected in Indian mynahs by an increase in head saccades, flight and alarm call rates. Surprisingly, responses acquired as a consequence of pairing pheasant and distress calls involved an increased rate of head saccades, but no changes in movement or vocal behaviour. The difference between the response acquired as a consequence of training and the spontaneous response evoked by a terrestrial predator raised two possibilities. First, some animals show responses to aerial predators that are qualitatively different to those evoked by ground predators (Evans et al. 1993a, b). Aerial threats may cause individuals to go quiet, increase vigilance, and to minimize movement, or changes in movement (Fentress 1968; Archer 1979; Evans et al. 1993a; Fanselow 1994). Consequently, the present finding that mynahs increased head saccade rates after training relative to before training and did not alarm call may have reflected acquisition of an antipredator response specific to raptors. For example, head saccades might facilitate distance judgements, either by generating motion parallax, in which near objects move faster across the retina than more distant objects, or a series of stimulus views, from which distance information can be extracted. It is well known that prey use distance information to select a subsequent antipredator response (Fanselow 1994; Lind et al. 2003).

Alternatively, an acquired response characterized by only an increase in head saccade rate may have reflected an increase in visual exploration of the training stimulus. Indeed, there is evidence that hens, *Gallus gallus*, increase the rate at which they move their heads in response to a novel object more than in response to a familiar conspecific (Dawkins 2002). It is thought that viewing the object with different areas of the retina, or even different eyes, may allow birds to collect different kinds of information about the stimulus (Martinoya et al. 1983; Maldonado et al. 1988; McKenzie et al. 1998; Land 1999a, b; Dawkins 2002; Andrew 2006). Dawkins' (2002) finding that visual exploration can be reflected by a change in head saccade rate suggests that pairing pheasant with distress calls may have mediated the acquisition of an investigative response, rather than an antipredator response. Experiment 2 was conducted to tease apart these two possibilities.

EXPERIMENT 2

The results of experiment 1 demonstrated that the sound of conspecific distress calls was sufficient to trigger learning about a novel stimulus. It remained unclear, however, whether mynahs acquired an antipredator response or a visual exploratory response. To separate these two possibilities, I elected to determine how Indian mynahs respond to a perched aerial predator and to a novel visual stimulus. Comparisons between spontaneous responses to each of these stimuli and that learnt as a consequence of training allowed me to explore the nature of the acquired response further. Specifically, if the response acquired in experiment 1 resembled that evoked by a prototypical raptor, then this would suggest that pairing pheasant with distress calls inculcated an antipredator response to the pheasant. In contrast, if the response learnt in experiment 1 resembled that evoked by a novel visual stimulus, this would suggest that distress calls inculcated rather a visual exploratory response to pheasant.

Methods

Subjects

Eighteen Indian mynahs served as subjects in experiment 2. None of them had taken part in experiment 1.

Visual stimuli

A taxidermic mount of a male brown goshawk, *Accipiter fasciatus*, was used as a prototypical representative of the greater class of raptors. There is abundant evidence that taxidermic models of aerial predators are effective stimuli for evoking antipredator behaviour in birds (e.g. Curio 1993). The same Reeves' pheasant model used to study learning in experiment 1 was used to measure responses evoked by a novel visual stimulus in experiment 2. To obtain a baseline level response with which to compare the effects of the predatory stimulus and the novel stimulus, I presented mynahs with the empty presentation platform during a blank control trial.

Test procedure

The test procedure was identical to that used during the pre- and post-training trials in experiment 1. Visual stimuli and the empty platform were presented for 60 s. Presentation order was balanced across subjects. Trials were conducted in the afternoon between 1300 and 1700 hours and separated by 24 h unless it rained, in which case trials were postponed until the next testing session.

Data analysis

Trials were scored and analysed in the same way as pre- and post-training trials in experiment 1. As in experiment 1, I measured changes in flight and walk rate from prestimulus baseline. For each of the three stimuli, I calculated the difference between the rate at which each behaviour occurred during the 60-s prestimulus baseline period and the rate at which each behaviour occurred during the 60-s presentation period. To analyse the effects of stimulus type

on each behaviour, I conducted a one-way repeated measures ANOVA using stimulus type as a repeated measures independent variable. As in experiment 1, I measured absolute rates of head movements. For each of the stimuli, frequency of head saccades was calculated during a 30-s time interval after stimulus onset. To analyse the effects of stimulus type on head saccade rate, I conducted a one-way repeated measures ANOVA with stimulus type as a repeated measures independent variable. Significant main effects were analysed further using Fisher's least significant difference (LSD) test, which protects against increased probabilities of Type 1 errors in multiple pairwise comparisons following a significant repeated measures overall ANOVA (Howell 1995). Finally, I tested the relationship between the probability of alarm calling and stimulus type using Cochran's Q.

Results and Discussion

Analyses of variance on locomotion revealed a main effect of stimulus type on flight rate and walk rate (ANOVA: flight: $F_{2,34} = 3.984$, $P = 0.028$; walk: $F_{2,34} = 3.522$, $P = 0.041$; Fig. 3). Pairwise comparisons indicated that the raptor evoked significantly higher flight rates than the pheasant and the blank control (LSD test: raptor versus pheasant: $t_{34} = 2.351$, $P = 0.025$; raptor versus blank: $t_{34} = 2.791$, $P = 0.016$), as well as significantly higher walk rates than the blank (LSD test: $t_{34} = 2.599$, $P = 0.014$). Comparisons

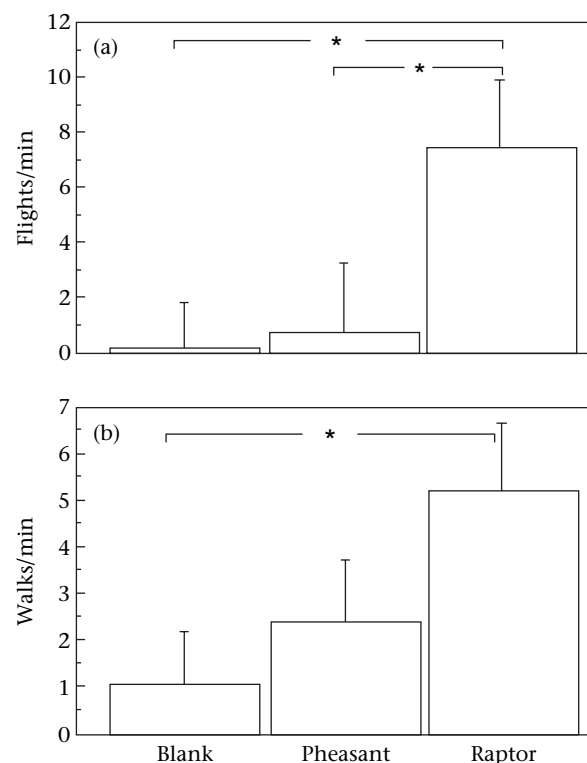


Figure 3. Locomotion evoked by a model hawk, a model pheasant and a blank control trial. The mean (\pm SE, $N = 18$) change in flight rate (a) and walk rate (b) from prestimulus baseline is indicated for a 60-s presentation period. * $P < 0.05$. See text for more details.

between pheasant and blank revealed no significant differences for either flight or walk (LSD test: flight: $t_{34} = 0.177$, $P = 0.860$; walk: $t_{34} = 0.828$, $P = 0.413$). In addition, three Indian mynahs gave at least one alarm call to the raptor while no mynah alarm-called to the pheasant or to the presentation device activated on its own. This difference was reflected by a marginally significant effect of stimulus type on the probability of alarm calling (Cochran's $Q = 6.0$, $P = 0.05$).

Analyses of variance revealed a significant main effect of stimulus type on head movement rate (ANOVA: $F_{2,34} = 8.444$, $P = 0.001$; Fig. 4). Furthermore, pairwise comparisons indicated that Indian mynahs increased the rate at which they moved their heads significantly more in response to both raptor and pheasant than in response to the blank control trial (LSD test: raptor versus blank: $t_{34} = 2.791$, $P = 0.009$; pheasant versus blank: $t_{34} = 4.007$, $P < 0.001$). However, head saccade rates evoked by raptor did not differ from those evoked by pheasant (LSD test: raptor versus pheasant: $t_{34} = 1.217$, $P = 0.232$).

These results show first that a model raptor and a novel visual stimulus evoke different kinds of responses in Indian mynahs when compared with an empty platform. While both raptor and pheasant caused head saccade rate to increase compared with the empty platform condition, only the raptor evoked increases in locomotion, and, in a small number of individuals, alarm calls. In so far that the goshawk was a representative member of the larger category of raptors and the pheasant a representative member of the larger category of nonpredators, differential responses strongly suggest that Indian mynahs discriminate between raptors and nonraptors. Interestingly, all mynahs were trapped in residential locations, in which exposure to raptors is unlikely to be common, suggesting that recognition of perched aerial predators may not be dependent upon specific experience with such stimuli. However, further research comparing exposure rates of urban and rural populations of Indian mynahs to raptors are needed to confirm this idea.

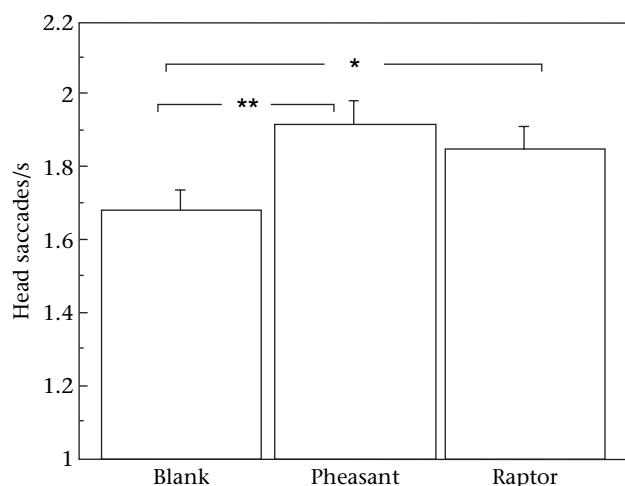


Figure 4. Head movements evoked by a model hawk, a model pheasant and a blank control trial. The mean (\pm SE, $N = 18$) head saccade rate is indicated for a 30-s time period after stimulus onset. * $P < 0.05$; ** $P < 0.001$. See text for more details.

Second, the present results corroborate earlier studies that have found that birds increase head saccades in response to novel stimuli (Dawkins 2002). Both raptor and pheasant evoked greater rates of head saccades than did the absence of any visual stimulus (blank control). However, head saccades evoked by the raptor were accompanied by an increase in flight rate, so I cannot exclude that they reflect the search for an escape route. In contrast, the pheasant evoked head saccades, but no change in locomotion. Higher head saccade rates in response to the pheasant than in response to the empty presentation platform (blank) suggest that head movements allowed mynahs to visually explore the pheasant. This finding is consistent with the suggestion that head movements may allow for a viewed object to be placed on different areas of the retina, or on different eyes, and allow for the processing of different kinds of information (Martino et al. 1983; Maldonado et al. 1988; McKenzie et al. 1998; Land 1999a, b; Lima & Bednekoff 1999; Dawkins 2002; Andrew 2006). The results of experiment 1 extend those of earlier work by demonstrating that learning can lead to increases in head saccade rates.

Finally, and most importantly, experiment 2 was conducted to better understand the nature of the response acquired as a consequence of pairing novel bird with distress calls in experiment 1. In experiment 1, mynahs increased head saccades in response to novel bird after training, but there were no changes in locomotion or alarm call rate. Results from experiment 2 revealed that spontaneous responses to a prototypical raptor involved head saccades, flight, and a tendency to alarm call, while those to a novel bird involved only head saccades. Consequently, acquired responses most closely resembled those evoked by a novel stimulus rather than those elicited by a perched raptor. I conclude that distress calls triggered the acquisition of a visual exploratory response, rather than an antipredator response specific to raptor.

DISCUSSION

The aim of the present study was to determine whether Indian mynahs acquired an antipredator response towards a novel stimulus after they had experienced it together with a playback of conspecific distress vocalizations. Results revealed that subjects increased the rate at which they made head saccades in response to a pheasant mount following paired presentations of pheasant and distress calls. A second experiment demonstrated that Indian mynahs respond spontaneously to a nearby perched raptor by increasing head saccade rate, locomotion and alarm calling, whereas their spontaneous response to a novel avian model involves only an increase in head saccade rate. Together, these findings suggest that distress calls constitute an antipredator signal that triggers the acquisition of a visual exploratory response in conspecific receivers, rather than an antipredator response.

Prior to selecting an appropriate antipredator response, animals presumably engage in some degree of visual exploration of the predatory stimulus. Information about the identity and the location of the predator might need

to be collected before an appropriate course of action is selected (Fanselow 1994; Lind et al. 2003). Therefore, it might be argued that training with distress calls inculcated a visual exploratory response that represented the very first stage of an antipredator decision process. However, in experiment 2, mynahs showed only a few seconds delay between the appearance of the raptor and subsequent increases in locomotion. Individuals that alarm-called also began to do so within seconds of stimulus onset. These observations suggest that predator recognition and response selection are very rapid processes, as functional considerations might predict. Post-training increases in head saccade rate were measured over a time period of 30 s after stimulus onset. This seems far too long to consider a potential predator before selecting a behavioural response. I conclude that the acquired visual exploratory response was purely investigative. More specifically, the pheasant became more interesting to the subjects as a consequence of its pairing with distress calls, but not more frightening.

The finding that distress calls can trigger learning is consistent with those of Maloney & McLean (1995) who found that New Zealand robins acquired an antipredator response towards a novel predator stimulus after they had experienced it together with conspecific distress vocalizations. Interestingly, the study revealed that the acquired response was of lower intensity, however, than that learnt after pairing predator with conspecific alarm calls. Robust predator avoidance learning using alarm calls has also been found in other systems, such as the European blackbird, *Turdus merula* (Vieth et al. 1980). Taken together, these studies point to a differential effect of distress calls and alarm calls on learning in receivers. Although the possibility of between-species differences cannot be ruled out, it is possible that distress calls are less effective social stimuli for triggering avoidance learning than alarm calls. This could explain the present unexpected finding that distress calls triggered acquisition of an exploratory response rather than an antipredator response. Differences between the effects of distress calls and alarm calls could also explain why one other study detected no evidence of learning following paired presentations of predator stimuli and a distress call playback (Conover & Perito 1981). Future work comparing the effects of alarm calls and distress calls on predator avoidance learning in Indian mynahs will help to explore potential differences between these antipredator signals further.

Any behaviour performed by a demonstrator and reliably associated with predation risk should have the potential to trigger learning of novel dangers in observers. For learning to provide a fitness benefit, however, observers should be able to adjust their acquired response to their level of predation risk (Ferrari et al. 2005). Accordingly, research on social learning of predators has reliably shown that post-training responses of observers are strongly correlated with levels of alarm behaviour displayed by demonstrators during training (reviewed in Griffin 2004). Distress calls are produced by individuals that are extremely alarmed because they have been caught by a predator; these vocalizations should, therefore, produce robust predator avoidance learning. On the other hand, in many avian species, distress calls are not only

produced by adults, but also by immature birds (Perrone 1980). In Indian mynahs, for example, approximately 50% of juveniles distress-call when handled by a human, as opposed to only about 25% of adults (A. S. Griffin, unpublished data). If vulnerability of juveniles to predation differs with that of adults (Hanson & Coss 1997), distress vocalizations may be a less reliable predictor of predation risk than an alarm call produced by an adult. Furthermore, there is strong evidence suggesting that distress calls might be directed primarily towards predators, even though these calls cause conspecifics to approach in some species (Stefanski & Falls 1972). In particular, they may serve to convey information about the quality of the caller to the primary predator (Laiolo et al. 2004), or to attract a secondary predator, that intervenes with the primary predator and creates escape opportunities for the prey (Curio 1976; Perrone 1980; Högstedt 1983). For either or both these reasons, this signal may be less likely to engage learning in receivers even though there is little doubt that their production reflects an extremely high emergency situation for the caller. More knowledge is needed about the effects of antipredator signals produced by juveniles, which are known to be less reliably associated with danger than those of mature individuals, on learning in adults (Mateo 1996a, b; Hanson & Coss 1997; Seyfarth & Cheney 1997; Hollen & Manser 2006).

In sum, the relationship between levels of alarm in demonstrators and levels of learning in observers may be more complex than it is usually thought. There is clearly a need for further studies that make formal comparisons between the effects of various antipredator signals on predator avoidance learning. Future research will help to establish the range of behaviours that trigger avoidance learning in observers, and therefore, the scope for social transmission of predator avoidance within a population.

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