

Temporal Limitations on Social Learning of Novel Predators by Indian Mynahs, *Acridotheres tristis*

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Abstract

Antipredator vocalizations of social companions are important for facilitating long-term changes in the responses of prey to novel predator stimuli. However, dynamic variation in the time course of acoustic communication has important implications for learning of predator cues associated with auditory signals. While animals often experience acoustic signals simultaneously with predator cues, they may also at times experience signals and predator stimuli in succession. The ability to learn about stimuli that are perceived not only together, but also after, acoustic signals has the potential to expand the range of opportunities for learning about novel events. Earlier work in Indian mynahs (*Acridotheres tristis*) has revealed that subjects acquire a visual exploratory response to a novel avian mount after they have experienced it together with conspecific distress vocalizations, a call produced in response to seizure by a predator. The present study explored to what extent such learning occurred if the avian mount was experienced after, rather than simultaneously with, distress calls, such as might happen if call production is interrupted by prey death. Results showed that mynahs that experienced a novel avian mount simultaneously with the sound of distress calls exhibited a sustained exploratory response to the mount after training relative to before that was not apparent in birds that received distress calls and mount in succession. This finding suggests that vocal antipredator signals may only trigger learning of environmental stimuli with which they share some temporal overlap. Recipients may need to access complementary non-vocal cues from the prey victim to learn about predator stimuli that are perceived after vocal behaviour.

Introduction

Antipredator signals play an important role in facilitating long-term changes in the responses of prey animals to novel predator stimuli with which they are associated. For example, conspecific chemical alarm substances trigger the acquisition of an antipredator response to previously unfamiliar predatory pike (*Esox lucius*) in predator-naïve fathead minnows (*Pimephales promelas*) (Chivers & Smith 1995). Likewise, the alarm responses of rhesus macaques (*Macaca mulatta*) to snakes lead to a similar acquired

alarm response in snake-naïve observer macaques (Mineka & Cook 1988, 1993). Although some antipredator signals contain both visual and acoustic components, it is well known that acoustic signals on their own are sufficient to trigger learning (Vieth et al. 1980; Maloney & McLean 1995; Griffin 2008).

Studies investigating the relationship between predator presence and alarm calls in prey consistently show that animals alarm call when a predator is sighted (Owings & Virginia 1978; Blumstein 1999; Goodale & Kotagama 2005; Leavesley & Magrath 2005). Whether animals continue to call thereafter

varies, however, across situations. For example, California ground squirrels (*Spermophilus beecheyi*) commonly maintain vocal alarm behaviour both whilst the predator is present and after it has disappeared, a phenomenon referred to as tonic communication (Schleidt 1973; Owings et al. 1986). Similarly, the rate with which chickens (*Gallus gallus*) produce ground alarm calls in response to the sighting of a terrestrial predator gradually builds up throughout the predator's presence and continues for several minutes after it has gone (Evans 1997). The temporal patterning of ground alarm call production is consistent with the hypothesis that these vocalizations are directed towards the predator and serve to inform it that it has been detected, thereby reducing the likelihood that it will attack (Evans 1997). In contrast, domestic chickens respond quite differently to aerial predators. First sighting of a flying raptor typically evokes only one to three aerial alarm calls followed by a period of silence, during which the caller maintains prolonged immobility while monitoring the overhead threat (Evans et al. 1993b; Bayly & Evans 2003). Aerial alarm calls, in contrast to ground alarm calls, appear to be directed towards nearby conspecifics, and function to warn them of an imminent aerial danger while minimizing risk to the caller (Evans et al. 1993a; Evans 1997; Bayly & Evans 2003).

Such dynamic variation in the time course of alarm call production has important implications for learning of novel predator stimuli associated with alarm vocalizations. In cases where alarm calls are maintained throughout the predator encounter, alarm call recipients are likely to experience the predator and alarm signals simultaneously. In contrast, in situations where call production is restricted to the early stages of the predation episode, recipients may sight the predator after they have detected alarm signals and, moreover, experience it in the absence of any further vocalizations. While it is well documented that predator stimuli that are perceived simultaneously with alarm vocalizations are learnt about (Curio et al. 1978; Magurran 1989; Mineka & Cook 1993; Maloney & McLean 1995; Griffin & Evans 2003), the possibility that predators might be observed during a period of non-calling subsequent to the detection of a conspecific alarm signal, raises the question of whether social learning can occur when alarm vocalizations and predators are experienced in succession, but with no temporal overlap.

The Indian mynah (*Acridotheres tristis*), also called the common myna, is a highly commensal Passerine that lives in close association with humans and can

be found in large roosts along the eastern coast of Australia (Tidemann 2006). This invasive species has expanded its range so quickly in the last few decades that it is now poses a threat to several native Australian bird species and is the target of ongoing pest control efforts. However, its highly social and adaptable lifestyle, together with its ability to produce a variety of antipredator vocalizations, make this species particularly well suited to empirical studies of social learning. Accordingly, earlier work in this system has demonstrated that Indian mynahs can learn socially (Griffin 2008).

Distress calls are one type of antipredator vocalization produced by Indian mynahs. This high amplitude broadband pulsatile vocalization, which is acoustically distinct from the lower amplitude broadband call made by free-flight mynahs when alarmed, is produced by about one-third of individuals including adults and juveniles, in response to seizure by a predator or a human (Pizzey and Knight 1998; A. S. Griffin, unpubl. data). Several hypotheses have been put forward to explain why birds from many species produce distress calls in response to capture by a predator. One hypothesis is that these vocalizations function to attract secondary predators that disrupt the predation event and afford prey an opportunity for escape (Driver & Humphries 1969; Curio 1976), an idea supported by evidence that these calls are highly attractive to predators and that they constitute an honest signal of bird quality (Perrone 1980; Högstedt 1983; Laiolo et al. 2004, 2007). Even though distress calls may be used primarily as an interspecific communication signal, experimental work in Indian mynahs has revealed that presenting distress calls simultaneously with a novel avian mount leads to the acquisition of a visual exploratory response (head saccade response) to the mount presented later on its own (Griffin 2008), suggesting that conspecific recipients can associate distress calls with a novel stimulus if the opportunity arises, corroborating earlier work in New Zealand robins, *Petroica australis*, (Maloney & McLean 1995). In cases where prey death interrupts call production, however, a receiver whose attention to a predator is captured by the sound of conspecific distress calls may experience distress vocalizations and predator stimuli in succession, rather than together. Consequently, the present study aimed to extend our understanding of the effect of distress calls on conspecific behaviour by exploring to what extent social learning was dependent upon temporal overlap of distress calls and novel stimulus. This question was addressed by testing whether mynahs acquire a

visual exploratory response to an unfamiliar avian mount after they experience it in succession, rather than simultaneously with, the sound of distress vocalizations.

Methods

Subjects and Husbandry

Subjects were 27 adult Indian mynahs. Subjects were allocated randomly to either a simultaneous group ($n = 13$, see below) or a contiguous group ($n = 14$, see below). Mynahs were caught in several distinct urban locations within Newcastle, a city on the eastern coast of Australia, using a walk-in baited trap specifically designed to trap this species (Tidemann 2006). The trap consists of two superimposed ($1 \times 1 \times 1$ m) cages. Birds access the lower one through two one-way tunnels located at ground height, and the top one through two one-way channels connecting the lower cage's roof to the top cage's floor. The trap works by allowing mynahs to enter the lower cage, collect food and fly up into the top cage where they roost on perches. As mynahs are the only species that willingly flies upwards through an opening to join conspecifics, the trap is relatively species-specific (Tidemann 2006). Dog pellets and water were available in both cages, which were covered in shade cloth to offer sun protection and cover. The trap was monitored twice daily and emptied each evening.

Upon capture, mynahs were placed in individual cotton bags and transported to the Central Animal House at the University of Newcastle. Before release into a large outdoor group aviary (depth $4.4 \times$ width $1.25 \times$ height 2.25 m), each individual was individually identified using one, or a combination of, plastic coloured leg band(s). As male and female mynahs cannot be distinguished on the basis of plumage, no attempt was made to control for sex. Mynahs had access to water, fresh vegetables and dog pellets *ad libitum*, and were left undisturbed for a period of at least 4 wk to acclimatize to captivity. Experiments spanned the breeding and non-breeding season of Indian mynahs.

The University of Newcastle Animal Care and Ethics Committee (ACEC) requested that mynahs be euthanized at the end of the study, because it feared that re-released subjects would not reintegrate a breeding territory or a social group. As recommended by the Australian and New Zealand Council for the Care of Animals in Research and Training

(Reilly 2001) and the ACEC (protocol 962 1007), euthanasia was achieved by exposing each individual to a lethal dose of CO_2 .

Acoustic and Visual Stimuli

Indian mynah distress calls were collected opportunistically during handling for the purposes of banding (for a spectrogram, see Griffin 2008). Vocalizations were recorded using a Sennheiser directional microphone connected to a Marantz analogue tape deck (model PMD 222, Saul Mineroff Electronics, Elmont, NY, USA) and digitized using a G3 iBook computer (sample rate 44.1 kHz, 16-bit amplitude encoding; Amadeus software, Hairersoft, Kenilworth, UK). Raw recordings were edited using Raven version 1.2.1 to make three distinct 2-min distress call sequences to sample natural variation in the acoustic structure of these vocalizations. To avoid startling the birds, each sequence began with a 4-s fade in (0–88 dB) and ended with a 4-s fade out (88–0 dB). Mean call rate was 69.2 calls per min, which approximated that observed naturally. Acoustic stimuli were then saved to type II analogue tapes and played back from the Marantz tape deck through a Clarion loudspeaker (model SRR1028, Clarion Corporation of America, Cypress, CA, USA; frequency response 45–30 000 Hz) located 1 m away from the test aviary. The volume of the distress calls was matched at the output using a digital sound level meter (Radioshack, model no. 33-2085, Radioshack Corporation, Fort Worth, TX, USA) and played back at a mean amplitude of 88 dB (± 1 dB) in front of each speaker.

To quantify learning, I used a taxidermically prepared mount of a Reeves pheasant (*Syrnaticus reevesii*). This species bears no resemblance to a natural predator of Indian mynahs and only exists in Australia under captive conditions where it is bred by bird fanciers. Consequently, urban mynahs are unlikely to have had any experience of Reeve's pheasants. The visual stimulus was presented on a platform (0.4×0.4 m) located 4 m away from the test aviary and 2 m above the ground. A 0.5-m high plastic screen, which could be operated by an experimenter in a hide located 8 m away from the test aviary, hid the pheasant mount when it was raised, and revealed the stimulus when it was lowered.

Experimental Protocol

For experiments, each Indian mynah was transferred to an outdoor individual test aviary (depth

1.0 × width 2.2 × height 1.95 m) where it was held for 3 d to acclimatize. The aviary was fitted with several perches, a nest box and food and water bowls.

Each mynah first underwent a pretest in which I measured its initial response to the pheasant mount. Mynahs allocated to the simultaneous group then received one training trial during which the pheasant mount was revealed simultaneously with the onset of a 2-min playback of distress vocalizations. Mynahs allocated to the contiguous group received a 2-min distress call playback followed immediately by a 2-min presentation of the pheasant mount. The specific distress call sequence used in each training trial was selected such that all three exemplars were equally represented in each group. After training, each bird received a post-test in which its response to the pheasant was measured once again. Pre- and post-tests lasted 6 min (2-min pre-stimulus, 1-min presentation and 3-min post-stimulus). Training trials lasted seven (simultaneous group) or nine (contiguous group) minutes (2-min pre-stimulus, 2-min (simultaneous group) or 4-min (contiguous group) presentation, 3-min post-stimulus).

It is important to note that mynahs from both groups received identical exposure to both distress calls and pheasant during training, but the simultaneous group experienced these stimuli simultaneously, while the contiguous group experienced the two stimuli in succession. Any differences between the behaviour of these two groups after training are therefore necessarily attributable to the differential temporal arrangement of distress calls and pheasant during training.

Data Analysis

All trials, including pre-tests, training trials and post-tests, were filmed using a digital camcorder. Behaviour was scored from video recordings using JWWatcher 1.0 (Blumstein et al. 2006).

As in previous work, I quantified social learning by measuring the head saccade response evoked by the pheasant before training, and comparing it with that evoked by the visual stimulus after training (Griffin 2008). Although birds have an excellent visual system including colour vision and good visual acuity, they have limited eye movements (Pratt 1982). Consequently, rather than moving their eyes to scan a visual scene, they move their heads (Nye 1969). Head movements may allow them to extract depth information by generating successive views of a stimulus, which can be compared (Wallace 1959; Ellard et al. 1984). Alternatively,

head movements may allow birds to derive different kinds, or quality of information, by placing the stimulus on spatially distinct high acuity areas within their fovea (Martinoya et al. 1983; Maldonado et al. 1988; McKenzie et al. 1998; Land 1999a,b; Mace 2000; Dawkins 2002; Andrew 2006). Consequently, changes in head saccade rate that occur as a consequence of social learning most likely reflect a change in visual exploratory behaviour (Griffin 2008).

As in earlier work, the number of head movements each individual made was counted during a 30-s time interval, which began as soon as the screen hiding the pheasant had stopped moving downwards and the mount was fully visible, during both pre- and post-tests. A head saccade was defined as any detectable movement of the head that occurred whilst the subject's body was immobile. As successive head movements can occur extremely rapidly, head saccades were scored from video footage played back at one-quarter normal speed. Subject and trial identity were encoded to ensure that head movements were scored blind. Head saccade rate was calculated by dividing the total number of head saccades by the total time immobile. To quantify the effect of presenting the pheasant mount together, or in succession, with distress calls, I calculated the difference between the head saccade rate in the post-test and that in the pre-test for each mynah. The mean pre/post difference in head saccade rate of the simultaneous group was then compared with that of the contiguous group using an unpaired t-test.

To better understand how mynahs responded to either simultaneous presentations of distress calls and pheasant (simultaneous group) or successive presentations of these stimuli (contiguous group), I analysed changes in flight behaviour during training trials. Flight is a well-known response of birds to danger (Blumstein 2003; Blumstein et al. 2006; Frid & Dill 2002). Furthermore, empirical work has revealed that captive Indian mynahs increase flight in response to a perched raptor (Griffin 2008). Consequently, changes in flight within the present context are most likely to reflect changes in antipredator wariness. Consistent with previous work in this system, flight was defined as any movement between a perch, the ground and the wire mesh of the aviary and ranged from 0.15 to 1.3 m. The person scoring flight had no knowledge of the experimental questions.

To quantify changes in flight behaviour, the number of flights was counted during a 60-s baseline time period that began 60 s before the first distress

call was detectable on video recordings for each individual mynah. I also counted the number of flights that occurred during four successive 60-s time periods starting from the first detectable distress call. Flight rate during each successive 60-s time period was determined by dividing number of flights by the duration of the time interval. Responses evoked by the training stimuli were then determined by calculating the change in flight rate from pre-stimulus baseline for each successive time interval and each mynah.

For each subject, I averaged the change from baseline flight rate for the first two post-stimulus 60-s time intervals, as well as for the following two post-stimulus 60-s time periods. For mynahs in the simultaneous group, average behaviour during the first two time periods reflected the mean flight response evoked by simultaneous presentation of distress calls and pheasant, while behaviour during the second two time periods reflected behaviour in the absence of any stimulus. For mynahs in the contiguous group, average behaviour during the first two time periods reflected the mean flight response evoked by the distress call sequence, while average behaviour during the second two time periods reflected the response evoked by the pheasant alone. Finally, I compared the flight behaviour of the simultaneous group with that of the contiguous group using a two-way, repeated measures ANOVA with factors for group (simultaneous, contiguous) and time (successive time intervals).

Finally to quantify the relationship between the flight response during training and the acquired visual exploratory response after training, I ran a Pearson's correlation on the change in flight rate from pre-stimulus baseline during the first 60-s time interval after distress call onset and the mean pre/post difference in head saccade rate. For mynahs in the simultaneous group, this period encompassed simultaneous presentation of both distress calls and pheasant, while for mynahs in the contiguous group it encompassed presentation of the distress call playback only. All statistical analyses were carried out on untransformed data using SPSS 16.0 (SPSS 2005). I used two-tailed tests throughout and alpha levels were set at 0.05.

Results

Mynahs that experienced a pheasant mount simultaneously with a playback of distress vocalizations maintained similar rates of head saccades in response to the pheasant after training relative to before train-

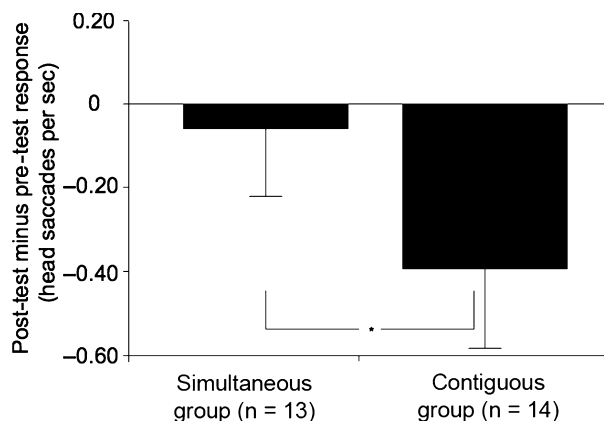


Fig. 1: Change in head movement response exhibited by mynahs in response to a pheasant mount after experiencing it either simultaneously with, or after the end of, a playback of conspecific distress calls. The \bar{x} (\pm SEM) difference between pre- and post-test was calculated for a 30-s time interval after stimulus onset for each treatment. For more details, see text.

ing (Fig. 1). In contrast, mynahs that experienced distress calls followed immediately by pheasant moved their heads at slower rates in response to the mount after training relative to before training (Fig. 1). The difference between the two groups' acquired response was reflected by a significant effect of group on the pre/post difference in head saccade rate (unpaired t-test: $t = 2.670$, $df = 25$, $p = 0.013$). Earlier research on social learning in Indian mynahs has shown that head saccades reflect a visual exploratory response (Griffin 2008). Consequently, the present between-group difference in acquired head saccade rate indicates that exposing mynahs to a novel stimulus simultaneously with an antipredator acoustic signal caused mynahs to maintain their visual interest in the novel stimulus after training relative to before training, while experiencing the novel stimulus only after the antipredator signal caused mynahs to lose interest in the mount. It appears therefore that the sound of distress calls made the pheasant more resistant to habituation, but only if vocalizations were experienced at the same time as the pheasant.

Analyses of locomotory behaviour during training revealed that both simultaneous and contiguous groups significantly increased flight rate during the first 120-s training time period relative to pre-stimulus baseline, an effect that was not present in either group during the second 120-s training time interval (ANOVA main effect time: $F_{1,25} = 8.675$, $p < 0.01$; main effect treatment: $F_{1,25} = 0.246$, $p = 0.624$; treatment by time interaction: $F_{1,25} = 0.022$, $p = 0.883$; Fig. 2). Such a

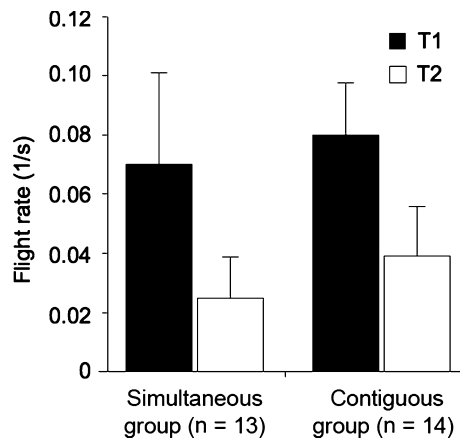


Fig. 2: \bar{X} (\pm SEM) change in flight rate during two successive 120-s time intervals after the onset of training stimuli. Birds in the simultaneous group received distress calls and pheasant simultaneously during the first time period (T1) and no stimulus during the second time interval (T2). Birds in the contiguous group received distress calls during T1 and pheasant during T2.

flight increase during a time period in which mynahs in the simultaneous group were exposed to both pheasant and distress calls, while mynahs in the contiguous group were exposed to distress calls only, suggests that distress calls on their own were sufficient to cause the change in locomotion. Furthermore, return of flight rate to baseline levels during the second 120 s time interval in both groups indicates that distress calls did not produce a locomotory effect that extended beyond the duration of the call, even if a novel stimulus was viewed immediately afterwards (Fig. 2).

Finally, an analysis of the relationship between responses during training and those after training revealed a significant positive correlation between flight rate during the first 60 s of the distress call playback and the acquired head saccade rate in mynahs that had experienced pheasant and antipredator signal simultaneously (Pearson's correlation, $r = 0.574$, $n = 13$, $p = 0.040$; Fig. 3). In contrast, there was no such relationship in mynahs that had experienced the distress calls and pheasant in succession (Pearson's correlation: $r = 0.093$, $n = 14$, $p = 0.751$).

Discussion

Socially transmitted recognition learning allows animals to use information provided by more experienced individuals to adjust their responses to previously unfamiliar stimuli, such as novel predators (Suboski 1990; Heyes 1994). Changes in behaviour attributable to learning typically occur after

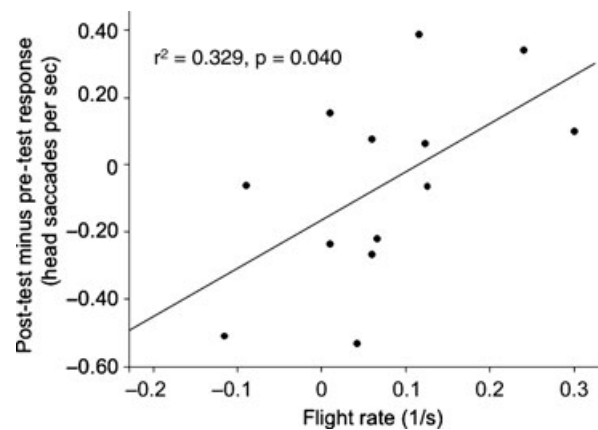


Fig. 3: Relationship between flight rate during the first 60-s time interval after the onset of the distress call playback and the appearance of the pheasant in birds that received these stimuli simultaneously during training ($n = 13$).

novel stimuli have been experienced simultaneously with social signals (Curio 1988; Mineka & Cook 1988; Magurran 1989; Suboski et al. 1990; Chivers & Smith 1995). The aim of the present study was to determine whether such learning occurs when antipredator signals and novel stimuli are experienced in succession, rather than simultaneously. Using Indian mynahs, I compared the effects of presenting a novel stimulus (pheasant) simultaneously with a social antipredator signal (mynah distress calls), with those of presenting antipredator signal and novel stimulus in succession. Results showed that mynahs that received training stimuli simultaneously maintained their visual exploratory response to the pheasant after training relative to before training, while mynahs that received the two stimuli consecutively lost interest in the pheasant.

The finding that presenting an object together with the sound of distress calls leads to a sustained visual exploratory response towards that stimulus is consistent with earlier work demonstrating that this antipredator vocalization triggers social learning (Maloney & McLean 1995; Griffin 2008). Indeed, even though the effect of the antipredator signal was rather to inhibit a decline in exploratory behaviour that occurred in mynahs that received distress calls and pheasant in succession, rather than to enhance behaviour, between group differences are the critical parameter demonstrating associative learning, and not within group comparisons of behaviour between before and after training (Shettleworth 1998; Griffin et al. 2000). Consistent with between group differences found here, Griffin (2008) showed that mynahs that received distress calls and novel stimulus

simultaneously showed a small increase in exploratory behaviour after training relative to before training. The acquired change in behaviour was significant, however, when compared to control mynahs that received antipredator signal and pheasant several hours apart, demonstrating the occurrence of associative learning in the simultaneous group. While cross-study comparisons should be made with caution, it appears that neither presenting a novel object just after a social antipredator signal, as in the present study, nor presenting these stimuli several hours apart, as in Griffin (2008), allows for signals and novel stimulus to become associated.

The present analysis extends earlier work in several ways. First, it appears that socially mediated effects of acoustic antipredator signals on conspecific responses to nearby environmental stimuli are restricted to events that share some temporal overlap with the acoustic signal. How much overlap is necessary, and whether it is less than the 88% used elsewhere (Griffin & Galef 2005), remains to be established. Second, analyses of behaviour during training suggest that the mechanism underpinning social learning is the ability of distress calls to trigger increased wariness, as reflected by changes in flight rate, which become associated with external events present at the same time. This idea is supported by a positive correlation between the flight response evoked by distress calls during training and the acquired head saccade response to novel stimulus after training in mynahs that received these stimuli simultaneously. Analyses of behaviour during training further revealed that flight rate waned as soon as distress calls stopped, even if interruption was followed immediately by a novel stimulus, suggesting that enhanced wariness does not carry over to stimuli experienced after the antipredator signal. This pattern of behaviour explains why distress calls do not trigger social learning about environmental stimuli that are sighted immediately after a social antipredator signal.

Distress vocalizations are produced in response to seizure by a predator or a human (Pizzey and Knight 1998), and opportunistic observations on free-living Indian mynahs suggest that individuals within ear-shot respond by approaching the source of the sound (A. S. Griffin, pers. obs.). Consequently, one situation in which distress calls and a novel predator stimulus may be experienced in succession, rather than simultaneously, may arise if a mynah is captured by a predator, and briefly distress calls before either losing consciousness or succumbing. A conspecific attracted to the predation site may experience the predator in the absence of any further social vocaliza-

tions. Successive detection of social alarm signals and predator may similarly occur when chickens encounter raptors. Indeed, senders only briefly produce aerial alarm calls when a predator is first sighted, so a recipient whose attention is captured by the social signal is likely to sight the predator in the absence of any further vocalizations. Overall, the findings from the present study suggest that such encounters may not allow for predator learning to occur.

While it may seem detrimental to restrict learning to stimuli that are perceived simultaneously with antipredator signals in so far that it limits learning opportunities, this strategy may provide the advantage that it might reduce the likelihood of wrongly identifying the cause of the conspecific's alarm, and consequently associating alarm signals with a harmless event. Under natural conditions, visual information emanating from the non-vocal behaviour of the prey after it stops calling may complement early acoustic information and play a role in learning. For example, studies of aerial alarm calls in chickens indicate that senders maintain frozen and alert body postures after vocalizing, thereby providing non-vocal visual information that recipients could associate with predator stimuli experienced simultaneously (Evans et al. 1993a). The fact that the first element of an aerial alarm call is localizable, while subsequent elements are less so, suggests that recipients have sufficient information to locate the caller and observe its non-vocal behaviour in conjunction with overhead threats (Evans et al. 1993b; Bayly & Evans 2003). In support of the idea that observers attend to the non-vocal behaviour of prey victims, conspecifics carried by a predator evoke a high level antipredator response (Lorenz 1931; Kruuk 1976; Conover & Perito 1981; Conover 1987; Barash 1976). Furthermore, such cues appear to play a role in social learning. Indeed, several avian species become more wary of a predator after they have viewed it holding a live or a dead conspecific (Kruuk 1976; Conover & Perito 1981; Conover 1987). Unfortunately, no study to date has teased apart the effects of experiencing a predator holding a prey from those attributable to taking part in mobbing aggregations around the predator. In sum, while the dynamic properties of acoustic communication alone may limit the array of opportunities for nearby conspecifics to learn socially about novel predator stimuli, a combination of vocal signals and non-vocal cues from prey may allow for such limitations to be overcome. Further research is needed to examine the contribution of each of these sources of social information on learning in recipients.

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