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Original Article

It's a trap! Invasive common mynas learn socially about control-related cues

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Social learning of novel threats coupled with adaptive generalization from learned to novel cues together provide the cognitive mechanisms by which adaptive avoidance of threats can spread rapidly both within and across generations. Whereas attention to effects of fishing and hunting on prey is increasing, nothing is known about how human predation can alter the behavior of invasive animals. Here, we examined whether common (Indian) mynas, *Acridotheres tristis*, one of the most widespread invasive birds in Australia and invasive to many other parts of the world, are learning to respond to anthropogenic predation. We analyzed behavior at an experimental food patch provisioned by 2 distinctly clothed persons both before and after mynas had observed one of the 2 persons seemingly capture conspecifics inside a trap placed at the food patch. After the demonstration, mynas landed in smaller numbers at the food patch and took longer to land. Further, mynas alarm called more when provisioned by the person who had been involved in trapping. Future work will determine whether narrow generalization gradients are a consistent feature of synanthropic species or whether they broaden as a function of human predation threat level as is predicted by the Predator Recognition Continuum Hypothesis. Practical implications for control are discussed.

Key words: **common myna, human predation, Indian mynah, invasive birds, pest bird management, social learning, threat perception.**

INTRODUCTION

The ability to alter behavior as a function of experience plays a fundamental role in survival and reproduction. Both vertebrates and invertebrates have been shown to be able to learn predictive relationships between novel cues and biologically important outcomes such as foraging or pain, as well as between their motor actions and resultant environmental consequences (Dukas 1998; Brembs 2003; Griffin 2003). Such prediction learning, referred to as classical and operant learning, respectively, provides the cognitive mechanism for adaptive changes in behavior and associated increases in fitness (Hollis 1984; Dukas 2004; Domjan 2005; Morand-Ferron et al. 2015).

Despite the possible intuition that antipredator behavior should be fully functional on first encounter with a threat, it is well established that animals can learn the features of novel predators (Mineka and Cook 1988; Heezik et al. 1999; Griffin et al. 2001; Shier and Owings 2007; Griffin 2008), the contextual cues that predict the appearance of predators (Fanselow 2000) and the places they appear in, and times at which predators are most likely to be present (O'Brien and Sutherland 2007; Ferrari and Chivers 2009; Griffin and Boyce 2009). Theoretical modeling of evolutionary scenarios indicates that when the costs of acquiring firsthand information are high, individuals should rely on social information (Kendal et al. 2005; Hoppitt and Laland 2013). Consistent with these predictions, acquisition of predator-related information from both conspecifics and heterospecifics within and across generations is commonplace (Mathis et al. 1996; Griffin 2004; Lönnstedt et al. 2012; Magrath et al. 2015).

Threat learning can vary in its specificity. Although classic work has demonstrated that prey acquire responses that are specific to trained cues (Mineka and Cook 1988; Chivers and Smith 1994), prey species often show adaptive patterns of generalization from learned to related cues without further pairings of these cues with indicators of risk (e.g., social alarm signals) or attack. For example, captive-born, fox-naïve wallabies (*Macropus eugenii*) that experience pairings of one predator species (fox, *Vulpes vulpes*) and an aversive human acquire a fear response to that predator, which generalizes to another predator species (cat, *Felis catus*) but not to a similar size nonpredator species (goat, *Capra hircus*) (Griffin et al. 2001). Similarly, juvenile rainbow trout (*Oncorhynchus mykiss*) conditioned to respond to predator scents via pairings with conspecific olfactory alarm signals acquire antipredator responses to trained predators but also generalize their acquired response to taxonomically closely, but not distantly, related predators (Brown et al. 2011). Learning specificity (i.e., the extent to which learning generalizes) has been found to depend on the level of risk associated with the known predator (Ferrari et al. 2008) and its certainty (Ferrari et al.

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2016) as predicted by the Predator Recognition Continuum (PRC) Hypothesis (Ferrari et al. 2008). Together, this large body of empirical work demonstrates the exquisite fine-tuning of animal antipredator systems to deal with variability in predation risk.

Humans have killed animals for food and garments for millennia. For these species, humans can pose an equal or even far greater mortality risk than natural predators (Darimont et al. 2009). In addition to significant demographic effects, anthropogenic predation can cause phenotypical change (Coltman et al. 2003; Kuparinen and Merilä 2007; Ciuti et al. 2012; Pigeon et al. 2016; Sullivan et al. 2017). The mechanisms underpinning these changes are generally attributed to both genetic and plastic processes (Law 2001; Darimont et al. 2009; Pigeon et al. 2016; Palkovacs et al. 2018), including transfer of information via social learning that can result in rapid behavioral changes (Askey et al. 2006).

Contrary to classical exploitation harvesting, such as hunting and fishing, whereby nondemographic effects have begun to receive some attention (Allendorf et al. 2008; Darimont et al. 2009), the consequences of control practices on the phenotypical composition of invasive animal populations remain mostly anecdotal and mechanisms of change largely untested (King 2010; Côté et al. 2014; Závorka et al. 2018). Control, be it poisoning, trapping, or shooting, differs from exploitative harvesting in several ways. Not only has exploitative predation existed for far longer, it is also typically much more intense in terms of pressure applied to target populations (Feare 1991; Newton 1998; Peacock 2007; Shine and Doody 2011; Darimont et al. 2015). Whereas exploitative predation can cause catastrophic decreases in population size, control measures are generally applied to populations over the long term, sometimes for decades and sometimes haphazardly through time and space (Britton et al. 2011; Lazenby et al. 2014; Kinnear et al. 2017). Although there are some ongoing attempts to scale successful eradications up from local to continental areas (Russell et al. 2015), instances of complete species removal are so far limited to small and isolated geographical spaces such as fenced-off areas and small islands (Courchamp et al. 2003; Saavedra 2010; Feare et al. 2017). Control measures applied over long periods of time give experience-dependent phenotypical change more chance to occur because more individuals can interact with and/or watch others encounter the control procedures and devices, with only a few dying.

Introduced alien species are responsible for severe environmental and economic damage worldwide (Mack et al. 2000; Pimentel et al. 2000). Potential behavioral adjustments in response to control could have important implications for managing pest animals (Závorka et al. 2018). On the one hand, these behavioral adjustments may lead to control-avoidant populations, therefore hindering the sustainability of control programs. On the other hand, problematic behaviors of the targeted species, such as competition with native endangered species, could increase. For example, an urban pest that is predated on in cities could move into more natural habitats, potentially increasing its impact on native, less urbanized species (King 2010). Whilst having important applied implications, studying responses to population management also provides a unique opportunity to investigate the role of cognition in adjusting to evolutionary recent forms of human predation and to quantify the specificity of learning.

Here, we consider the possibility that animals learn the cues associated with trapping. A wide range of mammals and birds are commonly trapped throughout the world as a means of population control (Gorenzel et al. 2000; Courchamp et al. 2003). Trapping presents animals with a variety of cues; which ones are learnt is likely to influence the extent to which learning generalizes. For example, if animals learn the specific place in which they viewed a trapped, alarmed conspecific, then learning is unlikely to generalize beyond that particular experience. In contrast, if animals learn that humans are associated with trapping, then they might become wary of humans more generally. Cross-species differences in the extent to which acquired information is generalized to stimuli beyond the learning experience might explain why some species, but not others, seem to acquire broad avoidance of humans in response to anthropogenic predation. For example, American crows, *Corvus brachyrhyncho*, respond specifically to the human who captured them (Marzluff et al. 2010), whereas rural house sparrows, *Passer domesticus*, avoid both hostile and unfamiliar humans (Vincze et al. 2015), and elephants behave more defensively to the voices of Maasai men in general (McComb et al. 2014).

Here, we studied the common myna, *Acridotheres tristis*, a medium-sized songbird, which was introduced to Australia in the mid-19th century. There is some evidence that mynas outcompete native secondary cavity-nesting birds for access to breeding cavities (Pell and Tidemann 1997; Grarock et al. 2012). As a result, the species has undergone heavy anthropogenic predation pressure over the last 20 years in an effort to reduce its range expansion across the Eastern seaboard (Ewart et al. 2019). For example, in the Australian Capital Territory alone, it is estimated that more than 53 000 individuals have been trapped and killed between 2005 and 2012 (Diquelou 2017). There are opportunistic observations of decreasing trapping success while population densities do not decline (King 2010). In addition, a recent large-scale comparative field study has found that in heavily trapped areas, mynas show changes in behavior consistent with increased risk perception, but whether cognition rather than selection is involved is not known (Diquelou et al. 2018). Studies of captive mynas have demonstrated that the species learns to recognize novel predators and dangerous places socially (Griffin 2008; Griffin and Boyce 2009; Griffin et al. 2010; Griffin and Haythorpe 2011). Therefore, we predicted that mynas would learn cues associated with trapping socially. By undertaking an experimental manipulation of social learning in free-ranging birds, our aim was to disentangle which cues associated with the trapping situation mynas would learn, if any. After an aversive trapping demonstration, no change in behavior would indicate the absence of learning; changes in behavior occurring specifically when the trapper was present would indicate human recognition learning, whereas changes in behavior occurring at the site when any human was present would indicate place avoidance learning or generalization of threat avoidance. By demonstrating learning under field conditions and further quantifying the specificity of learning, this study reveals the potential involvement of cognition in population phenotypical change of alien animal populations (Diquelou et al. 2018). Findings have important implications for our understanding of how fast animals can change their behavior and potentially avoid evolutionarily recent forms of human predation (Darimont et al. 2009).

METHODS

Experimental feeding locations

Fourteen experimental feeding patches were established in the Newcastle and Wyong local government areas, New South Wales, Australia. Experimental patches were situated at least 750 m apart to minimize chances of resampling. This distance was selected on the basis of extensive previous field work with this species as well as knowledge of its biology (Haythorpe et al. 2012; Sol et al. 2012; Diquelou et al. 2016; Diquelou et al. 2018). Although mynas can travel long distances (>40 km), they are typically sedentary and travel short distances from the roost to forage with home ranges less than 0.10 km^2 (Kang 1992; Peneaux and Griffin 2015). For this reason, it is highly unlikely that the same individuals were sampled across several feeding patches.

The feeding spots were established by walking across rural and suburban areas within 4 h of sunset or sunrise and provisioning groups of mynas found to be feeding on the ground in relatively undisturbed areas (i.e., with minimal passage of pedestrians and vehicles nearby) with an assortment of foods (white bread, dog pellets, and mealworms). Food was placed on the ground within approximately a 50-cm-diameter circle and the patch was watched from a distance of 10–30 m away for 10 min to determine whether any mynas approached the food.

The procedure was then repeated at each patch at the same time each day. The feeding location was considered established if mynas fed from the patch within 30 min on at least 3 successive days (14 out of 33 stations reached this threshold). Experimental feeding trials were initiated on the 4th day. The fact that birds came to wait at the same place at the same time each day supports the assumption that the same birds were present over consecutive trials.

Experimental trials

At each feeding location, we conducted in succession a series of predemonstration trials, 1 demonstration trial, and a series of postdemonstration trials. During the demonstration trial, we exposed free-ranging observer mynas to a staged aversive human-trapped myna interaction. During predemonstration and postdemonstration trials, we quantified the behavior of free-ranging mynas to detect changes indicative of learning.

In order to investigate the specificity of learning, we used an experimental design that not only demonstrated learning but also disentangled whether mynas restrict their learning to specific humans who trap or generalize to other humans not involved in trapping. The design required the experimenter to wear 2 different visual appearances, referred to as "mask" and "face." During the mask treatment, the experimenter wore a blank mask, a white lab coat, and a black hat. During the face treatment, the experimenter wore a dark jacket but neither a hat nor a mask.

During the demonstration trial, each experimental feeding location was randomly allocated to either the face or mask appearance (balanced across experimental feeding locations). The appearance used during the demonstration was referred to as "aversive," whereas the alternative appearance, which was only ever associated with feeding, was referred to as "neutral."

During predemonstration and postdemonstration trials, the experimenter alternated between face and mask appearances on successive days and the order of appearances was counterbalanced across experimental feeding locations. For logistic reasons associated with conducting research in public areas, any prior feeding involved in setting up the experimental locations (see Experimental feeding locations) was undertaken using the face appearance.

Predemonstration and postdemonstration trial procedure

Predemonstration trials involved 2 trials with each human appearance (face and mask) at each feeding station. These trials therefore took 4 days if mynas fed from the patch each day (see below). However, for logistic reasons, only 2 predemonstration trials, both with the face appearance, were conducted at the first 2 feeding locations.

At each location, all trials were undertaken at the same time of day. The experimenter placed food (the same quantity of white bread, dog pellets, and mealworms each day) in the patch and then watched and video-recorded the site from at least 10 m away. As soon as the first myna began feeding (time zero), the behavior of mynas at and around the food was recorded for 30 min. The number of mynas present at the feeding patch and its surroundings (i.e., within a 50-m radius of the food patch) was recorded every 5 min. The maximum number of mynas present at the feeding patch and in the surroundings was tracked continuously, as well as the number of alarm calls emitted. Latency of the first myna to feed from the patch after food was made available was recorded. The experimenter waited a maximum of 30 min (i.e., 1800 s) for a myna to feed from the patch. If no mynas fed, the trial was given a maximum latency of 1801 s. The procedure for the postdemonstration trials was identical to that of the predemonstration trials and the same behaviors, abundances, and latencies were recorded.

Whereas mynas most often landed at the food patch during predemonstration trials, this was not the case during postdemonstration trials. To be conservative (see Data analysis), we assumed the reasons for such "empty" trials could be stochastic and unrelated to the experiment (e.g., disturbance prior to the arrival of the experimenter; weather). For each empty trial, an additional trial was conducted on the following day using the same appearance (face or mask). If birds failed to feed during all 4 predemonstration (or postdemonstration) trials, a maximum of 4 additional trials could be conducted, totaling a maximum of 8 predemonstration (and/or postdemonstration) trials. In total, 20 additional trials were conducted in this study and most of them (17) were postdemonstration trials.

Demonstration trial procedure

The day after the end of predemonstration trials, an experimenter placed food at the patch and waited until the first free-ranging myna began to feed. The experimenter then waited an additional 20–40 s, which was long enough for most birds in the vicinity to begin feeding, before initiating the aversive demonstration. Feeding locations were randomly assigned to receive a demonstration performed with the face or mask appearance. Hence, the selected appearance constituted the aversive appearance for this site.

The experimenter approached the food patch slowly, carrying a Pignose 7–100 portable amplifier loudspeaker and a small birdcage (84 × 40.5 × 44.5 cm) covered with black material. Mynas typically responded to the slowly approaching human by moving away from the food but remaining in the vicinity from where they observed the subsequent events. The researcher placed the cage and loud speaker next to the food, removed the cage cover, revealing 2 live mynas inside, and started a 1-min playback of myna distress calls, an intense alarm signal mynas give when they are captured by a predator and known to trigger learning about novel threats under captive conditions (Griffin 2008, 2009). The distress call sequence was created by concatenating sequences of calls from 3 different mynas recorded during human handling and was played back at 75 dB (measured at 1 m with a sound level meter). The live demonstrator mynas were captive-held birds participating in other ongoing captive-based projects in the research group at the University of Newcastle. As these birds had been captured long before the study and in a variety of locations across Newcastle and surroundings, it is extremely unlikely that demonstrator birds were familiar to the free-ranging mynas.

During the 1-min myna distress call playback, and the following 4 min, the experimenter waved a small hand-held net inside the cage to simulate trappers of interacting with captured birds from traps (e.g., for feeding or capture). The birds in the cage exhibited a strong escape response to the experimenter involving flying rapidly from one side of the cage to the other. The combination of alarmed mynas and human capture constitutes a visual experience known to trigger place avoidance in observer mynas in captivity (Griffin and Boyce 2009; Griffin et al. 2010; Griffin and Haythorpe 2011). The 5-min aversive demonstration was terminated by covering the cage, collecting the equipment, walking away from the food patch and shielding the trapped mynas from free-ranging birds by placing the cage in a nearby vehicle. The experimenter then continued to record behavior of mynas at the food patch until 30 min after time zero (first bird feeding) had passed.

Data analysis

To be conservative, trials during which no mynas landed at the food source ("empty trials," see Predemonstration and postdemonstration trial procedure) were discarded from the data set, unless mynas also failed to land at the food patch during *any* of the additional trials. In this case, the last additional trial for each corresponding planned trial was retained. Our reasoning behind disregarding trials with no mynas was 2-fold. First, it excluded days on which, for unknown reasons, birds did not appear at the feeding location. Second, because we elected to conduct additional trials when no birds fed from the patch (see Predemonstration and postdemonstration trial procedure), including "empty" trials would have led to oversampling locations at which mynas had become wary postdemonstration. Hence, our approach was conservative in that it maximized the likelihood that any difference between predemonstration and postdemonstration trials were attributable to the demonstration trial manipulation and not to other unknown causes. Using this approach, the final data set included 4 predemonstration and 4 postdemonstration trials for all but 2 experimental feeding locations, which only included 2 predemonstration trials (total 108 trials).

Common mynas' latency to feed from the food patch was analyzed using survival analyses. Cox regressions are a semiparametric approach designed to analyze time-to-event variables that include censored times (Bradburn et al. 2003). The proportional hazards assumption was checked using the scaled Schoenfeld residual test (Grambsch and Therneau 1994). First, to determine whether one of the 2 human appearances (face and mask) was inherently aversive, a Cox regression model was fitted to the latencies to arrive at the food patch during the predemonstration trials including only human appearance as an explanatory variable. Second, to investigate to what extent mynas were reluctant to come and feed from the experimental patch after, relative to before, the demonstration, we analyzed the latency of mynas to feed from the patch during all trials, including trial type (predemonstration and postdemonstration), human identity (aversive and neutral), as well as their interaction, as explanatory variables.

Count data such as number of birds present and number of alarm calls emitted, which were recorded onsite by the experimenter, were analyzed with Poisson Markov chain Monte Carlo generalized linear mixed models (MCMCglmm). These models allow the integration of random variables such as location and trial, as well as to account for overdispersion of these variables (Hadfield 2010). These models were run with the MCMCglmm package (Hadfield 2010). Full models are presented, for which a weakly informative proper prior was used (see Supplementary Materials). Autocorrelation of successively stored iterations was checked to ensure that it was less than 0.1, and convergence was assessed visually from diagnostic plots. First, we investigated whether human appearance (face and mask) had an effect on the number of mynas present at the feeding patch at each scan point during predemonstration trials. To account for the repeated structure of the time variable, location and trial were entered as random variables and only human appearance was entered as a fixed explanatory variable. Second, we compared the number of mynas present at the patch and in the surroundings, as well as the number of alarm calls emitted, during postdemonstration trials relative to predemonstration trials. GLMMs included location and trial as random variables, and trial type (predemonstration and postdemonstration) and human identity (aversive and neutral), as well as their interaction, as fixed effects.

All statistical analyses were performed in R (Version 3.3.3; R Core Team 2017). All 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 Ethics Committee (protocol A-2011–129).

RESULTS

Neither the latency for birds to feed from the patch (Cox model: $z = -0.836$, $P = 0.403$), nor the number of birds present (Table 1) during predemonstration trials differed as a function of whether the human was masked or not, indicating that one human appearance was not inherently more aversive than the other.

Table 1

Poisson MCMCglmm on number of mynas at feeding station at each scan during predemonstration trials

Fixed effects	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample	pMCMC
(Intercept)	−0.894	−1.385	−0.309	1000	0.001
Human appearance (face)	0.128	−0.326	0.571	1000	0.602
Random effects					
Site	0.452	0.014	0.988	1000	
Trial	0.033	0.0002	0.135	828	

Human appearance refers to whether (mask) or not (face) the human wore a mask. Reference categories of categorical variables are noted between brackets beside the variable name.
CI, confidence interval.

Table 2

Poisson MCMCglmm on number of mynas at the food patch as a function of time since the first bird began feeding

Fixed effects	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample	pMCMC
(Intercept)	0.527	−0.141	1.156	1000	0.120
Time	−0.098	−0.117	−0.08	755	**0.001**
Trial type (postdemo)	−1.085	−1.625	−0.573	1000	**0.001**
Human identity (neutral)	−0.143	−0.677	0.301	1000	0.588
Trial type: human identity	0.190	−0.547	0.908	1000	0.596
Random effects					
Site	0.926	0.199	1.885	1064	
Trial	0.132	0.0003	0.377	394	

Trial type refers to whether the trial was run before (pre) or after (post) the staged aversive demonstration. Human identity refers to whether the human was the person involved in the aversive demonstration (aversive) or not (neutral). Note that human appearance (mask/face) was counterbalanced across human identity. Reference categories of categorical variables are indicated in brackets beside the variable name. Values is bold indicate significance at the 5% threshold.

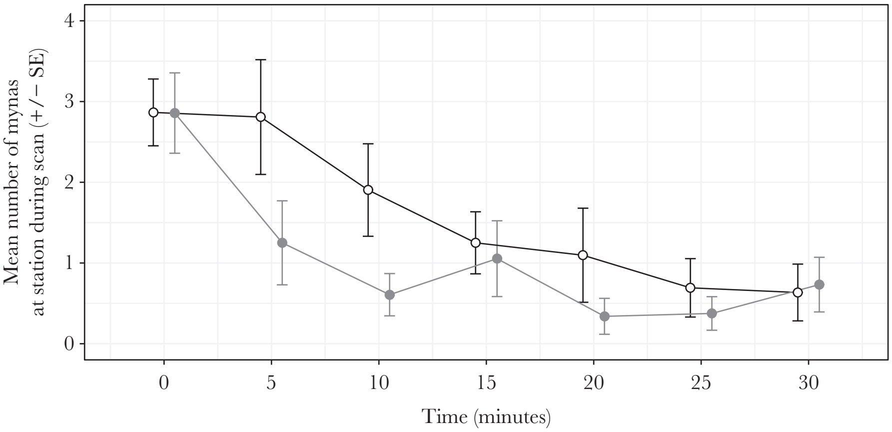

Figure 1

Mean number of birds at feeding station during 7 successive scans separated by 5-min sample intervals. Open circles: predemonstration trials; filled gray circles: postdemonstration trials.

Counts of mynas at the food patch revealed that myna presence was highest at the point in time when the first bird began to feed and decreased thereafter (Table 2; Figure 1). Because in many cases food remained at the end of the trial, the departure of mynas was not due to food depletion. Fewer mynas fed from the patch (Table 2; Figure 1) and fewer were present in its surroundings (Table 3) during postdemonstration trials than during predemonstration trials.

A Poisson MCMCglmm revealed significant effects of trial type and time on the number of mynas at the food patch (Table 2). To overcome mixing issues that arose with this model (autocorrelation of the trial parameter), potentially related to the fact that several postdemonstration trials contained 1 or 0 birds during every scan, we fitted a model to the maximum number of birds present during each trial. This analysis confirmed the strong effect of trial type indicating fewer birds were present after the demonstration than before it (Supplementary Table S1).

The number of mynas in the surroundings of the feeding location was not recorded during trials in which no mynas visited the patch (contrary to the number of mynas at the patch which was determined to be 0 under these circumstances). Hence, the number of mynas in the surroundings had fewer trials and scans than number of mynas at the feeding patch. The number of mynas within 50 m of the feeding patch decreased over time, as well as after the aversive demonstration, mirroring changes in the number of mynas at the food patch (Table 3).

On average, common mynas took just less than 6 min (350.3 s ± 47.4 standard error [SE]) to feed from the patch once food had been placed there. The Cox regression model revealed a strong effect of trial type on the latency to arrive at the patch (Table 4; Figure 2), showing that birds took longer to come to the food after the demonstration than before. However, the trial type variable did not follow proportional hazards assumptions (Schoenfeld residuals test; $\rho_{\mathrm{stage}} = 0.27$, $X^2_{\mathrm{stage}} = 12.3$, $P < 0.001$). Because only 5 of 108 trials contained capped values, we deemed it acceptable to use a model that did not account specifically for them. A Gaussian MCMCglmm was conducted and revealed an identical trial type effect to the Cox regression: latency to arrive at the station was longer after the demonstration had taken place than before (Supplementary Table S2).

Mynas commonly produced alarm calls during trials, often due to a bird of prey or a cat passing by. In total, alarm calls were detected on 87 of 108 trials. Analyses revealed a significant interaction between trial type and human identity, indicating that mynas emitted more alarm calls after the demonstration than before but only to the aversive human, that is, the human associated with the demonstration (Table 5; Figure 3).

An analysis of vigilance behavior during foraging was also performed in the context of this experiment. On average, 61% ± 0.03 SE of mynas were vigilant during trials but vigilance rate was not influenced by either trial type or stimulus (for all details see Supplementary Material 3).

Table 3

Poisson MCMCglmm on number of mynas in the surroundings of the food patch as a function of time since the first bird began feeding

Fixed effects	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample	pMCMC
(Intercept)	1.864	1.350	2.471	1000	0.001
Time	−0.009	−0.014	−0.004	949	**0.001**
Trial type (postdemo)	−0.297	−0.540	-0.045	1000	**0.018**
Human identity (neutral)	−0.037	−0.286	0.192	1000	0.774
Trial type: human identity	0.125	−0.205	0.459	1000	0.460
Random effects					
Site	0.909	0.276	1.713	1239	
Trial	0.123	0.070	0.182	1000	

Reference categories of categorical variables are indicated in brackets beside the variable name. See Table 2 for more details. Values is bold indicate significance at the 5% threshold.

Table 4

Cox regression model on the latency to feed from the food patch

	Estimate	Exp(coef)	SE(coef)	*z*	*P*
Trial type (postdemo)	−0.959	0.383	0.288	−3.077	**0.002**
Human identity (neutral)	−0.001	0.999	0.281	−0.005	0.996
Trial type: human identity	0.062	1.064	0.397	0.268	0.789

Reference categories of categorical variables are noted between brackets beside the variable name. See Table 2 for more details. Values is bold indicate significance at the 5% threshold.

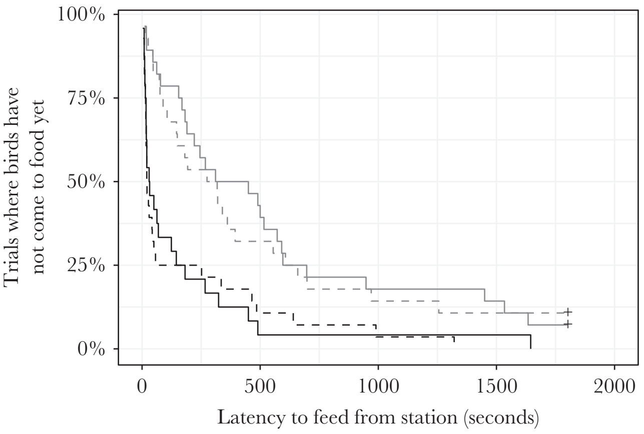

Figure 2

Kaplan–Meier survival curves of the latency of mynas to feed from the station during each trial. Predemonstration trials (black) and postdemonstration trials (gray) are presented, as well as trials with the aversive human identity (solid line) and the neutral human identity (dashed line). Human identity refers to whether the experimenter was wearing the appearance involved in the aversive demonstration (aversive) or not (neutral).

DISCUSSION

Social learning of novel threats coupled with adaptive generalization from learned to novel cues together provide the cognitive mechanisms by which adaptive avoidance of threats can spread rapidly both within and across generations (Cornell et al. 2012). Here, we investigated whether free-ranging common mynas, an invasive alien species in Australia and target in some areas of its distribution of heavy population control, are learning to respond to this evolutionary recent form of anthropogenic predation (King 2010). We analyzed behavior at an experimental food patch provisioned by what seemed like 2 distinctly clothed persons both before and after mynas had observed one of the 2 persons trying to capture conspecifics inside a trap placed at the food patch. Relative to before this staged trapping sequence, mynas landed in smaller numbers at the food patch and took longer to land. Further, whereas mynas responded initially equally to the 2 food-provisioning persons, after the staged trapping demonstration, mynas alarm called more when provisioned by the person who had been involved in trapping than when provisioned by the person who had not been involved. This study thus demonstrates fast changes in behavior in response to a novel anthropogenic threat indicative of learning. This is the first study to our knowledge to demonstrate that free-ranging invasive birds learn rapidly and specifically to recognize key cues associated with human predation.

The finding that mynas alarm called more to the person associated with trapping strongly suggests that, once habituated, the same individual mynas visited our feeding station repeatedly across days and further sampled and learnt provisioning- and threat-related information during their visits. Learning allowed mynas to update rapidly the status of a food provisioner from safe, before the staged trapping event, to dangerous after the trapping event. Our experimental design, which involved pairing only one of the 2 provisioners with visual and acoustic alarm signals and quantifying vocal behavior both before and afterward, demonstrates mynas learnt fast and specifically to associate the trapper with the dangerous context. Recognition of natural predators often relies on general features such as coat type or frontally placed eyes, the recognition of which facilitates generalization and foregoes the costs involved in having to learn about each predator separately (Caro 2005; Coss et al. 2005; Stankowich and Coss 2007). Responding to cues common to all humans would be detrimental to living in their proximity. This is because such broad generalization would induce a constant state of alert, potentially accompanied by chronic levels of high stress, which is contrary to our current understanding of synanthropy of

Table 5

Poisson MCMCglmm on the number of common myna alarm calls emitted during each trial

Fixed effects	Posterior mean	Lower 95% CI	Upper 95% CI	Effective sample	pMCMC
(Intercept)	0.661	−0.402	1.539	1008	0.158
Trial type (postdemo)	1.041	0.087	2.002	1140	**0.032**
Human identity (neutral)	0.195	−0.718	1.217	1667	0.668
Trial type: human identity	−1.447	−2.817	−0.099	1000	**0.036**
Random effects					
Site	1.384	0.095	3.308	1000	

Reference categories of categorical variables are indicated in brackets beside the variable name. See Table 2 for more details. Values is bold indicate significance at the 5% threshold.

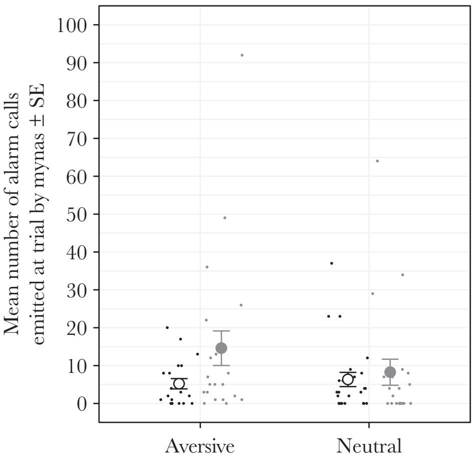

Figure 3

Mean (±SE) number of alarm calls emitted by common mynas during predemonstration trials (large open circle) and during postdemonstration trials (large gray closed circle) as a function of the human identity. Small dots represent the number of calls emitted at each predemonstration (black) and postdemonstration (gray) trial.

avian species (Partecke et al. 2006). Like many alien birds, common mynas are human commensals. Members of the myna family have a particularly long and close history of association with humans, given that their ability to mimic human speech has led them to be held as pets for thousands of years (Chopra 2017). Although the high specificity of learning found here is consistent with the intuitively appealing idea that human recognition is linked to a species' capacity to occupy anthropogenic environments, there is not yet enough consistent evidence that discriminating benevolent from malevolent persons are adaptations specific to human commensals (Belguermi et al. 2011; Vincze et al. 2015).

Common mynas learnt to recognize a specific human. This contrasts with findings from a large body of work on learning of natural predators. In general, animals trained to respond to one predator species show some degree of generalization to other predator species (Mason et al. 1991; Griffin et al. 2001; Griffin and Evans 2003; Ferrari et al. 2007; Ferrari et al. 2008; Ferrari et al. 2009; Davis et al. 2012). According to the PRC Hypothesis, generalization gradients should increase as the threat level associated with the predator, as well as predator diversity, increases (Ferrari et al. 2008). Even though human predation differs qualitatively from natural predation in that the level of threat people pose varies more across human predators than for nonhuman predators, the theory might nevertheless be useful in predicting the breadth of generalization gradients. Mynas in our study area do not have a history of undergoing trapping and may, hence, according to the PRC hypothesis, be expected to show narrow generalization gradients across humans. Future research should test whether mynas that have undergone historically high control, such as those in the Australian Capital Territory, show broader generalization gradients from aversive to innocuous humans.

Patterns of alarm calling demonstrate that mynas learnt which of the 2 food provisioners had been involved in trapping. However, after the aversive demonstrations, mynas also took longer to come to the patch and came in smaller numbers regardless of which experimenter was present. That one specific component of the alarm response (alarm calling) was stimulus specific, whereas other components (landing) were not, can be explained in several ways. Mynas may have higher caution thresholds for landing as this behavior may involve more risks (i.e., approaching the threat) than alarm calling, which can be performed while remaining at a safe distance from the threat. Such risky behaviors may, therefore, be expressed more conservatively. This would suggest that although mynas learnt to recognize the specific human involved in trapping, they generalized the avoidance response to all humans involved in the experiment.

Alternatively, delayed landing and a reduced willingness to land could be indicative of place learning. Place learning has been found in previous tests on captive mynas and is known to be dependent on observers viewing both alarmed conspecifics and the cause of their alarm (Griffin and Boyce 2009; Griffin et al. 2010; Griffin and Haythorpe 2011). In the current experiment, free-ranging birds were exposed to both social alarm cues and their cause (human). Based on previous experiments, this constitutes all information required for the spatial context of the event to be learnt. This interpretation is also consistent with studies quantifying the effects of trapping on myna abundances. Trapping reduces myna presence at a fine scale but not at a broad scale (Grarock et al. 2014), a pattern of spatial effectiveness which is compatible with mynas avoiding patches where they witnessed trapping. Hence, our study suggests that alien pest birds learn both the place and the identity of the human involved in a predation event.

Persistence in high threat environments can also induce behavioral changes in animals that are not a direct response to predator appearance per se. For example, fish that have experienced predators exhibit less risky behavior overall regardless of the presence of the predator (Lönnstedt et al. 2012). In tropical stonechats (*Saxicola torquata axillaris*), the presence of predators on the breeding territory leads to higher corticosterone levels and lower breeding rates (Scheuerlein et al. 2001). Mynas are also known to show generalized changes in risk-taking behavior governed by the perceived threat level of the environment (Diquelou 2017; Diquelou et al. 2018). Indeed, a recent study of free-ranging populations has shown that mynas living under high human predation risk areas stay closer to refuges, tend to form smaller groups, and are overall less detectable (Diquelou et al. 2018). Such changes in perceived predation risk makes it possible that increased caution of mynas toward experimental food patches found here was not only mediated by stimulus-specific (human/place) associative learning but also via more general changes in arousal as a result of exposure to danger (Lima 1998; Preisser and Bolnick 2008; Campos and Fedigan 2014), which might in turn provide a mechanism for how mynas in heavily trapped myna populations become more risk averse (Diquelou et al. 2018). However, such learning mechanisms are not mutually exclusive and it is possible that aversive human/myna interactions trigger both learning about specific trapping cues and changes in perceived predation risk simultaneously.

Ultimately, it will be important to understand the psychological processes that underpin avoidance learning in mynas. If avoidance comes from a purely associative mechanism, then ensuring that pairings of human and alarmed conspecifics do not occur, or at least are not visible to free-ranging birds, is paramount. Some groups involved in managing common mynas already recommend that approaching traps is restricted to nighttime (Dhami and Nagle 2009; Copsey and Parkes 2013; CIMAG 2017) following evidence of place avoidance learning in mynas (Griffin and Boyce 2009; Griffin et al. 2010; Griffin and Haythorpe 2011). In contrast, if acquired avoidance reflects a general change in risk-taking behavior triggered by observing alarmed conspecifics and capture events, then controlling these cues becomes more difficult. It is critical to determine the exact content of learning, as the degree of learning specificity will determine future control success. Nonassociative generalized changes in risk-taking behavior may reduce the likelihood of mynas approaching traps but also affect how they respond to alternative control methods such as poisoning and shooting. Such behavioral shifts would hence have further-reaching detrimental consequences for the control of the species.

In sum, this study revealed that human predation triggers rapid social learning in an invasive bird. Changes in alarm calling demonstrated that learning was highly specific to the human seen trapping conspecifics. Changes in landing behavior suggest that this other component of the avoidance response was not human specific, perhaps because landing is more dangerous than calling and the response was hence more conservative (i.e., generalized across humans). Alternatively, mynas could have learnt the place where the dangerous encounter occurred, an explanation supported by previous work (Griffin and Boyce 2009; Griffin et al. 2010; Griffin and Haythorpe 2011). Finally, behavioral changes were also consistent with a more generalized reduction in risk-taking. Avoidance behavior and vocalizations of mynas at the food patches would have made information available for transfer to naïve birds, potentially spreading the effects of experience within populations (Cornell et al. 2012). Future applied research should attempt to determine whether the breadth of generalization increases with increased levels of human predation as learning about one versus all humans and/or learning about one trapping location versus all trapping situations will have very different implications for the long-term success of control efforts.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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