

1 **Testing social learning of anti-predator responses in juvenile jackdaws: the importance of**  
2 **accounting for levels of agitation**

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9 **Abstract**

10 Social learning is often assumed to help young animals respond appropriately to potential  
11 threats in the environment. We brought wild, juvenile jackdaws briefly into captivity to test  
12 whether short exposures to conspecific vocalisations are sufficient to promote anti-predator  
13 learning. Individuals were presented with one of two models – a stuffed fox representing a  
14 genuine threat, or a toy elephant simulating a novel predator. Following an initial baseline  
15 presentation, juveniles were trained by pairing models with either adult mobbing calls,  
16 indicating danger, or contact calls suggesting no danger. In a final test phase with no  
17 playbacks, birds appeared to have habituated to the elephant, regardless of training, but  
18 responses to the fox remained high throughout, suggesting juveniles already recognised it as  
19 a predator before the experiment began. Training with mobbing calls did seem to generate  
20 elevated escape responses, but this was likely to be a carry-over effect of the playback in the  
21 previous trial. Overall, we found little evidence for social learning. Instead, individuals’  
22 responses were mainly driven by their level of agitation immediately preceding each  
23 presentation. These results highlight the importance of accounting for agitation in studies of  
24 anti-predator learning, and whenever animals are held in captivity for short periods.

25

26 **Keywords:** predator recognition, mobbing, corvids, captivity, habituation, personality

## 27 **Introduction**

28 The ability to recognise and respond appropriately towards predators is a critical component  
29 of fitness. Many young animals appear to recognise predators as being dangerous on their  
30 first encounter (1–3), be this through genetically determined responses (4) or through  
31 information acquired during development (5,6). For many species, however, learning during  
32 early life plays a major role in the development of predator recognition (7,8). Learned  
33 predator recognition is likely to be particularly advantageous in highly variable or  
34 heterogeneous environments, where predator assemblages and predation risk can vary  
35 spatially and/or temporally. Animals may learn about predators and potential sources of  
36 danger through personal experience of being chased, by observing predators attacking  
37 conspecifics (9,10) or through the anti-predator signals and cues of conspecifics alone  
38 (reviewed in 11). In aquatic environments learning about danger via social cues often involves  
39 the learned association of chemosensory information, such as the pairing of the chemical  
40 distress signals of an attacked conspecific with the scent of the predator (12,13). In contrast,  
41 in terrestrial systems information about predators is commonly conveyed by visual and  
42 acoustic means (11). Vocalisations made in response to predators can act as a warning of  
43 danger, eliciting flight responses, but many species also produce distinctive ‘mobbing’ alarm  
44 calls when a predator is spotted (14). These calls can encode information about the nature of  
45 the threat (15), triggering responses in both hetero- and conspecifics (16,17) that may either  
46 flee or may join the instigator in mobbing the target in an attempt to drive it away from the  
47 area (18).

48 A large body of experimental evidence shows that mobbing vocalisations can also help naïve  
49 individuals to learn socially about danger. In a pioneering experiment, Curio et al. (19)

50 instigated a mobbing response in observer blackbirds (*Turdus merula*) towards a stimulus that  
51 they had previously treated as being harmless (a model friarbird, *Philemon corniculatus*, or a  
52 plastic bottle), by allowing the observer to witness a demonstrator mobbing the model. The  
53 demonstrator was in fact mobbing a model owl that was hidden to the observer, but this  
54 learned association between the demonstrator's mobbing response and the (harmless)  
55 stimulus resulted in the transmission of mobbing responses along a chain of six individuals by  
56 using the observer as the demonstrator in each subsequent trial. While the great majority of  
57 research has been conducted in controlled laboratory settings, such cultural transmission of  
58 predator recognition has since been documented in the wild. For instance, American crows  
59 (*Corvus brachyrhynchos*) with no experience of being trapped or observing trapping socially  
60 learned to mob researchers who returned to the area wearing the same mask that had been  
61 worn when individuals from the previous generation of crows had been captured (20).

62 In recent decades a number of experiments have successfully trained naïve individuals about  
63 predators or brood parasites through pairing model predator or brood parasite presentations  
64 with a training stimulus. This stimulus was either a live conspecific demonstrator engaging in  
65 mobbing (19,21,22), mobbing calls paired with mounts of conspecifics (23), or mobbing calls  
66 alone (18,21,24), but in all cases the training phase lasted between 2 and 5 minutes. While  
67 such prolonged learning opportunities may reflect cases in which mobbing continues until the  
68 target moves away or the mobbing group loses interest (25–27), in many instances exposure  
69 to conspecifics' anti-predator responses are fleeting. For example, many predators are highly  
70 mobile, actively hunt their prey using the element of surprise and leave the area rapidly after  
71 an unsuccessful hunt (e.g. 28,29), providing prey species with only brief but vital opportunities  
72 for learning from conspecifics' responses. We tested whether a short, eight second exposure

73 to conspecific mobbing calls might be sufficient to train individuals to respond fearfully to a  
74 novel predator.

75 We conducted our study on wild jackdaws (*Corvus monedula*), highly social members of the  
76 corvid family. Jackdaws breed colonially, and short bursts of scolding calls are commonly  
77 heard in colonies in response to passing predators (G. McIvor, Pers. Obs. 2014). Jackdaw  
78 nestlings fledge from cavities from 30 days after hatching (30), and are dependent on their  
79 parents for up to 6 weeks thereafter (31,32). In response to predators, adult jackdaws  
80 produce distinctive anti-predator mobbing calls known as scold calls. Scold calls can be  
81 emitted singly to act as a warning of danger (e.g. if a predator is passing by), or repeated to  
82 recruit others to mob. These calls are likely to play a key role in helping young jackdaws learn  
83 about danger. Indeed, Lorenz (7) suggested, based on his observations of hand-reared  
84 jackdaws, that predator recognition is socially learned in this species, though this remains to  
85 be tested.

86 To control individuals' exposure to experimental stimuli and allow comparisons of their  
87 responses before and after exposure to social information, we brought juveniles temporarily  
88 into captivity for testing. This represents a compromise between testing in laboratory  
89 conditions, where the proximity of test stimuli and absence of distractions may artificially  
90 enhance social learning (33), and field experiments on unconstrained individuals where it can  
91 be extremely difficult to ensure that subjects attend to the relevant stimuli over repeated  
92 controlled presentations. Free-living juveniles were captured for the experiment 2 to 6 weeks  
93 after fledging using walk-in traps. Captured birds were transferred to a nearby aviary, and  
94 after an acclimatisation period given a series of presentations of one of two models – a stuffed  
95 fox to represent a genuine threat, or a toy elephant that simulated a novel predator. The first

96 presentation that each bird received was made with no accompanying playback, to gain a  
97 measure of their baseline response to the model stimulus. In conjunction with the second  
98 time the model was presented, the birds also received an 8 second playback of the calls of  
99 colony members – either scold calls that suggested danger, or contact calls that suggested no  
100 danger. Such brief calling events are common in jackdaw colonies. To test whether the  
101 scold/contact call playback in the training phase influenced the subsequent response of  
102 individuals towards the model, we presented the model a final time with no accompanying  
103 playback. We predicted that birds shown the elephant with scold calls would show a greater  
104 escape response to the model than those shown the elephant with contact calls, and would  
105 also direct scold calls at the model. In contrast, we expected the jackdaws to already recognise  
106 foxes as a threat and thus show an equally high escape response to the fox model regardless  
107 of which playback they had received. Finally, we predicted that the response of birds in the  
108 elephant-scold group would match the escape response level of those birds shown the fox  
109 model.

## 110 **Methods**

### 111 *Subjects and Housing*

112 The experiment was carried out over 14 days in July 2015. Forty-eight juvenile jackdaws were  
113 captured using a passive walk-in trap baited with bread and oats. Half of the birds used in the  
114 experiment had been ringed as chicks at our study site and had a known fledge date. On  
115 average these birds fledged from the nest 31 days before capture (range = 19 to 43 days). As  
116 breeding is highly synchronous across our jackdaw population (>90% of all nests fledge within  
117 a 14 day period; unpublished data), the 24 birds whose fledging date was unknown were likely

118 to have been at large in the environment for a similar length of time and have had a similar  
119 likelihood of having encountered predators as the birds with known fledging dates.

120 Once captured, individuals were removed from the walk-in trap and transferred to a separate,  
121 temporary aviary in a field 100m away. Although we cannot rule out the possibility that  
122 jackdaws flying past may have observed experimental presentations to other individuals  
123 before they themselves received them, this is very unlikely given that models were only  
124 displayed for a few seconds during presentations before being returned to a concealed  
125 position. The aviary consisted of a wooden frame (2x3x1.8m) covered by game-bird netting,  
126 which allowed the bird to see in all directions. A diagram of the experimental arena is  
127 provided in the supplementary materials. Half of the roof was covered in wooden boards to  
128 provide shade, and two screens were provided at the back of the aviary behind which the bird  
129 could hide. Branches were provided as perches in each corner, and a central beam ran across  
130 the middle of the arena that could also be used as a perch, as could the ledges than ran around  
131 the outside of the arena. All birds were provided with a dish containing food (rolled oats) and  
132 water. Birds were typically kept in the aviary for 25 to 35 minutes, after which they were  
133 released.

134

### 135 *Experimental Procedure*

136 Following transfer from the walk-in trap to the experimental aviary, each jackdaw was given  
137 10 to 15 minutes to calm down and acclimatise to its surroundings before the experiment  
138 commenced. This start time was consistent with the exception of 2 of the 48 trials, where the  
139 birds receiving longer periods because of farm machinery moving nearby (mean duration of

140 acclimatisation period (SE) = 12.75 (0.51) mins; range: 10-32 mins). The 10 to 15 minute  
141 period was considered to be an acceptable compromise between the need for time to  
142 acclimatise to the aviary and the ethical requirement of minimising the total length of time  
143 that juvenile birds were separated from their parents, upon whom they were still partially  
144 dependent. Birds were shown one of two models, in a series of three separate presentations:  
145 (1) *Baseline*, (2) *Training* and (3) *Test*. Twenty-four birds were shown a toy elephant to  
146 simulate a novel predator. This stimulus was deliberately chosen so as to avoid any potential  
147 resemblance to any animal the jackdaws may have encountered previously. To provide an  
148 ecologically relevant comparison, the other 24 birds were shown a taxidermy model of a red  
149 fox (*Vulpes vulpes*), a predator that is common around our study site and is frequently  
150 mobbed by jackdaws when encountered. The elephant model was of roughly equivalent  
151 height and length as the fox model. Birds were assigned to their model group at random, and  
152 received three presentations of the same model. The model was located in a hide 10m from  
153 the front of the aviary, and was mounted onto a skateboard to allow it to be smoothly moved  
154 in and out from the concealed position. Stones were piled in front where the models emerged  
155 so that the birds would only see the model, and not the skateboard. The skateboard's  
156 movement was controlled by an experimenter inside an adjacent hide by way of a connecting  
157 broom-handle (see figure S1 in supplementary materials).

158 Presentation 1 was intended to measure the *Baseline* response of the bird to the model, and  
159 involved the model being rolled from the concealed position and sitting stationary in the open  
160 for 8 to 10 seconds before returning to cover, with no accompanying playback. Five minutes  
161 after Presentation 1, the birds were shown the same model again in Presentation 2, the  
162 *Training* phase, where the model was accompanied by a playback. The playback contained



163 either contact calls that would suggest there was no danger posed by the model, or scold calls  
164 that would suggest that the model was dangerous. Both the model and playback type to  
165 which the birds were assigned were allocated at random, but with a limit of 12 individuals to  
166 each combination of model and playback type. The specific playback track that the bird  
167 received during the *Training* presentation was also allocated at random, from a choice of six  
168 playback tracks for both the Scold and Contact call groups.

169 All calls used for playbacks were collected using Olympus LS-100 digital recorders (Olympus  
170 Corporation, Tokyo, Japan), used in conjunction with two types of microphone. Contact calls  
171 were obtained by recording calls between pairs at nest boxes using AKG-C417PP lapel mics  
172 (AKG Acoustics, Vienna, Austria). Scold calls were collected using Sennheiser ME66 shotgun  
173 microphones (Sennheiser Electronic GMBH & Co. KG, Wedemark, Germany) with a Reinhardt  
174 windshield when nests were being visited by researchers. There is no evidence that the scold  
175 calls of jackdaws are predator specific, and previous experiments at our study sites show that  
176 playbacks of scold calls recorded in response to humans elicit collective anti-predator  
177 responses as if a predator were present (34). In our recordings, the identity of all callers was  
178 known, and only calls from adult individuals nesting in the colony where the experiment was  
179 carried out were used. Callers were not related to test subjects, and the parentage all marked  
180 juveniles was checked prior to the trials to ensure they had not been allocated a playback  
181 track that contained the calls of a parent. Each playback contained the calls of four birds, and  
182 each bird contributed 3 calls each. Playback tracks were prepared using the open source audio  
183 editing software Audacity ([www.audacityteam.org](http://www.audacityteam.org)), with normalised amplitude across all  
184 tracks. The playbacks were made through three separate FoxPro Fury (FOXPRO Inc.,  
185 Lewistown, PA, USA) speakers, to simulate a natural bout of calling by a group of jackdaws.

186 Speakers were set to volume level 18, simulating the amplitude of a calling bout 10 m away  
187 (c.72dB) as measured using a Voltcraft SL-100 sound level meter. The three speakers were set  
188 to the same operating channel to allow them to be controlled by a single handset. They were  
189 arrayed in an arc around the hide from which the model was presented, and each speaker  
190 contained a different track loaded in each position on their memory. This meant that all three  
191 speakers would play a different track of four calls simultaneously over an 8 second period.  
192 This produced a playback of 12 calls in total, containing calls from 3 individual birds, with each  
193 individual contributing 4 calls each (see Supplementary Materials S1). The playback slot was  
194 assigned at random for each bird. Each of the three tracks that occupied a memory slot had  
195 been prepared simultaneously in Audacity, and this ensured that they each achieved an  
196 identical effect. Playbacks were arranged so that the time between calls on the three  
197 synchronised tracks decreased as the playback continued, simulating the build-up of calls  
198 that occurs naturally during social chatter(contact call group) or recruitment to a mobbing  
199 event (scold call group).

200 Five minutes after the end of Presentation 2 the birds received the third and final *Test*  
201 presentation. The procedure was identical to Presentation 1, and served to test whether the  
202 responses of the birds changed as a result of the playbacks they heard in Presentation 2. Five  
203 minutes after the end of Presentation 3, the birds were removed from the aviary and  
204 released. The birds were filmed for the full time spent in the aviary using a Panasonic HC-X920  
205 camera (Panasonic Corporation, Osaka, Japan).

206

207 *Video and Data Analysis*

208 Videos were coded using Noldus Observer XT12 (Noldus Information Technology Inc.,  
209 Wageningen, Netherlands). Coding of videos was done blind to both the model and playback  
210 type to which the bird had been assigned, by a single observer (GM). The number of flights  
211 made by the bird in the 60 s prior to the model presentation, and 60 s following the  
212 presentation were recorded, as was the distance travelled during these flights. There was a  
213 high level of collinearity between the number of flights and distance travelled ( $r=0.964$ ), so  
214 the number of flights made was used as a response variable as this was less subjective. We  
215 also recorded any vocalisations made by the birds. We analysed the data using R version 3.1.2  
216 (R Core Team), and the packages *lme4*, *pastecs*, *ggplot2* for graphs, and *lmtest* for Breusch-  
217 Pagan tests.

218 We analysed the influence of the presentation number (1,2 or 3), model (fox or elephant),  
219 and playback type (scold or contact calls) on the number of flights that the birds made in the  
220 60 seconds after each presentation, which we interpreted as an indicator of individuals'  
221 stress/escape responses towards the model. We used general linear mixed models (*lme4*  
222 package), with focal bird identity and playback track fitted as random effects. The number of  
223 flights made by the birds in the 60 seconds before each presentation was included as an  
224 additional explanatory term in each model, to account for any captivity-induced agitation  
225 and/or carry-over effects from previous presentations. Over-dispersion in the raw data made  
226 Poisson error structure unsuitable, so we square root transformed the response variable  
227 (number of flights in 60 seconds post-presentation) which allowed the model to be fitted with  
228 a Gaussian error structure. Model plots were examined for evidence of violation of  
229 assumptions, and refitted as GLMs to allow a Breusch-Pagan test to check for  
230 heteroscedasticity in the data. We fitted 19 models in total, containing all potential

231 combinations of the three main explanatory variables (model, playback type, and  
232 presentation number) and the possible interaction terms, as well as the number of flights in  
233 the 60 seconds prior to the presentation as a main effect only.

234 To further examine the factors influencing responses in the test phase, we conducted an  
235 additional analysis, using only the data from the 60 seconds before and after Presentation 3.  
236 In this analysis we used linear regression models, to test the influence of the playback, model,  
237 and the number of flights made in the 60 seconds prior to Presentation 3 on the number of  
238 flights made by the birds in the 60 seconds after. The number of flights before and after the  
239 presentation was square-root transformed, as in the previous analyses.

240 We used an information theoretic (IT) approach to model selection, using Akaike's  
241 Information Criterion corrected for small sample sizes (AICc) to rank the models, following  
242 the approach advocated by Richards et. al (35). Models that had a  $\Delta AICc \leq 6$  of the model with  
243 the lowest AICc value (Table 1) formed the 'top set'. We then applied the 'nesting rule' (36)  
244 to the top set, whereby models that were more complex versions of nested models with a  
245 lower AICc value were removed from the top set so as not to retain unnecessarily complex  
246 models.

247

## 248 **Results**

### 249 *Effects of training on responses*

250 Individuals showed substantial variation in their responses to the three model (i.e.  
251 fox/elephant) presentations (Supplementary materials; Fig S3). In mixed model analysis, four  
252 models formed the top set (Table 1), and from these models numbers 6 and 9 were retained

253 (Table 2) following application of the nesting rule (36). In both models, the number of flights  
254 made in the 60 seconds prior to each presentation being made was a strong positive predictor  
255 of how many flights were made in the 60 seconds following the presentation (Table 2). Both  
256 candidate models also included an interaction between presentation number and model  
257 type. Birds shown the Elephant model displayed a substantial decrease in response to  
258 Presentation 3 compared to Presentation 1, while those shown the Fox did not ( $\bar{x}$ (SE)  
259 Number of Flights made in the 60 s after presentation: Fox Presentation 1 = 9.66 (1.59), Fox  
260 Presentation 3 = 9.46 (1.41); Elephant Presentation 1 = 9.75 (1.41), Elephant Presentation 3 =  
261 5.75 (1.28); Figure 1, Table 2).

262 Between Presentation 1 and Presentation 2 there was no change in the response of the birds  
263 to the presentation, regardless of the model shown or playback heard in Presentation 2, with  
264 the birds showing a similar level of alarm in each (Table 2, Figure 1). Birds that were played  
265 scolds in Presentation 2 generally flew more in response to presentations across all  
266 presentation periods and regardless of the model shown ( $\bar{x}$ (SE) Number of Flights made in  
267 the 60 s after presentation: Contact call group birds = 7.42 (0.76); Scold call group birds =  
268 10.56 (0.89)). However, while playback type was a term in the model with the lowest AICc  
269 (Model 6, Table 1), it did not appear to have a robust effect on the number of flights made in  
270 the 60 s after the presentation (estimate (SE) = 0.369 (0.226),  $t = 1.63$ ,  $p = 0.11$ ; Model 6,  
271 Table 2) and did not appear in the second best model (Model 9; Table 1).

272 Only two birds made scold calls during the experiment, and neither case occurred during the  
273 60 seconds after a model presentation. Both cases occurred between Presentations 2 and 3,  
274 with one bird (Fox-Scold group) directing the vocalisation at a passing buzzard (*Buteo buteo*),

275 while the other (Fox-Contact group) appeared to direct the vocalisation in the direction of the  
276 hide where the fox was concealed.

277

### 278 *Potential carry-over effects of playbacks*

279 In the analysis that considered only the responses to the final, Test presentation, there were  
280 three models in the top set, but after the nesting rule was applied only one was retained  
281 (p3.model4; Table 3, Supplementary Materials S2). As in the previous analysis, birds were  
282 likely to fly more in response to presentations of the fox than the elephant (Estimate (SE) =  
283 0.916 (0.245),  $t = 3.74$ ,  $p < 0.001$ , Figure 1) and the number of flights made in the 60 seconds  
284 pre- presentation predicted the number of flights after the presentation (Estimate (SE) =  
285 0.777 (0.077),  $t = 10.06$ ,  $p < 0.001$ ; Figure 2). The number of flights in the 60 seconds prior to  
286 the presentation (pre60) was by far the best predictor of post-presentation responses, with  
287 all models containing this term having an adjusted- $R^2$  ranging from 0.63 to 0.72 (Table 3).  
288 However, if we did not account for agitation, and left pre60 out of the analysis, then playback  
289 type changed from being a non-significant predictor of the birds' behaviour following  
290 Presentation 3 to having  $\alpha \leq 0.05$  (p3.model6 and p3.model9). On average, birds that had been  
291 played scolds in Presentation 2 flew more than those that had heard contact calls ( $\bar{x}$  (SE)  
292 Number of Flights made in the 60 s after presentation: Scold call group = 9.5 (1.4), Contact  
293 call group = 5.7 (1.3); Est (SE) = 0.886 (0.421),  $t = 2.10$ ,  $p = 0.04$ ).

### 294 **Discussion**

295 Predation is typically the main cause of mortality for fledgling birds (37–39), so there is great  
296 pressure on young individuals to quickly learn how to identify and respond to potential

297 predators. While experiments have demonstrated that birds can learn about novel predators  
298 through exposure to social information over several minutes (19,23), it remains unclear  
299 whether the very brief exposures to social information that often accompany natural  
300 predator attacks are sufficient to promote learning. Moreover, experimental tests of anti-  
301 predator social learning outside of controlled laboratory setting remain rare.

302 Here we found that, contrary to expectations, brief exposures to social information in the  
303 form of conspecific vocalisations did not appear to produce a consistent change in young  
304 jackdaws' responses to potential predators. If social learning had a strong effect, we would  
305 expect naïve birds to show low baseline responses to models which increased following scold  
306 call training and declined or remained constant following control call training. Instead, birds  
307 often showed high levels of agitation from the start of the experiment, with an overall decline  
308 in the number of flights made in response to the Elephant from presentation 1 to presentation  
309 3, while responses to the Fox remained elevated throughout, regardless of training. This  
310 suggests that the jackdaws may have habituated to the novel Elephant stimulus through  
311 repeated presentations, and that most if not all individuals already recognised the Fox as a  
312 threat from the start of the experiment. Although visual inspection of Figure 1 suggests that  
313 the responses of birds given scold call training may have remained elevated while those with  
314 contact call training declined, our analyses showed no clear statistical evidence for an  
315 interaction between presentation number and playback type. We did find some weak support  
316 for a main effect of playback type, with scold-trained birds tending to fly more than those that  
317 heard contact calls (playback type features in the top model, but does not have a significant  
318 effect at  $\alpha= 0.05$ ). However, this effect was consistent across both model groups, suggesting  
319 that it could be the result of birds still being in an elevated state of agitation as a result of

320 recently having heard scold calls, rather than specific learned responses towards the models.  
321 Indeed, the number of flights made in the minute before presentations was by far the  
322 strongest predictor of the subsequent responses to the presentations (Figure 2), indicating  
323 that captivity- and/or carry-over induced agitation rather than social learning was the primary  
324 driver of behaviour.

325 This conclusion is further supported by analyses honing in on responses to the final, test  
326 phase. Here, as in the main analysis, we found stronger responses to the Fox than to the  
327 Elephant but, as before, the strongest predictor was the number of flights in the minute  
328 preceding the presentation. Playback type did not appear to have a robust effect on  
329 responses, as it did not feature in the top model, and its inclusion produced only a 1%  
330 improvement in the variance explained (adjusted  $R^2$  of model 2 = 0.72; model 4 = 0.71). To  
331 the extent that there was some small increase in the responses of birds that heard scold calls  
332 compared to those that heard contact calls, this was consistent across both model types and  
333 is most likely to represent a carry-over effect from calls heard in training. It is important to  
334 note that, had we not accounted for levels of agitation prior to presentations, we could have  
335 reached very different conclusions, as playback type did appear to have a statistically  
336 significant effect ( $p < 0.05$ ) when pre-presentation flights were not included in the analysis.

337 Although our experiment failed to generate the predicted effects, it nevertheless has a  
338 number of important fundamental and practical implications. First, our results show that  
339 taking levels of agitation induced by captivity and/or carry-over effects into account is critical  
340 for studies attempting to train animals to respond to novel stimuli. Given the growing  
341 emphasis on harnessing social learning to promote adaptive behaviours in conservation  
342 contexts (40,41), accounting for agitation will be vital in the design and interpretation of such



343 research. This may be particularly important for species such as corvids that exhibit high levels  
344 of neophobia (42,43) and for *in situ* conservation and wildlife management schemes, where  
345 animals are not used to captive conditions. More generally, a failure to consider captivity-  
346 induced agitation could lead to false conclusions in any behavioural assay where animals are  
347 brought into captivity. For instance, some studies have interpreted movement around an  
348 enclosed space as indicative of exploratory tendencies, when it may in fact reflect agitation  
349 induced by spatial neophobia (reviewed in 44) and/or elevated stress levels due to capture  
350 and handling (45). The high flight responses observed in response to the first baseline  
351 presentation, regardless of the model shown, suggests that at this is likely to be the case here.  
352 While levels of agitation could, in principle, be reduced in experiments such as ours by  
353 allowing subjects more time to acclimatise to captive conditions, this must always be traded  
354 off against the ethical imperative to keep presentations as short as possible, particularly if  
355 they involve young animals that are still dependent on parents.

356 Second, our experiment showed that responses differed substantially between individuals  
357 (evident in figure S3). While such differences might be influenced by previous experience with  
358 predators (46,47), it is also possible that individual differences in agitation (possibly linked to  
359 variation in stress reactivity or coping styles; 48) could affect the potential for individuals to  
360 learn about novel predators, both in experimental and natural contexts. While a hormonally-  
361 mediated stress response is known to be necessary to promote aversion learning (49,50),  
362 there is some evidence that acute levels of stress can inhibit learning (51). Moreover, highly  
363 anxious individuals may be faster to flee upon hearing conspecific alarm calls, thus reducing  
364 their potential for learning to associate the calls with the presence of a novel predator. Given  
365 evidence that personality differences influence social information use in other contexts

366 (e.g.52,53), understanding how personality affects the development of anti-predator  
367 responses is a clear priority for future research.

368 Finally, our results raise questions about the stimuli needed to promote social learning of anti-  
369 predator responses. Whereas some studies on captive animals show that playbacks of  
370 mobbing or alarm calls are sufficient to promote learned fear responses towards novel stimuli  
371 (18,24), this did not appear to be the case in our experiment. Indeed, as the great majority of  
372 research on socially learned anti-predator responses has taken place under controlled  
373 laboratory conditions, it remains unclear whether vocalisations alone are sufficient to  
374 promote learning in the wild. Corvids, for example, show a range of distinctive behaviours in  
375 response to predators, including gaze fixing, aggressive postures, and diving flights directed  
376 at the threat (54–56). It is quite possible that the posture and directedness of the behaviour  
377 of conspecifics is as important as, or complimentary to, the vocalisations themselves in  
378 serving to reinforce learning and increase signal saliency. Such multimodal signals have been  
379 found to increase the speed at which predators learn to discriminate aposematic prey (57),  
380 and also enhance the responses of observers to anti-predator alarm signals compared to  
381 when such signals are presented singly (58).

382 Understanding how wild animals learn about new threats is an important priority for both  
383 fundamental and applied research. Tightly controlled laboratory experiments show that anti-  
384 predator responses can, in principle, be socially learned, but work on wild animals remains  
385 rare. We must now embrace the complexities of the real world, including individual variation  
386 and multi-modal signal structure, to better understand how such learning operates in  
387 practice.

388 **Ethics**

389 Birds were captured by trained bird ringers operating under licences issued by the British  
390 Trust for Ornithology (permit C5752), and held briefly in captivity under UK Home Office  
391 project licence PPL 80/2371. The experiment was carried out following methodological  
392 approval from the Biosciences Ethics Panel of the University of Exeter, and adhered to the  
393 standards outlined in the in the ASAB/ABS (2012) Guidelines for the Treatment of Animals in  
394 Behavioural Research and Teaching (59).

#### 395 **Data accessibility**

396 The data and R code are available from the Dryad Digital Repository at  
397 <https://doi.org/10.5061/dryad.9r8v0>

#### 398 **Author contributions**

399 Conceptualization GEM, AT; Data collection GEM, VEL; Video coding; GEM; Data analysis;  
400 GEM, Writing, GEM, VEL, AT. All authors gave their final approval for publication.

#### 401 **Competing interests**

402 The authors declare no competing interests.

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## 413 **References**

- 414 1. Veen T, Richardson DS, Blaakmeer K, Komdeur J. (2000) Experimental evidence for  
415 innate predator recognition in the Seychelles warbler. *Proc R Soc B*. **267**(1459):2253–  
416 8. (doi: 10.1098/rspb.2000.1276)
- 417 2. Göth A. (2000) Innate predator-recognition in Australian brush-turkey (*Alectura*  
418 *lathamii*, *Megapodiidae*) hatchlings. *Behaviour* **138**(1):117–36. Available from:  
419 <http://www.jstor.org/stable/4535809>
- 420 3. Ferrero DM, Lemon JK, Fluegge D, Pashkovski SL, Korzan WJ, Datta SR, et al. (2011)  
421 Detection and avoidance of a carnivore odor by prey. *PNAS* **108**(27):11235–40.
- 422 4. Sündermann D, Scheumann M, Zimmermann E. 2008. Olfactory predator recognition  
423 in predator-naive gray mouse lemurs (*Microcebus murinus*). *J Comp Psych*: **122**(2)  
424 146–55. (doi:/10.1037/0735-7036.122.2.146)
- 425 5. Ferrari MCO, Chivers DP. 2009. Sophisticated early life lessons: Threat-sensitive  
426 generalization of predator recognition by embryonic amphibians. *Behav Ecol*. **20**,  
427 1295–8.
- 428 6. Ferrari MCO, Chivers DP. 2010. The ghost of predation future: Threat-sensitive and  
429 temporal assessment of risk by embryonic woodfrogs. *Behav Ecol Sociobiol*. **64**, 549–  
430 55.

- 431 7. Lorenz KZ. 1952. King Solomon's Ring (English edition). The Reprint Society Ltd.  
432 (London); 146-198.
- 433 8. Kullberg C, Lind J. 2002. An experimental study of predator recognition in great tit  
434 fledglings. *Ethology*. **108**, 429–41.
- 435 9. Conover MR, Perito JJ. 1981. Response of starlings to distress calls and predator  
436 models holding conspecific prey. *Z Tierpsychol*. **57**,163–72. (doi:10.1111/j.1439-  
437 0310.1981.tb01320.x)
- 438 10. Griffin AS, Haythorpe K. 2011. Learning from watching alarmed demonstrators: Does  
439 the cause of alarm matter? *Anim Behav*. **81**, 1163–9.
- 440 11. Griffin AS. 2004. Social learning about predators: a review and prospectus. *Learn*  
441 *Behav* **32**, 131–40 (doi: 10.3758/BF03196014)
- 442 12. Brown GE. 2003. Learning about danger: Chemical alarm cues and local risk  
443 assessment in prey fishes. *Fish Fish*. **4**, 227–34.
- 444 13. Mitchell MD, Chivers DP, McCormick MI, Ferrari MCO. 2015. Learning to distinguish  
445 between predators and non-predators: understanding the critical role of diet cues  
446 and predator odours in generalisation. *Sci Rep* :13918. (doi: 10.1038/13918)
- 447 14. Bradbury JW, Vehrencamp SL. 1998. *Principles of animal communication*. Sunderland,  
448 MA: Sinauer Associates.
- 449 15. Suzuki, TN. 2014. Communication about predator type by a bird using discrete,  
450 graded and combinatorial variation in alarm calls. *Anim Behav* **87**, 59–65.  
451 (doi:10.1016/j.anbehav.2013.10.009)

- 452 16. Bílá K, Beránková J, Veselý P, Bugnyar T, Schwab C. 2017. Responses of urban crows  
453 to con- and hetero-specific alarm calls in predator and non-predator zoo enclosures.  
454 *Anim Cogn.* **20**, 43–51.
- 455 17. Fallow PM, Pitcher BJ, Magrath RD. 2013. Alarming features: birds use specific  
456 acoustic properties to identify heterospecific alarm calls. *Proc Roy Soc B.* **280** (1754):  
457 20122539–20122539. (doi:10.1098/rspb.2012.2539)
- 458 18. Vieth W, Curio E, Ernst U. 1980. The adaptive significance of avian mobbing. III.  
459 Cultural transmission of enemy recognition in blackbirds: Cross-species tutoring and  
460 properties of learning. *Anim Behav.* **28**, 1217–29.
- 461 19. Curio E, Ernst U, Vieth W. 1978. The Adaptive Significance of Avian Mobbing II.  
462 Cultural transmission of enemy recognition in blackbirds: effectiveness and some  
463 constraints. *Z Tierpsychol.* **48**, 184–202.
- 464 20. Cornell HN, Marzluff JM, Pecoraro S. 2011. Social learning spreads knowledge about  
465 dangerous humans among American crows. *Proc Roy Soc B.* **279** (1728), 499–508.  
466 Available from: <http://rspb.royalsocietypublishing.org/content/279/1728/499>
- 467 21. McLean IG, Hoelzer C, Studholme BJS. 1999. Teaching predator-recognition to a naive  
468 bird: implications for management. *Biol Conserv.* **87**, 123–30.
- 469 22. Feeney WE, Langmore NE. 2013. Social learning of a brood parasite by its host. *Biol*  
470 *Lett* **9**: 20130443.
- 471 23. Maloney RF, McLean IG. 1995. Historical and experimental learned predator  
472 recognition in free-living New-Zealand robins. *Anim Behav.* **50**, 1193–201.

- 473 24. Griffin AS, Galef BG. 2005. Social learning about predators: Does timing matter? *Anim*  
474 *Behav.* **69**, 669–78.
- 475 25. Tamura N. 1989. Snake-directed mobbing by the Formosan squirrel *Callosciurus*  
476 *erythraeus thaiwanensis*. *Behav Ecol Sociobiol.* **24**, 175–80.
- 477 26. Flasskamp A. 1994. The adaptive significance of avian mobbing V. An experimental  
478 test of the “move on” hypothesis. *Ethology.* **96**, 322–33.
- 479 27. Graw B, Manser MB. 2007. The function of mobbing in cooperative meerkats. *Anim*  
480 *Behav.* **74**, 507–17.
- 481 28. Barnard CJ. 1979. Interactions between house sparrows and sparrowhawks. *Brit*  
482 *Birds.* **72**, 569–73.
- 483 29. Cresswell W. 1996. Surprise as a winter hunting strategies in Sparrowhawks *Accipiter*  
484 *nisus*, Peregrines *Falco peregrinus* and Merlins *F. columbarius*. *Ibis.* **138**, 684–92.
- 485 30. Henderson IG, Hart PJB. 1993. Provisioning, parental investment and reproductive  
486 success in Jackdaws *Corvus monedula*. *Ornis Scand.* **24**, 142–8. Available from:  
487 <http://www.jstor.org/stable/3676364>
- 488 31. Coombs CJF. 1978 The Jackdaw. In: *The Crows: A study of the corvids of Europe*.  
489 London: B.T. Batsford Ltd, p. 111–29.
- 490 32. Cramp S, Perrins CM. 1994. Handbook of the Birds of Europe, the Middle East and  
491 North Africa. The Birds of the Western Palearctic. Crows to Finches, Vol. VIII. Oxford:  
492 Oxford University Press.
- 493 33. Thornton A, Malapert A. 2009. The rise and fall of an arbitrary tradition: an

- 494 experiment with wild meerkats. *Proc R Soc B*. **276**(1660), 1269–76.  
495 (doi:10.1098/rspb.2008.1794)
- 496 34. Woods RD. 2016. *Collective responses to acoustic threat information in jackdaws*.  
497 Unpublished PhD thesis, University of Exeter. (Available from:  
498 <https://ore.exeter.ac.uk/repository/handle/10871/25978>)
- 499 35. Richards SA, Whittingham MJ, Stephens PA. 2011. Model selection and model  
500 averaging in behavioural ecology: The utility of the IT-AIC framework. *Behav Ecol*  
501 *Sociobiol.* **65**, 77–89.
- 502 36. Richards SA. 2007. Dealing with overdispersed count data in applied ecology. *J Appl*  
503 *Ecol.* **45**, 218–27. (doi: 10.1111/j.1365-2664.2007.01377.x)
- 504 37. McFadzen ME, Marzluff JM. 1996. Mortality of prairie falcons during the fledging-  
505 dependence period. *Condor.* **98**, 791–800.
- 506 38. Yackel Adams AA, Skagen SK, Adams RD. 2001. Movements and survival of lark  
507 bunting fledglings. *Condor.* **103**, 643–647.
- 508 39. King DI, Degraaf RM, Smith ML, Buonaccorsi JP. 2006. Habitat selection and habitat-  
509 specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *J Zool.* **269**, 414–21.
- 510 40. Greggor AL, Thornton A, Clayton NS. 2017. Harnessing learning biases is essential for  
511 applying social learning in conservation. *Behav Ecol Sociobiol.* **71**, 16 (doi:  
512 10.1007/s00265-016-2238-4)
- 513 41. Whitehead H. 2010. Conserving and managing animals that learn socially and share  
514 cultures. *Learn Behav.* **38**, 329–36.



- 515 42. Greenberg R, Mettke-Hofmann C. 2001. *Ecological aspects of neophobia and*  
516 *neophilia in birds*. Current Ornithology Book Series (Vol 16) 119-178. Eds: Nolan Jnr  
517 VCFT 119-178. Eds: Thompson CF & Nolan Jnr VCFT. Kluwer Academic/Plenum  
518 Publishers, New York.
- 519 43. Greggor AL, Clayton NS, Fulford AJC, Thornton A. 2016. Street smart: Faster approach  
520 towards litter in urban areas by highly neophobic corvids and less fearful birds. *Anim*  
521 *Behav.* **117**, 123–33.
- 522 44. Greggor AL, Thornton A, Clayton NS. 2015. Neophobia is not only avoidance;  
523 improving neophobia tests by combining cognition and ecology. *Curr Opin Behav Sci.*  
524 **6**, 82–9.
- 525 45. Dickens MJ, Earle KA, Romero LM. 2009. Initial transference of wild birds to captivity  
526 alters stress physiology. *Gen Comp Endocrinol.* **160**, 76–83. ([doi:](https://doi.org/10.1016/j.ygcen.2008.10.023)  
527 [10.1016/j.ygcen.2008.10.023](https://doi.org/10.1016/j.ygcen.2008.10.023))
- 528 46. Griffin AS, Evans CS, Blumstein DT. 2001. Learning specificity in acquired predator  
529 recognition. *Anim Behav.* **62**, 577–89.
- 530 47. Ferrari MC., Gonzalo A, Messier F, Chivers DP. 2007. Generalization of learned  
531 predator recognition: an experimental test and framework for future studies. *Proc R*  
532 *Soc B.* **274** (1620), 1853–9. ([doi:10.1098/rspb.2007.0297](https://doi.org/10.1098/rspb.2007.0297))
- 533 48. Koolhaas JM, de Boer SF, Coppens CM, Buwalda B. 2010. Neuroendocrinology of  
534 coping styles: Towards understanding the biology of individual variation. *Front*  
535 *Neuroendocrinol.* **31**, 307–21. ([doi:10.1016/j.yfrne.2010.04.001](https://doi.org/10.1016/j.yfrne.2010.04.001))

- 536 49. Thaker M, Vanak AT, Lima SL, Hews DK. 2010. Stress and aversive learning in a wild  
537 vertebrate: the role of corticosterone in mediating escape from a novel stressor. *Am*  
538 *Nat.* **175**, 50–60.
- 539 50. Jones BC, Bebus SE, Ferguson SM, Bateman PW, Schoech SJ. 2016. The glucocorticoid  
540 response in a free-living bird predicts whether long-lasting memories fade or  
541 strengthen with time. *Anim Behav.* **122**, 157–68. (doi:  
542 10.1016/j.anbehav.2016.10.009)
- 543 51. Joëls M, Pu Z, Wiegert O, Oitzl MS, Krugers HJ. 2006. Learning under stress: how does  
544 it work? *Trends Cogn Sci.* **10**, 152–8.
- 545 52. Trompf L, Brown C. 2014. Personality affects learning and trade-offs between private  
546 and social information in guppies, *Poecilia reticulata*. *Anim Behav.* **88**, 99–106. (doi:  
547 10.1016/j.anbehav.2013.11.022)
- 548 53. González-Bernal E, Brown GP, Shine R. 2014. Invasive cane toads: Social facilitation  
549 depends upon an individual's personality. *PLoS One.* **9**(7) e102880.  
550 (<https://doi.org/10.1371/journal.pone.0102880>)
- 551 54. Yorzinski JL, Vehrencamp SL. 2011. The effect of predator type and danger level on  
552 the mob calls of the American Crow. *Condor.* **111**, 159–68.
- 553 55. Marzluff JM, Miyaoka R, Minoshima S, Cross DJ. 2012. Brain imaging reveals neuronal  
554 circuitry underlying the crow's perception of human faces. *PNAS.* **109**, 15912–15917.
- 555 56. Swift KN, Marzluff JM. 2015. Wild American crows gather around their dead to learn  
556 about danger. *Anim Behav.* **109**, 187–97.

- 557 (<http://dx.doi.org/10.1016/j.anbehav.2015.08.021>)
- 558 57. Rowe C. 2002. Sound improves visual discrimination learning in avian predators. *Proc*  
559 *R Soc B.* **269**(1498), 1353–7. (doi: 10.1098/rspb.2002.2012)
- 560 58. Partan SR, Larco CP, Owens MJ. (2009) Wild tree squirrels respond with multisensory  
561 enhancement to conspecific robot alarm behaviour. *Anim Behav.* **77**, 1127–35. (doi:  
562 10.1016/j.anbehav.2008.12.029)
- 563 59. Guidelines for the treatment of animals in behavioural research and teaching. 2006.  
564 *Anim Behav.* **71**, 245–53. Available from:  
565 <http://linkinghub.elsevier.com/retrieve/pii/S0003347205003337>

566

567

568 Table 1: Model selection table for the variables influencing the (square-root transformed)  
569 number of flights made by the jackdaws in the 60 seconds after each presentation. The grey  
570 area highlights the models that form the top set prior implementation of a model nesting rule  
571 (Richards, 2007) that filtered out those that should not be retained. When factors are included  
572 in the model this is denoted by the symbol ●, and numbers refer to the coefficients of numeric  
573 variables when these were included in the model, while \* denotes interaction terms between  
574 variables. sqrt.pre60 refers to the number of flights made in the 60 seconds prior to the  
575 presentation (square-root transformed), while model denotes the model shown  
576 (Elephant/Fox), pres.num the presentation number (1,2, or 3), and pb.group whether the bird  
577 heard scold calls or contact calls during presentation 2. Potential ‘top’ models are highlighted  
578 in bold, and these are reported in full in Table 2.  
579

Model ID	Intercept	sqrt.pre60	model	pb.group	pres.num	model* pb.group	model* pres.num	pb.group* pres.num	model* pb.group* pres.num	df	logLik	AICc	ΔAICc	retained	weight
<b>sqrt.sel6</b>	<b>1.815</b>	<b>0.521</b>	●	●	●		●			<b>11</b>	<b>-213.8</b>	<b>451.5</b>	<b>0.0</b>	<b>Yes</b>	<b>0.53</b>
<b>sqrt.sel9</b>	<b>1.991</b>	<b>0.527</b>	●		●		●			<b>10</b>	<b>-215.1</b>	<b>451.8</b>	<b>0.3</b>	<b>Yes</b>	<b>0.47</b>
sqrt.sel3	1.753	0.527	●	●	●	●	●			12	-213.6	453.7	2.1	No	
sqrt.sel5	1.943	0.508	●	●	●		●	●		13	-213.3	455.4	3.9	No	
sqrt.sel2	1.882	0.514	●	●	●	●	●	●		14	-213.2	457.6	6.1		
sqrt.sel15	1.679	0.526		●	●					8	-220.8	458.7	7.1		
sqrt.sel18	1.852	0.532			●					7	-222.1	459.0	7.5		
sqrt.sel12	1.637	0.522	●	●	●					9	-220.7	460.7	9.2		
sqrt.sel14	1.812	0.528	●		●					8	-222.0	461.1	9.6		
sqrt.sel1	1.869	0.504	●	●	●	●	●	●	●	16	-212.6	461.5	10.0		
sqrt.sel11	1.807	0.514		●	●			●		10	-220.4	462.4	10.9		
sqrt.sel7	1.573	0.529	●	●	●	●				10	-220.6	462.8	11.3		
sqrt.sel8	1.764	0.509	●	●	●			●		11	-220.3	464.6	13.1		
sqrt.sel17	1.472	0.525		●						6	-226.1	464.9	13.4		
sqrt.sel19	1.644	0.532								5	-227.4	465.3	13.8		
sqrt.sel4	1.701	0.516	●	●	●	●		●		12	-220.2	466.8	15.2		
sqrt.sel13	1.431	0.521	●	●						7	-226.1	466.9	15.4		
sqrt.sel16	1.605	0.528	●							6	-227.4	467.3	15.8		
sqrt.sel10	1.366	0.528	●	●		●				8	-225.9	468.9	17.4		

580

581

582 Table 2: Values from the GLMM models highlighted in Table 1 as the being the candidate  
 583 'best' models for predicting which factors influenced the (square-root transformed) number  
 584 of flights made by the birds around the experimental arena in the sixty seconds after the  
 585 model presentation. Bird identity and playback heard were included as random effects in each  
 586 model, with the variance (SD) of bird identity being 0.303 (0.55) in Model 6 and 0.331 (0.58)  
 587 in Model 9. Variance attributable to the playback track was zero in all models.  
 588

*Model sqrt.sel6 Summary*

Variable	Estimate	SE	t-Value	P-Value
Intercept	1.815	0.264	6.87	<0.001
sqrt.Flights in 60s prior to Pres	0.521	0.064	8.16	<0.001
Model: Elephant	0	0		
Fox	-0.257	0.318	-0.81	0.42
Playback Group: Contact	0	0		
Scold	0.369	0.226	1.63	0.11
Presentation Number: Pres 1	0	0		
Pres 2	0.067	0.275	0.25	0.81
Pres 3	-1.221	0.275	-4.43	<0.001
Presentation Number*Model	0			
Pres 2:Fox	-0.154	0.389	-0.40	0.693
Pres 3:Fox	1.216	0.389	3.13	0.002

*Model sqrt.sel9 Summary*

Variable	Estimate	SE	t-Value	P-Value
Intercept	1.991	0.247	8.07	<0.001
sqrt.Flights in 60s prior to Pres	0.527	0.064	8.22	<0.001
Model: Elephant	0	0		
Fox	-0.26	0.322	-0.81	0.42
Presentation Number: Pres 1	0	0		
Pres 2	0.068	0.275	0.25	0.81
Pres 3	-1.223	0.276	-4.43	<0.001
Presentation Number*Model				
Pres 2:Fox	-0.156	0.389	-0.40	0.69
Pres 3:Fox	1.217	0.389	3.13	0.002

589

590

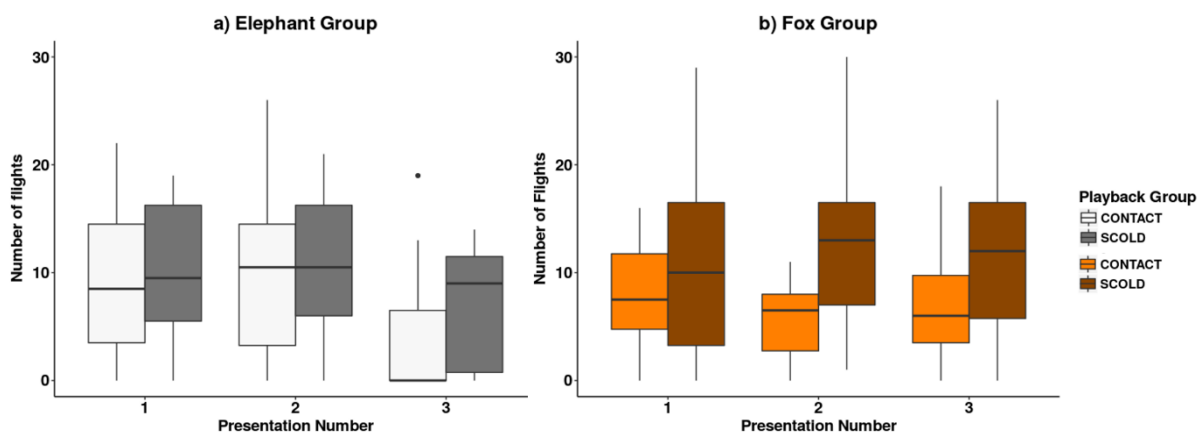
591

592 Table 3: Model selection table for the variables influencing the (square-root transformed)  
 593 number of flights made by the jackdaws in the 60 seconds after Presentation 3 only. The grey  
 594 area highlights the models that form the top set prior implementation of a model nesting rule  
 595 [36] that filtered out those that should not be retained. When factors are included in the  
 596 model this is denoted by the symbol ●, and numbers refer to the coefficients of numeric  
 597 variables when these were included in the model, while \* denotes interaction terms between  
 598 variables. sqrt.pre60 refers to the (square-root transformed) number of flights made in the  
 599 60 seconds prior to the model presentation, while model denotes the model shown  
 600 (Elephant/Fox), and pb.group whether the bird heard scold calls or contact calls during  
 601 presentation 2. The top model is highlighted in bold. As there was only one top model  
 602 following application of the nesting rule, model weights are provided for all of the models  
 603 listed.  
 604

model.ID	Intercept	sqrt.pre60	model	pb.group	model* pb.group	df	logLik	AICc	ΔAICc	weight	Retained
<b>p3.model4</b>	<b>0.305</b>	<b>0.777</b>	●			4	<b>-58.7</b>	<b>126.2</b>	<b>0.0</b>	<b>0.50</b>	<b>Yes</b>
p3.model2	0.201	0.754	●	●		5	-57.9	127.3	1.1	0.30	No
p3.model1	0.036	0.760	●	●	●	6	-57.0	128.1	1.9	0.20	No
p3.model7	0.733	0.792				3	-65.1	136.8	10.6	0.00	
p3.model3	0.636	0.770		●		4	-64.6	138.2	12.0	0.00	
p3.model6	1.302		●	●		4	-84.7	178.3	52.1	0.00	
p3.model8	1.745		●			3	-87.0	180.5	54.2	0.00	
p3.model5	1.210		●	●	●	5	-84.6	180.6	54.4	0.00	

605

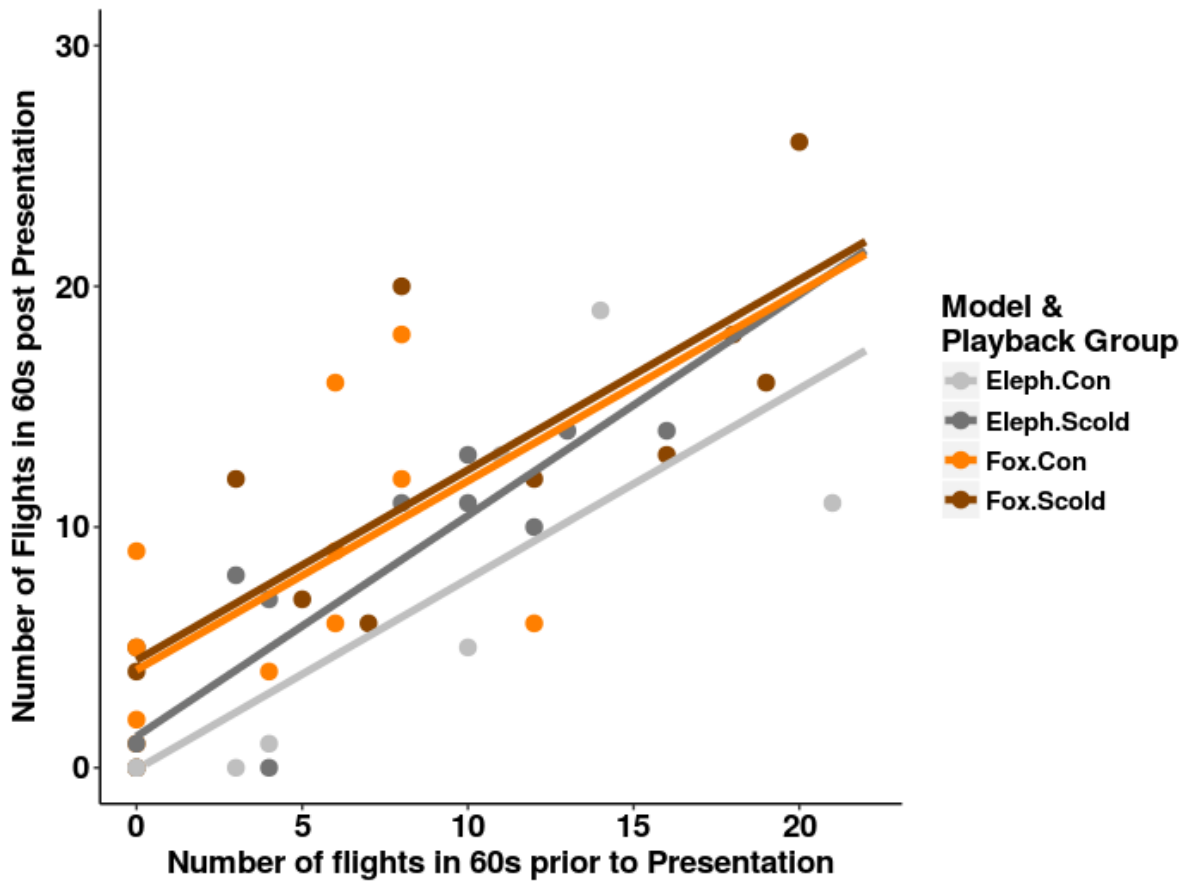
606 Figure 1: Plots of the raw data for the number of flights made by the birds in the sixty seconds  
 607 following the presentation of a) the model elephant, or b) the model fox. Light colours in each  
 608 represent birds from the Contact call group, while the darker plots display data from birds  
 609 played Scold calls in Presentation 2. There were no accompanying playbacks in Presentations  
 610 1 and 3.



611

612

613 Figure 2: Scatterplot of the number of flights made in the 60 seconds prior to the Presentation  
614 3, against the number of flights made in the 60 seconds after the presentation, highlighting  
615 the consistency of this relationship between groups, regardless of the model shown or the  
616 playback previously heard.



617