Nesting jackdaws' responses to human voices vary with local disturbance levels and the gender of the speaker

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The ability to detect and respond to indicators of risk is vital for any animal and, for many species, humans represent a key threat. We investigated whether wild jackdaws, *Corvus monedula*, a species that thrives in anthropogenic environments but is regularly persecuted by people, associate human voices with differential degrees of risk and differ in their responses according to local levels of human disturbance. Playbacks showed that nesting females did not discriminate between the voices of familiar men who posed differing levels of threat, generalize to unfamiliar individuals with similar regional accents or discriminate between familiar and unfamiliar accents and voices. They were, however, considerably more wary towards male than female human voices, which may reflect the greater likelihood of negative experiences with men than women. Responses to playbacks also differed across fine-scale spatial locations: females nesting in areas of the colony with high levels of disturbance were less likely to leave the nest cup in response to playbacks and were more wary on their return to the nest than birds nesting in less disturbed areas. Nevertheless, levels of local disturbance did not influence reproductive success. Together these results indicate that, although vocal cues alone may not suffice for wild jackdaws to discriminate between individual humans or generalize across categories of people, sensitivity to cues of gender and local disturbance may help jackdaws to optimize their defensive behaviour and maintain breeding success. Further research into plastic responses towards indicators of human risk is vital to understand and mitigate the impacts of increasing urbanization on wildlife populations.

Living near humans can provide wildlife with opportunities in the form of food, breeding sites, shelter and refuge from predators (Barrett et al., 2019; Lowry et al., 2013; Sih, 2013; Sol et al., 2013), but humans pose one of the main threats to the survival of many animals (Milleret et al., 2017; Revilla et al., 2001). The threat posed by humans and other predators can vary across different landscapes and habitat types, but also on finer spatial scales, such as within home ranges (Andruskiw et al., 2008; Gervasi et al., 2013; Hebblewhite & Merrill, 2007). Evaluating risks associated with humans is further complicated by the fact that some people may be more dangerous than others (e.g. Bolnick et al., 2003; McComb et al., 2014). In this age of rapid human-induced environmental change, it is increasingly important that we understand how animals respond to the challenges and opportunities of living around people (Goumas & Lee et al., 2020).

By being sensitive to spatiotemporal indicators of risk, animals may flexibly adjust behaviour to optimize trade-offs between investment in different activities such as foraging and vigilance (Hilton et al., 1999; Yasué et al., 2003). Animals can respond to humans by avoiding areas with anthropogenic structures and activity (Dyer et al., 2001; Kaartinen et al., 2005), by modifying vigilance behaviour and habitat use based on the times and seasons that hunting occurs (Ciuti et al., 2012; Lone et al., 2015; Sönnichsen et al., 2013) or by becoming more nocturnal (Gaynor et al., 2019). Such studies typically investigate effects over large spatial areas (e.g. Diquelou, McFarlane & Griffin, 2018), but both disturbance and threat levels can also vary at the scale of a few metres (Kuiper et al., 2015). This is especially true when human residents have highly contrasting attitudes towards certain species. For instance, while nearly half of the urban dwellers surveyed by Cox and Gaston (2015) felt either neutral or positive towards magpies, *Pica pica*, more either disliked or strongly disliked them. Such dislike is often acted upon, and in France as many magpies are trapped and killed

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in urban environments as in rural locations (Chiron & Julliard, 2013). The extent to which wild animals fine-tune their behaviour in response to this variation in attitudes and arising activities may have important impacts on population dynamics and viability (Goumas & Lee et al., 2020; Greggor et al., 2014; Lee & Thornton, 2021; Sol et al., 2005).

Given the wide range of human attitudes towards animals, it is perhaps unsurprising that some animals use human behaviours and characteristics to guide their behaviour around us. Urban herring gulls, *Larus argentatus*, are more likely to investigate items they have seen being handled by humans (Goumas et al., 2020) and various mammals and birds discriminate between people based on clothing (Bates et al. 2007; Feng & Liang, 2020) or facial features (Cornell et al., 2011; Davidson et al., 2015; Lee et al. 2011, 2016, 2019). In addition to visual features, there is now considerable evidence that animals attend and respond to the vocalizations of predators (Abbey-Lee et al. 2016; Hua et al., 2013; Zannette et al., 2011) and may even discriminate between vocalizations of predators of the same species. For instance, some pods of orcas, *Orcinus orca*, hunt mammals while others only hunt fish, and playback experiments indicate that harbour seals, *Phoca vitulina*, learn to discriminate between the calls of orca pods that are dangerous and those that are not (Deecke et al., 2002). Similarly, the responses of African elephants, *Loxodonta africana*, to human voices reflect differential levels of threat associated with the speaker's age, gender or ethnicity (McComb et al., 2014). However, little is known about whether and how wild animals generalize from past experience of human voices or adjust their responses across contexts.

A growing body of research shows that some animals discriminate between familiar and unfamiliar human voices in domesticated (Adachi et al., 2007; Saito & Shinozuka, 2013), captive (Leroux et al., 2018; Sliwa et al., 2011; Wascher et al., 2012) and wild settings (Dutour et al., 2021). Horses, *Equus caballus*, have also been shown to discriminate between the voices of different familiar humans (Proops & Mccomb, 2012). However, little is known about how wild animals generalize about stimuli encountered previously. Using generalization from past experience to guide responses could be especially valuable if certain groups or subgroups of people are more or less likely to behave in a particular way. For example, if hunting is a predominantly male activity, it could be advantageous for an animal to generalize from a negative experience with one man and avoid other men in future. Similarly, even within linguistic groups different subgroups may pose differing threat levels, so generalizing on the basis of markers of subgroup membership such as accents could therefore help to minimize risk. Moreover, the degree to which vocal properties reflect risk may vary across context: for instance, male voices might be associated with hunting in the countryside but not in urban areas.

We used playbacks to test whether wild jackdaws, *Corvus monedula*, adjust their responses to human voices according to (1) the fine-scale spatial location of the nest, (2) the gender, accent and familiarity of the speaker, and (3) whether they generalize their responses based upon their prior experience. Jackdaws are a highly social cavity-nesting member of the crow family. They readily utilize anthropogenic nest sites and have undergone steady population growth in the U.K. in recent decades (e.g. Gregory & Marchant, 1996; Keller et al., 2020). While they frequently live close to people, shooting is nevertheless the main cause of reported mortality for jackdaws in the U.K. (Henderson, 2002). Studies show that they remember the faces of threatening humans via individual learning (Davidson et al., 2015) and social learning (Lee et al. 2019). However, while some evidence suggests that captive corvids discriminate voices of familiar and unfamiliar humans (Wascher et al., 2012), it is not known whether and how corvids use information from human voice cues to adjust their responses to potential threats in the wild. Moreover, although men are more likely to pose a threat than women (in March 2019, 94% of all licensed firearms holders in the U.K. were male, Baxter, 2019), we do not know whether jackdaws discriminate the gender of human voices. We hypothesized that jackdaws nesting close to humans may use available cues to trade their own safety against the safety of their chicks: while responding too late to an approaching threat could prove to be fatal for the mother (Amat & Masero, 2004; Martin & Réale, 2008; Miller et al., 2007; Wiebe & Martin, 1998), leaving unnecessarily could advertise the location of the nest (Martin, 2000). It is therefore likely to be beneficial for females that are incubating or brooding to attend carefully to acoustic cues from the outside world when deciding whether to flee the nest (e.g. Suzuki, 2015).

In our experiments, we took advantage of two key characteristics of our study population: (1) the population uses nestboxes located on a busy farm, where disturbance levels range from being high throughout the day to areas where the birds are seldom disturbed, and (2) the jackdaws exhibit markedly different responses to different people, ignoring the farmworkers, who have strong regional Cornish accents, but showing marked antipredator responses towards the Scottish researcher, G.E.M. (see Methods). We therefore compared the responses of brooding females to playbacks of the voices of G.E.M. and a familiar farmer, across different areas of the farm. To test whether the birds generalized from past experience and attended to the gender of the speaker, we also played back tracks containing unfamiliar male and female voices with Cornish and Scottish accents. Californian accents (male and female) served as unfamiliar controls. We predicted that, if the jackdaws attended to and generalized about accents, they would be more likely to either move to the entrance of the nestbox to investigate the voice or flee playback of the scientist's voice than that of the farmer, and more likely to investigate/flee playbacks of unfamiliar Scottish voices than unfamiliar Cornish voices. As jackdaws are highly neophobic (Greggor et al., 2016), we expected they would be more likely to investigate/flee playbacks of the novel Californian accent than those with a Cornish accent. We also predicted that these differences would be likely to be most pronounced in areas of high disturbance, as birds in these areas are likely to be exposed to a greater number and diversity of voices. Moreover, being excessively wary in high disturbance areas may prevent females from keeping their clutch or brood warm. For females that fled the nest, we also investigated whether the features of the voices that they had heard influenced their behaviour upon returning to the nest. We measured the time spent away and the hesitancy of the female to enter the nestbox, predicting that both the time spent away from the box and the delay to enter would be longer when the females had heard voices that might be perceived as more threatening (Scottish and Californian accents) than those with the local Cornish accent. Finally, we used long-term breeding records to examine whether local disturbance levels generate differences in reproductive success.

METHODS

Ethical Note

This study was conducted with approval from the University of Exeter Research Ethics Committee and follows the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research. Jackdaws were colour ringed for individual identification by qualified ringers licensed by the British Trust for Ornithology (permits C5746 and C5752), and work at the nest was performed under a U.K. Home Office licence (project licence 30/3261).

Study Site

The experiment was carried out at a jackdaw nestbox colony on a farm in Cornwall in southwest England (50.198666, −5.169346) between 7 and 17 May 2015. Nestboxes were located throughout the farmyard and fields immediately surrounding the farm buildings and had been in use by jackdaws since 2013. The farmyard has a footprint of ca. 18,000 m^2, containing 13 buildings and barns of various sizes. Certain parts of the farmyard are busy throughout the day, while some barns are only visited intermittently, and others not visited daily by the farmworkers. Based on his knowledge of the daily activities on the farm, G.E.M. classified each box as being in either a high, medium or low disturbance zone prior to the experiment starting (Appendix Fig. A1). These classifications were confirmed as being accurate by the farmers, based on their perception of the daily activities on the farm. All the nestboxes had cameras permanently fitted in the roof space of the box with cabling to ground level (from handykam.com), which allowed digital video recorders to be connected for filming within-box activity with minimal disturbance.

Experimental Treatments

Of the 31 boxes occupied on the site during 2015, 17 were used in the study. Each box was scheduled to be played eight tracks in total and heard two tracks per day. Each playback track lasted about 2 min, contained the same paragraph of text (from Magnusson, 2001; see Appendix) being read by individuals with a local Cornish, Scottish (Borders region) or Californian (San Francisco Bay region) accent. Playback amplitudes were standardized using the open-source software Audacity (www.audacity.com) so that the amplitude of the tracks at peak volume would match that of a person talking directly beneath the box, as determined by a Voltcraft SL-100 sound level meter. Two playbacks were of familiar male voices that the birds had extensive previous experience of around the farm. One was of the resident Cornish farmer, who lives and works on the farm, and ignores the jackdaws as he carries out his daily duties such as husbandry of the cattle and direction of farm operations. The other was of the Scottish researcher G.E.M., who regularly captures adult jackdaws for colour ringing, both at their nest sites and using walk-in traps, as well as climbing to nestboxes every 3 days to remove and weigh chicks. Both men are present at the site every day throughout the breeding season. Jackdaws foraging in the farmyard take flight far earlier when

G.E.M. approaches than the farmer, and birds will fly to and from their nestboxes when the farmer works beneath them but will not approach when G.E.M. is present (McIvor, n.d.). Both men had been present on the site in each of the breeding seasons from the initiation of the colony in 2013. G.E.M. was the primary researcher at this site, and prior to the experiment had been responsible for more than 97% of all visits to the nests. In 2014 two female research assistants made eight visits to different nests, but this was the only time that anyone other than G.E.M. climbed to a nest prior to the experiment. In addition to playbacks of the voices of these two men, the birds also received another six playbacks, one exemplar of each gender of each accent type (Cornish, Scottish and Californian), of people who had never visited the farm before. Fig. 1 provides an overview of the experimental design and predictions.

To ensure all birds had similar exposure to the voices of the known men, both individuals were present on the study site each day after the first clutch was laid. The farmer was asked to talk about his daily activities as he walked around the farm so that the birds would hear this in addition to the conversations he had with the other farm staff over the course of the day. To ensure each nesting female had a standardized level of exposure to the familiar Scottish voice in an aversive context, GEM climbed each box and examined the contents three times before they received his voice as an experimental treatment, which required the brooding female to leave the nest. The first of these visits occurred during the incubation phase, when the eggs were removed from the nest, photographed and replaced. The others happened following the hatching of the first egg, where the chick(s) was removed from the nest and weighed. As these tasks required the focus of the experimenter, which could have generated variation in both the volume and extent of the monologue produced, a 20 min recording of his voice reading a different chapter of Magnusson (2001) to that used in the experimental trials was played on a loop through a portable Pignose P7-100 amplifier that he carried with him while he worked.

Each box had a playback track of each gender and accent allocated at random before the experiment started, with the order of tracks randomized. Playbacks were made to the brooding female when she was in the in the nestbox alone. A FoxPro Fury speaker was placed on the ground under the nestbox at least 10 min prior to the experiment starting, and a digital video recorder was set to record the behaviour of the female within the nestbox. Playbacks were triggered and controlled using a wireless remote, held by an experimenter (G.E.M. or V.E.L.) who was in a hide nearby. Hides were set up at least 30 min before the experiment commenced. Each playback was performed to simulate a person walking past the box while talking, with the experimenter manually increasing the volume using the remote control by standardized increments every 5 s (timed with a stopwatch) over a total of 40 s. The playback was then held at the peak amplitude for 10 s before being gradually decreased in the same way until silent. At times where the average wind speed was forecast to be over 20 mph, the peak volume was raised by a standardized increment to maximize the probability of the female hearing the playback over the environmental noise ($N = 8$). Treatments typically began 3–5 days after the first egg hatched and ran on 4 consecutive days but ranged from day 1 to day 10 posthatching. In four cases there was a 1-day intermission in the sequence due to there being insufficient time to run all the trials scheduled that day.

The response of the female to the playback was filmed on two devices simultaneously. The roof-mounted cameras filmed the behaviour of the female in the nestbox continuously from the start of the experiment until the end. In addition, the experimenter controlled a Panasonic HC-X920 HD video camera from within the hide, which filmed the response from the outside of the box.

Familiarity	Gender	Accent	Prediction
Familiar	♂	🏴󠁧󠁢󠁳󠁣󠁴󠁿	!!!
Familiar	♂	▪▪	=
Unfamiliar	♀	🇺🇸	!
Unfamiliar	♂	🇺🇸	!!
Unfamiliar	♀	🏴󠁧󠁢󠁳󠁣󠁴󠁿	!
Unfamiliar	♂	🏴󠁧󠁢󠁳󠁣󠁴󠁿	!!
Unfamiliar	♀	▦	=
Unfamiliar	♂	▦	=

Figure 1. An outline of all experimental treatments, showing the predicted strength of fear response (from = to !!!) if birds attend to familiarity, gender and accent cues. Accents are denoted by the relevant flags as Cornish (▪▪), Scottish (🏴󠁧󠁢󠁳󠁣󠁴󠁿) and Californian (🇺🇸).
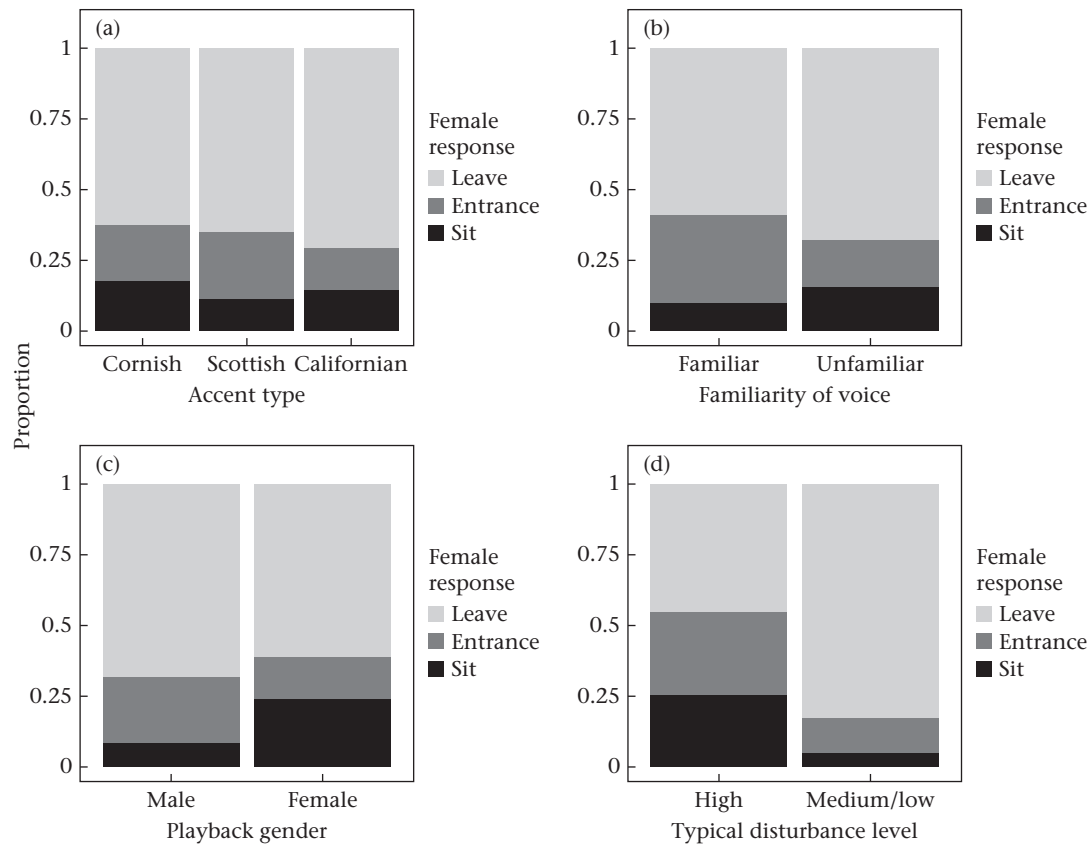
Figure 2. The proportion at which each level of the female's response was observed for the 110 playbacks at nestboxes, when the playback was of (a) a Cornish (N=40), Scottish (N=43) or Californian (N=27) accent, (b) a familiar (N=29) or unfamiliar (N=81) voice or (c) a male (N=69) or female (N=41) voice or (d) when the playback was made to a box in a farm zone that typically had high (N=51) or medium/low (N=59) levels of disturbance.

Playbacks were separated by a minimum of 14 min (median 22.5, range 14–67.5), and females had to have been in the box for 10 min prior to each playback.

Nine isolated nestboxes received presentations on their own. Where boxes had a close neighbour (within 5 m), we targeted the playback at a pair of boxes simultaneously, with the speaker located equidistant between them to ensure that each nestbox received each treatment only once. The speaker was never more than 4 m from a box, and in only one instance did the flight of one bird appear to trigger the flight response of the neighbour. Fourteen of the 17 boxes received all eight playbacks. The other three did not have a complete set, due to nest failure and/or insufficient time to test all boxes before the young no longer needed to be brooded by the female. Of the 14 boxes that received the full set of playbacks, seven had one or more playbacks that suffered technical issues (e.g. internal video feed failure or the female leaving the box with faecal sacs shortly after the start of the playback) that prevented us from getting full data for the box (12 cases in total). Overall, there were 110 successful trials across the 17 boxes.

Video Coding

Videos were coded using the software BORIS (Friard & Gamba, 2016) by G.E.M. The response of the female to each playback was scored as an ordinal variable with three levels: Nest, Entrance and Leave (see Supplementary videos). In the Nest outcome, females did not approach the entrance and remained on the nest. In the Entrance outcome, females left the cup and moved to the 8 cm diameter entry hole of the nestbox but did not fly away. In the Leave outcome, females left the nest and flew away from the nestbox. We recorded the time at which the female appeared to first notice the playback (typically a sharp movement of the head towards the entrance hole or leaving the nest cup), the time spent standing at the entrance and the time of departure if she left the box.

In the 72 cases where females left the nestbox in response to the playback, we also recorded their behaviour upon return in 53 trials. In the other 19 trials we were unable to record the female's behaviour upon her return to the box because of time constraints imposed by needing to run other trials at different nests. As a consequence of this, the data collected on females that had fled the second playback was biased towards females that had returned more quickly, and for this reason the playback number (first or second) for that day was included in the analyses of the females' behaviour upon their return to the nest. An additional case from the 53 observations was excluded because the male of the pair was perched at the entrance of the nestbox when the female returned, delaying her re-entry while she waited for him to feed the chicks and depart. We recorded the time that the female spent away from the box (seconds from take-off to landing on the perch), and the time between landing on the perch and the female entering the box (classed as the moment when her head and shoulders passed inside the entrance hole, blocking her view to the outside world), and whether she fed the chicks on return or returned immediately to brooding.

A subset of 18 of the 110 trials were coded blind to treatment by a second observer. All categorical/ordinal predictor scores matched. We also found the scores for the length of time the female spent away from the box, and how long she delayed at the entrance to be highly consistent between observers (time away: intraclass correlation coefficient, ICC (2) = 1, confidence interval, CI = 100,

Table 1
Model selection table for the variables influencing the response of the brooding female (Nest|Entrance|Leave) to the playback of the voice

Model	Intercept Nest|Entrance	Intercept Entrance|Leave	Accent	Familiar	No.	Gender	Zone	Accent*zone	Gender*zone	Familiar*zone	df	logLik	AICc	ΔAICc	Retained	Weight
ordin26	**−1.941**	**−0.088**				**Y**	**Y**				**7**	**−79.6**	**189.3**	**0.0**	**Yes**	**0.88**
ordin17	**−1.388**	**0.508**		**Y**		**Y**	**Y**				**8**	**−78.2**	**191.3**	**2.0**	**No**	
ordin34	**−1.349**	**0.349**					**Y**				**6**	**−83.4**	**192.4**	**3.0**	**Yes**	**0.06**
ordin32	**−3.381**	**−1.519**		**Y**							**6**	**−83.4**	**192.5**	**3.2**	**Yes**	**0.06**
ordin20	**−2.458**	**−0.569**			**−0.113**	**Y**	**Y**				**8**	**−79.2**	**193.2**	**3.9**	**No**	
ordin25	−2.883	−0.985		Y			Y				7	−82.1	194.5	5.2		
ordin6	−1.905	0.029		Y	−0.113	Y	Y				9	−77.9	195.3	6.0		
ordin10	−1.905	0.029		Y	−0.113	Y	Y				9	−77.9	195.3	6.0		

The lines in bold highlight the models that form the top set prior to implementation of a model nesting rule (Richards, 2007) that filtered out more complex models. Model weights are provided for those that were retained after the nesting rule was applied. When predictors are included in the model this is denoted by the letter Y, and numbers refer to the coefficients of numeric variables when these were included in the model, while * denotes interaction terms between variables. The intercept for each step in the response variable is provided. The variable names are as follows: familiar = whether the voice was that of someone who was familiar or unfamiliar; accent = the accent of the voice (Cornish|Californian|Scottish); no. = the playback number (1−8); gender = the gender of the voice played; zone = whether the nestbox was located in an area of the farm that had high disturbance levels or medium/low disturbance. logLik = log likelihood; AIC$_c$ = Akaike information criterion corrected for small sample size.

$P < 0.0001$; entrance delay: ICC (2) = 0.97, CI = 0.90−0.99, $P < 0.0001$). Other measures, in particular those based on calculations made from the point in time that the female was perceived to have first noticed the playback, were less repeatable, and so were not used in analyses (e.g. time between the female noticing and moving from the nest: ICC (2) = 0.76, CI = 0.35−0.91, $P = 0.003$).

Breeding Success

We monitored every nestbox at the farm each year between 2013 and 2021, with the same monitoring protocols being observed since 2014. The number of nestboxes used each year varied between nine in 2013 and 39 from 2017 onwards. Nests were checked daily from early April, providing exact laying, hatching and fledging dates. Each brood was ringed 26 days after the first egg of the clutch hatched. Nests were monitored until fledging using either the cameras fitted in the roof space of the boxes or pole-mounted inspection cameras, operated from the ground so as not to encourage premature fledging. Each box was checked daily in this way until the final chick fledged the nest.

Data Analysis

Data analysis was performed using R (R Core Team, 2016), and the packages ordinal (Christensen, 2015), MuMIn (Barton, 2018), lme4 (Bates et al. 2015), and lmerTest (Kuznetsova et al., 2017). We used a cumulative link mixed model (CLMM) with an ordinal response variable to test whether the response of the female to the playback (Nest/Entrance/Leave) was influenced by the playback accent (Cornish/Californian/Scottish), playback gender (male/female), playback familiarity (familiar/unfamiliar), playback number (1−8) and farm zone (high disturbance versus medium/low disturbance). Farm zone had been assigned to each box prior to the start of the experiment, and medium and low disturbance zones were pooled at the data exploration stage as both groups displayed identical patterns. Three interaction terms were also included in the maximal model, testing whether the response of the bird to the three features of the playback (accent, gender, familiarity) depended upon the farm zone in which the box was located. Three random effects were included in the models, with nestbox and playback ID being included to account for repeated measures, and the date on which the experiment took place was included to account for variation that might be attributed to wind and temperature. In total, 110 playbacks were analysed in the main analysis. We also performed a second subanalysis that compared the jackdaws' responses to the playbacks of the familiar voices only ($N = 29$), to determine whether they discriminated between familiar human voices associated with differing threat levels. This analysis contained the response to the playback (Nest/Entrance/Leave) as the response variable, with the threat level (scientist = threatening, farmer = nonthreatening), farm zone and playback number included as explanatory variables. An interaction term between farm zone and threat level was also included in the analysis, with nestbox and the date on which the experiment took place being included as random effects.

In cases where females left the nestbox in response to the playback, we also examined whether the length of time (s) that they spent away from the box was influenced by the playback accent, gender and familiarity. The number of days since the brood hatched was included to account for the reduction in urgency with which the female would need to return to the brood as they grew. Farm zone and whether the female fed on return, and whether it was the first or second playback of the day (due to the researchers needing to proceed on to the next location after trial 2, as mentioned above) were also included as explanatory variables,

Table 2
Summary of the top model ordin26 which received the most support in the model comparison in Table 1

	Estimate	SE	Lower	95% CI for odds ratio	Upper	Z	P
				Odds ratio			
Step							
Nest|Entrance	−1.941	0.731	0.15	0.67	2.98	−2.655	
Entrance|Leave	−0.088	0.689	0.88	4.26	20.53	−0.127	
Variable							
Playback gender							
Female	0						
Male	1.537	0.595	1.45	4.65	14.9	2.58	0.01
Zone							
High disturbance	0						
Medium/low disturbance	2.719	0.957	2.33	15.17	98.99	2.84	0.005

The values presented are from the CLMM model ordin26 which was highlighted in Table 1 as being the best candidate model for predicting which factors influenced the ordinal scored (Nest|Entrance|Leave) response of the brooding females to the playback simulating an approaching human voice. Bird ID, the playback heard and the date of the trial were included as random effects in the model, with the variance (SD) attributed to Bird ID being 1.934 (1.391) and that to Date 0.742 (0.861), while the variance of Playback ID was 0. CI: confidence interval.

while Box ID, Playback ID and date were again included as random effects. A single interaction term was included in this analysis, between farm zone and whether the female fed on return, as females nesting in the farmyard may need to travel further to forage and might spend longer away from the nest as a result. Finally, these same explanatory variables and random effects were also used in a third analysis, which examined factors influencing how long the females spent on the perch of the nestbox before entering. The time that the female had been away from the nest was also included as an explanatory variable in this analysis.

To analyse data from the experiment we used the dredge function of MuMIn (Barton, 2018) to compare models containing all biologically plausible combinations of explanatory variables. In our analysis of the response of the female to the playback, we limited the model to a maximum of five main effects and a single interaction to avoid overparameterization. Similarly, in our analyses of the behaviour of the females that fled the box upon their return, we limited the model to a maximum of five main effects or four main effects and an interaction term. We used an information theoretic approach to model comparison and selection, where models were compared and ranked based on their Akaike information criterion values corrected for small sample size (AICc) following the approach advocated by Richards et al. (2011). A penalty of $k = 4$ was applied for each additional parameter in the model, and models with a ΔAICc ≤ 4 of the model with the lowest AICc formed the 'top set'. We then applied the 'nesting rule' (Richards, 2007) to the top set, whereby models that were more complex models of nested models with a lower AICc value were removed from the top set so that unnecessarily complex models were not retained. The model weights were then calculated for the retained models, showing the level of support for each. We assessed model fit using standard

residual plot techniques, and response variables were square root transformed when necessary to meet model assumptions. Mixed models were also refitted as general linear models (GLMs) to allow application of a Breusch−Pagan test to check for heteroscedasticity in the data. Cook's distances were examined to check for influential cases (Cook's distance >1) but none were identified.

To evaluate whether differences in local levels of human disturbance influenced reproductive success we performed three further analyses using the breeding data from 2013 and 2021. In these, we used the number of chicks fledged (range 0−4), total mass of the brood at ringing, and the mean chick weight at ringing (i.e. total brood mass/number of nestlings) as our response variables, and the disturbance level of where the box was situated (high, medium or low) as our explanatory variable. Box was nested within year as a random effect, and both female and male ID were also included as random terms. To establish whether effects in the year of the experiment mirrored effects seen across years, we also repeated these analyses (as GLMs) using only data from 2015. Models with a Poisson error structure were checked for over- and underdispersion.

RESULTS

Response to Playbacks by Females on the Nest

The tendency of females to stay on the nest, go to the nestbox entrance or leave the nestbox in response to the playbacks simulating an approaching human was influenced by the gender of the voice heard and the typical level of disturbance in the area. There was no influence of either the accent or the familiarity of the voice on how the birds responded to the playback (Fig. 2a and b), nor was

Table 3
Summary of the only retained model from the model comparison table presented in Table A2

Variable	Estimate	SE	T	P
Intercept	25.75	2.693	9.312	<0.001
First or second playback				
First	0			
Second	−6.912	1.776	3.89	<0.001
Zone				
High disturbance	0			
Medium/low disturbance	−8.568	2.838	−3.019	0.01
Feed on return				
Yes	0			
No	−2.246	3.008	−0.727	0.477
Zone*Feed on return	0			
Medium/low*Yes	12.807	3.704	3.46	0.003

The values are from a GLMM model which tested which factors best explained the (square root transformed) length of time that the female spent away from the box if she left in response to the playback. The variance (SD) attributed to Box ID was 0.96 (0.98), that to Date was 3.19 (1.79) and that to Playback ID was 0.

there any evidence of habituation to the playbacks over time (Table 1). The best supported model from our analyses (ordin26, model weight = 0.88; Tables 1, 2) found that jackdaws were more likely to come to the entrance than remain on the nest and more likely to leave the box than remain at the entrance when the voice they heard was male than when it was female (Table 2, Fig. 2c). In addition, birds whose nestbox was in an area with medium/low levels of disturbance were more likely to come to the entrance than remain on the nest and more likely to leave the box than remain at the door than birds with nestboxes in areas of high disturbance (Table 2, Fig. 2d). Females remained in the box 54.9% of the time in high-disturbance areas ($N = 51$), but only 17% of the time when disturbance levels were lower ($N = 59$). The odds ratios of the predictors in the best-supported model indicate that females were 4.7 times more likely to respond to the playback with some form of investigation or flight behaviour when the voice was male rather than female, and 15.2 times more likely to do so if the nest was in an area of medium to low disturbance rather than high.

Our post-test check of the parallel slopes assumption (Harrell Jr, 2015) identified that the odds ratio for the gender of the playback did not apply equally across each step of our ordinal response. When considering only the birds that stayed in the nestbox (i.e. step 1 of the response variable) jackdaws were almost twice as likely to leave the nest cup and move to the entrance to investigate the sound of the approaching voice if that voice was male rather than female (37.5% for female voices, $N = 16$; 72.7% for male voices, $N = 22$). By contrast, when only birds that went to the entrance or left the nest were considered (step 2 of the response variable) 80.6% of the birds fled the nest when hearing a female voice ($N = 31$) compared to 74.6% when a male voice was played ($N = 63$). Our results therefore suggest that while the birds were more likely to investigate the sound of an approaching male voice than an approaching female voice, those that did leave the nest cup were just as likely to flee female voices as they were male voices.

When we compared data from playbacks containing familiar voices only, we found near-identical frequencies of Nest, Entrance and Leave responses to the 'nonthreatening' farmer or 'threatening' scientist (farmer: 2, 4, 9; scientist: 1, 5, 8, respectively | CLMM: estimate (SE) = 0.542 (1.049), $Z = 0.517$, $P = 0.6$). To confirm that the gender effect that we identified in the main analysis was robust,
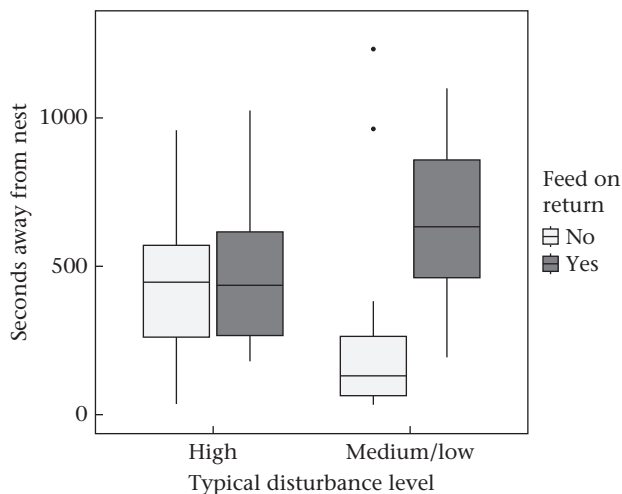
and not biased by responses to the voices of the familiar Cornish and Scottish men, we reanalysed the data set with the playbacks of the two familiar men excluded. This analysis returned an identical top model to that of the main analysis, with the gender of the playback (CLMM: estimate (SE) = 2.049 (0.800), $Z = 2.56$, $P = 0.01$) and the local disturbance levels (CLMM: estimate (SE) = 2.977 (1.095), $Z = 2.72$, $P = 0.007$) remaining important predictors of the jackdaws' responses. Similarly, as all playbacks of female voices were of unfamiliar voices, the gender effect we identified in our main analysis could potentially bias our interpretation of the responses to familiar/unfamiliar voices in the main analysis. We therefore repeated the analysis with a subset of data containing male voices only. This confirmed that there were no differences in response to familiar versus unfamiliar voices, with the local disturbance levels being the only variable retained in the best supported model (CLMM: estimate (SE) = 4.034 (1.685), $Z = 2.39$, $P = 0.02$).

Behaviour on Return to the Nest

Upon return to the nest, the behaviour of females that had fled the playbacks was primarily influenced by the typical disturbance

Figure 4. Box plots of the time that returning females spent at the entrance of the nestbox before entering, depending on whether (a) their nest was in an area of the farm with high or medium/low disturbance levels and (b) the female fed the chicks on her return to the box. Central bars represent the median values and boxes the interquartile range (IQR); whiskers extend to the maximum and minimum values excluding outlying points (those >(Q3 + 1.5×IQR)) which are denoted by circles.
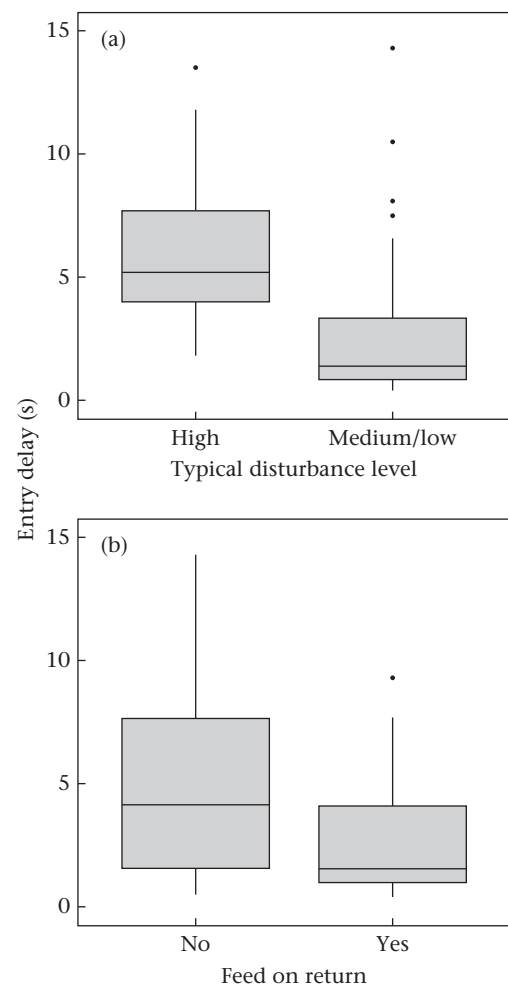

Figure 3. Box plots of the time that females that left the nestbox in response to the playbacks spent away from the nest, depending on whether their box was in an area of the farm with high or medium/low disturbance and whether they fed the chicks on their return to the box. Central bars represent the median values and boxes the interquartile range (IQR); whiskers extend to the maximum and minimum values excluding outlying points (those >(Q3 + 1.5×IQR)) which are denoted by circles.

levels around their nest, and whether they fed the chicks upon their return (Appendix Table A1). For the analysis investigating which factors influenced how long the females spent away from the box, only one model was retained once the nesting rule had been applied. This model contained an interaction between the local disturbance levels and whether the female fed the chicks upon returning to the box (Table 3, Fig. 3). Birds in medium/low-disturbance farm zones spent longer away from the nest when they fed upon their return than those that did not (GLMM: estimate (SE) = 10.589 (2.072), t = 5.11 P < 0.001; Fig. 3, Appendix Table A3). This contrasted with birds with nests in high-disturbance areas, where there was no difference in how long females spent away from the nest when they fed the chicks upon their return, compared to those that did not (GLMM: estimate (SE) = −5.492 (2.680), t = −2.05, P = 0.1; Fig. 3, Appendix Table A3). Return times were also significantly faster for the second playback than the first (Table 3), as the researchers needed to move on quickly to repeat the experiment at a different box. Playback accent, gender, familiarity or playback order had little effect on how long females spent away from their nest.

How long females remained on the perch before entering their nest was also influenced by disturbance zone and whether they returned with food (Appendix Fig. A2), but there was no influence of the interaction term in this analysis and it did not feature in the top set of models (Appendix Table A2). Females that nested in areas with high disturbance levels delayed entry for longer than those nesting in medium/low-disturbance zones (GLMM (model 257): estimate (SE) = −0.824 (0.358), t = −2.30, P = 0.04; Fig. 4a, Appendix Table A3). Females that fed their chicks on return to the nest also entered more quickly than those that did not (GLMM (model 5): estimate = −0.510 (0.196), t = −2.61, P = 0.01; Fig. 4b, Appendix Table A3). These outputs were obtained from the two models retained in the top set following the model selection procedure, which received similar levels of support (model 257 weight = 0.52, model 5 weight = 0.48; Appendix Table A2). There was no influence of the playback accent, gender or familiarity on how long the birds delayed before entering the nest, nor any influence of the number of playbacks previously heard, or whether it was the first or second playback that the birds had heard that day (Appendix Table A2).

Reproductive Success in Relation to Local Disturbance Levels

The number of chicks fledged from nests in areas of high disturbance was not different from those with either medium (GLMM: estimate (SE) = −0.114 (0.114), Z = −1.00, P = 0.32) or low levels of disturbance (GLMM: estimate (SE) = −0.175 (0.132), Z = −1.32, P = 0.19; Appendix Fig. A3a). We also found no difference in the mass of the brood at ringing when areas of high disturbance were compared with those with medium (GLMM: estimate (SE) = −22.70 (34.88), t = −0.65, P = 0.52) or low levels of disturbance (GLMM: estimate (SE) = −34.47 (38.81), t = −0.89, P = 0.38; Appendix Fig. A3b), nor when the average chick mass for each brood was compared (GLMM: high versus medium: estimate (SE) = 4.15 (4.85), t = 0.86, P = 0.40; high versus low: estimate (SE) = 6.05 (5.35), t = 1.13, P = 0.26; Appendix Fig. A3c). Analyses focusing only on breeding success data from 2015 (the year of the experiment) showed qualitatively the same results, with no differences across areas of differing disturbance (see Appendix Table A4).

DISCUSSION

Our results show that wild jackdaws' responses to human voices are sensitive to some aspects of vocal characteristics and show fine-scale spatial variation, reflecting levels of anthropogenic disturbance. Contrary to our predictions, we found no evidence to suggest that jackdaws associated specific familiar human voices with differing threat levels, discriminated between familiar and unfamiliar voices or generalized on the basis of regional accents. We did, however find that jackdaws were sensitive to the gender of the speaker, showing greater wariness upon hearing male than female voices. Responses to playbacks also depended on location: birds nesting in more disturbed areas were less likely to investigate and/or flee the playback and if they did flee the nestbox they typically showed higher levels of caution upon return than birds in areas of lower disturbance. Disturbance levels did not, however, influence breeding output, suggesting that plasticity in responses to local threat levels may enable jackdaws to maintain reproductive success despite variation in local conditions.

Corvids are known to discriminate between individual conspecifics' calls (Coomes et al., 2019; Kondo et al., 2012; Zandberg et al., 2014 etc) and carrion crows, *Corvus corone,* differentiate between familiar and unfamiliar human voices in captivity (Wascher et al., 2012). We had expected that jackdaws would discriminate between the voice of the researcher who regularly captured and disturbed them and that of a farmer who ignored them, but we found no evidence of differential responses by females either on the nest or upon returning to the nest. Similarly, we found no evidence of discrimination on the basis of familiarity. One possible explanation for this lack of discrimination is that under wild conditions the perceived risk associated with any approaching human voice is sufficiently high that it pays to be cautious regardless of the identity of the speaker. Similar findings have been reported in meerkats, *Suricata suricatta,* a species that lives under high predation risk, where individuals do not discriminate between the alarm calls of different group members even though the calls are acoustically distinct (Schibler & Manser, 2007). Alternatively, it may be that sensory/cognitive constraints limit the ability of jackdaws to discriminate between familiar individual humans on the basis of vocal cues alone (Carlson et al., 2020). Indeed, it is still not clear which cues humans use to distinguish speaker identity (Kriengwatana et al., 2015), and our abilities are sufficiently unreliable that they are not routinely accepted as evidence in courts of law (Latinus & Belin, 2011). It is possible that to discriminate accurately between familiar individuals, jackdaws may need to integrate visual information (e.g. facial features: Davidson et al., 2015; Lee et al. 2019) with acoustic cues (cf. Kondo et al., 2012). Some aspects of our experiment may also have made it particularly challenging for the jackdaws to discriminate between voices. First, whereas most previous research was conducted in controlled laboratory settings, wind conditions in the field vary from day to day (indicated by high variation associated with Date as a random term in our analyses) and playback sounds may have been attenuated by wind and other background noises. Second, we used a novel, long passage of text, whereas other studies have used between one and six words that the animals were already familiar and may have already formed associations with (Adachi et al., 2007; Dutour et al., 2021; Leroux et al., 2018; Proops & Mccomb, 2012; Saito & Shinozuka, 2013; Sliwa et al., 2011; Wascher et al., 2012). It is unclear whether the discrimination shown in these experiments would generalize to novel utterances by the same speaker (see Kriengwatana et al., 2015). For example, zebra finches, *Taeniopygia guttata,* differentiate human syllable sounds less accurately than conspecific song elements (Kriengwatana et al., 2016), suggesting that limitations in human voice recognition may arise quickly as the complexity and novelty of the sounds increase.

The lack of differentiation between the voices of familiar Scottish or Cornish men precludes investigation of the potential for generalization to novel, unfamiliar men with Scottish or Cornish

accents. However, the lack of differential responses towards Californian men indicates that jackdaws do not respond to human accents on the basis of familiarity. It remains to be tested whether jackdaws may be capable of distinguishing between broader-scale vocal characteristics such as languages (cf. elephants, McComb et al., 2014) as opposed to differing accents of the same language. Nevertheless, some aspects of human voices are clearly relevant, as jackdaws were almost twice as likely to leave the nest cup and move to the entrance if they heard a male than a female voice approaching. There are a number of potential explanations for this effect. One is that men typically speak at lower fundamental frequencies than women (Latinus & Belin, 2011), which reflects differences in fundamental frequency between male and female jackdaw vocalizations (Woods et al., 2018). These differences in frequency are likely to be discernible even in the presence of background noise, and lower frequencies may serve as indicators of size or threat level (Hardoiun et al., 2007; Hodges-Simeon et al., 2014; Ives et al., 2005; Puts et al., 2012; Reby et al., 2005) triggering greater wariness. Nevertheless, it is worth noting that jackdaws only show weaker responses to the higher-frequency alarm calls of conspecific females than males if the callers are unfamiliar, suggesting that experience plays an important role (Woods et al., 2018). In the current study, differential responses based on the gender of human voices may have also arisen, at least in part, through learning from past experiences. From the foundation of the colony in 2013, to the year of the experiment in 2015, female researchers had rarely climbed to the nests at this site (<3% of all visits), nor engaged in activities such as ringing that might lead the birds to view them as a threat. The birds may therefore have learned to recognize male voices as being potentially threatening by generalizing based upon their prior experiences with the researcher G.E.M. Moreover, as men are also far more likely than women to be involved in persecuting jackdaws (Baxter, 2019), it is possible that birds in our study population may have had negative experiences with men but not women outside of our nestbox colonies in the farmyard. Also note that the effect of speaker gender was apparent only when birds moved to the entrance, but not when they fled the nestbox altogether. This may be because, having taken action to investigate the sound but still being unable to identify the source, the birds may have left to collect more information (Dugatkin & Godin, 1992; Fishman, 1999).

Our results also show striking variation in responses over fine spatial scales, often as little as a few metres (Appendix Fig. A1). There was no evidence of habituation to our playbacks, and jackdaws nesting in areas of high human disturbance were consistently less likely to flee the nest in response to the playback than those that nested in areas with medium/low levels of disturbance. Females remained in the box 54.9% of the time in high-disturbance areas, but only 17% of the time when disturbance levels were lower. This effect could arise because individuals that are more tolerant of disturbance are more likely to occupy disturbed areas; (cf. Carrete & Tella, 2010; Holtmann et al., 2017; Martin & Reale, 2007; Rabdeau et al., 2019), but it is also likely to reflect behavioural plasticity. Indeed, studies on other species suggest that birds habituate to local disturbance levels after choosing a nest site (Conomy et al., 1998; Walker et al., 2006) and previous work on jackdaws highlights substantial plasticity in response to humans (Davidson et al., 2014; Lee et al. 2019; von Bayern & Emery, 2009). In our study population, jackdaws regularly move between areas with differing levels of disturbance during foraging and social interactions, so may benefit from adjusting their behaviour depending on their location. Moreover, our findings indicate that behaviour varied across contexts: among females that left the

nestbox in response to playbacks, subsequent behaviour was influenced not only by the level of disturbance in the area, but also by whether they had collected food for the chicks. Regardless of how long they had been away from the nestbox, females spent longer pausing on the perch before entering the nest if they were in areas of high disturbance and if they did not have food for the chicks. In low-disturbance areas the time spent away from the nest was longer when females returned with food than if they did not. This was not the case in high-disturbance areas, perhaps reflecting the need of females to spend time ensuring that any danger had passed before returning to the nest, regardless of whether they were bringing food. These results suggest that while jackdaws nesting in zones of high disturbance may be more resilient to this disturbance in general, individuals show plasticity in their nest attendance behaviour based on both perceived predation risk and context (Eggers et al., 2008; Goullaud et al., 2018; Krenhardt et al., 2021). Given that local levels of human disturbance did not influence the number of chicks fledged, the average nestling mass or the brood mass in our study, we suggest that this plasticity may be vital in allowing jackdaws to maintain reproductive success despite varying local conditions.

Although we found no evidence that jackdaws recognize the voices of different humans or generalize about the risk an approaching person might pose based on their accent, our results do highlight substantial sensitivity to cues of risk associated with humans near nest sites. Such sensitivity might help to explain why species such as jackdaws are able to thrive and breed successfully in the face of human-induced rapid environmental change. Further research is needed to understand how animals respond to the challenges of navigating human threats, and in particular to disentangle the effects of intrinsic individual differences and plasticity based on prior experience.

Author Contributions

G.E.M. and A.T. conceptualized the study, G.E.M. and V.E.L. collected the data, G.E.M. coded the videos and analysed the data, G.E.M. and A.T. wrote the manuscript with input from VEL. All authors gave their approval for publication.

Data Availability

Data and R scripts used for this study are available in the figshare repository https://10.6084/m9.figshare.19249673.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2022.08.006.

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Appendix

The passage of text used:

There was no time to lose. The Jacobites had learned a crucial lesson from previous campaigns — they had to take Edinburgh as quickly as possible and then, if there was to be any lasting success, march on London. There was no future in hanging around in the Highlands. The rebels waited only long enough for reinforcements to join them as word of the Raising of the Standard spread through the glens. Then they were up and away. They had the advantage of mobility, particularly because of the military roads which General Wade had constructed 25 years earlier to open up the central highlands from Lochaber to Inverness; these could also be used for opening up a way to the lowlands (Magnusson, 2001, p 590).

Table A1
Model selection table for the variables influencing how long the brooding female stayed away from the nest if she left in response to the playback

Model	Intercept	Day	Familiar	Feed	First/second	Accent	No.	Gender	Zone	Feed * zone	*df*	logLik	AICc	ΔAICc	Retained	Weight
397	25.075			Y	Y				Y	Y	9	−161.9	368.1	0.0	Yes	1
413	23.786			Y	Y	Y			Y	Y	11	−156.4	369.6	1.5	No	
461	26.045			Y	Y			Y	Y	Y	10	−160.0	370.5	2.4	No	
399	24.598	Y		Y	Y				Y	Y	10	−160.2	370.8	2.7	No	

All of the models displayed formed the 'top set' (ΔAICc<4) prior implementation of a model nesting rule (Richards, 2007) that filtered out those that should not be retained. Model weights are provided for only those that were retained after the nesting rule was applied. When factors are included in the model this is denoted by the letter Y, and numbers refer to the coefficients of numeric variables when these were included in the model, while * denotes interaction terms between variables. The intercept for each step in the response variable is provided. The variable names are as follows: day = the number of days since the first egg hatched, familiar = whether the voice was that of someone whose was familiar or unfamiliar, feed = whether the female fed the chicks on her return to the box (Y/N), first/second = whether the playback was the first or the second the female heard that day, accent = the accent of the voice (Cornish|Californian|Scottish), no. = the playback number (1−8) gender = the gender of the voice played and zone = whether the nestbox was located in an area of the farm that had high disturbance levels or medium/low disturbance. logLik = log likelihood; AICc = Akaike information criterion corrected for small sample size.

Table A2
Model selection tables for the variables influencing how long the returning female delayed at the entrance of the box before entering

Model	Intercept	No.	Familiar	First/second	Feed	Accent	Gender	Day	Zone	Feed *zone	*df*	logLik	AICc	ΔAICc	Retained	Weight
257	2.224								Y		6	−55.7	139.1	0.0	Yes	0.52
5	1.938				Y						6	−55.8	139.3	0.2	Yes	0.48
261	2.487				Y				Y		7	−53.4	139.9	0.7	No	

All models displayed formed the 'top set' (ΔAICc<4) prior implementation of a model nesting rule (Richards, 2007) that filtered out those that should not be retained. Model weights are provided for only those that were retained after the nesting rule was applied. When factors are included in the model this is denoted by the letter Y, and numbers refer to the coefficients of numeric variables when these were included in the model, while * denotes interaction terms between variables. The intercept for each step in the response variable is provided. The variable names are as follows: no. = the playback number (1−8), familiar = whether the voice was that of someone whose was familiar or unfamiliar, first/second = whether the playback was the first or second the female heard that day, feed = whether the female fed the chicks on her return to the box (Y/N), accent = the accent of the voice (Cornish|Californian|Scottish), day = the number of days since the first egg hatched, gender = the gender of the voice played and zone = whether the nestbox was located in an area of the farm that had high disturbance levels or medium/low disturbance. logLik = log likelihood; AICc = Akaike information criterion corrected for small sample size.

Table A3
Descriptive statistics for the analyses of factors influencing the length of time that females that left the box spent away from the nest, and how long they delayed entering the box when they returned

	Zone	Feed on return	Mean	SE	SD	Median	*N*
Seconds away from nest	High disturbance	Yes	471.7	82.9	262.3	435	10
	High disturbance	No	429.7	104.9	296.6	446.5	8
	Medium/low disturbance	Yes	649.6	61.3	260.1	634	18
	Medium/low disturbance	No	253.4	81.8	337.4	130	17
Entrance delay (s)	High disturbance	Yes	5.63	0.72	2.27	5.95	10
	High disturbance	No	6.51	1.78	4.71	4.30	7
	Medium/low disturbance	Yes	1.26	0.16	0.68	1.25	18
	Medium/low disturbance	No	4.38	0.99	4.06	3.30	17

The data are broken into subsets based on the key explanatory variables: whether the nestbox was in a farm zone with high or medium/low disturbance levels and whether the female fed the chicks upon her return.

Table A4
Output from the analyses of reproductive success for birds nesting in different areas of the farm, using data from 2015 only

| Variable	Estimate	SE	Z	P
Number of chicks fledged				
Intercept	0.587	0.236	2.49	0.01
Disturbance level				
High	0	0		
Medium	0.216	0.3	0.72	0.47
Low	0.277	0.329	0.84	0.4
Brood mass (g)				
Intercept	556.53	60.41	9.21	<0.001
Disturbance level				
High	0	0		
Medium	27.36	77.28	0.35	0.73
Low	−0.92	85.44	−0.01	0.99
Mean chick mass (g)				
Intercept	227.05	7.62	29.80	<0.001
Disturbance level				
High	0	0		
Medium	−4.01	9.75	−0.41	0.69
Low	−13.54	10.78	−1.26	0.22

Figure A1. A schematic layout of the farm, highlighting the location of barns, occupied houses and the typical disturbance levels of different areas of the farm. Nestbox locations are denoted by circles and are labelled with their identifying code.
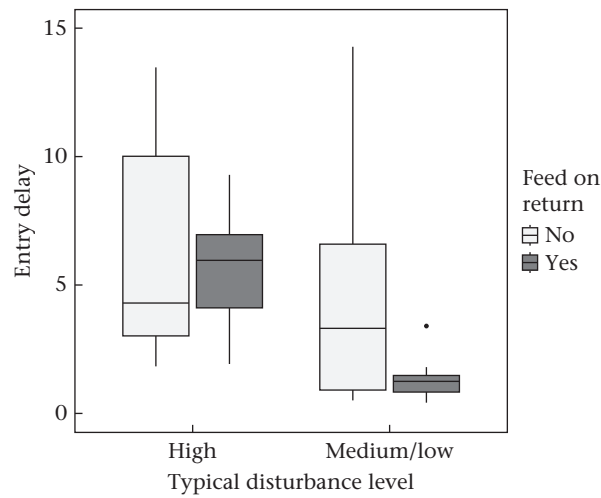
Figure A2. Box plots of the time that returning females spent at the entrance of the nestbox before entering, depending on whether their box was in an area of the farm with high or medium/low disturbance and whether they fed the chicks on their return to the box. Central bars represent the median values and boxes the interquartile range (IQR); whiskers extend to the maximum and minimum values excluding outlying points (those >(Q3 + 1.5×IQR)) which are denoted by circles.
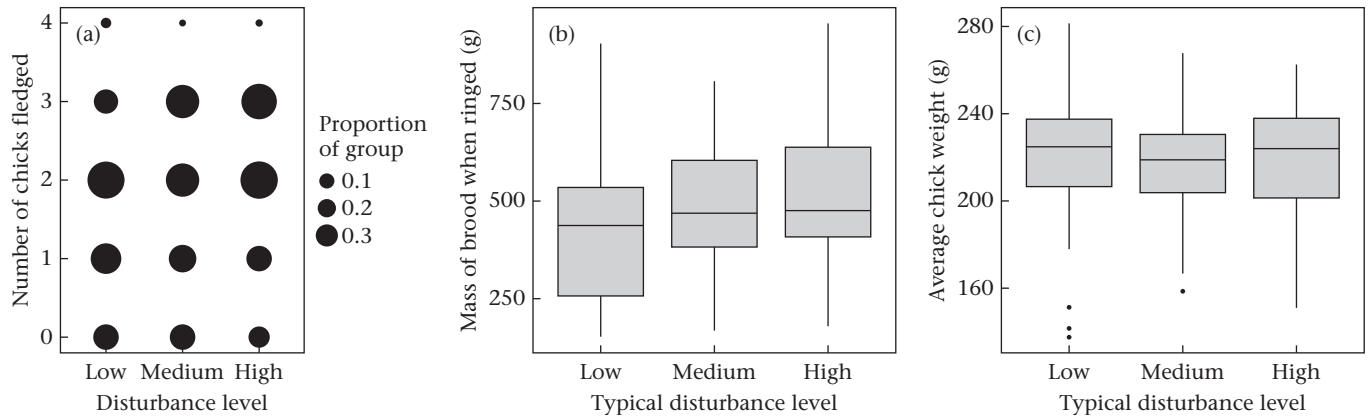
Figure A3. Plots displaying the variation in various measures of reproductive output, across areas of the farm with different levels of disturbance between 2013 and 2021. (a) The frequency at which jackdaws on the farm fledged different numbers of chicks per nesting attempt, with proportions calculated within each disturbance level (N for each: low = 75, medium = 119, high = 92). (b) The total mass (g) of broods at each site when the broods were ringed 26 days after the first egg of the clutch hatched. (c) The mean chick weight (g) within each brood when they were ringed at day 26. Central bars represent the median values and boxes the interquartile range (IQR); whiskers extend to the maximum and minimum values excluding outlying points (those >(Q3 + 1.5×IQR)) which are denoted by circles.