



Great tits, *Parus major*, increase vigilance time and reduce feeding effort during peaks of aircraft noise



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Antipredator vigilance may take a significant amount of time, leading to a trade-off between foraging and vigilance. Studies show that this trade-off is modulated by the perception of predation risk faced by individuals. Anthropogenic noise can disturb acoustic communication by masking both direct predator detection and the perception of conspecific alarm calls. We would expect a decrease in acoustic awareness to be compensated for by an increase in visual awareness. Thus, we tested whether increases in noise produced by commercial aircraft reduced foraging effort and increased vigilance time in great tits. We videotaped birds feeding on peanut feeders in the vicinity of Barajas airport (Madrid, Spain), and measured behavioural sequences before, during and after aircraft sound events. Our results show that, when aircraft noise peaked, the proportion of time devoted to vigilance was maximal, while that devoted to feeding was minimal. As a result, the ratio between vigilance and foraging was at its maximum when aircraft noise was loudest, being almost double that during baseline levels. The duration of vigilance episodes was strongly correlated with noise levels. Also, the duration of feeding bouts was at its lowest during the peak of noise, and increased after this period. We suggest that these behavioural modifications help foragers visually detect possible predators in those situations in which high levels of noise hamper sound perception. Our study suggests that behavioural plasticity could contribute to the resilience of avian populations exposed to anthropogenic disturbance.

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One of the most conspicuous forms of human disturbance for wild animals is noise (Barber, Crooks, & Fristrup, 2010). Anthropogenic noise is created by a variety of human activities, such as factories, construction or traffic. Recent literature in a wide variety of organisms has shown that the effects of noise can be detected in perturbations of behaviour, physiology and community ecology (Francis, Kleist, Ortega, & Cruz, 2012; Slabbekoorn et al., 2010). In the case of birds, a group characterized by a strong reliance on acoustic communication, noise limits the transmission and perception of signals (Brumm & Slabbekoorn, 2005; Gil & Brumm, 2014; Nemeth & Brumm, 2010), and can thus influence basic reproductive processes such as mate choice or territory defence (Francis, Ortega, & Cruz, 2009; Habib, Bayne, & Boutin, 2007; Halfwerk, Holleman, Lessells, & Slabbekoorn, 2011).

Birds also use acoustic signals to communicate in social situations. Social calls and alarm calls are produced by many species

while foraging in groups or in pairs, and are used to warn conspecifics about the presence of predators (Alatalo & Helle, 1990; Evans, Evans, & Marler, 1993). Additionally, other heterospecifics can profit from that information by eavesdropping on alarm calls (Hetrick & Sieving, 2012). Studies show that in many species there is a fine gradation in the information that is conveyed by these calls, including the immediate action to be taken by the signalling individual (Leavesley & Magrath, 2005), or an indication of the size of the predator that has been detected (Templeton, Greene, & Davis, 2005). If animals are subject to high levels of noise, social calls may go undetected (Klump, 1996), as shown in a captive study with starlings, *Sturnus vulgaris*, in which the perception of alarm calls was impaired when noise was being broadcast (Mahjoub, Hinders, & Swaddle, 2015).

Numerous studies show that, during foraging, the balance between the time devoted to foraging and vigilance is affected by the risk experienced by the individual (Beauchamp, 2015; Lima, 1998). Thus, animals increase vigilance and reduce foraging when they are alone or in small groups (Roberts, 1996), when predators approach (Creel, Winnie, Christianson, & Liley, 2008) or when the perception of predators is impaired by the landscape (Bednekoff & Blumstein,

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2009). Increased noise levels in this context would limit the detection of predators because alarm calls should become more difficult to perceive (Mahjoub et al., 2015), and also because direct detection of predators by acoustic cues would be affected (Chan, Giraldo-Perez, Smith, & Blumstein, 2010).

In general, data suggest that noise decreases auditory awareness, forcing animals to rely on visual cues (Barber et al., 2010; Chan & Blumstein, 2011). Most studies on this subject have so far been conducted in mammals. Thus, California ground squirrels, *Spermophilus beecheyi*, living in areas exposed to wind-turbine noise were more alert than those living in control areas (Rabin, Coss, & Owings, 2006), and pronghorn, *Antilocapra americana*, foraging close to roads were more vigilant and fed less than animals foraging far from roads (Gavin & Komers, 2006). A study in laboratory rats, *Rattus norvegicus*, has shown that individuals scan more often and eat faster when loud noise is being played back (Krebs, Weyers, Macht, Weijers, & Janke, 1997). Other recent studies in mammals suggest a close link between vigilance and noise disturbance (Larsen, Sherwen, & Rault, 2014; Shannon, Angeloni, Wittemyer, Fristrup, & Crooks, 2014). A study in birds, conducted with captive chaffinches, *Fringilla coelebs*, has shown that feeding bouts are shorter when noise is played back than during silence (Quinn, Whittingham, Butler, & Cresswell, 2006). However, further experimental data from wild birds are required to test whether a decrease in acoustic awareness because of noise is compensated for by an increase in visual awareness.

Noise produced by commercial aircraft is perceived as the loudest source of noise typically experienced by humans (Smith, 1989), and numerous national and international laws have been established to regulate its effects. We have previously shown that birds living near airports advance their dawn chorus, thus reducing the overlap with aircraft noise during their morning song periods (Gil, Honarmand, Pascual, Pérez-Mena, & Macías-García, 2015). This suggests that habitats exposed to aircraft noise are a good system in which to study the effects of noise in animal behaviour. Since animals are exposed continuously to this type of noise, it cannot be considered a novel or surprising stimulus (Quinn et al., 2006). In this study we took advantage of the loud noise created by taking-off and landing aircraft to analyse how feeding and vigilance behaviours are affected in great tits while they feed on peanut feeders.

METHODS

Study Area and Field Methods

The study was conducted during the winter of 2013–2014 in a zone adjacent to the final runway of Madrid Barajas airport (municipality of Paracuellos del Jarama). The study area is a riverine woodland, along the Jarama river, dominated by poplars, ash and willows, and contains a rich avian community, including sparrowhawks, *Accipiter nisus*, specialized avian predators. The river runs on the side of the outermost fence of the runway, in such a way that many planes fly very close to the forest after take-off or before landing. Thus, peaks of noise can reach very high levels (typically >85 dB, J. I. Klett-Mingo, I. Pavón & D. Gil, personal observations) when planes pass nearby (see the [Supplementary Material: Video S1](#)). The study area is delimited by the Lden isophones 65 and 70 dB (Lden is a noise indicator widely used to describe the annoyance caused by exposure to noise on people; Directive 2002/49/EC of the European Parliament and of the Council of 25 June 2002 relating to the assessment and management of environmental noise), according to the publically available 2013 Barajas airport noise map (Aena, 2013). Barajas ranked 27th in the 2014 list of busiest airports in the world (<http://www.aci.aero>), and flights

are very frequent over the study area (one plane every 2–5 min, J. I. Klett-Mingo, I. Pavón & D. Gil, personal observations).

In October 2013, we placed six cylindrical peanut feeders in the area (see [Supplementary Material: Video S1](#)), about 200 m apart. Feeders were modified by means of a thin plywood sheet, so that birds were forced to eat from one side of the feeder, thus providing a suitable view for the video recordings. We visited the feeders weekly, and filled them with seeds when necessary. Birds took some time to start using the feeders but, after a few weeks, peanuts were quickly being consumed. We chose peanuts instead of small seeds because birds need to peck at them through the wire mesh to break the nuts, and eat the fragments while sitting on the feeder, thus increasing manipulation time with respect to other smaller seeds that can be collected and manipulated elsewhere (Krams, 1998).

We placed digital video cameras (Sony Handicam 290) on tripods 5–10 m from the feeders and recorded continuously for periods of 4–5 h during January–February 2014. Recordings were conducted in the early morning (from 0800 to 0900 onwards). A total of 94 h of recordings were obtained from 7 recording days. Video cameras were zoomed on the feeder (8×) and recording volumes were set in all cameras at the same low level. Despite this measure, sound recordings were saturated during events of aircraft noise, and thus we were not able to calibrate each individual recording, and had to rely on post hoc average noise levels per period.

Behavioural Analyses

Recordings (mpg files) were transferred to a computer and we extracted the sound into wav files. We first identified instances of high noise levels by visually scanning wav files (using Raven Pro, Cornell Lab of Ornithology, Ithaca, NY, U.S.A.). These occurrences were visually inspected using a media-player (VLC software, <http://www.videolan.org>) to discard those in which the noise peak was produced by wind or other artefacts, and to select those recordings in which a single bird was feeding before and after the aircraft noise event. We avoided recordings in which more than one bird was feeding at the same time, or those in which fights, chases or aggressive displays were recorded. Most suitable recordings contained great tits, and we discarded those with less frequent species (e.g. blue tits, *Cyanistes caeruleus*, nuthatches, *Sitta europea*, great spotted woodpeckers, *Dendrocopos major* or robins, *Erithacus rubecula*). Using the video-editing software Movie-Maker (Microsoft Windows, Washington, U.S.A.) we tagged on the video files the sound saturation section corresponding to the passage of the plane, which had a mean duration of 10.2 s (SD = 2.2). Around this section, we labelled two sections of 10 s before the noise event and two further sections of 10 s after the noise, thus establishing five different time sections per observation. For some birds we could not obtain 10 s of observation in all periods, because the bird left before the end of the last period or did not stay for the whole 20 s before the noise event. We discarded periods that lasted less than 5 s or more than 15 s, and added duration as a covariate in all analyses.

Once the final set of available recordings was selected ($N = 122$), one of us (J.I.K.) visually scanned the recordings at half speed noting the occurrence of two types of behaviour: (1) feeding (time while the bird was pecking peanuts with its head down); and (2) vigilance (including time in which the bird had its head up, often scanning). Behavioural categories were recorded with the software Etholog (Otoni, 2000). During visual inspection, the observer switched off the sound. We calculated the average duration of feeding and vigilance episodes per period, as well as the number of episodes of each of these behaviours. In addition, we computed the

percentage of time spent feeding and in vigilance per period, as well as the ratio of vigilance to feeding time, a useful indication of alertness in foraging birds (Fernandez-Juricic & Telleria, 2000). We discarded recordings in which the bird was not feeding steadily in the first part of the sequence, rejecting those in which time devoted to vigilance was two or more times that devoted to feeding. This was done to avoid birds that were involved in some other behaviour than feeding, and whose behaviour was not stable.

Within each camera/recording site we strived to individually identify birds by looking at differences in plumage. This could be done for the majority of birds (14 males and nine females) but some were unidentified and a category of unidentified birds was created for each feeder. These categories were used as a random factor in the analysis to avoid pseudoreplication. We supplemented this analysis with a more conservative approach that does not rely on visual individual identification, categorizing all individuals according to the feeder and sex (males, females and unsexed individuals).

Evaluation of Noise Levels

Although we could not calibrate the sound levels of each individual recording due to sound signal saturation, we measured noise in a sample of aircraft noise sound signals, recorded in the same place and using the same procedure as in the behavioural observations. We videotaped an operating sound meter (CESVA SC-2c, fast mode: L_{AF}) during 22 instances of peaks of plane noise and visually annotated noise levels in each second of the whole time sequence. This allowed us to plot behavioural observations with respect to the typical sequence of average noise levels produced by the aircraft.

Statistics

Noise levels, mean feeding and vigilance durations, vigilance and feeding proportions and the ratio between vigilance and feeding were Box–Cox transformed to approximate normality by means of the function `boxcoxnc` (package 'AID') in R (R Core Team, 2015). These measurements were analysed by mixed linear models taking individual or sex-site categories as random factors using `lmer` (package 'lme4') in R. Count measurements (number of feeding or vigilance episodes) were analysed by means of generalized linear mixed models, using a Poisson distribution with the function `glmer`. Initial models contained the observation period as a factor and duration as covariate. The latter was dropped if its effect was not significant. Post hoc Tukey analyses between groups were performed using 'lsmeans' and 'multcomp' packages. Residuals were inspected for normality and homoscedasticity for linear models and overdispersion for Poisson models.

We had a priori expectations about the relationship between changes in noise levels and behaviour, namely that vigilance (proportion of time and duration of episodes) as well as the vigilance/feeding ratio should increase with increasing noise, whereas feeding duration and proportion of time feeding should show the opposite pattern. To test these hypotheses, we transformed the standard nondirectional heterogeneity tests (linear models) into ordered heterogeneity tests (Rice & Gaines, 1994). To this end, we calculated Spearman correlations between the ranks of periods in noise levels and the ranks observed in behavioural measurements. This correlation is combined with the P value of the linear model to produce a statistic (r_sPc) that measures to what extent the differences between groups match the ordered predictions, using two-tailed probability expectations (Rice & Gaines, 1994).

Ethical Note

The study was observational and we did not handle birds at any time. We made sure that the distance between the camera and the feeders did not disturb the birds. To this end, we ran a preliminary pilot study (with three feeders) in which we observed the birds returning to feed within 30 m of placing the camera, so we concluded that the procedure implied minimum disturbance to the birds.

RESULTS

Noise levels increased from 50.7 dB(A) 20 s before the aircraft passed to a peak of 76.8 dB(A) at its loudest moment (Fig. 1a). A mixed general linear model with repeated measures (10 observations per period) showed that there were strong differences between periods in noise levels ($X^2 = 3350.9$, $P < 0.001$). Post hoc analyses showed that all periods differed significantly from each other (see Fig. 1a for details). Incoming flight noise levels increased very steeply, whereas rearwards noise propagation, after the maximum burst of noise, had a slower decay (Fig. 1a).

There were significant differences between periods in both the proportion of time spent feeding and the proportion of time in vigilance (both models: $X^2 > 26.9$, $P < 0.001$). Since both measurements are complementary, the results are basically identical. The proportion of time in vigilance was highest during the maximum aircraft noise level (Fig. 1c) and, correspondingly, the proportion of time feeding was lowest (Fig. 1d; see Fig. 1c, d for post hoc tests). Results remained almost identical in all analyses regardless of whether individual birds or sex-specific categories per feeder were used as a random factor (data not shown). In the remainder of the analyses we refer to models that used visual identification of birds as a random factor.

There were significant differences between periods in the vigilance/feeding ratio ($X^2 = 28.7$, $P < 0.001$). Post hoc analyses showed that the vigilance/feeding ratio during the period of the aircraft noise burst was statistically higher than during the other periods (all $|z| > 2.7$, $P < 0.05$), except the first period ($z = -2.27$, $P = 0.15$). In absolute terms, quiet periods (e.g. 20 s before and after the noise event) were characterized by an even division of time between vigilance and feeding (ratios close to 1), whereas birds almost doubled their vigilance during the periods of maximum aircraft noise levels (Fig. 1b).

The duration of vigilance episodes changed between periods ($X^2 = 68.2$, $P < 0.001$), closely tracking noise levels (Fig. 1e). Despite this heterogeneity, post hoc analysis revealed few differences between particular groups (see Fig. 1e for post hoc tests). The duration of feeding episodes differed between periods ($X^2 = 68.2$, $P < 0.001$), increasing from the first to the last period (Fig. 1f). The episode of highest plane noise was characterized by the lowest duration of all (see Fig. 1f for post hoc tests). Number of vigilance and feeding episodes decreased progressively from the first to the last period in a similar fashion (vigilance bouts: $\chi^2 = 11.25$, $P = 0.023$, Fig. 1g; feeding bouts: $\chi^2 = 14.02$, $P = 0.007$, Fig. 1h), both correcting for duration of the period (both $\chi^2 > 42.5$, $P < 0.001$; see Fig. 1g, h for post hoc tests).

We tested the hypothesis that differences in behaviour were related to changes in noise levels. To this end we used the ordered heterogeneity test, in which the correlation between the ranking of periods in noise levels and the ranking of periods in behaviour is taken into account as an a priori expectation. We found that the duration of vigilance episodes was strongly and positively related to differences in noise levels ($r_sPc = 0.99$; $P = 0.001$). Neither the vigilance/feeding ratio, the duration of feeding episodes nor the proportion of time in vigilance or feeding was linearly correlated

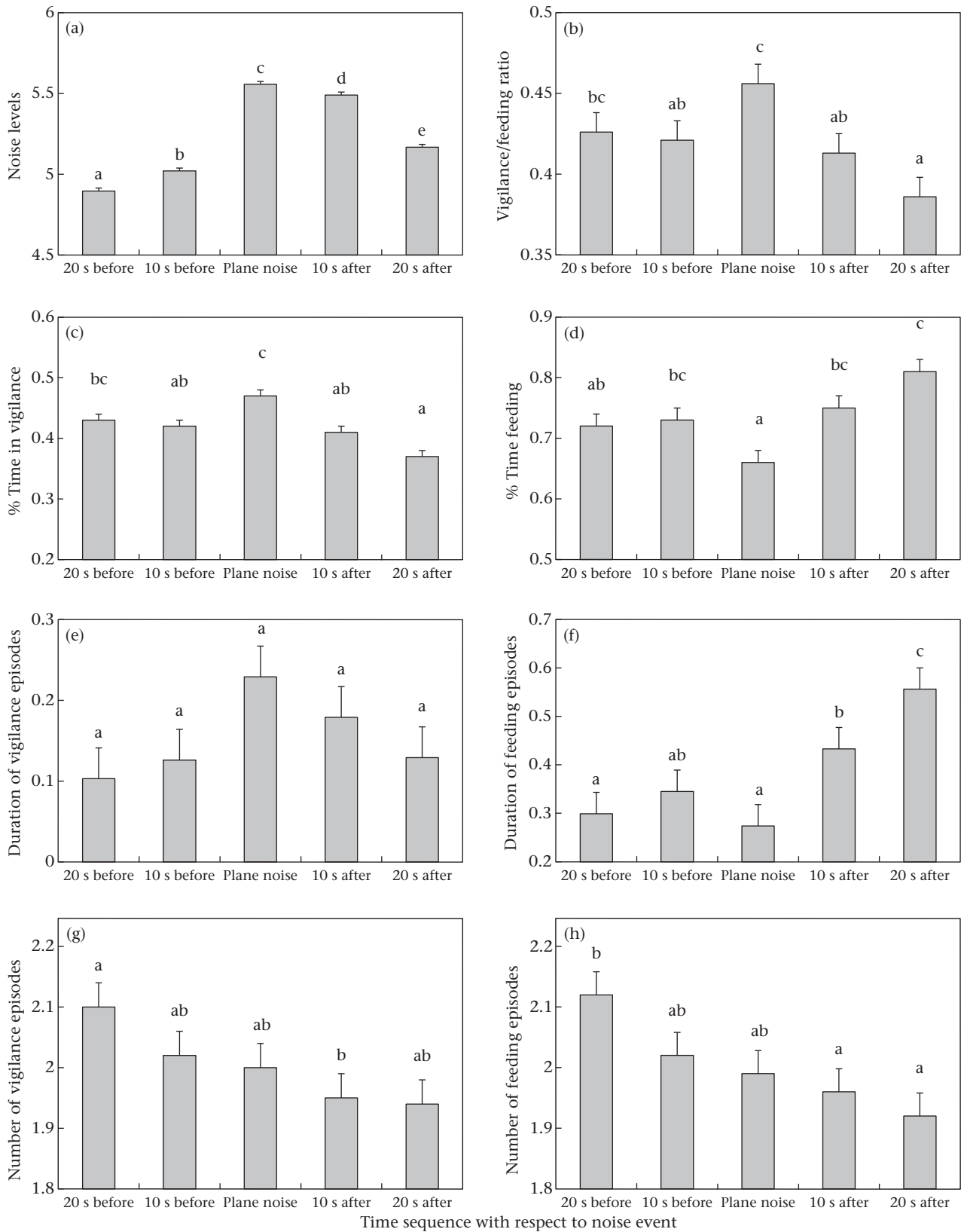


Figure 1. Least squared means (± 1 SE) of noise and the different behavioural categories divided by period with respect to maximum noise level produced by aircraft operation. (a) Noise level; (b) vigilance/feeding ratio; (c) % time spent vigilant; (d) % time spent feeding; (e) duration of vigilance episodes; (f) duration of feeding episodes; (g) number of vigilance episodes; (h) number of feeding episodes. Means represent estimates from the model on transformed data, taking into account other covariates and random effects. Axes have been zoomed individually per variable for clarity. Lowercase letters represent homogeneous groups after Tukey post hoc tests ($P < 0.05$). See text for statistics.

with differences in noise levels between periods (all $I_r P_{Cl} < 0.30$, $P > 0.15$).

DISCUSSION

Many studies show important reductions in fitness in avian communities affected by anthropogenic noise (Francis et al., 2009; Halfwerk et al., 2011; McClure, Ware, Carlisle, Kaltenecker, & Barber, 2013; Reijnen, Foppen, Terbraak, & Thissen, 1995). However, it is often difficult to distinguish between the multitude of factors that are brought about by human disturbance and pinpoint the precise mechanism by which noise impairs fitness. Several possibilities have been suggested, such as increases in signalling costs (Halfwerk et al., 2011), reduction in optimal parenting because of impaired parent–offspring communication (Schroeder, Nakagawa, Cleasby, & Burke, 2012) and increased predation (Francis et al., 2009).

Our study contributes with field-based evidence to the hypothesis that foraging and predation detection are compromised in noisy conditions (Chan & Blumstein, 2011), showing that foraging great tits reduce their feeding effort and increase vigilance when exposed to aircraft noise. This could impose important fitness costs in several ways. First, increased foraging costs would imply a reduction in habitat profitability in noisy areas, which could represent a constraining factor particularly in winter. Second, noise while foraging could increase stress, i.e. glucocorticoid levels (Bonier, 2012), and affect health and immunocompetence (Sapolsky, Romero, & Munck, 2000). Third, increased vigilance may not fully compensate for the higher predation risk under noisy conditions, and thus these bird populations could be subject to higher predation rates (Francis et al., 2009). Although the birds in our study were away from the runway of the airport, it could be argued that some could have been affected by the sight of the plane. However, plane sound and visual stimuli do not match in time, and the close match between vigilance ratio and plane sound levels suggests that birds were responding to noise disturbance.

Previous studies have shown that the capacity of birds to detect peripheral visual stimuli is reduced while individuals forage with their heads down (Lima & Bednekoff, 1999), particularly so if the feeding task is cognitively demanding (Dukas & Kamil, 2000). In addition, numerous theoretical and empirical studies show that noise impairs the detection of vocal signals (Klump, 1996; Mahjoub et al., 2015; Nemeth & Brumm, 2010), and thus it seems logical to assume that birds would be less likely to detect calls when noise is high. On the other hand, this lack of detection may be due to either sheer acoustic masking (Klump, 1996) or an increase in cognitive demands leading to limited attention and distraction (Chan et al., 2010; Dukas & Kamil, 2000).

Since our study was conducted on wild animals foraging in a situation in which noise events occur continuously, we can discount the effect we found being due to noise representing a novel stimulus (cf. Krebs et al., 1997). Our results are partly in agreement with a previous study in captive chaffinches (Quinn et al., 2006), in which birds were found to spend shorter head-down periods when noise was being broadcast than in quiet conditions, whereas the duration of head-ups was similar. This pattern is predicted by previous studies showing that predator detection is increased only by reducing the amount of head-down time and not by longer vigilance (Cresswell, 1994). In our study, feeding episodes were only marginally shorter than baseline levels, and the key modification caused by noise was an increase in the duration of vigilance episodes.

Although the average level of vigilance was higher during the maximum noise level produced by aircraft, additional variation within this period that we could not control renders our results

conservative. First, since our cameras could not measure the precise level of noise during the peak of the plane passage, it is likely that variation in these levels may introduce some heterogeneity in the response. Second, we did not have information on numerous characteristics of the focal individual that may affect the trade-off between foraging and antipredator behaviour, including hunger (Bachman, 1993) and dominance (Favati, Leimar, Radesater, & Lovlie, 2014; Krams, 1998).

It is well known by noise engineers that noise that is radiated rearwards, after plane passage, fades out more slowly than the increase in noise that is experienced when the plane arrives (Smith, 1989). We found the same pattern in relation to noise, and bird behaviour closely tracked these differences, suggesting that birds adjust the length of vigilance to absolute noise levels.

Several studies had suggested links between human disturbance and bird reproductive success (Bautista et al., 2004; Halfwerk et al., 2011), and the direct link between noise per se and bird behaviour has been experimentally demonstrated in recent studies (Francis et al., 2009; McClure et al., 2013). In general, birds in disturbed sites increase vigilance and reduce feeding (Fernandez-Juricic & Telleria, 2000). The risk disturbance hypothesis proposes that animals exposed to disturbance by humans will show behaviour typically expressed by individuals exposed to risky situations, such as antipredator behaviour, increased stress levels, flight responses and increased vigilance (Frid & Dill, 2002). Our study contributes with additional evidence to this general hypothesis, although in this case we were able to show that increased noise and no other type of human disturbance was responsible for the modification of behaviour that we detected (Chan & Blumstein, 2011). Furthermore, since we did not introduce any novel stimuli, and we worked with a wild species, the increase in vigilance that we found is unlikely to be an anomalous novel response, but rather a persistent behavioural modification.

Effects on foraging behaviour can have far-ranging implications for the avian community (Francis et al., 2012). Although increases in vigilance during feeding may help birds survive in habitats subject to high levels of anthropogenic noise, we still do not know the costs of this behavioural modification, particularly in terms of reduced intake rate and increased stress levels (Chan & Blumstein, 2011).

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.02.021>.

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