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Article

Anthropogenic noise reduces avian feeding efficiency and increases vigilance along an urban–rural gradient regardless of species' tolerances to urbanisation

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Anthropogenic noise can adversely impact urban bird populations by interfering with vocal communication. Less research has addressed if anthropogenic noise masks the adventitious sounds that birds use to aid predator detection, which may lead to increased vigilance and reduced feeding efficiency. We test this hypothesis using a controlled playback experiment along an urban–rural gradient in Sheffield (UK). We also test the related predictions that anthropogenic noise has the greatest impacts on vigilance and feeding efficiency in rural populations, and on species that are more sensitive to urbanisation. We focus on six passerines, in order from most to least urbanised (based on how urbanisation influences population densities): blue tit *Cyanistes caeruleus*, robin *Erithacus rubecula*, great tit *Parus major*, chaffinch *Fringilla coelebs*, coal tit *Periparus ater* and nuthatch *Sitta europaea*. We used play-back of anthropogenic urban noise and a control treatment at 46 feeding stations located along the urban–rural gradient. We assess impacts on willingness to visit feeders, feeding and vigilance rates. Exposure to anthropogenic noise reduced visit rates to supplementary feeding stations, reduced feeding rates and increased vigilance. Birds at more urban sites exhibit less marked treatment induced reductions in feeding rates, suggesting that urban populations may be partially habituated or adapted to noisy environments. There was no evidence, however, that more urbanised species were less sensitive to the impacts of noise on any response variable. Our results support the adventitious sound masking hypothesis. Urban noise may thus interfere with the ability of birds to detect predators, reducing their willingness to use food rich environments and increase vigilance rates resulting in reduced feeding rates. These adverse impacts may compromise the quality of otherwise suitable foraging habitats in noisy urban areas. They are likely to be widespread as they arise in a range of species including common urban birds.

Keywords: animal communication, antimicrobial capacity, antimicrobial defences, innate humoral immunity, sexual selection in females, *Sturnus unicolor*



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Introduction

Urbanisation is an increasingly important threat to biodiversity that destroys and degrades natural habitat, and is generally accompanied by marked changes in species

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composition and declines in species richness (Shochat et al. 2010, Aronson et al. 2014). Those species that remain face a host of challenges including reduced availability of food and nesting sites, changes in the nature of predation and competition, and increased air, light and noise pollution (McKinney 2002, Isaksson 2018).

Noise pollution has been implicated in reduced growth and body condition in several bird species (e.g. white-crowned sparrow *Zonotrichia leucophrys*, Phillips et al. 2018; tree swallow *Tachycineta bicolor* Injaian et al. 2018). It can cause oxidative stress and elevate production of stress hormones, thereby taxing resources needed for growth and maintenance (Partecke et al. 2006). However, the primary mechanism through which anthropogenic noise directly affects birds is thought to be ‘noise masking’, i.e. the disguising of other natural sounds such as birdsong (Barber et al. 2009). Vocalisations are used by birds in sexual display, territory defence, alarm calling and parent-offspring communication. The masking of such vocalisations has the potential to reduce mating success, increase risk of predation and affect offspring health. Extensive research has been conducted into the ways in which avian vocalisations, primarily song, have altered in response to anthropogenic noise, including changes in the length, timing, frequency and amplitude of songs, which may be adaptive in urban environments as they can reduce masking (Gil and Brumm 2014, Hill et al. 2018, Narango and Rodewald 2018). Noise masking of parent-offspring communication can also result in inadequate provisioning by parents and reduce chick responses to parental predator warnings (McIntyre et al. 2014, Meillère et al. 2015).

However, the effects of noise masking of adventitious sound, the non-deliberate sounds made by organisms in their environment, have been less well explored, and received at best minimal attention in recent reviews of the impacts of noise on birds (Ortega 2012, Blumstein 2014, Gil and Brumm 2014). Birds use sound to detect predators, and if audio cues are masked by urban noise, they could be forced to invest more time in assessing visual cues of predation risk. For example, in a laboratory environment chaffinch *Fringilla coelebs* from rural habitats increased the proportion of time they spent actively scanning the environment under experimental noisy conditions, and this increase in vigilance behaviour reduced their feeding efficacy (Quinn et al. 2006). Similarly, black-capped chickadee *Poecile atricapillus* along an urban gradient were less willing to visit a feeding station when exposed to noise playback, but unwillingness decreased with the degree of urbanisation, suggesting an adaptive habituation or other adaptation to noise (Van Donselaar et al. 2018). Masking of adventitious sounds may also explain why studies on northern cardinal *Cardinalis cardinalis* and superb fairy-wren *Malurus cyaneus* find that birds in areas with high levels of anthropogenic noise failed to exhibit predator avoidance responses to conspecific alarm calls (Grade and Sieving 2016, Zhou et al. 2019).

Here, we use a controlled experiment to investigate the effects of urban noise on passerine feeding behaviour along

a rural–urban gradient. Increased urban noise has been proposed to drive declines in species richness (Ortega 2012, Rodrigues et al. 2018), and to promote biotic homogenisation as noisy environments become dominated by the same restricted set of noise tolerant species (Francis et al. 2011b, Proppe et al. 2013, Cardoso 2014). These studies are, however, observational in nature and gradients in anthropogenic noise covary with multiple other factors along urbanisation gradients. Experimental studies are thus needed to quantify the impacts of noise in isolation of confounding factors. Such experiments are typically conducted in rural environments and have improved understanding of the impacts of anthropogenic noise (Halfwerk et al. 2011, Ware et al. 2015). Such rural experiments may be limited, however, in their capacity to inform understanding of the impacts of anthropogenic noise in urban locations as they assume that urban and rural bird populations exhibit similar responses to urban noise. Indeed, evidence is emerging that contradicts this assumption as urban individuals may be more adapted or habituated to noise (Van Donselaar et al. 2018).

Our primary objective is to test the prediction derived from the adventitious sound masking hypothesis that urban noise increases vigilance and thus reduces feeding rates. In addition, we test the prediction that bird populations occupying more urban sites are less sensitive to urban noise, as expected if they are habituated or otherwise adapted to noisy environments. Finally, we test if the least urbanised species are those that show the most marked impacts of urban noise on feeding rates and increased vigilance behaviour – such patterns are compatible with the suggestion that noise pollution in urban environments is a key factor that determines the composition of urban bird assemblages (Francis et al. 2011a, Cardoso 2014).

Methods

Site selection and urbanisation metrics

Work was conducted in and around Sheffield (53°22'N, 1°20'W), which is England's fifth largest city, with a population of c. 575 000. We defined urban areas as 1 × 1 km grid cells with more than 25% impervious surface (following Gaston et al. 2005) and selected 16 urban sites within 3 km of the city centre, 19 urban sites that were more than 3 km from the city centre and 11 rural sites that were between 1 and 3 km away from the city's outer limits (using the above definition of urban areas). This approach enabled us to haphazardly select sites that were spread across the urban to rural gradient (see below for quantification), with the fewest sites in rural areas due to their greater homogeneity in background noise levels. All sites within the urban area were public parks and green-spaces with some woody vegetation cover, and all rural sites were woodland (rather than the alternatives of moorland or farmland) to maximise the similarity of the focal bird community along the urban to rural gradient.

Urbanisation intensity was quantified at each site using the 'Urbanisation Index' software developed by Seress et al. 2014 (<<https://keplab.mik.uni-pannon.hu/en/urbanization-index>>). This software uses a semi-automated method where it takes a 1 km² area from google maps around the coordinates of each location, and then uses manually inputted training points to score each image for vegetation cover, forest, buildings and paved roads using 100×100 m² cells. It then uses principle component analysis (PCA) to calculate an urbanisation intensity score for each area. Our sampling sites capture substantial variation in urbanisation intensity (Supplementary material Appendix 1 Fig. A1).

Experimental design

Field work took place between the 12th February and 3rd April 2019. Our general approach was to assess avian feeding and vigilance rates at feeding stations under three experimental conditions: play back of urban noise and two control treatments (play back of natural noise and a silent control without playback). The urban recording was created by splicing together 5-min sound recordings from each of four locations in central urban Sheffield (Supplementary material Appendix 1 Table A1) using a Zoom H4n sound recorder and Cubase LE AI Elements 10, with a mixture of traffic, pedestrian and construction noise. The urban noise treatment was played at approximately 80 decibels (dbc), i.e. the typical volume of anthropogenic noise in busy urban areas during the day (Maryland 2018). The natural control used a mixture of songs of summer migrants (barn swallow *Hirundo rustica*; whinchat *Saxicola rubetra*; redstart *Phoenicurus phoenicurus* and common whitethroat *Sylvia communis*). Recordings were obtained from Xeno-Canto (2005–2019) and were vetted to ensure that they did not include alarm calls to ensure that this treatment did not include vocalisations to which birds using the feeders were likely to respond. The natural sound control treatment was played at approximately 40 decibels (dbc) that matched natural sound levels of avian vocalisations. The urban treatment lasted 40 min while each control lasted 20 min, with a 10-min habituation period between equipment set-up and beginning playback, and between the urban treatment and the two control treatments (which each lasted 20 min). We used two green, portable SONY SRS-XB10 Bluetooth controlled speakers (IPX rated 5) at each site located approximately a meter from the feeding station in a spatial configuration that created a surround sound effect.

Each site's feeding station was set up four to seven days before conducting the experiment to enable birds to habituate to the presence of the food source. Each station consisted of two standardised hanging feeders, each with two feeding ports, filled with sunflower hearts. These are a nutritious food source that has a negligible handling time and is thus widely used by a wide range of species. To reduce the risk of disturbance from grey squirrels *Sciurus carolinensis*, which can discourage birds from using feeders (Bonnington et al. 2014), poles were greased and sunflower hearts were coated in chilli powder (which squirrels avoid, whilst birds exhibit no adverse

response). Feeders were placed in relatively open locations to allow easy observation, but close to vegetation cover to encourage birds to approach and use the feeders. Feeding stations were located away from footpaths to minimise effects of human disturbance.

Treatments were applied in a randomised order at each site (with the three treatments being applied sequentially). Sites were visited in a haphazard manner with regard to the site's urbanisation score. All data collection took place at least 1.5 h after civil dawn and before civil dusk, to avoid spikes in bird activity early and late in the day. Data were not collected when it was snowing or raining (except occasional light drizzle), or at high wind speeds as such conditions interfered with activity levels and noise transmission.

Each treatment was filmed using a Panasonic (HC-X920) HD Camcorder and observed from an approximately 10 m to 15 m distance. Videos recorded birds feeding on the feeder and those feeding on spilt food beneath the feeder. If disturbance events occurred during the treatment, such as a human or dog passing close to the feeder, and interrupted birds' feeding behaviour, data collection was paused until birds resumed normal activity. Videos were analysed, and for each visit we recorded the species, visit duration (seconds), number of pecks (as a measure of feeding rate) and the amount of time (seconds) spent performing vigilance behaviour, defined following Quinn et al. (2006), as when the bird raised its head and scanned. For each site, the temperature (°C) and wind speed (kn) were also recorded using data from the nearest weather observation site (Met Office 2019). The seven weather stations used ranged from 220 m to 6.1 km away from the study site.

Statistical analysis

All statistical analyses were conducted using R Studio (RStudio Team 2016). Three response metrics were calculated from the videos for each species per treatment per site: 1) visit rate, i.e. the rate at which the species visited the feeder per hour of treatment, 2) the peck rate per hour of treatment and 3) the vigilance rate (in min) per h of time spent on the feeder. A total of 19 species were observed using the feeders or feeding on fallen seed on the ground below (Supplementary material Appendix 1 Table A2), of which six occurred at ten or more sites and were included in data analysis (great tit *Parus major* 46 sites; blue tit *Cyanistes caeruleus* 44 sites; coal tit *Periparus ater* 33 sites; Eurasian robin *Erithacus rubecula* 35 sites; nuthatch *Sitta europaea* 14 sites; and chaffinch *Fringilla coelebs* 13 sites). These species vary substantially in their ability to maintain high population densities in urban environments. This is indicated by their urbanisation scores as calculated by Evans et al. (2011), i.e. the ratio of urban to rural population densities obtained from Breeding Bird Survey data from approximately 3000 randomly selected 1×1 km squares located across the UK. These scores, from most to least urbanised species, are: blue tit 1.46; robin 0.99; great tit 0.74; chaffinch 0.25; coal tit 0.23, nuthatch 0.17. Matched paired t-tests demonstrated that each of these six

species' visit, peck and vigilance rates did not differ between the two forms of control (p ranges from 0.110 to 0.877; Supplementary material Appendix 1 Table A3) and these data were thus merged to form a single control treatment.

We modelled visit, peck and vigilance rates using mixed effect models (lme4 package; Bates et al. 2015). These models pool data across species and include the following main effects as predictors: species (fixed effect), treatment (fixed effect), the site's urbanisation intensity, date (number of days from the 1st of January), time of day (hours since sunrise), temperature ($^{\circ}\text{C}$), wind-speed (kn) and site (random effect). We also included the following interaction terms: species \times treatment \times urbanisation intensity (to test the predictions that treatment impacts vary with species and along the urbanisation gradient); species \times treatment (to test the prediction that species vary in their responses to treatment); treatment \times urbanisation intensity (to test the prediction that, regardless of species identity, urban populations are less sensitive to treatment effects); and species \times urbanisation intensity (to take into account the potential that species' vary in how their visit, peck and vigilance rates change along the urbanisation gradient, although such patterns are not associated with our objectives of assessing impacts of urban noise and are not explored further). A significant species \times treatment interaction term would indicate that species varied in their responses to the urban noise treatment. Consideration of the correlations between each species' parameter estimates from this interaction term and their urbanisation scores (from Evans et al. 2011; see above) enable us to assess if species with greater tolerance to urban development are less sensitive to treatment effects than species that are more impacted by urban development.

We start by building a full model that includes all main effects, the three-way interaction term and the three two-way interaction terms. We simplify this full model by removing non-significant interaction terms in a step-wise manner according to their p values, with significance being determined using the car package (Fox and Weisberg 2019) to calculate Wald chi-square statistics (Type III). We use this approach as the alternative of using information theoretic approaches based on criteria such as change in Akaike information criteria (AIC) is not recommended when models include interaction terms (Cade 2015).

Results

For all three response variables the three-way interactions between species, treatment and urbanisation intensity were not significant (visit rate $p=0.964$; peck rate $p=0.503$; vigilance rate $p=0.665$; Supplementary material Appendix 1 Table A4) and were thus removed from our models.

Exposure to the urban noise treatment significantly reduced visit rates, which were also significantly associated with species (with the three tit species visiting feeders more regularly than the other focal species), urbanisation intensity (fewer visits in more urban areas) and a significant interaction

between species and urbanisation intensity (with chaffinch and robin having reduced rates of decline in feeder use along the urbanisation gradient than other species; Table 1, Fig. 1a). There was no significant interaction between species and treatment ($p=0.976$; Supplementary material Appendix 1 Table A4) indicating that species' visit rates responded similarly to exposure to urban noise, and thus species' responses were not associated with their tolerances to urban environments (Supplementary material Appendix 1 Fig. A2).

Peck rates were significantly reduced by exposure to the urban noise treatment, and significantly varied with species (with chaffinch and robin having the lowest peck rates), urbanisation intensity (lower peck rates in more urban areas) and a significant interaction between treatment and urbanisation intensity with reduced impacts of treatment in more urban areas (Table 1, Fig. 1b). There was no significant interaction between species and treatment ($p=0.249$; Supplementary material Appendix 1 Table A4) indicating that species' peck rates responded similarly to treatment, and thus these responses were not associated with species' tolerances to urban environments (Supplementary material Appendix 1 Fig. A2).

Vigilance rates increased significantly in response to exposure to urban noise, and were also significantly associated with species (being lower in the three tit species than our other focal species) (Table 1, Fig. 1c). There was no significant interaction between species and treatment ($p=0.619$; Supplementary material Appendix 1 Table A4) indicating that species exhibited statistically similar increases in vigilance rates in response to the urban noise treatments, and thus these responses were not associated with species' tolerances to urban environments (Supplementary material Appendix 1 Fig. A2).

Discussion

Our results build on an increasing but still small body of work documenting single species responses in feeding behaviour to anthropogenic noise (Quinn et al. 2006, Klett-Mingo et al. 2016, Van Donselaar et al. 2018). We assess six species' responses along an urbanisation gradient. There is clear evidence for our core hypotheses that exposure to anthropogenic noise reduces willingness to visit feeders, increases vigilance whilst feeding and thus results in reduced feeding rates. Our results thus support the predictions of the adventitious sound masking hypothesis.

We find no evidence that species which exhibit markedly different tolerances to urban development, based on the ratio of breeding population densities in urban and non-urban habitats, vary in their response to the anthropogenic noise treatment. We thus find no support for previous suggestions that inter-specific variation in species' sensitivity to adverse impacts of anthropogenic noise influences their occurrence and distribution within urban areas (Francis et al. 2011a, Proppe et al. 2013, Cardoso 2014). These previous studies have, however, largely focused on inter-specific variation in

Table 1. Results of mixed linear models of avian visit rate (number per hour), peck rate (number per hour) and vigilance rate (minutes per feeding hour) in response to controlled experimental playback of urban noise along a gradient of urbanisation intensity. Parameter estimates are reported \pm one standard error. Species' parameter estimates are reported relative to blue tit (the most urban adapted species). Bold text indicates results for which $p < 0.05$ and grey highlighting indicates $0.05 < p < 0.1$.

Response	Urbanisation			Species x urbanisation			Treatment x urbanisation		
	Treatment	Temperature	Date	Wind speed	Time of day	intensity	intensity	intensity	
Visit rate	$p < 0.001$	$p = 0.022$	$p = 0.132$	$p = 0.521$	$p = 0.467$	$p = 0.002$			
	$X^2 = 118.134$	$X^2 = 5.229$	$X^2 = 2.266$	$X^2 = 0.412$	$X^2 = 0.528$	$X^2 = 19.470$			
	Chaffinch -19.118 ± 4.103	-2.303 ± 1.007	-0.158 ± 0.105	0.215 ± 0.335	-0.601 ± 0.827	Chaffinch 1.759 ± 1.636			
	Coal tit 3.38 ± 2.922					Coal tit -2.249 ± 1.381			
	Great tit 10.681 ± 2.632					Great tit -2.308 ± 1.211			
	Nuthatch -7.432 ± 4.008					Nuthatch -1.813 ± 2.074			
	Robin -15.672 ± 2.867					Robin 2.251 ± 1.2979			
	$p < 0.001$	$p = 0.001$	$p = 0.502$	$p = 0.721$	$p = 0.072$		$p = 0.020$		
	$X^2 = 44.746$	$X^2 = 12.171$	$X^2 = 0.451$	$X^2 = 0.127$	$X^2 = 3.246$		$X^2 = 5.395$		
	Chaffinch -69.015 ± 21.885	-12.413 ± 3.558	0.296 ± 0.440	$T = -0.357$	-6.357 ± 3.529		10.496 ± 4.519		
Coal tit -42.58 ± 15.707			-0.547 ± 1.532						
Great tit -0.122 ± 14.282									
Nuthatch 43.77 ± 21.256									
Robin -64.695 ± 15.444									
Vigilance rate	$p < 0.001$	$p = 0.550$	$p = 0.638$	$p = 0.628$	$p = 0.762$				
	$X^2 = 53.459$	$X^2 = 0.366$	$X^2 = 0.221$	$X^2 = 0.234$	$X^2 = 0.092$				
	Chaffinch 12.675 ± 2.602	0.162 ± 0.268	0.02 ± 0.043	0.068 ± 0.139	-0.108 ± 0.357				
	Coal tit -4.659 ± 1.448								
	Great tit -1.533 ± 1.276								
	Nuthatch 3.244 ± 2.084								
Robin 2.744 ± 1.55									

the potential for avian vocalisations to be masked by urban noise rather than the impacts of masking adventitious sound. Our analyses are also based on a limited number of species, and none of these are entirely absent from urban areas. It thus remains plausible that some species are excluded from towns and cities due to adverse impacts of anthropogenic noise. We encourage future experimental research that assesses feeding responses to anthropogenic noise across a larger and broader range of species than we are able to consider here. A larger database would also enable such research to benefit from taking phylogeny and other potentially confounding factors into account, such as relative eye size, which can determine species' reliance on auditory detection of predators (Martin 2017).

In contrast to the lack of inter-specific variation in the effect of treatment we find some evidence for intra-specific variation in response to treatment along the gradient of urbanisation intensity. The reductions in feeding rates induced by anthropogenic noise were less marked in more intensely urbanised areas. Such patterns are compatible with the suggestion that urban populations may exhibit phenotypic plasticity or adaptive responses that reduce adverse impacts of anthropogenic noise, as documented in the black-capped chickadee (Van Donselaar et al. 2018). Whilst we do not find equivalent patterns in visit rates or vigilance rates it is important to note that our measure of feeding rate is calculated per unit time of exposure to the treatment and thus incorporates the combined effects of visit and vigilance rates on feeding rates.

Despite the care taken in our experimental design one factor that is extremely difficult to control for is predation risk per se. The abundance and composition of predators will vary across our sampling sites and may do so in a systematic manner along the gradient of urbanisation intensity. Domestic cats will, for example, be more abundant in sites with higher densities of residential housing (Sims et al. 2007); conversely aerial predators such as sparrowhawk *Accipiter nisus* often occur at low densities in highly urbanised environments (Bell et al. 2010). It is thus difficult to assess how exposure to predators and associated perceived predation risk varies along the urban to rural gradient. It remains plausible that reduced impacts of anthropogenic noise on feeding rates in the most urban environments arise at least in part due to a reduced predation risk in such locations.

Notably, visit rates to supplementary feeding stations are reduced by anthropogenic noise and such reductions appear to be consistent in their magnitude along the urbanisation gradient. These results thus suggest that anthropogenic noise can reduce habitat quality by discouraging individuals from feeding in noisy areas – presumably because birds perceive an increased risk of predation due to anthropogenic noise masking adventitious sounds made by approaching predators. This finding adds to an increasing literature on 'fear ecology' which concludes that perceived predation risk is a strong determinant of habitat selection patterns in birds (Cimprich et al. 2005; but see Bonnington et al. 2015) and other taxa (Ripple and Beschta 2004, Benhaiem et al. 2008).

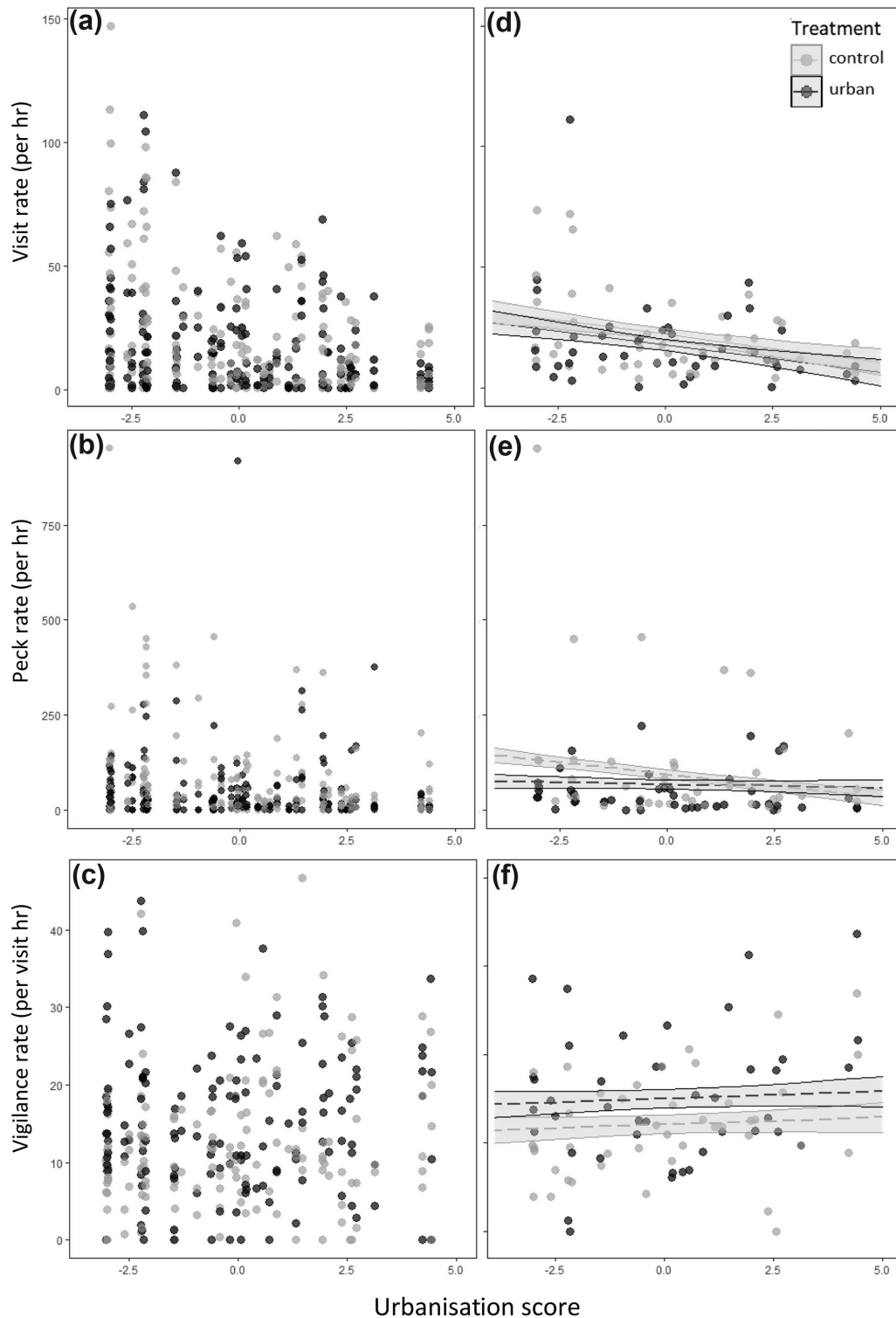


Figure 1. Variation in the effect of anthropogenic noise (dark grey) and control (pale grey) treatments on (a) visit rate (per treatment hour), (b) peck rate (per treatment hour) and (c) vigilance rate (minutes per visit hour) along a gradient of urbanisation intensity (higher scores indicate more urbanised sites). The anthropogenic noise treatment significantly reduces visit and peck rates, whilst increasing vigilance (Table 1). In the peck rate model there is a significant interaction between treatment and urbanisation intensity (Table 1) – with treatment induced reductions in peck rates being greatest at the least urban sites, i.e. the treatment \times urbanisation intensity interaction is significant. This interaction is not significant in models of visit and vigilance rates (Supplementary material Appendix 1 Table A4). Fitted lines represent predicted values along the urbanised gradient for blue tit (the reference species, which is the most urbanised of our focal species), calculated from the models presented in Table 1 when holding all other continuous variables at the mean value, and all factors at the reference value. Shading around the fitted lines is the standard error of predicted values.

Anthropogenic noise may thus reduce the quality of urban habitats, which otherwise appear to be very suitable based on assessments of food availability alone. Restoration and creation of avian habitats in urban environments may thus be more effective when focused on areas with relatively low levels of anthropogenic noise.

Whilst our results suggest that anthropogenic noise in urban areas will frequently disrupt feeding behaviour, the population level consequences of such disruptions are unclear. Urban areas in the UK have high rates of targeted supplementary feeding of garden birds (Reynolds et al. 2017), and the higher density of feeders may explain why feeder visit rates were lower in urban areas (although changes in the number of individuals along the urbanisation gradient could also contribute). Despite these high rates of supplementary feeding there is increasing evidence that population sizes of many urban bird species are limited by food availability, especially of natural food during the breeding season (Peach et al. 2014, Seress et al. 2020). It is therefore plausible that in food limited species the reduced feeding efficiency in response to anthropogenic noise that we document could limit reproductive success and population densities in locations with higher noise levels. Further work measuring long term changes in survival and reproductive rates in response to anthropogenic noise is required to confirm this, especially as urban noise can reduce the risk of nest predation by masking chick begging calls that predators use to locate nests (Francis et al. 2009).

Our study is unique in looking at the effects of noise on anti-predator and feeding behaviour across multiple species along a rural–urban gradient. It demonstrates that a wide variety of species exhibit adverse impacts of anthropogenic noise on their feeding behaviour, in part due to increased vigilance rates as predicted by the adventitious sound masking hypothesis. Adverse impacts on fitness or at the population level remain to be determined but there are plausible mechanisms for such reductions, including anthropogenic noise influencing local patterns of habitat use and reduced feeding rates in urban species whose breeding success is regulated by food availability. Implementation of acoustic barriers, which can include vegetation, around busy roads and other noise sources is likely to reduce such impacts (FHWA 2001, Han et al. 2018) whilst also reducing the harmful effects of noise pollution on people (Jarup et al. 2007, Braum and van Kamp 2017).

Transparent Peer Review

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Data deposition

Data will be available from the Dryad Digital Repository: <http://dx.doi.org/08kpr50d> (Merrall and Evans 2020).

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References

- Aronson, M. F., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., Warren, P. S., Williams, N. S., Cilliers, S., Clarkson, B. and Dobbs, C. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. – *Proc. R. Soc. B* 12: 281.
- Barber, J. R., Crooks, K. R. and Fristrup, K. M. 2009. The costs of chronic noise exposure for terrestrial organisms. – *Trends Ecol. Evol.* 25: 180–189.
- Bates, D., Maechler, M., Bolker, B., Walker, S. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Bell, C. P., Baker, S. W., Parkes, N. G., Brooke, M. D. L. and Chamberlain, D. E. 2010. The role of the Eurasian sparrowhawk (*Accipiter nisus*) in the decline of the House Sparrow (*Passer domesticus*) in Britain. – *Auk* 127: 411–420.
- Benhaïem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A. J. M., Morellet, N. and Verheyden, H. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. – *Anim. Behav.* 76: 611–618.
- Blumstein, D. 2014. Attention, habituation and antipredator behaviour: implications for urban birds. – *Avian urban ecology*, Oxford Univ. Press, pp. 41–53.
- Bonnington, C., Gaston, K. J. and Evans, K. L. 2014. Assessing the potential for grey squirrels *Sciurus carolinensis* to compete with birds at supplementary feeding stations. – *Ibis* 156: 220–226.
- Bonnington, C., Gaston, K. J. and Evans, K. L. 2015. Ecological traps and behavioural adjustments of urban songbirds to fine-scale spatial variation in predator activity. – *Anim. Conserv.* 18: 529–538.
- Braum, A. and van Kamp, I. 2017. WHO environmental noise guidelines for the European region: a systematic review of transport noise interventions and their impacts on health. – *Int. J. Environ. Res. Public Health* 14: 873.
- Cade, B. S. 2015. Model averaging and muddled multimodel inferences. – *Ecology* 96: 2370–2382.
- Cardoso, G. C. 2014. Nesting and acoustic ecology, but not phylogeny, influence passerine urban tolerance. – *Global Change Biol.* 20: 803–810.
- Cimprich, D. A., Woodrey, M. S. and Moore, F. R. 2005. Passerine migrants respond to variation in predation risk during stopover. – *Anim. Behav.* 69: 1173–1179.
- Evans, K. L., Chamberlain, D. E., Hatchwell, B. J., Gregory, R. D. and Gaston, K. J. 2011. What makes an urban bird? – *Global Change Biol.* 17: 32–44.
- FHWA. 2001. Noise barriers – design and construction [online] U.S. Department of Transportation, Federal Highway Administration. Available at https://www.fhwa.dot.gov/environment/noise/noise_barriers/design_construction/, accessed 20 Nov 2018.
- Francis, C. D., Ortega, C. P. and Cruz, A. 2009. Noise pollution changes avian communities and species interactions. – *Curr. Biol.* 19: 1415–1419.
- Francis, C. D., Ortega, C. P. and Cruz, A. 2011a. Different behavioural responses to anthropogenic noise by two closely related passerine birds. – *Biol. Lett.* 7: 850–852.
- Francis, C. D., Ortega, C. P. and Cruz, A. 2011b. Noise pollution filters bird communities based on vocal frequency. – *PLoS One* 6: e27052.
- Fox, J. and Weisberg, S. 2019. An R companion to applied regression, 3rd edn. – Sage, Thousand Oaks CA.
- Gaston, K. J., Warren, P. H., Thompson, K. and Smith, R. M. 2005. Urban domestic gardens (IV): the extent of the resource and its associated features – *Biodivers. Conserv.* 14: 3327–3349.

- Gil, D. and Brumm, H. 2014. Acoustic communication in the urban environment: patterns, mechanisms and potential consequences of avian song adjustments. – *Avian urban ecology*, Oxford Univ. Press, pp. 69–83.
- Grade, A. M. and Sieving, K. E. 2016. When the birds go unheard: highway noise disrupts information transfer between bird species. – *Biol. Lett.* 12: 20160113.
- Halfwerk, W., Holleman, L. J., C. K. Lessels and Slabbekoorn, H. 2011. Negative impact of traffic noise on avian reproductive success. – *J. Appl. Ecol.* 48: 210–219.
- Han, X., Huang, X., Liang, H., Ma, S. and Gong, J. 2018. Analysis of the relationships between environmental noise and urban morphology. – *Environ. Pollut.* 233: 755–763.
- Hill, S. D., Aryal, A., Pawley, M. D. and Ji, W. 2018. So much for the city: urban–rural song variation in a widespread Asiatic songbird. – *Integr. Zool.* 13: 194–205.
- Injaian, A. S., Taff, C. C. and Patricelli, G. L. 2018. Experimental anthropogenic noise impacts avian parental behaviour, nestling growth and nestling oxidative stress. – *Anim. Behav.* 136: 31–39.
- Isaksson, C. 2018. Impact of urbanization on birds. – In: *Bird species*. Springer, pp. 235–257.
- Jarup, L., Babisch, W., Houthuijs, D., Pershagen, G., Katsouyanni, K., Cadum, E., Dudley, M. L., Savigny, P., Seiffert, I., Swart, W. and Breugelmans, O. 2007. Hypertension and exposure to noise near airports: the HYENA study. – *Environ. Health Perspect.* 116: 329–333.
- Klett-Mingo, J. I., Pavón, I. and Gil, D. 2016. Great tits *Parus major* increase vigilance time and reduce feeding effort during peaks of aircraft noise. – *Anim. Behav.* 115: 29–34.
- Martin, G. R. 2017. *The sensory ecology of birds*. – Oxford Univ. Press.
- Maryland SHA. 2018. Sound barriers guidelines – highway traffic noise [online]. – State Highway Administration, Maryland Department of Transportation. <<https://www.roads.maryland.gov/Index.aspx>>, accessed 15 November 2018.
- McIntyre, E., Leonard, M. L. and Horn, A. G. 2014. Ambient noise and parental communication of predation risk in tree swallows, *Tachycineta bicolor*. – *Anim. Behav.* 87: 85–89.
- McKinney, M. L. 2002. Urbanization, biodiversity and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. – *Biosciences* 52: 883–890.
- Meillère, A., Brischoux, F. and Angelier, F. 2015. Impact of chronic noise exposure on antipredator behaviour: an experiment in breeding house sparrows. – *Behav. Ecol.* 26: 569–577.
- Merrall, E. S. and Evans, K. L. 2020. Data from: Anthropogenic noise reduces avian feeding efficiency and increases vigilance along an urban–rural gradient regardless of species’ tolerances to urbanisation. – *Dryad Digital Repository*, <<http://dx.doi.org/10.5061/dryad.08kpr50d>>.
- Met Office. 2019. *Weather Observations Website (WOW)* [online]. – WOW Met Office. <<https://wow.metoffice.gov.uk/>>, accessed 14 Feb 2019.
- Narango, D. L. and Rodewald, A. D. 2018. Signal information of bird song changes in human-dominated landscapes. – *Urban Ecosyst.* 21: 41–50.
- Ortega, C. P. 2012. Chapter 2: Effects of noise pollution on birds: a brief review of our knowledge. – *Ornithol. Monogr.* 74: 6–22.
- Partecke, J., Schwabl, I. and Gwinner, E. 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. – *Ecology* 87: 1945–1952.
- Peach, W. J., D. K. Sheehan and Kirby, W. B. 2014. Supplementary feeding of mealworms enhances reproductive success in garden nesting house sparrows *Passer domesticus*. – *Bird Study* 61: 378–385.
- Phillips, J. N., Gentry, K. E., Luther, D. A. and Derryberry, E. P. 2018. Surviving in the city: higher apparent survival for urban birds but worse condition on noisy territories. – *Ecosphere* 9: 02440.
- Proppe, D. S., Sturdy, C. B. and St. Clair, C. C. 2013. Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. – *Global Change Biol.* 19: 1075–1084.
- Quinn, J. J., Whittingham, M. J., Butler, S. and Cresswell, W. 2006. Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. – *J. Avian Biol.* 37: 601–608.
- Reynolds, S. J., Galbraith, J. A., Smith, J. A. and Jones, D. N. 2017. Garden bird feeding: insights and prospects from a north–south comparison of this global urban phenomenon. – *Front. Ecol. Evol.* 5: 24.
- Ripple, W. J. and Beschta, R. L. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? – *Bioscience* 54: 755–766.
- Rodrigues, A. G., Borges-Martins, M. and Zilio, F. 2018. Bird diversity in an urban ecosystem: the role of local habitats in understanding the effects of urbanization. – *Iheringia Sér. Zool.* 108: 2018017.
- RStudio Team. 2016. *RStudio: integrated development for R*. – RStudio, Inc., Boston, MA, USA.
- Seress, G., Lipovits, Á., Bókony, V. and Czúni, L. 2014. Quantifying the urban gradient: a practical method for broad measurements. – *Landscape Urban Plan.* 131: 42–50.
- Seress, G., Sándor, K., Evans, K. L. and Liker, A. 2020. Food availability limits avian reproduction in the city: an experimental study on great tits *Parus major*. – *J. Anim. Ecol.* 89: 1570–1580.
- Shochat, E., Lerman, S. B., Anderies, J. M., Warren, P. S., Faeth, S. H. and Nilon, C. H. 2010. Invasion, competition and biodiversity loss in urban ecosystems. – *BioScience* 60: 199–208.
- Sims, V., Evans, K. L., Newson, S. E., Tratalos, J. A. and Gaston, K. J. 2007. Avian assemblage structure and domestic cat densities in urban environments. – *Divers. Distrib.* 14: 387–399.
- Van Donselaar, J. L., Atma, J. L., Kruyf, Z. A., LaCroix, H. N. and Proppe, D. S. 2018. Urbanization alters fear behaviour in black-capped chickadees. – *Urban Ecosyst.* 21: 1043–1051.
- Ware, H. E., McClure, C. J., Carlisle, J. D. and Barber, J. R. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. – *Proc. Natl Acad. Sci. USA* 112: 12105–12109.
- Xeno-Canto. 2005–2019. *Sharing bird sounds from around the world* [online]. – Xeno-canto Foundation. <<https://www.xeno-canto.org/>>, accessed 6 Feb 2019.
- Zhou, Y., Radford, A. N. and Magrath, R. D. 2019. Why does noise reduce response to alarm calls? Experimental assessment of masking, distraction and greater vigilance in wild birds. – *Funct. Ecol.* 33: 1280–1289.

Supplementary material (available online as Appendix jav-02341 at <www.avianbiology.org/appendix/jav-02341>). Appendix 1.