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Short Communication

Differential impact of anthropogenic noise during the acoustic development of begging calls in Blue Tits (*Cyanistes caeruleus*)

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In many bird species, nestling begging signals play a key role in the interaction between parents and their offspring during development. The information conveyed by begging calls can be disrupted by anthropogenic noise, which is one of the major threats to biodiversity in increasingly urbanized landscapes. Here, we describe the developmental change in acoustic structure of begging calls in nestling Eurasian Blue Tits *Cyanistes caeruleus*; begging calls are pure-tone, low-frequency, soft calls during the first days of development and gradually turn into white-noise, hiss-like, powerful calls of broadband frequency. This strong developmental variation highlights the importance of an extended sampling scheme in developmental studies. Furthermore, we pinpoint two phases where begging calls could be most vulnerable to masking by anthropogenic noise. First, during early development, begging calls are very soft and low-pitched, closer to high-intensity noise bands of traffic noise. Secondly, around day 11, begging calls show reduced tonality, which implies higher degradation, and relatively low amplitude, which implies reduced signal range. We encourage future research to describe acoustic development of begging calls in other species, to provide a robust foundation that will make noise mitigation policies more effective.

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A major component of parental care in altricial birds is the provisioning of food to their nestlings, and such behaviour can strongly determine reproductive success (Ar & Yom-Tov 1978, Wojczulanis-Jakubas 2021). Nestling begging signals are thought to be an honest indicator of need and parents use them to adjust their provisioning rates accordingly (Marques *et al.* 2009, García-Campa *et al.* 2021). Among these signals, vocalizations (begging calls) are most conspicuous and transmit further than visual signals, especially in enclosed nests. Although begging is widespread among songbirds, the acoustic structure of these calls varies with developmental stage and between species (Briskie *et al.* 1999).

Acoustic communication can be disrupted by anthropogenic noise, which is one of the most common modifications of the environment caused by human activity (Barber *et al.* 2010, Mennitt & Fristrup 2015). Anthropogenic noise produced by transportation and industry is typically concentrated at lower frequencies (Gill *et al.* 2014, Sierro *et al.* 2017). As with any sound signal, chick begging calls that signal hunger or body condition may be masked by anthropogenic noise, leading to suboptimal parental provisioning behaviour (García-Campa *et al.* 2021). Experimental studies show that parents do not adjust provisioning rates in response to increased begging when environmental conditions are noisy (Leonard *et al.* 2015). Nestlings modify their calls under experimental noise exposure, which may improve communication efficiency (Leonard & Horn 2008), but may also be energetically costly. Although begging calls are used in close-range communication, it has been shown that predators use them to locate nests and prey upon nestlings (McDonald *et al.* 2009). Hence, a reduced range of acoustic signals due to masking by noise could have positive effects, as it may reduce predation risk, but it may also lead to negative effects on rearing the young if parent–offspring communication is also disrupted.

Anthropogenic noise has also been associated with higher stress in both adults and nestlings and may reduce growth rate or body condition (Potvin & MacDougall-Shackleton 2015, Injaian *et al.* 2018, Zollinger *et al.* 2019), although other studies have not found any detrimental effect of anthropogenic noise on nestling development (Liu *et al.* 2022) or fledging success (Leonard & Horn 2008). Potvin and MacDougall-Shackleton (2015) found that nestlings reared under experimentally increased noise conditions showed reduced weight gain in the early stages of development, but there was no difference in nestling mass compared with fledglings reared under quiet conditions. These apparently inconclusive results are complicated further because most studies of begging calls focus on a certain stage in nestling development (Popp & Ficken 1991, Christe *et al.* 1996, Briskie *et al.* 1999, Leonard & Horn 2012, Dakin *et al.* 2016), but begging vocalizations change during development. For example, Eurasian Magpie *Pica pica* nestlings decrease the frequency range of their begging calls as they grow (Redondo & De Reyna 1988) whereas the begging calls of Tree Swallows *Tachycineta bicolor* become longer, more powerful, lower and broader in frequency range (Leonard & Horn 2008). The differences in acoustic development between species highlight the importance of describing the changes in acoustic structure throughout development to understand the impact of anthropogenic noise on parent–offspring communication at each stage.

The acoustic structure of a sound determines how easy it is to locate the source as well as its transmission distance. For instance, it is easier to precisely locate the source of a broadband, white-noise sound than a tonal, narrowband sound (Knudsen & Konishi 1979). Low-frequency signals travel further and are less affected by reverberation and scatter than high-frequency sounds (Morton 1975, Wiley & Richards 1982). Some of these features, such as amplitude and frequency of vocalizations, are affected and/or constrained by body size (Tubaro & Mahler 1998, Kostoglou *et al.* 2022).

We investigated changes in the acoustic structure of begging calls of nestling Eurasian Blue Tits *Cyanistes caeruleus* (henceforth, Blue Tits) through development. We focused on multiple acoustic features that determine the transmissibility and locatability of the acoustic signals to explore how and when increased anthropogenic noise might have the greatest impact on parent–offspring communication at the nest. We recorded begging calls at eight different nests twice per day, resulting in higher temporal resolution than in previous studies. Furthermore, we quantified changes in the phonetic structure of the sound, by measuring the relative amplitude, the spectral characteristics and the tonality (or noisiness) of begging calls, which determine the transmission distance of sounds as well as the locatability by the receiver. We aim to set specific predictions for when anthropogenic noise will have a stronger masking effect on the begging calls of nestling Blue Tits. Identifying vulnerable phases during the reproductive cycle is a fundamental step to produce efficient conservation policies that protect wildlife from human disturbance.

METHODS

Study population and study design

We studied the begging behaviour of nestling Blue Tits, a well-studied species commonly used as a model in behavioural ecology (Mainwaring & Hartley 2019). The study population was located in the woods surrounding Lancaster University, UK (54.01°N, 2.78°W), where it has been monitored for over 20 years (Leech *et al.* 2001). In this study, we aimed to describe the developmental changes in the acoustic structure of begging calls in Blue Tit nestlings. To that end, we strapped autonomous recording units (Bioacoustic Audio Recorders ™ -BAR-, Frontier Labs, www.frontierlabs.com.au/support) to the outside of each nestbox, with the microphone inserted through a hole in the lid, placing it around 10 cm away from the nestlings. We made two 30-min long recordings per day, the first beginning 1 h after sunrise and the second beginning 5 h after sunrise (WAV format, sampling rate: 48 kHz, 16 bits). We made daily recordings at eight different nests throughout development, but because of other ongoing studies, not all nests could be recorded during the entire nestling period (see Results). Blue Tits typically leave the nest between the 17th and the 20th days after hatching, so we analysed calls from day 1 until day 16, where day 0 was the day the first egg hatched. Blue Tit nestlings may vary in age within broods, as there is some hatching asynchrony. In this population, eggs in a clutch normally hatch within 1–2 days of each other, with most of the brood hatching together on day 0 (Mainwaring *et al.* 2010). We assigned an age class to each recording based on the number of days after the first day of hatching. Despite the hatching asynchrony, this measure is a good proxy for nestling age. Any variation in age within broods is likely to cause only minor variation in calls but not any bias in relation to the hypotheses.

Part of the study was to identify vulnerable periods in nestling development when increased anthropogenic noise would have the greatest negative impact on communication. For this, we made audio recordings near a busy motorway (the M6 motorway at Lancaster University) using a similar protocol of two recording sessions per day during five consecutive days. In this case the microphone was placed inside an empty nestbox that was located 13.6 m from the closest lane of the motorway (see Measuring noise profiles). All fieldwork involving Blue Tits was approved by the Lancaster University animal welfare and ethical review board.

Acoustic analysis

Using the labelling tool in Audacity (Mazzoni & Dannenberg 2014), we manually selected a maximum of 50 single, individualized, begging calls that were clearly separated in the spectrogram from other vocalizations (Fig. 1). In the spectrogram, we placed manual time marks on individual begging calls to locate them in the recording (Fig. S1). As nestlings often call simultaneously upon the arrival of an adult (i.e. begging bouts),

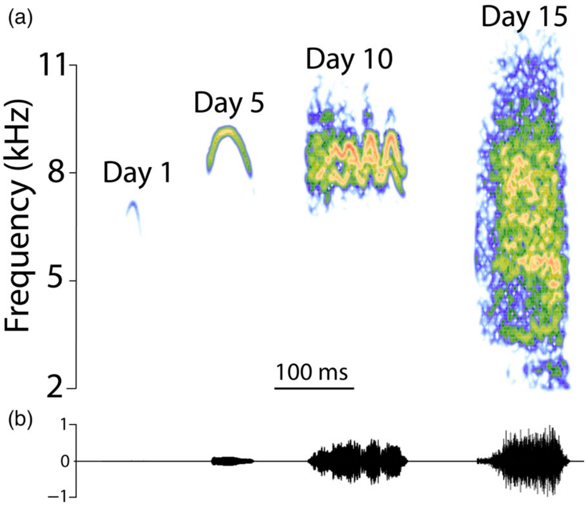

Figure 1. Spectrogram of examples of begging calls of nestling Blue Tits from the same brood during development (a) with the associated amplitude waveform (b).

we were more likely to find the isolated calls of individuals a few seconds into the begging bout. This was necessary to measure duration of individual calls. Although it is possible that initial begging calls may differ from the calls produced later in a begging bout, this should not bias our results because the same criterion was used systematically for all nests and age classes, so the data are suitable to investigate developmental changes within broods.

To measure the duration of each call, we used manual marks that were placed clearly inside the begging call and used this reference point to identify the start and end points of each vocalization in the recording automatically with R (R Core Team 2022). These were the first point before and the first point after the manual time mark, in which the amplitude fell below 20% of the maximum amplitude during a time window of 10 ms. This was measured in the normalized amplitude envelope, within a segment of 0.3 s cut around the manual time mark (Fig. S1). We measured relative vocal amplitude of individual vocalizations on a linear scale as bits in the digital recording. These values were normalized so that a value of 1 was the maximum amplitude that could be recorded with the recording equipment and settings before clipping. This value was then transformed into a decibel scale where 0 dB was the maximum relative amplitude. This study design, although not suitable to derive absolute values of sound level, was suitable to investigate relative changes in acoustic structure during development. We measured the spectral variables (peak, minimum and maximum frequencies) in the normalized power spectrum (max dB = 0) following Podos (1997). The peak frequency was the frequency with the highest amplitude whereas the maximum and minimum frequencies were the highest and lowest frequencies in the power spectrum above an amplitude threshold of −20 dB. Finally, we measured spectral entropy using the Shannon entropy function (H) in *seewave* (Sueur *et al.* 2006). This is an index of the tonality of the sound, where high values represent noisy sounds (i.e. hiss-like sounds) and low values represent tonal sounds (i.e. a whistle sound without frequency modulation). We confirmed that the function returned values close to 1 when applied to synthetic white noise (0.99 ± 0.0004, $n = 100$), but the spectral entropy measured in a synthetic pure tone was 0.23 ± 0.02 ($n = 100$). This value is rather higher than 0, which is the predicted value for a pure tone. Hence, we re-scaled the index derived from the original function by setting 0.23 as the lowest value (pure tone). We further observed a marginal, positive effect of sound duration on the measure of spectral entropy in noisy sounds ($r = 0.74$, slope = 0.0014, $P < 0.0001$, df = 998, $N = 1000$). Hence, to avoid this small ‘duration bias’, we systematically measured entropy on a clip of 20 ms cut from the middle of the call (all calls were longer than 20 ms). Finally, given that differences in signal-to-noise ratio of the calls, determined by the amplitude of the call over the ambient noise, could also affect the measurement of spectral entropy, we applied a bandpass filter from 1 kHz below to 1 kHz above the measured minimum and maximum frequency, respectively.

Measuring noise profiles

Noise profiles were measured from nestboxes at different distances from the motorway traffic source. From recordings taken near the motorway, we selected parts of the audio with a clear view of the ambient noise while avoiding other transient noises such as bird vocalizations. We extracted the noise profile by computing the mean power-spectrum of all audio clips and transforming it into a dB scale as explained above. The sample of audio segments selected to extract the noise profile added to 20:01 minutes of recording across 10 sessions made during five consecutive days (mean ± sd = 2:00 ± 1:04 min per recording). In order to obtain a similar profile of the natural ambient noise in a quiet area of the study site, we selected several parts of the recordings made in a box located 3.02 km from the motorway. Again, we selected audio clips with a clear view of the ambient noise, avoiding any transient noises. This was one of the boxes used to record begging calls so there were fewer parts of the audio without transient noises. This sample of audio segments added to a total of 10:55 min across 12 recordings on six different days (0:55 ± 0:18 min per recording).

We overlaid the noise profiles over the power-spectrum profiles of begging calls of one nest for which we had the longest period of recorded begging calls from day 1 to day 16. We selected four age classes, days 1, 5, 10 and 15, that arbitrarily split the entire nestling period into same length intervals. For each age class we computed the mean power spectrum of all individual calls selected in that day (day 1: $n = 50$, day 5: $n = 48$, day 10: $n = 41$ and day 15: $n = 46$ individual calls).

Although we did not calibrate the microphones at each location, amplitude profiles can be compared because we used the same models for the recording machine and microphone and identical recording settings. It is important to note that amplitude is not measured as absolute sound level but only relative to the maximum amplitude recorded (maximum dB = 0). The resulting Figure 2 shows the noise profiles recorded in these specific nests and we use them only as a visual aid in our discussion. As a theoretical exercise, we also calculated how begging calls would be perceived at 1 m from the sound source, after applying the following formula for sound attenuation over distance (Fig. 2a):

$$\mathrm{SPL}_2 = \mathrm{SPL}_1 - 20\log\left(\frac{R_2}{R_1}\right)$$

where SPL_1 is the relative amplitude in dB as measured in the recording, R_2 is the distance for which we want to estimate the SPL levels (SPL_2) and R_1 is the original distance from the microphone to the sound source (nestlings). Power-spectrum profiles of begging calls in Figure 2b are calculated for an R_2 of 1 m and R_1 of 0.10 m (Fig. 2b). This estimate does not account for the sound attenuation due to the wooden walls of the nestbox (25 mm thick). Note that ambient noise would barely change after moving 1 m from the nestbox.

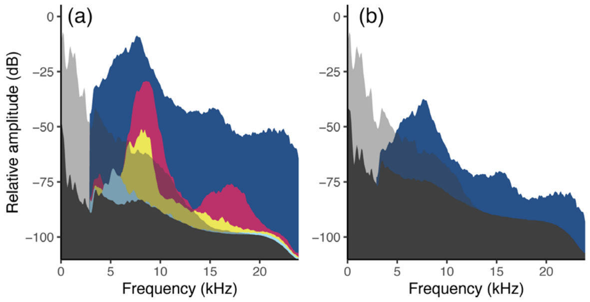

Figure 2. Power-spectrum of begging calls of nestling Blue Tits at different age classes (light blue, yellow, pink and dark blue) recorded in an urban woodland with low ambient noise, overlaid with the ambient noise profile (black) recorded in a rural woodland with natural ambient noise and the motorway noise profile (grey) recorded in an empty nestbox near the motorway with identical recording equipment and settings. We show only four age classes that split the entire nestling period into equal-length intervals, day 1 (light blue), day 5 (yellow), day 10 (pink) and day 15 (dark blue). (a) Power-spectrum of each sound as originally recorded, normalized for the maximum amplitude with the current recording settings and transformed into dB (logarithmic scale). (b) Estimated signal-to-noise ratio at 1 m distance from the nestbox (see Methods for details).

Statistical analysis

To investigate the developmental variation in the acoustic structure of begging calls, we fitted generalized additive mixed models (GAMMs). These models describe a response variable as a series of unknown smooth functions and are suitable to model non-linear variation of time series. We fitted six models, each with one of the acoustic variables (duration, relative amplitude, maximum, minimum and peak frequency, and spectral entropy) as the response variable, as a function of days from hatching within the smooth function. Cross-validation was used to estimate the optimal amount of smoothing using cubic regression splines (Zuur *et al.* 2009). To control for pseudo-replication, we included the recording session ID and the nest ID as random effects. After fitting each model, we analysed the slope on the GAMM splines to define whether there was a significant increase or decrease in the response variable as well as the inflection points. The inflection points or change points were defined as the days after hatching where the slope (i.e. first derivative of the spline function) changed significantly, from being significantly positive to neutral or negative, after estimating the 95% confidence intervals of the slope at each point in the splines (https://rpubs.com/hrlai/gam_inflection; Fig. S2). From these models we determined: (1) whether the acoustic structure changed significantly during development; (2) whether this change was a directional increase or decrease; and (3) the point during development (days from hatching) of any inflection point(s). All measures are presented as mean ± one standard deviation (sd), unless otherwise indicated.

RESULTS

Begging calls through development

We analysed a total of 3813 individual begging calls (28.6 ± 11.7 sd number of calls per recording session) from eight different nests during a mean of 10.5 ± 4.1 sd days of recording per nest. Brood size varied across nests (7.5 ± 2.6 sd chicks per nest), but was not associated with sampling effort at different ages (Table S1).

We found that all acoustic variables measured in begging calls varied significantly with nestling age in a non-linear pattern, as shown by the effective degrees of freedom being significantly different from 1 (Table 1, Figs. 1 and 3). The points of change in slope are presented as rounded to the integer in the text (days from hatching) but the exact values estimated in the models are shown

Table 1. Results from a generalized additive mixed model, fitted to investigate acoustic development in begging calls of Blue Tit nestlings.

Smooth terms

Dependent variable: Fixed effect	EDF	*F*	*P*
Call duration: days from hatch	4.451	45.627	<0.001
Relative amplitude: days from hatch	3.714	82.393	<0.001
Peak frequency: days from hatch	6.59	48.405	<0.001
Maximum frequency: days from hatch	6.538	75.681	<0.001
Minimum frequency: days from hatch	5.8	77.169	<0.001
Spectral entropy: days from hatch	4.447	166.65	<0.001

Parametric terms

Dependent variable: Fixed effect	Estimate	2.5% CI	97.5% CI	*T*
Call duration: intercept	72.419	61.66	83.178	13.193
Call duration: days from hatch	77.079	64.004	90.155	11.664
Relative amplitude: intercept	−36.052	−40.066	−32.037	−17.602
Relative amplitude: days from hatch	31.473	27.821	35.124	17.053
Vocal consistency: intercept	7.54	7.137	7.943	36.674
Peak frequency: days from hatch	0.328	0.063	0.593	2.452
Maximum frequency: intercept	8.72	8.12	9.319	28.504
Frequency: days from hatch	3.059	2.727	3.391	18.224
Minimum frequency: intercept	6.42	6.16	6.68	48.343
Frequency: days from hatch	−1.562	−1.909	−1.215	−8.909
Spectral entropy: days from hatch	0.361	0.329	0.393	21.872
Spectral entropy: days from hatch	0.414	0.381	0.446	25.414

The table shows the estimated coefficients for the smooth and the parametric terms derived from the three models. The upper half of the table show the Effective Degrees of Freedom (EDF) for the smooth terms and the test statistics derived from the frequentist properties of Bayesian confidence intervals for smooths (Marra & Wood 2012).

in Table S2. Call duration was shortest from day 1 to day 4, after which it increased significantly until day 10. From day 10 to day 16 call duration remained stable (Fig. 3). Amplitude was lowest in the first day of development and increased significantly with age throughout the entire nestling period (Fig. 3). Peak, maximum and minimum frequencies followed very similar patterns. All three measures increased until days 6–7, but then decreased significantly after day 8. Minimum frequency continued to decrease until day 15, whereas peak and maximum frequency increased again from days 13 and 12, to days 14 and 15, respectively (Fig. 3). Spectral entropy was lowest and stable during the first 4 days of development when begging calls were tonal sounds of narrow bandwidth. After day 4, entropy increased significantly until day 16, reaching high values that indicate white-noise, chaotic (non-tonal) sounds in the final nestling period (Fig. 3).

DISCUSSION

Our study shows that the acoustic properties of begging calls change significantly and non-linearly during development. We can define three phases: a first phase from 1 to about 5 days, a second phase from about 5 to 12 days, and a third phase from about 12 to 16 days after hatching. In the first phase, begging calls are narrow-band sounds (i.e. pure tones) of very low amplitude and relatively low frequency. During the second phase, begging calls are louder tonal sounds with higher frequency and wider frequency modulations. In the third phase begging calls transform into loud, hiss-like sounds of broadband frequency.

Based on these data, we hypothesize that there are two points in the development of nestling Blue Tits when their begging calls might be particularly vulnerable to interference from road traffic noise. The first vulnerable point is during the entire first growth phase and a second vulnerable point is during the transition between the second and third phases at around day 11. Begging calls during the first phase are short vocalizations of very low amplitude and relatively low frequency, making them easily masked by anthropogenic noise, despite being tonal sounds, which are less susceptible to degradation. At the end of the second and beginning of the third phases, begging calls change from highly tonal

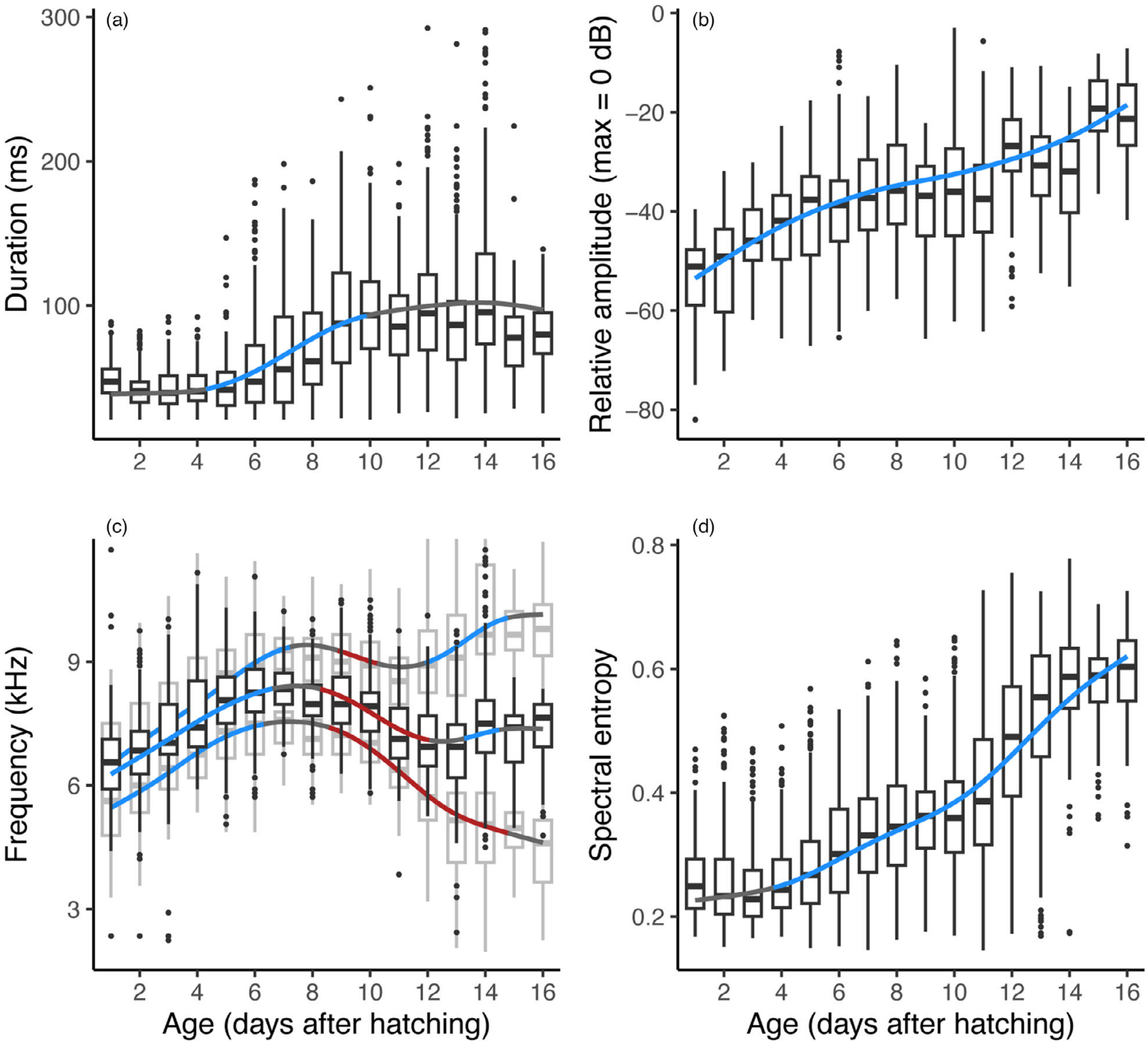

Figure 3. Generalized Additive Mixed Models (GAMMs) of variation in acoustic characteristics of the begging calls of Blue Tits during development, from day 1 to day 16 after hatching. Call duration (a), relative amplitude (b), frequency (c) and spectral entropy (d) all vary significantly and non-linearly during development. In (c), the peak frequency is shown in black boxes with transparent, grey boxes in the background indicating the maximum frequency (above) and the minimum frequency (below). Box and whisker plots show median, higher and lower quartiles and 1.5 interquartile range. Lines show the GAMM splines coloured with the slope indicated by colour codes: flat slope (grey), positive slope (blue) and negative slope (red).

sounds to chaotic, noisy sounds. These hiss-like sounds degrade faster under noisy conditions, and, at this point, sound amplitude is not yet as high as in later development, when it would partly compensate for the masking by noise from traffic.

In areas with high levels of anthropogenic noise, we predict that parent–offspring communication will be particularly affected at these two vulnerable points of nestling development. From the receiver's perspective, we predict that parents will be unable to assess begging calls adequately, and this could lead to a mismatch between provisioning rates and offspring need. The observed pattern of variation in acoustic structure could explain why experimental noise exposure has been associated with a lag in growth rate only during some parts of nestling development in Zebra Finches *Taeniopygia* *guttata* (Potvin & MacDougall-Shackleton 2015, Zollinger *et al.* 2019). Leonard *et al.* (2015) showed, in Tree Swallows, that noise disrupts parent–offspring communication but did not find an effect on nestling mass at the end of the nestling period. It could be that parent–offspring communication is disrupted during certain vulnerable periods, as we have predicted, leading to suboptimal provisioning behaviour and therefore reduced growth rate, but parents may be able to compensate for such a detrimental effect if communication is efficient during other periods of development. Through an experimental and a meta-analytic study, Liu *et al.* (2022) did not find any effect of chronic traffic noise on growth rates of nestlings, although parents showed increased nest attendance under high levels of noise. In this scenario, even though reproductive success seems unaffected, it is possible that provisioning parents could suffer greater costs under noisy conditions, which may compromise their own survival (Nur 1984, Santos & Nakagawa 2012). At a population scale, vulnerable points in development where communication is inefficient under noisy conditions could lead to lower resilience of bird populations in urbanized habitats (Senzaki *et al.* 2020).

From the point of view of a signaller, it has been shown that nestlings modify their calls in response to environmental noise, producing vocalizations that transmit better under noisy conditions (Leonard *et al.* 2015, Dharmasiri *et al.* 2022) but the extent of variation in amplitude and frequency of sounds is limited by body size, and hence the ability to produce adaptive signals may vary through development. For instance, very young nestlings may be unable physically to increase the power or frequency of their begging calls. Moreover, by increasing the power of vocalizations, nestlings may incur energetic costs with consequences that may depend on the developmental stage (Moreno-Rueda 2010, Dunn *et al.* 2018).

The vulnerable phases which are most prone to masking by environmental noise may vary between species. Our findings of developmental changes of begging calls in Blue Tits are nearly identical to those described for Tree Swallows (Leonard & Horn 2008), leading to similar predictions for that species. In the case of Eurasian Magpies, a much larger species, begging calls seem to develop into narrower bandwidth sounds (Redondo & De Reyna 1988), which is different from the pattern observed in Blue Tits. Clearly, acoustic properties of begging calls vary between species, so variation in developmental changes is also expected, making further research necessary to find evolutionary patterns that lead to robust conclusions.

The negative impact of urbanization on natural ecosystems is well established (Grimm *et al.* 2008) and some studies point towards anthropogenic noise causing lower reproductive success in birds (Halfwerk *et al.* 2011, Senzaki *et al.* 2020). Identifying vulnerable points during the reproductive cycle of animals, when anthropogenic factors could have the highest impact, may be key to developing effective conservation policies.

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AUTHOR CONTRIBUTIONS

Javier Sierro: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; visualization; writing – review and editing; software; formal analysis; data curation; validation; project administration. **Selvino R. de Kort:** Conceptualization; writing – review and editing; supervision; methodology. **Ian R. Hartley:** Conceptualization; writing – review and editing; supervision; resources; project administration.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

ETHICAL NOTE

None.

FUNDING

None.

Data Availability Statement

All data supporting the findings of this study are publicly available at the FigShare repository (DOI: 10.6084/m9.figshare.24581823).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Automatic method to measure call duration.

Figure S2. Statistical analysis of the slope along the GAMM splines to identify inflection points, related to Fig. 2.

Table S1. Brood size variation between nestboxes, with the total days of begging call recording and the oldest brood age recorded in each nestbox.

Table S2. Change points in slope for the generalized additive mixed models, indicated as days from hatching.