



## Noise annoys: effects of noise on breeding great tits depend on personality but not on noise characteristics

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Anthropogenic noise can have serious implications for animals, especially when they communicate acoustically. Yet, the impacts of noise may depend not only on noise characteristics but also on an individual's coping style or personality. We tested whether noise is more disturbing if it masks communication signals, and whether characteristics of both the noise and the individual affect its impact. Using a unique population of personality-typed great tits, *Parus major*, we tested whether the kind of noise and parental personality affect parental nestbox visits and nestling begging. Nestboxes were exposed to automated noise playbacks, differing in spectral composition (noise masking begging calls, nonmasking noise or no noise). Parental nestbox visits were recorded using RFID transponders. Video and audio recordings were used to quantify nestling begging. Nestlings mainly begged in silence and in the presence of parents. Parents reduced nestbox visits during noise treatments regardless of the kind of noise and initially reacted more strongly to nonmasking noise. Moreover, slower explorers took longer to enter the nestbox during noise than faster explorers. Total visit rates during noise depended on parental sex and personality. In females, bolder individuals, but in males shyer individuals, reduced total visits during noise. These results extend previous findings in showing experimentally that the disturbance effects of noise do not depend on whether or not the noise directly interferes with information exchange by masking signals. Moreover, personality- and sex-specific responses to noise indicate that anthropogenic disturbance can differentially affect individuals within populations, which will influence mitigation strategies.

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The continuing expansion of human activities has led to the widespread occurrence of anthropogenic noise. Increases in noise can have serious implications for animals including humans (Barber et al. 2009). Noise can affect internal processes such as gene regulation, physiological processes such as blood pressure or immune response, sleep, fearfulness, attention and cognition (Kight & Swaddle 2011), all of which may affect an individual's behaviour and fitness. An important factor explaining variation in response to noise is the type of noise to which an individual is exposed (Luther & Gentry 2013; Naguib 2013). Some noises may simply disturb

individuals, while others may also interfere with signals, thus directly affecting social interactions. In vocally communicating animals, environmental noise can mask a range of acoustic signals affecting reproduction and survival, such as song, contact and alarm calls, or nestling begging calls in birds (Brumm & Slabbekoorn 2005; Warren et al. 2006). Research on vocal communication in noise has mainly focused on such masking effects, revealing that animals in noisier habitats show temporal or spectral shifts in their signals away from the signal space covered by noise (Brumm & Slabbekoorn 2005; Brumm & Naguib 2009; Luther & Gentry 2013) or to signals at higher volume (Brumm & Zollinger 2011). Songbird nestlings react to masking noise by altering their begging calls (Leonard & Horn 2005, 2008) and by reducing responsiveness to parental calls (Leonard & Horn 2012). Masking noise can also affect the parents, which may change their feeding pattern, because they miss information provided by begging calls masked by noise (Glasse & Forbes 2002; Kilner & Hinde 2008). Nonmasking noise that simply distracts receivers can also have fitness consequences with respect to foraging

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behaviour or alertness to predators (Dukas 2004; Purser & Radford 2011) but such disturbance effects have not received much attention in studies on vocal communication and parental provisioning.

Beyond the nature of the noise, responses to such disturbances also depend on the context and the characteristics of the individual itself. Indeed, the internal mechanisms that are affected by noise (Kight & Swaddle 2011) vary depending on an individual's coping style or personality (Koolhaas et al. 2010), so that for humans it has been suggested that responses to noise may depend on personality (Ellermeier et al. 2001; Västfjäll 2002). Like humans, other animals differ in how they cope with environmental challenges (also referred to as animal personality; Gosling 2001; Groothuis & Carere 2005), so that taking animal personality traits into account can contribute to a better understanding of the effects of noise on a larger scale. Indeed, personality-dependent effects may lead to microevolutionary changes within populations owing to a reduction of within-group diversity in noisy areas. Personality traits in animals are commonly described along a bold–shy or slow–fast explorer continuum and are measured in standardized tests using novel objects or environments as mild stressors. Quantifying behavioural characteristics in these ways has been useful in quantifying consistent individual differences in behaviour that explain variation in a broad range of behavioural and life history traits across various taxa (Wolf et al. 2007; Sih & Bell 2008; Bell et al. 2009; Dingemanse et al. 2010). A series of studies on great tits, *Parus major*, one of the best studied model organisms for ecology and animal personality traits in the wild, has shown that exploratory behaviour in a novel room (as an operational measure of personality) explains, among other traits, variation in mate choice (van Oers et al. 2008), resource defence (Amy et al. 2010), aggression (Verbeek et al. 1996), learning (Titulaer et al. 2012) and fitness (Dingemanse et al. 2004; Both et al. 2005). Thus, variation in the way animals cope with noise may depend not only on the nature of the noise, but also on their own characteristics, that is, their personality traits.

We used wild great tits with known personality traits, to investigate the effects of masking and nonmasking noise on nestling begging behaviour and parental nestbox visits and to test whether the kind of noise and the personality of the individual affect an individual's response. During parental care, masking and nonmasking noise may interfere differently with the foraging and provisioning behaviour of parents, which may be reflected in a reduced number of visits to the nestlings. To determine the effects of noise on begging behaviour and parental nestbox visits, we conducted automated playback experiments at nestboxes using three experimental treatments: (1) mask-and-disturb noise (noise covering the frequency spectrum of nestling begging calls), (2) disturb-only noise (noise above and below the frequency spectrum of begging calls) and (3) silent control. Parental nestbox visits were recorded automatically using transponder and video devices complemented by audio recordings of nestlings begging inside the nestbox. We expected that masking noise would have stronger effects on begging and parental behaviour than nonmasking noise, regardless of sex or personality, because parents will be less able to gauge information on offspring need from begging calls in addition to being distracted by the stimulus. During noise that disturbs but does not mask the begging calls, parents are still able to hear their offspring and thus may still feed them according to their demand. Moreover, we expected that slower explorers would be better able to cope with the stressors as they are assumed to be more flexible in their behavioural responses (Verbeek et al. 1994) and thus adjust quicker to changes in the environment (Exnerova et al. 2009; Guillette et al. 2010; Amy et al. 2012). Because personality effects can differ between the sexes (Dingemanse et al. 2004; Titulaer et al. 2012), we also took the sex of the parent and the personality of the respective partner into account in the analyses.

## METHODS

### *Subjects and Study Site*

The study was conducted from March to May 2011 at West-erheide, near Arnhem, the Netherlands, using a long-term nestbox population of personality-typed great tits. The site (ca.100 ha) contains more than 200 regularly distributed nestboxes with another ca. 200 nestboxes in adjoining areas. Nestboxes were initially checked weekly for nest building and egg laying. Hatching dates were determined by checking the nestboxes daily around the anticipated hatching date, which is around 12 days after the last egg is laid. In this study we used 39 breeding pairs and their offspring as subjects for noise playback experiments. The playback experiments were conducted from 6 to 18 May, when offspring were 9–11 days old and each nestbox was used only once. All parents were equipped on one leg with an RFID transponder (pit tag), glued to three colour rings. Birds were equipped with the transponders either during roosting at night in nestboxes prior to breeding (in early March), or by catching the parents when offspring reached day 5 posthatch, by trapping them with automatic doors that close the nestbox entrance after nestbox visits.

### *Experimental Set-up and Design*

To control for effects of differences in the onset of breeding and for weather conditions, we assigned three synchronous nestboxes to triplets to be tested on a given day. In total, 39 nestboxes were used of which 33 nestboxes were assigned to 11 triplets with each triplet containing each treatment, and six nestboxes assigned to three duos consisting of two treatments. In two cases recordings failed, leaving 37 boxes. Playback treatments were (1) mask-and-disturb noise ( $N = 13$ ), (2) disturb-only noise ( $N = 13$ ) and (3) no noise (silent control;  $N = 11$ ). The mask-and-disturb noise (bandwidth 10 kHz) ranged from 2.5 to 12.5 kHz, covering the frequency range of nestling begging calls (peak at ca. 7.6 kHz, bandwidth ca. 6–9 kHz at –15 dB from the peak; Fig. 1). The disturb-only noise (also a bandwidth of 10 kHz to standardize the two noise treatments) ranged from 1.5 to 6.5 kHz and from 9.5 to 14.5 kHz, and therefore excluded the main frequency range of nestling calls (Fig. 1). The noise was synthesized as a 1 min white noise file using Adobe Audition on a PC. The noise file had smooth envelope ramps increasing the amplitude over the first 25 ms (and decreasing over the last 25 ms) to avoid distortions by the loudspeaker caused by sudden noise onsets and offsets (Naguib et al. 2000). The noise was then bandpass filtered according to the spectral characteristics of the two noise treatments and replicated 60 times for each (see below). Adobe Audition was also used to generate the file with no noise (silence) which was also replicated 60 times for each noise treatment (see below). The noise was broadcast at 80 dB (measured over the full spectrum; thus at a lower volume within each frequency band), as measured with a Voltcraft digital sound-level meter inside the nestbox. In a pilot experiment in 2010, we had placed the loudspeaker outside the nestbox (revealing similar effects as those reported below) but here decided to follow methods used by others (Leonard & Horn 2008) and placed the loudspeaker inside the nestbox, mainly because birds respond to visual changes outside their nestbox in a personality-dependent way (Garamszegi et al. 2008). Begging calls were still audible (and just visible on the spectrogram) within the masking noise.

All playback experiments were conducted in the morning, starting between 0815 and 1030 hours. The evening before an experiment started with a given nestbox, nestbox lids were replaced by lids with a built-in camera and a small loudspeaker (Goobay Soundball speaker; positioned so that it faced the nest). Additionally, a small microphone was placed inside the nestbox, at

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