

# Article

# Snake-like calls in breeding tits

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# Abstract

Hole-nesting tits belonging to the family Paridae produce a hissing display that resembles the exhalatory hiss of a snake. When a predatory animal enters the nest hole of a tit, tits often hiss vigorously, while lunging their head forward and shaking their wings and tail, until the intruder retreats. We assessed the acoustic similarity between such hiss calls from 6 species of tits, snake hisses, and tit syllables used in alarm vocalizations, as well as white noise as a control. Tit hiss calls showed a high degree of similarity with snake hisses from 3 different snake families. Tit hisses had lower similarity to syllable alarm calls, suggesting convergence of tit hisses in their spectral structure. Hiss calls would only be effective in protecting nest boxes if nest predators responded to these calls. In order to test this hypothesis, we trained individual Swinhoe's striped squirrels, Tamiops swinhoei hainanus, a common predator of egg and nestling tits, to feed at feeders in proximity to nest boxes. We compared the aversive response of squirrels to tit's hiss calls and white noise, presented in random order. Squirrels showed a higher degree of avoidance of feeders when hiss calls were played back than when white noise was presented. In conclusion, our study suggests that hole-nesting birds have evolved convergent snake-like hiss calls, and that predators avoid to prey on the contents of nest boxes from which snake-like hisses emerge.

Key words: frequency-dependent selection, hiss call, mimicry, squirrels, tits

In evolutionary biology, mimicry refers to the evolved resemblance between one organism and another object, which is often another species (the model). For instance, mimicry occurs when a mimic resembles a dangerous model, thereby avoiding or reducing the risk of attack by a predator. The efficiency of such mimics relies on confusion of the mimic with the model (Bates 1862; Ruxton et al. 2004). Well-known examples of mimicry involve vocal signals. For instance, fork-tailed drongos Dicrurus adsimilis produce almost perfect false alarm calls to scare other species and steal their food (Flower et al. 2014). Similarly, when burrowing owls (Athene cunicularia) are scared, they produce hisses that resemble a rattlesnake's rattle (Rowe et al. 1986). A key review of this topic argued that

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most reported cases of vocal mimicry lacked solid experimental evidence, and that vocal mimicry requires a specific learning process to adopt model features (Kelley et al. 2008). This restrictive definition, however, favors one particular mechanism underlying the origin of mimicry while disregarding evolutionary convergence (Dalziell and Welbergen 2016). Furthermore, it misses one fundamental point behind the origin of mimicry, namely its function: the function arises from an increase in fitness of the mimic through the production of a trait, which is mistaken by the perceptual system of the receiver (Vane-Wright 1980; Wickler 2013).

Snakes produce a highly defensive hiss that they use when they are cornered or challenged. Snake hisses are poorly structured

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sounds, and they have been described as "nothing more than loud, forced ventilation" (Young et al. 1999). They are present in all snake taxa although they are far more common in terrestrial than in arboreal species (Young 2003). Not all snake species hiss in the same way; although some hiss through the nose, others do so through the mouth, and there are large differences in hiss duration (Young 2003). However, there are few systematic studies that tackle the evolution of these signals. The only comparative analysis that we know included only 7 species and concluded that there were no important differences among taxa (Young et al. 1999). However, a more recent study has shown a possible case of minicry of viper hisses by the harmless viperine snake *Natrix maura* (Aubret and Mangin 2014).

Many species of birds produce a hissing display that closely mimics the sound of snakes when confronted by humans or other potential predators inside a nest hole or a nest box (e.g., Hinde 1952; Löhrl 1964; Gompertz 1967; Klump and Shalter 1984; Krams et al. 2014; Møller et al. 2020). Incubating or brooding female great tits hiss when encountering nest intruders (Krams et al. 2014) even before the intruder has entered the nest (Electronic Supplementary Material Video S1). The female great tit first raises its head to ca. 60° above horizontal, with the white cheek-patches ruffled and the crown feathers sleeked, eyes "bulging," and wings raised. The bird repeatedly rises on its tarsi, uttering an explosive hiss while the head being thrust forward like a snake, violently snapping shut its mandibles (Hinde 1952; Gompertz 1967). Simultaneously, the wings are brought sharply down, often striking against the sides of the nest cavity, while the tail is fanned and the outermost tail feathers are conspicuously displayed. Most predators retreat following such an encounter with a snake mimic, thereby increasing the survival prospects of the hissing bird (Krams et al. 2014).

To human perception, a tit hiss is remarkably similar to a snake hiss. Different snakes show a high degree of acoustic similarity in their hiss, and this sound is characterized by wide frequency pattern with the poor tonal structure typical of white noise (Young et al. 1999; Young 2003; Aubret and Mangin 2014). A similar example of convergence concerns the similarity between burrowing owl hisses *Athene cunicularia* and rattlesnake hisses (Owings et al. 2002; Rainey and Grether 2007). Thus, there is a low level of acoustic specialization in the sounds produced by snakes, providing an efficient common warning display to improve defence as in Müllerian mimics, possibly reinforcing the function of the scary hiss even when many snakes are not venomous and hence not as dangerous.

The high degree of similarity in snake and tit hisses makes this an ideal model for the study of the evolution of mimicry by birds. Indeed, spectrograms of snake hisses and hisses made by great tits are strikingly similar, consisting of highly repeated syllables of similar duration and frequency (Cramp and Perrins 1993, p. 273; Young et al. 1999, p. 2285). Previous studies repeatedly argue that tit hisses are a prime example of mimicry (Sibley 1955; Krams et al. 2014), but no study so far has objectively measured sound similarity or tested for a reaction of potential predators to the hiss.

Snake predation is a key selective process for bird reproduction (Weatherhead and Blouin-Demers 2004). It is very common on breeding tits inside their cavities (Møller et al. 2020), and indeed snakes are commonly found within the same type of cavities (Møller et al. 2020). Common hole-nesting birds of the Paridae family have been reported to mimic the hiss of venomous snakes. When humans place their hands near the nest of tits belonging to this family, the incubating female performs a hissing display that mimics the inhalation hiss of a viper or that of another snake. In a previous study

(Møller et al. 2020), we have shown that females that flew away from their nest box were less likely to hiss than those that did not fly away. This pattern is consistent with great tits either cautiously flying away or staying put on their nest while actively defending it. Tits that flew away produced fewer chicks than those staying and hissing. In addition, the hissing display was more common when snakes were more abundant, both seasonally and geographically. The frequency of nest predation was higher in sites with no snakes, and the frequency of predation increased with decreasing frequency of hissing display (Møller et al. 2020).

Here we extend our first study by experimentally testing for functional explanations of hissing displays in tits. First, we recorded hisses from incubating tits and compared the acoustic structure of these hisses to snake hisses, species-specific tit alarm calls and white noise, thereby testing for convergence in hisses between tits and common snakes. Second, we tested how a common predator of eggs and nestlings in cavity nests of tits, Swinhoe's striped squirrels *Tamiops swinhoei hainanus*, fled in response to playback of white noise versus hiss calls.

## **Material and Methods**

#### Recording hissing displays

We obtained a total of 40 recordings of different birds of the Paridae subfamily performing defensive hissing displays while incubating (see Supplementary Table S2 and Supplementary Figure S5). Most recordings for *Parus major* and *P. monticolus* were collected by the authors across China (see below for details of field sites). When we visited nest boxes, we opened the lid of the box and placed a hand on the rim. This often led the incubating female to produce hiss calls, and this behavior was recorded. An example of a hissing display including sounds and movements can be found in the attached video (Electronic Supplementary Material Video S1).

We added recordings for other Paridae species from Xenocanto (www.xeno-canto.org), the Macaulay Library (macaulaylibrary.org) of the Cornell Lab of Ornithology (Ithaca, USA), and the Wildlife Sound section of the British Library (sounds.bl.uk). These additional recordings came from an area from Pakistan across the Middle East and Europe to the UK (see Supplementary Table S2).

Our recordings were obtained with a portable video camera (Sony HDR-PJ30EDV; Shanghai Suoguang Electronics Co. Ltd., China) or a digital recorder (JWD DV-58G; JWD Inc., Shenzhen, China). Soundtracks were extracted from video files by means of Audacity software, and all sound files were converted to mono 44.1 kHz. We avoided low-quality recordings with either low signal-to-noise ratios, or those that had been filtered within the frequency band that we chose for comparisons (200–7,000 Hz).

#### Sound similarity analysis

Hissing displays contain both mechanical sounds and vocal hisses (see Results section). For sound analysis, we chose high-quality tit recordings with clear, long hisses (n = 18, Supplementary Figures S5). From each recording, 3–5 high-quality individual hisses were sampled for each of the recordings (mean = 3.7, standard deviation [SD] = 0.64). To perform acoustic cross-correlations, it is important to control for differences in sound duration and amplitude (Khanna et al. 1997). From each call, we selected a series of randomly chosen 100 ms clips using the analysis software Raven Pro. 1.5. (Center for Conservation Bioacoustics, 2014) and saved it as individual amplitude-standardized wav files. We made sure that this selection

was not overlapped by other mechanical sounds such as those produced by the beak and wings of the bird when startled in the box (see Supplementary Video S1).

Cross-correlation is a bioacoustics technique that aims to compare the similarity of 2 sounds by analyzing the degree of overlap between 2 signals (Khanna et al. 1997). Since amplitude and duration were controlled by selecting samples of fixed length and standardizing amplitude, the correlation score computes the similarity in spectral shape between samples.

We obtained 3 different categories of sounds for comparison with hisses: white noise, snake hisses, and tit alarm calls. For the white noise, we obtained 2 different white noise sample recordings (Uniform and Gaussian distributions) from www.audiocheck.net. We included white noise so as to count with a random broad frequency signal, without tonal structure, which could be used as a measurement stick for comparisons. However, white noise is an artificial sound that does not occur as such in nature.

Snake recordings were obtained from sound libraries. We used all species with recordings of hisses that we could find (Supplementary Table S3 and Supplementary Figures S6), and chose one recording for each of the following snake species: Colubridae: *Coronella austriaca, Malpolon monspessulanus, Natrix natrix,* and *Pituophis melanoleucus*; Elapidae: *Naja naja, Ophiophagus Hannah,* and *Walterinnesia aegyptia*; and Viperidae: *Bitis arietans, B. gabonica, Cerastes vipera, Vipera berus, V. raddei,* and *V. russelii* (see Supplementary Table S3 for details of the recordings). We chose expiratory hisses rather than inhalatory hisses because the former hisses are louder and are produced by all snakes, whereas some species do not have the inhalatory hiss component (Aubret and Mangin 2014). As for the bird hisses and calls, we avoided poor quality recordings and those with low signal-to-noise ratios.

Control calls were also obtained from bird sound libraries. We chose high-quality recordings and we attempted to find a wide variety of calls uttered in alarm contexts, and selected 4–7 syllables common and distinct for different species (see Supplementary Table S4 and Supplementary Figures S7).

Peak cross-correlations between spectra were calculated in Raven Pro 1.5 using a Hahn window with FFT (Fast Fourier Transform) length of 1,024 samples (61.9 Hz frequency width), a frequency grid of 1,024 samples (grid spacing = 43.1 Hz), and a time grid of 50% overlap (hop size = 512 samples). We band-filtered all calls between 200 and 7,000 Hz, and we included amplitude normalization. Before deciding on these parameters, we also explored FFT lengths of 512 and 256, which provided extremely similar cross-correlation scores (Khanna et al. 1997).

### Study areas

The great tit field study was conducted in Southern and Central China between March and June 2013, at 2 places: Diaoluoshan National Nature Reserve ( $18^{\circ}40'$ N,  $109^{\circ}55'$ E), Hainan, which is covered with tropical forests (see Liang et al. 2016 for more details), and at Dongzhai National Nature Reserve ( $32^{\circ}15'$ N,  $114^{\circ}25'$ E), Henan, an evergreen broadleaf forest between subtropical and temperate zones (see Yang et al. 2012 for detailed descriptions of the study sites). All nest boxes were made of wood and of a similar size (35 cm in height and 11 cm in width and depth, with a 4-cm diameter entrance hole). They were all situated at a height of 4–5 m along roads near forest edges. Because snakes or mammals had depredated nests in 2012, the poles were provided with a plastic cover in 2013 to prevent access to nests by nest predators.

#### Field and lab experiments on squirrels

We tested whether Swinhoe's striped squirrels Tamiops swinhoei hainanus, a common predator of eggs and nestlings of birds in cavity nests, reacted to playback of white noise or hiss calls in a foraging context. This was done on 14 different squirrels on the Campus of Hainan Normal University, Haikou, Hainan Island, China (19°59'52.13"N, 110°20'20.06"E). We made sure that we used different individuals by conducting the experiment in distant sites across the large campus, at distances greater than observed home ranges. This is an open habitat with scattered bushes and trees. This tropical site is close to the coast at an elevation of 13 m. a.s.l. We first attracted squirrels to peanuts provided on the top of a nest box (3-4 m above ground), waiting at a distance of 15-20 m until the squirrel took the first peanut. This was done to ensure that squirrels had learned the location and the nature of the peanut reward. When the second peanut was provided, we played back the recording of either white noise or hisses (random order), and we determined the distance in units of 10 cm to the location where the squirrel moved to eat the peanut. The playback speaker was concealed inside the nest box. We determined the proportion of the second peanut that was taken when a hiss or white noise was played back at the same time as when the second peanut was provided.

In the second experiment that took place in the lab with 9 different squirrels that were allowed to eat peanuts, we played back either white noise or hiss calls when the squirrels started eating. The response to playback was quantified as whether the squirrels stopped eating depending on the type of call played back (white noise or hiss call).

Both white noise and hisses lasted for 3 min. White noise was used as a control stimulus with the range 1-10 kHz. We used 3 different hiss recordings with 14 different squirrels in order to avoid pseudoreplication. Each individual squirrel received 1 single hiss recording. These 3 hisses were recorded from 1 individual in Jilin (named great tit\_1) and 2 individuals in Hainan (named great tit\_2 and great tit\_3) in the 2015 breeding season. Background noise and calls of other species were deleted from these recordings using Goldwave 5.25 (GoldWave Inc., Canada). Call rate was 38 notes per min in great tit\_1 recording, 21 notes per min in great tit\_2 recording, and 25 notes per min in great tit\_3 recording. We adjusted the maximum amplitude to 75-85 dB (measured at a distance of 1 m above the speaker) when conducting playback. This amplitude approximated the natural amplitude of great tit hisses in the field. Playback was made with a BV210 Bluetooth speaker (80 Hz-18 kHz, Shenzhen See Me Here Electronic Co. Ltd., China). The experiments were taped from a distance of 15 m using a portable Sony HDR-PJ30EDV (Shanghai Suoguang Electronics Co. Ltd., China), and observations were taken from the videos in the lab. Squirrels were 0.5 m from the speaker.

#### Ethical standards

The experiments comply with the current laws of China, which is the country were these were performed. Experimental procedures were in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (permit no. HNECEE-2012-003).

#### Statistical analyses

In the case of the bioacoustics analyses, we took several clips (3-5, mean = 3.76, SD = 0.62) from each sound recording to increase reliability. However, to avoid pseudo-replication, in each comparison of 2 recordings, we calculated the average of the cross-correlation matrix of all clips, and this single value was used for each

comparison. We built random models in R (package "lme4"), considering both recordings being compared as random factors nested within each category, as well as tit species. *P* values were calculated for fixed effects in mixed models by using the Kenward–Rogers approximation (package "afex" in R). Differences between factor levels were obtained by the "lsmeans" R package, following Tukey's correction for multiple comparisons. The cross-correlation scores were normalized by means of the Box–Cox procedure to maximize normality (package "MASS" in R).

In the case of behavioral experiment, we compared the reaction of 14 squirrels with either white noise or hisses, when the second peanut was provided, by comparing the distance the squirrels retreated using a Wilcoxon matched-pairs signed-rank test. Likewise, we determined the proportion of the peanuts that were taken when a hiss or white noise was played back again using a Wilcoxon matched-pairs signed-rank test.

Similarly, in the second experiment for 9 squirrels in the lab, we tested whether squirrels that had just been allowed to eat continued or stopped eating, when we played back white noise or a hiss call, using a Wilcoxon matched-pairs signed-rank test. Statistical analyses of the playback experiment were made using JMP (SAS 2012).

# **Results**

#### Hiss calls in hole-nesting birds

Hiss calls were produced by incubating birds when disturbed by the presence of a researcher who opened the nest box. The birds

typically crouched on the nest and produced a display, which consisted of 1 or 2 different components: a mechanical sound produced by a quick snap of the wings on the walls of the box (Supplementary Information: Video S1) and a hissing sound (Figure 1). In most species, the 2 components appear together, except for great tits, in which 40% of displays lacked the hiss. Displays varied greatly in length among individuals (Supplementary Table S2), but species did not differ statistically in duration ( $F_{5,34} = 2.28$ , P = 0.07) or calling rate ( $F_{5,34} = 0.35$ , P = 0.88). Among the 2 species that we observed in the field, hiss calls occurred in 27% of 314 breeding great tits in nest boxes in Denmark and in 71% of 14 tits in China. Hence hissing is a common and widespread behavior among breeding great tits and its prevalence varies among areas.

# Similarity in the spectral structure of bird hiss calls and snake hisses

We performed cross-correlation analyses between a total of 24 hisses belonging to 5 different tit species (Supplementary Table S2), hisses of 14 snake species belonging to the families Viperidae, Elapidae, and Culebridae (Supplementary Table S3), white noise samples (a control), and a selection of syllables commonly used in alarm calls by tits (Supplementary Table S4). The resemblance between tit and snake hisses was in general very high (Figure 1 and Supplementary Information S5 and S6). To be able to understand cross-correlation figures, it is important to consider that the mean (SD) cross-correlation that we obtained between 2 clips of the same signal is 0.45 (0.09). A mixed model comparing cross-correlation

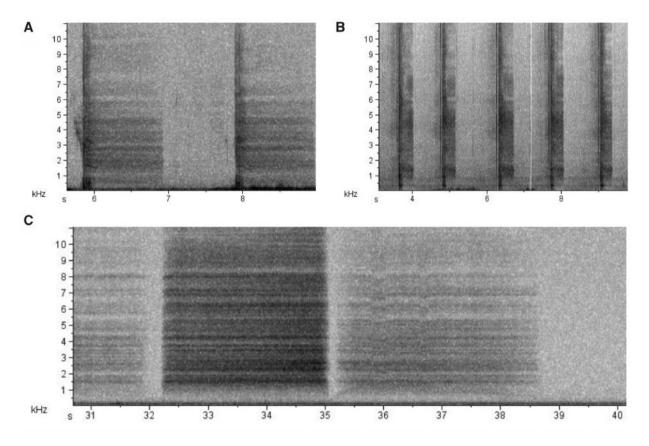


Figure 1. Two examples of tit hisses: (A) *Parus major* (Xenocanto, code XC71684, recording by Marco Dragonetti) and (B): *Parus monticolus* (authors' recording GB22), as well as a typical snake hiss (C): *Vipera berus* (British Library, code BLOWS2311, by Reg Genever), showing both the exhalatory and the inhalatory components. Spectrograms were produced in Raven Pro. 1.5, using a Hahn window (1,024 samples, 61.9 Hz filter bandwidth) with a frequency grid of 1,024 samples (grid spacing = 43.1 Hz), and a time grid of 50% overlap (hop size = 512 samples).

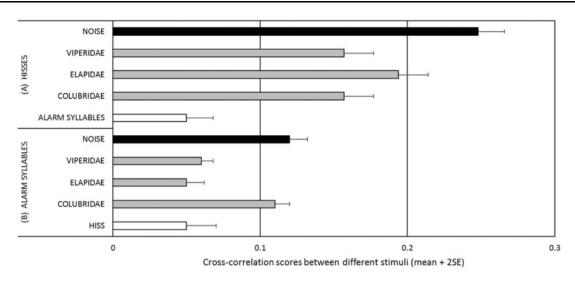


Figure 2. Cross-correlation scores between tit hisses and other calls. (A) Bars show mean cross-correlation scores (+2 SE) between tit hisses and white noise (black), snake hisses (gray), and tit alarm syllables (white). (B) Bars show mean cross-correlation scores (+2 SE) between alarm syllables and white noise (black), snake hisses (gray), and tit hisses (white). The figure shows direct descriptive statistics from the data, untransformed, and not corrected by tit species and uneven sampling.

scores between tit hisses and the remainder of the sounds showed a significant difference among categories ( $F_{4,21.7} = 28.04$ , P < 0.001): resemblance of tit hisses with snake hisses was intermediate between alarm syllables (lowest) and white noise (highest) (Figure 2A). Comparisons between estimated means showed that resemblance with alarm syllables was significantly lower than for the rest of the categories (*t*-ratio > 5.5, P < 0.001), and resemblance with noise was larger than with Colubridae and Viperidae (*t*-ratio > 3.1, P < 0.05). Noise and Elapidae hisses showed similar levels of resemblance with tit hisses, and tit hisses showed similar cross-correlations with all snake families (Tukey *t*-ratio < 1.5, P > 0.53).

In contrast, alarm syllables were much less similar to snake hisses, tit hisses, or white noise (Figure 2B), and cross-correlation scores did not differ among sound categories ( $F_{4,12.01} = 2.45$ , P = 0.10). Pairwise comparisons showed no statistically significant differences among groups (Tukey *t*-ratio < 2.46, P > 0.16).

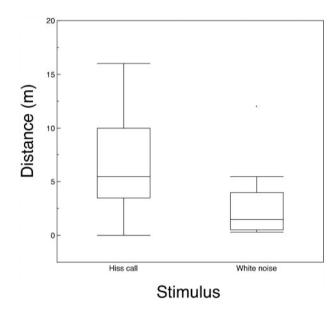
#### Predators respond to and avoid hiss calls

The median distance from the location where the peanut was eaten and the box with playback of hiss calls was 5.5 m, while the distance was shorter (median = 1.5 m), when playing back white noise (Figure 3; paired *t*-test: t=3.28, df = 13, P = 0.0066). While only 43% of 14 squirrels took a peanut when we played back a hiss call, all 14 did so when we played back white noise (Wilcoxon matchedpairs signed-rank test, S = -18, P = 0.0078).

A much larger percentage of squirrels stopped eating and showed an escape response when we played back hisses than when playing back white noise. A total of 78% of 9 squirrels played back hiss calls versus 11% of 9 squirrels played back white noise (Wilcoxon matched-pairs signed-rank test, S = 10.5, P = 0.031).

#### Discussion

Snake-like behavior including hiss calls has been documented in more than 20 species of birds, mainly tits belonging to the family Paridae but also other hole nesters (e.g., Sibley 1955; Møller et al. 2020). Human observers typically report that the hiss of birds resembles that of snakes, and humans are startled even when hearing



**Figure 3.** Box plots of distance from eating location for 14 Swinhoe's striped squirrels to nest boxes playing back white noise or hiss calls. The box plots show medians, quartiles, 5- and 95-percentiles, and an extreme value.

the hiss repeatedly (Sibley 1955). Tit hiss calls are similar in spectral structure to snake hisses from 3 different snake families. Syllable alarm calls had a much lower similarity to snake hisses than did tit hisses, showing convergence of tit hisses, but not of tit calls to snake models. Although common squirrels were able to distinguish between hiss calls and white noise, they were more cautious when encountering playback of hisses than playback of other types of calls.

Our spectrographic analysis showed that tit hisses were similar in spectral structure to snake hisses, both not very far from white noise. In contrast, typical syllables used by tits in their alarm calls showed a very low resemblance to hisses. Thus, by choosing hisses, tits produce a signal similar to that used by snakes. The high resemblance of tit and snake hisses with artificial white noise suggests that these signals cover a wide range of frequencies without minimal tonal structure, following a generalized structural rule that links sound harshness with aggressive intention (Morton 1977).

For Batesian mimicry to evolve, a perfect mimic is not necessary as long as the receiver of the signal perceives the signal as if produced by the noxious species (Dalziell et al. 2015). Rare variants relative to the abundance of models have a disproportionate advantage in terms of elevated survival resulting in stable polymorphisms (Mallet and Joron 1999). Predator receivers have been assumed to gain information only from direct experience with the dangerous model (Speed and Turner 1999; Ruxton et al. 2004). However, that cannot always be the case because death would then almost invariably result from encounters with venomous snakes. We found no differences in similarity between tit and snake hisses of 3 different families, suggesting that snakes are likely to have converged on a common warning display to improve defence in terms of Batesian mimicry. This may have facilitated the common evolution of inherited snake recognition mechanisms in most animals.

It is debatable whether vocal mimicry requires learning in order to evolve (Kelley et al. 2008; Dalziell et al. 2015). Vocal learning is not a likely mechanism for the evolution of hisses in birds since birds would be required to be exposed to this sound and subsequently learn it. However, a hiss is only uttered when snakes are threatened by a predator, which is an unlikely event to be witnessed by shortlived birds. Thus, it is more likely that this is a case of evolutionary convergence probably favored by a widespread motivation-structural rule that makes a wide-frequency harsh hiss a noxious signal (Morton 1977; Silaeva 1996). Learning is an unlikely prerequisite for this type of vocal mimicry, and we support the view that mimicry is best defined by its functional consequences in relation to the receiver of the signal (Daziell et al. 2015). The efficiency of hiss calls relies on the fact that predators or competitors respond to hisses, and that mimics thereby gain an advantage in terms of survival prospects and reproduction (Wickler 2013). Here we tested whether a common mammal predator of the contents of nest cavities responded by fleeing when exposed to hiss calls or white noise (a control). We showed both in the field and in the lab that Swinhoe's striped squirrels kept a longer safe distance to a nest box that played back hisses compared with a box that played back white noise. Squirrels avoided boxes that played back hisses rather than white noise, showing that squirrels associated tit hisses with something more dangerous than white noise. These findings provide evidence of a common predator of great tits responding to the playback of hiss calls.

The fact that squirrels were able to detect the difference between noise and hisses despite the high spectrographic similarity between the 2 signals that we found suggests that there is enough information in the calls to convey specific and context-dependent meaning. In addition to spectral structure, the duration, amplitude variation, and the additional sounds that accompany a hiss (wing snap, mechanical sounds of the bird as it starts in the nest) likely provide additional richness to the signal.

Different species of cavity-nesting birds vary in the finer structure of their hiss calls, but the propensity to emit a hiss also differs among species of birds. We hypothesize that such differences may be linked to the probability of nest take-overs or the risk of predation by snakes.

In conclusion, tit hisses have converged toward snake-like hiss calls. Such resemblance had significant effects on the response of Swinhoe's striped squirrel, a common nest predator, because tits behaved more cautiously toward playback of hisses compared with playback of white noise. These findings suggest that tits gain fitness advantages by emitting hisses that resemble those produced by venomous snakes that constitute the real danger.

# **Data Accessibility**

Data from this study will be made available upon acceptance of this manuscript.

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# **Conflict of Interest**

The authors declare that all authors have no conflict of interest.

# **Supplementary Material**

Supplementary material can be found at https://academic.oup.com/cz.

# References

- Aubret F, Mangin A, 2014. The snake hiss: potential acoustic mimicry in a viper-colubrid complex. *Biol J Linn Soc* **113**:1107–1114.
- Bates HW, 1862. Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. *Trans Linn Soc Lond* 23:495–566.
- Center for Conservation Bioacoustics, 2014. Raven Pro: Interactive Sound Analysis Software (Version 1.5). Ithaca (NY): The Cornell Lab of Ornithology.
- Cramp S, Perrins CM, 1993. *The Birds of the Western Palearctic*. Vol. 7. Oxford: Oxford University Press.
- Dalziell AH, Welbergen JA, 2016. Mimicry for all modalities. *Ecol Lett* **19**: 609–619.
- Dalziell AH, Welbergen JA, Igic B, Magrath RD, 2015. Avian vocal mimicry: a unified conceptual framework. *Biol Rev* **90**:643–668.
- Flower TP, Gribble M, Ridley AR, 2014. Deception by flexible alarm mimicry in an African bird. *Science* **344**:513–516.
- Gompertz T, 1967. The hiss-display of the great tit *Parus major*. *Vogelwelt* 88: 165–169.
- Hinde RA, 1952. The behaviour of the great tit *Parus major* and some other related species. *Behaviour Suppl* 2:1–201.
- Kelley LA, Coe RL, Madden JR, Healy SD, 2008. Vocal mimicry in songbirds. *Anim Behav* 76:521–528.
- Khanna H, Gaunt SLL, McCallum DA, 1997. Digital spectrographic cross-correlation: tests of sensitivity. *Bioacoustics* 7:209–234.
- Klump GM, Shalter MD, 1984. Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm calls. II. The functional significance and evolution of alarm calls. Z Tierpsychol 66: 189–226.
- Krams I, Vrublevska J, Koosa K, Krama T, Mierauskas P et al., 2014. Hissing calls improve survival in incubating female great tits *Parus major*. Acta Ethol 17:83–88.

- Liang W, Møller AP, Stokke BG, Yang C, Kovařík P et al., 2016. Geographic variation in egg ejection rate by great tits across 2 continents. *Behav Ecol* 28:859–865.
- Löhrl H, 1964. Verhaltensmerkmale der Gattungen Parus (Meisen), Aegithalos (Schwanzmeisen), Sitta (Kleiber), Tichodroma (Mauerläufer) and Certhia (Baumläufer). J Ornithol 105:153–181.
- Mallet J, Joron M, 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annu Rev Ecol Evol Syst* 30:201–233.
- Møller AP, Flensted-Jensen E, Liang W, 2020. Behavioral snake mimicry in breeding tits. *Curr Zool* 67. doi: 10.1093/cz/zoaa028.
- Morton ES, 1977. Occurrence and significance of motivation structural rules in some bird and mammal sounds. *Am Nat* 111:855–869.
- Owings DH, Rowe MP, Rundus AS, 2002. The rattling sound of rattlesnakes Crotalus viridis as a communicative resource for ground squirrels Spermophilus beecheyi and burrowing owls Athene cunicularia. J Comp Psychol 116:197–205.
- Rainey MM, Grether GF, 2007. Competitive mimicry: synthesis of a neglected class of mimetic relationships. *Ecology* 88:2440–2448.
- Rowe MP, Coss RG, Owings DH, 1986. Rattlesnake rattles and burrowing owl hisses: a case of acoustic Batesian mimicry. *Ethology* 72:53–71.
- Ruxton GD, Sherratt TN, Speed MP, 2004. Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry. New York: Oxford University Press.

- SAS Institute Inc., 2012. JMP. Version 10.0. Cary (NC): SAS Institute Inc.
- Sibley CG, 1955. Behavioral mimicry in the titmice (Paridae) and certain other birds. *Wilson Bull* 67:128–132.
- Silaeva OL, 1996. Hissing as a multifunctional and interspecific signal of animals. *Izvest Akad Nauk Ser Biol* 5:628–635.
- Speed MP, Turner JRG, 1999. Learning and memory in mimicry: II. Do we understand the mimicry spectrum? *Biol J Linn Soc* 67:281–312.
- Vane-Wright RI, 1980. On the definition of mimicry. *Biol J Linn Soc* 13:1–6. Weatherhead PJ, Blouin-Demers G, 2004. Understanding avian nest preda-
- tion: why ornithologists should study snakes. J. Avian Biol 35:185–190.
- Wickler W, 2013. Understanding mimicry with special reference to vocal mimicry. *Ethology* **119**:259–269.
- Yang C, Liang W, Cai Y, Wu J, Shi S et al., 2012. Variation in russet sparrow *Passer cinnamomeus* breeding biology in relation to small-scale altitudinal differences in China. *Zool Sci* **29**:419–422.
- Young BA, 2003. Snake bioacoustics: toward a richer understanding of the behavioral ecology of snakes. *Q Rev Biol* 78:303–325.
- Young BA, Nejman N, Meltzer K, Marvin J, 1999. The mechanics of sound production in the puff adder *Bitis arietans* (Serpentes: Viperidae) and the information content of the snake hiss. *J Exp Biol* 202: 2281–2289.

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