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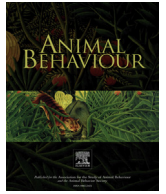
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Mechanisms of mobbing call recognition: exploring featural decoding in great tits

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Recent research on bird calls has unearthed a striking result: birds sometimes react to the calls of other species that are neither geographically nor phylogenetically close. One mechanism explaining this response may be the recognition of specific acoustic features, also present in their own vocalizations, rather than the recognition of complete notes, with the result that unfamiliar calls may be understood if they contain the critical feature. Parids and other passerines produce mobbing calls with similar properties that are responded to across species (i.e. noisy, large frequency range notes reaching low frequencies and with numerous harmonics) that are therefore good candidates for recognition based on features. In a playback experiment, we explored the featural interpretation hypothesis by testing the response of free-ranging great tits, *Parus major*, to artificial mobbing calls with varying acoustic properties. We first confirmed that they respond to artificial calls sharing all the targeted spectral properties (large frequency range, low frequency, noise and harmonics). In contrast, great tits did not respond to calls with the same rhythmicity but without the targeted features. We then tested whether great tits respond to calls that possess only one of the four above-mentioned properties. We show that great tits did not respond to any of the four treatments, and therefore no single specific spectral feature seems likely to explain great tits' response to unknown calls. We discuss alternative mechanisms for decoding novel calls, notably through a similarity threshold.

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Acoustic communication plays a crucial role in animals and is especially significant among specific taxonomic groups such as birds and anurans (Bradbury & Vehrencamp, 2011). This form of communication predominantly takes place between individuals of the same species, but research has described a growing number of occurrences where communication happens between distinct species (Krams, 2010; Magrath et al., 2015; Pepperberg, 2017). This interspecific communication emphasizes the importance of networks in transfers of information (Farine et al., 2015) and the various costs and benefits implicated in such exchanges (Baigrie et al., 2014). In the case of birds, this interspecific communication often occurs in winter flocks and mostly informs receivers about

the availability of food (Mahurin & Freeberg, 2009) or potential threats (Magrath et al., 2015).

The decoding processes involved in heterospecific communication are diverse. Several studies suggest the involvement of learning mechanisms (Haff & Magrath, 2012; Keen et al., 2020). Indeed, several avian species have exhibited the ability to associate a novel sound with a specific stimulus (i.e. associative learning, Curio et al., 1978; Dutour, Léna, et al., 2019; Vieth et al., 1980), which may provide an understanding of how distinct species are able to respond to each other's alarm calls. On the other hand, certain species may react to unfamiliar calls, rendering the theory of learning improbable (Magrath et al., 2015). These unfamiliar calls can be allopatric species' calls (Fallow et al., 2011) or even artificial calls (Fallow et al., 2013). To explain these unexpected responses, two possible mechanisms have been discussed in the literature. One is based on global acoustic similarity between unfamiliar and

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familiar calls. Following this hypothesis, a multiplicity of acoustic features plays a role in determining an overall level of acoustic similarity, and a threshold determines whether an unfamiliar call does or does not trigger the relevant behaviour. This hypothesis has been suggested to be the mechanism at play in several articles that examined responses to unfamiliar calls (e.g. Debracque et al., 2023; Fallow et al., 2011). However, a recent review (Schlenker et al., in press) has emphasized the lack of experimental validation of this hypothesis, especially when contrasted with a second hypothesis: featural interpretation.

Featural interpretation states that a particular acoustic feature rather than an entire call may be responsible for triggering the target behaviour (Schlenker et al., in press). While several acoustic properties have been identified as good candidates for recognition (e.g. the peak frequency, Fallow et al., 2013; Johnson et al., 2003), the thorough testing of one specific feature has been limited. For instance, Aubin and Brémond (1989) postulated that for two bird species (European herring gull, *Larus argentatus*, and European starling, *Sturnus vulgaris*), a slow frequency-modulated slope is decisive for triggering distress behaviour. They showed this by creating simplified versions of distress calls (note with numerous harmonics with or without a slow frequency modulation); without the slope, they failed to trigger the behaviour. However, when a positive slope was present, the artificial call triggered the behaviour in the tested species. Following this idea, unfamiliar call recognition may occur not because of acoustic similarity between calls, but rather on the decoding of particular features. The convergent evolution of specific features in different species may be an efficient evolutionary strategy facilitating heterospecific communication (Schlenker et al., in press).

One difficulty in deciding between these two hypotheses is that featural interpretation and acoustic similarity might go in the same direction (Schlenker et al., in press). For instance, in the above-mentioned experiment (Aubin & Brémond, 1989), it might be that the addition of a slope to the pure tone versions of the calls was enough to make them reach a threshold of acoustic similarity to the original sound. One effective, albeit untested, method to differentiate these two hypotheses is to simultaneously consider multiple features: consider an artificial call AB which shares feature A with the original call but not feature B, and another artificial call AB which shares feature B but not feature A. One may argue that, by some plausible measure of acoustic similarity, they are equally similar to the original call. If a bird responds to one but not the other, one could identify which of feature A or B is critical. To explore this idea, we need to isolate specific features from calls; one method that has already been proved efficient in bioacoustics is to use artificially created sounds (e.g. Lengagne et al., 2001). A second necessary component is to create calls that trigger unambiguous responses from the receivers. Mobbing behaviour possesses all the characteristics needed to test such a hypothesis; it is a quick, clear and unambiguous aggressive response, readily elicited in playback experiments on wild, free-ranging animals (Carlson & Griesser 2022).

We specifically focused on mobbing calls of a common Paridae species, the great tit, *Parus major*. Great tits have been observed to respond to the vocalizations of other species (Dutour et al., 2017) and even to unfamiliar species sharing the same call organization (Randler, 2012; Salis et al., 2021, 2023), while their mobbing calls are responded to by a large number of species in return (Carlson et al., 2020). This prominent role can be attributed to their ability to convey consistent information about the perceived threat through their mobbing calls ('community informant' status, Carlson et al., 2020). During mobbing events, great tits predominantly produce a call consisting of two distinct components: initial high-pitched notes (hereafter referred to as F notes, Salis, 2022)

followed by a sequence of broad-spectrum notes (known as D notes, Hailman, 1989; Dutour, Lengagne et al. 2019). This F-D organization is shared by most Paridae (Salis et al., 2024) and is considered to be one mechanism by which these species recognize meaningful mobbing calls (Salis, 2022). The D notes of the great tits and of the other Paridae have similar features: first, they are notes with a large frequency range, reaching both the lower and higher frequencies of the birds' repertoire (Hailman, 1989; Salis, 2022). Marler (1955) has suggested that a large frequency range is crucial to enhance the localization of the calls, which is very useful in a mobbing context and is indeed present in several other species' mobbing calls (e.g. the common grackle, *Quiscalus quiscula*, or Hutton's vireo, *Vireo huttoni*, Ficken & Popp, 1996). In great tits, the D notes are made of a series of flat harmonics, a trait that is also shared with other Paridae species (Hailman, 1989). Finally, following the motivation – structural rule of Morton (1977), D notes possess 'harsh' characteristics. This is due to the presence of nonlinearities, mostly noisy parts, hypothesized to emerge because of increased excitation and hostility from the caller.

The D notes of great tits therefore share four properties with those of other Paridae four properties: they typically begin at low frequencies, exhibit a wide frequency range, include numerous harmonics and display nonlinear phenomena such as noise (Salis, 2022; Hailman, 1989). As a result, these four features in the D notes are considered strong candidates for featural interpretation, possibly explaining the response of great tits to allopatric Paridae species. Peak frequency has also been identified as an important candidate in other alarm calls (Fallow et al., 2011; Johnson et al., 2003). In great tits, D notes possess most of their energy between 3000 Hz and 5000 Hz. However, this feature is not shared with the coal tit, *Periparus ater* (peak frequency between 5000 Hz and 7000 Hz), although great tits do respond to them (when the call organization matches their own, Salis et al., 2023). We therefore did not select this parameter in the following experiment. Finally, temporal features, rather than spectral features, are also well known to trigger different mobbing responses in birds (Charrier & Sturdy, 2005; Méndez & Sandoval, 2016), including great tits (Salis et al., 2022). By controlling the call rate of artificially created calls, we choose to isolate the role of specific spectral features.

We devised playback experiments involving free-ranging, wild great tits, with the aim of answering two questions: (1) do great tits react to synthetic F-D calls with D notes that possess all four of these features, and (2) do great tits respond to synthetic F-D calls with D notes that possess only one of these specific features? For question (1), we compared responses to a 'complete' artificial call (i.e. a synthesized call composed of simplified F and D notes sharing the characteristics of the natural notes) relative to a 'null' artificial call (i.e. a synthesized call with the same F notes but with D notes that possess none of the four features, yet still with the correct call rate and note repetition) and a natural great tit's call sequence. Both hypotheses (acoustic similarity and featural interpretation) lead one to predict that only the artificial call with all the mobbing features would elicit a mobbing response from great tits. This is a plausible prediction for acoustic similarity because the null artificial call shares so little with the natural call that it is unlikely to reach any reasonable threshold of acoustic similarity. This is also a plausible prediction for featural interpretation because each of the four candidate features has been suppressed in the null call.

If the expected outcome is observed, we can conclude that temporal organization alone is insufficient to trigger mobbing behaviour in great tits. However, this outcome would not distinguish between the acoustic similarity hypothesis and the featural interpretation hypothesis. Doing so is the purpose of the second experiment: if the great tits respond to one of the four single-trait acoustic treatments, this suggests that they employ a simple

featural interpretation mechanism for decoding new calls. Responding to more than one treatment would still be compatible with featural interpretation but may rather indicate redundancy in the signal. By contrast, responding to none of them would indicate that featural interpretation based on only one trait is not the mechanism used by great tits to decode novel signals.

METHODS

General Organization

We performed playback experiments on free-ranging adult great tits in the Ain department, France. Tests were performed at the onset of the reproductive season: between 4 and 12 April 2023 for experiment 1 and between 13 and 27 April 2023 for experiment 2, which in this region corresponds to the brooding period (laying eggs and brooding occurred between 6 and 25 April in a monitored population of great tits in 2021, 10 km from the tests of the current experiment). We performed tests only on days with no wind nor rain, and selected rural habitats (parks, small villages, trails) as great tits are common in these areas and familiarized to human presence. Tests were performed between 0600 and 1200, matching the peak activity of great tits. We performed a total of 210 tests (30 tests for each acoustic treatment) and each individual was tested only once. We tested between seven and 17 individuals each fieldwork day (mean ± SD: 11 ± 3 tests) and rotated among our treatments to avoid spatial and temporal autocorrelation. Any two test sites were separated by at least 150 m to avoid the risk of testing the same bird twice (a 100 m distance is sufficient to avoid this risk, Salis et al., 2022). Birds were tested sequentially, with a minimum of 5 min between each test to avoid any potential effect of the previous test on the next one (13 of 210 tests; median: 17 min; Q1: 10 min; Q3: 30 min). This latency time, associated with the distance and the different treatments at each point, was made to avoid any carryover effects on the subsequent tests, allowing us to consider our tests as statistically independent (Dutour et al., 2017; Salis et al., 2023). We never went on the same pathway twice (moving to different villages/parks each day). Tests were of short duration and individuals were tested only once to avoid any negative impact on the bird tested.

We divided the experiment into two parts: first, we tested whether the response of great tits differed when hearing natural conspecific calls compared to (1) artificial calls possessing all characteristics of a mobbing call ('complete' treatment, Table 1, Fig. 1) or (2) artificial calls possessing the rhythmic characteristics but none of the spectral characteristics of the original call ('null' treatment, Table 1, Fig. 1). We then tested the response of great tits

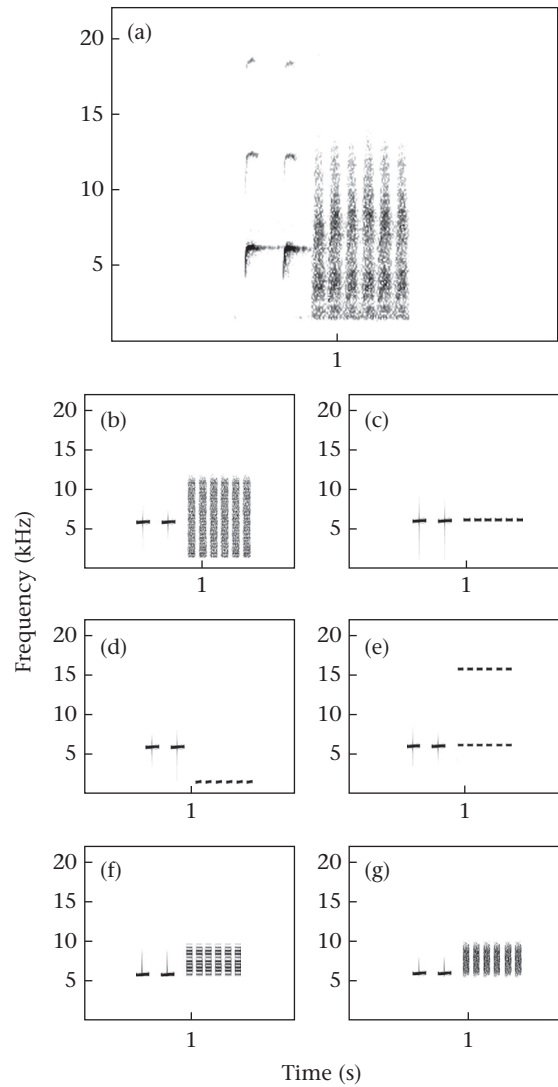


Figure 1. Spectrograms of our seven playback treatments. Experiment 1: (a) 'natural' = unmodified great tit call, (b) 'complete' = artificial signal with the four features of mobbing calls and (c) 'null' = with none of the four features. Experiment 2: (d) 'low' = signal with low frequencies and no other relevant feature, (e) 'range' = signal with a large frequency range only, (f) 'harmonics' = signal with harmonics only and (g) 'noise' = white noise (nonlinear phenomenon). Each call contains F and D notes, but only the D notes are modified in the different artificial playbacks. An audio with an example of each treatment is available as Supplementary material.

to four treatments in which the D notes possessed only one of the four spectral characteristics previously chosen (large frequency range, low frequency, noise and harmonics, Table 1, Fig. 1).

Playback Preparation

To create the artificial soundtracks, we first analysed the natural mobbing calls of great tits. Great tits produce mobbing calls that are a combination of F notes (high-frequency pure notes) followed by a series of D notes (large frequency range elements, with noise and harmonics). While D notes alone can also be used when mobbing, only the F-D sequence can trigger a complete mobbing response from conspecifics (Salis et al., 2021). The majority of Paridae species exhibit this F-D call organization when mobbing, leading to the hypothesis that heterospecific recognition may be partly dependent on this particular syntax (Salis, 2022). We therefore decided to create playbacks with the combinatorial F-D call and modified only

Table 1
Summary of the characteristics of the seven treatments used in the playback experiments

Treatment	Low frequency	Large frequency range	Harmonics	Noise
Experiment 1				
Natural	✓	✓	✓	✓
Artificial complete	✓	✓	✓	✓
Artificial null	x	x	x	x
Experiment 2				
Low	✓	x	x	x
Range	x	✓	x	x
Harmonics	x	x	✓	x
Noise	x	x	x	✓

Spectrograms are given in Fig. 1 and an audio example of each treatment is provided in the Supplementary material.

the D notes between our different treatments. To do so, we analysed recordings obtained in 2019 by A.S., in the Ain department. Great tits were exposed to a playback comprising a chorus of three birds mobbing simultaneously (experimenter placed 10 m from the loudspeaker with a Fostex FR2LE digital recorder connected to a Sennheiser ME67-K6P highly directional microphone). All recorded birds closely approached the loudspeaker and performed wing-flicking behaviours, confirming that they were mobbing (Hinde, 1952; Salis et al., 2021).

We selected 30 recordings and, in each recording, three F notes and three D notes from different calls with the best signal-to-noise ratio. We used a high-pass filter at 1 kHz or 2 kHz, depending on the background noise. With the semiautomatic measurement window from Avisoft SASLab (Avisoft Bioacoustics, Berlin, Germany), we measured the length of the note, the minimum dominant frequency and the frequency range (distance between the lowest and highest dominant frequency). We also extracted for the D notes the space between two harmonics. These measurements (for more details see the Appendix) were sufficient to create the artificial mobbing calls. The duration of the natural F notes was 0.11 ± 0.04 s (mean \pm SD) and F notes consisted mostly of flat pure tones with a minimum frequency at 6048 ± 1381 Hz (in some F notes, a frequency modulation was found at the beginning, but we chose to simplify the signal and not include this modulation, Fig. 1a). The F notes were therefore created with the graphical synthesizer of Avisoft SASLab and were designed as flat pure tones of 0.10 s with a peak frequency at 6000 Hz. The natural D notes were 0.05 ± 0.01 s, with a minimum frequency at 1566 ± 237 Hz, a bandwidth of 9661 ± 1922 Hz, and harmonics spaced by 405 ± 66 Hz (Fig. 1a). We created the artificial D notes in two steps. First, we created a 0.05 s note with a series of flat harmonics with the same amplitude, spaced from 400 Hz, beginning at 1500 Hz and ending at 11 000 Hz. We used the graphical synthesizer of Avisoft SASLab by clicking and dropping flat lines (pure tones) at the anticipated positions. We then superimposed these notes with white noise (also limited to 1500 Hz and 11 000 Hz) to add some nonlinear phenomena in the notes (same amplitude level of the noise and the notes, Fig. 1b). White noise was also created with Avisoft (with the insert white noise function) then cropped with the time domain IIR filter. The 'null' D notes were created as notes that do not possess any of the four features of D notes (i.e. no harmonics, no large range of frequency, no low frequency and no noise). The null D notes were therefore simple flat pure tones with peak frequency at 6000 Hz (same level as the F notes) and a duration of 0.05 s (Fig. 1c).

To create the F-D calls, we followed the natural organization of great tits' mobbing calls: two F notes followed by six D notes (space between the two F notes: 0.10 s; space between the F and D notes: 0.10 s; space between the D notes: 0.3 s). The amplitude of F notes is naturally higher than that of D notes (Appendix, Fig. A1). We kept this difference by homogenizing the amplitude of F notes at 75% and the amplitude of D notes at 35%. We repeated the same call 15 times in 1 min with the same intercall interval (the natural rhythm of great tits, Kalb et al., 2019). Since the creation of these artificial notes could be prone to experimenter variation and unpredictable variation because of the noisy parts, we created three replicates of each note (final measurements of the three replicates are given in the Appendix, Table A1).

To create the natural treatment (great tits' natural mobbing calls: positive control), we used the 30 recordings analysed above to create 30 soundtracks. In each recording, we kept the five calls (from the same individual) with the best signal to noise ratio and replicated this series three times to obtain a rhythm of 15 calls/min (the intercall interval was kept the same as the artificial sequences). To ensure that the comparison between the natural and artificial treatments was feasible, we homogenized the number of F and D

notes in each call (two F notes followed by six D notes), suppressing or duplicating notes when necessary. The space between notes and the amplitude of the notes was the same as for the artificial treatments (see Appendix for details).

To create the playbacks for the second experiment, we modified the artificial D notes to obtain notes with only one of the four spectral features we originally identified (only low frequency, only large frequency range, only harmonics or only noise). For the low-frequency treatment, we created notes very similar to the null treatment, except that the peak frequency of the notes was at 1500 Hz (the lowest frequency of the natural D notes), instead of 6000 Hz (Fig. 1d). For the only large frequency range treatment, we created notes with two flat lines: one at 6000 Hz, like the null treatment, and one at 15 500 Hz. This resulted in a note with a frequency range of 9500 Hz, which is the natural frequency range of great tits (Fig. 1e). Note that this rigid choice to not go below 6000 Hz (to be sure that it is not a lower frequency that is recognized by great tits) meant that the treatment was possibly outside the hearing range of great tits (Klump et al., 1986). We none the less chose to keep this treatment in our experiment, to show the complete rationale underlying the protocol (see Discussion for more details). For the two last treatments, we needed to incorporate noise or harmonics but without a large frequency range. We therefore designed notes with a frequency range below the natural range of great tits (3000 Hz, as the lowest range we found in our population was 4680 Hz). For the harmonics treatment, we used the harmonics of the artificial complete treatment but suppressed the frequencies below 6000 Hz and above 9000 Hz (seven harmonics left, Fig. 1f). Similarly, for the noise treatment, we used the noise of the artificial treatments, but filtered below 6000 Hz and above 9000 Hz (Fig. 1g).

Playback Procedure

The protocol used to record great tits' mobbing response follows previous work done in the same region (Salis et al., 2021, 2022, 2023). Once a foraging, isolated, calm individual was detected, one experimenter placed a loudspeaker ~20 m from the bird (19 ± 3 m, mean \pm SD, $N = 210$) and then retreated to ~10 m from both the bird and the loudspeaker. The loudspeaker was always placed above the ground (~1 m) and close to a potential roost (typically, a tree in a 3 m radius) to allow the bird to approach. We then launched a 1 min soundtrack at 75.67 ± 1.55 dB SPL (mean \pm SD); measured at 1 m from the loudspeaker with a sound level meter Solo (01dB-Metravib, Limonest, France). A second experimenter (10 m from the bird and the loudspeaker, and 5 m from the first experimenter) recorded the birds' responses with binoculars and a voice recorder for 90 s (60 s of call sequence followed by an additional 30 s). We recorded whether the focal bird produced mobbing calls and the distance the bird travelled from its starting point to its closest point to the loudspeaker during the test. If the focal individual came at least halfway from its starting point, we considered it as approaching (Salis et al., 2020, 2022). If the individual both called and approached, it was then noted as 'mobbing'. We combined these two common variables used to assess mobbing (Carlson & Griesser, 2022) since approaching behaviour on its own might be considered as reflecting curiosity rather than mobbing and calling from a distance may arise for reasons unrelated to our acoustic stimuli. Note that, although we chose not to include approach alone, the same tendencies were found as with the mobbing behaviour (the natural and artificial complete treatments triggered the approach of more than 60% of the tested birds, while the birds approached the null treatment or any of the 'only one feature' treatments in less than 30% of the tests). In addition, we noted the number of scans (180° head turns while keeping the rest

of the body still) produced by the focal bird as a proxy for vigilance behaviour (Suzuki et al., 2016; Dutour, Lengagne, et al., 2019; Salis et al., 2020). We chose this variable to be able to detect more subtle behavioural responses (i.e. individuals may adapt their behaviour and increase their vigilance when hearing new sounds yet choose not to invest in mobbing).

All observations were made by the same experimenter (A.M.) who was previously trained by an experienced ornithologist (A.S.) to correctly assess scanning behaviour. To confirm that this measure was not prone to variation between observers and that the observations were stable during the experiment, both A.S. and A.M. independently (at a distance of 10 m from each other) counted the scans in nine tests during experiment 2. Scan counts matched perfectly in four tests, diverged by one scan in four tests and diverged by two scans in the remaining test. When scans diverged, it was always A.S. that counted more scans, indicating that A.M. was more conservative and that differences between treatments are not likely to be due to variation between observers. For each test, we recorded the total time the bird was seen, and we discarded tests for which birds were seen for less than 60 s. On no occasion did the birds approach the experimenters rather than the loudspeaker. Mobbing is often a cooperative behaviour, hence leading to several birds approaching the playbacks. While we could not fully control the social environment of our focal bird, we circumvented the potential problem of having other birds influencing our focal bird's response by (1) discarding our test if another bird responded before our focal bird and (2) performing short tests (90 s) to ensure that the subsequent response of other birds did not strongly influence our focal bird.

Ethical Note

Humans were always at a minimum of 10 m to any tested bird. However, since the calls broadcasted were mobbing calls, hence potentially stress-inducing calls, we limited birds' disturbance by (1) testing the birds for only 90 s and (2) testing each bird only once. Moreover, after our tests, we checked that all birds returned to their pretest behaviour in less than 5 min. We tested a total of 210 birds to have a sample size of 30 individuals per treatment; which is an anticipated equilibrium between statistically robust results (expected level of responses to be 50% of response when mobbing is high, and 10% when mobbing is low, Salis et al., 2022, 2023) and limited disturbance to the birds. Our experiment did not need any special permit, as the birds were free ranging in a territory of 25 km around our town. We followed our institutional rules of procedure regarding field work. We complied with the ASAB/ABS Guidelines for the Use of Animals in Research and with The European Code of Conduct for Research Integrity.

Statistical Analyses

All analyses were performed in R Studio, with R v. 4.2.3 (R Core Team, 2021). To compare the mobbing response of great tits in our different acoustic treatments, we considered the mobbing response (i.e. whether the individual both approached and called, dichotomous variable) and the number of scans produced during the test. For both variables, we ran generalized linear models (GLMs) with the acoustic treatment as explanatory variable. We first tested whether we obtained different responses between the natural calls, the complete and the null treatments. We did not include the sex of the individuals in our models (determined by the broad black line on the chest which is thicker in males than females) as it led to singular fit issues (note that the sex ratio was similar each treatment within each part, so that sex differences will not bias our results; females/males for experiment 1: complete = 11/19, null

and natural 10/20; experiment 2: range = 4/25 with one unidentified sex, harmonics = 4/26, low = 5/24 with one unidentified sex and noise = 8/22). For mobbing behaviour, we ran a logistic regression (binomial distribution and logit link function). For scanning behaviour, we used a negative binomial distribution (overdispersion detected with the `check_overdispersion` function, package `performance`, Lüdecke et al., 2021) and we added the amount of time the bird was seen as an offset (84 ± 8 s, minimum 60 s, maximum 90 s, function `glm.nb`, package `MASS`, Venables & Ripley, 2002) to all models. As we were interested in the differences between treatments, we calculated the estimated marginal means (package `emmeans`, Lenth, 2021), with the results on the response scale (this permitted us to obtain the effect sizes of the differences) and with a Sidak correction for multiple testing.

We then tested whether we could detect different responses to the four 'only one feature' treatments. However, as we obtained very low responses for the mobbing occurrences, and since one treatment obtained a percentage of response of 0%, the GLM failed to converge. The biological conclusions of this part of the experiment being straightforward (no response to any of the four treatments), we did not run any models for experiment 2. For the scanning behaviour, we used the same pathway of analysis as for experiment 1 (negative binomial GLM and two-by-two comparisons with a Sidak correction).

RESULTS

Experiment 1: Test of Artificial Calls

Great tits responded to their conspecific calls with both mobbing behaviour (36% of the individuals both approached and called in response to conspecific calls, Fig. 2a) and vigilance (11.57 ± 4.56 scans on average during the 90 s tests, Fig. 2b). A similar percentage of birds mobbed the artificial sequences that possessed all characteristics of a typical mobbing call: 33% of the birds approached and called (Table 2, Fig. 2a). Great tits also scanned in response to these artificial, complete sequences (8.8 ± 4.52 scans on average, Fig. 2b) and the difference from the natural calls was not statistically significant (Table 2). In contrast, few individuals responded to the null treatment (sequences with the correct temporal organization but none of the spectral features of a typical mobbing call, Fig. 2a). Only 3% mobbed to the null treatment, a significant difference from the other two treatments (Table 2). They also scanned half as much as to conspecific calls (5.5 ± 4.31 scans on average, Fig. 2b). The difference in scan number between the complete and the null playbacks was statistically significant (Table 2).

Experiment 2: Test of Simple Featural Interpretation

None of the four playbacks triggered a significant mobbing response from the birds (only one bird approached and called in three treatments, and none for the harmonics treatment, Fig. 3a). Similarly, no playback treatment led to a higher vigilance response: the number of scans was overall low (highest average: 6.87 ± 5.39 scans for the noise playback, Fig. 3b), and we detected no differences between the four treatments (Table 2).

DISCUSSION

Our first experiment established that great tits can appropriately respond to an artificial version of the mobbing call F-D, made of artificial F notes with a flat frequency (constant across conditions), followed by artificial D notes with four features of the natural D call (low frequency, large frequency range, harmonics and

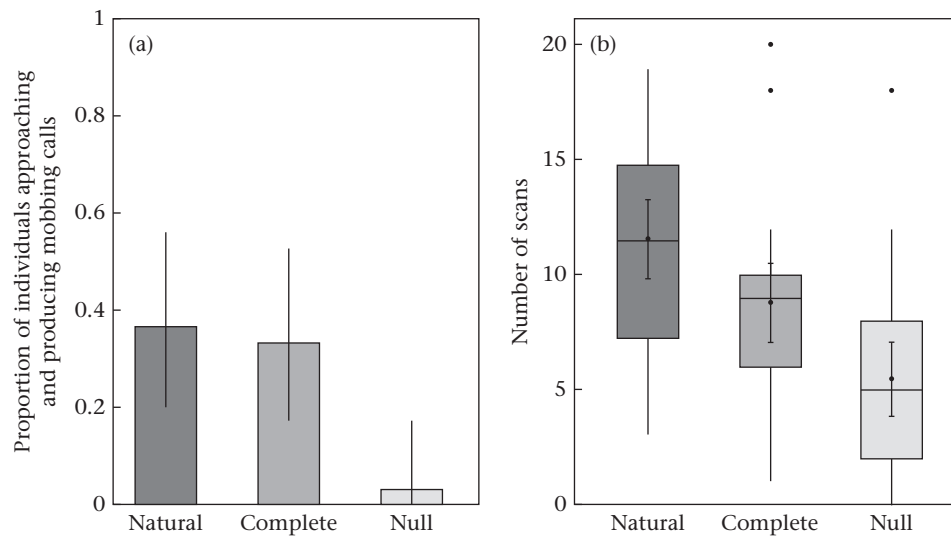


Figure 2. Responses of great tits to natural calls, complete calls (artificial signal with the four features of mobbing calls) and null calls (artificial signals with none of the four features); $N = 30$ for each treatment. (a) Proportion of individuals that approached and produced mobbing calls when hearing the playbacks (dichotomous variable) and (b) vigilance behaviour estimated as the number of scans (180° head turns) during the 90 s tests. The proportions in (a) and means in (b) (black dots) are accompanied by 95% confidence intervals (error bars). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Table 2

Results of the pairwise comparisons between our playback treatments (estimated with a Sidak correction)

		Ratio	SE	Z	P
Experiment 1					
Mobbing	Natural – Complete	1.16	0.63	0.3	0.96
	Natural – Null	16.80	18.20	2.6	0.03
	Complete – Null	14.50	15.78	2.46	0.04
Scans	Natural – Complete	1.35	0.18	2.20	0.07
	Natural – Null	2.09	0.30	5.20	<0.001
	Complete – Null	1.55	0.23	3.00	0.007
Experiment 2					
Scans	Low – Range	1.11	0.23	0.50	0.96
	Harmonics – Range	1.33	0.27	1.39	0.50
	Harmonics – Low	1.20	0.25	0.89	0.81
	Noise – Range	1.44	0.29	1.77	0.29
	Noise – Low	1.29	0.26	1.26	0.58
	Noise – Harmonics	1.08	0.22	0.37	0.98

We provide the effect size of the difference (ratios and SE), the Z ratio and the P value (significance threshold at 0.05). Experiment 1: natural = unmodified great tit call, complete = artificial signal with the four features of mobbing calls, null = with none of the four features. Experiment 2: low = signal with low frequencies and no other relevant feature, range = signal with a large frequency range only, harmonics = signal with harmonics only and noise = white noise (nonlinear phenomenon). Significant P values ($P < 0.05$) are shown in bold.

noise). By contrast, a control condition with the artificial D note produced with the same rhythm (modelled after natural F-D sequences) but no spectral differences between F and D notes yielded no effect. This shows that rhythmic properties of F-D alone do not suffice to trigger mobbing, but that the addition of four crucial features to the D part does. Repetition rate has been repeatedly identified as an important feature used to decode heterospecific signals (Randler & Förschler, 2011; Dutour et al., 2022; Wheatcroft, 2015). Our results demonstrate that the natural mobbing call rate alone (present in the null treatment) is insufficient to trigger mobbing behaviour in great tits. None the less, great tits are sensitive to call and note repetition in their mobbing calls: greater mobbing call rate led to higher vigilance behaviour (Salis et al., 2022). Our results, in combination with this previous experiment, suggest that the F-D call organization is a necessary feature of mobbing recognition in great tits and that call rate specifies the intensity of the situation (Salis et al., 2022).

The second experiment tested whether any individual feature out of the four sufficed to trigger mobbing behaviour. The outcome was negative: we found no evidence in favour of interpretation based on a single feature. While the interpretation of the absence of a mobbing response to any of these four treatments is relatively straightforward, that of scanning behaviour is not as it is a continuous variable. Nevertheless, we can compare this result with previous experiments done in the same population: great tits performed the same number of scans to our four acoustic treatments and to our null treatment in experiment 1 as they did to background noise (Salis et al., 2021), heterospecific song from a sympatric species (Salis et al., 2022) or an allopatric species (Salis et al., 2021) and heterospecific calls with different syntax and acoustic properties in their D notes (Salis et al., 2023). We can therefore safely conclude that our four acoustic treatments did not trigger a strong increase in vigilance in great tits. While previous research has linked the presence of F notes to vigilance behaviour in great tits (Dutour, Lengagne, et al., 2019), the number of scans observed in our experiment did not show a direct correlation with the number of F notes in the sequence (this number was stable in all our treatments). This finding aligns with a recent study on the same species (Salis et al., 2022) which found that varying numbers of D notes in F-D calls resulted in different scan numbers. As such, we interpret the scanning behaviour as an indication of general vigilance rather than a behaviour specifically influenced by the presence of a particular note type.

Our results suggest that it is unlikely that only one specific feature is sufficient to trigger a mobbing behaviour in great tits. This is in line with previous work on mobbing calls of apostlebirds, *Struthidea cinerea* (Johnson et al., 2003) and black capped-chickadees, *Poecile atricapillus* (Charrier & Sturdy, 2005) concluding that the mere presence of a particular acoustic trait (in this case, broadband elements) was not sufficient to trigger a response. One criticism of our treatments, however, is that because we shifted the beginning of the frequency range from 1500 Hz to 6000 Hz for the only range treatment, the upper part of the signal may not have been detected by the great tits. The great tit's sensitivity to high frequencies has been shown to be low (above 10 kHz, Klump et al., 1986). On this assumption, the only range treatment might have been perceived in the same way as the null treatment:

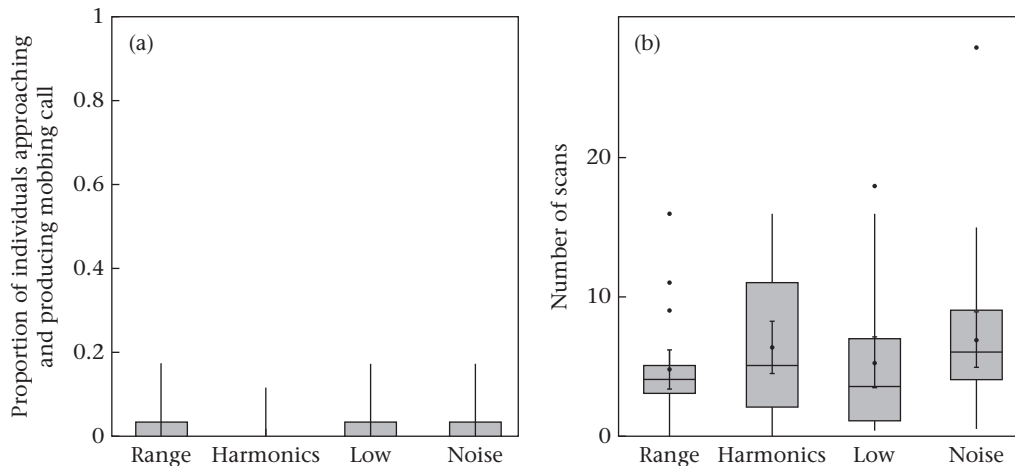


Figure 3. Responses of great tits to artificial sequences ($N = 30$ for each treatment) that possessed only one of the four features identified in mobbing calls: 'range' = signal with a large frequency range only, 'harmonics' = signal with harmonics only, 'low' = signal with low frequencies and no other relevant feature, 'noise' = white noise (nonlinear phenomenon). (a) Proportion of individuals that approached and produced mobbing calls when hearing the playbacks (dichotomous variable), and (b) vigilance behaviour estimated as the number of scans (180° head turns) during the 90 s tests. The proportions in (a) and means in (b) (black dots) are accompanied by 95% confidence intervals (error bars). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

the large frequency range may not have been thoroughly tested, and therefore cannot be definitively ruled out as the characteristic used by great tits to recognize unfamiliar mobbing calls. We chose to keep this treatment in our experiment, to show the complete rationale underlying the protocol, but we suggest that future experiments should develop additional, intermediate treatments to counterbalance this potential caveat in our methodology (for example, testing large frequency ranges that are none the less below 10 kHz).

Our results raise the general question of what the necessary and sufficient conditions are for a signal to trigger a reaction, that is, to carry meaning and be interpreted as such. We have shown that none of the specific features we selected was sufficient to trigger a mobbing reaction from great tits. By contrast, the combination of four features did trigger a reaction (the 'complete', yet artificial signal). It could be that some combinations of features are necessary and sufficient to trigger a reaction, even if no single feature is. In that scenario, producing artificial calls with two specified features, but with contrasting scores for the other two features (for instance, a low frequency, accompanied by noise, yet lacking harmonics and with a low frequency range) may provide valuable insights. It could also be that a more strictly global acoustic similarity approach is correct. Under that assumption, no particular subset of features is necessary. Rather, what is critical for great tits to respond to a signal is that it contains enough features (say, two of four features). That is, the artificial call should be sufficiently similar to the original call, no matter what the similarities and differences are. Finally, while we chose to apply a rigid 'presence/absence' framework to our treatments, it may be important to explore more subtle variations by gradually modifying/degrading the complete mobbing calls. This has been done in studies of the importance of song features in field sparrows, *Spizella pusilla* (Nelson, 1988) and the calls of black-capped chickadees (Charrier & Sturdy, 2005) and could be applied to the model of the great tit's mobbing calls. Shedding more light on these questions is fundamental to understanding comprehension in and across a variety of species.

The hypothesis of featural decoding has larger implications than testing the mobbing responses of great tits. Heterospecific communication is increasingly described in all clades, and particularly in birds, and the ubiquity of these exchanges raise questions on the mechanisms and evolutionary processes implicated. While simple associative learning has been well described and demonstrated, other mechanisms such as the recognition of syntax are

beginning to emerge (Salis et al., 2023; Suzuki et al., 2017). Featural decoding has the benefit of being a simple yet efficient mechanism explaining heterospecific communication and may indeed explain why calls that necessitate recruitment from a large number of birds (such as mobbing calls) share strong similarities (Morton, 1977). Recent work has demonstrated that humans and crocodiles do rely on specific acoustic features when hearing distress calls from another species; but that the features they focus on do not necessarily match (Thévenet et al., 2023). There is therefore a great need for more studies on other species to understand the extent to which our results are specific to our focal species.

To conclude, we tested the presence of featural decoding processes in the great tit's mobbing calls. We demonstrated that artificial calls trigger a response from great tits but that none of the four isolated features was sufficient to trigger a mobbing response. This absence of response from great tits is far from uninformative as it allows us to rule out a simple decoding process and permits the development of alternative hypotheses (combinations of features versus global acoustic similarity processes). Using artificial signals to understand the mechanisms used in heterospecific communication is a powerful tool and may greatly help the understanding of the mechanisms of heterospecific communication, ultimately enlightening the evolution of such mechanisms.

Author Contributions

Ambre Salis: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Flavien Badaire:** Writing – review & editing, Investigation. **Camille Coye:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Maël Leroux:** Writing – review & editing, Methodology, Investigation. **Thierry Lengagne:** Writing – review & editing, Resources, Methodology. **Philippe Schlenker:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Emmanuel Chemla:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Data Availability

The R code and data sets used in this study can be found at <https://doi.org/10.5281/zenodo.11207822>.

Declaration of Interest

The authors declare they do not have any conflict of interest relative to this work.

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Supplementary Material

Supplementary material associated with this article is available in the online version at <https://doi.org/10.1016/j.anbehav.2024.07.020>.

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frequencies and then calculate the space between these bursts. Fig. A1 also illustrates how we calculated the amplitude ratio between the F notes and the D notes (in our example, the F notes have an amplitude 2.14 times higher than the D notes). For the artificial complete calls, we provide in Table A1 the final measurements of the three exemplars we created, obtained with the Avisoft SASLab semiautomatic measurement tool.

Appendix: Playback Preparation

To create the simplified, artificial mobbing calls, we first analysed the natural call sequences of great tits (details in the main text). We provide in Table A1 the values obtained for the different measures of the F and D notes. We analysed three F notes and three D notes with the best signal to noise ratio from 30 different recordings (the same recordings were then used to create the ‘natural’ treatment). We extracted the minimum frequency, the frequency range (bandwidth button), and the duration of each type of note (Fig. A1). To extract these measurements, we used the automatic parameter measurement tool and measured these parameters for the entire element. The threshold to correctly detect each note was manually adapted to each note to ensure a correct analysis. Note that we could not always measure the space between harmonics because of a lot of noise in the calls. We chose to select the recordings for which this measure was clearcut, hence reducing the sample size to seven. We calculated this measure by plotting the amplitude spectrum of a small portion of a note (0.01 s) to obtain the bursts of energy at specific

Table A1
Measurements of the natural soundtracks used to determine great tits’ natural mobbing calls, and the artificial complete treatments used in our playback experiments

	Great tits’ natural call sequences	Artificial complete calls
F notes		
Minimum frequency (Hz)	6048 ± 1381	5933 ± 115
Frequency range (Hz)	1283 ± 1156	1100 ± 0
Duration (s)	0.11 ± 0.04	0.10 ± 0.009
D notes		
Minimum frequency (Hz)	1566 ± 237	1200 ± 100
Frequency range (Hz)	9661 ± 1922	10 133 ± 305
Duration (s)	0.05 ± 0.01	0.045 ± 0.003
Space harmonics (Hz)	405 ± 66	
Space between notes		
F-F	0.10 ± 0.03	0.10 ± 0.002
F-D	0.09 ± 0.04	0.10 ± 0.002
D-D	0.03 ± 0.006	0.03 ± 0.006
Other measure		
Ratio amplitude F/D	2.15 ± 0.72	2.14

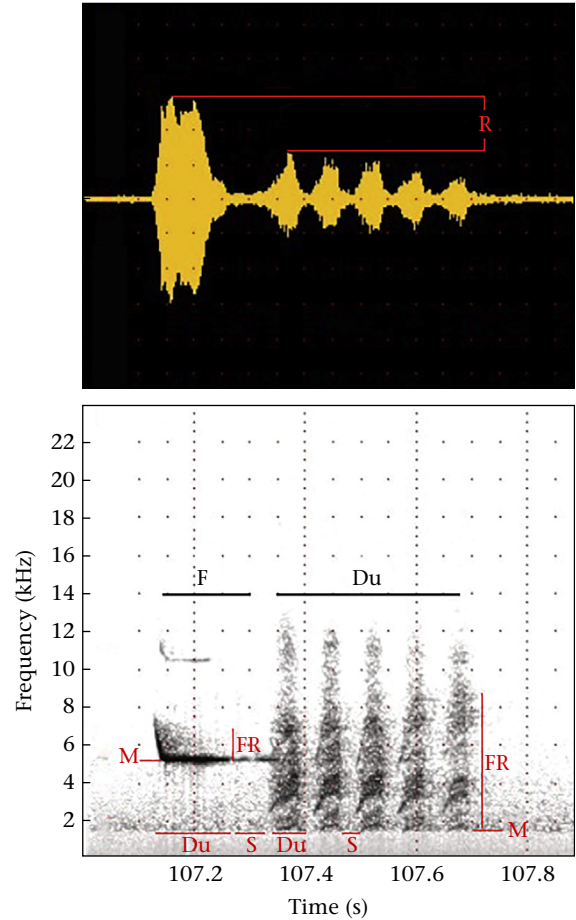


Figure A1. Example of a call analysed to determine the natural mobbing call properties of great tits. In this example, the F-D call contains one F and five D notes. Du = duration, M = minimum frequency, FR = frequency range, R = ratio between the amplitude of the F notes and the D notes (here, 30/14 = 2.14), S = space between notes. The acoustic measures were estimated with the semiautomatic measurement tool from Avisoft SASLab.