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Mobbing calls: a signal transcending species boundaries

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Mobbing calls: a signal transcending species boundaries

When they perceive a potential predator, many species of birds and mammals emit specific alarm calls (Seyfarth et al., 1980; Klump & Shalter, 1984; Rainey et al., 2004; Graw & Manser, 2007; Magrath et al., 2007). These calls are often classified as flee alarm calls, which are associated with an immediate escape of the emitter while spurring receivers to freeze or flee, or mobbing calls, which are associated with the approach and harassment of the predator by the emitter, while spurring receivers to join the caller (Hartley, 1950; Curio, 1978; Hurd, 1996; Kennedy et al., 2009; Magrath et al., 2015). Mobbing calls are usually intended toward a potential non-hunting predator, and are expected to decrease its hunting efficiency, either

through distracting it or by chasing it away (Hoogland & Sherman, 1976; Curio, 1978; Pettifor, 1990; Flasskamp, 1994; Pavey & Smyth, 1998). Both the intensity of mobbing and its success in deterring the predator are positively related to the size of the crowd gathered by the caller (Becker, 1984; Robinson, 1985; Verbeek, 1985; Picman et al., 1988). Although mobs can be formed exclusively by conspecifics, they often involve heterospecifics prey (Hurd, 1996; Suzuki, 2016; Dutour, Lena, & Lengagne, 2017). Hence, this phenomenon makes them well-suited to investigate communication at the community level. Indeed, as it implies a cooperative act, i.e. joining the mob, this makes it easier to distinguish between "simple" eavesdropping on heterospecific signals and more elaborate interspecific communication. For instance, while some species will take part in the crowd, others will not, although they perceive the same threat (Davies & Welbergen, 2009; Ito & Mori, 2010). As for other alarm calls, mobbing calls require the ability to gather relevant information from heterospecific signals (i.e. interceptive eavesdropping, *sensus* Peake, 2005; see Magrath et al., 2015 for a review). In particular, individuals can recognize heterospecific mobbing calls.

Both learned and innate processes could be involved in the mechanisms enabling the recognition of heterospecific mobbing calls (Hurd, 1996; Ramakrishnan & Coss, 2000; Magrath et al., 2009; Fallow et al., 2011; Wheatcroft & Price, 2013). By nature, associative learning is more flexible than innate process but it requires a previous experience to take place. Such experience could occur when heterospecific preys encounter each other when detecting and mobbing the same predator. However, several innate processes could also play a central role in the recognition of heterospecific mobbing calls. In particular, as for other alarm calls, strong ecological constraints apply on the acoustic structure to enhance call efficiency. In the case of mobbing calls, loudness and repeated features can be expected to be selected in order to facilitate emitter location (Marler, 1955; Klump & Shalter, 1984; Ficken & Popp, 1996; Bradbury & Vehrencamp, 1998; Jones & Hill, 2001). Hence, these calls can also be

used in other contexts for which an accurate localization of the emitter is necessary such as pair contact situation or food presence discovering (Marler, 1956; Mahurin & Freeberg, 2009; Suzuki, 2012). Moreover, calls inevitably incorporate some features such as harshness or broad-bandwith pulses of sound related to the psychological state of the emitter, such as fright in the case of flee calls or arousal in the case of mobbing calls. All these characteristics can be expected to lead to acoustic similarity of mobbing calls across species, which could arise from phylogenetic conservation or evolutionary convergence of mobbing calls (Ficken & Popp, 1996; Johnson et al., 2003; Randler, 2012). Finally, one may not exclude that both associative learning and innate process could enhance recognition of heterospecific mobbing calls. In particular, similitudes in acoustic features of mobbing calls among heterospecific species could greatly enhance heterospecific mobbing call recognition through the mechanism of generalization which is often involved in learning process (Weary, 1991; Sturdy, Bloomfield, Charrier, & Lee, 2007). Studies in some Paridae species suggest that they learn to recognize their own mobbing calls and that they generalize to other unfamiliar calls that are acoustically similar.

Mechanisms involved in the recognition of heterospecific alarm and mobbing calls are still poorly understood despite heterospecific responses becoming well documented (Magrath et al., 2015). One way to fill this gap is to investigate the variation in response to unfamiliar alarm calls. Unfortunately, such data remain scarce in the case of mobbing calls. While in one study, individuals did not respond to the allopatric mobbing calls (Nocera et al., 2008), in other cases individuals recognized the allopatric mobbing calls (Johnson et al., 2003; Langham et al., 2006; Randler, 2012; Wheatcroft & Price, 2013). Because almost all studies just focused on one pairwise comparison of emitter-receiver species, any comparison across species remains difficult, if not impossible. Moreover, while studies focused on more than one pair of emitter-receiver, heterospecific species responding to playbacks have not been

identified and prevent us from understanding responses in the light of the phylogeny**.** Hence, there is a need for a larger pairwise comparison of emitter-receiver species in order to unravel the importance of the relationship among species to explain their behavioural responses in an antipredator strategy.

In this study, we conducted playback experiments to investigate the variation in the response of four passerine birds exposed to three allopatric species mobbing calls. Additionally, we measured similarity among mobbing call of the studied species to determine if acoustic similarity could be viewed as a general mechanisms involved in heterospecific communication. To this aim, we selected the four receiver species among European passerine birds and the three emitter ones among North American birds, since mobbing is well documented in both communities and found to be based on a similar alarm-calling system (Langham et al., 2006; Templeton & Greene, 2007; Sieving et al., 2010; Dutour et al., 2016). Then, according to a first study suggesting a possible phylogenetically conserved response among Paridae family (Randler 2012), we used sound track of three American Paridae species: two of them corresponding to mobbing call while the third one was a control one (i.e. territorial call). Additionally we choose to use a non Paridae call to compare mobbing responses obtained from two different families.

METHODS

Study Species

To test whether a response to mobbing calls can occur without a learning process linked to these calls, we tested four European species with playbacks of three North American passerine species. The following European species were selected because they are known to exhibit mobbing behaviour when confronted with a predator and give specific mobbing calls: great tit (*Parus major*), blue tit (*Cyanistes caeruleus*), coal tit (*Periparus ater*) and common

chaffinch (*Fringilla coelebs*) (hereafter chaffinch) (Thompson, 1969; Curio, 1971; Zimmermann & Curio, 1988 ; Krams & Krama, 2002; Lind et al., 2005; Berzins et al., 2010; Randler, 2011; Randler & Vollmer, 2013; Dutour et al., 2016; Carlson et al., 2017). These European species were exposed to mobbing calls of three North American passerine species, black-capped chickadee (*Poecile atricapillus*), tufted titmouse (*Baeolophus bicolor*) and Carolina wren (*Thryothorus ludovicianus*). All of them are known to mob predators (Morton & Shalter, 1977; Hurd, 1996; Sieving et al., 2004; Betts et al., 2005; Templeton et al., 2005; Templeton & Greene, 2007; Bartmess-LeVasseur et al., 2010; Hetrick & Sieving, 2011). Tests involved 132 different European individuals (for the detailed number of tests conducted for each combination, see Table 1). Additionally, to ensure that the response was not due to call novelty (i.e. that the individuals did not simply respond to any novel sound) we used territorial call of the boreal chickadee (*Poecile hudsonicus*), an American songbird found throughout Canada and northern United States (Ficken et al., 1996), as a control (50 tests, see Table 1). Finally, to compare the relative intensity of mobbing response obtained to American species, we also broadcast conspecific mobbing calls to each of the four European species studied (44 tests, see Table 1).

Acoustic Analysis

Recordings were in 16-bit WAV format and analyzed with Avisoft SASLab© software. We used spectrograms with a FFT length of 512 points for the measurements. We selected 5 recordings per species and analyzed up to 10 songs per recording (on average 5.97 ± 2.43 SD). To properly characterize the mobbing production of each studied species and to measure the variation across species, seven shared acoustic properties were measured on each call sound track: (1) duration (s); (2) peak frequency (the frequency for which amplitude is maximum in Hz); (3) maximum frequency (highest frequency of the call in Hz); (4) minimum

frequency (lowest frequency of the call in Hz); (5) frequency bandwidth (differences in Hz between maximum frequency and minimum frequency measure on a linear amplitude spectrum (threshold -20dB)); (6) number of elements; (7) number of different elements per song, an indicator of call complexity (frequency modulated element or dee element or both, see Fig 1).

Study Sites and Playback Experiments

All experiments were conducted on wild passerines inhabiting a large mixed deciduous-coniferous forest (c.a. 570 km²) located in South-East France (45°80'N, 4°52'). We never went back twice on the same forest path and two successive playbacks were always separated by more than 100 m (200 m for two tests performed on the same species). Hence although birds were not individually ringed the probability to test a second time a given individual remain very low. Moreover, all tests were conducted over a relatively short period during the breeding season (end of April to mid-July) in order to avoid a seasonal effect. In addition, we avoided any temporal effect during our experiments by evenly distributing the playbacks of the different species across the study period.

Once a focal bird was identified, we placed the loudspeaker used to broadcast the acoustic signal 30 m away from the bird at the bottom of a tree. The focal subject was always the one that was nearest to the playback source. We performed our playback experiments only at times when there were no other passerines observed near the focal individual, to avoid any interference with the behaviour of other passerines. All tests for which another bird mobbed before the focal one were discarded because we could not determine whether the focal individual responded to our playback test or to the mobbing call emitted by the other bird. Two observers with binoculars were positioned opposite each other at vantage points at least 15 m from the loudspeaker and observed bird response during the test. In order to limit the

risk of interference with non focal birds, the experimental duration was voluntary shortened compared to what it is usually done (including our own previous studies, Dutour et al. 2016, see also Randler & Vollmer, 2013). More precisely, each experimental test was divided into a 1 min baseline of silence followed by playback of signal containing a series of individual calls following a natural rhythm (1 min). We found no evidence that our arrival disturbed the behaviour of the focal individual before the playback. During the playback, focal birds either did not approached the loudspeaker (i.e. staying around 30 m apart from it) and continued their usual activity (i.e. singing, foraging or resting) or approached it within a 15 m radius. We therefore used this distance of approach to assess the mobbing propensity of focal birds as Hua et al. (2016). A preliminary analysis confirmed that animals approaching the soundtrack within a 15 m radius were 20 times more likely to emit mobbing calls than animals that did not approach it (CI 95%: 21.75 – 59.15). Furthermore, approaching birds also exhibited other mobbing behaviours (circling the loudspeaker, restless movements), although these behaviours were not quantified. Neither the latency to approach (i.e. time of arrival), nor the closest approach (i.e. the minimal distance from the loudspeaker) were found related to the emission of mobbing call among approaching birds (see supplementary material 1, Table A1). Data on species identity and mobbing response of the focal birds were collected mainly by one observer (MD), and were supplemented by a second observer who recorded behavioral observations on bird individuals.

Choice of Experimental Stimuli and Playback Materials

In the field, the amplitude level of mobbing call emitted by these species has never been measured accurately (precise distance between the bird and the sound level meter taking into account the exact position of the head of the bird). Hence, we decided to match by ear signal amplitude of the signals used during our test to a natural calls emitted by passerine

birds while mobbing. Then, the average amplitude used for the playback experiment was obtained by way of a sound level meter placed at one meter from the loudspeaker (86.2 ± 3.07 dB, mean ± SD, Lutron SL-4001, C weighting, slow settings, re: 20 µ Pa). The same volume was used for all species. We broadcast sound tracks using a Shopinnov 20 W loudspeaker (frequency response 100 Hz -15 kHz) that include a memory to store sound file.

Concerning the signal used during playback, we used mobbing calls produced by passerines in response to an Eurasian pygmy owl (*Glaucidium passerinum*) and to conspecific mobbing calls. Calls were recorded with a Fostex FR2LE digital recorder connected to a Sennheiser ME67-K6P microphone. We also used mobbing calls obtained from the Macaulay Library (Cornell Lab of Ornithology, http://macaulaylibrary.org) or from the Xeno Canto online database (www.xeno-canto.org). In order to avoid pseudoreplication (Hurlbert, 1984; Kroodsma, 1989, 1990), calls from 40 individuals were used (five from each species). Each stimulus was played back at the same volume to copy natural calling amplitudes.

Statistical Analyses

To compare the acoustic similarity of European calls to those of the North American species, we carried out four Principal Components Analysis (PCA) using acoustic measurements taken from mobbing calls of the 7 species (Fig. 1). These four PCA analyses including peak frequency, minimum frequency, frequency bandwidth, number of different elements and number of elements. Furthermore, the PCA of great tit and blue tit including duration. For chaffinch and coal tit this acoustic measurement was excluded because it was strongly correlated with number of elements (chaffinch: $r^2 = 0.89$, coal tit: $r^2 = 0.86$, $P < 0.001$). Maximum frequency was excluded for each of the four European species because it was strongly correlated with frequency bandwidth ($0.84 < r^2 < 0.99$, $P < 0.001$). Analyses

were done in R v.2.15.1 (R Development Core Team 2012) using the ade4 package (Dray & Dufour, 2007).

Because none of the focal bird (whatever the receiver species) mobbed when exposed to the novelty signal (i.e. the territorial call of the boreal chickadee; $N = 50$), it was not possible to include this experimental treatment in a parametric analysis. For each receiver species, we therefore used a Fisher exact or Chi-square homogeneity tests to compare the mobbing propensity, as revealed by the relative frequency of mobbing birds, between the novelty signal and the other three heterospecific mobbing stimuli (black-capped chickadee, tufted titmouse and Carolina wren mobbing calls). For each receiver species, a similar test was also performed to compare the mobbing propensity between the novelty signal and the conspecific mobbing stimulus. We then used a generalized mixed models (GLMM) to investigate the variation in mobbing propensity among the receiver species and according to the mobbing stimuli broadcast, thus discarding the novelty signal treatment from the analysis. More specifically, the individual binary response (mobbing response = 1; no mobbing response = 0) was introduced as the dependent variable using a logit link and a binomial distribution for the error term, and the receiver species, the mobbing stimuli and their interactive effect were introduced as explanatory terms in the fixed part of the model. Because five different playback soundtracks of each mobbing stimulus were used twice for each receiver species, soundtracks were introduced in the model as random effects. All coal tits mobbed when a conspecific mobbing call was offered that resulted in aliasing between this explanatory term combination and a complete set of soundtrack random effects (i.e. the coal tits mobbing calls). We therefore used the Laplace optimization method to circumvent the optimization problem and to allow a log-likelihood estimation of the model required to perform likelihood ratio tests (LRT). The significance of the random effect was tested using a likelihood ratio test (LRT) on the full model. LRT were also used to test the significance of

explanatory terms, and non-significant explanatory terms were removed to obtain the final model. We then performed an analysis of deviance to examine the relative importance of the variation explained by the heterospecific status of the stimuli. For this purpose, we constructed a concurrent but reduced model for which all heterospecific stimuli were regrouped within a unique category and compared to the conspecific one. An F statistic was then calculated in order to test the significance of the variation caught by this group. We used a similar approach to investigate whether the difference of response between the conspecific and the heterospecific mobbing calls observed among receiver species could be explained by their phylogenetic relationship at the family level (hereafter family origin). For this purpose, the mobbing stimuli were regrouped into two classes (heterospecific versus conspecific calls) and the receiver species were regrouped according to their family origin. Finally, we performed a separate analysis on the conspecific mobbing call treatment to control for variation of mobbing propensity according to the receiver species. We also performed a partial analysis for each receiver species in order to investigate the variation of mobbing propensity according to the mobbing stimuli using LRT based contrasts. For both these two analyses, the soundtrack random effect could not be estimated reducing the models to generalized linear models (GLM). Analyses were done using SAS 9.3 (SAS Institute Inc., Cary, NC, U.S.A.) software.

Ethical Note

All tested birds returned to normal activity relatively quickly after our experiments (usually within one minute), so we were confident that our experiments were not unduly stressful. All behavioural observations performed during this study complied with the legal requirements in France and followed the ASAB/ABS Guidelines for the Use of Animals in Research. The study complied with the ethical rules set by University Lyon 1 concerning the

use of wildlife species in research programs. The study was conducted with the approval of the Prefecture du Rhône (Ref 2015-13).

RESULTS

Acoustic similarity of mobbing calls

A PCA was performed on acoustic characteristics for each of the four European species in order to determine the similarity of their mobbing calls with those emitted by allopatric species (Fig. 2). In two cases, chaffinch and coal tit, we observed a strong dissimilarity between the focus species and allopatric ones (Fig. 2a and 2b). Concerning great tit, PCA revealed an important overlapping with allopatric mobbing calls of the three allopatric species (Fig. 2c). At last, blue tit mobbing calls showed a strong similarity with black-capped chickadee but no overlapping with mobbing calls emitted by Carolina wren and tufted titmouse (Fig. 2d).

Response to Mobbing Calls

As highlighted in the methods section, none of the European species responded to the novelty signal (i.e. the territorial call of the boreal chickadee). Nonparametric tests showed that all European species responded significantly less to the novelty signal than to conspecific mobbing calls (Nonparametric tests: territorial call versus. conspecific mobbing calls; great tit: $N = 25$, $P < 0.001$; blue tit: $N = 21$, $P = 0.001$; coal tit: $N = 24$, $P < 0.001$; chaffinch: $N = 24$, $P < 0.001$). Furthermore, our results showed that all three tit species responded significantly less to the novelty signal than to the three mobbing calls of American species (black-capped chickadee, tufted titmouse and Carolina wren grouped) (Nonparametric tests: territorial call versus. mobbing calls; great tit: $N = 48$, $P < 0.001$; blue tit: $N = 41$, $P = 0.002$; coal tit: $N = 44$, $P = 0.009$). Concerning chaffinch, the response did not differ significantly

between the novelty signal and mobbing calls (N = 49, P = 0.167). Responses to the novelty signal were thus discarded for the rest of the analyses.

According to the generalized linear mixed model (GLMM) used to analyze the response variation among the receiver species and across the different mobbing signals, we detected a significant soundtrack random effect ($\chi^2 = 3.60, P = 0.03$; see Table 2). The pattern of responses to the different mobbing signals also varied significantly among the receiver species, as indicated by a significant interactive effect between the receiver species and the mobbing signals ($\chi^2 = 18.92, P = 0.03$; see Table 2). As revealed by a deviance analysis, a significant part of this interactive effect could be explained by the variation among the receiver species of the relative response difference between heterospecific and conspecific mobbing calls ($F_{7,8} = 4.04, P = 0.03$; see Table 2 for details). Although all species responded to conspecific mobbing calls (see partial analysis below), the relative strength of this response when compared to all grouped heterospecific calls varied significantly across receiver species (Fig. 3). Furthermore, this variation of response between the conspecific and the heterospecific calls observed among receiver species was at least partly explained by their family origin ($F_{3,12} = 5.42, P = 0.01$; see Table 2 for details).The chaffinch showed a higher response to conspecific rather than heterospecific mobbing calls, whatever the emitter species, while this difference was relatively less and more heterogeneous within the tit species (Fig. 3; Table 3). Partial analysis of the response towards conspecific mobbing calls did not indicate a significant variation in mobbing propensity among species ($\chi^2 = 6.93, P = 0.074$), although the response exhibited by the coal tit was stronger than that of the other three species. Separate analyses performed for each receiver species indicate that both coal tit and chaffinch were significantly more prone to respond to conspecific calls than to heterospecific ones while this was not the case of both the great tit and the blue tit (see Table 3 and Fig. 3). Contrarily to the great tits and the chaffinches, both the blue tit and the coal tit exhibited some variations in

their response towards the three different heterospecific calls despite these variations were not statistically significant (see Table 3 and Fig. 3).

DISCUSSION

We found that European birds responded selectively to the broadcast of mobbing calls of North American passerines but not to the boreal chickadee territorial call, which is usually directed at conspecifics, whereas the mobbing calls are addressed to both conspecifics and heterospecifics. These results corroborate the study of Randler (2012) showing that great tits responded more strongly towards allopatric chick-a-dee mobbing calls than towards the allopatric territorial call. In that study, 31.3% of individuals (5 out of 16) approached the loudspeaker during the black-capped chickadee territorial call playback, while during our boreal chickadee territorial call playback, no individual (0 out of 50) mobbed the loudspeaker. Unlike us, the author started their trials at the beginning of the territorial phase of great tits (Hölzinger, 1997). The stronger response to an allopatric territorial call at the beginning of the territorial phase could be explained by a modification of mobbing response according to the stage in reproduction behaviour.

Our results clearly show that among three out of four receiver species studied, i.e. the three species of tit, prior experience of the heterospecific mobbing call is not required to elicit a response. Moreover, during our experimental tests, American mobbing call playbacks elicited mobbing responses from 9 other bird species, including different genuses, such as *Troglodytes*, *Regulus*, *Sitta*, *Lophophanes*, *Poecile*, *Turdus* and *Garrulus*. As expected, as natural selection might favour the strongest response to their own mobbing calls. Indeed, European passerines reacted most strongly towards European conspecific mobbing calls than those of North American species. Nevertheless, focusing on differences among species, we found great variations in their behavioural response. In particular, the propensity of the

chaffinch to respond to heterospecific mobbing calls is clearly lower than that found for the three tit species. Furthermore, although tits responded well to heterospecific mobbing calls, to some extent their responses remained heterogeneous. Like the chaffinch, the coal tit responded less to the allopatric calls than the conspecific calls. Therefore, these results strongly suggest variability among species, which could well explain the incongruence among previous studies (Johnson et al., 2003; Nocera et al., 2008; Randler, 2012).

Three hypotheses, not mutually exclusive, could be suggested to explain the responses observed to unfamiliar mobbing calls: (i) phylogenic conservatism of the signal structure, (ii) evolutionary convergence due to similar constraints exerted on the signal structure, and (iii) acoustic communication system complexity.

(i) Several studies suggest a phylogenetic relatedness on existing sensory bias in the receiver and in the call structure used by the emitter (Ryan & Rand, 1993; Ryan, 1998; de Kort & ten Cate, 2001). Calls of different species can be acoustically similar as a result of calls retaining features of their acoustic structure from a common ancestor (de Kort & ten Cate, 2001), thus enabling interspecific responses among related species. Such a hypothesis could well explain the response of the chaffinch to allopatric mobbing calls we observed in our study, since none of the three emitter species we used came from its own family. The response of the European tit species to the American tit species could also be due to the highly conserved call structure of the Paridae throughout the Holarctic (Langman, 2006; Randler, 2012).According to the study conducted by Randler (2012) suggesting that response of great tit to allopatric mobbing calls could be phylogenetically conserved, we observed in the present study a strong overlapping between characteristics of mobbing call emitted by this species and three other allopatric species. Surprisingly, all three tit species responded as strongly to the Carolina wren mobbing call as to the mobbing calls of the two tit species.

Hence, the difference in response across the heterospecific mobbing calls may not be explained by the family concordance between the receiver and emitter species.

(ii) The second mechanism to explain the responses observed to allopatric mobbing calls could be due to a similarity of the acoustic features resulting from an evolutionary convergence (Johnson et al., 2003). In order to facilitate emitter localization and recruitment for mobbing, acoustics signals frequently involved repeated calls, strongly modulated in amplitude, with a large frequency band and emitted with high amplitude (Brown, 1982; Marler, 1955; Bradbury & Vehrencamp, 1998; Aubin & Jouventin, 2002). In the same way, many studies suggest that flee alarm calls emitted by several species share the same acoustic structures due to the fact that the emitter should not be localized by the predator while calling (Shalter, 1978; Brown, 1982; Jones & Hill, 2001). The strong selective pressure imposed by predators on the communication process (being localized in the case of mobbing calls or being not localized in the case of flee alarm calls) may lead many species to share the same acoustic structures and could at least partially explain heterospecific communication (Marler, 1955; Bradbury & Vehrencamp, 1998; Johnson et al., 2003; Fallow et al., 2011). Previous studies suggest that both acoustic similarity and learning are important for interspecific responses to alarm calls (Fallow et al., 2011; Haff & Magrath, 2012). In the present study the fact that three out of four European species responded to mobbing emitted by allopatric American species suggests that acoustic structure similarities could explain our results (Fallow et al., 2011). Nevertheless, our acoustic analysis revealed a contrasted situation (Fig. 2). Acoustic similarity could explain behavioural response to allopatric species both in chaffinch (strong acoustic differences with allopatric call and low behavioural responses) and in great tit (strong acoustic similarities and strong behavioural responses to allopatric species). Great tits responded to calls that were acoustically similar to their own. This suggests that they generalize responses from conspecific calls to unfamiliar calls that are acoustically

similar (Ghirlanda & Enquist, 2003). Indeed, if a great tit learns to recognize its own mobbing calls, then with generalized responding, any calls that it hears that are acoustically similar enough to those mobbing calls would be treated as "mobbing calls" (Weary, 1991; Sturdy, Bloomfield, Charrier, & Lee; 2007). On the other hand, acoustic similarity did not explain behavioural response to allopatric species in coal tit (strong behavioural responses to allopatric call in spite of strong acoustic differences with them) and blue tit although for this species results are more complex (Fig. 2d and Fig. 3).To sum up, similarity of the acoustic features seems not to be a universal hypothesis to explain our results as suggested by Wheatcroft and Price (2013).

(iii) A third hypothesis, dealing with acoustic communication system complexity, may explain the fact that the three European tit species responded strongly to American mobbing calls while the chaffinch did not. Indeed calling is structurally complex in tits and chickadees because of the presence of different elements (Suzuki et al., 2016), and the fact that the number of C or D notes elicited different responses (Freeberg & Lucas, 2002). Previous studies have suggested that mobbing calls contain information about the degree of threat that a predator represents (Baker & Becker, 2002; Templeton et al., 2005; Hetrick & Sieving, 2011). Paridae exhibit two very different signals in response to flying or perched predators. Finally, most of these species exhibit rich territorial call repertoires. On the other hand, the chaffinch calling system seems to be less structurally complex than that of chickadees. For instance, the call rate was the most significant determinant on whether other birds interpreted the vocalization as a mobbing call (Randler & Förschler, 2011). Therefore, the complexity of call structures used by the emitter, which is probably associated with the cognitive capacity of the receiver to decode information, may explain the differences observed between the responses of European tits and chaffinches. Further studies focusing on species for which the

mobbing system is based on a simple variation in call rate would be interesting to assess how birds might respond differently to heterospecifics.

In conclusion, our study has emphasized that prior experience is not a prerequisite for heterospecific communication. The allopatric response to mobbing calls of three American species by four European ones shows that a mobbing response could be obtained without previous learning process of these calls. We found that among two out of four receiver species studied, acoustic similarity could explain behavioural response to allopatric species. Nevertheless, the complexity of the communication system in many passerine species probably prevents us to find a general phenomenon that can be applied to all species. For instance, in chickadee species, within a given mobbing call sequence, some elements involved early experience while other not (Hughes, Nowicki, & Lohr, 1998). Further studies, including the use of different passerine species with different complexity levels of their communication system are now necessary to assess differences in phylogenetic relationships, acoustic parameters and acoustic communication system complexity.

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Table 1

The number of tests conducted for each combination in this study. *N* = 226

	Playbacks				
	Mobbing calls				Song
	Black-capped chickadee	Tufted titmouse	Carolina wren	Conspecific	Boreal chickadee
Coal tit	11	11	10	12	12
Blue tit	10	10	11	11	10
Great tit	13	10	10	10	15
Chaffinch	13	11	12	11	13

Table 2

Deviance and AIC according to the terms introduced in the fixed part of the generalized mixed model

Explanatory terms in the fixed part of the models	Nb parm	Deviance	AIC
Receiver | E(conspecific versus heterospecific)	8	196.09	214.09
R(tits versus chaffinch) | E(conspecific versus	4	206.36	216.36
R(tits versus chaffinch) + E(conspecific versus	3	208.53	216.53
R(tits versus chaffinch) |Emitter	8	199.03	217.03
Receiver | Emitter	16	185.66	219.66
Receiver + E(conspecific versus heterospecific)	5	207.94	219.94
Receiver + Emitter	7	204.58	220.58
Receiver	4	218.41	228.41
Emitter	4	220.23	230.23
Intercept	1	235.32	239.32

The « | » character indicates the addition and interaction between the explanatory terms. Receiver: 4 receiver species, Emitter: 4 mobbing call stimuli, R(tits versus chaffinch): receivers species grouped into two class according to the family of origin, E(conspecific versus heterospecific): mobbing call stimuli grouped into two classes, heterospecific versus conspecific calls. Nb parm: Number of parameters in the fixed part of the model. The significance of explanatory terms was tested using a likelihood ratio test or a F test in the case of constrained structures for the receiver or the emitter effect (see main text). For all models, the playback soundtrack of each mobbing stimulus as a random factor in the response. N = 176

Table 3

Overall difference of responses between birds exposed to heterospecific calls and those exposed to the conspecific one, and overall difference of responses among birds exposed to different heterospecific calls.

comparison	receiver	df	χ^2	*P*
Conspecific versus heterospecific calls	Blue tit	3	5.6	0.13
	Coal tit	3	21.86	< 0.0001
	Great tit	3	0.85	0.84
	Chaffinch	3	13.38	0.004
Difference between heterospecific calls	Blue tit	2	4.84	0.09
	Coal tit	2	4.92	0.09
	Great tit	2	0.85	0.65
	Chaffinch	2	1.46	0.48

All comparisons were based on a partial analysis for each receiver species using a LRT based contrast. df: degrees of freedom. See supplementary material 3 Table A3 for detail pairwise comparisons of responses between all mobbing call stimulus for each receiver species.

APPENDIX

Table A1

Influence of the latency and the closest approach on the mobbing call propensity. Df: degrees of freedom

Explanatory term	Numerator df	Residual df	F value	P value
Latency	1	60	0.04	0.8467
Closest approach	1	60	0.05	0.8235
Latency*Closest approach	1	60	0.33	0.566

A logistic model was used to examine whether the latency (i.e. time of arrival within the 15 meter radius around the loudspeaker) and the closest approach (i.e. the minimal distance from the loudspeaker) were related to the emission of mobbing call among approaching birds. Neither the latency nor the closest approach was found related to the mobbing call propensity.

Table A2

Pairwise comparisons of the two principal components between each European birds mobbing calls and the North American birds ones

	Tufted titmouse		Black-capped chickadee		Carolina wren	
	PC1	PC2	PC1	PC2	PC1	PC2
Chaffinch	**0.008**	**0.008**	**0.008**	0.151	**0.008**	0.151
Coal tit	**0.008**	0.548	**0.008**	0.309	**0.008**	0.548
Great tit	**0.032**	0.548	0.841	0.690	0.548	0.548
Blue tit	0.548	**0.008**	0.690	0.841	0.095	**0.008**

PC1 and PC2 respectively for the first and the second principal components. All comparisons were done using a Wilcoxon exact test given the low sample size (i.e. N = 10 for each test), p values were not corrected for multiple comparisons. Significant P values are indicated in bold.

Table A3

Pairwise comparisons of responses between all mobbing call stimulus for each receiver species

Receiver species	Pairwise comparison	χ^2	*P*
Blue tit	conspecific *vs* BC	0.02	0.89
	conspecific *vs* CW	0	1
	conspecific *vs* TT	3.96	0.04
	BC *vs* CW	0.02	0.89
	BC *vs* TT	3.29	0.07
	CW *vs* TT	3.96	0.04
Coal tit	conspecific *vs* BC	6.83	0.009
	conspecific *vs* CW	12.32	0.0004
	conspecific *vs* TT	20.36	< 0.0001
	BC *vs* CW	1.18	0.28
	BC *vs* TT	4.92	0.03
	CW *vs* TT	1.24	0.27
Great tit	conspecific *vs* BC	0.01	0.94
	conspecific *vs* CW	0.22	0.64
	conspecific *vs* TT	0.2	0.65
	BC *vs* CW	0.18	0.67
	BC *vs* TT	0.31	0.58
	CW *vs* TT	0.84	0.36
Chaffinch	conspecific *vs* BC	11.81	0.0006
	conspecific *vs* CW	5.45	0.02
	conspecific *vs* TT	6.99	0.008
	BC *vs* CW	1.44	0.23
	BC *vs* TT	0.6	0.44
	CW *vs* TT	0.16	0.69

All comparisons were based on a partial analysis for each receiver species using a LRT based contrast. BC for black-capped chickadee, TT for tufted titmouse and CW for Carolina wren. df: degrees of freedom.

FIGURE LEGENDS

Figure 1. Spectrograms of the mobbing calls of studied species. Spectrograms were produced with Avisoft SASLab© (frequency sampling 44.1kHz, FFT length 512 points). See text for further details of measurments.

Figure 2. Principal Components plot of the acoustic characteristics of European birds mobbing calls (◆): (a) chaffinch (PC1: 40.9% and PC2: 23.2%), (b) coal tit (PC1: 50.3% and PC2: 22.3%), (c) great tit (PC1: 40.1% and PC2: 26.5%), (d) blue tit (PC1: 33.2% and PC2: 21.9%) with North American birds mobbing calls (tufted titmouse (■), a black-capped chickadee (▲), a Carolina wren (○)). The contour lines indicate the 68% probability of belonging to each putative cluster (i.e. species) which can be used to examine graphically the similitude between species. See supplementary material 2 Table A2 for pairwise comparisons performed separately on PC1 and PC2 between European and North American mobbing calls.

Figure 3. Proportion of European birds responding to the presentations of a tufted titmouse (light grey square), a black-capped chickadee (dark grey triangle), a Carolina wren (white circle) and a conspecific (black diamond) mobbing call. Error bars represent standard errors. See supplementary material 3 Table A3 for detail pairwise comparisons of responses between all mobbing call stimulus for each receiver species.

Figure 1.

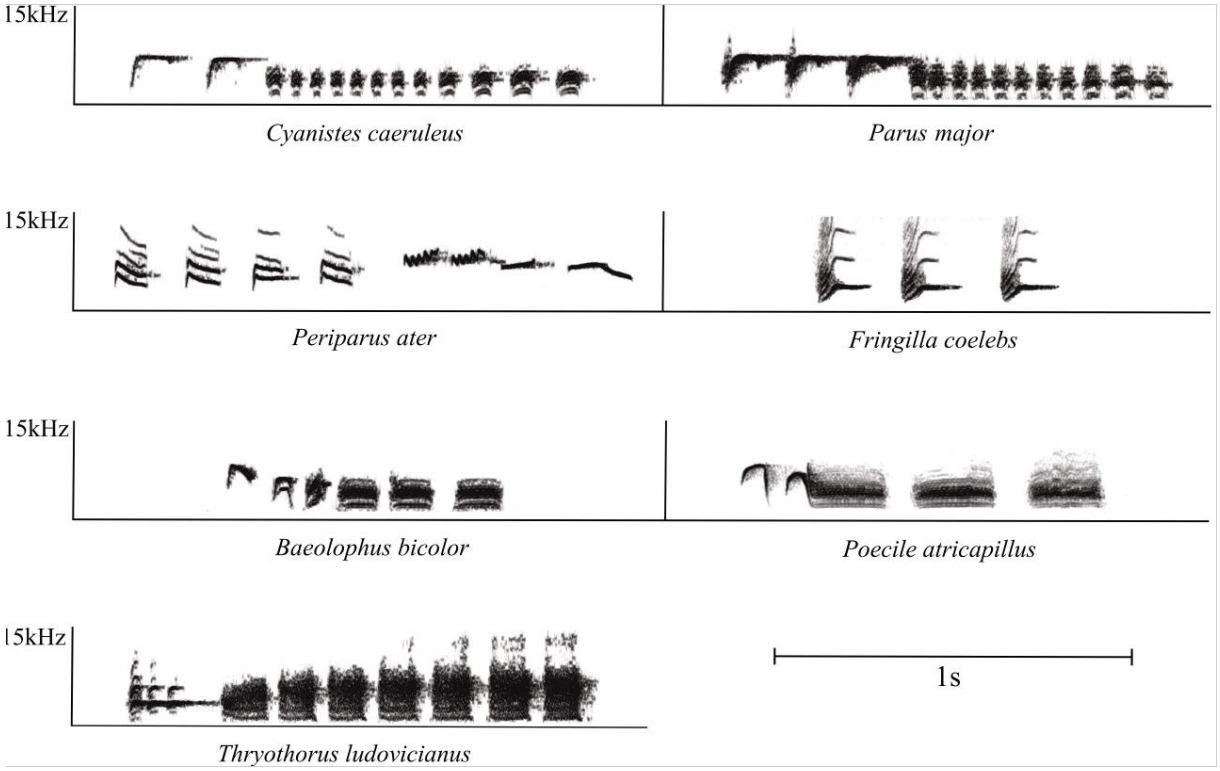

15kHz
Cyanistes caeruleus
Parus major
15kHz
Periparus ater
Fringilla coelebs
15kHz
Baeolophus bicolor
Poecile atricapillus
15kHz
1s
Thryothorus ludovicianus

Figure 2.

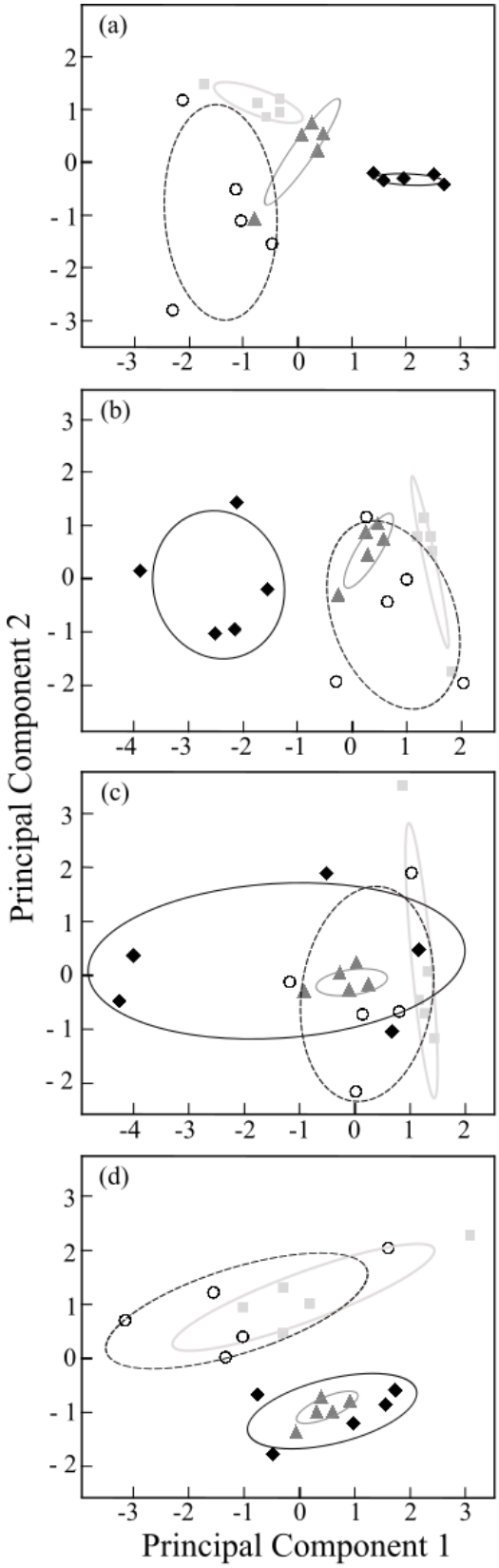
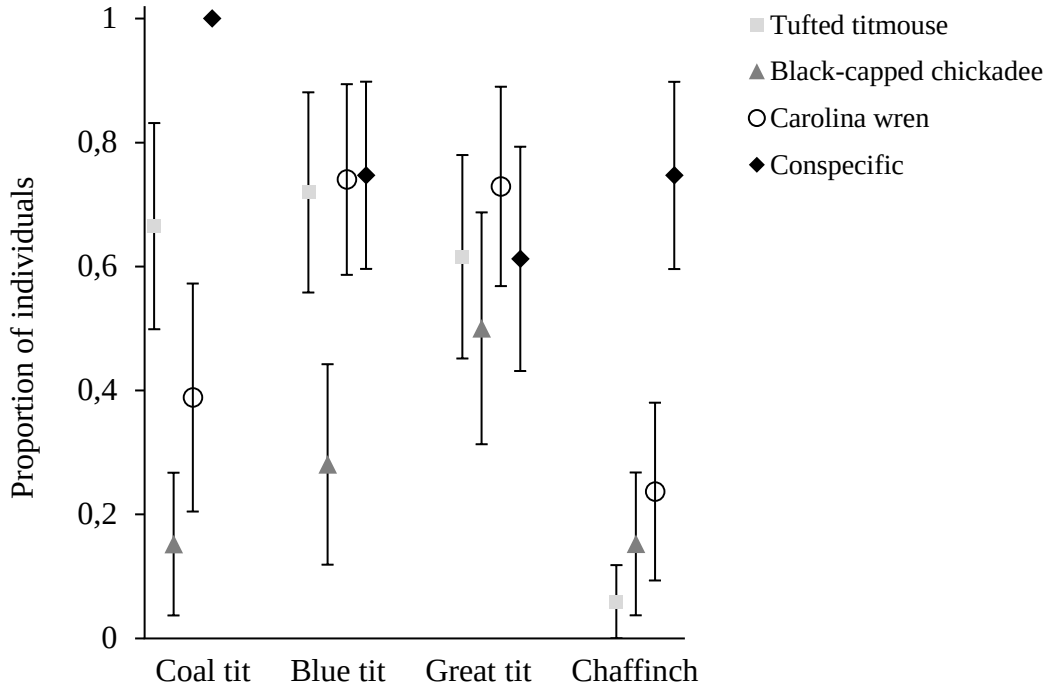


Figure 3.


1
0,8
0,6
0,4
0,2
0
Proportion of individuals
Coal tit
Blue tit
Great tit
Chaffinch
Tufted titmouse
Black-capped chickadee
Carolina wren
Conspecific