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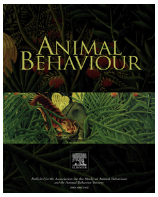

Mobbing calls: a signal transcending species boundaries

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When they detect a predator, some prey exhibit mobbing behaviour and produce mobbing calls that quickly draw a mixed conspecific and heterospecific group against the predator. While the efficiency of this strategy is often linked to interspecific communication, it raises the question of how animals recognize these signals as mobbing calls. It is usually suggested that associative learning about a predator when heterospecific mobbing calls are heard plays a crucial role in communication among species. Alternatively, phylogenetic conservation or evolutionary convergence could also explain this communication process. To determine whether prior experience is required to express a mobbing response, we conducted playback experiments with four European passerine species: great tit, *Parus major*, blue tit, *Cyanistes caeruleus*, coal tit, *Periparus ater*, and common chaffinch, *Fringilla coelebs*. The aim of the study was to examine whether they would respond to the mobbing signals of several North American passerines. As expected, because natural selection might shape a strong response to conspecific mobbing calls, our focal species reacted more strongly towards their own mobbing calls than towards those of American species. Nevertheless, for the three European species of tit, prior experience of heterospecific mobbing calls was not required to elicit a response. Additionally, for great tit and chaffinch, we found that acoustic similarity could explain behavioural responses to allopatric species. In contrast, such similarity was probably not the main mechanism underlying the response for the other two European species. Heterospecific response to mobbing calls probably involved many different mechanisms. Further studies focusing on each of these should allow us to understand their relative contribution to heterospecific communication.

When they perceive a potential predator, many species of birds and mammals produce specific alarm calls (Graw & Manser, 2007; Klump & Shalter, 1984; Magrath, Pitcher, & Gardner, 2007; Rainey, Zuberbühler, & Slater, 2004; Seyfarth, Cheney, & Marler, 1980). These calls are often classified as flee alarm calls, which are associated with the caller escaping while spurring other individuals to freeze or flee, or mobbing calls, which are associated with the caller approaching and harassing the predator while encouraging others to join it (Curio, 1978; Hartley, 1950; Hurd, 1996; Kennedy, Evans, & McDonald, 2009; Magrath, Haff, Fallow, & Radford, 2015). Mobbing calls are usually directed at an apparently nonhunting predator, and are expected to decrease its hunting efficiency, either by distracting it or by chasing it away (Curio, 1978; Flasskamp, 1994; Hoogland & Sherman, 1976; Pavey & Smyth, 1998; Pettifor, 1990). Both the intensity of mobbing and its success in deterring the predator are positively related to the size of the group gathered by the caller (Becker, 1984; Picman, Leonard, & Horn, 1988; Robinson, 1985; Verbeek, 1985). Although mobs can be formed exclusively by conspecifics, they often involve heterospecific prey (Dutour, Lena, & Lengagne, 2017; Hurd, 1996; Suzuki, 2016). Hence, this phenomenon makes mobs well suited for investigating 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 mob, 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, sensu Peake, 2005; see Magrath et al., 2015 for a review), especially to recognize heterospecific mobbing calls.

Both learned and innate processes could be involved in the mechanisms enabling the recognition of heterospecific mobbing calls (Fallow, Gardner, & Magrath, 2011; Hurd, 1996; Magrath,

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Pitcher, & Gardner, 2009; Ramakrishnan & Coss, 2000; Wheatcroft & Price, 2013). By nature, associative learning is more flexible than innate processes but it requires previous experience to take place. Such experience could occur when heterospecific prey 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. As for other alarm calls, there are strong ecological constraints on the acoustic structure of mobbing calls to increase their efficiency. Loudness and repeated features can be expected to be selected to facilitate locating the caller (Bradbury and Vehrencamp, 2011; Ficken & Popp, 1996; Jones & Hill, 2001; Klump & Shalter, 1984; Marler, 1955). Hence, these calls can also be used in other contexts that require accurate location of the caller such as maintaining contact with a partner or finding food (Mahurin & Freeberg, 2009; Marler, 1956; Suzuki, 2012). Moreover, calls inevitably incorporate some features such as harshness or broad bandwidth pulses of sound related to the psychological state of the caller, 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, McNaughton, Shelley, & Blumstein, 2004; Randler, 2012). Finally, both associative learning and innate processes could enhance recognition of heterospecific mobbing calls. Having similar acoustic features could greatly enhance the recognition of heterospecific mobbing calls through the mechanism of generalization which is often involved in the learning process (Sturdy, Bloomfield, Charrier, & Lee, 2007; Weary, 1991). Studies in some species of Paridae 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, Taylor, & Ratcliffe, 2008), in others they did recognize them (Johnson et al., 2004; Langham, Contreras, & Sieving, 2006; Randler, 2012; Wheatcroft & Price, 2013). Because almost all studies have focused on one pairwise comparison of caller–receiver species, any comparison across species remains difficult, if not impossible. Moreover, in the studies on more than one caller–receiver pair, the heterospecific species responding to playbacks were not identified, preventing an understanding of responses in the light of the phylogeny. Hence, there is a need for a larger pairwise comparison of caller–receiver species 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 response of four passerine birds exposed to the mobbing calls of three allopatric species. Additionally, we measured similarity among mobbing calls of the studied species to determine whether acoustic similarity could be viewed as a general mechanism involved in heterospecific communication. To test this, we played the calls of three North American passerine species to four European species, since mobbing is well documented in both communities and based on a similar alarm-calling system (Dutour, Lena, & Lengagne, 2016; Langham et al., 2006; Sieving, Hetrick, & Avery, 2010; Templeton & Greene, 2007). Then, as one study suggested a possible phylogenetically conserved response among the Paridae (Randler, 2012), we used sound tracks of three American species of Paridae: two corresponding to a mobbing call and one as a control (i.e. territorial call). Additionally, we chose to use a non-Paridae call to compare mobbing responses obtained from two different families.

METHODS

Study 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, Jöngren, Nilsson, Schönberg Alm, & Strandmark, 2005; Berzins et al., 2010; Randler & Förschler, 2011; Randler & Vollmer, 2013; Dutour et al., 2016; Carlson, Healy, & Templeton, 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 (Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Betts, Hadley, & Doran, 2005; Hetrick & Sieving, 2011; Hurd, 1996; Morton & Shalter, 1977; Sieving, Contreras, & Maute, 2004; Templeton & Greene, 2007; Templeton, Greene, & Davis, 2005). 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 the territorial call of the boreal chickadee, *Poecile hudsonicus*, an American songbird found throughout Canada and the northern United States (Ficken, Mclaren, & Hailman, 1996), as a control (50 tests, see Table 1). Finally, to compare the relative intensity of mobbing responses to American species, we also broadcast conspecific mobbing calls to each of the four European species (44 tests, see Table 1).

Acoustic Analysis

Recordings were in 16-bit WAV format and analysed with Avisoft SASLab software (Avisoft Bioacoustics, Berlin, Germany). We used spectrograms with a fast Fourier transform length of 512 points for the measurements. We selected five recordings per species and analysed up to 10 songs per recording (on average 5.97 ± 2.43 SD). To properly characterize the mobbing calls of each 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 (Hz) is maximum); (3) maximum frequency (highest frequency of the call in Hz); (4) minimum frequency (lowest frequency of the call in Hz); (5) frequency bandwidth (differences

Table 1
The number of tests conducted for each combination in this study

	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

$N = 226$.