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Batesian acoustic mimicry in mammals: bats mimic hymenopteran sounds to deter predators

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Mimicry, in its multiple forms, represents one of the most fascinating phenomena in nature [1]. The traits of these often complex, finely tuned, and sometimes extravagant relationships among species have evolved to deceive predators or prey. Indeed, mimicry has most often evolved to discourage predation: the "mimic" belongs to a species that exhibits phenotypic convergence towards a non-related "model" organism which is inedible or harmful, so that a given predator, or "receiver", will refrain from attacking, handling or ingesting the mimic. Among animals, mimicry is well-known for invertebrates [2] and several vertebrate classes e.g. [3], yet in most cases, it only concerns visual resemblance between mimics and models. Despite the importance of acoustic signals in animal communication, antipredatory acoustic mimicry has been long neglected until recently. Acoustic mimicry *per se* occurs when the receiver alters its behaviour after detecting the acoustic resemblance between the mimic and the model in such a way as to confer a selective advantage to the mimic. Distinguishing the different mechanisms by which sound deters predators, i.e., aposematism, mimicry, or startle, is based on how receivers respond to the signal, and on the existence of a model [4]. Aposematism is associated with unpalatability and requires a predator to learn such association [5]. Similarly, mimicry also requires a learning phase by the receiver, yet it may or may not be combined with unpalatability (Müllerian and Batesian systems, respectively). Startling sounds instead deter the receiver from persisting in the predation attempt for the short time the prey needs to evade the attack [6], and require no learning from the receiver.

In this experimental study, we investigate on the first documented case of interspecific acoustic mimicry among mammals, and hypothesize that distress calls broadcast by greater mouse-eared bats (*Myotis myotis*) when handled discourage their avian predators by mimicking sounds of stinging social hymenopterans. We first compared the acoustic similarity of buzzing sounds emitted by distressed *M. myotis* and four species of social hymenopterans during handling by exploring the degree of multivariate separation in structure. We then conducted playback experiments by broadcasting bat, hymenopteran and control sounds respectively to captive adult owls (8 barn owls, *Tyto alba*, and 8 tawny owls, *Strix aluco*). Each owl was exposed once to each treatment (a buzz from *M. myotis*, from honeybees *Apis mellifera*, from hornet *Vespa crabro*, and a non-buzzing bat sound as control). Owl's behaviours during and after each playback were videorecorded. We tested whether and how behavioural responses by owls differed according to treatment. To assess whether genuine mimicry actually occurred, we included, as experimental subjects, both wild owls, expected to be potentially experienced with bats and hymenopterans, and captive-raised individuals, considered as fully naïves to the selected stimuli.

When handled, bats and insects readily produced distress buzzes (sequences of steep frequency-modulated calls at high repetition rates – Figure 1A). Multivariate discrimination reached 95.4% correct classification among bats and hymenopterans, yet such measure dropped to 53.7% when only call variables comprised within the owl's hearing range were considered, with higher confusion rates between calls of *M. myotis* and those of *V. crabro*.

Behavioural responses by owls were significantly influenced by individual experience, stimulus type, and their interaction. Owls consistently reacted to hymenopteran and bat buzzes in the same way by increasing the distance from the speaker, whereas they approached it in response to the control stimulus, as expected from a non-mimetic vocalization produced by potential prey. Such spatial response was more pronounced in experienced vs. naïve owls (Figure 1B). The stimulus type *per se* influenced predatory behaviours: control sounds elicited such behaviours more frequently than did buzzes. Moreover, experienced owls inspected and performed escape attempts more often than naïve individuals (Figure 1C). In all cases, post-hoc comparisons resulted in significant differences among responses to control versus each of all other stimuli (all $p<0.05$).

We show that the buzzes emitted by a distressed bat resemble those of noxious hymenopteran insects when the acoustic parameters taken for comparison are those falling within an owl's hearing range, and that insect and bat buzzes exert a consistent avoidance reaction in avian predators. We thus provide strong support to a novel Batesian acoustic mimicry system, involving a mammal as the mimic, insects as models, and predatory birds as receivers. This represents the first documented example of interspecific mimicry between mammals and insects and one of the few examples of acoustic mimicry systems known to date.

Our results also fit into the framework established by Dalziell & Welbergen [7] and Font [8], i.e., that mimetic systems comprise three elements as actors (model, mimic and receiver), and that mimicry may be tuned to the species-specific perceptual abilities of one or more receivers. Several bat species emit buzzes [9], and other animal species inhabiting tree or rock cavities are also anecdotally known to buzz when they are disturbed at their nest, and these buzzes are sometimes described as similar to those made by bees, as in North American flickers (*Colaptes auratus*; [10]), so the system we describe here may represent an example of a more common phenomenon. Whether other taxa play a role in a widespread acoustic mimetic system, with vertebrates mimicking insect models, has yet to be tested, leaving room for further research on the ecological interactions that lead to signal evolution in animal interspecific communication.

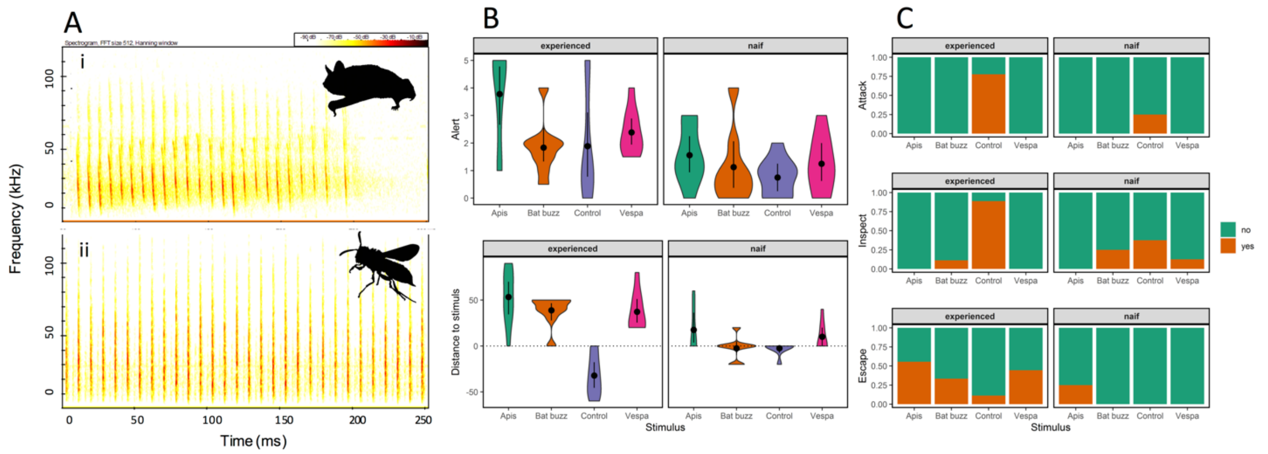

Figure 1. Structural resemblance between bat and hymenopteran buzzes, and behavioural responses of owls buzzes and control stimuli.
(A) Spectrograms of buzzes emitted by distressed i) Greater mouse eared bat (*Myotis myotis*) and ii) European hornet (*Vespa crabro*). (B-C) Behavioural responses (n scored behaviours=5) by 16 captive owls (*Tyto alba*, n=8; *Strix aluco*, n=8) to the playback of 4 acoustic stimuli (Apis: buzz of domestic bee *Apis mellifera*; Control: social call by European fee-tailed bat Tadarida teniotis; Bat buzz: distress buzz of greater mouse-eared bat *Myotis myotis*; Vespa: buzz of European hornet *Vespa crabro*), separately for experienced (n=8) and naif individuals (n=8).

SUPPLEMENTAL INFORMATION

Supplemental Information includes two tables, detailed experimental procedures, and supplemental references.

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