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REVIEW

Bats are still not birds in the digital era: echolocation call variation and why it matters for bat species identification[1]

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Abstract: The recording and analysis of echolocation calls are fundamental methods used to study bat distribution, ecology, and behavior. However, the goal of identifying bats in flight from their echolocation calls is not always possible. Unlike bird songs, bat calls show large variation that often makes identification challenging. The problem has not been fully overcome by modern digital-based hardware and software for bat call recording and analysis. Besides providing fundamental insights into bat physiology, ecology, and behavior, a better understanding of call variation is therefore crucial to best recognize limits and perspectives of call classification. We provide a comprehensive overview of sources of interspecific and intraspecific echolocation call variations, illustrating its adaptive significance and highlighting gaps in knowledge. We remark that further research is needed to better comprehend call variation and control for it more effectively in sound analysis. Despite the state-of-art technology in this field, combining acoustic surveys with capture and roost search, as well as limiting identification to species with distinctive calls, still represent the safest way of conducting bat surveys.

Key words: bat detector, bioacoustics, Chiroptera, classification, spectrogram.

Résumé : L'enregistrement et l'analyse de cris d'écholocalisation sont des méthodes fondamentales utilisées pour étudier la répartition, l'écologie et le comportement des chauves-souris. Il n'est toutefois pas toujours possible d'identifier les chauves-souris en vol sur la base de leurs cris d'écholocalisation. Contrairement aux chants d'oiseaux, les cris de chauves-souris présentent une grande variabilité qui peut souvent rendre l'identification difficile. Les outils matériels et logiciels numériques modernes utilisés pour l'enregistrement et l'analyse des cris de chauves-souris n'ont pas encore permis de surmonter complètement cette difficulté. En plus de renseignements fondamentaux sur la physiologie, l'écologie et le comportement des chauves-souris, une meilleure compréhension de la variabilité des cris est donc nécessaire pour mieux établir les limites et les perspectives que présente la classification des cris. Nous présentons un survol exhaustif des sources de variabilité interspécifique et intraspécifique des cris d'écholocalisation, en illustrant ce que cette variabilité signifie pour l'adaptation et en soulignant les lacunes sur le plan des connaissances. Nous notons que d'autres travaux sont nécessaires pour mieux comprendre la variabilité des cris et l'intégrer efficacement à l'analyse des sons. Bien que des technologies de pointe soient disponibles dans ce domaine, l'approche la plus sûre pour réaliser des relevés de chauves-souris demeure le jumelage de relevés acoustiques à la capture et l'inspection de dortoirs tout en restreignant l'identification aux espèces dont les cris sont distinctifs. [Traduit par la Rédaction]

Mots-clés : détecteurs de chauves-souris, bioacoustique, chiroptères, classification, spectrogramme.

Introduction

Echolocation is a form of active sensing in which an individual generates sound to ensonify the surrounding space and analyzes the corresponding echoes to detect obstacles, orientate, and acquire information on the presence and location of food and other key spatial resources (e.g., Fenton 2013). The sense is especially valuable for animals that are active in the dark, such as bats, or dwell into deep or turbid water, such as toothed whales (Jones 2005; Fenton 2013).

Bats (order Chiroptera) are one of the most diverse mammal groups — ca. 1300 species so far known to science, over 80% from which use laryngeal echolocation (Fenton and Simmons 2014). Bats that echolocate using sounds produced in the larynx stand out of the several vertebrate groups that have independently evolved echolocation (Fenton 1984) for the remarkable acoustic diversity of their echolocation calls, with frequencies ranging between 8 and >200 kHz (Altringham 2011).

The acoustic diversity of bats is expressed at two levels: (1) interspecific, represented by the structural differences of echolocation calls that occur among species, and (2) intraspecific, occurring within species over different spatial and temporal scales (e.g., Jones and Holderied 2007). Both levels arise from a complex network of selective pressures that have led to one of the most compelling examples of "good design" obtained through evolution by natural selection (Dawkins 1986). Theory of acoustics and sonar, as well as radar engineering, may in fact predict the design of bat calls effectively because calls are often ideally suited to face the sensorial challenges posed to the echolocator by its environment (Jones and Holderied 2007).

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[1] This review is one of a series of papers arising from "*Learning to Listen* — Second International Symposium on Bat Echolocation Research: Tools, Techniques, and Analysis" that was held in Tucson, Arizona, USA, 26 March – 1 April 2017. Invited speakers were encouraged to submit manuscripts based on their talks, which then went through the normal *Canadian Journal of Zoology* peer-review process.

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Scientists often exploit echolocation calls to study bats because acoustic surveys overcome the difficulties posed by the nocturnal habits of these mammals and their elusiveness, rendering detection possible (and noninvasive) when direct observation or capture would be of little or no use (e.g., Fenton 2013; Russo and Voigt 2016). To identify bat species from their echolocation calls, species-specific, diagnostic differences must be recognized. At first glance the process might be likened to how ornithologists use songs to identify bird species; however, bird song functions in intraspecific communication and is therefore stereotyped to convey unambiguous messages to conspecifics only (Barclay 1999). Bird song is also often elaborate in structure, with complex and species-specific songs having evolved through sexual selection. Echolocation has primarily a sensory scope, and echolocation calls may therefore be similar among species, not only because of phylogenetic relatedness (i.e., a certain call structure has been retained from a shared common ancestor), but also due to adaptive convergence evolved under similar habitat pressures. An important source of overlap in call characteristics is individual flexibility, i.e., bats may change call structure to optimize echolocation performances in different habitat structures or to fulfil different tasks (e.g., Obrist 1995; Barclay 1999), so that their calls may at times resemble those of other species. This considerable variability often makes recognizing diagnostic call traits for species identification problematic.

In the early years of bat acoustic surveys, attempts were made to recognize bat species qualitatively. By making ultrasound audible through portable devices such as heterodyne (and later, time expansion) bat detectors, the operator performed species recognition in the field judging the "best heard" frequency and evaluating qualitative species "fingerprints" such as rhythm and tonal qualities of sound emission (e.g., Ahlén 2002). Because this approach relies on personal sound memory and having a musical ear, its validity has been questioned (e.g., Vaughan et al. 1997; Barclay 1999; Russo and Jones 2002). Barclay (1999) remarked that "bats are not birds", highlighting the importance of being aware of limitations and degree of reliability of the technique and recognizing the central role of call variation as an obstacle to identification. Another issue deserving attention is that self-determined, unassessed experts sometimes use echolocation calls recorded from free-flying bats as species-specific templates for identification. Although bat calls used for reference should have been identified from other features (e.g., morphology or even genetic validation of the bat that emitted the call), their identity is in fact established from the calls themselves, making the argument circular.

In the last two decades, acoustic identification of bats has undergone a step change. Thanks to digital technology, today some researchers rely on automated recorders and direct ultrasound sampling, as well as algorithms that classify bat calls to species (Russo and Voigt 2016). The principle common to all algorithms is the comparison of an unknown call with a library of calls of known identity: the unknown call is assigned to the species whose calls are most similar based on a set of spectral and temporal descriptors (Russo and Voigt 2016). The process is operator-independent (but see Russo and Voigt 2016) and repeatable. The new technology has been welcome especially by consultants given the ever-growing demand for bat surveys where wind turbines or roads (which may cause bat mortality; e.g., Fensome and Mathews 2016; O'Shea et al. 2016) are planned or developed, or their effects need to be monitored. Although screening recordings and identifying species have reached an unprecedented speed thanks to the new tools, and our knowledge of the echolocation calls of more and more species has expanded, identification is still far from being error-free (Russo and Voigt 2016; Rydell et al. 2017). Barclay's (1999) cautionary note is still valid: in the digital era, bats are still "not birds", and call variation remains as a major obstacle to species identification in many cases.

The aim of this article is to offer a comprehensive review of echolocation call variation and discuss its implications for species identification, recognizing limitations, and providing perspectives in this field. We categorize variation as occurring across species (interspecific acoustic diversity) and within species, further dividing these categories into subcategories according to the causes of the variation. It is important to bear in mind, however, that as with all classifications, the one we adopted is inevitably simplistic and interactions occur among factors, so these categories are not always independent from one another. For example, geographic differences are often difficult to separate from a species' phylogenetic history, or may result from evolutionary pressures exerted by the local bat community to partition food niches or to separate communication channels; intersexual differences in calls may occur in some populations but not in others, or their direction (i.e., which sex typically emits calls of higher frequency) may differ across populations.

Interspecific acoustic variation

Echolocation behaviour and call structure

Echolocation behaviour may be classified according to duty cycle, i.e., the proportion of time echolocation calls are "on" relative to the silence intervals between them (e.g., Jones and Holderied 2007; Fenton et al. 2012). Most bats are low duty cycle (LDC) echolocators, i.e., they broadcast brief calls whose subsequent long silence interval is used by the bat to listen to the returning echo to process time delay and work out position and characteristics of surrounding objects. In this case, sound is on for <30% (Jones 1999) and pulse and echo are separated in time to avoid overlap between returning echoes and outgoing calls (forward masking; e.g., Fenton 1999; Fenton et al. 2012). These echolocators emit calls that are frequency modulated (FM), i.e., frequency changes as a downward sweep over time, or call structure includes at least a substantial FM component (Fenton et al. 2012). A minority of bats are high duty cycle (HDC) echolocators; their signals are "on" most of the time (>30%), so forward masking is not avoided. These bats use constant frequency (CF) echolocation calls and detect the acoustic "glints" encoded in the returning echo. Acoustic glints are sudden changes in echo amplitude and Doppler shifts in frequency induced by the wing fluttering of the insects that bats pursue in cluttered habitats such as the forest (Fenton et al. 2012). HDC echolocators are most sensitive to a given (individual) frequency value (Schuller and Pollak 1979).

When flying, HDC bats reduce call frequency to compensate for Doppler shifts generated by their own movement (Schnitzler 1968), so that the echo frequency matches exactly the high auditory sensitivity of their acoustic fovea (Schuller and Pollak 1979). The outgoing call and returning echoes are separated in frequency rather than in time, so that unlike LDC bats, HDC bats may broadcast calls and receive echoes at the same time and thus tolerate forward masking (Fenton et al. 1995; Fawcett et al. 2015). This echolocation mode is most effective in cluttered habitats such as forests where call–echo overlap occurs frequently (Fenton et al. 2012). Unlike calls of LDC echolocators, those of HDC echolocators are dominated by a long, pure CF component (Schnitzler et al. 2003; Fig. 1). LDC bats foraging in open space use narrowband calls: operational range is increased by concentrating energy in a narrow band of low frequencies that being less subject to atmospheric attenuation may travel farther (Lawrence and Simmons 1982). This call type provides coarse resolution, but finer resolution is not needed by open-space foragers. In this habitat type, a relatively long call duration provides a longer operational range; since the acoustic image does not need to be updated frequently, call emission rates are typically low enough to avoid forward masking. Broadband, FM (Fig. 1) calls are typically recorded from bats foraging in clutter such as a forest (Neuweiler and Fenton 1988; Neuweiler 1990). The high frequencies that often dominate

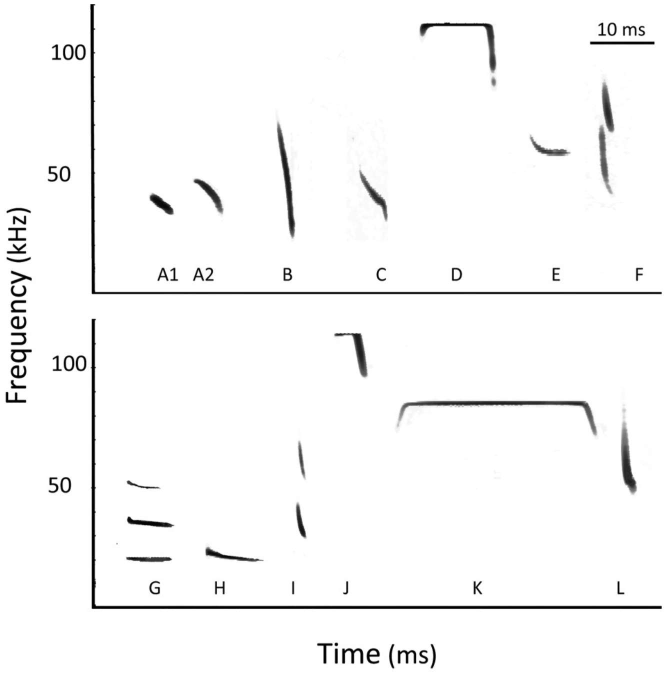


Fig. 1. Examples of different echolocation calls for 12 bat species from two geographic regions. Top panel — bats from central Apennines (Italy): (A1, A2) western barbastelle, *Barbastella barbastellus*; (B) Natterer's bat, *Myotis nattereri* (Kuhl, 1817); (C) Alcathoe myotis, *Myotis alcathoe* von Helversen and Heller, 2001; (D) Mediterranean horseshoe bat, *Rhinolophus euryale*; (E) soprano pipistrelle, *Pipistrellus pygmaeus*; (F) brown big-eared bat, *Plecotus auritus* (L., 1758). Bottom panel — bats from the Negev desert (Israel): (G) Egyptian tomb bat, *Taphozous perforatus* E. Geoffroy, 1818; (H) European free-tailed bat, *Tadarida teniotis*; (I) Christie's big-eared bat, *Plecotus christiei* Gray, 1838; (J) trident leaf-nosed bat, *Asellia tridens* (E. Geoffroy, 1813); (K) Geoffroy's horseshoe bat, *Rhinolophus clivosus*; (L) Bodenheimer's pipistrelle, *Hypsugo bodenheimeri* (Harrison, 1960). Cases A1, A2, B, C, F, and I represent frequency-modulated (FM) calls, whereas E, H, and L are frequency-modulated – quasiconstant frequency (FM–QCF) calls. All such cases refer to low duty cycle species, whereas D, J, and K (characterized by FM–CF or FM–CF–FM structure, where CF is constant frequency) are typical of high duty cycle species. Note call alternation in A1 and A2 and the use of harmonics in F, G, and I.

FM calls undergo strong atmospheric attenuation (Lawrence and Simmons 1982), so they are only effective over the short range needed by a clutter specialist, but confer the sonar beam a higher directionality and return stronger echoes from smaller targets (Siemers and Schnitzler 2004). Besides, the echoes of broadband calls reflected from targets include constructive and destructive interference — amplitude peaks and nulls depending on the texture of the surface ensonified — named "echo colours" (Smith 2008). "Colours" increase the echo's informational content (e.g., Schmidt 1992) and help with tracking small (down to 0.2 mm) prey movements on the ground or in the foliage (Neuweiler 2000). By illuminating the sonar scene with a broad range of frequencies, frequency-dependent differences are highlighted in the echo and background details characterized to aid prey discrimination (Siemers and Schnitzler 2004). In dense vegetation, proximity to surrounding objects makes it necessary to update the acoustic image more frequently by increasing call emission rate; forward masking is then avoided by decreasing call duration (Schnitzler and Kalko 2001).

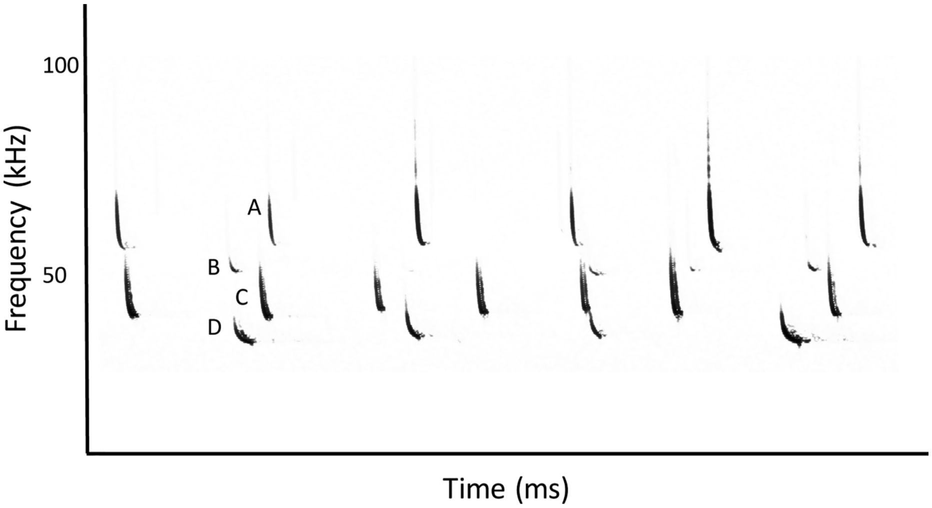
In LDC echolocators, narrowband and broadband components may be combined in the same call to increase operational range through the narrowband component while providing details on the target through the broadband component (Simmons and Stein 1980; Fenton 1999). Such calls are common in bats that hunt along habitat edges such as pipistrelles (e.g., Jones and Van Parijs 1993) and are referred to as FM–CF, or FM–QCF calls (e.g., Russo and Jones 2002; Figs. 1, 2). "Q" stands for "quasi", because in this portion, frequency is not rigorously constant but still decreases within a narrow frequency range unlike the "true" pure CF calls of HDC echolocators (Kalko and Schnitzler 1993). CF calls of HDC species instead include initial and (or) terminal FM portions, the latter of which is used in target ranging (Trappe and Schnitzler 1982), so such call type might be referred to as CF–FM or FM–CF–FM (Altringham 2011; Fig. 1).

It is useful to consider features of echolocation calls according to a classification often used in sonar and radar (detection, localization, and classification). Narrowband or CF calls are effective for target detection, whereas FM calls are adaptive in target localization. Indeed, many edge bats switch from using calls dominated by a narrowband component to broadband calls after a target has been detected and needs to be captured. Target localization and detection are traded off against one another, so an FM call that provides strong localization potential has weak detection abilities. Conversely, a narrowband call that has strong detection potential is poorly suited for localization. Pure CF calls also provide information about prey wingbeat characteristics that can be used for target classification (e.g., Schnitzler and Denzinger 2011).

Some species, such as those of the genus *Nyctalus* Bowditch, 1825, alternate between relatively broadband and narrowband calls during nonforaging contexts (e.g., Waters et al. 1995), whereas in the greater sac-winged bat (*Saccopteryx bilineata* (Temminck, 1838)), alternation between low- and high-note calls is limited to foraging (Ratcliffe et al. 2011). More generally, several species alternate between calls whose structures differ in their frequency, duration, and harmonic structure (reviewed in Kingston et al. 2003; Fig. 1). To date, no univocal explanation is available for all cases (Kingston et al. 2003). Proposed explanations include social or antijamming roles (Kössl et al. 1999), detecting prey over longer distances by facilitating assignation of echo to call (so that echoes from close objects returning from the second call are not confused with echoes from the first call from distant targets) (Fenton et al. 1998), allowing detection over different ranges or of targets of different size (Heller 1995), integrating long-range detection and localization (Denzinger et al. 2001), or improving target identification (Heller 1995). The western barbastelle (*Barbastella barbastellus* (Schreber, 1774)) broadcasts two calls that differ in structure (Fig. 1): one is a short, narrowband FM call (type 1), whereas the other (type 2) is longer and covers higher frequencies (Denzinger et al. 2001). The species adopts a "stealth" hunting strategy: it may approach tympanate moths, sensitive to ultrasound, by emitting faint calls that do not alert prey (Goerlitz et al. 2010). Seibert et al. (2015) have shown that type 1 signals are emitted through the mouth and directed downwards, whereas type 2 signals are weaker, directed upwards, and emitted through the nostrils. Whereas type 2 calls would be used to detect prey in the "stealth" mode, type 1 calls would be used for spatial orientation thanks to their greater amplitude and longer operation range.

Some bats emit echolocation calls made of one acoustic element only, whereas others show several harmonics, i.e., a fundamental (the lowest in frequency) plus one or more harmonics whose frequencies are integer multiple of the fundamental (Jones and Teeling 2006; Fenton et al. 2011). Harmonics broaden call bandwidth, increasing resolution and detection of details (Simmons et al. 1975; Fig. 1). In some cases, the fundamental contains the highest energy, but in others most energy is in higher harmonics, for instance in the second harmonic of horseshoe bats, or shifted between the fundamental and higher harmonics in the same sequence (Russo and Jones 2002; Fenton et al. 2011). Shifts between higher and lower harmonics may increase echolocation resolution or operational range, respectively (Fenton et al. 2011). The

Fig. 2. Frequency call partitioning among some European pipistrelles. The spectrogram shows echolocation calls of four individual bats of four different species recorded together: (A) soprano pipistrelle (*Pipistrellus pygmaeus*), frequency of maximum energy (Fmaxe) of ca. 55 kHz; (B) common pipistrelle (*Pipistrellus pipistrellus*), Fmaxe of ca. 45 kHz; (C) Kuhl's pipistrelle (*Pipistrellus kuhlii*), Fmaxe of ca. 40 kHz; (D) Savi's pipistrelle (*Hypsugo savii* (Bonaparte, 1837)), Fmaxe of ca. 35 kHz.



allotonic frequency hypothesis predicts that the high call frequencies of HDC echolocators are an adaptation to bypass tympanate moths' auditory sensitivity, which is highest between 20 and 60 kHz (Fullard 1987). Such lepidopterans are in fact frequently eaten by HDC bats (Jones 1992), but in some cases the same fate happens to moths sensitive to higher frequencies, which should detect HDC bats (Jacobs et al. 2008). Moreover, the numbers of rhinolophid species whose call frequencies fall, respectively, within and outside moth hearing ranges do not differ from each other (Stoffberg et al. 2011). Overall, although the allotonic frequency hypothesis has received some support in the past (Fullard 1998; Schoeman and Jacobs 2003), high frequencies used by many rhinolophid and hipposiderid bats may have evolved for other reasons, e.g., to operate effectively over short ranges in clutter (Lazure and Fenton 2011).

Another factor varying across species is call intensity, whose adaptive significance has received less attention than that of call frequency or duration, yet it has important implications for prey detection, discrimination, and capture. Aerial-hawking bats use intense echolocation calls to search for insect prey: such calls are in fact among the most intense airborne animal vocalizations (Holderied et al. 2005; but see Goerlitz et al. 2010). Call intensity may also vary across different aerial-hawking species sharing similar hunting habits to counter the frequency-specific effect of atmospheric attenuation and hence achieve similar detection distances. In a bat assemblage of 11 species studied in Panama, species broadcasting the highest intensities also produced the highest frequencies that are more strongly attenuated, so that they covered similar ranges of those bats broadcasting weaker calls at lower frequencies (Surlykke and Kalko 2008). Calls of species trawling prey from water surfaces are also intense: these bats exploit and integrate the echoes generated by prey with indirect reflections from the water surface to improve detection and localization of prey close to, resting above, or protruding from the water surface (Zsebok et al. 2013). Some bats glean prey from foliage or from the ground, when echolocation is often not effective for prey detection because echoes from the cluttered substrate can mask prey echoes. Moving prey generates rustling sounds that are located by passive listening (e.g., Arlettaz et al. 2001; Russo et al. 2007*a*; Jones et al. 2016). Passive gleaners produce weak calls that do not mask the faint prey-generated noise (Russo et al. 2007*a*) or alert ultrasound-sensitive prey (e.g., Jones and Rydell 2003). Echolocation may still be needed by passive listeners to detect the surroundings and orientate (Fenton 1990; Schnitzler et al. 2003). Some species still use echolocation to detect silent and motionless prey from substrate (active gleaning). The common big-eared bat (*Micronycteris microtis* Miller, 1898) does so by combining hovering flight and frequent production of short broadband calls (Geipel et al. 2013). Based on acoustic tomography representations of prey resting on substrate, Clare and Holderied (2015) proposed that bats perceive changes in the depth profile and acoustic shadows cast by prey, especially when the surface ensonified is smooth (detection would be more difficult for cluttered surfaces, where prey might be concealed acoustically). Echolocation may also be used by gleaners to recognize the shape of specific plant species that are likely to host prey (Siemers 2001; Hulgard and Ratcliffe 2014).

Scaling of bat call variables with body mass

Body size is clearly related to echolocation call structure. An exhaustive review is given in Jones (1999), so here we will only synthesize the main points. Because larger vocal tracts generate lower frequencies than do smaller ones, generally speaking the larger the bat species (at least within families), the lower the dominant call frequency. Jones (1999) found this pattern to be consistent across five bat families (Rhinolophidae, Hipposideridae, Emballonuridae, Vespertilionidae, and Molossidae) from both bat suborders Yangochiroptera and Yinpterochiroptera (Teeling et al. 2005), but not for Phyllostomidae. Although it has been proposed that high frequencies in bats might not be related to a small body size, but instead be used by small bats (characterized by a smaller gape) in open space to achieve more directional sonar beams (Jakobsen et al. 2013), this hypothesis was not supported in a recent large-scale analysis with phylogenetic control (Thiagavel et al. 2017).

The emission rate of calls is also linked with body size, as bats tend to produce one call per wingbeat to synchronize echolocation with flight and reduce the cost of call emission (Speakman and Racey 1991). Wingbeat frequency is inversely proportional to body size (Pennycuick 1972), so small species have a higher call emission rate than do large species (Jones 1999). However, this analysis is somewhat simplistic because bats approaching targets such as foraging gleaners may broadcast low-intensity batches of calls during one exhalation to trade call intensity against repetition rate and mitigate echolocation's energetic costs (Jones 1999). Call duration tends to scale positively with body mass because large bats fly faster and may probe for more distant objects, so there is little risk of call–echo overlap, whereas small bats, which detect closer targets, need to broadcast short calls to avoid forward masking (Jones 1999). However, this pattern seems to be less pronounced than the others described above.

The relationship between call intensity and species' body size is unclear. Among vespertilionids, larger species broadcast more intense calls (Holderied and Von Helversen 2003); in rhinolophids, a similar trend is not apparent (Schuchmann and Siemers 2010).

Effects of phylogenetic relatedness and adaptive convergence on call structure

Echolocation call design may be at least partly predicted from species' phylogenetic history (Jones and Teeling 2006; Collen 2012; Jung et al. 2014) because evolutionary history clearly influenced body size and, in turn, call structure, and in part habitat use (Stoffberg et al. 2011; Collen 2012). A typical example of phylogenetic similarities is given by the steep FM calls common to the many species in the genus *Myotis* Kaup, 1829 (Russo and Jones 2002). Collen (2012) considered 410 species from all 19 families of echolocating bats and found one set of call variables associated with body mass (peak frequency, characteristic frequency, call duration, and call bandwidth) to have been more constrained by phylogenetic relatedness, less by habitat, whereas another set (maximum frequency, minimum frequency, total slope, and dominant slope) was best explained in terms of adaptation to habitat-specific echolocation tasks. Noticeably, evolutionary history exerted a greater influence than environmental conditions on call design.

Another potentially strong influence on call design comes from adaptive convergence: echolocation calls from species that are not closely related with one another may converge structurally to cope with similar environmental tasks such as those arising from foraging in similar habitat. A Neotropical insectivorous bat, the black myotis (*Myotis nigricans* (Schinz, 1821)), uses echolocation calls unusual for that genus and most similar to those broadcast by pipistrelle bats (Siemers et al. 2001). Just like pipistrelles, *M. nigricans* mostly forages in open space or along vegetation edges: the common ecological niche that bats of these taxa exploit has imposed similar evolutionary pressures leading to converging call structures. HDC echolocation and Doppler-shift compensation, suited to detect fluttering targets in clutter, appeared twice in the evolutionary history of bats (Jones and Holderied 2007), namely in the family Rhinolophidae (Yinpterochiroptera) and in Parnell's mustached bats (*Pteronotus parnellii* (Gray, 1843); family Mormoopidae (Yangochiroptera)). However, the former emits sound through the nostrils, while the latter emits sound through the mouth (Jones and Teeling 2006), and also the auditory cortex shows a different organization in the two cases (O'Neill 1995). Bats in the families Megadermatidae (Yinpterochiroptera) and Nycteridae (Yangochiroptera) also show morphological convergences and similar call design, best adapted to dwell in dense vegetation where they find prey by passive listening (Fenton et al. 1983; Jones and Holderied 2007). Overall, phylogenetic relatedness and habitat adaptations are both needed to explain echolocation call design and behaviour, but disentangling their effects may be operationally difficult unless phylogenetic affiliations can be mapped onto call features (Jones and Teeling 2006; Collen 2012).

Echolocation diversity and community structure: evolutionary pressures from resource partitioning and intraspecific communication

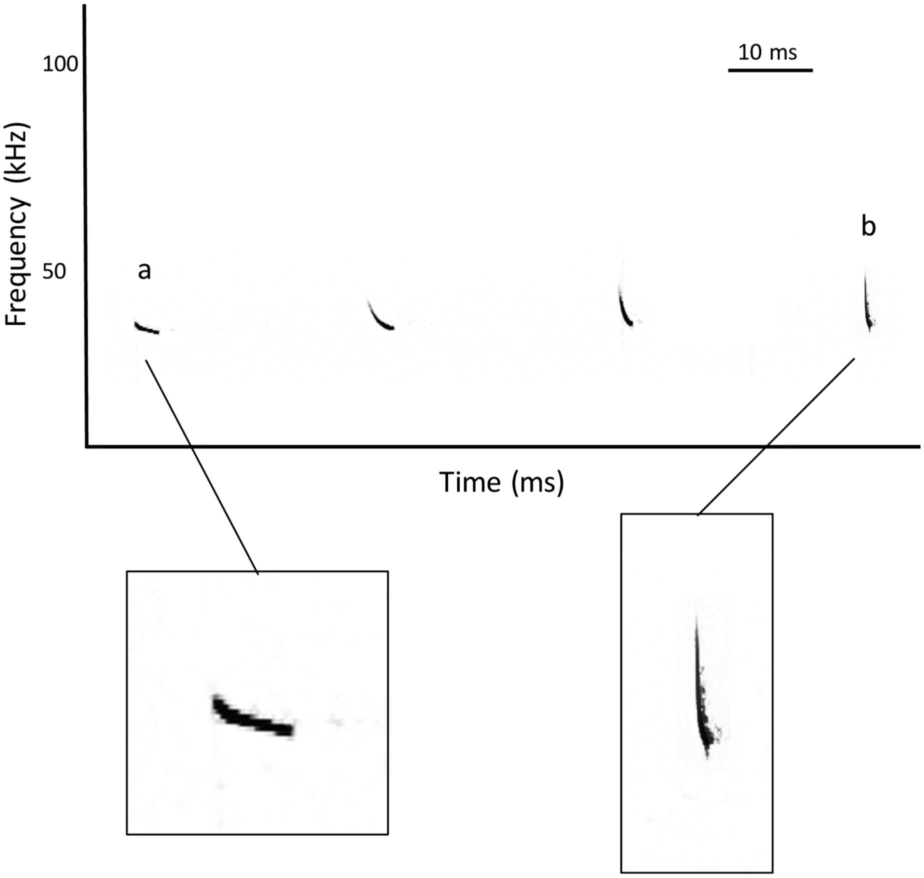
Species that compete for the same resources cannot coexist in space and time: to minimize interspecific competition, species must segregate their temporal or spatial niches (e.g., Begon et al. 2006). For bats, differences in wing shape (Norberg and Rayner 1987) or echolocation (Neuweiler 1989; Denzinger and Schnitzler 2013) may lead to niche partitioning through differences in habitat use, and in turn, dietary segregation (Aldridge and Rautenbach 1987; Mancina et al. 2012; Emrich et al. 2014). Echo strength drops for sound wavelengths greater than the target circumference (Pye 1993), so bat species broadcasting higher frequencies would detect smaller prey than bats broadcasting lower frequencies, setting the basis for potential partitioning of food resources by prey size (Jones 1995*a*, 1995*b*, 1996). In other words, call frequency might be likened to bill shape in birds: just like the latter changes across species under the selective pressures posed by the need to access different resources, frequencies of different bat species might diverge ("acoustic character displacement") to minimize niche overlap (Jones 1997). Moreover, call frequencies may affect detection performances in cluttered vs. uncluttered habitat because increasing frequency values improve resolution at the cost of operational range, so frequency divergence might lead to resource partitioning via habitat segregation (Fig. 2).

There are a few debatable points, however, in the niche partitioning paradigm in bats, from the difficulty in controlling for the effects of body size on frequencies in analysis to whether insect food is actually limiting for bats. In general, there is a paucity of strong, global evidence that food can be limiting in bats (e.g., roosts may be a more limiting resource) and thus prompt interspecific competition. Even in absence of current competition for food, however, niche differentiation as observed today might represent a "ghost" of past competition occurred when food was limiting (Connell 1980; Fukui et al. 2009). In speciose bat communities such as those encountered in tropical regions, pressures from interspecific competition have been proposed to lead to resource partitioning via call frequency displacement. Research has not provided unequivocal answers. Heller and von Helversen (1989) observed this pattern for 12 rhinolophoid species in a Malaysian assemblage. Kingston et al. (2000), however, could not support it when 15 species from the same community — the former 12 species of Heller and von Helversen (1989) plus another 3 species — were taken into account. The same community still showed nonrandom morphological overdispersion that was probably shaped by present or past competition.

Competition might, in theory, be especially harsh between species showing similar morphology. The two sibling mouse-eared bat (*Myotis myotis* (Borkhausen, 1797)) and lesser mouse-eared bat (*Myotis blythii* (Tomes, 1857)) segregate niches by exploiting different habitats (bare ground, short mown grass, or forest leaf litter vs. dense grassland), where they find different food items (mostly carabid beetles vs. tettigoniids, respectively) detected and located by passive listening (Arlettaz et al. 2001). These bats land on the ground to glean prey. Whereas *M. myotis* typically broadcasts a rapid sequence of calls ("landing buzz") soon before landing probably to assess the distance to the ground, *M. blythii* does not (Russo et al. 2007*a*). Typical *M. blythii* prey are tympanate, so ultrasound might alert them and compromise capture success: the absence of a buzz might therefore arise from niche segregation in these cryptic species of bats.

In several cases, divergence in the frequencies of echolocation calls have been found insufficient to support resource partitioning (Kingston et al. 2001; Jones and Barlow 2004; Jacobs et al. 2007), so the evolutionary forces that have caused it must be elsewhere. Although bat echolocation calls primarily serve a sensory scope, there is mounting evidence of their importance for intraspecific communication (for a review see Jones and Siemers 2011). Acoustic character displacement may, therefore, rather be selected for to maintain "private communication channels" and avoid unwanted information transfer among heterospecifics broadcasting similar frequencies (Thabah et al. 2006; Jacobs et al. 2007; Russo et al. 2007*b*). A social selection process has also been postulated: assortative mating and ultimately sympatric speciation might potentially be driven by changes in echolocation call frequencies if these influence mate recognition (Kingston et al. 2001; Kingston and Rossiter 2004; Puechmaille et al. 2014).

Fig. 3. Variation induced by habitat structure in echolocation calls of Savi's pipistrelle (*Hypsugo savii*) recorded in Italy, moving from open space (*a*) to clutter (*b*). Call shapes typical of the two extreme conditions are shown in detail in the boxes.



Implications of interspecific acoustic variation for bat call identification

Echolocation call structure is generally the first, important clue used in identification to assign an unknown call to a given category. As we will see ahead, however, bats may change call shape dramatically depending on the habitat or the task that they are facing, so the resulting spectrogram may differ considerably from the expected categories described above. For instance, a pipistrelle bat that often broadcasts FM–QCF calls will emit steep ("*Myotis*-like") FM calls when flying in dense vegetation or near objects, causing confusion (Fig. 3). Alternation between echolocation call structures in species that do so aids species identification, but alternation is not consistent. An example from the European bat fauna is given by Leisler's bat (*Nyctalus leisleri* (Kuhl, 1817)): when flying near clutter, alternation is suppressed and the resulting calls resemble those of other often sympatric species such as the common serotine (*Eptesicus serotinus* (Schreber, 1774)).

Calls that include high frequencies may also cause problems in identification or detection because such frequencies undergo strong atmospheric attenuation (Lawrence and Simmons 1982). The highest frequencies in broadband calls such as those of *Myotis* bats may therefore not appear in the recordings of distant individuals, potentially leading to identification problems. HDC bats, characterized by high-frequency calls, may often be go undetected for the same reason. Other calls frequently overlooked are the weak ones broadcast by "whispering" species such as the genus *Plecotus* E. Geoffroy, 1818 or other gleaners.

Convergence in call design due to phylogenetic relatedness or resulting from similar evolutionary pressures is also another main obstacle to species identification: a good example is given by European *Myotis* species, which show large overlap in call structure across species.

Intraspecific variation

Intraspecific variation can occur both among and within individuals of a species and is influenced by factors covered below.

Habitat structure

Individual LDC bats may change echolocation call characteristics dramatically according to the degree of habitat clutter (e.g., Obrist 1995; Barclay et al. 1999; Murray et al. 2001; Kingston et al. 2003; Rodríguez-San Pedro and Simonetti 2014). Such adjustments represent transitory modifications of individual call structure rather than static differences among individuals specialized in foraging in different environmental situations (Wund 2006). Call plasticity is especially evident in LDC species specialized in exploiting open-space or edge habitats (Kalko and Schnitzler 1993; Jacobs 1999; Russo and Jones 2002; Ibáñez et al. 2004; Mora et al. 2005, 2011). When such bats move from open-space to cluttered habitat (e.g., forest), they tend to increase frequency values and pulse rates of their calls and, to avoid forward masking, decrease duration (Fig. 3). Bats do so to maximize operational range (a priority in open habitat), optimize discrimination power, and avoid masking (essential in cluttered space). Captive studies suggest that LDC bats may adjust habitat-specific echolocation call characteristics over time by learning to improve foraging efficiency (Wund 2005; Chen et al. 2016).

In other cases, bats use different call structures according to habitat structure (Jones 1995*a*, 1995*b*; Kingston et al. 2003). When bats approach background clutter, such as when close to the ground, they must detect an "edge space" within which call design is modified to avoid forward masking (Kalko and Schnitzler 1993; Schnitzler and Kalko 1998; Siemers et al. 2001; Schaub and Schnitzler 2007; Gillam et al. 2009). The number of harmonics or the way energy is spread across them may also change according to the degree of clutter, most likely to increase bandwidth to improve target ranging and resolution (e.g., Macías and Mora 2003; Fenton et al. 2011). The Brazilian free-tailed bat (*Tadarida brasiliensis* (I. Geoffroy, 1824)) increases duration and decreases frequencies and pulse rate for altitudes >100 m above ground, i.e., in clutter-free space (Gillam et al. 2009). This might compensate for decreased sound propagation associated with elevation-dependent differences in atmospheric conditions or increased difficulties in echo detection caused by stronger wind speeds at higher altitudes; alternatively, it might increase detection range to pursue high-altitude, more dispersed prey.

Habitat effects are probably the most substantial and frequent source of variation that renders acoustic identification of LDC bats a complex task. The habitat in which recordings were made is therefore an important piece of information to be aware of potential identification difficulties, but even in open space, a bat may occasionally fly low above ground or near isolated objects altering call structure significantly.

Effects of conspecifics

Several studies have found that when flying together LDC bats shift call frequencies to avoid masking of their echoes by the loud calls of conspecifics flying nearby, or confusion between their own echoes and those of other bats (Ibáñez et al. 2004; Ratcliffe et al. 2004; Ulanovsky et al. 2004; Gillam et al. 2007; Bates et al. 2008). In this phenomenon, called "jamming avoidance response", bats would detect and unambiguously recognize the echoes of interest by separating in frequency their own calls from those of conspecifics. Over the years, some authors have expressed serious doubts about the existence of jamming avoidance, suggesting that it might be more convincingly explained as a reaction to clutter (Obrist 1995; Ratcliffe et al. 2004; Fawcett and Ratcliffe 2015). Cvikel et al. (2015) applied miniature on-board microphones and GPS receivers to naturally foraging greater mouse-tailed bats (*Rhinopoma microphyllum* (Brünnich, 1782)), providing a "point-of-view" picture of bat behaviour. If jamming avoidance occurs, call frequencies should be shifted in such a way to maximize differences between the emitter's calls and those of surrounding conspecifics. In that experiment, however, all monitored bats increased call frequencies and bandwidth, shortening duration, and in most cases, increasing pulse rate. This response reminds of a simple reaction to the "cluttering" of surrounding space determined by the presence of conspecifics rather than a way to avoid call jamming. Another study on the common pipistrelle (*Pipistrellus pipistrellus* (Schreber, 1774)) reached similar conclusions (Götze et al. 2016).

Other studies controlled for potential clutter effects. Gillam et al. (2007) found jamming avoidance in European free-tailed bats (*Tadarida teniotis* (Rafinesque, 1814)) in response to playback of echolocation calls, in which case the clutter effect was ruled out. Cvikel et al. (2015) argue that, as in other previous studies, recordings were altered by Doppler shift, differential acoustic attenuation, and angle between the emitting bat and the microphone, and that calls experimentally played back from the ground would be perceived as unnatural by the bats tested. Amichai et al. (2015) found that Kuhl's pipistrelle (*Pipistrellus kuhlii* (Kuhl, 1817)) increased call intensity and extended signal duration when subjected to playbacks of conspecific calls in a flight room. Although small spectral changes in signals were noted during playbacks, such shifts were insufficient to decrease the spectral overlap with potential jamming calls. Bartonička et al. (2007) recorded jamming avoidance when *P. pipistrellus* or soprano pipistrelle (*Pipistrellus pygmaeus* (Leach, 1825)) flew in monospecific groups, but the presence of heterospecifics did not elicit the frequency shift expected if the "clutter effect" occurred. Because calls of the two pipistrelle species differ by ca. 10 kHz, this separation would be enough to recognize their own calls in the absence of jamming avoidance responses.

The issue of jamming avoidance responses in HDC bats is less investigated: these bats cannot shift frequencies because echoes would fall out of the best detected individual frequency encoded in their auditory fovea, making bats deaf to their own echoes. Fawcett et al. (2015) looked at the effects of the presence of both conspecifics and heterospecifics on echolocation calls of the Cape horseshoe bat (*Rhinolophus capensis* Lichtenstein, 1823). Conspecifics or LDC heterospecifics — namely, the Natal long-fingered bat (*Miniopterus natalensis* (A. Smith, 1833)) — flying nearby mostly elicited the same changes in echolocation calls that the presence of obstacles would cause, again advocating against the existence of jamming avoidance (Fawcett et al. 2015). Reactions included a reduction in call intensity plus, for the sole terminal FM-sweep call component (thought to be used for accurate ranging), an increase in duration and a decrease in minimum frequency. It is unclear, however, why shorter calls were broadcast when the larger heterospecific Geoffroy's horseshoe bat (*Rhinolophus clivosus* Cretzschmar, 1828) was encountered. In the absence of jamming avoidance response, both LDC and HDC bats would probably still be able to recognize their own echoes based on other call characteristics, including individual signatures (Jones et al. 1992; Fenton 1994; Masters et al. 1995; Obrist 1995; Cvikel et al. 2015).

The effect of conspecifics may lead to changes in call structure of LDC species similar to those described for the influence of habitat, so its consequences should be taken into account when recordings of bats foraging together or leaving the roost in groups are examined.

Effect of environmental noise

Although this is probably a negligible issue with respect to call identification, it is worth mentioning that call intensity and duration are increased in response to masking noise (e.g., Amichai et al. 2015; Luo et al. 2015), the so-called "Lombard effect".

Several studies show changes in echolocation call characteristics in the presence of environmental noise, seemingly often aimed at avoiding jamming. Playback of experimentally manipulated insect sound showed a positive correlation between insect sound frequencies and frequencies of echolocation calls in *T. brasiliensis*, probably so the bats can avoid interference from background noise and echolocate using noise-free frequency values (Gillam and McCracken 2007). In the big brown bat (*Eptesicus fuscus* (Palisot de Beauvois, 1796)), experimentally broadcast CF noise induced shifts in the frequencies of the end (CF) portion of calls up or down to move them away from noise frequency, provided this lay within 2–3 kHz of their baseline frequency, otherwise no reaction was recorded (Bates et al. 2008). The Lombard effect, i.e., increases in call amplitude when broadband noise is present, also occurs in both LDC and HDC bat species (Simmons et al. 1978; Bates et al. 2008; Tressler and Smotherman, 2009 Hage et al. 2013). Reactions to noise may depend on the noise bandwidth, or its proximity in frequency to a species' best frequencies of hearing. In *T. brasiliensis*, broadband noise elicits a typical Lombard response (increase in call duration and amplitude), whereas responses to band-limited noise are different and depend on both the frequency range of the noise and call characteristics (Tressler and Smotherman 2009). In stationary greater horseshoe bats (*Rhinolophus ferrumequinum* (Schreber, 1774)), narrowband (i.e., with a bandwidth of 20 kHz) noise centred on the bat's frequency of maximum energy at rest elicits an increase in call amplitude, and increases in call frequency are triggered by other frequencies across the species' hearing range, even if well below its echolocation frequency range, i.e., in the range of most anthropogenic noise sources (Hage and Metzner 2013; Hage et al. 2013). Overall, the studies so far conducted suggest that noise pollution caused by human activities may have important consequences for bat foraging efficiency, survival, and reproduction. Indeed, activity levels of *T. brasiliensis* are reduced at gas compressor sites where ultrasound from the compressors may mask call frequencies emitted by the bats. The bats also produce longer, more narrowband calls at compressor sites, maybe to enhance target detection (Bunkley et al. 2015). Call duration also increases in noise by 1–5.3 dB in the pale spear-nosed bat (*Phyllostomus discolor* Wagner, 1843), augmenting detectability (Luo et al. 2015).

Effects of individual characteristics

Spectral and temporal characteristics of echolocation calls may differ among conspecifics (e.g., Burnett et al. 2001; Murray et al. 2001; Mora et al. 2005) according to their age, family membership (Masters et al. 1995), sex (Kazial and Masters 2004), reproductive state (Kazial et al. 2008), or body condition (Puechmaille et al. 2014), potentially playing an important role for communication of individual characteristics and status (reviewed in Jones and Siemers 2011). Bats may learn individual characteristics of conspecific calls and use them for recognition. Flexibility in individual signatures recorded in certain cases points to a potentially plastic communication system (Mora et al. 2005). Mounting evidence from playback experiments shows that bats use echolocation calls to recognize the emitter's sex (Kazial and Masters 2004), body condition (Puechmaille et al. 2014), reproductive status (Grilliot et al. 2015), or to distinguish between familiar vs. unfamiliar subjects (Yovel et al. 2009; Voigt-Heucke et al. 2010). Individual differences are often difficult to detect in free-flying LDC species because they may be confounded by overwhelming sources of variation such as habitat structure effects (Obrist 1995). More information is available for HDC bats: the study of individual differences is easier in these species because individual-specific frequencies may be recorded from hand-held bats ("resting frequencies", hereafter RF) to eliminate potentially confounding factors such as Doppler-shift compensation present in flying subjects. RF may vary with sex, body condition, forearm length, and age (Jones et al. 1992; Jones 1995*a*, 1995*b*; Guillén et al. 2000; Russo et al. 2001; Siemers et al. 2005; Armstrong and Coles 2007). Sex differences in RF may or may not occur, and in the former case differ in direction across species (e.g., Jones et al. 1992; Jones 1995*a*, 1995*b*; Russo et al. 2001, 2007*b*; Salsamendi et al. 2006; Chen et al. 2009) or populations (Guillén et al. 2000; Siemers et al. 2005; Odendaal and Jacobs 2011; Ramasindrazana et al. 2015). Frequencies between sexes may differ from what would be expected from body size (according to which the larger sex — generally females — should broadcast the lower frequencies), and are generally too small to propose a role for intersexual resource partitioning (e.g., Chen et al. 2009; Odendaal and Jacobs 2011; Puechmaille et al. 2014). RF values in Mehely's horseshoe bats (*Rhinolophus mehelyi* Matschie, 1901) might advertise body condition, being higher for larger bats (Puechmaille et al. 2014). Females may select males with higher RF values in mate choice, and such males sire more offspring (Puechmaille et al. 2014). However, there is no unequivocal evidence on the use of RF to signal body condition in HDC bats (Russo et al. 2007*b*; Schuchmann and Siemers 2010). Schuchmann and Siemers (2010) found that in the lesser horseshoe bat (*Rhinolophus hipposideros* (Bechstein, 1800)) males call at lower intensities than do females, but the reason for this is unclear.

The ontogeny of vocalization in infant bats is well studied in several species (e.g., Brown et al. 1983; Schuller and Moss 2004). Here we will only mention that echolocation calls may differ between volant juveniles and adults and change over an individual's life. A common pattern in rhinolophids is that juveniles broadcast lower frequencies than do adults (e.g., Jones and Ransome 1993; Russo et al. 2001). In *R. ferrumequinum*, after an initial increase across years 1–3, RF decreases over the rest of an individual's life (Jones and Ransome 1993), probably because older bats lose sensitivity towards higher frequencies. In this and probably other HDC species, infants are thought to possess a genetic template for call structure, but the fine-tuning of echolocation call frequencies is vertically learnt from their mothers (Jones and Ransome 1993; Chen et al. 2009). Learning also plays a role among adults, as individuals experimentally added to a colony tend to shift their RF value to match those of their new colony mates (Hiryu et al. 2006; Chen et al. 2016). Overall, vocal production learning is perhaps widespread across bats and might account for some of the observed individual variability; yet, especially for echolocation, the process is still largely unexplored (Knörnschild 2014).

Individual differences in echolocation calls may sometimes cause identification problems, at least for HDC bats. For instance, in some rhinolophid species, juveniles emit calls at lower frequencies than do adults and their call frequencies may overlap with those of other species occurring in sympatry: an example is given by juvenile *R. mehelyi*, whose calls may be confused with those of adult Mediterranean horseshoe bats (*Rhinolophus euryale* Blasius, 1853) (Russo et al. 2001).

Geographic variation

Within species, populations from separate regions often express some differences in echolocation call characteristics (Conole 2000). Whether genetically or culturally determined, the degree of isolation plays a substantial role in influencing geographic variation of acoustic traits by countering gene flow and (or) cultural contacts between populations (Jiang et al. 2013, 2015; Mutumi et al. 2016), so comparisons between islands and the mainland may prove ideal in highlighting the existence of local variants (Russo et al. 2007*b*). Site effects on echolocation call characteristics may also be evident at a smaller scale, i.e., within populations, over geographical gradients (Chen et al. 2009) or in different colonies (Guillén et al. 2000). Locally evolved anatomical differences may or may not explain the existence of acoustic variation (Jiang et al. 2013, 2015). Correlations between call frequency and morphology may be weak or absent when general traits, e.g., body size, are considered (Jiang et al. 2013, 2015), but may emerge when the morphological variables considered are directly related to sound production or processing, such as nasal chamber size, justifying the occurrence of acoustic variants (Armstrong and Coles 2007; Odendaal and Jacobs 2011).

Although geographic variation is often too small to imply differential sensory performances, it may still be important for communication, especially if used by bats to discriminate between members of their own population and those of other populations. There is growing evidence in support of this hypothesis (Bastian and Jacobs 2015; Lin et al. 2016). This process has implications for the recognition of sexual partners, assortative mating, and potentially for speciation.

The origin of this variability, i.e., the relationship between echolocation differences and population history, appears complex and multifaceted (Chen et al. 2009). Local call variants may arise from several potential causal factors, including genetic or cultural drift, social selection in allopatry (Jones 1997; Yoshino et al. 2008; Chen et al. 2009; Odendaal et al. 2014); local adaptation to environmental conditions or specific resources (Armstrong and Coles 2007; Jiang et al. 2015; Ramasindrazana et al. 2015); and community-induced acoustic displacement to partition food resources (e.g., Emrich et al. 2014) or ensure "private communication bandwidths" (e.g., Thabah et al. 2006; Russo et al. 2007*b*).

Among the potential drivers of geographic adaptation in echolocation calls, climate may play a significant role. Atmospheric attenuation of sound depends on relative humidity, temperature, and sound frequency (Lawrence and Simmons 1982), so call frequencies of highest energy may be locally adapted to adjust for geographically different attenuation within the trade-off between operational range (increasing for lower frequencies) and target resolution (higher for higher frequencies) (Snell-Rood 2012; Jiang et al. 2015). Lower frequencies would perform better at high humidity levels because they undergo less attenuation (Lawrence and Simmons 1982; Hartley 1989), yet the few studies investigating relationships between humidity and call frequencies do not provide a unequivocal picture (Guillén et al. 2000, Jiang et al. 2010, 2010; Mutumi et al. 2016). Modelling applied to an Australian HDC species, the orange leaf-nosed bat (*Rhinonicteris aurantia* (Gray, 1845)), rejects the view that its small geographic variation in call frequencies (6 kHz) compensates for the operational range alteration caused by different relative humidity or atmospheric temperature (Armstrong and Kerry 2011). Ambient temperature may also influence body temperature and in turn call frequency (Huffman and Henson 1991; Jones and Ransome 1993). The impact of temperature and humidity on call frequency is interesting because it provides a framework for understanding how echolocation calls may adapt to climate change. Luo et al. (2013) argued that prey detection ranges will differ in species with different call frequencies, as well as in different climates. Bat species using lower frequencies may benefit from global warming, but the frequency threshold where detection volume decreases will vary according to local climate (Luo et al. 2013). Atmospheric conditions will also affect recordings of bats made with bat detectors in similar ways that they affect bats (though signal transmission from bat to microphone is one way, rather than two ways in echolocation), and bioacoustics researchers should be aware of the effects of factors such as temperature and humidity on the recording process.

Correlative evidence between genetic and acoustic differences in studies may be misleading, and interactions among call frequency and genetic differentiation can be subtle and differ in different environments (Odendaal et al. 2014). For instance, in Taiwanese populations of the Formosan lesser horseshoe bat (*Rhinolophus monoceros* K. Andersen, 1905), RF values correlate linearly with geographical and, apparently, genetic distances within regions, but no direct relationship exists between echolocation and genetic distances because both covary with geographical distance (Chen et al. 2006, 2009). Genetic drift is unlikely to explain variation in call frequency in *R. capensis*. Lower call frequencies used by bats in less cluttered environments are thought to have evolved by local adaptation favouring increased detection distances in such habitats (Odendaal et al. 2014).

The extent of geographic variation in echolocation calls is unknown for most species. Therefore, special prudence is needed in using reference calls from different geographic regions to carry out identification in new study areas for which no local libraries are available even for widespread, easy-to-identify species.

Existence of sympatric acoustic variants

Sympatric differences in echolocation call frequencies may indicate the existence of cryptic species or suggest the occurrence of a differentiation pattern ultimately leading to different species (e.g., Thabah et al. 2006; Ramasindrazana et al. 2015). Changes in echolocation frequencies may drive evolutionary radiation and speciation. The most compelling example is given by three sympatric size morphs of the large-eared horseshoe bat (*Rhinolophus philippinensis* Waterhouse, 1843) studied in Indonesia (Kingston and Rossiter 2004). The dominant harmonic of their CF calls (i.e., that containing the highest energy) has switched in the course of their evolutionary history so that the three morphs show substantial differences in frequency values (ranging between ca. 27 and 54 kHz). The harmonic-hopping process has led the morphs to achieve different target resolution and thus trophic niche segregation, triggering disruptive selection. Given the likely role of CF calls as communication signals and the recent genetic divergence observed for these morphs, acoustic divergence may have also led to reproductive isolation and potentially might have initiated sympatric speciation (Kingston and Rossiter 2004).

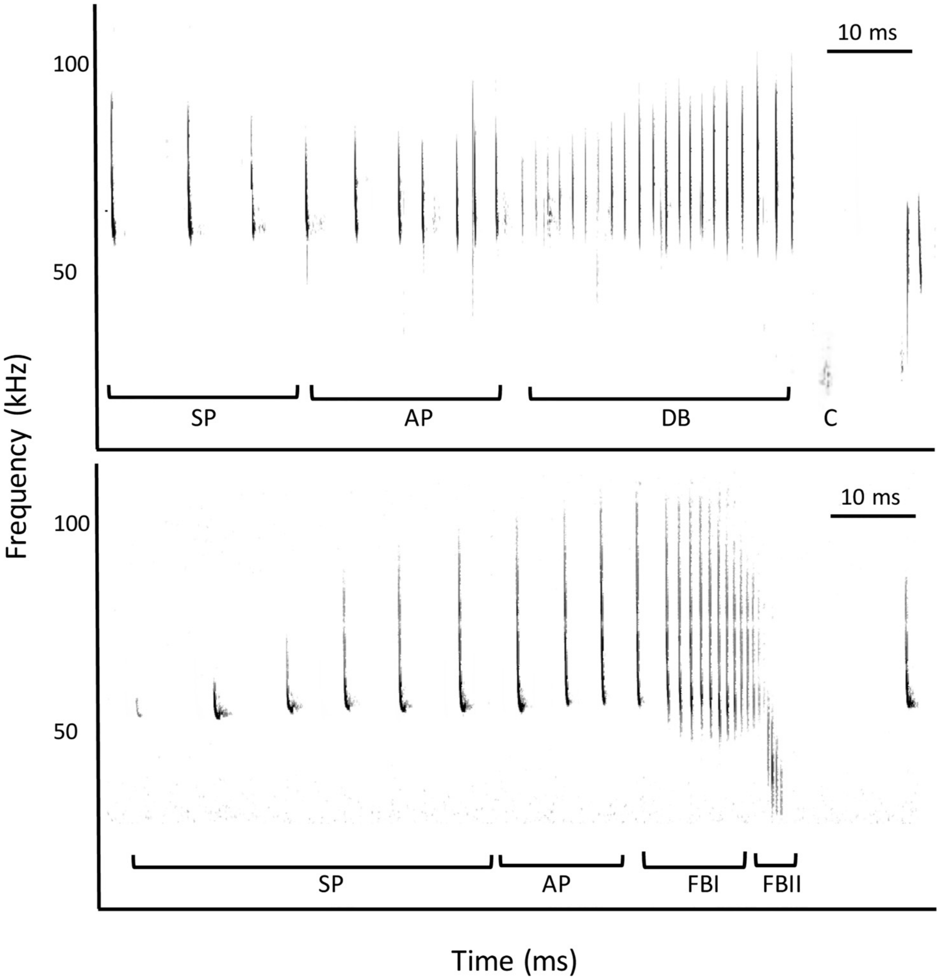
Perhaps the best-known case of acoustic differences between cryptic species is offered by two European pipistrelle bat species (*P. pipistrellus* and *P. pygmaeus*) that were once considered a single species. An approximate 10 kHz difference between echolocation call frequencies of highest energy recorded in sympatry represented the first clue suggesting the two phonic types were actually different species, later confirmed by ecological, behavioral, and genetic differences (Jones and Parijs 1993; Barlow and Jones 1997; Barratt et al. 1997; Jones 1997). The differences in call frequency are likely to have evolved in allopatry (Hulva et al. 2007). Separation in call frequencies observed in sympatric acoustic variants may make identification from their echolocation calls relatively easy. For example, *P. pipistrellus* and *P. pygmaeus* are hard to distinguish based on morphology alone, and apart from molecular methods and social calls, echolocation calls offer often a reliable way to establish species identity. Nonetheless, some overlap between species may occur, so problems may still arise in absence of other evidence.

Intraindividual echolocation plasticity in response to different sensory tasks

Besides habitat effects, intraindividual variability of echolocation calls is also caused by adjustment of echolocation call structure or production of specific call sequences occurring to fulfil specific sensory tasks. Three typical echolocation phases are described for aerial hawking bats, especially evident in LDC species (Fig. 4). A first phase, called search phase, is shown by bats commuting or searching for food. Once the target is detected, an approach phase begins, i.e., frequency values and pulse rate increase (respectively, to provide a greater target resolution while updating the sonar image more frequently), pulse interval decreases, and call duration decreases (to avoid forward masking). When the bat homes in on its prey, the approach is concluded by increasing pulse rate and decreasing call duration further in a rapid sequence (100–200 calls/s) of steep FM sweeps (Fig. 4). This feeding or terminal buzz (Griffin et al. 1960) provides last-instant precise target localization (Schnitzler and Kalko 2001; Jakobsen and Surlykke 2010; Ratcliffe et al. 2010; Schmieder et al. 2010). The buzz often comprises two parts, named buzz I and buzz II, respectively, with the latter being characterized by an abrupt frequency drop (Surlykke et al. 1993; Schnitzler and Kalko 2001; Ghose and Moss 2003; Ratcliffe et al. 2010). There is evidence that by lowering call frequency bats broaden the sonar beam (Jakobsen and Surlykke 2010; Matsuta et al. 2013; Russo et al. 2016), which helps track fast-moving insects and may constitute an adaptive response to counter evasive manoeuvres made by some ultrasound-sensitive insect species (Fullard 1998; Miller and Surlykke 2001; Ratcliffe et al. 2013). When drinking on the wing or landing on substrate, bats also broadcast drinking (Griffiths 2013; Russo et al. 2016) or landing (e.g., Russo et al. 2007*a*) buzzes, respectively, that lack buzz II, as expected because in these cases the buzz is only needed to assess precisely the distance between the emitter and a static (water or ground) surface (Fig. 4). The relative durations of buzz I and II may be adjusted according to the specific foraging task. In the trawling long-fingered bat (*Myotis capaccinii* (Bonaparte, 1837)), which preys upon both fish and insects (e.g., Biscardi et al. 2007; Aihartza et al. 2003), feeding buzzes broadcast while fishing show a longer buzz I and a shorter buzz II, in this way achieving a better discrimination ability while reducing sonar beam width because the prey are nonflying and may be incapable of last-instant evasive manoeuvres (Aizpurua et al. 2014). Buzzes are also observed in HDC species, where the duration of the CF portion decreases and the bandwidth of the final FM sweep increases (Altringham 2011).

Another dynamic adjustment associated with flight is observed in HDC species, which lower the frequency of their calls' CF component to compensate for the Doppler effect induced by movement to match the frequencies that their hearing is most sensitive to, as perceived by their acoustic fovea (Schuller and Pollak 1979).

Fig. 4. Drinking (top) and feeding (bottom) buzzes in soprano pipistrelle (*Pipistrellus pygmaeus*) recorded in Italy. SP, search-phase calls; AP, approach-phase calls; DB, drinking buzz; C, contact with water; FBI, buzz I; FBII, buzz II.



Task-specific changes in call intensity have received less attention, but at least one example, regarding the desert long-eared bat (*Otonycteris hemprichii* Peters, 1859) in the Negev desert, shows a switch from intense to faint calls depending on foraging mode. During aerial hawking, intense calls are emitted that allow for longer operational distance; when gleaning nonaerial arthropods from the ground such as scorpions, weak calls are produced that prevent self-deafening and thus favour detection of prey-generated rustling noise (Hackett et al. 2014).

Few case studies regard the emission of context-dependent calls, a so-far little-known source of variation. For instance, Gillam et al. (2010) found that *T. brasiliensis* uses specific call structures during roost emergence from densely populated roosts, whose exact function is unclear but which may be needed to coordinate flight and avoid forward or backward masking (the latter is produced by interfering signals following the target echo, such as clutter echoes; Schnitzler and Kalko 2001). After controlling for environmental clutter and presence of conspecifics, Berger-Tal et al. (2008) found that echolocation calls produced by *P. kuhlii* during the search phase in four different flight situations (emergence from a roost, commuting to and from foraging sites, foraging, and returning to a roost) differed from one another in terms of duration, pulse rate, maximum frequency, and bandwidth, and that emergence calls were highly variable. In both this species and Geoffroy's bat (*Myotis emarginatus* (E. Geoffroy, 1806)) (Schumm et al. 1991), search phase calls emitted while foraging in the open are significantly longer than those broadcast while commuting. This type of variation likely expresses intrinsic behavioural changes that would deserve further consideration.

Changes in echolocation call structure associated with specific sensory tasks may have profound implications for bat call identification. Approach calls differ markedly from search phase calls, but published description of echolocation calls for many species only regard search phase calls. Therefore, their usefulness as reference to identify approach sequences is limited and comparisons may lead to unreliable diagnoses.

The scales of call variation

The sources of variation so far described are expressed at different scales (Fig. 5). The temporal scale has major importance: whereas call structure may be changed instantaneously to negotiate different degrees of clutter or to fulfil different tasks, call features that depend on body size, condition, or age change over a lifetime; cultural effects, cultural or genetic drifts, or evolutionary responses take longer to emerge, sometimes changing over generations. Some sources of variation are expressed at the individual level (e.g., task, habitat structure, age, body condition, or sex effects), whereas cultural effects, adaptive responses, or drifts are detectable at the colony or even more strongly at the population level. Interactions may exist, such as the direction of call sexual dimorphism that may differ among colonies or populations.

Fig. 5. Acoustic diversity of bats is the synergistic effect of emerging properties acting at three different scales, from individual to population through colony. Causal factors represented here are either recognized or hypothesized in the scientific literature and illustrated as spheres whose relative size reflects their magnitude. Contact with icons representing the three scales expresses the occurrence of influences, whereas overlap between spheres points at interactions between factors. Individual variation originates from several potential sources, among which the effects of habitat structure (degree of clutter) and sensory task play an overwhelming role, with further influences of sex, body size, and body condition. Cultural effects may be detected at colony level and interact with sex, as call sexual dimorphism may be expressed differently in different colonies. Calls of colonies within populations may also be affected by environmental pressures linked with climatic gradients. Echolocation calls of allopatric populations in absence of significant gene flow and (or) cultural influences may show differences arising from environmental pressures, sexual selection, cultural or genetic drifts, and acoustic displacement to achieve resource partitioning or “private communication bandwidths”. Arrow symbolizes the time scale, from instantaneous changes to those emerging over evolutionary time scales. Colour version online.

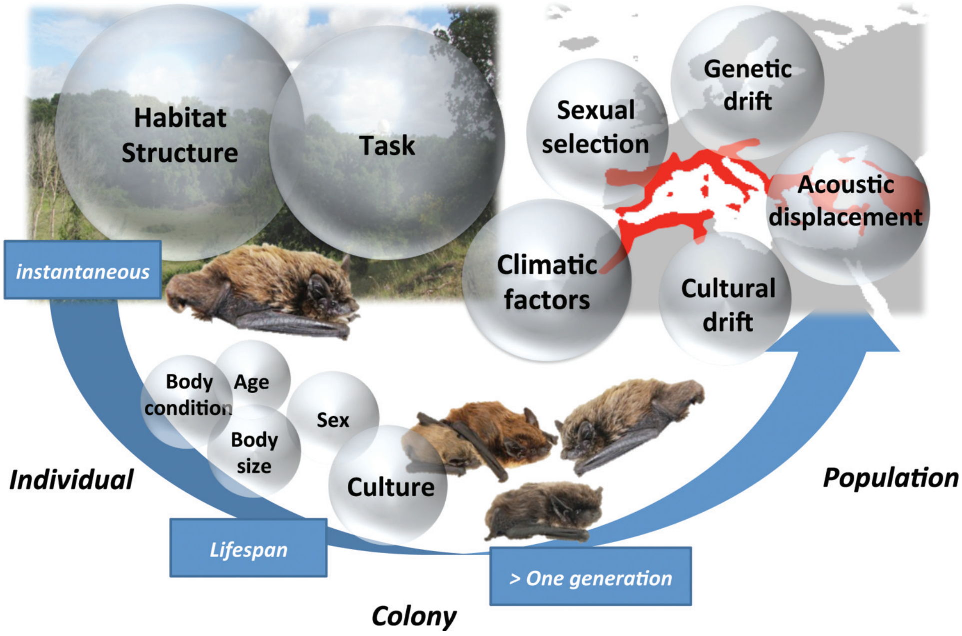
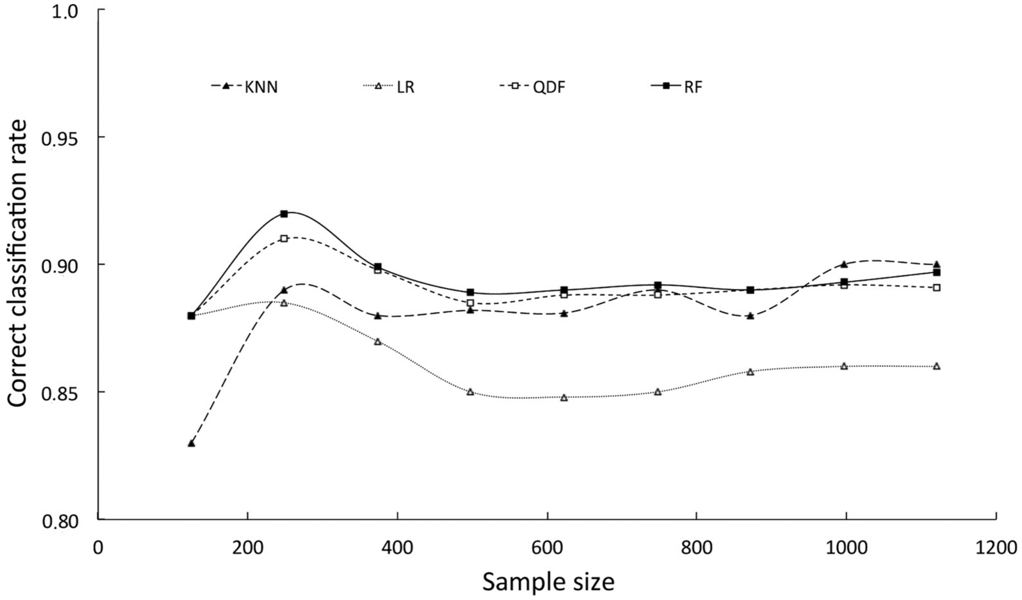


Fig. 6. The effect of sample size on classification performances of *k* nearest neighbors (KNN), logistic regression (LR), quadratic discriminant function (QDF), and random forest (RF) calculated for three species broadcasting similar calls (common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*Pipistrellus pygmaeus*), and Schreibers’s long-fingered bat (*Miniopterus schreibersii* (Kuhl, 1817)). The correct classification rates were assessed for randomly extracted 10%–90% subsets of a training or validation library of 1245 echolocation calls; variables used for classification were end frequency, frequency bandwidth, and duration (D. Russo and B. Silva, unpublished data). Note that a drop in classification performances is observed for all algorithms for sample sizes more than ca. 250 calls.



Conclusions

The problem of identifying bat species from calls is in some ways analogous to that faced in the morphological identification of species. In fact, the issue is largely about disentangling two variability components: (1) diagnostic species-specific variation (analogous to key morphological characters used in classical taxonomy for direct examination of specimens) and (2) the often overwhelming background noise generated by nondiagnostic variation (the equivalent of convergent characters, age-related variation, sexual dimorphism, and other individual differences that may confound morphological identification).

Call variation therefore includes both the problem and the solution and its full understanding is central to address the challenging issue of bat identification. Although much information is now available on echolocation call variation, much still remains to be learnt or awaits clarification — e.g., the existence of jamming avoidance during group flights. Identification is especially problematic for LDC species because their calls show the greatest intraspecific (in fact intraindividual) flexibility associated with habitat effects and different sensorial tasks. LDC species are often overrepresented in most geographic regions and habitats and convergence in call design may result from phylogenetic relatedness or adaptive convergence in syntopy. HDC species pose fewer problems, at least in regions where few such species occur, but still some overlap is possible (Russo et al. 2001; Schuchmann and Siemers 2010), and sex, age variation, and Doppler compensation may increase overlap in call frequencies among species.

Statistical approaches to call identification may in many cases provide encouraging results (e.g., Parsons and Jones 2000; Russo and Jones 2002; Walters et al. 2012; Zamora-Gutierrez et al. 2016), but in our opinion, we are still far from achieving safe identification for all species, especially in geographic regions characterized by extensive bat diversity (Russo and Voigt 2016; Rydell et al. 2017). Whatever the algorithm used, its performance will heavily depend on the reference library employed for comparison, its comprehensiveness, sample size, and quality. The issue of quality is especially sensitive because on the one hand it would be desirable to use reference calls recorded from subjects of known identity, i.e., hand-released or emerging from roosts of known composition. However, especially for open-space or edge foragers recorded in this way, clutter effects may be strong enough so that call structure differs considerably from that typically observed in commuting or foraging flights, where definitive identification of distant bats can be problematic (Parsons 1998). On the other hand, using library calls recorded in more natural conditions identified on the basis of their structure and used for reference is a circular argument. Identification performance is also expected to decrease for libraries featuring greater numbers of species, such as those developed for regions characterized by higher bat diversity. To account for as much variation as possible, libraries should also include many calls per species, but algorithms might show variable performance for different sample sizes as biases related to sample size such as overfitting or different degrees of variation-generated "background noise" may affect the outcome (Fig. 6). Finally, classification performances of automated classifiers are generally calculated using the training data set only: training calls are extracted iteratively one at a time and treated in turn as "unknown", then compared with the remaining data set to obtain a likelihood of correct classification for all species in the library. However, this procedure tends to overestimate identification performances, whereas using a separate validation data set would provide more realistic results (Clement et al. 2014). Overall, we feel the problem of call variability in quantitative acoustic identification is all about the quality and numbers of calls featured in libraries, as well as the quality of the recordings where identification is being attempted. Many calls recorded in field surveys are emitted by distant animals or by bats that are off-axis from the microphone. Such calls may be unrepresentative of "typical" calls of the species, e.g., because calls from distant bats will lose high frequencies because of frequency-dependent atmospheric attenuation. Although the technological problem of classification has surely made considerable progress, the biological problem of call variation is still significant. Further research is needed to comprehend it better and control for it more effectively in identification. Thus far, combining acoustic techniques with capture and roost search (Flaquer et al. 2007), as well as limiting manual or automatic identification to species with distinctive calls, still represents the wisest approach to employ in field studies of bats.

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