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Article *in* Ecological Indicators · July 2017

DOI: 10.1016/j.ecolind.2017.03.023

Ecological Indicators 78 (2017) 416–420

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Testing the performances of automated identification of bat echolocation calls: A request for prudence

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ARTICLE INFO

Article history:
Received 5 October 2016
Received in revised form 9 March 2017
Accepted 13 March 2017

Keywords:
Biosonar
Methodology
Software
Species identification
Ultrasound

ABSTRACT

Echolocating bats are surveyed and studied acoustically with bat detectors routinely and worldwide, yet identification of species from calls often remains ambiguous or impossible due to intraspecific call variation and/or interspecific overlap in call design. To overcome such difficulties and to reduce workload, automated classifiers of echolocation calls have become popular, but their performance has not been tested sufficiently in the field. We examined the absolute performance of two commercially available programs (SonoChiro and Kaleidoscope) and one freeware package (BatClassify). We recorded noise from rain and calls of seven common bat species with Pettersson real-time full spectrum detectors in Sweden. The programs could always (100%) distinguish rain from bat calls, usually (68–100%) identify bats to group (*Nyctalus/Vespertilio/Eptesicus, Pipistrellus, Myotis, Plecotus, Barbastella*) and usually (83–99%) recognize typical calls of some species whose echolocation pulses are structurally distinct (*Pipistrellus pygmaeus*, *Barbastella barbastellus*). Species with less characteristic echolocation calls were not identified reliably, including *Vespertilio murinus* (16–26%), *Myotis* spp. (4–93%) and *Plecotus auritus* (0–89%). All programs showed major although different shortcomings and the often poor performance raising serious concerns about the use of automated classifiers for identification to species level in research and surveys. We highlight the importance of validating output from automated classifiers, and restricting their use to specific situations where identification can be made with high confidence. For comparison we also present the result of a manual identification test on a random subset of the files used to test the programs. It showed a higher classification success but performances were still low for more problematic taxa.

1. Introduction

Acoustic methods of species identification represent a powerful approach to studying the distribution, ecology and behaviour of animals that broadcast sound for communication or echolocation (Towsey et al., 2014). In many cases, such as for bird- and cricket songs (e.g. Briggs et al., 2012; Lehmann et al., 2014), this approach involves reliable species identification. Bats are not birds or crickets, however, and, more importantly, echolocation calls, which generally are used to identify bats, are not songs (Barclay, 1999). While songs have the primary objective of announcing the identity of the singer, echolocation calls provide information for tasks such as orientation or prey detection, and therefore vary dramatically depending on task (Obrist, 1995). Moreover, different species often solve similar tasks using similar calls (Jones and Holderied, 2007), which means that considerable overlap in call structure is expected. Hence, species recognition based on echolocation calls is not nearly as straightforward as recognition based on e.g. bird or cricket songs and often leads to substantial challenges (Russo and Voigt, 2016).

Developments in ultrasonic technology have revolutionized the study of bats over the last few decades, and ultrasound detectors or "bat detectors" are now used routinely to study and survey bats in the field all over the world (Parsons and Szewczak, 2009). Over the years, researchers have moved from manual species identification, listening to heterodyned and/or time-expanded sound sequences (Ahlén, 1981), to analyses of displayed call sequences using various software (e.g. Russo and Jones, 2002). Recently, different automated

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http://dx.doi.org/10.1016/j.ecolind.2017.03.023
1470-160X/

approaches, typically employing multivariate sets of spectral and temporal variables of bat calls, have been attempted with variable results (e.g. Parsons and Jones, 2000; Walters et al., 2012; Zamora-Gutierrez et al., 2016). Freeware and commercial software used to speed up the screening of long recordings, select echolocation calls and identify species have recently appeared and are used extensively. The frequent use of automatic recorders triggered by bat calls and generating large audio data-sets when left unattended in the field for long periods have made such software welcome, because it saves time and facilitates analysis of large data-sets.

Software producers certainly provide warning notes on the risk of misclassification for some species or under certain recording conditions, but the temptation of using automatic tools non-critically remains strong. This may be especially true for ecological consultants with little or no experience with bats. Another reason for concern is that the performance of automated classification software has not been sufficiently validated before release into the market (Russo and Voigt, 2016). Although the limitations of automated classification have been highlighted by showing that different software packages identify calls of unknown bat species in different ways (Lemen et al., 2015), the reliability of identifying species of known identity remains little known. A first step is to test the performances of some popular software in the field under normal working conditions. This would give users a better grasp of the possibilities and limitations of these tools. To help fill this gap, we tested the absolute identification performances of three popular packages by recording echolocation calls from free-flying bats of known identity (i.e. the recorded bats were identified beforehand based on several complementary criteria – their real identity was therefore accurate and not based solely on our own sound identification ability).

Hence, the aim of this work was to test the program performance in an "absolute" sense, i.e. against known bats, or at least as absolutely as we could. We also tested whether the software can distinguish environmental noise such as rain from bat echolocation calls. For comparison with human identification performance, we also asked three colleagues to manually identify a small, random subset of the files that had been used for the programs (e.g. Jennings et al., 2008; Lewandowski and Specht, 2015). Finally, we provide some preliminary guidelines on how automated classifiers for the identification of bat species may and may not be used and highlight some obvious pitfalls with respect to both automatic and manual identification of bat calls.

2. Materials and methods

2.1. Field recordings

We made recordings of free-flying bats in Sweden in 2013–2016, using Pettersson D1000X and D500X bat detectors (Pettersson Elektronik AB, Uppsala, Sweden; www.batsound.com). The recordings were 3–4 s long full spectrum real time sequences with good signal to noise ratio sampled at 384 or 500 kHz and 16 bits. For each species we used 1–4 sets of recordings made in various parts of the country and under different conditions (specified in supplementary material 1). However, the identification performances of the programs turned out to be very similar across all the sets within each species, and we therefore pooled the sets before presentation. We used only recordings for which there was no doubt of the identity of the bat being recorded.

The identities of the recorded bats were established as follows:

a) Individuals of *Pipistrellus pygmaeus*, *Myotis brandtii* and *Plecotus auritus* were recorded as they were seen to emerge from or return to roosts where the bats had been identified beforehand, usually morphologically (captured individuals). We avoided making recordings of bats that did not use typical search-phase echolocation pulses, i.e. those being < 20 m from the roost exit. The exception is *P. auritus*, which was also recorded inside roosts (churches), where colonies had been identified visually beforehand. *P. auritus* emerging from roosts could always be recognized on its large and diagnostic ears.
b) Individual *Eptesicus nilssonii* and *Vespertilio murinus* were recorded at specific feeding territories where they have been observed regularly over long periods during previous studies. In these cases the recordings were made at close range (<10 m) and under good light conditions prevailing during the light nights of summer in Scandinavia. The bats' identities were thus confirmed based on a combination of size, wing shape and colour and, in addition, echolocation calls, by use of the bat detector. The light bellies and smaller sizes distinguish the two species from *Nyctalus noctula*, although all three sometimes co-occur in the area where the recordings were made, and may emit similar echolocation calls (authors' unpublished observations).
c) We used recording sequences containing intermittent and diagnostic social calls of presumed *V. murinus* to identify the bats unambiguously (Zagmajster, 2003). Search phase echolocation call sequences from these recordings were used in the test, but the social calls were excluded.
d) Recordings of *E. nilssonii* and *M. brandtii* were made in subarctic Lapland, where no other bats occur (Ahlén, 2011, author's unpublished observations). In this case, the identifications were facilitated by very good visual views, sometimes in sunlight.
e) We recorded *M. daubentonii* at a locality in southernmost Sweden, where it is the only bat species foraging low over water (trawling). We only recorded these bats as they flew over water and hence immediately and unambiguously were recognized to species.
f) *B. barbastellus* was recorded at a known feeding territory and near a hibernaculum, in both cases in places regularly used by several individuals over long periods. We made sure that all recordings used in the analysis included the pulses diagnostic for this species (Görlitz et al., 2010).
g) To minimize the risk that the recorded rain (noise) files actually were from bats, they were recorded in Tärendö in northernmost Sweden, an area where no bats are known to occur.

To simplify the classification tasks as far as possible and make our analysis conservative, we excluded all files containing calls from several individuals and more than one species. We also excluded social calls and sequences emitted in close proximity to roosts or clutter. However, for *P. auritus* we included the short broadband sweeps typically used in cluttered situations, which is the normal foraging habitats of this species, and also sequences with its characteristic low frequency sweeps (Anderson and Racey, 1991; Furmankiewicz et al., 2013), some of which were recorded inside the roost (a church loft). To simplify the task even further we made sure that all sequences used in the analysis were recorded under typical flight conditions for each species, e.g. *M. daubentonii* low over water, *E. nilssonii*, V. *murinus* and *P. pygmaeus* in more or less open space, *M. brandtii* and *B. barbastellus* in semi-open situations or ecotones, and *P. auritus* in clutter. Some typical sequences used in the test are provided as supplementary material 2.

2.2. Software tested

Using SonoChiro v. 3.3.3 (Biotope, France; www.biotope.fr), Kaleidoscope Pro 3.14B (Wildlife Acoustics, U.S.A; www.wildlifeacoustics.com) and BatClassify version 2014-07-14 (Chris Scott and John Altringham, U.K.; https://bitbucket.org/chrisscott), we tested whether the software could correctly attribute recorded call sequences to species group, an output provided by two (SonoChiro and BatClassify) packages, and species, provided by all three packages. Species groups were *Nyctalus*/*Vespertilio*/*Eptesicus* ("NVE"), *Pipistrellus*, *Myotis*, *Plecotus* and *Barbastella*. All three programs were provided with the same sets of recordings, but some files were discarded by the programs or were attempted but without any species being suggested ("no id"). The remaining sequences were either identified correctly or erroneously.

We used the default settings; for SonoChiro – type of recorder, region (North Boreal), time expansion (x1), maximum call duration (0.5), and sensitivity (7), for Kaleidoscope – filter (filter noise files, keep noise files), signal of interest (8–120 kHz, 2–500 ms, minimum 2 calls), classifiers = bats of Europe 3.1.3 (−1 more sensitive). No setting choices were available for BatClassify. Neither *V. murinus* nor *E. nilssonii* files was used to test BatClassify at the species level as its reference libraries only cover species occurring regularly in the U.K. However, the recordings of these species were tested to group level.

All software classified the sequences (files) according to the echolocation calls they contain, so results were expressed as percent of files correctly or erroneously classified to species groups or species. The programs provided "probabilities" of correct classification and one of them (Kaleidoscope) also suggested alternative species. However, as we found no way to interpret and standardize this information we did not use it.

To facilitate comparison of the program performance with that of manual identification (Lewandowski and Specht, 2015), we presented a small and random subset of the files to three colleagues. They were asked to identify each file according to group ("NVE" or to genus) and species in the same way as for the programs. The colleagues were given the information that the recordings were made in Sweden, but nothing else.

3. Results

Each program was given 2275 files containing bat calls and 190 containing only noise from rain. All rain files were distinguished from bat sound by all packages (Table 1). The frequency of rejected or not identified files varied between the programs and even more so between species within each program. Files with *E. nilssonii* were rejected particularly often by SonoChiro (41%) and Kaleidoscope (44%), and the latter also rejected many (55%) *P. auritus* files. The two programs that classify to group (SonoChiro and BatClassify) did so correctly in most cases (87–100%), although *E. nilssonii* and *V. murinus* were only correctly classified to their group ("NVE") about half the time (55% by Sonochiro, for the two species combined), as many files (40%) were rejected (not attempted).

Identification at the species level was highly variable both among programs and bat species. Two species that employ either a unique frequency band (*P. pygmaeus*) or unique alternating call sequences (*B. barbastellus*) were identified with good or at least reasonable accuracy by all software (97–99% and 62–95% correct, respectively). In contrast, *E. nilssonii* and *V. murinus*, belonging to the NVE group with several species using similar calls, were classified correctly only about half the time or less (49–54% and 16–20%, respectively). However, for *E. nilssonii* the low score was not primarily a result of errors, but of many rejected files.

Classification of *M. brandtii* and *M. daubentonii* was extremely variable and inconsistent (4–93% and 0–98% correct, respectively) with error rates as high as 96–100% in some cases (*M. brandtii* by SonoChiro and *M. daubentonii* by BatClassify, respectively; Table 1). *P. auritus* was usually identified correctly by two programs (80% and 89% for SonoChiro and BatClassify, respectively), but not at all by the third (0% for Kaleidoscope). In the latter case the files (95%) were usually rejected, only three identification attempts were made, all resulting in errors (Table 1). We double-checked Kaleidoscope's performances on *P. auritus* by trying various settings but always obtained the same result.

Misclassifications (false positives) occurred within genera (e.g. *M. brandtii* and *M. daubentonii* misidentified as other *Myotis* spp.) but also across genera and groups of genera (Table 2). For example, *E. nilssonii* was identified as belonging to five different genera, including *Myotis* and *Barbastella* and was particularly often identified as *M. dasycneme* (82% of the misidentifications by SonoChiro) and *Nyctalus leisleri* (64% by Kaleidoscope). Likewise *V. murinus*, which is notoriously difficult to identify manually from sonograms because of its broad frequency overlap with other species (Ahlén, 1981), was misidentified as belonging to four genera, including *Nyctalus* spp. (88% of the misclassifications by Kaleidoscope) and *Eptesicus serotinus* (40% by SonoChiro), but also quite frequently as *P. auritus* (32% by SonoChiro).

Our colleagues performed better than the programs both at the group and species levels (Table 3) with higher scores in most cases. The exceptions were when identifying *V. murinus* and *Myotis* spp. to species. Hence, these problems, so evident from the result of the automatic identification, were highlighted again, as the errors occurred in two out of the three cases (colleagues 1 and 2). *V. murinus* was misidentified as *Nyctalus noctula* and *Eptesicus serotinus* and *M. brandtii* and *M. daubentonii* were misclassified as other *Myotis* species. One colleague (colleague 3) was unfamiliar with one of the presented *P. auritus* call types, resulting in 50% error rate in this particular case.

4. Discussion

Although the software packages that we tested showed inconsistent performances, some generalizations can be made. For example, rain noise was distinguished from bat calls successfully by all programs, suggesting that they can be used to sort files containing bat calls from those containing only rain noise. However, environmental noises other than rain, such as sounds from rustling leaves, strong winds or running water, were not tested, so we cannot generalize across all sorts of environmental noise. We also caution that the high rejection rate of some bat calls, such as the short sweeps of *P. auritus* flying in clutter, suggests that there may be a risk that true bat calls were rejected as noise.

Generally, the programs successfully classified bat calls into broad groups (genera or in one case a group of genera) or identified the species with the most characteristic echolocation calls such as *P. pygmaeus* and *B. barbastellus*. This suggests that the programs may be used to survey these particular genera or species. However, it must be stressed that our study took place in a country with relatively low diversity of bats (19 species, Ahlén, 2011), so that the task was much simpler than in more species-rich sites. It was also simpler than it would have been if we had included calls from atypical habitats, social calls or calls from more than one individual or even several species at the same time. Indeed, serious shortcomings were evident for most species, including *V. murinus* and *E. nilssonii*, as already discussed, and also *M. brandtii* and *M. daubentonii*. Generally, many *Myotis* species, including those that we included in this test, use similar echolocation calls which may be difficult to classify (Parsons and Jones, 2000). We recorded the two *Myotis* species only in their most typical habitats *M. brandtii* in forest and *M. daubentonii* low over water, respectively. Since none of the programs could distinguish the two species nevertheless, it seems unlikely that any Scandinavian *Myotis* can be recognized reliably. It was also unexpected that *B. barbastellus* was so frequently misclassified. This species uses two unique call types that alternate at different frequencies, unlike any other bat in Scandinavia. Bar-

Table 1
The performance of three automatic bat identification programs given as % of files submitted to the programs (N). SonoChiro and BatClassify identified to species group and species, Kaleidoscope only to species. "No id" files were not attempted by the programs or attempted but not resulting in any identification. Dashes mean that the species were not included in the package, because they are not recognized members of the U.K. fauna. An asterisk denotes that the output actually was *Myotis brandtii*/*Myotis mystacinus*.

Species	*N*	Performance (% of *N*)												
		Sonochiro					Kaleidoscope			BatClassify				
		No id	Group		Species		No id	Species		No id	Group		Species	
			Right	Wrong	Right	Wrong		Right	Wrong		Right	Wrong	Right	Wrong
Pipistrellus pygmaeus	381	1.6	98.4	0.0	96.6	1.8	3.1	96.6	0.3	0.3	99.7	0.0	99.0	0.7
Vespertilio murinus	50	30.0	52.0	18.0	20.0	50.0	0.0	16.0	84.0	0.0	92.0	8.0	–	–
Eptesicus nilssonii	490	42.4	55.3	2.3	53.7	3.9	45.1	49.0	5.9	0.0	52.7	47.3	–	–
*Myotis brandtii**	831	0.0	99.5	0.5	4.0	96.0	6.0	50.3	43.7	0.0	93.4	6.6	93.4	6.6
Myotis daubentonii	102	0.0	100	0.0	57.8	42.2	0.0	88.2	11.8	0.0	98.0	2.0	0.0	100
Plecotus auritus	64	7.8	87.5	4.7	79.7	12.5	95.4	0.0	4.6	0.0	89.0	11.0	89.0	11.0
Barbastella barbastellus	357	0.3	95.2	4.5	95.2	4.5	25.5	61.9	12.6	0.0	96.4	3.6	96.4	3.6
Total	2275	10.3	87.8	1.9	49.4	40.3	19.1	59.1	21.8	0.1	86.2	13.7	89.6	10.3
Rain	190		100	0.0				100	0.0		100	0.0		

Table 2
Misclassifications at the species level, where *n* is the number of misclassifications of the species by the program in question. In addition to those shown in the table, misclassifications also occurred frequently at the group level. Dashes mean that the species were not included in the package, because they are not recognized members of the UK fauna. *Nyct/Vesp/Epte* refers to species in the genera *Nyctalus*, *Vespertilio* and *Eptesicus*.

Correct species	Misidentified as	SonoChiro		Kaleidoscope		BatClassify	
		n	%	*n*	%	*n*	%
Pipistrellus pygmaeus	*Pipistrellus pipistrellus*	7	100.0	1	100.0	3	100.0
Vespertilio murinus	*Nyctalus* spp.	25	24.0	42	88.1	–	–
	Pipistrellus pygmaeus		4.0		0		–
	Eptesicus serotinus		40.0		11.9		–
	Plecotus auritus		32.0		0		–
Eptesicus nilssonii	*Nyctalus leisleri*	17	0	28	64.3	–	–
	Pipistrellus pipistrellus		5.9		0		–
	Eptesicus serotinus		11.8		10.7		–
	Myotis dasycneme		82.3		21.4		–
	Barbastella barbastellus		0		3.6		–
Myotis brandtii	*Nyct/Vesp/Epte*	797	0	363	0	56	25.0
	Pipistrellus pipistrellus		0.2		0.3		21.4
	Myotis spp.		99.4		99.8		53.6
	Barbastella barbastellus		0.1		0		0
	Plecotus auritus		0.1		0		0
Myotis daubentonii	*Nyct/Vesp/Epte*	43	0	11	0	102	2.0
	Myotis spp.		100.0		100.0		98.0
Plecotus auritus	*Nyctalus leisleri*	1	0	3	33.3	3	0
	Pipistrellus pygmaeus		0		0		100.0
	Vespertilio murinus		0		33.3		0
	Eptesicus serotinus		0		33.3		0
	Myotis myotis		100.0		0		0
Barbastella barbastellus	*Nyct/Vesp/Epte*	16	0	44	0	14	21.4
	Pipistrellus spp.		0		13.6		28.5
	Eptesicus nilssonii		12.5		18.4		0
	Eptesicus serotinus		0		2.3		0
	Myotis spp.		87.6		61.3		28.5
	Plecotus auritus		0		0		21.4

bastelles were identified as *Myotis* spp., *Pipistrellus* spp., *E. nilssonii* and even *P. auritus* (Table 2).

It is striking that basic discriminant analysis or neural network approaches attempted many years ago (Parsons and Jones, 2000; Russo and Jones, 2002) did better than the suite of algorithms currently used in the modern software that we tested. Our results raise serious concerns about the risk of making considerable identification errors by using automated identification of bat calls, and this may bring about potentially detrimental consequences for conservation and species management. Needless to say, identification performances ranking well below 100% of correct classification should not be used for mapping species distributions, but obviously other surveys would also be compromised by incorrect identifications. Overall, our work confirms the concerns expressed by Russo and Voigt (2016) on the reliability of automated identification software and calls for prudence in the adoption of such tools for acoustic surveys and research.

We also highlight that manual identification of bat calls suffers from misidentification risks, just like automatic identification, although apparently to a lesser degree. Nevertheless, the performance of manual identification attempts may also need a thorough and critical evaluation. Individual differences in experience and ability among analysts also create noise in identification success (Jennings et al., 2008). We identify two specific cases where there is a clear risk of considerable errors even with the manual method, namely when identifying *Myotis* spp. and *V. murinus* to species.

Table 3
The performance of three colleagues that were asked to manually identify a subset of the sound files ($N = 10$ for each species, each colleague was given the same set). Explanations as in Table 1. An asterisk means that we accepted the suggested identification as *Myotis brandtii*/*Myotis mystacinus*, although all files actually were of *M. brandtii*.

Species	Performance (% of $N = 10$)														
	Colleague 1					Colleague 2					Colleague 3				
	No id	Group		Species		No id	Group		Species		No id	Group		Species	
		Right	Wrong	Right	Wrong		Right	Wrong	Right	Wrong		Right	Wrong	Right	Wrong
P. pygmaeus	0	100	0	100	0	0	100	0	100	0	0	100	0	100	0
V. murinus	20	80	0	50	30	10	90	0	50	40	0	100	0	100	0
E. nilssonii	0	100	0	90	10	0	100	0	100	0	0	100	0	100	0
*M. brandtii**	0	100	0	80	20	0	100	0	70	30	0	100	0	90	10
M. daubentonii	0	100	0	90	10	0	100	0	30	70	0	100	0	100	0
P. auritus	0	100	0	100	0	0	100	0	100	0	0	50	50	50	50
B. barbastellus	0	90	10	90	10	0	90	10	90	10	0	100	0	100	0
Total	2.9	95.7	1.4	85.7	11.4	1.4	97.2	1.4	77.1	21.5	0.0	92.9	7.1	91.5	8.5

In the latter case we strongly recommend extreme prudence and advise to refrain from identifying free-flying bats to species using sound alone. Needless to say, a similar situation may apply to several other European bats as well.

We recognize that automated identification of bat echolocation calls can be valuable for specific purposes and provided that certain caveats are met. For example, it may be effective for classifying some particular easy-to-recognize species in particular areas such as *Pipistrellus pipistrellus* and *P. pygmaeus* in the U.K. (Rowse et al., 2016). Removal of these abundant species then makes manual identification of the remaining files a manageable task. Also our results suggest that it is sometimes preferable to classify bats to species groups rather than to species, as error rates were relatively low for the former, although pooling different species may sometimes be insufficient to provide the information needed.

Acknowledgments

We acknowledge Johan Ahlén, Arjan Boonman and Espen Jensen (in random order) for help with the manual identifications and the reviewers for many useful suggestions. Funding was provided by the Swedish Energy Agency through the Vindval program (2016-000101) to JR.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.03.023.

References

Ahlén, I., 1981. Identification of Scandinavian Bats by Their Sounds. Report 6. Swedish Univ. Agric. Sci. Dep. Wildlife Ecology, Uppsala1–56.

Ahlén, I., 2011. Fladdermusfaunan i Sverige. Arternas utbredning och status. Fauna flora Stockholm 106, 2–19.

Anderson, E., Racey, P.A., 1991. Feeding behaviour of captive brown long-eared bats *Plecotus auritus*. Anim. Behav. 42, 489–493, http://dx.doi.org/10.1016/S0003-3472(05)80048-X.

Barclay, R.M.R., 1999. Bats are not birds – a cautionary note on using echolocation calls to identify bats. J. Mammal. 80, 290–296, http://dx.doi.org/10.2307/1383229.

Briggs, F., Lakshminarayanan, B., Neal, L., Fern, X.Z., Raich, R., Hadley, S.J.K., Hadley, A.S., Betts, M.G., 2012. Acoustic classification of multiple simultaneous bird species: a multi-instance multi-label approach. J. Acoust. Soc. Am. 131, 4640–4650, http://dx.doi.org/10.1121/1.4707424.

Furmankiewicz, J., Duma, K., Manias, K., Borowiec, M., 2013. Reproductive status and vocalisation in swarming bats indicate a mating function of swarming and an extended mating period in *Plecotus auritus*. Acta Chiropterol. 15, 371–385, http://dx.doi.org/10.3161/150811013X678991.

Görlitz, H., Hofstede, H.M.ter, Zeale, M.R.K., Jones, G., Holdereid, M., 2010. An aerial-hawking bat uses stealth echolocation to counter moth hearing. Curr. Biol., http://dx.doi.org/10.1016/j.cub.2010.07.046.

Jennings, N., Parsons, S., Pocock, M.J.O., 2008. Human vs. machine: identification of bat species from their echolocation calls by humans and by artificial neural networks. Can. J. Zool. 86, 371–377, http://dx.doi.org/10.1139/Z08-009.

Jones, G., Holderied, M.W., 2007. Bat echolocation calls: adaptation and convergent evolution. Proc. R. Soc. Lond. B 274, 905–912, http://dx.doi.org/10.1098/rspb.2006.0200.

Lehmann, G.U.C., Frommolt, K.-H., Lehmann, A.W., Riede, K., 2014. Baseline data for automated acoustic monitoring of Orthoptera in a Mediterranean landscape, the Hymettos, Greece. J. Insect Conserv. 18, 905–925, http://dx.doi.org/10.1007/s10841-014-9700-2.

Lemen, C., Freeman, P., White, J.A., Andersen, B.R., 2015. The problem of low agreement among automated identification programs for acoustical surveys of bats. West. North Am. Nat. 75, 218–225, http://dx.doi.org/10.3398/064.075.0210.

Lewandowski, E., Specht, H., 2015. Influence of volunteer and project characteristics on data quality of biological surveys. Conserv. Biol., http://dx.doi.org/10.1111/cobi.12481.

Obrist, M., 1995. Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. Behav. Ecol. Sociobiol. 36, 207–219, http://dx.doi.org/10.1007/BF00177798.

Parsons, S., Jones, G., 2000. Acoustic identification of 12 species of echolocating bats by discriminant function analysis and artificial neural networks. J. Exp. Biol. 203, 2641–2656.

Parsons, S., Szewczak, J.M., 2009. Detecting, recording, and analyzing the vocalizations of bats. In: Kunz, T.H., Parsons, S. (Eds.), Ecological and Behavioral Methods for the Study of Bats. , 2nd ed. The Johns Hopkins Univ. Press, Baltimore, pp. 91–111.

Rowse, E.G., Harris, S., Jones, G., 2016. The switch from low-pressure sodium to light emitting diodes does not affect bat activity at street lights. PLoS ONE 11, e0150884, http://dx.doi.org/10.1371/journal.pone.0150884.

Russo, D., Jones, G., 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. J. Zool. Lond. 258, 91–103, http://dx.doi.org/10.1017/S0952836902001231.

Russo, D., Voigt, C.C., 2016. The use of automated identification of bat echolocation calls in acoustic monitoring: A cautionary note for a sound analysis. Ecol. Indic. 66, 598–602, http://dx.doi.org/10.1016/j.ecolind.2016.02.036.

Towsey, M., Parsons, S., Sueur, J., 2014. Ecology and acoustics at a large scale. Ecol. Inform. 21, 1–3, http://dx.doi.org/10.1016/j.ecoinf.2014.02.002.

Walters, C.L., Freeman, R., Collen, A., Dietz, C., Fenton, M.B., Jones, G., Obrist, M.K., Puechmaille, S.J., Sattler, T., Siemers, B.M., Parsons, S., Jones, K.E., 2012. A continental-scale tool for acoustic identification of European bats. J. Appl. Ecol. 49, 1064–1074, http://dx.doi.org/10.1111/j.1365-2664.2012.02182.x.

Zagmajster, M., 2003. Display song of parti-coloured bat *Vespertilio murinus* Linnaeus, 1758 (Chiroptera, Mammalia) in southern Slovenia and preliminary study of its variability. Nat. Slov. 5, 27–41.

Zamora-Gutierrez, V., Lopez-Gonzalez, C., MacSwiney Gonzalez, M.C., Fenton, M.B., Jones, G., Kalko, E.K.V., Puechmaille, S.J., Stathopoulos, V., Jones, K.E., 2016. Acoustic identification of Mexican bats based on taxonomic and ecological constraints on call design. Methods Ecol. Evol. 7, 1082–1091, http://dx.doi.org/10.1111/2041-210X.12556.