

REVIEW

Using on-board sound recordings to infer behaviour of free-moving wild animals

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ABSTRACT

Technological advances in the last 20 years have enabled researchers to develop increasingly sophisticated miniature devices (tags) that record an animal's behaviour not from an observational, external viewpoint, but directly on the animals themselves. So far, behavioural research with these tags has mostly been conducted using movement or acceleration data. But on-board audio recordings have become more and more common following pioneering work in marine mammal research. The first questions that come to mind when recording sound on-board animals concern their vocal behaviour. When are they calling? How do they adjust their behaviour? What acoustic parameters do they change and how? However, other topics like foraging behaviour, social interactions or environmental acoustics can now be addressed as well and offer detailed insight into the animals' daily life. In this Review, we discuss the possibilities, advantages and limitations of on-board acoustic recordings. We focus primarily on bats as their active-sensing, echolocating lifestyle allows many approaches to a multi-faceted acoustic assessment of their behaviour. The general ideas and concepts, however, are applicable to many animals and hopefully will demonstrate the versatility of on-board acoustic recordings and stimulate new research.

KEY WORDS: Bats, Tag, Acoustic recording, On-board, Animal-borne, Acoustic behaviour, Foraging, Environmental acoustics, Predator-prey, Sensory ecology

Introduction

Throughout their life, animals face critical decisions that will influence their fitness. Some come up only at certain times, including whom to mate with and when to migrate. Some have to be made on a daily basis, like where and what to forage or where to roost. Animals receive different types of information gathered by their own senses and provided by other individuals, and they additionally can rely on memory of their previous experience. It is difficult to assess how animals make these decisions in the wild. Studying decision making in the field is extremely challenging, because it requires monitoring not only an animal's movement but also its foraging and interactions with other individuals (particularly conspecifics). Many studies are therefore performed in laboratories under controlled conditions. This scientific gap has primarily been a result of technological limitations. However, with the rapid miniaturization of electrical circuits and power supplies, the science of animal-borne sensors, known as biologging, is experiencing

an exciting explosion of possibilities (Bridge et al., 2011; Kays et al., 2015; O'Mara et al., 2014; Ropert-Coudert and Wilson, 2005).

The number of studies in the field is growing exponentially and each study is producing increasing amounts of accurate animal localizations. These data provide rich information about animal movements, but it is not always easy to infer much about the animal's behaviour or about its physical or social environment based on movement alone. The lack of additional behavioural information is limiting our ability to go beyond the description of an animal's trajectory. It impairs our ability to address questions related to the mechanisms underlying the animal's decisions of where and how to move. For example, we can determine which migratory route an animal chose, but it is hard to assess whether this decision was for example related to its foraging success prior to the decision to migrate, or whether it migrated alone or in a group. Thus, researchers have deployed multiple complementary sensors in order to address these gaps (Kays et al., 2015; Wilmers et al., 2015). The most commonly used sensors are tri-axial (3D) accelerometers (often accompanied by 3D gyroscopes and 3D magnetometers), which can provide information on movement dynamics (Brown et al., 2013; Martín López et al., 2016; Williams et al., 2017; Wilson et al., 2018) and on the animal's behavioural state like flying versus foraging (Nathan et al., 2012; Shamoun-Baranes et al., 2012; Shepard et al., 2008). Other complementary sensors include heart-rate and body-temperature sensors to monitor physiology (Bishop et al., 2015; Dechmann et al., 2011; O'Mara et al., 2017a,b; Stawski and Currie, 2016), ambient sensors to measure environmental parameters such as illumination (Bowlin et al., 2010; Bridge et al., 2013; Fudickar et al., 2012; Weller et al., 2016) and cameras mounted on larger animals to monitor behaviour and sociality (Goldbogen et al., 2017; Moll et al., 2007; Rutz and Troscianko, 2013; Rutz et al., 2007).

In this Review, we discuss the advantages of an uncommon sensor – a microphone – enabling sound recordings. Sound recordings on-board the animal can complement movement data and provide valuable information about the animal's behaviour and environment (Yovel and Greif, 2018). We focus mostly on echolocating bats, which are useful models for acoustic behavioural assessment, as they are active-sensing animals. This means that in order to perceive their environment, they produce echolocation calls, which we can conveniently eavesdrop on (Corcoran and Moss, 2017; Moss and Surlykke, 2010; Schnitzler et al., 2003). However, we will also demonstrate how audio recordings can be beneficial for studying many additional organisms.

Using sound to study foraging

Echolocating bats emit biosonar signals and analyse the returning echoes in order to search for and intercept prey, avoid obstacles, land and probably also navigate (Schnitzler and Kalko, 2001; Surlykke et al., 2014). Importantly, bats alter the acoustic parameters of their calls according to the task they are performing. This provides an

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excellent opportunity to infer the behaviour of a wild animal through sound recordings (Fig. 1A) conducted with miniature microphones that are mounted on-board the bat (Fig. 1B). An important behaviour that can be easily detected using such sound recordings is an ‘approach’. When a bat approaches an object (e.g. a wall or a prey item), it will emit a typical sequence of echolocation signals with decreasing intervals between them and shortening signal durations (Fig. 1A, inset) (Corcoran and Moss, 2017; Yovel and Greif, 2018). Inter-species variability in the echolocation approach behaviour can be substantial, but the general characteristics are maintained. Distinguishing between a landing event and an attack on prey can be difficult based on echolocation alone, but is made easier through analysis of secondary acoustic cues like chewing or landing noise (Stidsholt et al., 2018). Alternatively, GPS and acceleration data could be used to separate the two. For example, the animal’s location and height (based on GPS) during the approach and its movement pattern after the approach can provide context and assist in determining whether the bat has landed or attacked prey. The documentation of attacks on prey can be used to study fundamental questions in behavioural ecology such as the relationship between movement strategy and the probability of finding prey, i.e. what characterizes the movement of individuals that are more successful in finding prey (Egert-Berg et al., 2018).

In some cases, when the prey emits sound, it can be used to identify the type of prey that has been attacked. For example, in bats that detect prey such as katydids or frogs based on their emitted sounds, these emissions can be picked up by the on-board microphone (Fig. 1C,D; Audio 1 and 2). Moreover, depending on prey type, the recordings can sometimes be used to determine whether an attack was successful according to the presence (or absence) of chewing sounds immediately afterwards (Stidsholt et al., 2018). Identifying prey type and the success of the attack allows us to obtain a rather accurate estimate of the caloric intake of the bat (Encarnação and Dietz, 2006). Alternatively, when studying a specialized forager, which relies almost exclusively on a specific type of prey, it is enough to recognize chewing in order to estimate caloric intake. This is the case, for instance, with the greater mouse-tailed bat (*Rhinopoma microphyllum*), which forages almost exclusively on *Camponotus* ants during August–September in northern Israel (Levin et al., 2009).

Using sound to infer foraging might also be the case with non-predatory bats, like fruit bats, where chewing sounds could provide information about the amount of consumed fruit (Fig. 1E; Audio 3) (Michal Handel, Tel Aviv University, personal communication). In insectivorous bats, a successful attack is equivalent to the capture of a single prey item. In contrast, when using chewing to infer the

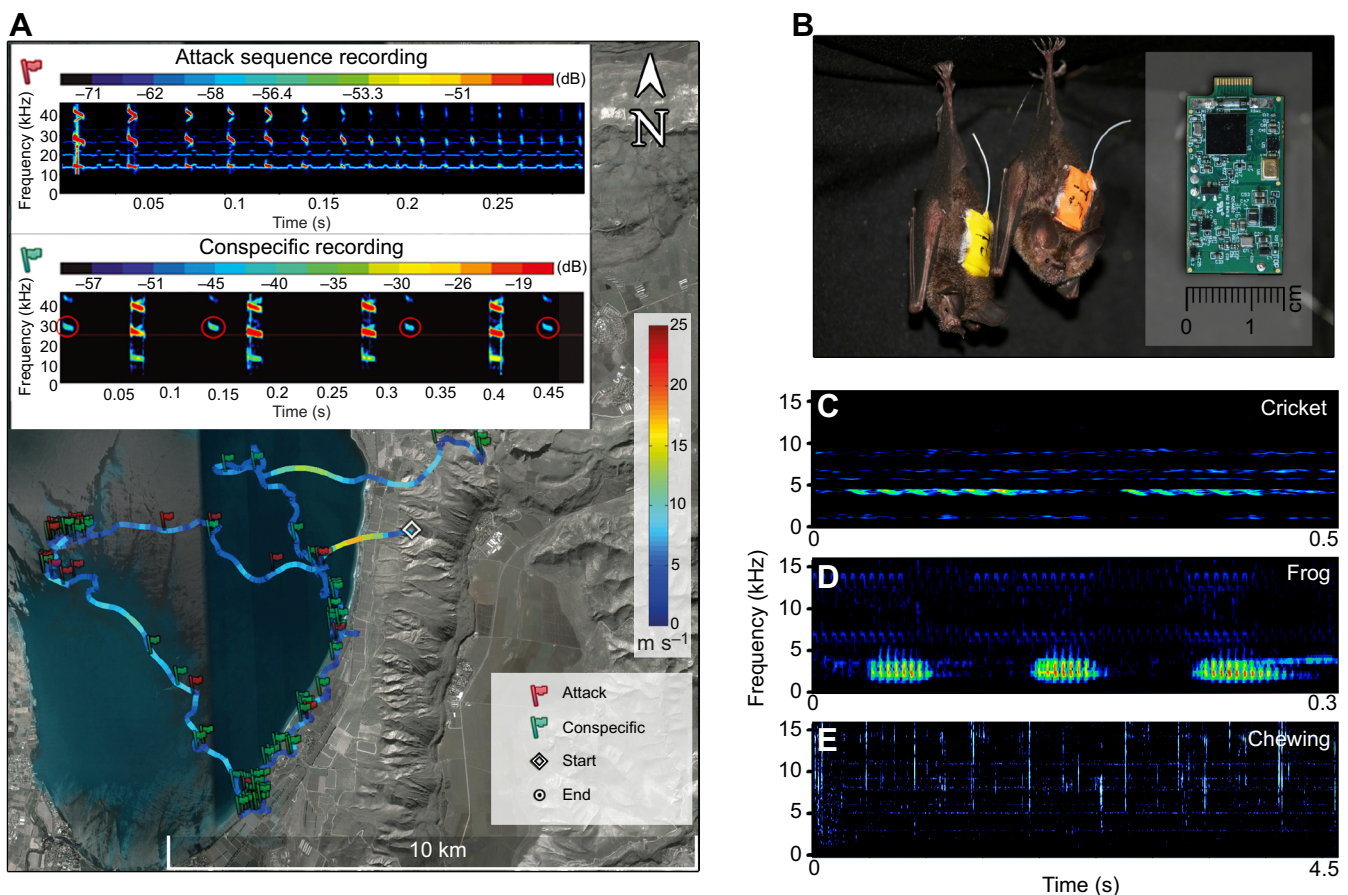


Fig. 1. Recordings of echolocation and environmental sounds. (A) A GPS track (one night) of a *Rhinopoma microphyllum* bat in Israel. The colour of the track codes for flight speed and the red and green flags mark attacks on prey and recordings of a conspecific (detected based on on-board audio recordings). The inset shows two spectrograms of on-board recordings: at the top, a typical echolocation attack sequence, and at the bottom, the echolocation calls of a searching bat that encounters a conspecific (calls in red circles). Adapted from Cvikel et al. (2015). (B) Two *Trachops cirrhosus* bats with attached multisensory tags (shown in the inset). Photo credit: S.G. (C) Spectrogram of a cricket, recorded with a tag on a *Hipposideros armiger* bat in Thailand. (D) Spectrogram of a frog calling, recorded on a *Trachops cirrhosus* bat in Panama. (E) Spectrogram of chewing noises, recorded on a *Rousettus aegyptiacus* bat eating fruits in Israel. Sounds C–E can be listened to in Audios 1–3.

amount of fruit eaten, recordings should be compared with a reference library. Here, captive bats are recorded feeding on different types of fruit while the amount they eat is monitored using video. Assessing food intake using sound is of course not restricted to bats and can be performed on any other organism for which chewing or food processing is audible, as has already been demonstrated in several animals, including humans (Bi et al., 2016), lions (Wijers et al., 2018) and mule deer (Lynch et al., 2013; Nelson et al., 2005).

Recording sound on-board free-flying bats allows us to connect foraging behaviour to environmental conditions. For example, sound recordings could potentially be used to study how bats adapt their signals to different ambient conditions (such as temperature, humidity or rain), which are known to affect sound attenuation and can therefore affect prey detection range (Goerlitz, 2018; Luo et al., 2013). Recordings are also useful for studying how bats weigh different sensory modalities; for example, whether and how they adjust echolocation (signal intensity and frequency) according to the availability of visual cues (Gorresen et al., 2017). By recording sound on-board Egyptian fruit bats (*Rousettus aegyptiacus*), which are known to rely heavily on vision, we recently showed that these bats will use echolocation even when foraging in high light levels, probably benefiting from the accurate ranging information provided by echolocation and integrating it with vision when landing on fruit trees (Danilovich et al., 2015). On-board echolocation recordings can also reveal how bats deal with noisy conditions and specifically whether, and how, they adapt to anthropogenic noise. These questions can similarly be addressed using stationary ground-microphones placed at foraging sites where bats are active (Koblitz, 2018; Luo et al., 2015a), but recording sound on-board the animal provides a rare opportunity to study the question from an individualistic point of view; that is, how one individual tunes its sensing to the changing environment. Additionally, it allows for more continuous and precise measurements.

Intriguingly, the use of audio to infer foraging success (see above) can be combined with recordings of ambient noise in order to examine the effect of the latter on the former (Luo et al., 2015b; Siemers and Schaub, 2011). This is also true for non-echolocating animals: for instance, if attacks can be inferred from acceleration recordings (e.g. in cheetahs; Wilson et al., 2018) then complementary sound recordings could reveal whether background noise (such as anthropogenic noise) influences the attack rate (Blair et al., 2016; Shannon et al., 2016). Additionally, on-board anthropogenic noise recordings could also be quantified and further used to explain other noticeable behavioural changes in acceleration or tracking data, thus describing noise-related avoidance behaviour (Johnson and Tyack, 2003; Madsen et al., 2006). How animals adjust to urban environments is a 'hot' topic in ecology. A textbook example of adaptation claiming that song-birds raise their song frequencies to overcome anthropogenic noise (Slabbekoorn and Peet, 2003) has been criticized as being the result of recording and analysis artefacts (Nemeth et al., 2013). Using on-board microphones (instead of the terrestrial ones currently used) would help to resolve this and similar debates.

It should be mentioned that research into toothed whales, another active-sensing group of animals, has greatly benefited from the deployment of tags. These animals also emit sound in order to find and attack prey and, like bats, emit a typical sequence of signals when approaching a target (Madsen and Surlykke, 2013). Many of the discussed foraging-related questions can therefore be studied in this group with similar techniques. In recent years, researchers have provided great examples of how to combine different sensors

(e.g. pressure sensors, accelerometers, video cameras), enabling a better understanding of foraging, diving and sensory perception (Fais et al., 2016; Watwood et al., 2006; Wisniewska et al., 2015). As toothed whales are large animals, researchers were able to pioneer the development and use of on-board acoustic tags in this group (Johnson, 2014; Johnson et al., 2009). However, despite this early start, the use of on-board acoustic recordings for studying toothed whale echolocation is still sparse. Because sound travels much farther under water, recordings on-board toothed whales can pick up not only the animal's emissions but also the returning echoes, thus allowing the study of how animals adjust their sensing in response to incoming information (e.g. how is emission intensity controlled as a function of echo intensity). It is not easy to record faint reflected echoes on-board bats but this has recently been done, opening up a more intimate view of the bat's world (Stidsholt et al., 2018).

Using sound to study sociality

One of the greatest advantages of on-board audio recordings is the window they open into studying animal sociality (Hughey et al., 2018). It is extremely difficult to observe groups of individuals over long periods in the field, especially when studying small, elusive animals. Up to now, researchers have used video or radar for tracking large groups over short periods, but once the group starts moving beyond the field of view of the system, it is impossible to keep track of individuals. For some localized, slow-moving species like meerkats, Arabian babblers or chimpanzees, habituating the animals to human observers has worked well (Gall and Manser, 2017; Wright et al., 2001), but for the majority of species a different monitoring approach of social interactions is needed. We are now seeing the first studies where all or many individuals of a group have been tracked with GPS (Flack et al., 2018; Jones et al., 2018; Nagy et al., 2010; Strandburg-Peshkin et al., 2015), allowing detailed insight into group behaviour. In addition, on-board audio recordings allow unique opportunities to study animal sociality using sound to infer the presence of conspecifics and without the need to directly track numerous individuals (Cvikel et al., 2015; Egert-Berg et al., 2018). Acoustic recordings are ideal for monitoring interactions in species that rely on vocal communication, but they could also allow identifying interactions when no vocalizations are emitted, by detecting non-communicative sounds such as sniffing, movement or physical altercations. In deer, the fighting sounds of colliding males could give an indication of courtship efforts, while in spring the shedding of antler skin on trees might be recorded. Even in the otherwise barely vocal tortoises, acoustic on-animal recording could be used to evaluate mating efforts when the male rams the female repeatedly over a considerable time (and subsequently squeaks during copulation). Because it is not always trivial to interpret these non-communicative sounds, it is generally a good idea to create a reference audio library by coupling video and audio recordings where the animal's behaviour can be clearly observed in parallel to recorded sound (Stowell et al., 2017).

In echolocating bats, which constantly emit sound, recordings on-board one individual will also reveal its interactions with conspecifics. The presence of nearby conspecifics, or even heterospecifics, can be identified (Fig. 1A), and in some cases the intensity of the conspecific's emission can be used to estimate its distance from the individual carrying the microphone. Exact distance is impossible to obtain, because the position of the tag relative to the calling conspecific (i.e. on- or off-axis to its mouth) would make a huge difference in the received intensity. When assuming an emission intensity (which is well studied in bats), the maximum distance can be estimated, and when taking into account

the sensitivity for different frequencies, this estimate can be further improved. Moreover, when examining a sequence of conspecific emissions, one can often determine whether it is moving towards or away from the tagged bat, which allows an even better estimate. We have shown that such a crude estimate of conspecific distance correlates nicely with the expected echolocation response of a bat to a nearby conspecific (Cvikel et al., 2014). Future tags equipped with two (or more) microphones will make it possible to roughly estimate the direction of the conspecific in relation to the tagged animal (Johnson et al., 2009). By combining the probability of encountering conspecifics (deduced from the audio) with a statistical model of the animal's movement, the density of a species' population in a region can be estimated (Marques et al., 2013). For example, when the movement of individual bats can be modelled based on GPS data, one could examine how many individuals should be present to explain the encounter rate observed through acoustic recordings. Such estimations are obviously limited, but they could be used in order to set bounds to the actual density. We used a similar approach to show that bats were intentionally aggregating more than expected by chance (Cvikel et al., 2015; Egert-Berg et al., 2018). In bats, it is easy to distinguish the echolocation signals of the bat carrying the device from those of a nearby conspecific based on differences in intensity. Because of the strong attenuation of high sound frequencies in air, the echolocation calls of a conspecific will always be much weaker than those of the tagged bat (Fig. 1A, inset). This is not always the case when dealing with low-frequency social calls of nearby bats or other organisms such as birds or toothed whales. The vibration of the body resulting from the sound emission can be used to solve this problem (Anisimov et al., 2014; Goldbogen et al., 2014) and other, acoustic-based solutions to identify the emitter have also been suggested (Stimpert et al., 2015; Stowell et al., 2017).

Because bats adapt their signals based on the task they are performing, when two bats encounter each other, their interaction can be characterized. We have recently used this to address a

fundamental riddle in bat sensing – how bats deal with sensory interference generated by the signals of conspecifics when flying in groups with high density (Cvikel et al., 2014). In theory, because conspecifics emit signals with very similar frequencies, when flying with nearby neighbours, bats face the problem of detecting weak prey echoes amid the cacophony of neighbouring bat signals. Unlike some previous studies (Gillam et al., 2007; Ulanovsky et al., 2004), we have not found any evidence that bats perform a jamming avoidance response, i.e. that they shift the emitted frequencies aiming to decrease spectral overlap with nearby conspecifics (Cvikel et al., 2014). Our on-board recordings allowed us to more accurately estimate the frequencies emitted by the bats and the conspecific interference that they were exposed to, as previous studies had to rely on ground stationary recordings. Another laboratory study showed that bats can distinguish between the echolocation signals of specific individuals (Yovel et al., 2009), an ability which could facilitate a solution to the problem of distinguishing one's own echoes from the echoes of conspecifics. Thus far, we have mainly concentrated on echolocation recordings in bats, but they also exhibit a wide array of social vocal communication (Fig. 2A) (Pfalzer and Kusch, 2003). On-board sound recordings can therefore be used to study other aspects of bat sociality, which are hard to unravel from echolocation, such as courtship singing or patch defence behaviour (Corcoran and Conner, 2014; Smotherman et al., 2016).

Recording the sounds of conspecifics on-board a wild animal could enable us to address many more exciting questions related to the animal's social environment, including the following. (1) Do animals maintain consistent groups while moving? Computational methods like canonical discriminant analysis or machine learning classifiers sometimes permit recognition of individuals based on their calls (Kirschel et al., 2011; Prat et al., 2016; Stowell and Plumbley, 2014; Yovel et al., 2009). This might allow us to study whether bats or other animals move with the same individuals around them, and how the social dynamics of such groups work. (2)

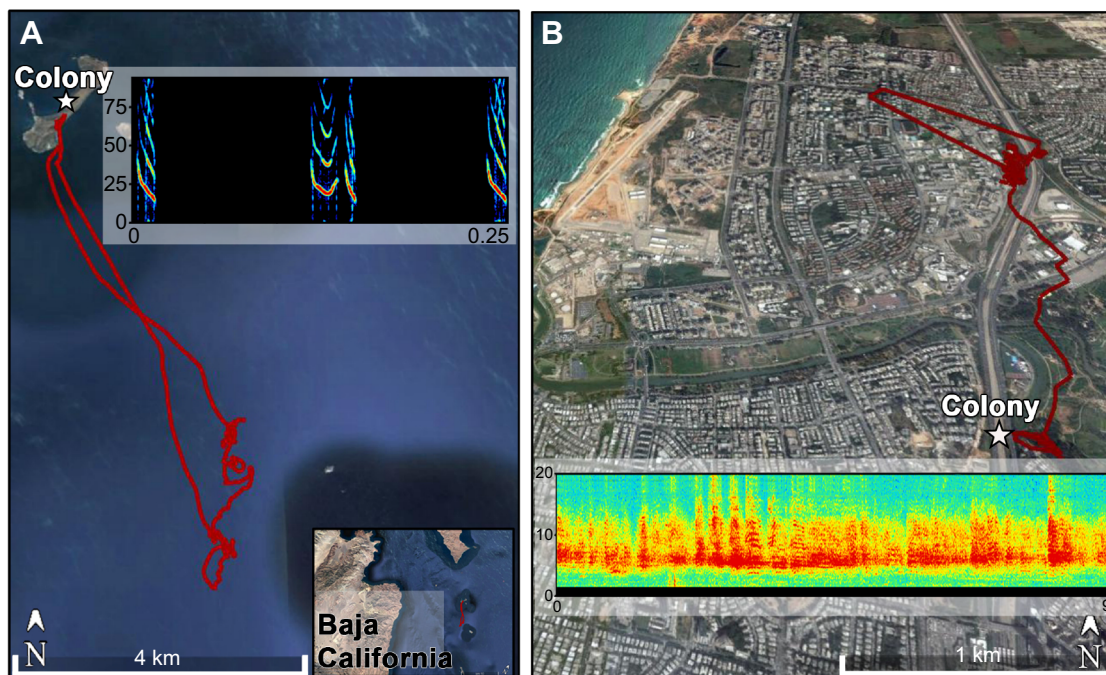


Fig. 2. Social communication in bats. (A) GPS track (one night) and social calls of a *Myotis vivesi* bat, recorded only near the colony site. (B) Social call cacophony of *Rousettus aegyptiacus* bats inside a colony found with GPS and audio recordings. The insets depict frequency (kHz) on the y-axis and time (s) on the x-axis.

How do animals maintain a coherently moving group? By combining audio recordings with acceleration and locational measurements, the dynamics of flight (or other types of movement) can be compared when the individual is flying alone or in a group. Numerous mathematical models have been suggested to explain how animals move in coherent groups (Couzin et al., 2005; Herbert-Read, 2016), but these models have received comparatively little support from field data until recently (Flack et al., 2018; Nagy et al., 2010; Strandburg-Peshkin et al., 2015). Recording sound to determine the density of the group accompanied by fine movement measurements (such as acceleration and localization) could further help to narrow this gap in the data. (3) How do animals optimize foraging when foraging in a group or when competing with others? Audio recordings can be used to test some of the classical optimal foraging models, such as the marginal value theorem, which postulates that an animal should leave a food patch when the marginal feeding rate in the patch drops below the average rate of the habitat (Charnov, 1976); or the ideal free distribution theory, which suggests that animals will spread between foraging sites with an inverse relationship to their profitability (Kacelnik et al., 1992). In both of these cases, monitoring the foraging success of the animal (see above) and the density of conspecifics is extremely valuable. (4) How do animals interact with heterospecifics? Research usually focuses on a specific species, and thus very little is understood about inter-species interactions. Recent studies on bats showed that they can learn from heterospecifics in captivity (Clarín et al., 2014; Patriquin et al., 2018). On-board sound recordings will allow us to examine whether such inter-species interactions are more or less common in the wild (Hügel et al., 2017). A classic example in vertebrates is alarm calls that can be used by heterospecifics to avoid danger and illicit anti-predator behaviour (Magrath et al., 2015).

Many of the ideas discussed above on how to exploit sound recordings for inferring behaviour are not exclusively relevant to bats, and can be applied to study many additional species. Clearly, the most prominent research direction is using sound to record social vocalizations. On-board recorded vocalizations can be used to study different aspects of sociality in the animal's natural habitat. Some examples include the species' vocal repertoire, courtship patterns, group communication or aggressive behaviour (Anisimov et al., 2014; Choi et al., 2017; D'Amelio et al., 2017; Gill et al., 2015). On-board microphones can also replace external microphones in studies focusing on vocal learning and vocal ontogeny, allowing researchers to address these questions in the wild. Sound recordings on-board non-echolocating animals might also be valuable for movement and navigation-related studies. For example, using the calls of animals typically travelling in groups would allow estimation of the density of nocturnal, migratory birds (Salamon et al., 2016) or characterization of the movement dynamics of individual animals within a group (e.g. meerkats, parrots, swifts) (Couchoux et al., 2015; Gall and Manser, 2017; Van Oosterom et al., 2016).

Using sound to extract additional information

Recording audio on-board wild animals can help ecological surveying. Acoustic monitoring using stationary microphones is a common way to assess species abundance and population density (Marques et al., 2009, 2013; Ross et al., 2018). To go even one step further, one could imagine that when mounting microphones on animals in the field, they essentially become mobile sensors that move through the environment. In some cases, such a survey animal can reach places that human surveyors cannot, allowing us to record sound in the depth of the ocean, high above ground or deep in dense

vegetation. Obviously, unlike human surveyors or stationary recorders, animals move according to their needs, so their movement biases must be taken into account when analysing the results. Using a combination of GPS and sound recordings on-board wild animals can also reveal the locations of unknown colonies or social meeting points, which might be important for the conservation of species that have a poorly studied ecology. We often find locations of new bat colonies based on acoustic recordings (Fig. 2B). Yet, the potential for surveying the environment with sensor-mounted animals is not limited to detecting conspecifics. The population of any other species that is present in the activity area of the tagged animal could also be assessed as long as this species emits sound (Towsey et al., 2018). In this way, one easy to catch species can reveal the presence of other, more cryptic species. With our microphones on bats, we have recorded other bat species, insects, frogs and other un-recognized species. When coupling the acoustic data again with GPS localizations of those heterospecific encounters, a rough distribution map of the population could be generated. For example, on a tagged fruit bat in Tel Aviv, we have recorded the howling of golden jackals, thus documenting its recent expansion into more urban environments in Israel.

On-board sound recordings can also be used creatively to replace or supplement other sensors. For example, in the absence of an accelerometer, audio recordings can be used to detect wind or changes in air pressure induced by different movement patterns. When analysing the recordings performed on-board flying bats or birds, it is often possible to infer wingbeat rate as the wings produce noticeable noise when cutting through the air (Fig. 3A; Audio 4) (Fournier et al., 2013). Such data can also provide insight into the synchronization between sensing and movement. In Fig. 3B, we show the coupling of echolocation with the bat's wingbeat, which has been suggested to reduce energy costs of sound production (Amichai et al., 2015; Voigt and Lewanzik, 2012). Changes in wingbeat pattern can also reveal behavioural phases, like distinguishing between active and gliding flight. Further differences can be recorded when an animal moves from a commuting locomotion to a foraging locomotion like sprinting after prey or hovering in front of a flower. Additional foraging events could be detected based on changes in air pressure around the microphone, created for example by the swift manoeuvres of a predator (Wilson et al., 2018). This could be a peregrine falcon stooping down on a pigeon or a gannet piercing the water surface when hunting fish (Ropert-Coudert et al., 2004). The sound of the wind induced by flight (occurring between wingbeats or when gliding) could potentially be used for estimating the speed of the animal (Goldbogen et al., 2007). Separating movement-induced wind noise from actual wind is a challenge that must be dealt with in many of these applications. When the animal is stationary or slow moving, the intensity of ambient wind could be assessed to some extent and could possibly inform movement patterns of terrestrial animals that want to avoid wind exposure. Additional creative uses of sound can be thought of when looking at activity-generated sounds (Couchoux et al., 2015; Parsons and Wilson, 2006). In walking animals, one can distinguish between different locomotion modes (e.g. resting, trotting, running), thereby giving insight into activity patterns and circadian rhythms (Insley et al., 2008; Itai and Yasukawa, 2007; Iyengar et al., 2007; Wijers et al., 2018). In Fig. 3B,C, we show an example of a bat that commutes steadily in the open air space versus a bat that flies in a restricted air space where it has to make not only faster wingbeats but also stronger ones (as visible in the louder wingbeat noise). In some animals, it might be possible to

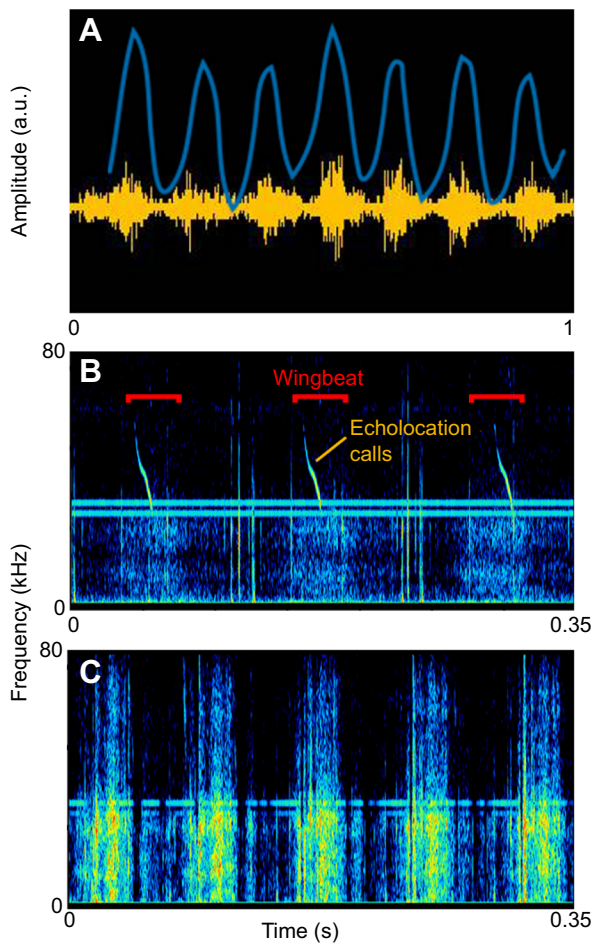


Fig. 3. Acoustic information from a bat's wingbeat. (A) Acoustic recordings can at times depict wingbeat quite accurately. The yellow oscillogram of the audio recording is showing the same wingbeat rhythm as the z-axis acceleration (blue). Amplitude is in arbitrary units (a.u.). The wingbeat sounds can be listened to in Audio 4. (B) A spectrogram of three wingbeat sounds during a commuting flight of *Leptonycteris yerbabuena* in Mexico. It further shows a coupling of wingbeat and echolocation calls. (C) A spectrogram showing the clearly different flight pattern of the same *Leptonycteris* bat when flying in a constrained space, while approaching a cactus flower. The wingbeat is faster and sounds noisier. Echolocation calls are not visible as bats (especially Phyllostomids) reduce emission amplitude drastically in such situations.

discriminate between different habitats (e.g. when hedgehogs or beetles are moving in a silent meadow or a rustling understory) (Goerlitz et al., 2008). Similarly, analysis of echoes can reveal how close bats and whales are to nearby objects or environmental features (Johnson et al., 2009; Stidsholt et al., 2018). Finally, acoustic sensors mounted on marine mammals can also be used to record respiratory rate or heart rate as proxies for metabolic measurements (van der Hoop et al., 2014a; Rojano-Doñate et al., 2018; Storch et al., 1999).

A few technical notes about on-board sound recordings

Microphones can be miniature and therefore mounted even on very small animals (several labs have developed a telemetry microphone circuit that weighs ~1 g) (Gill et al., 2016; Hiryu et al., 2007; Lancaster et al., 1992). However, audio recordings have one main disadvantage compared with acceleration or localization data: they create a lot of data, requiring a large storage capacity and are hard to transmit. This problem is even more pronounced when studying bat

echolocation. Recording high frequencies creates even more data as, according to the Nyquist ratio, the sampling rate should be at least twice the highest frequency that needs to be recorded (i.e. for a bat calling up to 100 kHz, sampling rate should be at least 200 kHz). One way to overcome this difficulty is to run auto-detection algorithms and to store (or transmit) only those parts of the data where sounds of potential interest have been detected. This approach can be combined with a flexible time schedule (e.g. only recording the dawn chorus of birds) (Stowell et al., 2017) or with a movement-generated activation mechanism which is operated by other sensors (e.g. accelerometers), and which only activates the recordings during the activity periods of the animal (Jurđak et al., 2013; Oletic et al., 2018). If the actual precise acoustic parameters are not essential for the study, compressed audio file formats like mp3 may be preferred over the 10 times larger lossless standard wav format (Araya-Salas et al., 2017). Going even further, an on-board sound analysis and classification algorithm could save only the time and outcome/category of the event (e.g. call, species, chewing), which would reduce the amount of data drastically (Akamatsu et al., 2005; Deniz et al., 2017). Naturally, some of these algorithms are heavy power consumers, so they must be used wisely. Additionally, on-board pre-filtering (e.g. with a band-pass filter) can improve signal quality, promising a better dynamic range in the desired frequency spectrum. A good signal to noise ratio (and therefore dynamic range) is especially important where big amplitude differences can be expected. The calls of bats can for example be very loud, frequently reaching peak values around 130 dB SPL (Surlykke and Kalko, 2008), whereas the rustling sound of potential prey, like beetles crawling over a leaf-covered ground, is around 50 dB SPL or lower (Goerlitz et al., 2008). This can create difficult recording situations, as can be seen in Fig. 3C. When hovering in a constrained space, the wingbeats of the *Leptonycteris* bat become faster and louder. At the same time, the bat reduces the amplitude of the calls drastically, making it at times impossible to record because the calls are too faint compared with the noisy wingbeats. In this case, our control recordings from a stationary microphone (with a better dynamic range and away from the wings) did not have this problem and confirmed continuous echolocation by the bat. Small microphones (e.g. MEMs) which are often used nowadays for recording with tags have a limited depth of 12–16 bit, providing a dynamic range of approximately 72–96 dB.

Some of the research suggestions made above require accurate estimates of the absolute intensity or spectrum of the emitted sound. For example, when studying vocal learning, obtaining high-quality recordings might be crucial. It should be noted that estimating the absolute intensity of the signals emitted by an animal and their exact spectrum might be challenging when using on-board microphones. In many cases, the microphone will be placed on the animal's body and often on its back (e.g. between the shoulders in bats). This means that in order to estimate the intensity and precise spectrum of the signals, the difference between the on-axis and the rear emission must be known. Head movements relative to the microphone (e.g. due to changes in gaze) might further complicate estimations. Nevertheless, when an omni-directional microphone can be situated very close behind the emitter (i.e. the mouth), as we do with bats (Fig. 1B), then head movements will not translate into big changes in amplitude or spectrum at the microphone. This is because the microphone can be almost fully omni-directional and it is always positioned at the rear of the emitter, even when the head moves. The characteristics of the microphone are extremely important here. Small microphones that are commonly used for miniature sensors (e.g. the Knowles FG series) are almost omni-directional, but their

frequency response is far from flat (i.e. the recording is biased towards certain frequencies). These parameters should be taken into account when analysing the acoustics (Adams et al., 2012; Ratcliffe and Jakobsen, 2018). However, even with these limitations, on-board recordings are often more accurate than ground stationary recordings, which additionally suffer from artefacts resulting from Doppler shifts (whenever the animal is moving) and from the directionality properties of the microphone and the animal emission (Cvikel et al., 2014; Jakobsen et al., 2013; Ratcliffe and Jakobsen, 2018).

When combining audio recordings with other sensors like acceleration or GPS, special care should be taken to secure a proper synchronization of the system as sampling clocks might be drifting, especially when no GPS clock is available. External synchronization can be achieved by providing an input signal that can be received by all sensors. For example, a simple way to achieve rough synchronization is tapping the tag on a surface. This will lead to a noticeable signal in the acceleration and audio channel and will allow synchronization of ca. 10–50 ms. Such synchronization signals should be given at the beginning and the end of the recording or, if possible, at regular intervals. Another challenge here is to bring data from different sensors together with each other or with environmental data to evaluate behaviour in greater detail (Dodge et al., 2013; Kays et al., 2015; Kranstauber et al., 2011; Obringer et al., 2017; Walker et al., 2015).

Before recording, thought should be put into the analysis of the audio data (Hopp et al., 1998; Johnson, 2014; Sueur, 2018). Unlike GPS data, where millions of location points can be plotted as a single trajectory, it is challenging to view large audio datasets with a single simple representation (Towsey et al., 2014, 2015). Audio recordings are also much more power consuming than GPS. Tags with many gigabytes of storage already exist, so whether the factor limiting recording duration is battery or storage will depend on the capacity of the battery as well as the audio-recording duty cycle and sampling rate. To this end, new research efforts have focused on segmentation and classification algorithms that automatically detect events of interest (Salamon et al., 2016; Stowell, 2018; Stowell et al., 2017; Towsey et al., 2018). The marine bio-acoustics community has been dealing with this challenge for many years because of their immense amount of recordings and they have developed some useful strategies (Johnson, 2014; Johnson et al., 2009). Similarly, the relatively new scientific direction of soundscape ecology or ecoacoustics is addressing comparable issues of large data acquisition and classification (Farina and Gage, 2017; Pijanowski et al., 2011; Ross et al., 2018). As mentioned previously, creating a reference library will often be necessary and help to create useful classifiers for machine learning algorithms (Mac Aodha et al., 2018; Prat et al., 2016).

While telemetry microphones, which transmit data to a receiving unit, are often lighter than logging tags, they have several disadvantages. Most critical is that they suffer from a very limited transmission range, typically not exceeding dozens of metres (Johnson, 2014). As such, telemetry microphones are better for studies in enclosed areas/laboratories or for very small animals with a restricted, small-scale home range. Additionally, when using telemetry microphones in the wild, they can be susceptible to transmission artefacts (e.g. through the tag position in relation to the receiving antenna), which can degrade the recorded signal (Lancaster et al., 1992). Storing the data on the tag instead of transmitting it allows for greater flexibility in experimental design. However, it currently requires retrieval of the tag, either by recapturing the animal or by collecting the dropped tag. In the

future, wireless data transfer through receiver stations in known regular locations like a bat roost or a bird's nest, might simplify data retrieval and reduce handling stress for the animal.

Last but not least, it is imperative to keep in mind any potential effects that tags might have on the animal's welfare and the data itself (Wilson and McMahon, 2006). Here, a distinction between long-term and short-term experiments should be made as, in the latter case, a slightly higher tag weight might be more acceptable. There are quite a few studies on a range of species that have studied the impact of tagging (Barron et al., 2010; Bodey et al., 2018; Lameris and Kleyheeg, 2017; Sergio et al., 2015); however, considerations should be species specific (Vandenabeele et al., 2012) and controls should be performed (Egert-Berg et al., 2018). Particularly when studying flying or swimming animals, scientists should place special focus on tag shape and placement in order to reduce drag and therefore the impact on the animals (Fiore et al., 2017; Jones et al., 2013; Vandenabeele et al., 2014). Moreover, the behaviour of tagged animals always has to be evaluated carefully and critically, because tag deployment might alter the regular behavioural patterns (van der Hoop et al., 2014b). In this respect, studies of mid- to long-term duration are especially valuable as initial aberrant behaviour might be reduced or ceased after habituation to the tag.

Compared with birds, bats seem to be less affected by tags: a weight loss comparison after recapture between bats equipped with a GPS tag and a tiny 0.3 g radio transmitter did not reveal significant differences (Egert-Berg et al., 2018). Furthermore, when bats with GPS tags were caught after several days, they were usually back to capture weight. The behavioural data in these short-term experiments show very wide-ranging movement and a seemingly normal behaviour compared with the literature. However, our understanding of the effects of tagging is still limited and further studies (e.g. control experiments with light radio tagged bats and measurements of energy expenditure) should be conducted wherever possible and will surely come.

Conclusions

For researchers working with acoustically active-sensing animals like bats or toothed whales, the use of acoustics for behavioural analyses outside the communication range comes naturally (e.g. to understand their environmental perception). The advancements in animal-borne acoustic tags will surely increase possibilities for their use in many more animals. While the primary research area will probably be communication between individuals, we hope to have illustrated here a wider range of possible applications for on-board acoustic recordings. Stationary, ground recordings can only give us a snapshot of an animal's life, but with on-board recordings we are now changing our perspective to the animal's view and therefore gain greater insight through continuous monitoring. With ever-changing technology and miniaturization, we are truly witnessing an exciting time for animal behavioural research and the future promises an even wider scope for applications and opportunities.

Acknowledgements

We would like to thank Mor Taub for help with the figures and Shannon Currie for comments. We would further like to thank Rachel Page, Gerald Carter, Edward Hurme, Aya Goldshtein, Lee Harten and Michal Handel for supplying data.

Competing interests

The authors declare no competing or financial interests.

Funding

Y.Y. was supported by the European Research Council (ERC), grant number ERC-2015-StG-679186_GPS-Bat. S.G. was supported by the Minerva Foundation and Sagol School of Neuroscience.

Supplementary information

Supplementary information available online at
<http://jeb.biologists.org/lookup/doi/10.1242/jeb.184689.supplemental>

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Audio 1: Song of a cricket, recorded with a tag on a *Hipposideros armiger* bat in Thailand.

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Audio 2: Calls of a frog, recorded on a *Trachops cirrhosus* bat in Panama.

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Audio 3: Chewing noises, recorded on a *Rousettus aegyptiacus* bat eating fruits in Israel.
Headphones are advised for listening to the faint sounds.

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Audio 4: Wingbeat sounds of *Rousettus aegyptiacus* on a commuting flight in Israel.

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