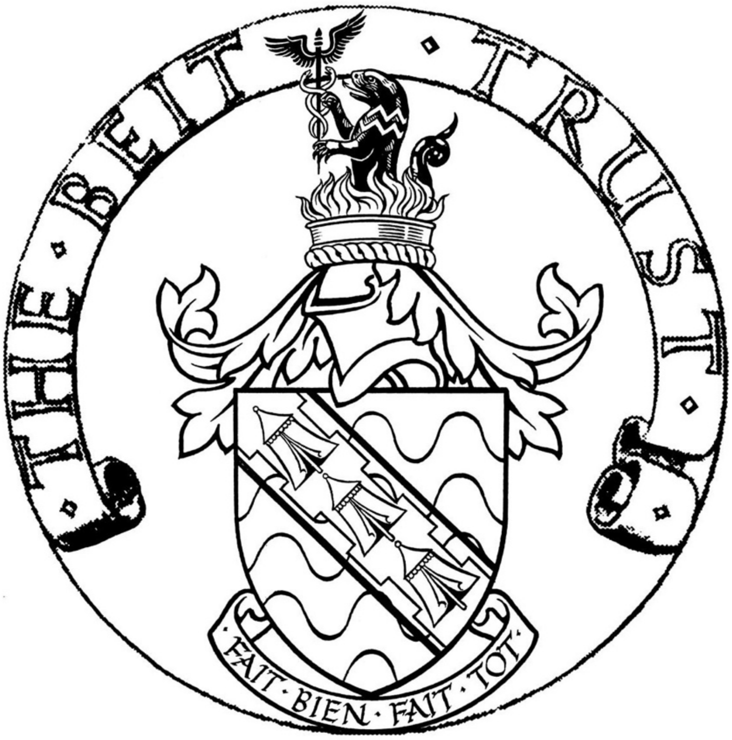
The application of acoustic sensing technology to African lion (*Panthera leo*) ecology and conservation

Matthew C. Wijers

Thesis submitted for the degree of Doctor of Philosophy

St Cross College, University of Oxford

Trinity 2019


THE BEIT TRUST
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Knowledge is like a lion; it cannot be gently embraced.

(South African proverb)

Abstract

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Recent technological advances are revolutionizing the field of ecology and conservation by providing tools and techniques to overcome many of the challenges that have previously limited the understanding of particular animal species and their environments. Significant improvements in acoustic sensing tools have led to an increase in their use for the research and management of vocally active species, particularly those that are difficult to monitor visually and continuously. However, the application of acoustic monitoring methods is often limited by high equipment costs and poor knowledge of many species' vocal behaviour. This is indeed the case for African lions (*Panthera leo*) which are well known for their characteristic roars, but for which an in-depth understanding of vocal behaviour has been difficult to acquire due to the complexities of directly observing and manually recording vocalizations. In this work, I investigate the use of animal-borne and static acoustic recording technology for improving the understanding of lion behaviour and explore its application as a monitoring tool for the species. I begin by testing a novel acoustic biologging approach for recording animal behaviour remotely and find it to be an effective technique for acquiring rich, long-term datasets on lion activities. Coupled with machine learning methods, I then apply this approach to investigate patterns of lion vocal behaviour and show that territorial males are more likely to roar under atmospheric conditions that favour long-distance sound transmission and also adjust their vocal behaviour depending on spatial attributes. Next, I present an affordable, custom-designed passive acoustic sensing tool capable of localizing animal call signals over long ranges (> 1 km) owing to a novel multi-microphone hardware design. Finally, I demonstrate the use of this tool for localizing lion roars and, combined with on-animal audio recordings, discover an individually unique call feature that enables vocal differentiation of individual lions which could facilitate collar-free tracking. Collectively, the findings presented in this thesis highlight the value of acoustic sensing for both understanding animal behaviour and monitoring individual movements over time and space.

Prologue

I have always been passionate about wildlife conservation having spent most of my childhood surrounded by nature. This led me to pursue a BSc in Conservation Ecology at the University of Stellenbosch where I received valuable training in ecological concepts and research techniques but, admittedly, had little exposure to the computational tools and approaches that are currently revolutionizing the field of ecology. Recent technological advances such as the miniaturization of electronic components and the development of powerful machine learning algorithms have provided unique opportunities for scientists to study the natural world in ways that were previously unimaginable. Recognising these opportunities, I proposed this project which aimed to explore the conservation and research applications of novel audio recording tools. Consequently, this work was largely focused on the interface between technology and ecology. In order to explore this relatively new theme effectively, I spent a considerable amount of time learning concepts and skills more commonly associated with computer science.

Working with new technology is exciting, particularly when first reviewing the data retrieved from devices that offer insight into aspects of animal's lives that are yet to be explored. These are the moments that motivate and drive me as a researcher. Being able to successfully retrieve the necessary data from these novel devices requires many hours of design and preparation to ensure that projects run smoothly and effectively. Inevitably, however, there are frequent occasions when field work does not go according to plan. The data collection procedure may prove to be ineffective, devices can be destroyed by the animals themselves and electronic components can malfunction. It is during these moments that one learns the most, not only about the issue being faced, but about one's own capacity to persevere and remain positive in times of failure. For me, this test was most pronounced when a full set of static audio recording devices, that we had designed and built, malfunctioned in a single night, causing significant damage to the electronic components. Without any devices to collect the data required, the project was in jeopardy. I subsequently spent many days trying to deduce the cause of the failures while also arranging for spare components to be sent to me from Oxford. Once these spares arrived, I attempted to repair each device; carefully resoldering resistors and capacitors using creative techniques in desperate hope of restoring device functionality. Thankfully, the repairs proved to be effective and enabled me to continue with project, albeit behind schedule. This was not the only time I encountered technical difficulties with the new tools being tested. Over the course of this research I also worked on developing a second generation acoustic biologger which would be attached to existing lion GPS collars and record audio and movement data for a period of up to six months (a significant improvement on the first generation biologger described in this thesis). Despite several iterations, we continually faced challenges with both hardware and software functionality which meant that these devices could not be used for this project. Although these continual setbacks were frustrating, the lessons learned have paved the way for progress and development on a separate project.

Having initially been unaware of the challenges associated with developing new technological tools, one of the main lessons I take from this research is that failures are an inevitable but necessary part of development and should be considered as opportunities to advance one's skills and knowledge. I would therefore encourage ecologists embarking on a similar project involving technology, to take advantage of collaborative partnerships with the technical disciplines and to persevere through the challenges. While some argue that technology is creating a disconnect between ecologists and their study systems, I believe that the tools developed through such collaborations have immense potential to improve our understanding of natural systems and thereby facilitate better, data-driven decisions for wildlife conservation.

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I am indebted to my supervisors, Professor David Macdonald, Dr Andrew Loveridge and Professor Andrew Markham. David, I admire your achievements and commitment to wildlife conservation across the world. Thank you for believing in me as a young graduate and for your guidance and support over the past four years. I feel privileged to have been part of the WildCRU. Andrew L., thank you for giving me the opportunity to volunteer with your team in Hwange. It was those experiences that convinced me to pursue a career in wildlife conservation. I am also extremely grateful for all your input on my project as well as your advice on field work and lion conservation in general. Andrew M., you have supported me immensely. Thank you for the many hours you dedicated to our projects and for your patience with my technical naivety. I learned so much from you and thoroughly enjoyed building gadgets under your watch.

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Hunt and Justin Seymore-Smith, thank you for your friendship, assistance and words of advice throughout my DPhil journey. Dr Dawn Burnham, Jennifer Spencer and Emma Stewart-Wood, thank you very much for your administrative support and commitment to my project.

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1 General Introduction

1.1 Introduction

Over the course of evolution, mammals have evolved complex sensory systems to extract information from internal and external environments. Although many important evolutionary developments have occurred in olfaction and vision, the changes in mammal auditory form and function are thought to have been the most pronounced (Stebbins, 1980). Originating as simple, substrate vibration detectors, the complex hearing adaptations of extant mammals, such as echolocation in bats and the discrimination of subtle acoustic variations by primates, highlight the dramatic transformations that have occurred over time (Stebbins, 1980).

Animal vocal communication is considered to have evolved in synchrony with auditory perception as the consequence of the emission of a particular signal is entirely dependent on the receiver's mechanism for decoding the transmitted signal (Wiley, 1983). A commonly accepted approach to understanding the evolution of communication considers signalling to be a manipulative behaviour whereby selection favours individuals that use signals to manage the behaviour of others in their best interests (Owings and Morton, 1998; Wiley, 1983). Although a signaller cannot directly alter the way in which a signal is processed by the receiver's auditory system, it can change the detectability of its signal (Wiley, 1983). Acoustic communication has therefore evolved in such a way as to increase the reliability of detection and discrimination of signals by the intended receivers. This has been achieved by increasing the contrast between signal and noise, incorporating redundancy through repetition to reduce the chances of missed detection and including alerting components to attract attention (Wiley, 2013).

In the study of animal communication in general, particular attention has been paid to determining whether signals evolved to be “honest” (a signal reliably reflects the quality of the signaller) or “dishonest” and, if signals are honest, what mechanisms maintain this honesty over the possible advantages of deception (Searcy and Novicky, 2006). Maynard Smith and Harper (1995), make the distinction between cost-added signals (originally referred to as “handicaps” by Zahavi (1975)) and indices, each of which, provide possible explanations for the evolution of honest signalling. The former refers to strategic signals that incorporate a greater production cost than is required to transmit the information while the latter refers to signals that are directly associated with a specific quality of the signaller and cannot be “faked”. Animal vocal signals have been shown to contain honest cues to individual characteristics (e.g. size and age) and identity and therefore function as indices. The transmission of this information can be explained by the source-filter theory (Fant, 1960) which describes how the characteristics of a vocalization and the resulting spectral envelope of the signal arise from anatomical variations in the larynx (source) and the cavities of the vocal tract (filter).

African lions are well known for their characteristic long-distance vocalizations which are highly conspicuous and repetitive, enabling detection over large distances (Stander and Stander, 1988; Ramsauer, 2005). This adaptation in vocal communication is a core component of sociality in the species and allows individuals to advertise ownership of large territories and maintain group cohesion (Ramsauer, 2005). The same features that facilitate effective communication between individuals can also be exploited by wildlife researchers and conservationists to remotely monitor species populations.

In order to design and implement effective acoustic monitoring systems, it is important to understand animal vocal behaviour and how certain social and environmental factors might influence an individual's decision to vocalize or remain silent. In addition, an understanding of the information encoded in vocal signals can further improve acoustic surveys by allowing inferences to be made about individual animal characteristics such as identity (Terry et al., 2005), sex (Rendall et al., 2004) and size (Charlton et al., 2013). Knowledge of the acoustic features that enable vocal discrimination of individual animals is particularly valuable as several modern survey methods rely on reidentification of individuals over time.

One of the main factors limiting the use of acoustics for species monitoring is the difficulty in obtaining sufficient data to investigate animal vocal attributes and behaviour (Rocha et al., 2016). Many vocally active species are nocturnal or inhabit environments that are difficult to access and therefore the use of manual audio recording methods in these scenarios is often ineffective. Recent technological innovations have, however, provided opportunities to capture acoustic data in a variety of environments. One of the most ambitious recording locations is, perhaps, directly on an animal. Animal-borne recording devices provide an unparalleled opportunity to record high quality animal vocal signals. In addition, the acoustic information obtained from an animal's surrounding environment can offer valuable insight into animal behaviour as specific activities are often characterized by distinct sounds (Lynch et al., 2013). For example, the repetitive thuds of an animal's footfalls are clearly indicative of locomotion while the sound of bone crunching and lapping water are typical of feeding and drinking behaviour.

The implementation of acoustic surveys is also reliant on specialized equipment. The development of the autonomous recording devices used for this purpose has received considerable attention over the last decade. Although commercially available recorders are effective and reliable in most cases, their expense can be prohibitive. Recently, several low-cost, custom-designed devices have been unveiled and are increasing in popularity amongst field biologists (Hill et al., 2018; Whytock and Christie, 2017). One functional limitation of these new innovations, however, is their inability to localize sound signals. Sound localization provides valuable information on the relative position of vocalizing animals and can potentially facilitate tracking of individual animal movements. Several publications have highlighted the need for further development of low-cost acoustic recording systems that provide information on sound source location (Kalan et al., 2016; Marques et al., 2013).

Acoustic sensing technology has immense potential to improve our understanding of animal behaviour (e.g. constructing time budgets or uncovering patterns of vocal behaviour) and supplement conventional population monitoring methods. The work in this thesis demonstrates the application of this technology to African lions and offers insight into the species' vocal behaviour.

1.2 The role of technology in wildlife research and monitoring

Wildlife tracking and monitoring technologies are thought to have evolved from bird banding in the 1800s, although, the first record of a bird carrying metal rings on the tarsus originates from Germany in 1710 (Lincoln, 1921). The first rigorous study involving banding was conducted on storks, teals and starlings in 1899 by Herr Mortensen of Denmark who is considered the pioneer in scientific bird banding (Lincoln, 1921). Half a century later, the Craighead brothers developed the first radio-collars which were used to study grizzly bears (*Ursus arctos horribilis*) in Yellowstone National Park (Craighead and Craighead, 1965). The collars were designed to emit a high frequency radio pulse which could be detected using a radio receiver and directional antenna. Prior to their work, little was known about the behaviour of wild grizzly bears as the species is nocturnal and generally inhabits areas with thick vegetation and rugged terrain and are therefore difficult to observe. The introduction of these devices revolutionised their study, allowing collared individuals to be located from distances of 15-20 miles and revealed information on prehibernation and denning activities (Craighead and Craighead, 1965, 1972). Since then, the field of biotelemetry (a collective term for the techniques used to remotely record data from free-living animals) has advanced rapidly, further transforming the way in which researchers acquire information. Today, the availability of satellite tracking and archival data-loggers which provide automated data collection and in some cases, wireless transmission to a central database, allows researchers to receive data directly from their study animals in near real time from almost anywhere in the world (Brown et al., 2013). Apart from the convenience offered by these innovations, other advantages include the ability to record data at a high frequency and with unprecedented levels of precision. Perhaps the greatest advantage, however, is the opportunity to collect data that is not limited to or biased by the ability of a human observer (Hebblewhite and Haydon, 2010). Like the grizzly bear, species that are typically elusive, nocturnal or wide-ranging have previously been challenging to study but the advances in sensor technology have provided solutions for monitoring a range of species from small birds (Hernández-Pliego et al., 2017) to large pachyderms (Soltis et al., 2012).

Despite the many advantages offered by newly developed tools, the financial costs associated with commercially available devices are often prohibitive, particularly for smaller projects with limited funding. GPS collars for large terrestrial carnivores and ungulates range in price from US$ 2000 – 8000 depending on collar features with an additional monthly expense for satellite data transfer subscriptions (Hebblewhite and Haydon, 2010). Other static data recording tools such as camera traps and acoustic recording devices are also costly with prices exceeding US$ 400 for medium-range units (Rovero et al., 2013), particularly considering that a large number need to be purchased in order to carry out meaningful surveys. Although these costs are likely to be justified, due to the time and expertise required to develop such tools, the use of these technologies will generally be restricted to well-funded studies.

1.2.1 Open source and custom-designed tools

The term 'open source' refers to a product that is distributed free of charge with permission to use the design documents or code (Lerner and Tirole, 2001). The open source movement, initially associated with software design, emerged as a result of the rapid expansion of the internet and accessibility of computers. More recently, the collaborative efforts have extended to electronic hardware development enabling the production of bespoke data collection devices. Several software and hardware innovations born from this movement have provided highly effective solutions for many ecological studies and through continued development are becoming commonplace alongside proprietary products. QGIS (QGIS Development Team, 2019), which was first released in 2002, is an example of a popular, open source geographic information system that is often used for spatial analyses and mapping applications in ecology (Deacon and

Smit, 2017; Habel et al., 2015). Similarly, the statistical programming language, R (R Development Team, 2019), first developed in 1993, is now one of the top five platforms for data analytics (Ihaka and Gentleman, 1996; Ozgur et al., 2017). From a hardware perspective, numerous data recording tools have been designed following the introduction of open source micro-controllers such as the Arduino (Arduino LLC, Scarmagno, Italy) and Rasberry Pi (Raspberry Pi Foundation, Cambridge, UK). These devices are essentially tiny, low-cost computers that run programs written by the user (Fisher and Gould, 2012). Many auxiliary sensor components are also available as add-ons (e.g. microphones, GPS etc.) which can be selected based on the intended function of the device. The freedom to select sensor features and define the functionality of a device has provided opportunities to collect data previously beyond the reach of researchers. Furthermore, the lower costs associated with custom-designed devices allows for the production of a larger number of units which effectively increases study sample sizes (Greenspan et al., 2016).

One restriction associated with the use of these modular circuit boards is their fixed size and power consumption. Wildlife research applications involving the attachment of devices to study animals are limited by size, mass and battery capacity and therefore require circuit boards that are extremely light and highly efficient. For this reason, several researchers have designed their own devices from scratch, some of which weigh less than 1 gram and can operate for up to 40 days on a single, small battery (Shipley et al., 2018). The production of such devices generally requires greater software and engineering expertise and are consequently developed through collaborations between ecologists, engineers and computer scientists. These transdisciplinary partnerships have led to the production of several other popular ecological tools such as the Audiomoth, an open source acoustic detector (Hill et al., 2018) and the Daily Diary, an animal movement and tracking tag (Wilson et al., 2008). Carey et al. (2019) highlight the value and importance of collaborations between ecologists and computer scientists in particular, suggesting that the field of ecology is likely to benefit substantially from the additional technical expertise especially in relation to data acquisition and processing. The work described in this thesis is the direct result of a partnership between the Wildlife Conservation Research Unit (WildCRU) and the Department of Computer Science and further exemplifies the benefits that can accrue through similar collaborations.

1.2.2 Biologging

The term 'biologging' refers to the practice of attaching miniaturized electronic data recorders to animals for the purpose of collecting information on movement, behaviour, physiology and surrounding environment (Rutz and Hays, 2009). The ongoing development of the data recorders, collectively known as biologgers, has facilitated incredible biological discoveries. Bishop et al. (2015), for example, used implantable devices to uncover an energetically advantageous flight strategy in bar-headed geese (*Anser indicus*) migrating across the Himalayas. The ability to record information in harsh, inhospitable environments (e.g. polar regions and deep marine habitats) is one of primary advantages of this technology and is increasing our understanding of rare and elusive species that have previously been impossible to monitor (Block et al., 2011; Cooke, 2008). Biologgers also provide significant advantages over direct observation in cases where human presence is likely to influence animal behaviour and thereby introduce potential biases to experimental studies (Caine, 1990). These innovative tools have been used to address a variety of research themes (Rutz and Hays, 2009) which include the study of global climate change and its implications for animal conservation (e.g. measuring physiological plasticity in aardvarks (*Orycteropus afer*) to predict possible consequences of a warmer climate (Rey et al., 2017)), examining animal adaptations using controlled experimentation (e.g. How do birds orient over familiar terrain? (Biro et al., 2007)) and comparing life-history traits across populations and species (e.g. How does migratory behaviour vary between white stork (*Ciconia ciconia*) sub-populations (Flack et al., 2016)).

A broad range of biologgers has been designed, often with specific sensors for particular research purposes. One of the most common measurements recorded by these devices is body acceleration which is determined using an electro-mechanical instrument called an accelerometer. Between 2002 and 2012, the number of published studies using accelerometers in animal behaviour research increased exponentially (Brown et al., 2013). In many cases, acceleration is measured along three axes (Fig. 1.1) which, together, can provide a realistic representation of three-dimensional body movement and posture (Shepard et al., 2008). Another sensor that is a common component of biologger devices is the magnetometer which detects changes in orientation relative to the Earth's magnetic field. Although not as widely used as accelerometers, the sensitivity of modern tri-axial magnetometers allows for fine scale calculations of animal heading and angular rotation that are often associated with particular behaviours (Williams et al., 2017). By combining both these sensor types in biologger designs and capitalizing on their different frames of reference, researchers are able to acquire a rich dataset on animal movement.

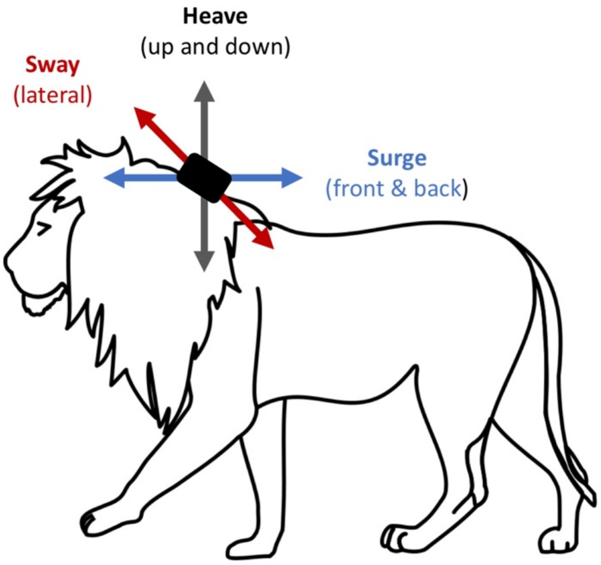

Figure 1.1 Three-dimensional body acceleration measured by an accelerometer.

In most cases where biologgers have been used to investigate animal behaviour, simple measures of acceleration or magnetic heading are not of direct relevance to the study. Generally, raw biologger data needs to be "converted" into animal behavioural states through a calibration process. Calibration involves mapping observations of behaviours of interest to corresponding movement data in order to be able to associate particular patterns of acceleration or angular rotation with particular behavioural states. Ground-truth observations required for calibration are typically obtained from time synchronized video recordings of the animal (Kawabata et al., 2014; Lush et al., 2015; McClune et al., 2014).

In some studies, microphones have been included in biologgers and have allowed for behaviour determination directly from acoustic cues (Couchoux et al., 2015; Insley et al., 2008; Lynch et al., 2013). Continuous audio recordings could therefore provide an alternative and valuable source of ground truth for calibration, eliminating the need for video recorded observations that require visual contact with the animal. Apart from the calibration benefits of acoustic biologgers, on-animal audio recordings can also provide valuable information on animal vocal behaviour that often cannot be acquired using manual methods (Couchoux et al., 2015).

1.2.3 Big data and machine learning

Although the development of biologgers has created opportunities for data acquisition and ecological research that previously never existed, it has brought with it new challenges associated with data management and interpretation. Devices often generate millions of multidimensional data points that are difficult to process. These challenges are however, not unique to ecology; extremely large, complex datasets, often referred to as 'big data' are becoming more common in all domains of science owing to the recent advances in networking, data storage and data collection technologies (Wu et al., 2014). Analyses of such datasets are typically beyond the capabilities of conventional software tools and therefore require innovative management and processing approaches. A key challenge for researchers is being able to extract relevant information from highly dimensional data in reasonable time frames. The most effective solutions to this problem are often provided by machine learning techniques.

Machine learning (ML) is a branch of computer science that involves the development of algorithms capable of making data-driven decisions (Thessen, 2016). These algorithms are generally used to make predictions based on complex patterns in the data. The use of ML techniques is relatively common in the field of ecology and has been applied in studies investigating habitat suitability (Garzón et al., 2006), animal behaviour (Valletta et al., 2017) and the classification of animal calls (Acevedo et al.,

2009) amongst others. More recently, advanced ML methods for computer vision are being used to track illegal wildlife trade on social media (Di Minin et al., 2018) and to classify camera trap images automatically (Tabak et al., 2019).

Machine learning methods can be broadly separated into three groups based on the learning approach: supervised, unsupervised and reinforcement learning. Supervised methods model the relationship between a set of known inputs and outputs and therefore require labelled ground truth data. Conversely, unsupervised methods are used to infer patterns in the data without reference to known outcomes (Olden et al., 2008). In reinforcement learning, the information available to the model only provides an indication of whether an action is correct or not and is used to achieve a solution through trial and error (Jordan and Mitchell, 2015). Several ML techniques within the supervised and unsupervised categories are commonly applied in ecological studies, a list of which is shown in Figure 1.2. The use of reinforcement learning is, however, relatively uncommon in ecology and is therefore not discussed further.

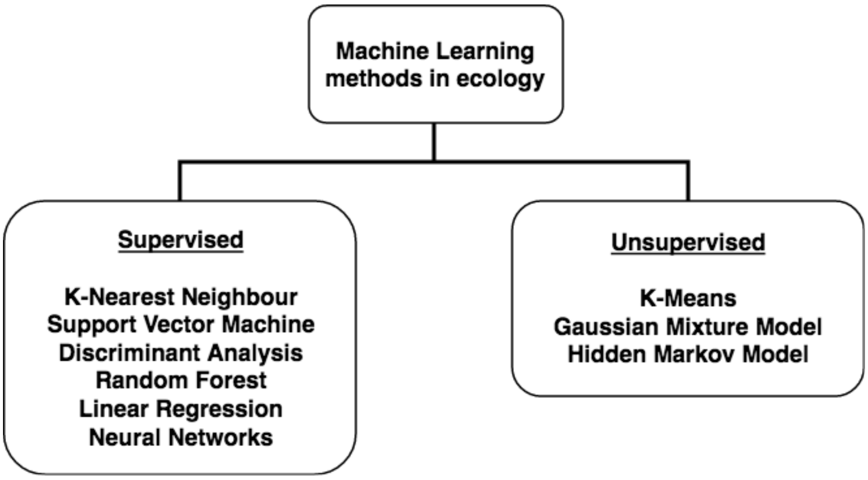

Figure 1.2 Machine learning methods (supervised and unsupervised) commonly used in ecology.

Random forest and hidden Markov models are the primary methods used for data classification in this thesis and therefore warrant further description.

The random forest (RF) method is a popular classification algorithm developed by Breiman (2001). As the name suggests, RFs consist of a number of individual decision trees. Each tree iteratively splits the data based on a rule resulting in the divided groups being more homogenous than the group before (Thessen, 2016). The output of each decision tree can vary considerably depending on the training (ground truth) data and therefore a single tree alone is likely to offer poor predictive performance. Combining the results of multiple trees, however, can improve prediction by taking the majority vote over all predictions of each tree in the forest (Crisci et al., 2012). RFs are computationally fast, robust to outliers and can deal with small sample sizes and mixed data types (Cutler et al., 2007).

A hidden Markov model (HMM) is a statistical tool for modelling sequential data and is widely used in speech recognition systems. In essence, an HMM maps ‘hidden’ model states to a sequence of observations. Although considered an unsupervised model, for many applications HMMs are trained in a supervised manner (Tamposis et al., 2019). Based on a number of training examples, a set of parameters that maximize the joint probability of sequences and class labels are estimated using an Expectation Maximization algorithm called the Baum-Welch algorithm (Baum et al., 1970; Tamposis et al., 2019). Single models are trained for each class which are then used to estimate the likelihood that an unknown sequence matches the underlying model. The model with the highest likelihood is assumed to be the class associated with the test sequence.

1.3 Acoustics and ecology

The recording and analysis of acoustic signals is a common research approach in biology and has been used to address a diverse range of research topics such as animal communication (McComb et al., 2003), animal sound production and auditory physiology (Garstang, 2004), acoustic ecology (Nowacek, 2005) and the evaluation of acoustic tools and methods (Hill et al., 2018). In general, all studies investigating aspects of sound in relation to animals are encompassed in a single broad branch of biology known as bioacoustics.

1.3.1 Passive acoustic monitoring

One particular discipline within the field of bioacoustics that is progressing rapidly as a result of recent technological advances is passive acoustic monitoring (PAM). Traditional methods of monitoring and surveying wildlife populations have generally relied on visual observations of target species coupled with distance sampling techniques (Buckland et al. 2001) or involved methods of physical capture and marking of individual animals (Nichols, 1992). Many species, however, produce sounds to communicate with conspecifics and in so doing reveal information relating to their location and species identity. Passive acoustics offers opportunities to exploit the information available from emitted vocal signals to monitor the distribution and occurrence of populations over time. PAM is particularly advantageous for species that are elusive, visually cryptic, or difficult to capture (Marques et al., 2013). It is therefore no surprise that the majority of studies which have relied exclusively on passive acoustics have been conducted in marine environments, particularly as sound propagation is more efficient in water than in air (Marques et al., 2013). Although PAM related research has not been as common in terrestrial environments, new microphone, processor and data storage technologies have facilitated the development of powerful, autonomous acoustic recording tools for land-based applications. The commercially available ‘Song Meter’ range offered by Wildlife Acoustics Inc., Massachusetts, USA, is a case in point and has been the equipment of choice for a large number of bioacoustics studies (Adams and Kwiecinski, 2018; La and Nudds, 2016).

PAM has a variety of ecological applications ranging from relatively simple acoustic surveys determining species presence or absence (Celis-Murillo et al., 2012) to more complex uses involving the acoustic tracking of individual animals (Spillmann et al., 2017). The technique has also been implemented in law enforcement initiatives aimed at reducing environmental disturbances such as logging and poaching (Astaras et al., 2017). While PAM is frequently used in species management related research it has also been used to provide insight into species biology such as determining the relationship between calling activity and daily weather conditions to predict the potential implications of climate change (Ospina et al. 2013).

Key factors to consider when designing acoustic surveys are the number and arrangement of recording units. Single, isolated recording devices are typically used to investigate community structure metrics such as species richness and composition (Blumstein et al., 2011). In some cases, however, researchers may also wish to know the specific location of a sound source (e.g. to enable multiple individuals to be distinguished from one another) which can only be achieved using an array of multiple, synchronized recording units. In the latter case, the location of the source can be estimated by calculating the time delay and difference in signal intensity between recorders at known locations.

1.3.2 Vocal individuality

A large number of studies have been dedicated to investigating the information content of animal vocal signals, particularly regarding the presence of individually distinct features in certain call types (Clemins and Johnson, 2005; Ji et al., 2013; Root-Gutteridge et al., 2013). Results of these studies have shown that vocal individuality is a characteristic of many species and is likely a consequence of the subtle morphological variations in vocal apparatus between individuals (Reby and McComb, 2003). Mammal vocal production is thought to consist of two stage process known as the source – filter theory (Fant, 1960). According to this theory, calls are created by the larynx (the source) which is a cartilaginous structure situated in the lower part of the throat (Taylor and Reby, 2010). Folds of membranous tissue, known as the vocal folds, extend across the interior of the larynx forming the glottis. It is here that sounds are produced through vibration of the vocal folds. The rate of vibration is dependent on the length and mass of the vocal folds which ultimately determines the fundamental frequency of the sound wave (Taylor and Reby, 2010). Following production of the vocal signal, the sound then passes through the air passages of the vocal tract (pharynx, mouth and nasal cavities). Here, the sound is filtered by selective enhancement and dampening of specific frequency ranges resulting in energy peaks in particular frequency bands that are called 'formants' (Fitch, 2000; Taylor and Reby, 2010). Individual variations in the fundamental and formant frequencies of animal calls can therefore be attributed to differences in the length and shape of the vocal tract. The extent to which the fundamental and formant frequencies encode individuality is, however, not consistent across species. For example, the individual calls of red-bellied lemurs (*Eulemur rubriventer*) are best distinguished by variation in the formant frequencies (Gamba et al., 2012), while the howls of eastern grey wolves (*Canis lupus lycaon*) appear to encode individual identity in the fundamental frequency (Root-Gutteridge et al., 2013). In some species, such as fallow deer bucks (*Dama dama*), both the fundamental and formant frequencies contribute towards vocal individuality (Reby et al., 1998).

The presence of individually unique features in animal vocal signals facilitates vocal recognition of conspecifics. This function is essential for social species which rely on the reception of identity information to locate and maintain contact with group members (Ramos-Fernández, 2005). Vocal recognition is also important for territorial species that use vocalizations to advertise territorial boundaries and helps to ensure adequate spacing between potentially hostile neighbours (Frommolt et al., 2003). While vocal individuality has clear benefits for animals, individually unique signals can also be valuable for wildlife conservation and management. Call features that encode identity can be used as non-invasive "marks" allowing individuals to be reidentified over time. For example, Delport et al. (2002) investigated the territory turnover of African wood owls (*Strix woodfordii*) using recordings of owl hoot-calls collected over a 12-year period. Their study was entirely dependent on the accurate classification of calls which enabled identification of specific individuals that were otherwise difficult to detect visually.

1.3.3 Animal vocal behaviour

Research investigating the spatial patterns of animal vocal behaviour is scarce mainly due to the difficulty in determining the accurate locations of calling individuals, particularly for nocturnal species (Delgado and Penteriani, 2007). The intensity of animal space use and territorial behaviour is likely to vary within a home range considering that certain habitat features (e.g. den sites and areas of high food availability) may be more valuable for survival and reproduction than others (Burt, 1943). Species that rely on vocalizations to advertise territory ownership are known to vary their calling rates according to their location (Darden and Dabelsteen, 2008; Delgado and Penteriani, 2007; Sunde and Bolstad, 2004).

In addition to spatial factors, animal vocal behaviour may also be affected by environmental conditions. Sound propagation through the air is influenced significantly by the acoustic features of the signal itself as well as the atmospheric conditions and physical features of the environment. In general, the attenuation and degradation of an acoustic signal will increase with increasing distance from the source as a result of energy absorption and wave deflection from objects and gradients within the medium (Wiley and Richards, 1978). The rate of attenuation is, however, dependent on the frequency of the sound signal; higher frequency signals are more rapidly absorbed compared to lower frequency signals. Furthermore, variations in atmospheric conditions such as temperature, humidity and turbulence alter the state of the air column through which sound waves propagate. Larom et al. (1997), suggested that the predictable daily fluctuations in these factors create periods of enhanced sound transmission in which animals are likely to concentrate their vocal activity. Wolves, for example, refrain from howling in turbulent conditions and are therefore more likely to vocalize during calm periods of the day (Rocha et al., 2016).

When integrated with acoustic sensing and recording tools, knowledge of animal vocal behaviour and individuality is particularly valuable for monitoring vocally active species. With the recent technological advances highlighted earlier in this chapter, there exists considerable potential for acoustic sensors to be incorporated into and improve current methods of monitoring African lions (*Panthera leo*). In order to achiever this, however, it is necessary to understand how lions convey identity information in their calls and to identify factors that influence vocal behaviour. Further work is also required to develop an affordable passive acoustic monitoring tool that is capable of signal localization in order to facilitate tracking of individual lion movements.

1.4 The African lion

1.4.1 Description and ecology

The African lion, a member of the Felidae family, is the largest terrestrial carnivore on the continent (Fig. 1.3). Adult males weigh approximately 190 kg and possess impressive manes; a feature lacking in female lions which are also much smaller, weighing only 120 kgs. This sexual dimorphism is a unique characteristic of the species amongst the felids (Macdonald et al., 2010). An additional attribute distinguishing lions from other members of the family is their highly gregarious nature. Dominant males typically form coalitions of between 1 and 9 individuals and closely guard groups of 1 to 18 females and their dependent offspring (West and Packer, 2002). The overall composition and ranging behaviour of these social groups, known as prides, remain relatively constant over time although within-pride fission-fusion dynamics are common (Schaller, 1972). Lion home-ranges are typically between 50 and 700 km^2 in area and vary according to pride size as well as prey abundance and distribution (Loveridge et al., 2009). In arid ecosystems such as the African Kalahari region, home ranges can be as large as 4300 km^2 (Zehnder et al., 2018).

Figure 1.3 A female (left) and male (right) African lion

Lions are highly territorial and both male and female members of the pride cooperate to defend access to resources. Although territorial defence can involve physical encounters, challenges often lead to serious injury or even death (Schaller, 1972). Consequently, lions have evolved alternative strategies, including olfactory and acoustic communication, to advertise territory ownership without physical confrontation (Ramsauer, 2005). Scent marking generally occurs throughout the entire territory but particularly along passages that are frequently used for travel in order to maximize detection by other individuals (Ramsauer, 2005). Vocal signalling, by contrast, is more conspicuous and acts as an instant threat display to neighbouring animals. Lion vocalizations, known as roars, are loud, low frequency calls that can travel distances of several kilometres. A single roar consists of a series of moans followed by several deep-throated roars and a terminating sequence of grunts (McComb et al., 1994). In addition to advertising territorial boundaries, lion vocalizations are also important for maintaining contact with distant companions.

Several studies have explored aspects of lion vocal communication. Schaller (1972), was one of the first to document the nocturnal temporal patterns of lion vocal behaviour from his observations of prides in the Serengeti. Almost two decades later Stander and Stander (1988) carried out a detailed investigation of the characteristics of lion roars in Etosha National Park which corroborated Schaller's observations. Following their pioneering work on the subject, further studies have been carried out on the functional role of the roar which have revealed that lions can distinguish between familiar and unfamiliar vocalizations and are also able to assess group size from roar choruses (Gilfillan et al., 2016; McComb et al., 1993, 1994). Vocalizing has also been shown to be a flexible behaviour that is partly driven by the costs and benefits of revealing information to potential eavesdroppers. This is evidenced by the 'low profile' behaviour of nomadic males which tend to remain silent to avoid detection by aggressive territorial males (Grinnell and McComb, 2001). Despite the advances in acoustic recording technology that have arisen over the past two decades, only one study has attempted to investigate the acoustic features (e.g. fundamental frequency) of lion roars and the potential information encoded by certain attributes (Pfefferle et al., 2007). A possible reason for the lack of research on this topic, as mentioned by Pfefferle et al. (2007), is the extreme difficulty associated with manually recording lion roars which are predominantly emitted at night when visibility is poor.

1.4.2 Conservation status and monitoring

The African lion is classified as vulnerable by the IUCN Red List as a result of an overall population decline of 43% between 1993 and 2014 (Bauer et al., 2016). This figure, however, conceals a much more drastic decline of 60% in populations outside of Botswana, Namibia, South Africa and Zimbabwe (Bauer et al., 2016). In these southern African nations, lion numbers have increased by 12% as a result of population growth in most small, fenced reserves (Bauer et al., 2015). In some countries such as Angola, Central African Republic and South Sudan, knowledge of the status of lion populations is scarce.

Robust population assessments are vital for the development of effective lion management and conservation strategies. In general, lion population estimates have been obtained using either spoor transect metrics (Funston et al., 2010; Stander, 1998), call-up surveys (Ferreira and Funston, 2010; Midlane et al., 2015) or forms of intensive monitoring that incorporate mark-recapture models (Castley et al., 2002; Rosenblatt et al., 2014). All three methods have their inherent advantages and disadvantages, but in most cases, these methods are labour intensive and can take several weeks or months to complete depending on the size of the area (Elliot and Gopalaswamy, 2017). Autonomous data collection tools such as camera traps can reduce the human effort required to collect data and have recently been used to estimate lion density in the Ngamiland District of northern Botswana (Rich et al., 2019) and the Serengeti National Park in Tanzania (Cusack et al., 2015). Although all conventional lion survey methods involve visual detection of animals or their cues, Rodgers (1974) attempted to calculate lion density from vocalizations by listening for roars along transect routes. With the ongoing development of autonomous acoustic recorders, passive acoustic monitoring may, in future, be used to supplement conventional survey methods. Considerable research and development are, however, still required to produce reliable tools and methods for monitoring and assessing lion populations using acoustic approaches.

1.5 Study area

1.5.1 Location and history

The research described in this thesis was conducted in the Bubye Valley Conservancy (BVC), located in southern Zimbabwe between latitudes 21.209° and 21.851° South and longitudes 29.798° and 30.521° East (Fig. 1.4). The BVC, measures approximately 3400 km^2, is the largest privately-owned wildlife area in the country and also one of the largest in southern Africa. Prior to the establishment of the Conservancy in 1994, cattle ranching was the primary land use in the area. Wildlife species, including lions, that competed with or preyed upon cattle were actively eliminated, although some species such as leopards (*Panthera pardus*) remained present at low densities. A devastating drought that occurred in 1992 affected the future viability of the local cattle industry and led to the sale of a number of properties. Several neighbouring ranches were subsequently purchased by local and international investors with the purpose of establishing a wildlife enterprise based on a sustainable use model. A double, electrified fence was erected along the perimeter of the newly defined conservancy to comply with veterinary regulations and prevent human wildlife conflict.

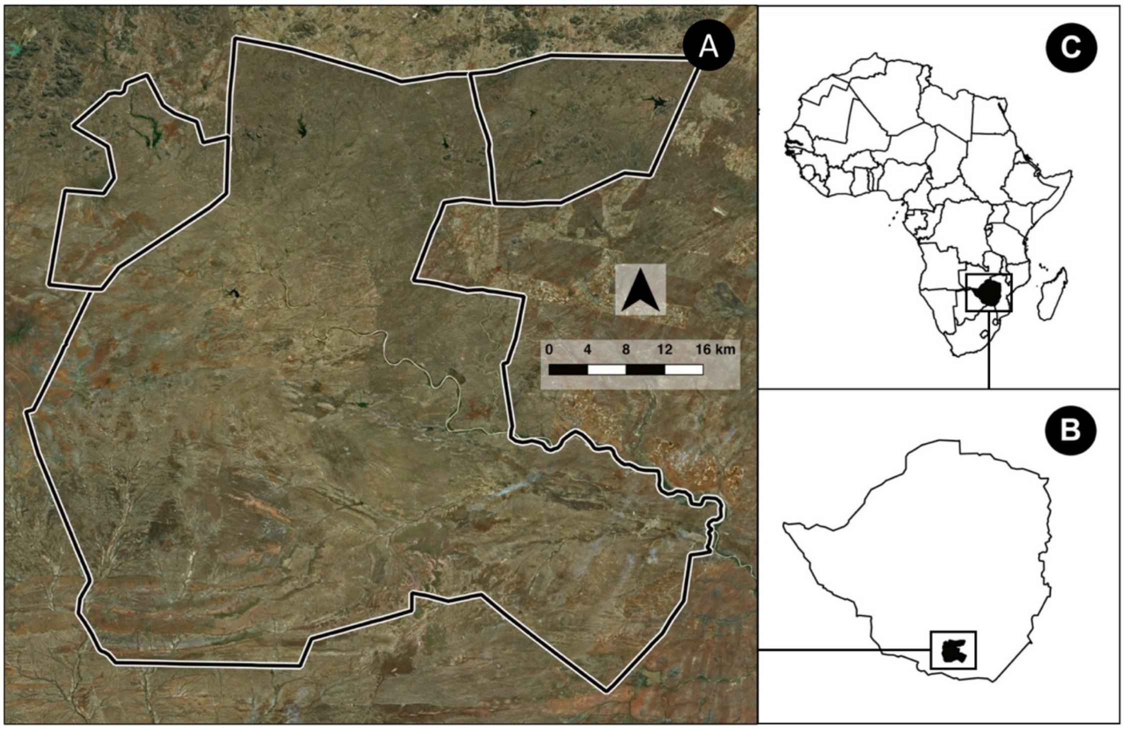

Figure 1.4 The Bubye Valley Conservancy (A) with position in relation to Zimbabwe (B) and Africa (C).

1.5.2 Wildlife

A variety of indigenous megafauna were introduced to the Conservancy in the year following its establishment. The BVC now supports high densities of herbivore species, the most abundant of which include plains zebra (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*) and greater kudu (*Tragelaphus strepsiceros*). The abundance of prey has also facilitated a rapid increase in the large carnivore species populations which include, in decreasing order of density, brown hyaena (*Hyaena brunnea*), lion, spotted hyena (*Crocuta crocuta*) and leopard (*Panthera pardus*). The initial lion population in 1997 consisted of 13 individuals that were introduced from South Africa and additional 4 young animals that broke into the Conservancy during the same period. A recent survey carried out in July 2018 estimated the lion population density to be approximately 0.123 ± 0.044 km^{-2} which equates to 325 individuals (M. Wijers, unpublished).

1.5.3 Vegetation and surface water

The vast majority of the BVC consists of mopane (*Colophospermum mopane*) woodland savannah with some riparian woodland, characterized by *Acacia* species, occurring along seasonal river lines. The Bubye river, which runs through the centre of Conservancy, is the largest watercourse and generally flows in the late wet season between December and March. Other smaller rivers exist in the south western section but only flow for a few days following heavy rain. Water is retained in numerous small pools along these rivers until the middle of the dry season. In addition to the natural surface water, many artificial sources are provided from boreholes distributed across the Conservancy.

1.5.4 Climate and topography

The BVC, situated in the semi-arid lowveld region of Zimbabwe, receives low annual rainfall of approximately 350 mm between December and March (du Preez, 2014). Maximum daily temperatures during the summer, from October to April, are generally high and often exceed 40°C. By comparison, winter months from May to September are typically mild and dry.

The majority of the Conservancy is relatively flat with few, small isolated hills scattered throughout the central and south eastern sections. The terrain in the northern section is, however, more variable and characterized by numerous small, granite hillocks (~ 100 m high).

1.6 Research aims and thesis structure

The overarching aim of this research is to explore the application of animal-borne and static acoustic recording technology to the study of lion behavioural ecology and to investigate its potential as an alternative monitoring tool for the species. Sound signals offer a rich source of information about the surrounding environment and can provide unique insights into animal behaviour. I demonstrate the value of audio as a data source for determining animal behaviour remotely, investigating animal vocal signals and as a monitoring tool for lion conservation. Previous work in the field of bioacoustics has highlighted the importance of future research on species vocal behaviour and the development of new hardware and software tools for locating and identifying animal acoustic signals.

1.6.1 Chapter 2

Listening to lions: Animal-borne acoustic sensors improve biologger calibration and behaviour classification performance

Biologging technology has advanced rapidly over the last decade, allowing researchers to remotely acquire a wide range of data on their study species. Despite these developments, one of the main challenges associated with interpreting the data recorded by these devices is relating movement metrics to behaviour. This calibration process, generally conducted using video footage of the instrumented animal, requires direct observation of animal behaviour. This approach is limited by the ability of the observer to record sufficient samples of all behavioural states and may also introduce biases as a result of observer presence. Previous research has shown that on-animal audio recordings provide effective cues from which the behavioural state can be inferred. I therefore attempt to test the use of audio as a source of ground truth for calibrating biologgers fitted to lions. In addition, I investigate how acoustic features can be used to improve automated classification of animal behaviour.

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1.6.2 Chapter 3

The influence of spatial features and atmospheric conditions on African lion vocal behaviour

Vocalization is a flexible behaviour that is dependent on the relative costs and benefits of emitting a signal under certain environmental and social conditions. Few studies have attempted to investigate the influence of spatial factors on animal vocal behaviour, most likely because of the difficulty in manually recording vocalization events with simultaneous location information. Understanding how environmental features affect vocal behaviour is, however, important for informing acoustic monitoring methods. Given that lions vocalize to advertise territory ownership, and that areas within a home range are not equally important for the holder, the distribution of roar events is unlikely to be spatially homogenous. Furthermore, atmospheric conditions are known to alter sound propagation and thus reduce or enhance the range of a vocal signal. Like several other vocal species, such as wolves, lions may concentrate vocal behaviour in periods that are more favourable for long-range signalling. In this chapter, I investigate how spatial features, specifically proximity to rivers and water points and position relative to home range, and surface atmospheric conditions such as temperature, humidity and wind speed influence lion vocal behaviour. To do so, I make use of the acoustic biologger approach described in Chapter 2 to infer lion vocalizations from movement metrics.

[Prepared for submission to *Behavioural Ecology*]

1.6.3 Chapter 4

CARACAL: A versatile passive acoustic monitoring tool for wildlife research and conservation

Passive acoustic monitoring is an effective technique for studying and monitoring vocally active wildlife species but most applications have relied on commercially available recording devices which are often expensive and therefore limits the number of recorders used in research studies. With the increasing availability of open-source hardware and software and the collaborative partnerships between ecologists and computer scientists, affordable, custom-made devices are becoming more popular. These innovations are, however, still incapable of facilitating localization of sound sources. In this chapter I describe and test a novel, custom-made, multi-microphone hardware and software system called CARACAL, designed to localize animal vocal signals over large areas.

[Resubmitted to *Bioacoustics* for final decision]

1.6.4 Chapter 5

Vocal discrimination of African lions and its potential for collar-free tracking

Vocal individuality is a common trait amongst many species and has frequently been highlighted as a means of remotely identifying individual animals over time and space. A number of playback experiments have established that lions are able to identify conspecifics by their vocal signals but knowledge of the acoustic features that might encode individual identity has been lacking. In this chapter, I investigate whether the fundamental frequency of the full-throated unit of a roar contains individually distinct elements that are sufficiently consistent to enable individual discrimination. I present the analysis firstly, in the context of a number of other studies that have addressed vocal individuality, and secondly, using a unique approach that considers sequential patterns in the fundamental frequency contour. In addition, I demonstrate how vocal signal differences can be exploited to track individual lion movements.

[Prepared for submission to *PNAS*]

1.6.5 Chapter 6

General discussion

In this final chapter, I review and discuss the main findings of the study and highlight how the tools and knowledge gained from this work are interlinked. I further discuss the relevance of these findings to the development of a passive acoustic monitoring system for lions and also consider the wider application and conservation implications.

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2 Listening to lions: Animal-borne acoustic sensors improve biologger calibration and behaviour classification performance.

Matthew Wijers, Paul Trethowan, Andrew Markham, Byron du Preez, Simon Chamaillé-Jammes, Andrew Loveridge, David Macdonald

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Authorship: SC-J, AL and DM conceptualized the addition of audio sensors to biologgers. AM designed the biologgers and assisted in the extraction and analysis of data. Study animals were captured and fitted with biologgers by PT and BdP. MW carried out the data analysis and wrote the manuscript with input from all authors.

2.1 Abstract

Efforts to better understand patterns of animal behaviour have often been restricted by several environmental, human and experimental limitations associated with the collection of animal behavioural data. The introduction of new biologging technology has offered an alternative means of recording animal behaviour continuously and is being used in an increasing number of studies. Accurately calibrating these biologgers, however, still remains a challenge in many cases. Using lions as an example species, we test how audio recordings from animal-borne acoustic sensors can improve calibration and behaviour classification. Through a collaborative effort between computer scientists, engineers and zoologists, custom-designed acoustic biologgers were fitted to eight lions and recorded audio simultaneously with accelerometer and magnetometer data. Audio recordings were then used as the source of ground truth to train random forest classification models as well as to provide additional predictor variables for behaviour classification. We demonstrated near-perfect classification performance for five lion behaviour classes when all component variables were combined, with an average per-class precision of 98.5%. Using accelerometer features only, the audio-trained classifier predicted behaviours with an average per-class precision of 94.3%. On-animal audio recordings are therefore able to provide a valuable source of ground-truth for calibrating biologgers while also offering additional predictive features for increasing the accuracy of behaviour classification. This technological innovation has wide ranging application and provides a useful tool for behavioural ecologists wishing to collect fine-scale behavioural data for animal research and conservation.

2.2 Introduction

Remote data-logging, also referred to as biologging or biotelemetry, has evolved rapidly with new available technologies. Initially, studies focusing on animal spatial ecology were revolutionized by the introduction of GPS tracking methods in the 1980's which provide accurate and long-term location information at varying resolutions (Rutz and Hays, 2009). More recently, there has been a shift in focus to providing behavioural information in conjunction with location data using similar archival data-loggers in order to better understand the drivers of animal behaviour. To achieve this, a substantial collaborative effort between zoologists, computer scientists and engineers has been required. The resulting technological advances have transformed the field of behavioural ecology with an increasing number of studies now relying on animal-attached sensors to record behaviour (Brown et al., 2013). This rapid transition likely resulted from the need to overcome a number of difficulties associated with direct observation. These difficulties may include biases suffered as a result of observer presence (Caine, 1990; Gutzwiller et al., 1994) or the inability continuously to observe the focal animal if it is an elusive species, or a species that occurs in inaccessible habitats. In addition, direct observations require considerable time and effort on the part of the observer and thus can be heavily influenced by human physical limitations (Cagnacci et al., 2010).

While biologgers provide a solution to most of these challenges, they also have several drawbacks of their own. Firstly, the size of such devices may limit their use on smaller animals where it is not feasible to design a unit that weighs less than 2% of the animal's body mass. This is necessary to prevent behavioural changes and increases in energy expenditure (Cooke et al., 2004). Secondly, in most cases, researchers are still required to spend time in the field observing the study animal in order to calibrate the data generated by the biologger. This is commonly done using video cameras held by the observer with subsequent video labelling that can be matched to the corresponding biologger data by time stamps (Kawabata et al., 2014; Lush et al., 2015; McClune et al., 2014; Wang et al., 2015). Thirdly, and perhaps a more fundamental problem is that many types of biologgers do not achieve desirable results in discerning between behaviours. Recent studies still fail to differentiate accurately between more than three basic activities (Grünewälder et al., 2012; Lush et al., 2015; Wang et al., 2015).

The majority of biologgers used in animal behaviour studies generally rely on one or a combination of three microelectromechanical systems (MEMS) sensors: accelerometer, magnetometer and a gyroscope. An accelerometer measures the acceleration forces of the body to which it is attached (Albarbar et al., 2009) while a magnetometer measures magnetic field strength and direction (Herrera-May et al., 2016). Gyroscopes, although not as common, are used to measure angular rate of rotation (Piyabongkarn et al., 2005). In some cases, animal-borne video cameras have been included to provide ground truth for directly calibrating accelerometer data but only provide visual validation for short periods due to the high power and data storage requirements for recording video (Pagano et al., 2017; Volpov et al., 2015; Watanabe and Takahashi, 2013). Audio recording can also be used to collect behavioural information as shown by Insley et al. (2008) on fur seals (*Callorhinus ursinus*) and Lynch et al. (2013) on mule deer (*Odocoileus hemionus*). These studies inferred animal behaviour by visually reviewing spectrographic patterns but did not incorporate any statistical learning for automatic behaviour classification. To our knowledge, the use of audio recordings as a method of calibrating on-board movement sensors as an alternative to video footage and direct observation has not been tested. In this study, we present a novel method for calibrating biologger signals using simultaneously captured on-collar audio recordings from a custom-designed biologger. In so doing, we provide suggested improvements to the issues surrounding biologger calibration and behaviour differentiation. We further demonstrate near-perfect (>99%) classification accuracy when we combine audio features with other sensor data, especially for behaviours which are typically misclassified using motion sensors alone (e.g. drinking water). Thus, capturing synchronized audio and multi-sensor data has not only the potential to provide detailed ground-truth, but also provides extremely accurate automatic behaviour classification.

2.3 Materials and methods

2.3.1 Study site

The study took place on the privately-owned Bubye Valley Conservancy (BVC). The BVC is approximately 3400km^2 and is located in the lowveld region of southern Zimbabwe between latitudes 21.209° and 21.851° South, and longitudes 29.798° and 30.521° East. We focused on the south-western section of BVC where an ongoing lion research project has been conducted since 2009. For a full description of the study site see du Preez et al. (2014).

2.3.2 Biologgers

Biologgers were custom-designed through a collaborative research partnership between zoologists, computer scientists and engineers with the overall objective of developing a device capable of recording lion behaviour continuously and accurately. The loggers were manufactured to attach onto existing lion tracking collars produced by Africa Wildlife Tracking (AWT), Pretoria, South Africa and measured approximately 50 x 20 x 30 mm with a mass of less than 150g (Fig. 2.1). Each unit comprised a triaxial accelerometer and magnetometer, with both sensors sampling at 32 Hz per axis and a mono-electret microphone sampling audio at 16 kHz with an 8-bit resolution. The microphone circuit used a compander to provide dynamic gain adjustment where more amplification is made when the ambient audio is quiet. Custom firmware was written for an 8-bit AVR microcontroller which also included a low-power 802.15.4 radio unit which was used for time-synchronizing the biologger to a base station upon deployment. Data was logged to a 32 gigabyte micro-SD card. The biologger was powered by 3 CR123A lithium cells and encased in an epoxy resin-reinforced housing, with a hydrophobic vent for the microphone. Table 2.1 shows the relative current draw for each particular sensor, including the cost of logging to the SD card. As can be seen, the audio sensor consumes nearly 100 times as much power as the accelerometer, and this is mainly due to the cost of storing the audio data into the SD card, as 16 kilobytes needs to be written per second, compared with 96 bytes per second for the accelerometer or magnetometer.

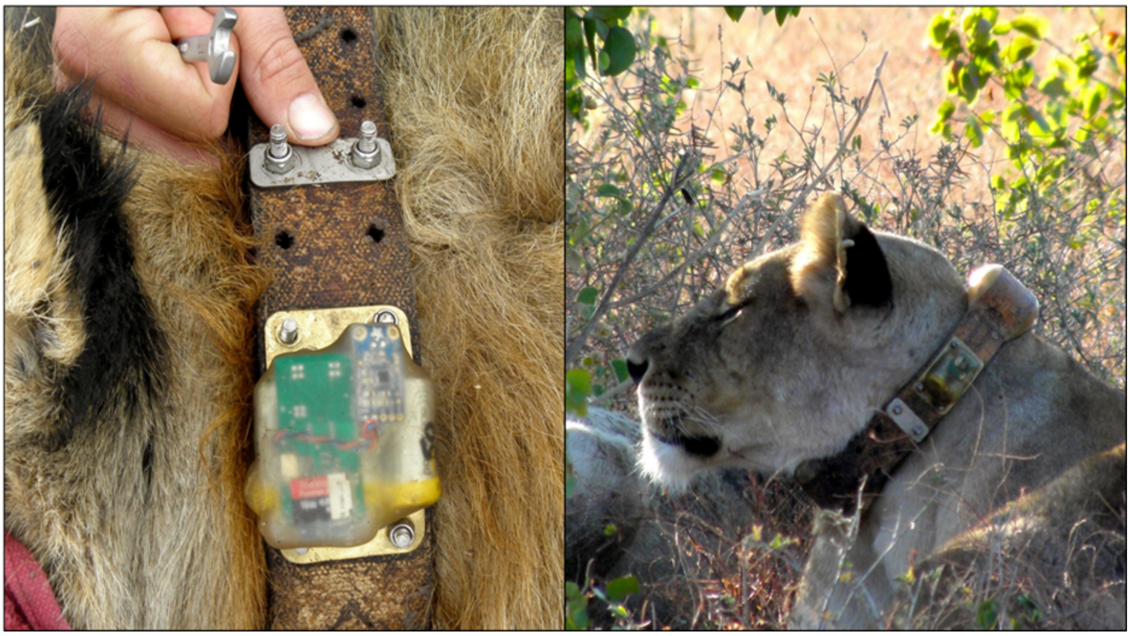

Figure 2.1 Image showing biologger bolted to a GPS collar fitted to a lioness.

Table 2.1 Current draw and estimated lifetime using different sensors.

Active Sensor	**Total current draw (mA)**	**Estimated lifetime (days)**
Accelerometer only	0.35	535
Magnetometer only	0.50	375
Microphone only	26.0	7

2.3.3 Ethical statement

This study was carried out in accordance with the recommendations of the Use of Animals in Research, ASAB/ABS. The protocol was approved by the University of Oxford Animal Welfare and Ethical Review Board and the University Veterinary Services Department. Project staff were qualified to capture and handle the study animals by attendance at Zimbabwe's Physical and Chemical Capture of Wild Animals Course and held valid drugs licenses (Dangerous Drugs License No. 2014/16). The animals were captured with permission from the landowner and conservancy management.

2.3.4 Data collection

In November 2014, we captured eight lions (five males and three females) that had been previously fitted with standard AWT satellite GPS collars. For a full description of the capture method see du Preez et al. (2015). Once the animals had been immobilized, the biologgers were bolted on to the existing GPS collars and started recorded audio (8 bit, 16 kHz mono) and three-dimensional accelerometer and magnetometer data (32 Hz) continuously until the batteries failed between 4 and 10 days later. Lions were recaptured approximately one month after initial capture and the loggers removed for data extraction.

2.3.5 Data management

In total, 80 predictor variables were calculated from the three accelerometer and magnetometer axes (40 variables for each component) for each 1 second window of data (Table 2.2). Many of the predictor features chosen for the movement sensor data have also been used in other studies (Gerencser et al., 2013; Wang et al., 2015). In addition to these features, 48 predictor variables were calculated from the corresponding audio recordings creating a combined feature set of 128 variables (see Table 2.2 for a description of each feature). Energy mean and variance were used as audio variables as they represent the zeroth and first order statistical moments of power in the 24 frequency bands as is often used in speech recognition (Kos et al., 2013). The energy mean captures whether a tone is present or not over a window, while energy variance better captures impulsive sounds such as foot falls during running.

For each individual lion, random sections of audio recordings were labelled manually into one of five behavioural states (fast, slow, stationary, eat and drink) by two lion ecologists with a minimum of two years of experience working on lions. We grouped running and trotting together as ‘fast’ behaviour while walking was classed as ‘slow’ behaviour. We were able to distinguish between these two behavioural states by the sound and pace of the lion’s footfalls. Eating behaviour was discernible by the sound of chewing and bone crunching along with aggressive vocalisations that are often associated with group feeding. Drinking events were recognized by the sound of lapping water with regular swallowing. We labelled a total of 20.5 hours of audio which was then matched to logger measurements by corresponding time stamps. This resulted in a total labelled dataset of 73930 samples each 1 second long. We randomly subsampled this dataset to 16223 1-second samples by balancing across behavioural state and individual where possible to ensure that each individual and behaviour were sufficiently represented (Table 2.3). Poor representation of certain behavioural classes has been shown to reduce classification performance (Grünewälder et al., 2012). Additionally, class imbalances can result in a bias towards the over-represented classes (Stumpf and Kerle, 2011).

Table 2.2 Predictor variables calculated over each second of data, used for RF classification.

Component	Feature	Definition	Number of Variables
Accelerometer and Magnetometer	Average axes values	Mean for X,Y,Z axes	6
	Variance in each axis	Variance for X,Y,Z axes	6
	Pitch	Ratio between X,Y & Z axes	2
	Roll	Angle between Y and Z axes	2
	Overall dynamic body acceleration	Sum of the dynamic acceleration values for X,Y & Z axes	2
	Standard deviation of magnitude	Standard deviation of the square root of the sums of squares of values in X,Y & Z axes	2
	Fast Fourier Transformations	Energy level in 8 x 4Hz frequency bins for each axis	48
	Peak frequencies	Frequency bin with maximum energy level for each axis	6
	Peak amplitudes	Power of frequency bin with maximum energy level for each axis	6
Audio	Mean energy	Mean energy in 24 frequency bands between 20Hz & 8kHz using Gabor filter bank	24
	Energy variance	Variance in energy in 24 frequency bands between 20Hz & 8kHz using Gabor filter bank	24

2.3.6 Statistical learning to predict behaviour

We used the Random Forest (RF) classification method developed by Breiman (2001) to infer behaviour from biologger measurements. This method is advantageous as it is computationally fast, robust to outliers and noise and also offers variable importance estimates for classification (Breiman, 2001). The analysis was done using the randomForest package (Breiman, 2001) in the R statistical program (R Core Team, 2016), within the R studio integrated development environment (RStudio Team, 2016). For all models, we set the number of trees (ntree) to 1000 and used the recommended value ($\sqrt{(number\ of\ variables)}$) for the number of variables considered at each split (*mtry*) which has been shown to yield optimal performance (Díaz-Uriarte and Alvarez de Andrés, 2006).

We carried out a 5-fold cross-validation to train and test two RF models, one with all component features combined and another with only accelerometer features. We compared the behaviour classification performance of the models using accuracy, precision and recall. Accuracy is a measure of overall model performance and is defined as the proportion of correctly classified data. Precision is defined as the proportion of correctly predicted positive classifications for a particular behavioural state while recall (also called sensitivity) refers to the proportion of data of a particular behavioural state that is classified correctly as positive (Bidder et al., 2014; Sokolova and Lapalme, 2009). We used accuracy as the overall performance metric due to its simplicity and the fact that it takes into account all classification outcomes (Bidder et al., 2014; Wang et al., 2015). To evaluate prediction performance for each behavioural state, we used precision as the main performance metric as it is most applicable to biological inferences which generally rely on true positive classifications, as was the case in this study (Bidder et al., 2014). We included recall as recommended by Bidder et al. (2014) for novel classification methods.

Table 2.3 Summary of balanced dataset showing number of seconds for each behaviour and individual.

Tag ID	Sex	Drink	Eat	Fast	Slow	Stationary	Total
A1	Female	684	1021	429	598	515	3247
A3	Female	196	0	163	598	515	1472
A4	Male	684	330	227	548	514	2303
A8	Male	684	1020	209	597	514	3024
A9	Male	684	1020	237	63	514	2518
A10	Male	0	0	226	598	514	1338
A11	Male	668	209	332	598	514	2321
Total		3600	3600	1823	3600	3600	16223

2.4 Results

We collected a total of 44 lion-days of useable data from 7 individual lions. One female lion was excluded from the final dataset as the magnetometer malfunctioned from the time of deployment. Our final subsampled dataset consisted of 16223 data points with an hour of data for each behavioural class except 'fast' for which we could only accumulate 1823 seconds of data.

2.4.1 Behaviour classification performance

Combining all component features resulted in near perfect classification performance with an average per-class precision of 98.5% (Table 2.4). Drink, fast, slow and stationary behaviours were predicted with approximately 99% precision while eating was approximately 3% lower with a precision of 96.2%. Training the classifier using accelerometer features only, resulted in an average per class precision of 94.3% (Table 2.5) with only eating behaviour being predicted with less than 90% precision.

Table 2.4 Confusion matrix of actual (rows) vs predicted (columns) behaviours for audio, accelerometer and magnetometer features combined.

Behaviour	Drink	Eat	Fast	Slow	Stationary	Recall (%)	Precision (%)
Drink	3514	53	0	12	21	97.6	98.8
Eat	21	3537	14	11	17	98.3	96.2
Fast	0	7	1814	2	0	99.5	99.2
Slow	5	38	1	3553	3	98.7	99.2
Stationary	15	40	0	3	3542	98.4	98.9

Table 2.5 Confusion matrix of actual (rows) vs predicted (columns) behaviours for accelerometer features only.

Behaviour	Drink	Eat	Fast	Slow	Stationary	Recall (%)	Precision (%)
Drink	3433	118	0	5	44	95.4	95.1
Eat	149	3122	14	170	145	86.7	87.7
Fast	0	5	1811	6	1	99.3	99.1
Slow	3	221	2	3371	3	93.6	94.9
Stationary	26	94	0	0	3480	96.7	94.7

2.5 Discussion

Recording the active behavioural states of African lions such as running, drinking or eating by directly observing study individuals can often be difficult as lions are mostly active at night and can be challenging to follow in areas with thick vegetation such as BVC. Adult lions, weighing in excess of 150kg, are capable of carrying biologging devices attached to collars which can offer unique insights into their behavioural patterns.

Using custom-designed acoustic biologgers, we found that audio can be used as an effective source of ground truth for training accurate behaviour classification models.

Six years ago Grünewälder et al. (2012) suggested that the collection of behavioural observations for calibrating biologging devices could be done remotely in the near future. Achieving this objective, however, required the integration of technological and zoological knowledge and skills both for the development and data analysis phases, which was achieved through an interdisciplinary research partnership. Our results indicate that remotely collected audio recordings can be used as a reliable source of ground truth for calibrating biologgers by matching audio labels to logger data following logger retrieval and thereby eliminate the need for calibration from direct observations (Figure 2.2 illustrates how audio and movement sensor data are synchronized).

It is useful to note that a relatively small number of ground truth labels (1 hour per behavioural state) were required to build an accurate classifier, although it is important to ensure that all behavioural classes are sufficiently represented in the training dataset (Grünewälder et al., 2012). This requirement can be fulfilled by continuously logging audio over several days which increases the likelihood of recording rarer behavioural events.

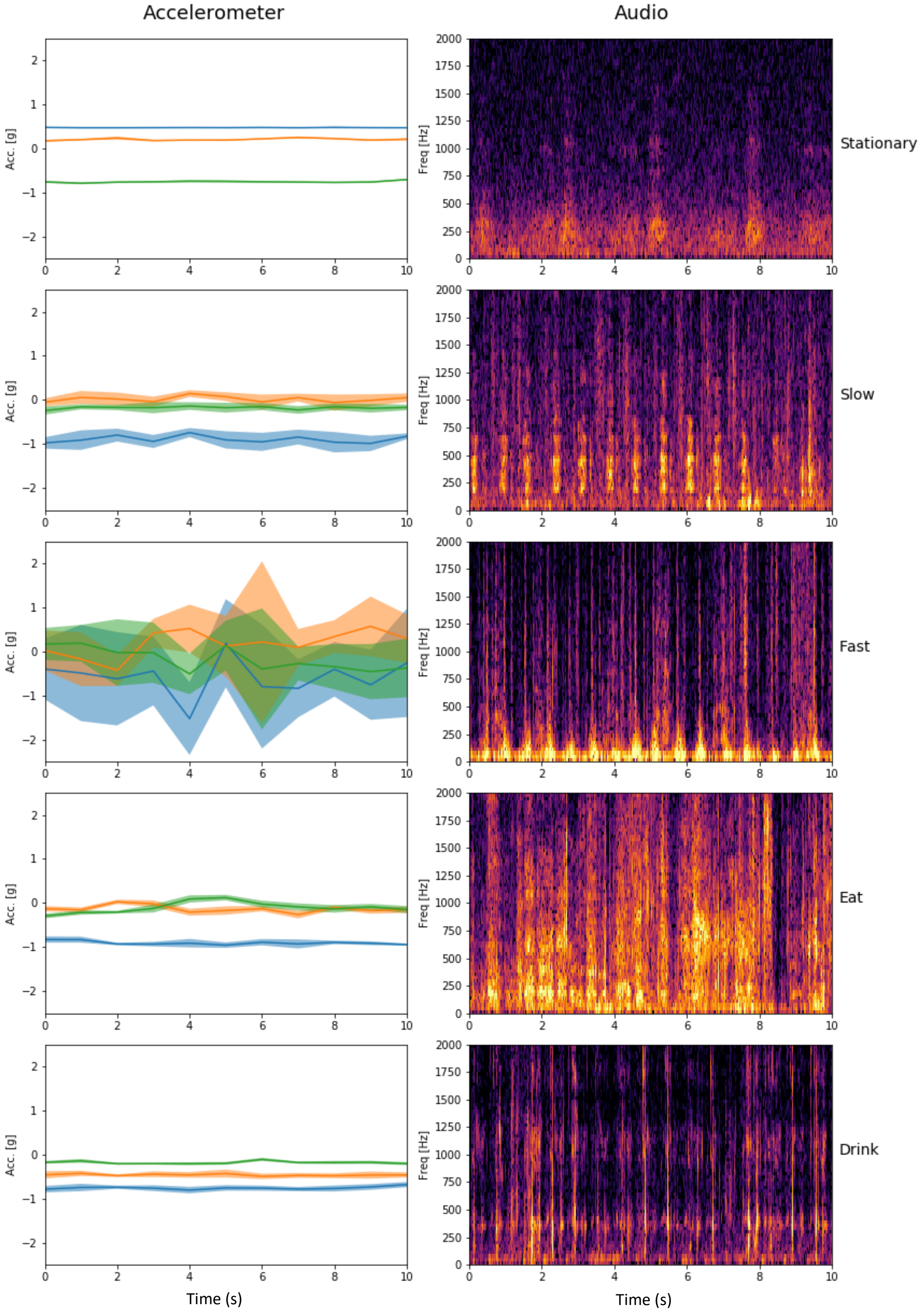

Figure 2.2 Synchronized accelerometer data and audio spectrograms for each behavioural state. *Lines and shaded regions on accelerometer plots represent mean and standard deviation for 1 second windows, respectively for each accelerometer axis.*

The total of 44 lion-days of audio from 7 individuals provided considerably more data for calibration of rarer behavioural events (eat, drink and fast) than could have been realistically achieved using video footage recorded by an observer or a video collar. In comparison, Pagano et al. (2017) recorded a total of 140 hours of video for accelerometer validation from ice bears (*Ursus maritimus*) fitted with video collars. Although visual determination of animal behavioural states is likely to be more objective than those which are determined audibly from sound recordings, we found that in general, the behaviour of the study animal could be determined easily from certain acoustic cues as outlined in section 2.3.5. Insley et al. (2008) who also made use of an animal-borne acoustic recording device reported being able to clearly differentiate between resting and other active behaviours of northern fur seals. Similarly, Lynch et al. (2013) list in detail, the audible behaviours that could be captured by their animal-borne acoustic devices fitted to wild mule deer. Where more than one person is responsible for labelling behaviours from audio recordings, particularly complex behaviours, it may be necessary to conduct an analysis on inter-coder consistency in order to quantify potential observer-biases. No such analysis was carried out in this study as the five behaviours of interest were clearly discernible by the listeners. While most behaviours may be easily recognizable using this method, short periods of ambiguous sound signals will likely be recorded and, depending on the objective of the research, may require concurrent observational data collection to confirm the behavioural state (Lynch et al., 2013). In some cases, interference from other sound sources may also make it difficult to determine behaviour. Such interference may result from self-vocalizations, vocalizations emitted by other species, anthropogenic sources (e.g. vehicles) or environmental sources (e.g. wind and rain). The use of this approach should also consider the acoustic characteristics of the species of interest as the behaviour of certain species may not be sufficiently audible, even at close range.

The results from the model built using the different component datasets showed that audio and magnetometers can also be used as additional sensor modalities for classification with high model predictive performance when accelerometer, magnetometer and audio features are combined. However, due to the considerably higher power consumption of audio recording and the battery capacity limits on current biologgers, it is unlikely that continuously logging raw audio would be a suitable sensor modality for long-term logger deployments. However, scheduling (e.g. sampling for only a few hours a day) could dramatically increase lifetime whilst still providing a sufficiently representative training set. Despite this drawback, we still demonstrated good model predictive performance using the audio labels and accelerometer features only. Thus, a small subset of animals can be equipped with audio and motion loggers to provide ground-truth calibration for a larger set of animals equipped only with motion loggers.

While we have primarily highlighted the use of audio for training behaviour classifiers, biologgers fitted with microphones may also be useful tools for other study purposes such as investigating how species respond to environmental acoustic stimuli or exploring patterns of animal vocal behaviour (Stowell et al., 2017; Wisniewska et al., 2018). The audio recordings collected from our biologgers often revealed the presence of other species (e.g. antelope and baboon alarm calls) and in some cases also allowed for the identification of captured prey species from the prey distress vocalizations. Such contextual information could be particularly useful where opportunities for visual observations are rare. Furthermore, we were able to identify 297 roar events from the 5 male lions in this study. This data alone could be used to assess vocalization rates as well as provide insight into the spatial patterns of vocalizations when combined with GPS collar data.

In future, acoustic biologgers could be greatly enhanced by intelligent on-board processing functions aimed at reducing battery load by either limiting recording to sounds of interest or by storing audio variables rather than raw audio samples. Consideration must also be given to the mode of data retrieval with wireless data transmission being a preferred option. These advancements would be particularly beneficial to studies on smaller species, where battery capacity is limited, and elusive species, where logger retrieval is difficult.

Few published studies have reported the use of micro-sensors to investigate aspects of lion behaviour (Wilson et al., 2018) however, with advances in technology and the development of interdisciplinary research partnerships, opportunities to overcome previous study limitations have arisen. Gao et al. (2013) suggested that one of the main challenges associated with analysing accelerometer data from wild animals is that there is often very little observational data to generate an accurate behaviour classifier. We have demonstrated how on-animal audio recordings can be used to collect a large amount of ground truth data for training accurate classifiers. Acoustic biologgers have wide-ranging application and this work can inform the design and development of future biologgers for other animal behaviour studies.

2.6 Acknowledgments

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3 The influence of spatial features and atmospheric conditions on African lion vocal behaviour

Matthew Wijers, Paul Trethowan, Byron du Preez, Simon Chamaillé-Jammes, Andrew Loveridge, David Macdonald, Andrew Markham.

Prepared for submission: *Animal Behaviour*

Authorship: SC-J, AL and DM conceptualized the addition of audio sensors to biologgers. AM designed the biologgers and assisted in the extraction of data. Study animals were captured and fitted with biologgers by PT and BdP. MW conceptualized and built the vocalization classifier, carried out the data analysis and wrote the manuscript with input from all authors.

3.1 Abstract

Long-distance vocalization is a characteristic of African lion (*Panthera leo*) behaviour and is important for maintaining territorial boundaries as well as locating distant group members. Vocal signalling is, however, a flexible behaviour that involves varying costs and benefits depending on environmental, social and spatial factors. Acoustic communication is likely to be preferred under atmospheric conditions that enhance sound propagation. In addition, vocal behaviour may be influenced by an animal's home range geography where valuable resources are distributed unevenly. We therefore hypothesize that lions prefer vocalizing closer to rivers and water points within their home range and in cool, calm and humid conditions. Due to the challenges associated with obtaining records of lion vocalizations in the wild, the influence of atmospheric conditions and spatial features on lion vocal behaviour has been poorly understood. Motivated by these previous data collection limitations, we developed a novel approach to investigate these questions using on-animal acoustic and accelerometer biologgers. To compensate for the short lifetime of the acoustic biologger, we developed a machine learning model to detect lion roars from long term acceleration signals which yielded over 500 nights of data from 7 individual lions. Analysis of detected roar events revealed that vocalizations occurred mainly at night with a peak just before dawn. The relative likelihood of vocalization was negatively related to wind speed and temperature and positively related to absolute humidity suggesting that lions preferred to roar under conditions that reduce sound attenuation and thereby maximize calling area. Roar occurrence was found to be dependent on an animal's location relative to its home range with lions demonstrating an apparent avoidance for vocalizing beyond the home range boundary. Lions were also more likely to roar repetitively while closer to rivers and water

points within their home range core. This study is the first of its kind and not only improves the understanding of lion vocal behaviour but can inform new approaches for recording animal vocalizations remotely as well as the development of passive acoustic monitoring systems.

3.2 Introduction

Animal vocal communication has been a topic of considerable interest over the past century with the majority of research being dedicated to three main aspects which include function, structure and production (Garcia and Favaro, 2017). Vocal signalling fulfils a variety of biological functions including territorial defence (Darden and Dabelsteen, 2008) contacting members in a social group (Rendall et al., 1996), foraging (Rydell et al., 2002), navigation (Moss and Surlykke, 2010) and deterring predators (Zuberbühler et al., 1999). Long distance vocal communication functions, in general, as a spacing mechanism between territorial individuals and allows distantly separated group members to locate each other (Marler, 1967; Mitani and Nishida, 1993). It is widely accepted that vocal signals are produced in a two-stage process, known as the source-filter theory, which involves independent contributions from different parts of the vocal apparatus, namely, the larynx and cavities of the vocal tract (Fant, 1960; Taylor and Reby, 2010). Given that the resulting signal is dependent on these anatomical features, variations in signal structure can encode information related to specific characteristics of the caller (e.g. size and age) and thus convey this ‘honest’ information to receivers (Taylor and Reby, 2010). The spectral structure of animal calls also has implications for signal transmission due to the physical constraints on signal propagation in the atmosphere which vary according to frequency (Wiley and Richards, 1978).

The transmission of acoustic signals has traditionally been viewed as an interaction between a sender and a single receiver, however, in social groups, transmitted information can be received by multiple listeners within the signalling range (Fichtel and Manser, 2010). While broadcasting to a number of individuals can facilitate the maintenance of group cohesion and territorial advertisement, signals can also be intercepted by eavesdroppers (Fichtel and Manser, 2010). Revealing information about identity, fitness, behaviour and location to potentially hostile listeners can be costly and result in unwanted conflict depending on the context. Like other behaviours, an animal's decision to vocalize or remain silent is therefore likely to be based on a trade-off between the relative costs and benefits of calling under certain conditions (Mcfarland, 1977). Studies on territorial species have shown that nomadic individuals avoid vocalizing in order to reduce the risk of attracting attention from territory owners (Campioni et al., 2010; Grinnell and McComb, 2001; Harrington and Mech, 1979). Dominant individuals may also show varying degrees of preference and avoidance behaviour depending on their location within their home range. For example, territorial swift foxes (*Vulpes velox*; Darden and Dabelsteen, 2008) and eagle owls (*Bubo bubo*; Delgado and Penteriani, 2007) have been reported to increase vocal effort in the core of their home ranges while tawny owls (*Strix aluco*; Sunde and Bolstad, 2004) appear to prefer vocalizing in peripheral areas. Variation in vocal intensity may also be influenced by the distribution of important resources within a territory such as nests, access to mates, or areas of highest food availability (Jacobsen et al., 2013).

In addition to spatial variation in the costs and benefits of vocalizing, the efficacy of long-distance acoustic communication is subject to changes in atmospheric conditions which result in varying degrees of signal degradation. Factors such as wind speed, temperature and humidity can significantly increase or reduce an animal's calling area which is the size of the region in which the call can be detected (Larom et al., 1997b; Wiley and Richards, 1978). Garstang et al. (1995) found that the range of elephant vocal signals doubled in magnitude under optimum atmospheric conditions that often occurred 1-2 hours after sunset. Such optimum conditions were generally characterized by low wind speeds and low-level vertical changes in temperature known as temperature inversions (Larom et al., 1997b). Studies on wolf and coyote vocalizations have shown an overlap between peak periods of vocalization and the hours of best sound transmission (Harrington and Mech, 1979; Laundre, 1981).

African lions are well known for their impressive, long-distance vocalizations commonly referred to as 'roars'. These signals typically consist of a series of moans leading to several full-throated roars and end with a sequence of short grunts (Grinnell and McComb, 2001; McComb et al., 1994). Lion vocal communication has been well studied particularly in relation to roar characteristics (Stander and Stander, 1988), individual recognition (Gilfillan et al., 2016; McComb et al., 1993), information content of the signal (McComb et al., 1994; Pfefferle et al., 2007) and the limitations imposed by unwanted receivers (Grinnell and McComb, 2001). The majority of these studies have used playback experiments to test hypotheses and thus there are few cases where researchers have relied on records of natural roaring events to investigate aspects of lion vocal behaviour. This preference may be partly related to the difficulty in obtaining sufficient quantities of roar records especially as wild lions vocalize almost exclusively at night (Pfefferle et al., 2007; Stander and Stander, 1988). Apart from the observations of Schaller (1972) and Stander and Stander (1988) little is known about the temporal or spatial patterns of lion vocal behaviour that may arise as a result of spatial and temporal variations in the costs and benefits of communication. Lehmann et al. (2008) documented an apparent preference for roaring along drainage lines and within 500 m of water but were limited by sample size and therefore encouraged further research on this topic. At a home range scale, lions are known to positively select areas closer to water which are characterized by high prey abundances (Davidson et al., 2012). Such areas within a territory are high value resources and are therefore likely to be more intensely protected with increased territorial behaviour such as scent marking and roaring.

In this study, we aimed to investigate whether lions exhibit spatial preferences for vocalizing, specifically with regards to proximity to rivers and water points and an individual's location relative to its home-range. Previously, it has been impossible to manually obtain sufficient data on spontaneous lion vocalizations with concurrent location information. To overcome this issue, we developed novel acoustic-accelerometer biologgers combined with innovative machine learning techniques to detect lion vocalizations from accelerometer data alone. Generally, animal activity recognition from accelerometers has been limited to locomotion and feeding and therefore, this work presents the first example of vocalization detection using the same approach. We hypothesized that lions would show a preference for vocalizing closer to rivers and water points as an attempt to retain and protect these valuable territory features and avoid roaring outside their home ranges due to the risks of provoking conflict with neighbouring individuals. We also aimed to test how lion vocal behaviour is influenced by atmospheric conditions. In this case we hypothesized that conditions with lower temperatures and wind speed and higher absolute humidity would be preferred given that such conditions maximize the calling range.

3.3 Materials and methods

3.3.1 Study site

The study was conducted in the Bubye Valley Conservancy (BVC), a privately-owned wildlife area in southern Zimbabwe located between latitudes 21.209 and 21.851°

S and between longitudes 29.798 and 30.521° E. The BVC measures approximately 3400 km^2 in area and hosts a large lion population along with a variety of other indigenous megafauna. Mopane woodland savannah dominates the majority of habitat within the Conservancy with some riparian woodland occurring along seasonal river lines. Annual rainfall is low, averaging 351 mm, and falling mostly during the summer months from November to March (du Preez et al., 2014). Daytime temperatures are generally high in summer, regularly exceeding 40 °C, with mild conditions in winter. Permanent surface water is artificially provided from boreholes (approximately 5.9 / $100km^2$). The study was conducted in the south-western section of the conservancy where an ongoing lion research project was established in 2009.

3.3.2 Weather data

Weather data which included air temperature, relative humidity and wind speed were obtained using a portable weather station (HOBO® Weather Station Data Logger—H21- 001, Onset Computer Corporation, Massachusetts, USA). The unit was erected in an open area in the study site and set to record measurements at 5-minute intervals (Trethowan et al., 2017). Because we were interested in the sound attenuation effects of humidity, we converted relative humidity (RH) to absolute humidity (AH). AH is a more appropriate measure than RH as the interaction of water molecules with oxygen contributes towards the largest proportion of molecular attenuation (Griffin, 1971). AH in g/m^3 was calculated from relative humidity and temperature using the following formula (Mander, 2012):

$$AH = \frac{6.112 \times e^{\left[\frac{17.67 \times T}{T+243.5}\right]} \times RH \times 2.1674}{273.15 + T}$$

where RH is relative humidity in % and T is temperature in °C. Data were then summarized into hourly means for each variable.

3.3.3 Spatial variables

Two spatial variables were used in this study: i) distance to closest river or water point and ii) position relative to home range. Using GIS layers of rivers and water points within the study site, we generated a raster proximity surface in Quantum GIS 2.14 (QGIS Development Team, 2016) indicating the distance of each cell to the closest river or water point. Home range zones were estimated from GPS collar data using the local convex hull (LoCoH) method (Getz et al., 2007) with heuristic value $k = \sqrt{n}$ (n = number of locations). Three home range zones were defined: i) core (within 50% isopleth), ii) peripheral (between the 50% isopleth and 90% isopleth) and iii) outside (beyond the 90% isopleth).

3.3.4 Biologgers

Between January and July 2014, we fitted thirteen lions (9 males and 4 females) with custom designed accelerometer biologgers (Biotrack / University of Oxford) that recorded accelerometer data at 16 Hz in 3 orthogonal dimensions. In November 2014, eight lions (5 males and 3 females) were fitted with custom-designed acoustic-accelerometer biologgers (Biotrack / University of Oxford) that recorded audio (8 bit, 16 kHz mono) and accelerometer data (32 Hz, 3 dimensions) simultaneously. Six (4 males and 2 females) of these study animals were recaptures from the initial accelerometer biologger deployment. All biologgers were manufactured to attach onto existing GPS satellite collars (Africa Wildlife Tracking, Pretoria, South Africa) and measured ~ 50 x 20 x 30 mm with a mass of < 150 g. The GPS collars (mass of 1.2 kg) recorded 16 geographical locations per day at an hourly interval between 17:00 and 07:00 local time and one point in the middle of the day at 14:00. From the accelerometer biologgers we collected a total of 1069 lion days of useable data from 12 lions (no data was recorded for one male lion). Due to the higher power requirements for recording audio, the acoustic-accelerometer biologgers provided a comparatively smaller dataset with a total of 60 lion days of concurrent audio and accelerometer data from all 8 individuals.

3.3.5 Animal capture procedure

Each study animal was chemically immobilized using 75-100 mg Zoletil (Virbac RSA (Pty) Ltd, Halfway House, South Africa) combined with 5 mg medetomidine (Kyron Laboratories, Johannesburg, South Africa). Immobilization drugs were delivered intramuscularly by 1 cc darts (Pneudart, Williamsport, Pennsylvania, USA) projected from a Dan-Inject CO_2-pressurized dartgun (Dan-Inject, Børkop, Denmark) at a distance of 15-20 m from the animal. Following clear signs of immobilization and a time period of approximately 15 minutes, the animal was carefully approached and blindfolded. The front legs were then secured together with a rope and earplugs inserted to reduce auditory stimuli. At approximately 60 minutes after initial drug injection, ~ 25 mg atipamazol (Antisedan, Pfizer Animal Health, Johannesburg, South Africa) was administered to reverse the effects of medetomidine allowing the animal to recover within 15 – 90 mins.

3.3.6 Roar classifier

From the raw audio recordings recovered from the acoustic-accelerometer biologgers we manually labelled the start and end times of roar events in Audacity 2.1.1 (Audacity Team, 2019). A total of 297 roars was found for the five male lions. The three females did not roar and could only be heard uttering soft moans. We further labelled random segments of audio according to other identified, non-vocalizing, behaviours (run, walk, feed, drink, rest) as described in Wijers et al. (2018). All behaviour labels were then matched with concurrent accelerometer data to obtain a labelled dataset for training classification algorithms. Figure 3.1 illustrates the synchronized audio and accelerometer data for a single roar bout. Considering that the training dataset contained no female roars, we chose to limit further analyses to males as it was impossible to validate a roar classifier for females.

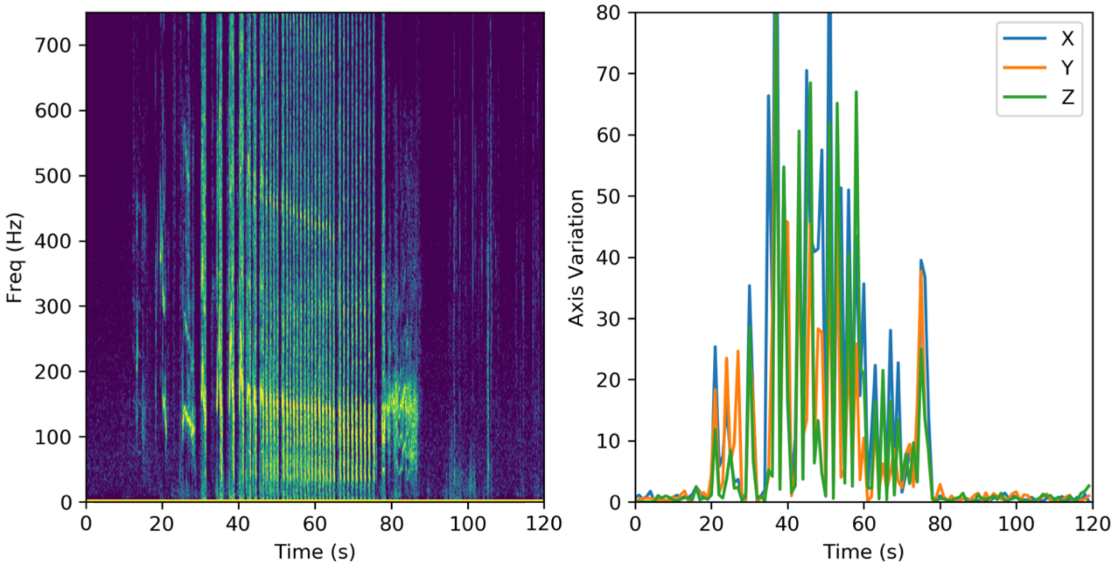

Figure 3.1 Roar spectrogram (left) with corresponding 3-axis accelerometer data (right).

Since roar events can overlap with active behaviours such as walking we noticed distinct differences in the roar acceleration signal when an animal was stationary compared to when it was active. Active behaviours appeared to override the roar acceleration signal making it more difficult to determine the presence or absence of a roar. Given that our objective was to investigate patterns of lion vocal behaviour, it was essential that the classifier functioned with high precision (no false positives). Initial attempts to build a classifier that could identify roars in both active and stationary behavioural states produced a high number of false positives. We therefore decided to exclude periods of active behaviour from our analysis and focus on vocalizations occurring while the animal was stationary. We reasoned that this approach was valid as the majority (68%) of roars obtained from the acoustic-accelerometer biologgers occurred when animals were stationary. This finding was also consistent with the observations of Stander and Stander (1988) who found that 70% of roars emitted by Etosha lions occurred while animals were sitting, lying or standing.

A second important consideration in our analysis was being able to link location with a roar event. Given that the GPS satellite collars only recorded location on the hour at an hourly interval we systematically sampled the accelerometer data by extracting 20-minute windows centred on the hour associated with each GPS point (Fig. 3.2). We chose a 20-minute period as a trade-off between maximizing the time available to detect roars and minimizing the potential drift from the recorded location. We used the same sampling method to investigate the diel distribution of roars but used all hours of the day in order to determine vocalization rates during daylight hours as well as at night.

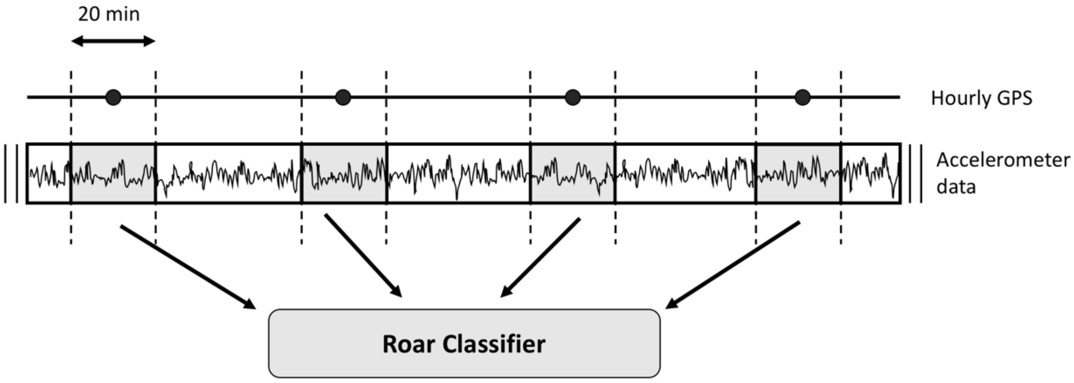

Figure 3.2 Schematic representation of the sampling approach used to link behaviour with location.

To extract roar events from accelerometer data we built a hierarchical classifier consisting of hidden Markov models (HMM) to distinguish between active and stationary behaviour, and a random forest (RF) to differentiate between roars and non-roars (Fig. 3.3). We first trained 3-state HMMs for active and stationary behaviour based on overall dynamic body acceleration (ODBA) which is a single, integrated measure of body motion (Gleiss et al., 2011). ODBA sequences could then be tested against each HMM to determine which model (active or stationary) was most likely to produce the given sequence (based on log-likelihood). A 4-fold cross-validation procedure resulted in 100% recall and precision indicating perfect classification of active and stationary sequences. Accelerometer windows that were classified as stationary in the first step were then passed to the RF (1000 trees and √(number of variables) considered at each split) which was trained to classify each second of the 20 min window as 'roar', 'rest' or 'other' (the features used for RF classification are described in Table S3.1 in the Appendix). The RF classification performance was tested using 5-fold cross validation where each fold represented data from only one of the five individual lions. Roars were classified with 93.3% recall and 86.1% precision (Appendix - Table S3.2). We used this approach to simulate the scenario where the classifier would be required to predict behaviour on individual animals not included in the training set. The predicted series of behaviours generated by the RF were then converted into 1s and 0s where a ‘1’ indicated a roar and a ‘0’ indicated a non-roar. This allowed for the application of a gaussian filter which effectively filtered out isolated 1s that were likely to be false positives (considering that a single lion roar bout lasts for approximately 40 s). We selected a classification threshold of 0.82 which was found to yield high roar precision (100%) and satisfactory recall (68.9%). All stages of roar classification were carried out in Python using the hmmlearn 0.2.2 (hmmlearn Development Team, 2019) and Scikit-learn (Pedregosa et al., 2011) libraries.

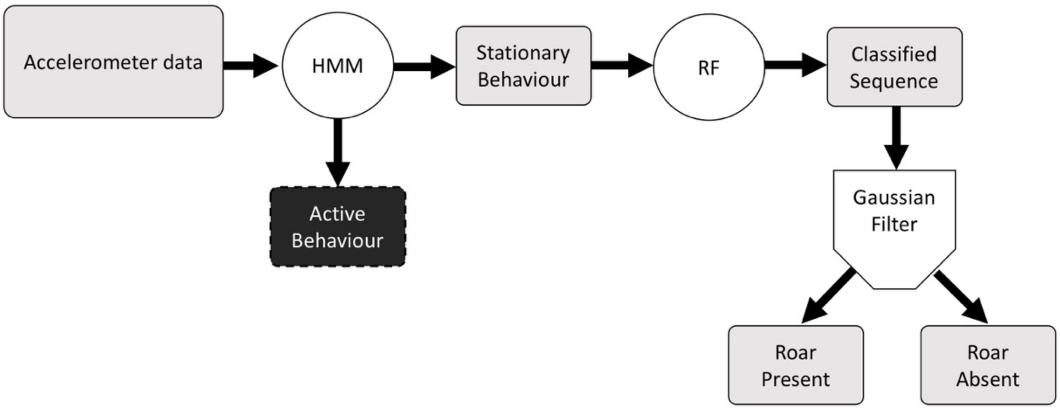

Figure 3.3 Flow diagram illustrating the sequence of steps in the roar classifier.

3.3.7 Statistical analyses

Diel distribution of roars

To determine the diel distribution of roars from the accelerometer data, we first calculated the total number of roars (frequency) in each hour for each individual. The hourly frequencies were then divided by the total number of stationary windows in each hour to account for potential variations in sampling effort across hours. For each individual, hourly frequencies were normalized by expressing each frequency as a fraction of the maximum frequency in order to compare distribution patterns across individuals. The resulting relative hourly frequencies were averaged across each individual and plotted with a nonparametric loess smoothing function and 95% confidence intervals to remove low-frequency variability (Cleveland, 1988). We used the same method to plot the diel distribution of roars obtained from the raw audio recordings on the acoustic-accelerometer biologgers. However, because all data were used, it was not necessary to account for any variation in sampling effort.

Effect of location and atmospheric conditions on vocalization likelihood

Lion vocalizations were analysed at two levels. Firstly, we simply considered the presence or absence of vocalizations in each 20-min window (roar occurrence). Secondly, we accounted for the number of vocalizations in each window in order to investigate possible differences in vocalization preferences when lions choose to roar repetitively. In the latter case, we only considered windows in which two or more roars were detected (repetitive roars). Because lions primarily roar during the night, we restricted our analyses to the period between 18:00 and 06:00 local time.

To test whether the likelihood of roar occurrence and repetitive roaring was a function of location relative to home range and proximity to rivers and water points, we compared roar location characteristics to all non-roar stationary locations. Generalized linear mixed models (GLMM) with a binomial distribution and logit link function were used from the 'lme4' package in R (Bates et al., 2015). The response variable was coded as 1 (roar) and 0 (no roar). In each model lion identity was included as a random intercept, which accounted for individual-level variation in vocalization behaviour and allowed for inference to the population level. This use-availability design allowed for robust comparison of locations chosen by lions for roaring to those available to them. We considered five candidate models consisting of each of the explanatory variables alone, combined and in interaction. Using the same GLMM approach, we also tested for effects of atmospheric conditions on vocalization likelihood. Specifically, we investigated whether roar likelihood was a function of temperature, wind speed and absolute humidity. Eight potential models were considered that consisted of the explanatory variables alone and in all possible combinations. Due to gradual changes in atmospheric conditions through the night and through the year we included random intercepts for night period (evening: 18:00 – 21:00; mid-night: 22:00 – 02:00; morning: 03:00 – 06:00) and for month. A random intercept was also included for individual identity. Model selection was carried out using the R package MuMin (Bartoń, 2019) with all potential models ranked according to Akaike Information Criterion corrected for small sample sizes (AICc). The model with the lowest AICc was considered the most plausible, however, models with a ΔAICc ≤ 2 were also considered to have substantial support. If no single model was clearly superior, we performed model averaging on all models with ΔAICc ≤ 2 to obtain unconditional coefficient estimates and confidence intervals (Burnham and Anderson, 2002). Results were then interpreted in terms of odds ratios (OR) and their 95% confidence intervals (CI).

3.4 Results

Home range analyses indicated that 7 out of the 8 male lions with functioning accelerometers were territorial males with clearly defined, static home ranges. One male, however, was not resident in any one area and appeared to only move along the boundary fence. A total of 990 roars was detected from the 7 territorial males (mean ± SE = 1.98 ± 0.33 roars/day) with only 19 roars (0.63 roars/day) detected from the nomadic male. Due to the low number of detected roars and in order to reduce possible bias as a result of social status, the nomadic male was excluded from further vocalization analyses.

3.4.1 Diel distribution of roars

The diel distribution of classified roars derived from the accelerometer data indicated that the territorial male lions roared predominantly during the night. Relative frequency of roars increased steeply between 5pm and 8pm and then stabilized until shortly after midnight, before peaking between 3am and 5am. Relative frequency then steeply decreased at sunrise between 5am and 7am with relatively few roars detected during daylight hours. The hourly distribution of roars obtained from the acoustic biologgers shows an almost identical pattern with an obvious peak just before dawn between 3am and 5am (Figure 3.4).

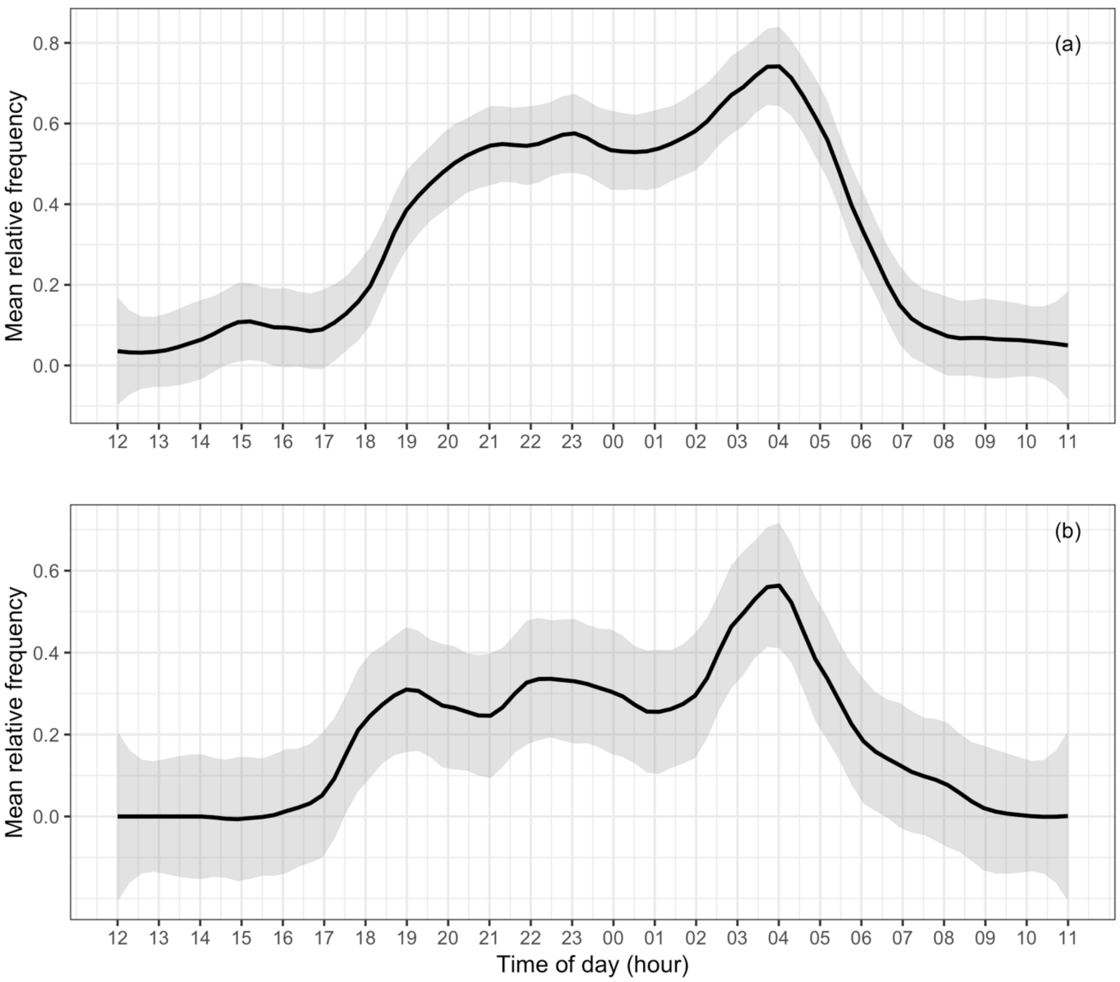

Figure 3.4 Diel distribution of roars obtained from accelerometer biologgers (a) and from acoustic biologgers (b). *Shaded areas denote 95% confidence intervals.*

3.4.2 Effect of atmospheric conditions on vocalization likelihood

The likelihood of roar occurrence in relation to atmospheric conditions was best explained by a model consisting of temperature, wind speed and absolute humidity (Table 3.1). Wind speed had the greatest effect with the odds of vocalization decreasing by ~ 40% for every 1 m/s increase in speed (OR: 0.596, CI: 0.500 – 0.710). Comparatively, a 1°C rise in temperature decreased the odds of vocalization by ~ 6% (OR: 0.938, CI: 0.907 – 0.970) while a 1 g/m^3 increase in absolute humidity increased the odds of vocalization by ~ 7% (OR: 1.069, CI: 1.022 – 1.119). When assessing the relationship between repetitive vocalizations and atmospheric conditions, the best model consisted of all three atmospheric predictor variables as was the case for roar occurrence (Table 3.1). The odds of repetitive roars occurring decreased by ~ 53% with every 1 m/s increase in wind speed (OR: 0.472, CI: 0.323 – 0.689), decreased by ~ 9% for every 1°C rise in temperature (OR: 0.906, CI: 0.847 – 0.968) and increased by ~ 10% for every 1 g/m^3 increase in absolute humidity (OR: 1.098, CI: 1.014 – 1.189).

Table 3.1 Summary of model selection statistics for mixed effects logistic regression analysis of the relationship between the response variables (vocalization occurrence and repetitive vocalization occurrence) and the explanatory variables: wind speed (Wind) absolute humidity (AH) and temperature (Temp)*.*

A random intercept was included in each model for individual animal, month and night period. Selection statistics include log-likelihood (LLH), Akaike Information Criterion corrected for small sample sizes (AICc), AICc difference from the most plausible model (Δi), Akaike weight (w_i*) and the number of parameters (K). Models highlighted in bold indicate the most plausible models with AICc* ≤ 2*.*

Response	Model	Rank	LLH	AICc	Δi	w_i	K
Vocalization occurence Present (1) vs Available (0)	**Temp + AH + Wind**	**1**	**-1557.590**	**3129.2**	**0.00**	**0.952**	**7**
	Temp + Wind	2	-1561.656	3135.3	6.13	0.045	6
	Wind	3	-1565.832	3141.7	12.47	0.002	5
	Wind + AH	4	-1564.916	3141.9	12.64	0.002	6
	Temp + AH	5	-1577.366	3166.8	37.55	0.000	6
	Temp	6	-1579.005	3168.0	38.82	0.000	5
	Null	7	-1589.093	3186.2	56.99	0.000	4
	AH	8	-1589.057	3188.1	58.92	0.000	5
Repetitive vocalization Present (1) vs Available (0)	**Temp + AH + Wind**	**1**	**-602.863**	**1219.8**	**0.00**	**0.758**	**7**
	Temp + Wind	2	-605.489	1223.0	3.24	0.150	6
	Wind	3	-607.319	1224.7	4.90	0.066	5
	Wind + AH	4	-607.207	1226.4	6.68	0.027	6
	Temp + AH	5	-613.058	1238.1	18.38	0.000	6
	Temp	6	-614.861	1239.7	19.98	0.000	5
	Null	7	-618.762	1245.5	25.78	0.000	4
	AH	8	-618.721	1247.5	27.70	0.000	5

3.4.3 Effect of location on vocalization likelihood

The best model explaining the likelihood of roar occurrence in relation to spatial variables consisted of location relative to home range as the only explanatory variable, however, two other models were also plausible (Table 3.2). The second model included an interaction between location relative to home range and distance to nearest river or water point while the third included location relative to home range and distance to nearest river or water point without an interaction. We performed model averaging to obtain unconditional estimates and confidence intervals for each variable. Only the location relative to home range variable contributed significantly to the averaged model. A Tukey Post-hoc analysis revealed that the odds of a lion roaring outside its home range was ~ 52% lower compared to its home range core (OR: 0.475, CI: 0.298 – 0.756) and ~ 42% lower compared to the periphery (OR: 0.575, CI: 0.356 – 0.928). No significant difference was found between the likelihood of roar occurrence in the home range core and the periphery (OR: 0.826, CI: 0.659 – 1.037). The best model explaining the likelihood of repetitive vocalizations consisted of an interaction between location relative to home range and the distance to nearest river or water point (Table 3.2). The effect of distance to rivers and water points therefore depended on an individual's location relative to its home range (Appendix - Figure S3.1) with the odds of repetitive vocalizations increasing by ~ 79% for every 1 km decrease in distance to rivers and water points in the home range core (OR: 1.786, CI: 2.717 – 1.174) and decreasing by ~ 82% for every 1 km decrease to rivers and water points outside the home range boundary (OR: 0.182, CI: 0.046 – 0.717). No significant effect was detected for the influence of distance to rivers and water points on the likelihood of repetitive roaring within the periphery (OR: 0.983, CI: 0.703 – 1.376).

Table 3.2 Summary of model selection statistics for mixed effects logistic regression analysis of the relationship between the response variables (vocalization occurrence and repetitive vocalization occurrence) and the explanatory variables: location relative to home range (Zone) and proximity to closest river or water point (Dist).
A random intercept was included in each model for individual animals. Selection statistics include log-likelihood (LLH), Akaike Information Criterion corrected for small sample sizes (AICc), AICc difference from the most plausible model (Δi), Akaike weight (w_i) and number of parameters (K). Models highlighted in bold indicate the most plausible models with ΔAICc ≤ 2.

Response	**Model**	**Rank**	**LLH**	**AICc**	**Δi**	**w_i**	**K**
Vocalization	**Zone**	**1**	**-1562.052**	**3132.1**	**0.00**	**0.499**	**4**
occurence	**Zone*Dist**	**2**	**-1559.554**	**3133.1**	**1.02**	**0.299**	**7**
	Zone + Dist	**3**	**-1561.968**	**3134.0**	**1.84**	**0.199**	**5**
Present (1) vs	Dist	4	-1568.836	3143.7	11.56	0.002	3
Available (0)	Null	5	-1570.629	3145.3	13.15	0.001	2
Repetitive	**Zone*Dist**	**1**	**-594.6**	**1203.2**	**0.00**	**0.973**	**7**
vocalization	Zone + Dist	2	-601.2	1212.4	9.15	0.010	5
	Zone	3	-602.3	1212.7	9.44	0.009	4
Present (1) vs	Dist	4	-603.6	1213.3	10.03	0.006	3
Available (0)	Null	5	-605.8	1215.5	12.30	0.002	2

3.5 Discussion

Recording animal vocal behaviour with simultaneous location information is challenging, particularly for species such as lions which are mostly active at night and therefore difficult to identify. The use of biologgers provides a unique opportunity to monitor animal movement continuously and thereby overcomes many of the difficulties associated with direct observation (Rutz and Hays, 2009). Lion vocalizations involve consistent movements of the animal’s head and neck which can be captured by three-dimensional accelerometer loggers. To our knowledge, this study is the first to retrieve animal vocalizing behaviour from accelerometery data. Although our detection method was limited to stationary behaviour and retrieved ~69% of roar events it still provided more than three times the number of roars than the raw audio recorded by the acoustic-accelerometer biologgers. On-animal audio recordings may be preferable for detecting all roars emitted by tagged animals but the lifetime of an acoustic biologger is considerably lower (~ 8 days) than an accelerometer biologger (~ 100 days) due to the higher power requirements for recording audio.

The diel distribution of roars obtained from both biologgers indicated that lions vocalize mainly at night with a distinct peak just before dawn. This pattern corresponds closely with observations reported by Schaller (1972) and Stander and Stander (1988) who also noted a consistent peak in the hours before sunrise.

Larom et al. (1997b) suggested that lion calling behaviour is likely to be driven by predictable atmospheric fluctuations that enhance the range of vocal signal propagation. Optimal conditions occur when there is a strong surface temperature inversion and no wind as acoustic energy is refracted downwards and thereby increases sound levels near the ground (Larom et al., 1997a). Although it was not possible to determine the strength of daily temperature inversions, our results indicated that lions strongly avoided vocalizing with increasing wind speed. Strong winds cause vertical and horizontal mixing of air and thus prevent the development of a surface temperature inversion. Furthermore, wind has the added effect of causing fluctuations in the received signal and introduces considerable low frequency noise that overlaps with low frequency vocal signals, such as lion roars, resulting in acoustic masking (Larom et al., 1997b; Wiley and Richards, 1978). Considering the multiple negative effects of wind on signal propagation and reception it is probable that lions actively avoid vocalizing during these periods as doing so would result in proportionally reduced benefit. Similar avoidance behaviour has been recorded for maned wolves (Rocha et al., 2016) and timber wolves (Joslin, 1967). In addition to the effects of wind speed, our results also indicated relatively weaker but significant effects for temperature and absolute humidity with lions showing an apparent preference for vocalizing in lower temperatures and higher humidity. For frequencies below 1 kHz, sound attenuation decreases with increasing humidity and increases with increasing temperature (Griffin, 1971; Harris, 1966). Low frequency vocalizations emitted in cold, humid conditions are therefore likely to travel further compared to signals emitted in warm, dry conditions. It is likely that lions also choose to exploit these conditions by roaring more frequently when temperatures are low and humidity is high in order to maximize calling area.

Although atmospheric conditions are likely to be a primary factor influencing lion vocal behaviour, spatial attributes may also impact an individuals' decision to vocalize. When assessing patterns of roar occurrence, the primary spatial feature affecting vocalization likelihood was the animal's position relative to its home range. Despite little difference in the likelihood of roar occurrence between core and peripheral areas, lions appeared to strongly avoid vocalizing outside of their home range. This result is consistent with the findings of Grinnell and McComb (2001) who reported, from anecdotal observations, that resident male lions in the Serengeti and Ngorongoro crater refrain from roaring beyond their territory boundaries. This avoidance behaviour can be attributed to the increased costs of engaging in conflict with other territorial males and the reduced benefits of vocalizing away from owned resources. Similar 'low profile' behaviour is commonly displayed by nomadic individuals that do not possess a territory as was evident in this study where the nomadic male vocalized less than the territorial males (Campioni et al., 2010; Grinnell and McComb, 2001; Harrington and Mech, 1979). The locations of repetitive vocalizations appeared to be influenced by proximity to the nearest river or water point with the effect being dependent on the animal's position relative to its home range. Within the home range core, lions showed a weak preference for vocalizing repetitively while closer to rivers and water points but strongly avoided doing so when outside of their home range. Several studies have shown that rivers and water points are important features for lion prey acquisition and reproduction (Davidson et al., 2013; Mosser et al., 2009; Valeix et al., 2010). Lions may therefore choose to increase vocalization effort when closer to valuable territory features within their home range core in order to deter potential invaders. Other species such as fallow bucks are known to increase vocalization rates as a threat display directed at rival males particularly in contexts requiring protection of a resource such as access to females (Mcelligott and Hayden, 1999). The apparent avoidance of repetitive vocalizations closer to rivers and water points beyond an individual's home range boundary reflects the increased risks of inviting attacks from aggressive resident males that may be more willing to engage in conflict when access to a valuable resource is challenged.

Although the objective of this work was to investigate the influence of spatial features and atmospheric conditions on lion vocalizations, it is important to note that there are other potential factors that can affect an animal's decision to vocalize or remain silent. For example, some predatory animals reduce vocalization rates during foraging as prey are able detect vocal signals and respond with antipredator behaviour (Deecke et al., 2004). Considering that lion prey species are generally located near water, lions may avoid vocalizing in these areas while hunting despite the potential benefits of doing so to protect valuable territory features. Social factors may also play a role; in this study the three lionesses did not produce full throated roars and could only be heard uttering soft moans, likely as a means of short distance communication between other members of the pride. Although this was unexpected, the presence of small cubs in the prides may have contributed to a temporary cessation of long-distance vocalization. Similar behaviour has been reported for wolves where adults appeared to stop howling until pups had reached an age of 6-9 weeks; a strategy that is thought to be employed to protect pups from predators (Joslin, 1967). In the case of lions, avoiding long-distance vocalization may reduce the risks associated with attracting potentially infanticidal males (Grinnell and Mccomb, 1996). We acknowledge, however, that three lionesses does not constitute an adequate sample size and therefore further work would be required to support this assumption.

In this study we have shown that lion vocal behaviour is influenced by both spatial and atmospheric variables. Lions appear to select conditions that maximize calling area as suggested by Larom et al. (1997b) and also adjust vocal effort depending on their location in order to defend resources and minimize inter-pride conflict. Understanding how environmental factors influence animal vocal behaviour is not only important for interpreting patterns relating to species ecology but can also directly benefit species conservation through passive acoustic monitoring (PAM; Marques et al., 2013). To our knowledge, no study has attempted to monitor lions from their vocalizations, but with rapidly advancing technology, PAM could provide an alternative, cost effective option for future lion research and conservation initiatives. This work has highlighted some important considerations for PAM system design such as the time of peak vocalization and the influence of habitat features and environmental conditions. Furthermore, the methods employed in this study to obtain data on lion vocalizations may also be applicable to other species that move in a unique and consistent manner while vocalizing. In future, biologgers could be improved by incorporating on-board classification of vocalizations to eliminate the requirement for continuous audio and thereby improve device lifetime.

3.6 Acknowledgements

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3.8 Appendix

Table S3.1 Features used for RF classification.

Feature	Definition	Number of variables
Variance in each axis	Variance for X,Y and Z axes	3
Pitch	Ratio between X,Y and Z axes	1
ODBA filter	The difference between median filters of the sum of the dynamic acceleration values for X,Y and Z axes taken from a 200 second window and a 40 second window	1
Relative Frequency	The difference between Gaussian filters of average peak frequency (frequency bin with the maximum energy level) with sigma level 70 and 10.	1
Roll Variation	The variation in the angle between the Y and Z axes across a 9 second window	1
Mean Maximum Peak Frequency	The mean maximum peak frequency from X, Y and Z axes across a 9 second window	1
Mean Average Peak Frequency	The mean average peak frequency from X,Y and Z axes across a 9 second window	1
Mean Frequency Range	The mean difference between the maximum and minimum peak frequencies across a 9 second window	1

Table S3.2 Confusion matrix of actual behaviours (rows) vs predicted behaviours (columns).

Activity	Roar	Rest	Active	Recall %	Precision %
Roar	3522	82	171	93.3	86.1
Rest	24	4807	54	98.4	96.7
Active	545	81	4445	87.7	95.2

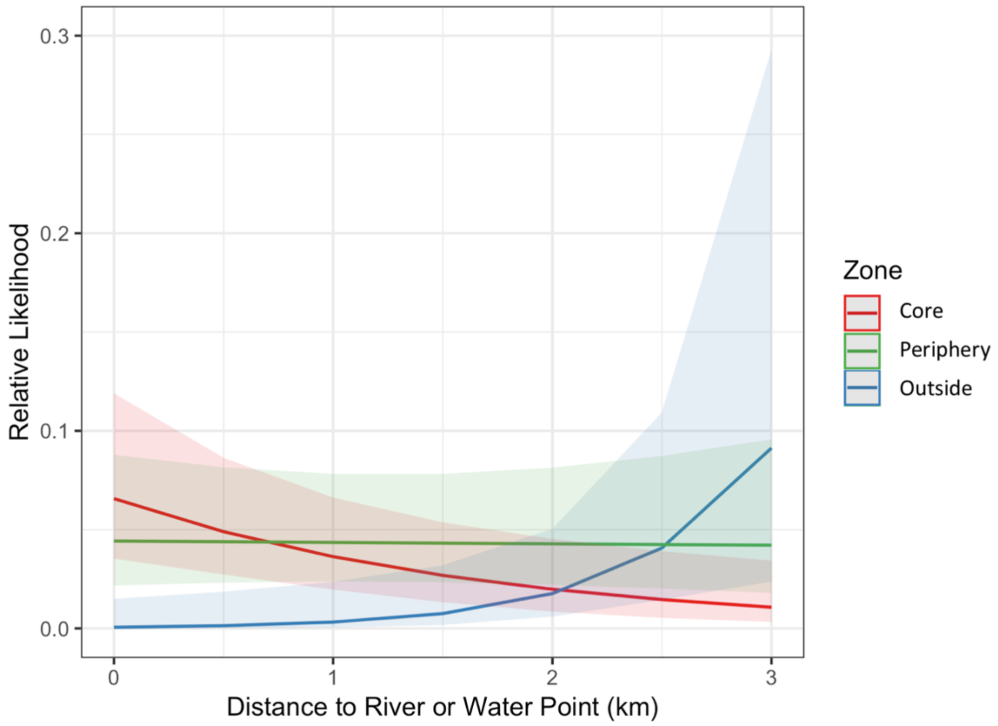

Figure S3.1 Relationship between relative likelihood of repetitive vocalization and the interaction between location relative to home range and distance to rivers and water points. *Shaded areas denote 95% confidence intervals.*

4 CARACAL: A versatile passive acoustic monitoring tool for wildlife research and conservation

Matthew Wijers, Andrew Loveridge, David Macdonald, Andrew Markham.

Resubmitted for final decision: *Bioacoustics*

Authorship: MW and AM conceived of the study; AM designed the CARACAL hardware and software; MW assembled the hardware and carried out the field tests and experiments; MW performed the data analysis with assistance from AM; MW wrote the manuscript with input from all authors.

4.1 Abstract

Acoustic localization technology has been widely tested and applied for passive acoustic monitoring and ecological research, however, hardware costs of commercially available devices limit scalability. Furthermore, few studies have explored its use with low-density arrays. We present a low-cost, custom-designed hardware and software system termed ‘CARACAL’ that is able to extract and localize weak acoustic signals. The key to this is the use of four microphones on each logger, allowing for phase-based measurements and the ability to enhance signal-to-noise ratio through beamforming. As a proof of concept, we test the functionality of the CARACAL system by conducting a gunshot localization experiment and demonstrate animal call detection and localization from a lion predation event. Results show the system could locate gunshots with an average accuracy of 33.2 ± 15.3 m within an array of 7 stations 500m apart, on par with commercially available devices. When applied to animal call positioning, we show long range (> 1 km) localization of three different species’ calls, Cape buffalo (*Syncerus caffer*), chacma baboon (*Papio ursinus*) and spotted hyaena (*Crocuta crocuta*). With a cost of approximately £150 per unit, the CARACAL system provides a cost-effective solution for acoustic localization over large areas. The system is open source and can be customized and adapted to suit a variety of applications related to wildlife research.

4.2 Introduction

Ecosystem monitoring is a key aspect of effective conservation strategies that provides baseline evidence for determining wildlife population trends and habitat use (Gibbs et al., 1999). Monitoring is equally important for facilitating the detection of environmental disturbances threatening the viability of these populations or the ecosystem as a whole (Astaras et al., 2017). Numerous survey methods exist for monitoring wildlife, however, in many cases there are fundamental challenges with scaling across space and time (Noon et al., 2012). National parks and other wildlife areas often span several thousand square kilometres and lack the infrastructure to facilitate frequent access for repeatable surveys. Similarly, obtaining long-term datasets with high temporal resolution for these areas can be constrained by cost and human physical limitations. One technology which has the potential to address some of the challenges faced by traditional surveys is passive acoustic monitoring (Wrege et al., 2017).

Passive acoustic monitoring (PAM) is an emerging tool in ecology and resource management which collects and processes environmental audio data for research and monitoring purposes. Though the challenges of marine mammal monitoring prompted most of the early development of PAM technology, terrestrial PAM usage has been stimulated by substantial increases in digital recorder capabilities, reductions in recorder costs, and the emergence of adaptable analytical software (Gibb et al., 2018; Marques et al., 2013). The majority of terrestrial PAM research has been conducted on birds (McGregor et al., 1997; Mennill et al., 2006; Frommolt & Tauchert, 2014; Sebastián-González et al., 2015), anurans (Crouch and Paton, 2002; Ospina et al., 2013), insects (Mankin et al., 2002; Pinhas et al., 2008; Riede, 1998) and bats (O’Farrell et al., 1999; Newson et al., 2017). PAM systems have a number of ecological applications such as determining species occupancy from presence and absence data (Heinicke et al., 2015), population assessment (Adi et al., 2010; Marques et al., 2013), monitoring of environmental disturbances and their effects on species behaviours (Hatch et al., 2008; Pirotta et al., 2015; Wrege et al., 2017), animal movement and territory use (Clark et al., 1996; Kalan et al., 2016) and investigating animal vocal behaviour (Payne et al., 2003). While the functionality of PAM systems varies according to research and monitoring objectives, several studies have outlined the importance of further development on automated sound detection and localization (Ali et al., 2009; Kalan et al., 2016; Marques et al., 2013).

Automated sound signal detection is critical for processing the vast quantities of data produced from multi-sensor acoustic arrays. Common detection techniques include hidden Markov models (Zilli et al., 2014), cross-correlation (Mellinger and Clark, 2000) and supervised machine learning such as decision trees and support vector machines (Heinicke et al., 2015; Sebastián-González et al., 2015; Newson et al., 2017). Variable performance results have been reported for detection algorithms with recall rates (proportion of correctly classified sound signals) often below 60% (Digby et al., 2013; Heinicke et al., 2015; Swiston and Mennill, 2009). Performance is likely to be species-related as some animal vocal signals may be more amenable to detection than others due to the acoustic characteristics of the calls (Mellinger et al., 2007; Newson et al., 2017). Acoustic signal quality also affects the probability of successful detection and may be influenced by the presence of overlapping, non-target sound signals from both natural and anthropogenic sources, the distance of the animal from a sensor and local environmental factors (Gibb et al., 2018).

Acoustic localization, while not as common as acoustic detection, is generally achieved using an array of three or more spatially separated audio sensors where differences in time of arrival (ToA) of an animal call signal can be used to calculate signal source location (Ali et al., 2009; Wilson et al., 2014). Other methods for determining location are based on angle of arrival of the signal (on a multichannel recorder) and differential signal strength (Ali et al., 2009). Acoustic localization accuracy can be affected by a number of environmental and array-specific factors. Dense vegetation, variable topography and the presence of large temperature and humidity gradients affect sound speed and attenuation and can be difficult to account for, thereby reducing the accuracy of location estimates (Darras et al., 2016). The degree of accuracy is also an intricate function of the locations of microphones in an array. More spatially extensive measurements of the arriving wavefronts leads to greater accuracy, yet larger spacing between microphones can decrease received signal strengths and coherence, degrading the accuracy of those wavefront measurements. In practice, location accuracy often decreases when the sound source originates from outside the convex hull of the sensor array (McGregor et al., 1997; Ali et al., 2009; Frommolt and Tauchert, 2014). Locating sound sources over large distances, even in flat, open areas, has therefore been challenging (Frommolt and Tauchert, 2014).

An important consideration in the design of passive acoustic arrays is the magnitude of the active space of the signal of interest. Acoustic localization has mostly been applied to the research of birds, frogs and small mammals with relatively short-range vocal signals which have therefore required dense sensor arrays (McGregor et al., 1997; Bower and Clark, 2005; Ali et al., 2009; Collier et al., 2010). The use of sparse arrays for localizing comparatively longer-range vocal signals, such as those emitted by African lions and spotted hyaenas, remains largely untested on land. In addition, audio recording devices capable of capturing data suitable for acoustic localization have been limited and thus the majority of studies have relied on commercially available recorders such as the Wildlife Acoustics Song Meters as used by Mennill et al. (2012). Modern, GPS-equipped commercial devices cost upwards of US$930 (Wildlife Acoustics, 2019) which restricts their use to smaller, well-funded surveys. With the recent advances and availability of microcontroller technology, many researchers are now turning to custom-made devices to suit their own needs at a fraction of the cost (Beason et al., 2018; Hill et al., 2018; Whytock and Christie, 2017). Most of the recent open-source innovations are, however, incapable of offering acoustic localization functionality.

In this study we present a low-cost, open-source hardware platform called CARACAL (Conservation at Range through Audio Classification And Localization) and associated signal processing software that is able to detect, match and localize sound emitters. We demonstrate the functionality of this system by using a sparse sensor array to locate gunshots and animal calls from ranges of more than 1 km. This system is intended to provide researchers and wildlife managers with a cost-effective tool to study and monitor ecosystems remotely by employing long range acoustic positioning.

4.3 Materials and methods

4.3.1 Sensor design

CARACAL circuit boards consisted of an ARM (Advanced RISC Machines) M4 Cortex microcontroller, interfaced to four PDM (digital) MEMS (microelectro-mechanical systems) microphones, placed at the cardinal compass points on an 8.4 cm diameter circle. Data are saved to micro-SD cards and accurately timestamped using GPS

PPS signals. The prototype unit costs under £150 to fabricate with hardware designs and firmware openly available at https://github.com/OpenWild.

4.3.2 Signal processing pipeline

A complete software pipeline was developed to automatically process audio files recorded by the CARACAL hardware (Fig. 4.1). Acoustic events are extracted from the raw multichannel audio based on a threshold of magnitude squared coherence (MSC) between pairs of channels. The MSC between two signals (x and y) is defined by:

$$C_{xy}(f) = \frac{|S_{xy}(f)|^2}{S_{xx}(f)S_{yy}(f)}$$

where $S_{xy}(f)$ is the cross spectrum density and $S_{xx}(f)$ is the power spectral density of signal x (Ramírez et al., 2008). The quadrophonic (four separate channels) audio per station are fused into a single (mono) channel using generalized cross correlation (GCC) beamforming (Knapp and Carter, 1976). Beamforming involves coherent addition of channels by estimating the relative delay (equivalent to a phase shift) per microphone. Signals correlated across all four microphones are enhanced by superposition, whereas uncorrelated signals (e.g. white noise, wind) are non-coherently summed. In an ideal case, the overall signal to noise ratio is boosted, for a four-microphone array, by a factor of 4 (6dB). However, the microphones on the CARACAL circuit board are spaced so closely that many sound pressure fluctuations in the audio range will be correlated to some degree which will reduce the actual signal to noise ratio.

Extracted events are then matched across all other station audio files to determine the relative time-delay with a likelihood metric measuring the confidence of the match.

Matched events are subsequently passed to a locator function which uses time of arrival differences to output an estimated position of the event. A log-likelihood (LLH) of the position provides a measure of confidence of each estimate. All functions are contained in a Python library and demonstrations made with Python notebooks which are open-source.

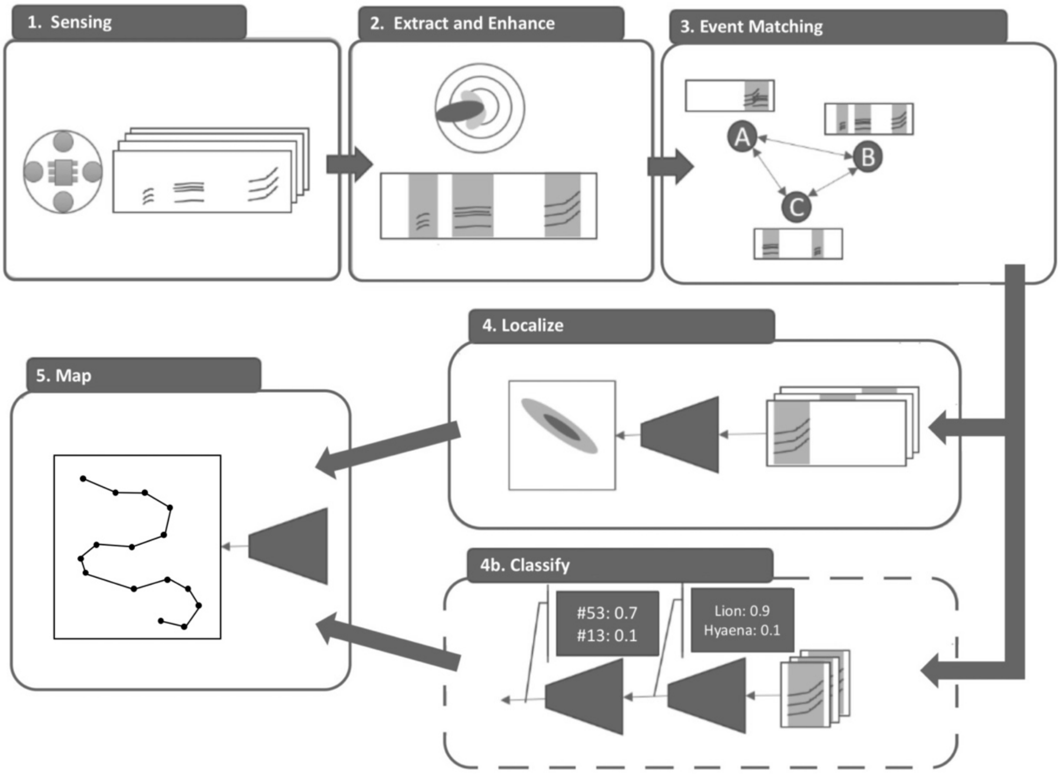

Figure 4.1 . Flow diagram illustrating the sequential steps of the CARACAL audio processing pipeline. *Step 4b can be included as an additional step in the processing sequence, but is not used in this study.*

4.3.3 Field deployment

Each CARACAL circuit board was mounted on a 3D printed plastic frame, fixed within a simple clip-seal plastic container (Fig. 4.2). We drilled three rows of 3 mm holes around the side of the container to allow free sound signal propagation to the microphones and secured polyester wadding material against the inner sides to reduce noise from wind. A 30 cm diameter, 3 mm thick acrylic disk, mounted on a 40 mm wooden cube block was fixed to the top of the container to provide protection from rain and direct sunlight. The containers, housing the circuit boards, were then mounted on top of 5 m high telephone poles (Appendix - Fig. S4.1).

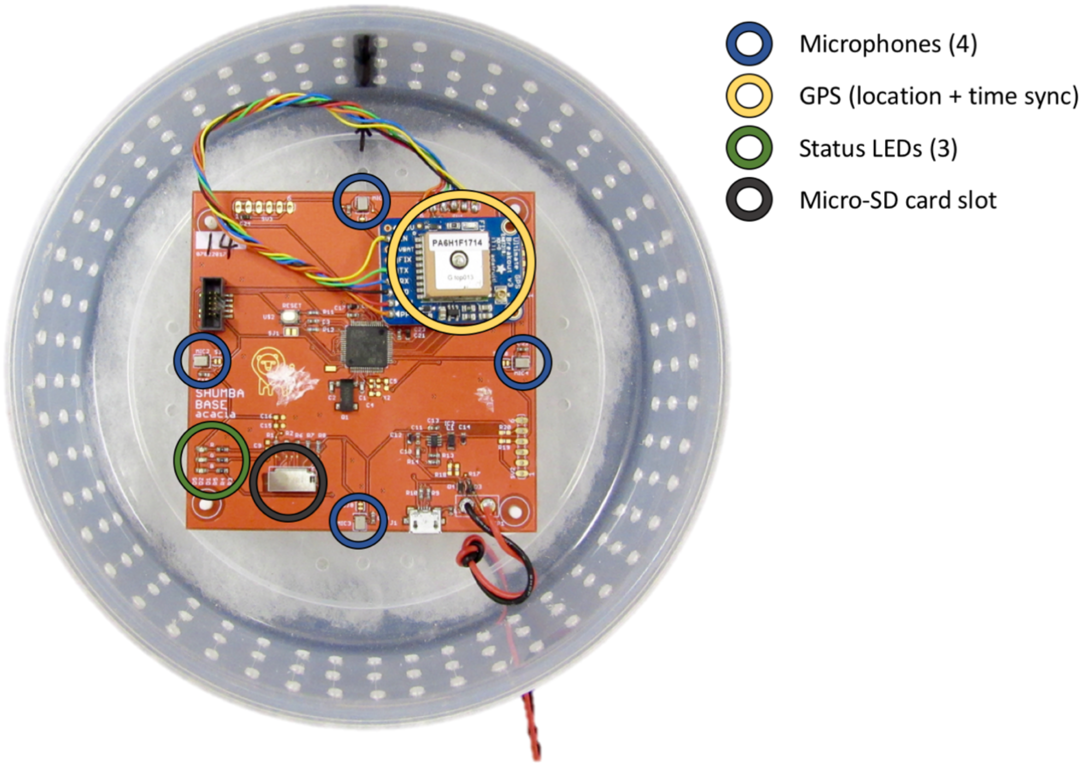

Figure 4.2 Image showing CARACAL circuit board with major components, secured within a plastic container.

We deployed a total of 8 CARACAL recording stations in a grid layout across a ~6 km^2 study area in the south western section of the Bubye Valley Conservancy (BVC), a privately managed wildlife area in southern Zimbabwe (Appendix - Fig. S4.2). The BVC hosts a large number of vocally active mammals such as African lions (*Panthera leo*), spotted hyaena (*Crocuta crocuta*), African bush elephant (*Loxodonta africana*), Cape buffalo (*Syncerus caffer*) and chacma baboon (*Papio ursinus*) making it an ideal study site to test the functionality of the CARACAL system with long-distance animal vocalizations. Each station was separated by a distance of ~500 m from the nearest neighbouring station. Care was taken to ensure all stations were horizontally orientated with one microphone consistently facing North. While CARACAL circuit boards can be powered with a variety of battery options (3-12 V), we used a battery bank consisting of six AA 2500 mAh rechargeable batteries in series (~8 V) which was secured on top of the plastic container, below the acrylic disk. Audio data were written to a 64 GB microSD card which could store 48 hours of continuous recording (44.1 kHz, 16 bit, 4 channel).

4.3.4 Case study: Gunshot localization

This study aimed to test the accuracy of sound signal localization using the CARACAL system. Gunshots were chosen as the test signal as the characteristic gunshot blast is easily identifiable and propagates over long distances. Additionally, gunshots often reveal the presence of illegal poaching activities in wildlife areas where early detection and accurate localization could reduce reaction times to such incidents.

Using a LM-5 assault rifle, we fired 28 controlled gunshots along roads with a spacing of ~250 m between shot locations. For each shot, GPS coordinates were recorded using a handheld Garmin eTrex GPS. All recordings were downloaded and imported into Audacity software, version 2.1.1 (Audacity team, 2019), where the arrival time of each gunshot was marked and recorded for each station by visual inspection of spectrograms. The ToA data were passed through the CARACAL localization algorithm with the

Euclidean distance in two dimensions between the estimated and true location calculated for each shot. When assessing localization accuracy, it is necessary to distinguish between shots originating from inside and outside the convex hull (CH) of the array as signals outside the array are generally localized poorly in comparison to those within the array. Since the localization results were not normally distributed based on a Shapiro-Wilcoxon normality test, we tested whether accuracy differed between the two regions by carrying out a Mann-Whitney U-test.

We also sought to investigate the localization performance using ToA data from between 3 and 7 stations as sparser deployments are likely to be more cost effective but may impact localization performance. For every combination of each number of stations, the localization error was calculated for each gunshot occurring within the CH of the tested array. A cumulative distribution function of the gunshot localization errors was plotted for each number of stations.

4.3.5 Case study: Animal call localization

This study was based on a single lion predation event, where a pride of 6 lionesses attacked, and later killed, a Cape buffalo within the study area. We aimed to demonstrate the ability of the CARACAL system to localize a variety of long-distance animal calls and to compare manual annotation of calls with the automated processing pipeline. Only four CARACAL stations were deployed on the night of this predation event (stations 7, 8, 10 and 14) but still provided sufficient data for localization. We selected 300 seconds of continuous audio starting from the beginning of the event (first bellow of the buffalo in distress). We also included a 100 second period of audio from ~ 40 minutes after the start which contained additional long-distance animal calls. Following the method stated above for gunshot localization, spectrograms of the audio associated with the predation event were labelled manually with the arrival times of each animal call. Each call was also manually classified according to species. Using the CARACAL localization algorithm and ToA data, position estimates for each call were mapped relative to the array and surrounding landscape features (riverbeds and conservancy boundary).

Using the manually labelled data as a benchmark, we also assessed the performance of the CARACAL audio processing pipeline. All audio files were passed through the pipeline for event detection, matching and localization. We first tested the performance of the CARACAL signal detector (coherence detector) using a receiver operating characteristic (ROC) analysis and included a naïve energy detector to provide a comparative measure of performance. Energy detectors are often used with more typical, single-channel recordings. We then tested the efficacy of the locator function using a high LLH threshold (LLH > 0) in order to minimize the number of incorrectly localized events (false positives). The resulting output of localized events were compared with the manually labelled audio.

4.4 Results

4.4.1 Gunshot localization

Time synchronized audio data were collected from seven out of the eight stations as station 6 malfunctioned during the test. Gunshots originating within the CH (convex hull) of the functioning 7-station array were localized with significantly lower errors than those from outside the CH ($U = 32.0$, $n_{inside} = 12$, $n_{outside} = 16$, $p < 0.01$). The mean localization error for gunshots inside the CH was 33.2 ± 15.3 m (mean ± 1 sd), while shots outside were localized with a mean error of 83.3 ± 58.1 m (mean ± 1 sd). The median localization errors for each region were 32.0 m and 61.8 m respectively. Locations of the true and estimated locations of gunshots were plotted relative to the array stations along with the distributions of the errors in each region (Fig. 4.3).

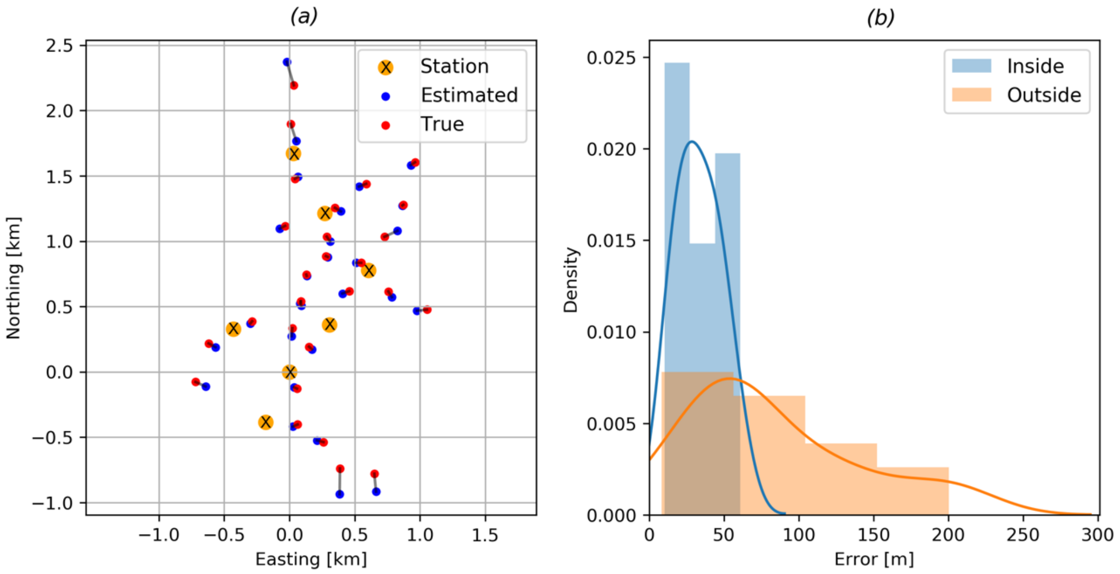

Figure 4.3 Relative positions of true and estimated locations of gunshots (a), and corresponding distribution of localization errors for shots originating inside and outside the CH (b).

When all 7 functional stations were used to localize gunshots within the convex hull of the array, 100% of shots were localized within 100 m of the true location. When stations were experimentally reduced to 6, 5, 4 and 3, the percentage of shots localized within 100 m reduced to 99%, 89%, 80% and 53% respectively (Appendix - Fig. S4.3).

4.4.2 Animal call localization for predation event

Manual processing

Detailed manual inspection of the audio associated with the predation event revealed 64 distinct animal calls in the vicinity of the array. Twenty-four of these calls were identified as Cape buffalo (*Syncerus caffer*) bellows, 29 as chacma baboon alarm calls (*Papio ursinus*) and 11 as spotted hyaena (*Crocuta crocuta*) calls. A temporal progression of the localization of all 64 calls (Fig. 4.4) showed an initial cluster of buffalo bellows closely distributed around co-ordinates x = 250 m, y = 900 m. Less than two minutes later, two clusters of baboon alarm calls were estimated to have occurred near station 7 (600 m, 950 m) and ~ 100 m south of station 14 (0 m, -50 m). Two separated bouts of spotted hyaena calls were then recorded, one at a time of 3 minutes and another at 40 minutes. The first bout was localized south east of the array (900 m, -250 m) and the second outside the Conservancy boundary (-900 m, -100 m). Although no ground truth was available against which estimated positions could be compared, a fine scale plot of the estimated positions of each buffalo bellow showed these locations to be distributed within ~ 70 m of the carcass (Appendix - Fig. S4.4).

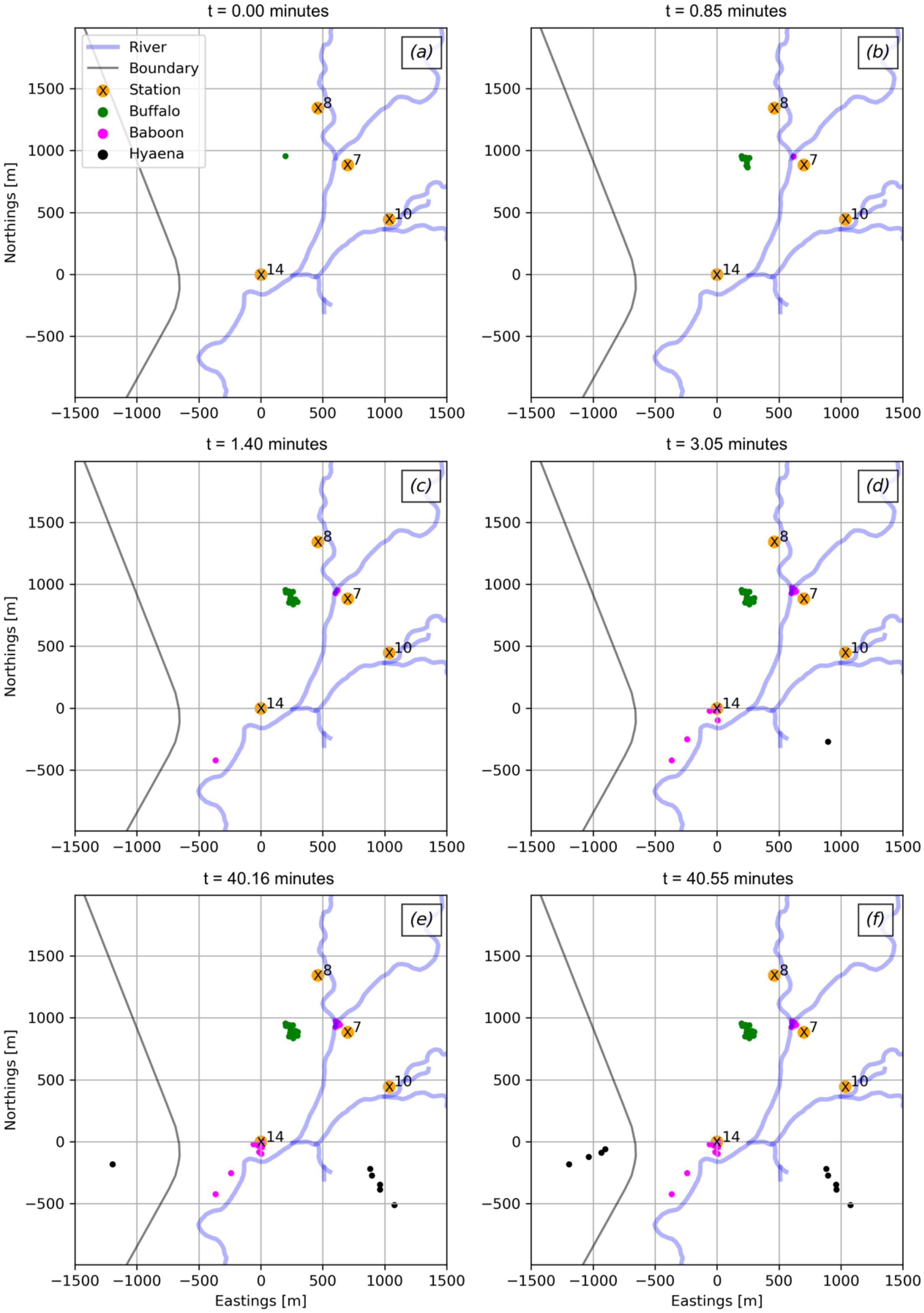

Figure 4.4 A series of maps showing overlaid localizations of animal calls. *First bellows from buffalo being attacked by lions (a); First alarm call from baboon troop near station 7 (b); First alarm call from baboon troop near station 14 (c); First spotted hyaena call south east of the array (d); First spotted hyaena call from a second animal outside the conservancy boundary, south west of the array (e); Last call from spotted hyaena outside the boundary (f).*

Automated processing

Using the manually labelled dataset as a benchmark, we assessed the performance of the automated processing pipeline. The ROC analysis (Fig. 4.5) revealed high discriminatory power for the coherence detector (area under the curve (AUC): 0.95) against comparatively poorer discriminatory power for the energy detector (AUC: 0.52). The events detected by the coherence detector were then passed to the signal matching and locator function. With an LLH threshold > 0, the locator function produced position estimates for 53.1% of the manually labelled events. Of these positions, 88.2% were found to have been localized correctly. Overall, the automated processing pipeline was able to detect and accurately localize 46.9% of the true acoustic events (Fig. 4.6) Manual classification of these events showed species-specific recall of 83.3% for buffalo, 13.8% for baboon and 54.5% for spotted hyaena. The processing rate for the automated pipeline was approximately 3 minutes of 4-channel audio per minute. For an 8-station array, the system would take approximately 2 hours 40 minutes to process a 1-hour period of audio which is equivalent to 32 channel hours (8 stations x 4 channels x 1 hour).

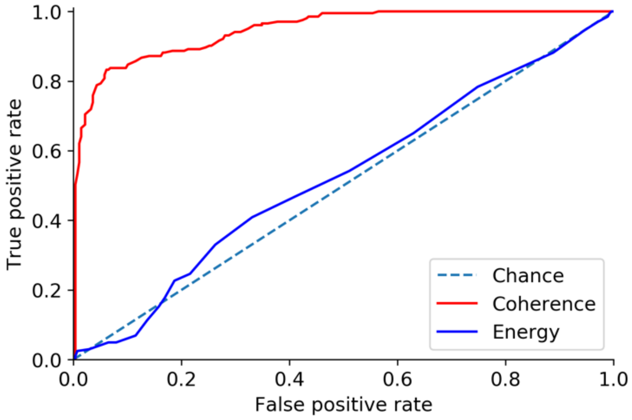

Figure 4.5 Receiver Operator Characteristic (ROC) curve comparing detection performance of the coherence detector used by the CARACAL system against that of an energy detector.

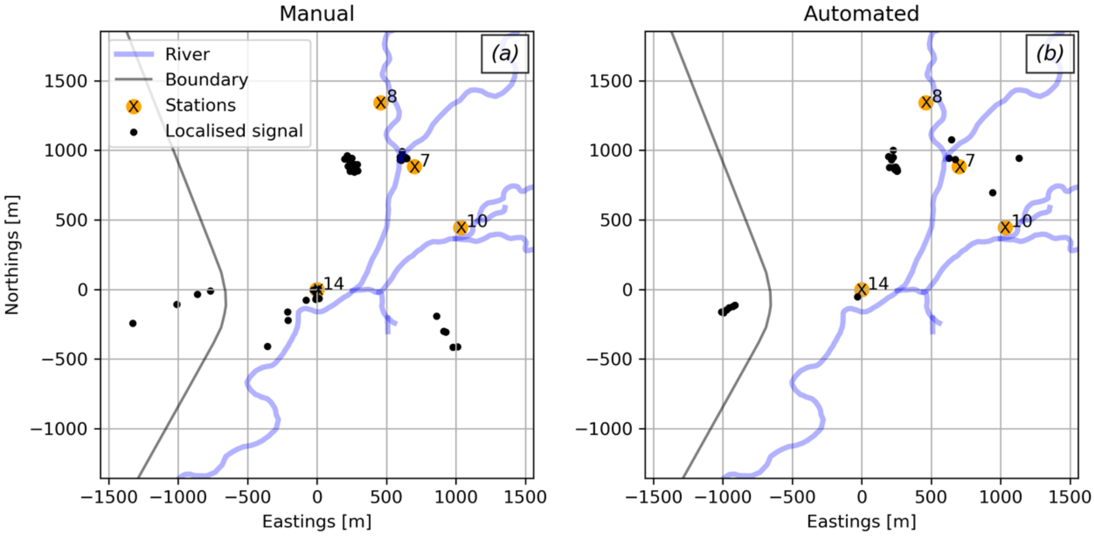

Figure 4.6 Maps showing position estimates of animal calls identified manually (a) and using the automated signal processing pipeline (b).

4.5 Discussion

A major factor limiting the scalability of PAM systems has been the hardware costs associated with commercially available audio recorders (Gibb et al. 2018; Mennill et al. 2012). Only recently have cheaper, open source devices, such as the Audiomoth, become accessible to researchers and facilitated larger deployments (Beason et al., 2018; Hill et al., 2018). However, the main focus of Audiomoth to date has been on quantifying the acoustic soundscape and automated signal detection rather than localization, due to its lack of precise time-synchronization across loggers. At a cost price of ~ £150 per unit, the CARACAL system fits into this category and provides weak signal detection and localization through the use of a time-synchronized, multi-microphone hardware design. Using a sparse array of CARACAL stations, we found that relatively accurate acoustic localization can be achieved over large ranges (> 1 km), offering valuable information on disturbance events, such as gunshots, and animal species' presence and distributions.

Although gunshot localizing and reporting technology already exists in modern cities (e.g. 'ShotSpotter' (ShotSpotter, 2019)), their size, cost and power requirements prohibit their use in remote, natural environments where the necessary supporting infrastructure does not exist (Hill et al., 2018). Several studies have tested the application of small, autonomous audio recorders to gunshot detection as the use of high-powered guns for poaching is a relatively common occurrence in many wildlife areas (Astaras et al., 2017; Hill et al., 2018; Wrege et al., 2017). Using data from the seven functioning stations, and with no information on environmental variables (e.g. temperature and humidity), the CARACAL system was able to localize gunshots occurring inside the array within 33.2 m of the true location on average. The majority of studies that have conducted acoustic localization have done so using station separation distances of between 15 and

75 m and have reported localization errors of less than 3 m (McGregor et al., 1997; Bower and Clark, 2005; Mennill et al., 2006; Ali et al., 2009). While closely spaced detectors may be favourable for some species in small areas, such configurations would not be practical or cost-effective for monitoring large areas (e.g. >1000 km^2). Our results are, however, similar to those reported by Kershenbaum et al., (2019) who used commercially available recording devices spaced 1-3 km apart to localize wolf howls and achieved an average distance error of 83 m. Although the localization errors for sparse deployments are likely to be considerably higher than those for dense arrays, highly accurate (< 3.0 m error) localizations may not be necessary for monitoring species with large home ranges.

Minimizing the number of stations available in an area to detect and locate animal calls is likely to be a priority when designing sparse acoustic arrays. Although a minimum of three detectors is required for localization, results from the simulated removal of stations showed considerable improvements in localization accuracy when ToA data from more than three stations were available. The relatively poor localization performance observed for three stations is likely a result of the dual localization solutions produced for some combinations of arrival time differences in this configuration (Spencer, 2007). Acoustic localization systems that are dependent on ToA would therefore benefit from deployment patterns that enable signal detection from at least four stations. In order to reduce array density, the use of techniques that facilitate detection of signals from greater distances would be advantageous. The multi-microphone design used in CARACAL enabled the use of beamforming; a method which enhances the signal to noise ratio of sound from certain directions, which effectively increases the acoustic detection area (Mellinger et al., 2007). In addition to this feature, The CARACAL system utilizes a coherence detector (a threshold of similarity between a pair of signals) which provides a significant improvement over standard signal strength (energy) detection where it can be difficult to set detection thresholds. Signal coherence is also more consistent across varying degrees of signal strength and is especially effective for weak signals (Fig. 4.7).

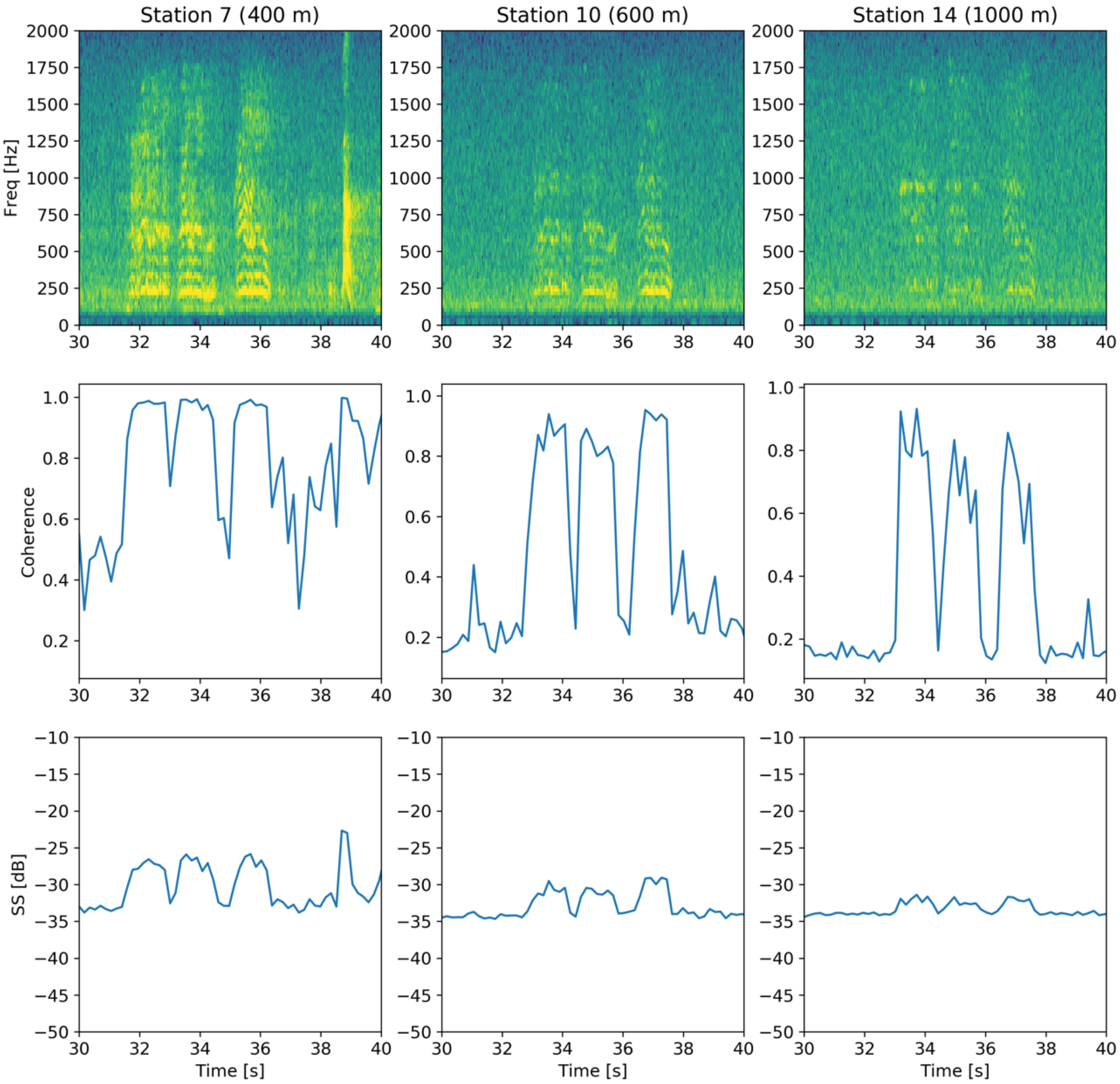

Figure 4.7 Comparison between signal coherence and signal strength for progressively weaker buffalo call signals (left to right) recorded at three different stations with increasing distance from the animal.

It is important to note that signal coherence relies on the availability of signals from two or more spatially close microphones which is a core design feature of the CARACAL hardware. A further benefit of the quadrophonic microphone design is the ability to estimate the Angle of Arrival through the delay matrix estimated during the beamforming process. This can be used in combination with ToA to reduce density further and enhance the capacity to distinguish between calls from multiple sources, offering a significant improvement over single sensors for point count applications. We therefore suggest this as a promising future direction of research.

Many species actively emit vocal signals for communication, and by doing so, offer information on their presence at a particular location (McGregor, 1993). We demonstrate that long-range localization of animal calls can provide valuable information on biological events, such as predation, which would otherwise be difficult to detect. Although the CARACAL audio processing pipeline demonstrated good detection performance and successfully localized the majority of the buffalo bellows, it failed to accurately localize many of the baboon alarm calls and a whole bout of spotted hyaena calls. The poor performance for baboon calls is likely related to the short, repetitive vocal behaviour of the species which creates challenges when matching signals from each station as one call may be incorrectly matched with another. Furthermore, different species' calls frequently overlapped which each other which also impacted the matching of calls between stations. The pipeline is likely to function effectively when animal calls do not overlap with those of conspecifics or those from other species. The presence of overlapping signals is, however, a common issue for most extant detection algorithms which leads to low recall (Gibb et al., 2018). Despite these limitations, the CARACAL processing pipeline can act as an effective initial filter by scanning through many hours of audio and identifying locations with high vocal activity which can then be investigated further. The alternative approach of manually processing long periods of raw audio would be unfeasible given the time and effort required to locate and match signals across several stations. The speed and functionality of the processing pipeline can also be enhanced through the use of parallel computing and cloud technologies (Ahmad et al., 2018; Varghese and Buyya, 2018), as well as with the addition of sound classification techniques that assign species labels to extracted events (Mielke and Zuberbühler, 2013).

Acoustic localization allowed us to recreate a biological event by offering considerably more contextual information than would be available from other forms of monitoring technology used in wildlife research such as single channel acoustic recorders (Hill et al., 2018; Whytock and Christie, 2017) and camera traps (Kays et al., 2011). Data obtained from such events could be used to investigate a variety of animal behaviour patterns including inter- and intraspecific interactions and competition, habitat use and species vocal communication. Our study also highlights the potential for acoustic detection and localization to complement conventional GPS tracking which still remains a popular method for studying animal movement behaviour and habitat use (Kays et al., 2015). The procedures required to fit GPS tracking devices to study animals are often invasive and can require substantial resources and veterinary expertise thereby limiting the number of individuals that can be tagged. The CARACAL system can overcome some of these challenges by facilitating remote localization, over large areas, for any vocalizing individual. Kershenbaum et al. (2019) showed this to be possible for wolves in Yellowstone National Park but used costly commercial recording devices which would likely limit scalability.

While acoustic localization may be advantageous in many ways, there are several limitations with this approach. Firstly, localization is reliant on the emission of a sound signal from the animal of interest and therefore may not be a suitable method where regular and consistent location information is required or where study species do not vocalize at all. Secondly, being able to identify individual animals is a fundamental requirement for studies investigating animal movements or estimating density from spatially explicit mark recapture. Several studies have reported finding unique vocal signals for individuals of certain species, however, vocal individuality remains largely untested for most taxa (Gibb et al., 2018; Mathevon et al., 2010; Soltis et al., 2005). Thirdly, and perhaps a more common problem, is that sound signals are often indistinct as a result of high noise levels and overlapping signals from other sources (Frommolt and Tauchert, 2014). Further work is required to build accurate signal extraction, separation and classification algorithms that will provide useful data to end users.

Weaknesses associated with the CARACAL system in its current form are mainly related to the lack of on-board processing. With ~ 30 GB of raw data produced by each station every day, SD cards had to be replaced every second day which was costly and time-consuming. This could be extended to a week or more by using larger SD cards (e.g. 512 GB) but these typically cost more than the logger itself. Retrospective examination of the audio also resulted in large time lags between event occurrence and detection, limiting its use for reacting to time-critical events such as poaching. The weaknesses identified from this study will be used to inform further development of the CARACAL system. Future iterations will combine hardware and software developments that will facilitate on-device and in-network data processing. Acoustic detection and localization can also be improved by incorporating angle of arrival and signal strength variables and by accounting for sound wave diffraction around the array structure (Gillett et al., 2008). Coupled with power supply improvements, through integration with solar panels for example, these enhancements will increase the autonomy and independence of the system and deliver real-time alerting.

Marques et al. (2013), suggested that future research on PAM systems should focus on, among others, the development of reliable and low-cost autonomous sensor arrays that are capable of ranging. Similarly, Kalan et al. (2016) noted that PAM systems could be improved by automated individual caller identification, acoustic localization and real-time data transmission. We have demonstrated the ability of the CARACAL system to address some of these gaps by providing cost-effective acoustic detection and source localization over large ranges using novel hardware configurations and data processing techniques. CARACAL can be customised and developed further or used in its current form to investigate a variety of biological questions where knowledge of the locations of sound sources are required.

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4.9 Appendix

Figure S4.1 Image showing field deployment of CARACAL logger.

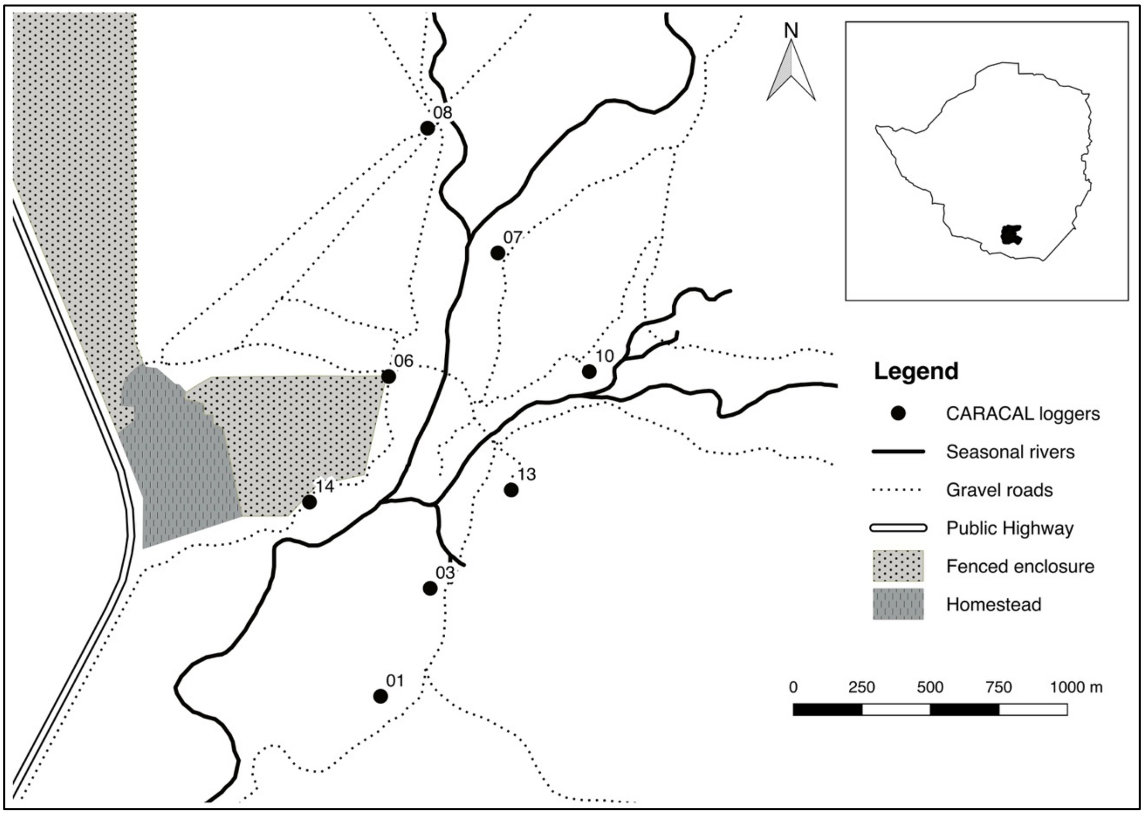

Figure S4.2 Map of the study area showing locations of CARACAL loggers. Inset map shows location of BVC in Zimbabwe.

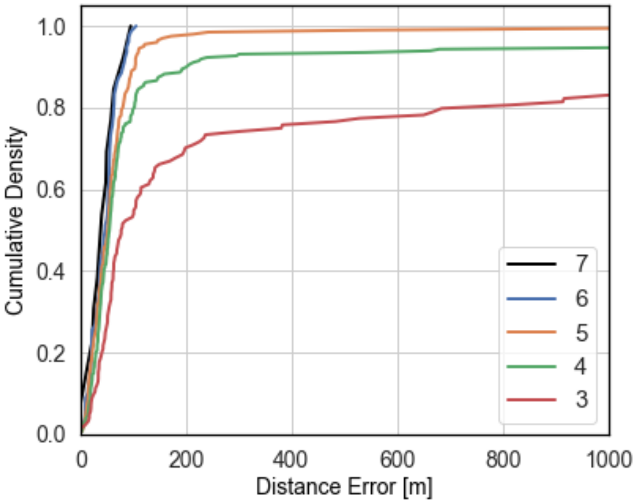

Figure S4.3 Cumulative distribution functions for the gunshot localization errors for each number of stations.

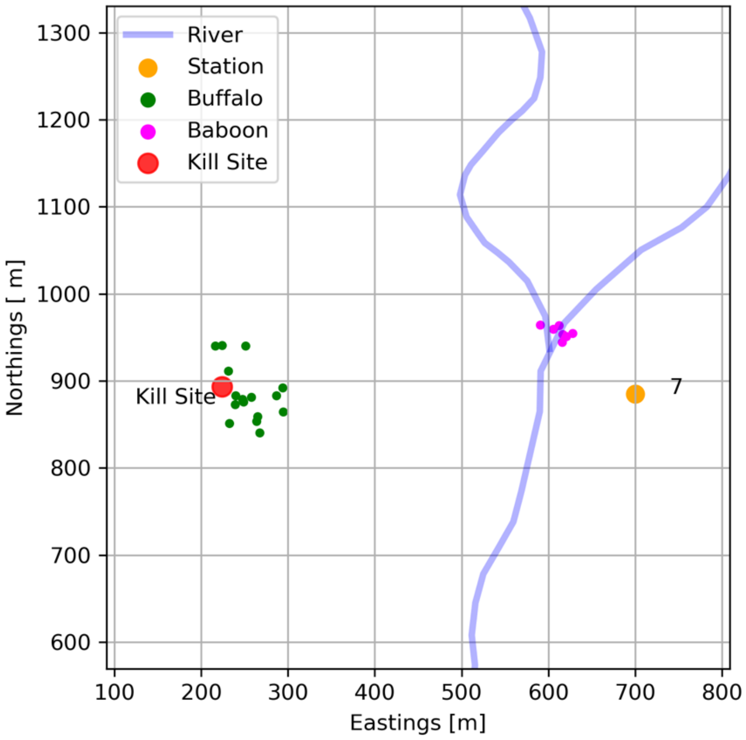

Figure S4.4 High resolution map showing estimated locations of buffalo bellows relative to the kill site.

5 Vocal discrimination of African lions and its potential for collar-free tracking

Matthew Wijers, Paul Trethowan, Byron du Preez, Simon Chamaillé-Jammes, Andrew Loveridge, David Macdonald, Andrew Markham.

Prepared for submission: *PNAS*

Authorship: SC-J, AL and DM conceptualized the addition of audio sensors to biologgers while MW conceived of the study design and analytical approach. AM designed the biologgers and passive acoustic recorders and assisted in the extraction of data. Study animals were captured and fitted with biologgers by PT, BdP and MW. MW assembled the passive acoustic recorders, recorded lion vocalizations, carried out the data analysis and wrote the manuscript with input from all authors.

5.1 Abstract

Many animal species are known to encode individual identity in their vocalizations. In some cases, vocal individuality can provide researchers with a valuable means of monitoring individual animals. The loud, long-distance roar of an African lion is an important behavioural trait facilitating maintenance of territory boundaries and likely conveys information relating to caller identity. A number of playback studies have shown that lions have the ability to discriminate between conspecific vocalizations, but little is known about how lions are able to transmit identity information in their roars. Using biologgers and a passive acoustic array, we test for lion vocal individuality in the fundamental frequency (*f*0) of roars from 5 male lions and explore the use of passive acoustic monitoring for lion tracking. Vocal discrimination is tested first, using simple summary features, and then by modelling the temporal pattern of the fundamental frequency contour using hidden Markov models. We then use a combination of GPS tracking, acoustic localization and vocal discrimination to demonstrate identification and localization of roars from two male lions. Results indicated that the use of simple *f*0 summary features only allows for vocal discrimination with 71.3% accuracy. By comparison, vocal discrimination can be achieved with an accuracy of 91.5% based on individual differences in the temporal pattern of the *f*0 sequence. We further demonstrate that passively recorded lion roars can be localized and identified with similar accuracy, highlighting the value of passive acoustic monitoring for tracking lion movements. The existence of individually unique *f*0 contours in lion roars and their relatively lower attenuation indicates a likely mechanism by which individual lions can identify conspecifics over long distances. These differences can be exploited to track individuals across the landscape and thereby supplement conventional GPS tracking.

5.2 Introduction

African lions (*Panthera leo*) are well known for their loud, characteristic roars, frequently audible from several kilometres away. Lions are, however, just one of many terrestrial mammalian species that are capable of communicating vocally over large distances. The basic function of long distance signalling is to aid individuals in locating and avoiding each other and therefore facilitating group cohesion and the maintenance of territorial boundaries (Marler, 1967; Mitani and Nishida, 1993; Ramsauer, 2005). A key component of the information conveyed to conspecifics through the use of long-distance calls is individual identity. Reception of this information is crucial for influencing the response of the receiver. For example, in the context of territoriality, identifying a call from a neighbouring animal in their usual location will likely elicit a different response to that of an unfamiliar animal (McGregor, 1993). Several studies on terrestrial mammals such as elephants (*Loxodonta africana*; Clemins et al., 2005), orangutans *(Pongo pygmaeus wurmbii*; Spillmann et al., 2017), tigers (*Panthera tigris*; Ji et al., 2013), wild dogs (*Lycaon pictus*; Hartwig, 2005) and wolves (*Canus lupus*; Root-Gutteridge et al., 2013) have shown that certain elements of vocal signals are unique to individuals and thereby convey information relating to caller identity. Typically, researchers seek to uncover the mechanisms for vocal individuality (e.g. temporal variations in frequency or amplitude) and to assess the stability of individually unique signals over time (Feng et al., 2014; Zdenek et al., 2018). The evolution of individuality has also attracted considerable interest with sociality thought to be one of the primary drivers of this phenomenon (Pollard and Blumstein, 2011). The production of individually unique signals is likely related to variations in the morphology (e.g. length and stiffness) of the vocal apparatus between individuals (Fitch, 1997; Ey et al., 2007). Encoding information on individual identity is therefore inevitable and provides an ‘honest’ signal to receivers which cannot be ‘faked’. This is in contrast to strategic or cost-added mechanisms of signal honesty whereby fitter individuals can invest more energy in higher quality signals that are more costly to produce (Zahavi, 1975).

Despite the ability of many animals to encode individually unique features within their calls, sound signals degrade progressively as they propagate through the environment. Higher frequencies are more rapidly absorbed through air and incur greater scattering by small objects (e.g. vegetation) compared to lower frequencies, resulting in changes to the spectral structure of the original signal (Forrest, 1994; Wiley and Richards, 1978). This degradation can impair the ability of distant receivers to extract information. Several studies on birds have shown that individuals responded more strongly to undegraded calls than to degraded calls (McGregor et al., 1983; Mathevon and Aubin, 1997). Despite the loss of information incurred during signal propagation, some species are able to learn and accurately recognize the degraded call of a conspecific through experience (Mouterde et al., 2014).

Knowledge of how species transmit information relating to individual identity is important for understanding species communication mechanisms. In some cases, vocal individuality can also be exploited by researchers and conservationists to monitor and survey species populations using individually distinct vocal features as a non-invasive marking method (Terry et al., 2005). For example, Gilbert et al. (2002) investigated the survival and movements of great bitterns (*Botaurus stellaris*) using spectrogram measures of vocalizations. Similarly, Delport et al. (2002) relied on vocal identification of African wood owls (*Strix woodfordii*) to monitor territory turnover. However, despite the large number of studies that have explored vocal individuality, there are relatively few published examples of how acoustic monitoring of individuals can be applied in practice, particularly for mammalian species (Peake and McGregor, 2001).

In order to assess animal vocal individuality, acoustic features must first be extracted from the call recordings. Although this can be done automatically using state-of-the-art deep learning techniques (Stowell et al., 2018), a more common approach to feature extraction entails separating the original signal into multiple discrete frequency components (collectively referred to as a filter bank), using fast Fourier transformations. A variant of this method involves the calculation of Mel-frequency cepstral coefficients (MFCCs) which effectively warps the frequency axis to the Mel-scale under the assumption that the species perceives frequencies on a logarithmic scale (Clemins and Johnson, 2005). The use of MFCCs is prevalent in human-speech recognition and is becoming more popular for the identification of animal vocalizations (Clemins et al., 2005; Mielke and Zuberbühler, 2013; Spillmann et al., 2017). Feature extraction can also be done manually, whereby simple summary variables (e.g. min, max, mean) associated with the fundamental frequency and the harmonics are calculated (Fan et al., 2019; Ji et al., 2013). Following feature extraction, pattern recognition algorithms are implemented to 'learn' the acoustical features associated with each individual and subsequently classify 'unseen' call signatures. The recognition models are assessed based on their ability to classify the 'unseen' calls correctly. Several algorithms have been used for this purpose, including discriminant functions (Blumstein and Munos, 2005; Fan et al., 2019), artificial neural networks (Mielke and Zuberbühler, 2013; Reby et al., 1998), Gaussian mixture models (Cheng et al., 2010) and hidden Markov models (Clemins et al., 2005; Ji et al., 2013). One of the main issues affecting the classification performance of vocal recognition models is the presence of background noise. Noise from any natural or anthropogenic source introduces additional sound information and thereby increases model variation and classification uncertainty (Terry et al., 2001). The majority of studies have dealt with this issue by removing samples with overlapping signals (Clemins et al., 2005; Reby et al., 1998).

Lions emit loud, low-pitched vocal signals referred to as ‘roars’. A single roar is typically delivered in a bout consisting of one or two soft moans followed by several full-throated roars and a terminating sequence of short grunts (Grinnell and McComb, 2001; McComb et al., 1994). The low fundamental frequency of the roar (~ 150 Hz) can be attributed to the long and heavy vocal folds, characteristic of the species’ vocal anatomy (Weissengruber et al., 2002). Both male and female members of a pride are known to roar and will do so to either maintain contact with distant companions, or to advertise territory ownership (Grinnell and McComb, 2001; McComb et al., 1994). Lions also use roars to transmit information relating to group size. A series of overlapping roars emitted by three or fewer individuals provides an honest indicator of the number of individuals present, allowing receivers to assess their chances of successfully deterring potential competitors (McComb et al., 1994). Several studies have reported evidence of vocal recognition in lions. For example, McComb et al. (1993) found that adult females are able to distinguish between playbacks of familiar, resident males and those of unfamiliar males by noting changes in female response to different calls. Similarly, individual lions have been shown to display stronger responses to situations where a familiar call does not match a familiar lion, suggesting that specific calls are associated with specific individuals (Gilfillan et al., 2016). Other studies have examined the attributes of individual roars and have found differences in the temporal pattern and acoustic features between male and female roars, however, little is known about whether consistent differences exist between individuals (Pfefferle et al., 2007; Stander and Stander, 1988). This knowledge gap is likely attributable to the difficulties associated with obtaining sufficient samples of roar recordings from known individuals in the wild and highlights the need for a new approach to acquire data on animal vocalizations.

Lions defend large territories, often in excess of 500 km^2 (Tumenta et al., 2013; Zehnder et al., 2018). Given that the primary functions of the roar require receivers to differentiate between individuals in order to respond appropriately (Grinnell and McComb, 2001), it can be reasoned that the transmission of information relating to caller identity over long distances would be advantageous. It can therefore be expected that selection would favour animal calls that transmit information efficiently by minimizing degradation of the intended signal. Despite many studies being dedicated to lion vocal behaviour, little is known about how lions convey information relating to individual identity in their call structure. In this study, we investigate lion vocal individuality based solely on the fundamental frequency of full-throated lion roars; the frequency that is likely to suffer the least degradation over large distances. To achieve this, we use a novel acoustic biologger which facilitates the acquisition of a relatively large dataset of lion roar events. We also demonstrate the conservation implications of our findings by testing the application of acoustic recognition and localization for tracking individual lion movements.

5.3 Materials and methods

5.3.1 Study site

The study took place in the Bubye Valley Conservancy (BVC), a privately-owned wildlife area located in southern Zimbabwe between latitudes 21.209 and 21.851° South, and longitudes 29.789 and 30.521° East. The BVC measures approximately 3400 km^2 in area and hosts a variety of indigenous megafauna including a high density of African lions (du Preez et al., 2015). Habitat within the Conservancy is dominated by mopane woodland savannah with riparian woodland occurring along several seasonal river lines. Annual rainfall is typically low, averaging 351 mm, and falling mostly in summer between November and March (du Preez et al., 2014). Maximum daily temperatures are high (> 40°C) in the summer months and comparatively mild in winter.

5.3.2 Data collection

Biologgers

Given that lions vocalize predominantly during the night and can be difficult to identify and observe, we used an on-animal audio recording approach to investigate lion vocal individuality. In November 2014 we fitted custom-designed acoustic biologgers to five male and three female lions as described in Wijers et al. (2018). Study animals were chemically immobilized using 75-100 mg Zoletil (Virbac RSA (Pty) Ltd, Halfway House, South Africa) combined with 5 mg medetomidine (Kyron Laboratories, Johannesburg, South Africa). Immobilization drugs were delivered intramuscularly by 1 cc darts (Pneudart, Williamsport, Pennsylvania, USA) projected from a Dan-Inject CO2-pressurized dartgun (Dan-Inject, Børkop, Denmark). After fitting the biologger, ~ 25 mg atipamazol (Antisedan, Pfizer Animal Health, Johannesburg, South Africa) was administered to reverse the effects of medetomidine allowing the animal to recover within 15 – 90 mins. The biologgers recorded continuous audio (8 bit, 16 kHz mono) for between 4 and 10 days before the batteries were depleted. Study animals were then recaptured and the data downloaded for processing and analysis.

Acoustic array

To explore the application of acoustic recognition and localization for lion tracking, we set up a custom-designed passive acoustic array system within the home-range of a coalition of two male lions (neither of which had been previously fitted with biologgers) fitted with GPS collars (set to record geographic location every hour between 17:00 and 07:00 local time). Animals were captured using the same capture technique as described in the preceding section. The acoustic array consisted of 8 time-synchronized audio recording stations each separated by ~ 500 m from the nearest station. When operational, each station recorded audio continuously (32 bit, 44.1 kHz, 4 channel). The array was activated on selected nights between June and November 2018 when weather conditions were optimal (dry and low wind speed).

5.3.3 Vocal individuality

Roar extraction

All lion audio recordings were processed manually in Audacity 2.1.1 (Audacity Team, 2019) by visually inspecting spectrograms and annotating the position of lion roar events. Labelled lion roars were then extracted and classified by individual identity. Roars containing interference (e.g. noise from natural or anthropogenic sources) or overlapping roars of nearby lions were excluded from the analyses. Because the aim of our study was to test for individual differences in the full-throated (FT) roars for each study animal, we further annotated and extracted audio segments containing the FT roar units for each roar bout (Fig. 5.1). As described in several other studies, the FT roars are the high amplitude signals emitted after the initial soft moans and before the sequence of short grunts (Grinnell and McComb, 2001; McComb et al., 1994; Stander and Stander, 1988).

Fundamental frequency extraction

For each FT roar unit, we first applied a bandpass filter function to focus further analyses on the fundamental frequency (*f*0) between 40 Hz and 230 Hz. We extracted the peak frequency contour for this bandwidth (the *f*0 contour) by computing the short-time Fourier transformation (STFT) for the signal using a 2048-point moving Hann window with 68% overlap and zero-padding to four times the window length. The above extraction process was conducted in Python using the 'SciPy' library (Jones et al., 2001).

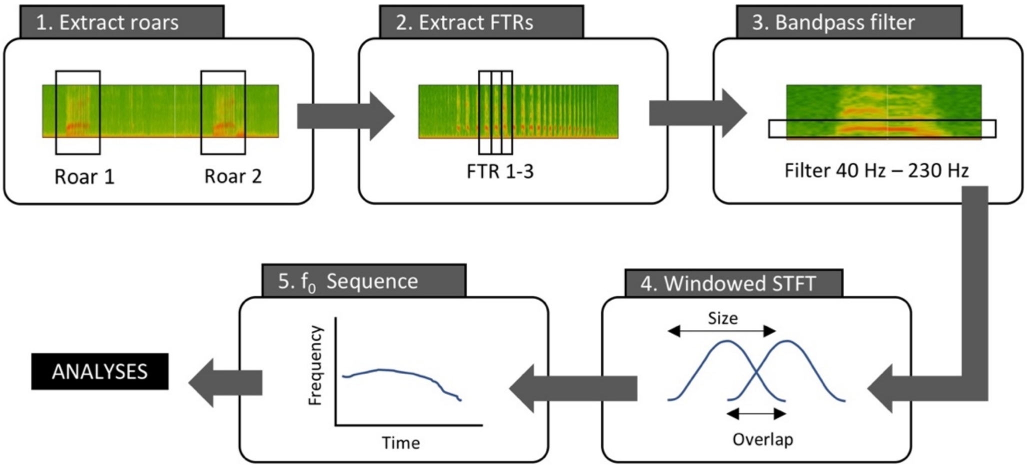

Figure 5.1 Fundamental frequency extraction process.

Fundamental frequency summary features

Following the method used by Ji et al. (2013), we aimed to investigate whether four *f*0 summary features differed between individuals: maximum *f*0, minimum *f*0, mean *f*0 and roar duration. Because the data were non-normal, we used the Kruskal Wallis method to test the hypothesis that the median feature value of least one individual differed from that of at least one other individual. Post-hoc pairwise multiple comparisons were then conducted using Dunn's test with Bonferroni adjustment. In addition to the statistical analyses, we used the k-nearest neighbours (K-NN) algorithm to test the classification ability of models built using the four *f*0 features, individually and combined. The purpose of this test was to measure the discriminative ability of each *f*0 feature and to determine whether the combined feature set was sufficient to accurately discriminate between individuals. Each K-NN classifier was assessed using the overall accuracy metric produced from a repeated 10-fold cross-validation (3 x 10 cv). All statistical analyses were conducted in R (R Core Team, 2019).

HMM classification of f0 contour

A hidden Markov model (HMM) is a statistical tool for representing the probability distributions over a sequence of observations and is therefore useful for modelling time series data (Ghahramani, 2001). An additional benefit of HMMs is their ability to model patterns of varying length as would be expected from variable duration lion roars. We used HMMs to model the temporal pattern of the *f*0 contour for each individual lion. The roar recognition experiment was implemented using the leave-one-out cross validation method whereby 10-state Gaussian HMMs were trained for each individual using all but one sample of the *f*0 sequences. Note that a sample, in this case, consists of FT roar *f*0 sequences from the same bout. The unseen *f*0 sequences were then tested against each HMM by determining which model was most likely to produce the given sequence (using the log-likelihood metric). This process was repeated for all samples, ensuring that all tests were carried out on examples not used for training while also allowing for large training set sizes. Classification performance was assessed by calculating overall accuracy, recall and precision metrics of classified sequences. HMM classification was performed in Python using the 'hmmlearn' library (hmmlearn Development Team, 2019).

5.3.4 Lion tracking application

We used an acoustic array to record roars from two known male lions fitted with GPS tracking collars. Identified roars were manually matched across at least 4 stations with the time of arrival (ToA) of the signal recorded for each roar at each station. The difference in the ToA of the signal between stations allowed us to localize the source of the roar with an accuracy of ~ 100 m using custom-written functions in Python. Estimated roar locations were then compared with GPS collar data from the two lions to determine the identity of the caller. An example of the comparison between GPS collar positions and roar localizations is shown in Figure 5.2. In this particular example, the second male lion was not near the array, allowing us to confidently identify the individual vocalizing. For the analysis, we excluded roars that contained noise from other sources (e.g. wind) as wells as roars for which the identity of the caller was uncertain (e.g. when lions roared while in close proximity to one another). To test roar recognition performance, we used audio recorded by the closest station to the lion. Raw 44.1 kHz audio was first down-sampled to 16 kHz, followed by FT roar and *f*0 extraction. We then trained 4-state

Gaussian HMMs for each individual and carried out tests using the leave-one-out cross validation method as described previously.

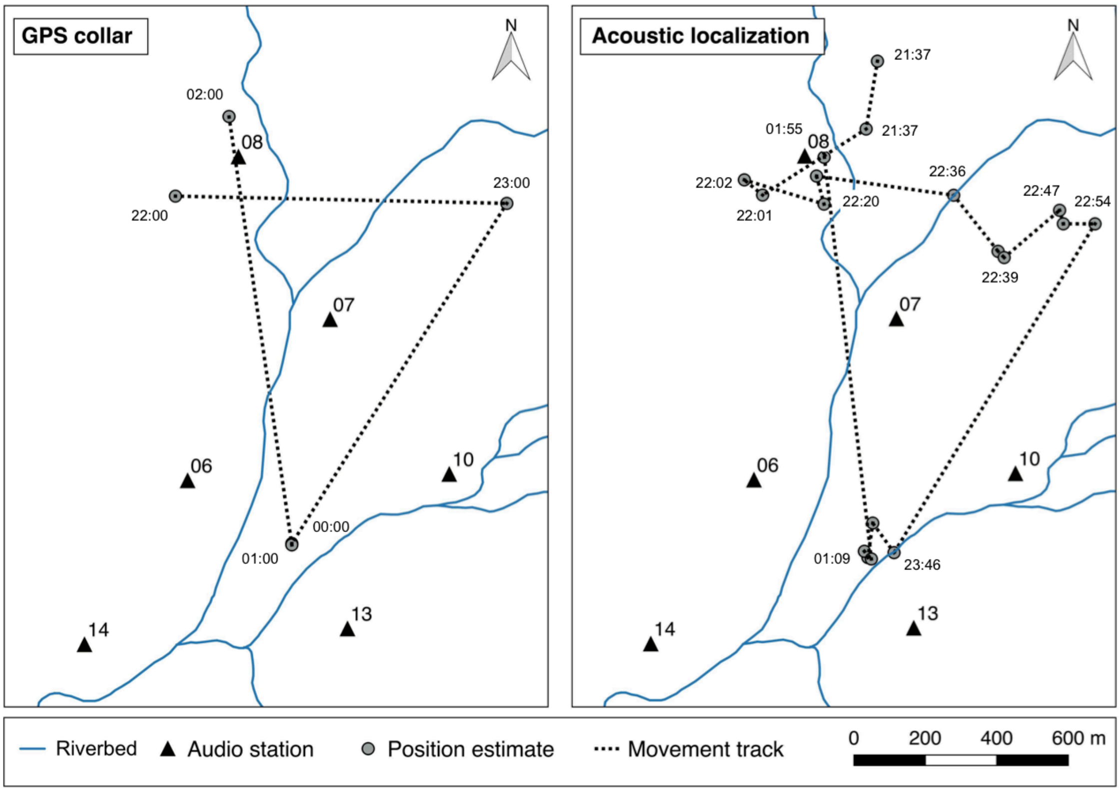

Figure 5.2 Comparison between collar GPS positions (left) and roar localization (right) for a 4-hour period from a single lion. *Where possible, timestamps are provided next to each position estimate.*

5.4 Results

5.4.1 Vocal individuality

We recorded a total of 60 lion-days of audio from the eight lions fitted with biologgers. Manual inspection of the audio revealed a total of 297 roaring bouts from the 5 male lions. The 3 female lions did not appear to roar and only uttered soft moans. Of the total number of bouts, only 78 were useable as the majority contained overlapping roars from conspecifics. From the useable roar bouts, a total of 164 FT roars were extracted, ranging from 24 (lion ID: A10) to 40 (lion ID: A9) for each individual male.

Fundamental frequency summary features

Results of the Kruskal Wallis tests, produced *p* values below 0.001 for all *f*0 features indicating significant differences in max *f*0, min *f*0, mean *f*0 and duration between at least one pair of individuals. Post-hoc analyses using the Bonferroni-Dunn test revealed that *f*0 features did not differ significantly between all individuals (Table 5.1). Roars emitted by lion A4, in particular, were found to have significantly lower maximum *f*0 (median = 162.1 Hz), mean *f*0 (median = 122.3 Hz) and duration (median = 1.01 s) compared to other lions. Consistent differences between lions A8, A9, A10 and A11 were not as apparent (Fig. 5.3). All lions were of similar age and size, however, precise body measurements such as those taken by Pfefferle et al. (2007) were not collected due to time constraints which therefore precluded analysis of the relationship between animal traits and vocal characteristics.

The analysis of the classification ability of K-NN models built using each of the *f*0 features showed a performance range of between 26.2% (min *f*0) and 52.4% (max *f*0) when single features were used (Table 5.1) Overall classification accuracy increased to 71.3% when all four features were used together. Optimal performance was achieved using a k value of 7.

Table 5.1 Results of Kruskal Wallis tests (chi-squared and p values) and overall accuracy of the K-NN classifiers for each of the four f0 features.

Feature	**K-NN Classifier**	**Kruskal Wallis**		**Pairs that were significantly different**
	Accuracy	χ^2	*P value*	
Min *f*0	26.2	37.6	< 0.001	A9-A10; A10-A11; A10-A4; A9-A8
Max *f*0	52.4	79.4	< 0.001	A9-A10; A9-A4; A10-A4; A11-A4; A9-A8; A8-A4
Mean *f*0	46.1	98.2	< 0.001	A9-A10; A9-A11; A9-A4; A10-A4; A11-A4; A9-A8; A4-A8
Duration	34.6	71.4	< 0.001	A9-A4; A10-A4; A11-A4; A4-A8

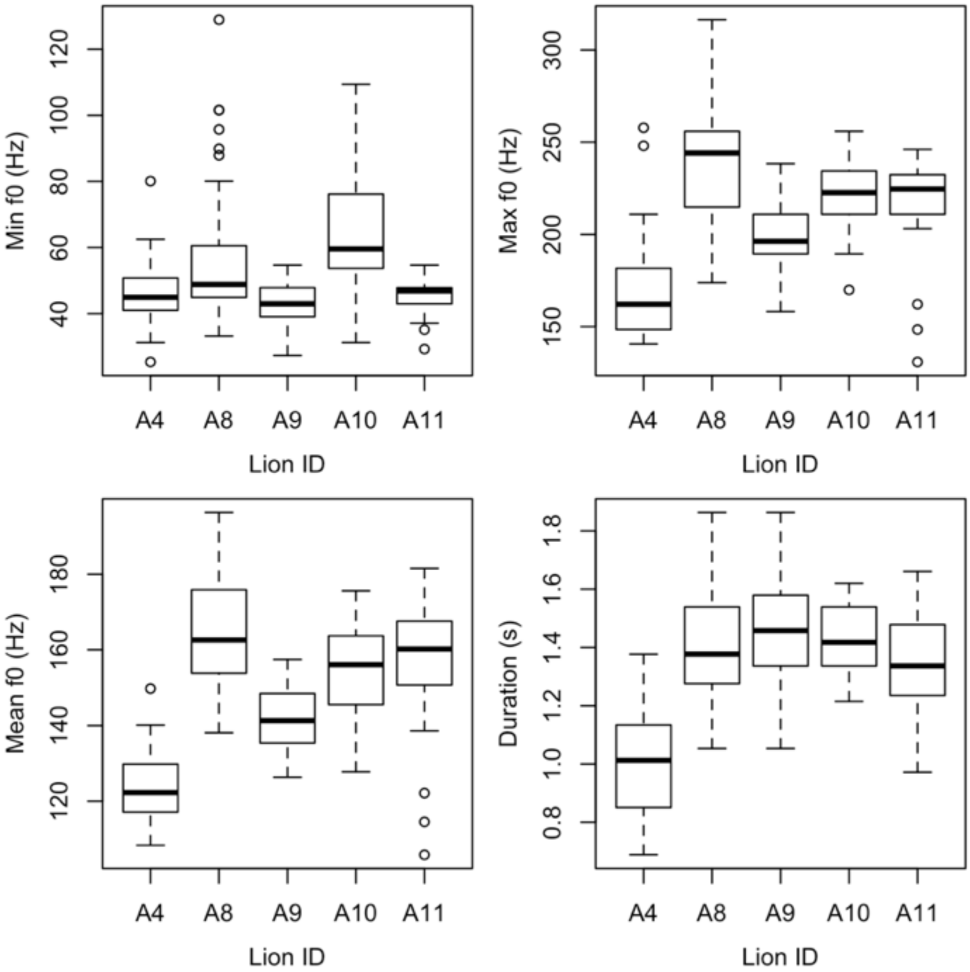

Figure 5.3 Boxplots of the four f0 summary features for each lion.

HMM classification of f0 contour

Visible differences in the shape of the *f*0 contour were evident in the FT roars for each lion (Fig. 5.4). Modelling the temporal pattern of individual *f*0 sequences resulted in high classification performance with an overall accuracy of 91.5% and average recall and precision of 91.0% and 91.7% respectively (Table 5.2). Four out of the five lions were classified with recall greater than 90%. Recall for lion A10 was found to be lower at 83%. We also investigated classification performance using training set sizes of between 40 (approx. 8 roars per individual) and 160 (approx. 32 roars per individual) roars. Performance was found to increase considerably from 40 to 120 roars and then more gradually beyond 120 roars (Fig. 5.5). Optimal performance is therefore likely to be achieved with datasets consisting of 24 or more roars per individual.

Table 5.2 Confusion matrix of actual lion IDs (rows) vs predicted IDs (columns) for biologger recorded roars.

Individual	**A4**	**A8**	**A9**	**A10**	**A11**	**Recall %**	**Precision %**
A4	36	0	2	0	0	94.7	100.0
A8	0	33	0	0	2	94.3	84.6
A9	0	2	36	1	1	90.0	92.3
A10	0	2	1	20	1	83.3	95.2
A11	0	2	0	0	25	92.6	86.2
Average						91.0	91.7

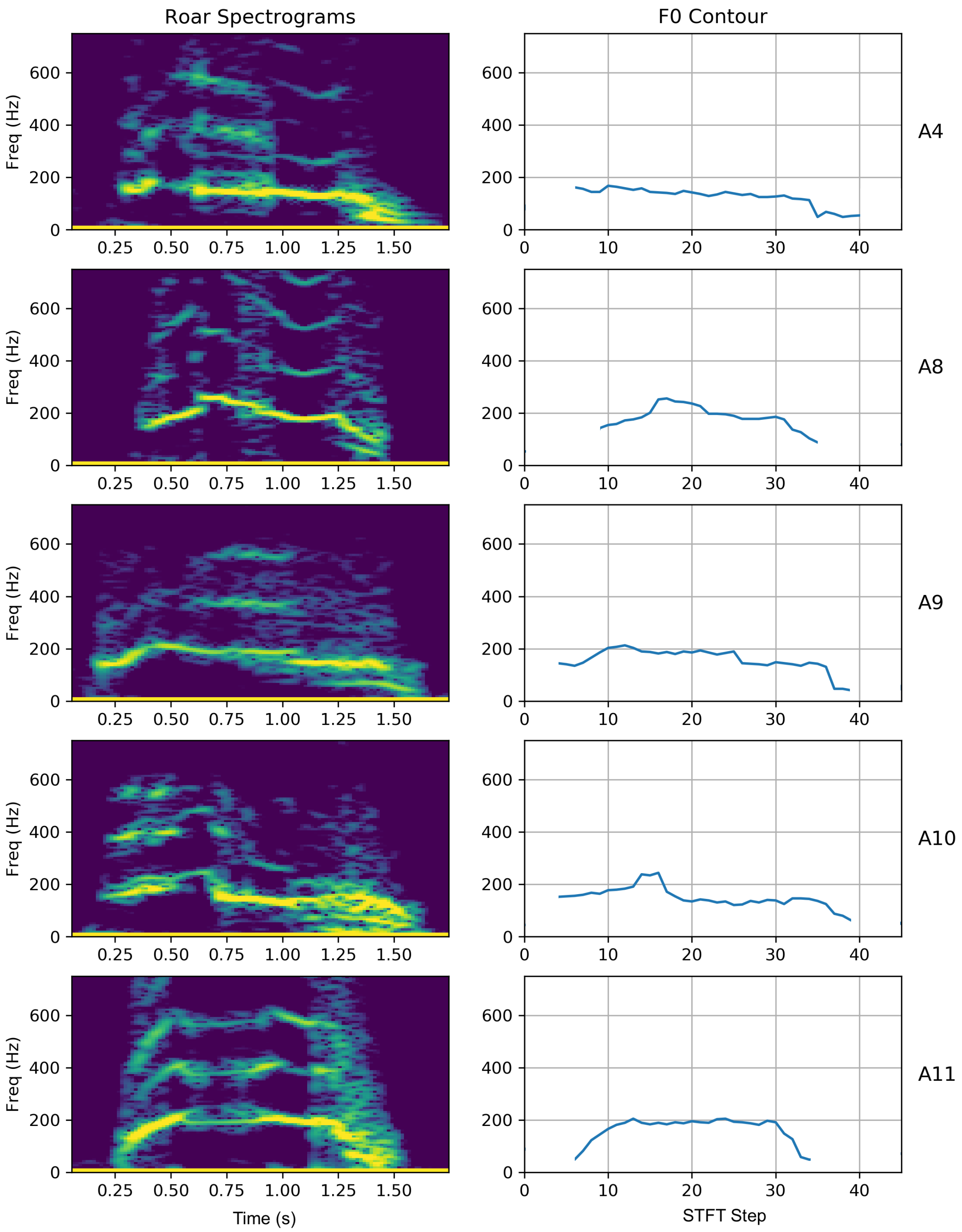

Figure 5.4 Examples of FT roar structure and corresponding f0 contour pattern for each individual as recorded by the animal-borne biologgers.

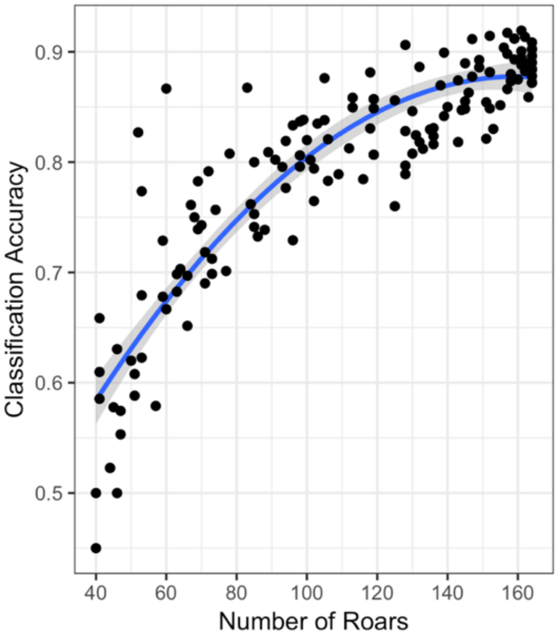

Figure 5.5 Classification accuracy using an increasing number of training set samples. *Shaded area shows 95% confidence intervals.*

5.4.2 Lion tracking application

We extracted a total of 50 FT roars from 31 roaring bouts emitted by the two collared males while they were in the vicinity of the acoustic array. The FT roars were then localized using ToA differences and identity assigned according to corresponding collar GPS data. Results of the HMM classification showed that, using passively recorded audio, we could differentiate between the two individuals with an overall accuracy of 90.0%. Recall was slightly higher for lion B1 compared to lion B2 (Table 5.3). Vocalizations used for identification originated from distances ranging from 45 m to 1094 m with incorrectly classified calls distributed relatively evenly across the distance spectrum (Fig. 5.6).

Table 5.3 Confusion matrix of actual lion IDs (rows) vs predicted IDs (columns) for passively recorded roars.

Individual	B1	B2	Recall %	Precision %
B1	25	2	92.6	89.3
B2	3	20	87.0	90.9
Average			89.8	90.1

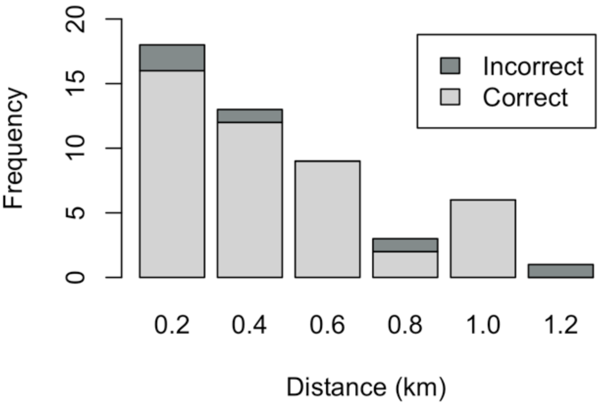

Figure 5.6 Distance distribution of correct and incorrectly classified roars.

5.5 Discussion

Previous research dedicated to African lion vocal communication focused on receiver responses to experimental playbacks with few studies exploring variations in the acoustic structure of calls (Gilfillan et al., 2016; Grinnell and McComb, 2001; McComb et al., 1993). While these playback-response experiments have undoubtedly provided important insight into the function of vocal signalling (e.g. territorial advertisement and maintaining group cohesion) and the possible information content of the signal (e.g. identity and sex), knowledge of how this information is conveyed has been lacking. In this study, we have demonstrated that the temporal pattern of the fundamental frequency of lion roars is a possible mechanism for lion vocal identification and is useful for automated digital differentiation of individuals.

We acquired our lion roar dataset using a novel acoustic biologging method which made it easy to obtain a sufficient number of roar recordings from each individual and to be able to reliably associate roars with lion identity. When recording animal vocalizations manually, it can be difficult to tell which individual is vocalizing (Clemins et al., 2005). This is particularly true for identifying lions in the wild where the only clues to identity are subtle differences in whisker spot patterns or unique scars (Pennycuick and Rudnai, 1970). Furthermore, lions roar mostly during the night which can make it even more difficult to accurately differentiate between individuals. Manual recording approaches are also costly and time consuming and can potentially influence animal behaviour as a result of observer presence.

Results of the statistical analysis exploring differences in roar duration and maximum, minimum and mean fundamental frequency between individuals showed that these factors were not consistently different between all individuals. This suggests that simple overall summary features that do not incorporate temporal variation may not provide optimum discriminatory power to differentiate between individual lions. This was confirmed by the relatively poor classification accuracy of the K-NN model which could only classify 71.3% of calls correctly, although, this is still better than chance (20%). Similar classification performance (69.9%) was reported by Ji et al. (2013) for tigers, using these same four features. Other $f0$ features have been used in vocal identification studies on spotted hyaenas (Mathevon et al., 2010), monkeys (Fan et al., 2019) and wolves (Root-Gutteridge et al., 2013) with varying success (32%-88%). The roars emitted by lion A4 appeared to be significantly shorter and had lower maximum and mean fundamental frequencies compared to the other four lions. Lion A4, although resident in the study area, was known to have originated from the Tuli Block in eastern Botswana from where it dispersed more than 60 km before breaking into the fenced Bubye Valley Conservancy. The differences observed for this lion alludes to the possible existence of vocal dialects. Variations in vocalizations between populations of other species are known to exist and may occur between different lion populations (Deecke et al., 2000; Martins et al., 2018; Mitani et al., 1992). Indeed, Stander and Stander (1988) also reported that Etosha lions have shorter roars than lions in other parts of Africa. While these variations may be dialectal, Conner (1982) makes an important distinction between 'dialects' and 'geographical variation' and highlights the fact that differences arising as a result of geographic barriers to geneflow do not constitute dialects. Such differences are more likely due to genetic or anatomical differences, rather than the cultural evolution of learned traits which result in true dialects. In order to define the vocal variation between lion populations it would be necessary to obtain call recordings from each population along with genetic and anatomical data (e.g. size) on each individual from which calls are recorded. If individuals from each population are not genetically or anatomically distinct, then the possibility that variation is dialectal may be explored further (Mitani et al., 1992).

Although the use of $f0$ summary features resulted in relatively poor classification performance, when we modelled the temporal pattern of the $f0$ sequence using HMMs, classification performance improved considerably to an overall accuracy of 91.5%. The overall shape of the $f0$ contour is therefore a defining characteristic that allows for better discrimination between individual lions. This finding is consistent with studies on other species which have found that the frequency distribution of vocalizations from each individual are similar but the temporal patterns of the signals are unique to each individual (Clemins et al., 2005; Ji et al., 2013). The key novelty of our approach is in the use of the *f*0 sequence as the only feature for identification rather than the more common approach of using filter bank or MFCC features derived from a range of frequencies which include the harmonics. As shown in Figure 5.7, the higher frequencies of a full-throated lion roar degrade noticeably more than the fundamental frequency which is more consistent across space. Information contained in the fundamental frequency is therefore likely to be preserved over distance and received effectively by a listener. A study on long-distance communication between elephants (*Loxodonta africana*) also showed that the higher formant frequencies of a call are unable to carry information related to individual identity over long distances (3 km) and therefore identity is more likely to be discerned from the lower frequency harmonics in the 115 Hz region (McComb et al., 2003). Our results support this theory and thereby provide a likely explanation for the mechanism underpinning individual vocal recognition amongst African lions. We acknowledge, however, that it would be necessary to conduct playback experiments using spectrally modified calls in order to determine the extent to which lions are able to recognise conspecifics purely by the fundamental frequency of their calls. Recognition can be determined from differential response to modified calls as has been used in other studies (McComb et al., 1993). We therefore suggest this as a beneficial avenue for future research in lion communication and as well as for other species.

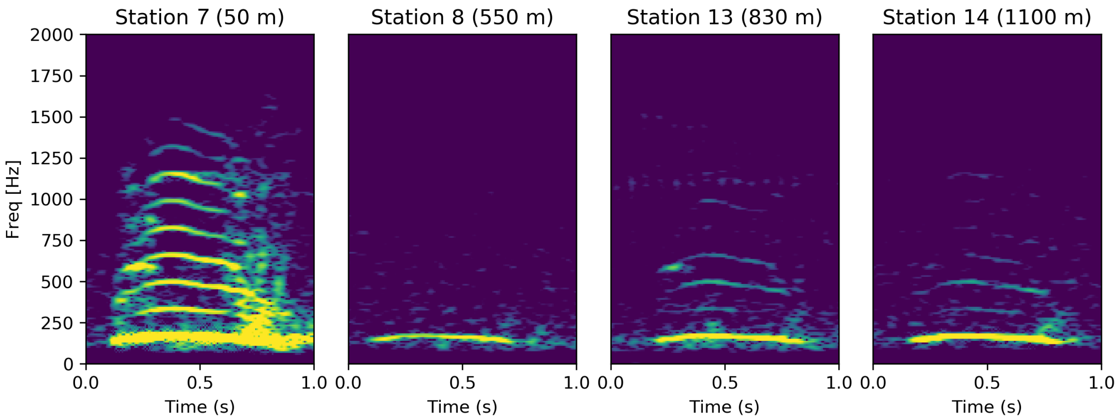

Figure 5.7 Spectrograms of the same FT roar recorded at varying distances from the animal.

Understanding how lions are able to recognise conspecifics from their vocal signals is not only important for advancing our understanding of lion ecology, but also provides a useful feature by which lions could be identified using autonomous, acoustic recorders. Traditionally, abundance estimates for lion populations have been achieved using call-in surveys (Ferreira and Funston, 2010), spoor transects (Stander, 1998) and camera trap surveys (Cusack et al., 2015). Vocal identification of lions may allow for the use of passive acoustic monitoring methods which have the potential to be fully automated using detection and recognition algorithms. Automation would facilitate longer term or even continuous surveys and significantly reduce the number of man-hours required for data management; a challenge that is inherent to camera trapping when individuals need to be manually identified.

Hartwig (2005) highlighted the value of individual vocal identification of African wild dogs (*Lycaon pictus*) as a supplement to radio telemetry and visual recognition. Similarly, one of the primary benefits of acoustic monitoring of lions would be its facilitation of collar-free tracking which is likely to provide movement information for a greater number of individuals at lower cost compared to animal-borne systems. Using an acoustic array and sound signal localization techniques, we were able to obtain position estimates for several roars emitted by two resident male lions. The locations of the roars corresponded closely with collar GPS positions which provided reliable ground truth information for assigning identity labels to each roar in order to build individual recognition models. Models trained for each individual were able to accurately classify ‘unseen’ roars from varying distances. We therefore show that, with sufficient training data, it would be possible to locate and identify lion roars and thereby track individual movements across the landscape using passive acoustics as illustrated in Figure 5.2. Furthermore, by integrating in-network data processing, real-time tracking would be achievable, particularly as the data content of the $f0$ contour is extremely small and therefore easily transmitted over the air. However, despite the roar classification performance being considerably better than chance, we acknowledge that this experiment was conducted for only two individuals, whereas in practice, discrimination between several different lions may be required including out-of-set (unknown) individuals. Obtaining a sufficient number of clean vocalization samples from known lions without the use of biologgers is a difficult task. As shown in our results, too few training samples can lead to reduced classification performance. This is especially true when attempting to distinguish between signals that have a greater degree of similarity (Trifa et al., 2008). Collecting such data is likely to present the biggest challenge to the development of large-scale, collar-free lion tracking systems. However, with the development of machine learning methods, particularly unsupervised clustering approaches, discriminating between individuals may be possible without the need for manual training (Frasier et al., 2017; Stowell et al., 2019, 2018).

Although we have shown that lion FT roars are individually unique, it is necessary to highlight that lion vocal behaviour can vary across space, time and social circumstances. None of the three tagged female lions in this study emitted full throated roars. This was unexpected, but could be related to the presence of small cubs in the pride, however, we acknowledge that further work would be required to confirm this assumption. Similarly, other research has shown that resident male lions tend to avoid roaring when outside of their territories while nomadic males roar at greatly reduced rates or avoid roaring entirely until they have gained prides (Grinnell and McComb, 2001). Surveys that rely entirely on roaring may therefore be biased by the fact that not all lions vocalize consistently across the landscape or through time. In addition, communal roaring by several members of a pride is a common occurrence and can make it particularly difficult to dissociate individual roars, resulting in reduced classification performance of recognition algorithms. Another important consideration for long term surveys is the temporal consistency of individual calls. Age-related variations in the calls of other species have been reported (Ey et al., 2007; Ota and Soma, 2014). Our study was conducted over a short period and therefore it remains uncertain as to whether the structure of an individual lions' roar varies with age.

In this study, we have shown that the roar of an African lion contains an individually unique identifier in the form of the fundamental frequency contour. Our method of modelling the extracted $f0$ sequences using HMMs is unprecedented in the field of animal vocal recognition and is likely applicable to a number of species which emit loud, long distance calls. We have also demonstrated the conservation value of our findings through the use of a passive acoustic array to localize and identify individual lion roars. This work highlights the value of passive acoustic monitoring for African lion research, particularly as current GPS tracking methods, although reliable, are highly expensive and involve invasive capture procedures. With rapidly advancing technological innovations, especially open-source tools, monitoring vocally active wildlife species is likely to become more efficient and affordable, providing new avenues for research and conservation.

5.6 Acknowledgments

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6 General Discussion

6.1 Main findings

The miniaturization of electronic components such as processors, solid-state memory and microphones have provided unique opportunities to manufacture small, robust data recorders that can be attached directly to animals. The acoustic biologger, described in Chapter 2, is an example of such a device and was designed to record raw audio in addition to movement metrics. The continuous audio recorded by these instruments contained informative cues from which behaviour could be inferred. This ground truth data was highly effective for training machine learning models to predict lion behaviour from accelerometer and magnetometer measures and was particularly valuable for obtaining data on behaviours that can be relatively difficult to observe (e.g. running and drinking). In addition, the inclusion of acoustic features as predictive variables can considerably improve the accuracy of automatic behaviour classifiers, enabling almost perfect recognition of behaviour states. This suggests that acoustic sensors can be a valuable addition to biologgers and provide an effective means of remotely classifying a rich range of animal behaviours.

The continuous, on-animal audio recordings also provided valuable data on lion vocalizations. Although the short length of the raw recordings limited the investigation of vocal behaviour exclusively from audio, vocalizations could be inferred from long term accelerometer signals using machine learning models (Chapter 3). Surface atmospheric conditions and spatial features were found to significantly influence vocal behaviour. Lions were more likely to roar when conditions favoured long-distance sound propagation, particularly when wind speeds were low. This provides a likely explanation for the peak in the number of vocalizations just before dawn. Lions also appeared to avoid roaring beyond their home range boundaries and were more likely to vocalize repetitively while nearer rivers and water points within their home range core. These findings offer valuable insights into lion vocal behaviour that, previously, were unattainable due to the challenges associated with manually recording spontaneous vocalizations with corresponding location information.

Although many species are known to encode individual identity within their call signals, the knowledge of how this information is conveyed in the spectral structure of the call is often lacking, as has been the case for African lions. Analysis of the raw audio recordings of individual roar events indicated that the shape of the fundamental frequency contour of the full-throated roar unit is a feature that is individually unique and sufficiently consistent to enable vocal discrimination of individual lions (Chapter 5). The importance of the temporal pattern of this feature is highlighted by the relatively poor discriminative ability of simple summary features (e.g. maximum and minimum) of the fundamental frequency that are often used in studies on animal vocal individuality. This knowledge of vocal signal variation between individuals contributes towards an understanding of individual recognition in the social context and is likely to motivate further research on the auditory perceptual abilities of the species.

Understanding lion vocal individuality is also an important prerequisite for remote tracking of individual lion roars. This, however, is also dependent on the cost and functionality of acoustic monitoring equipment. The low-cost CARACAL system, described in Chapter 4, was able to localize sound signals with similar accuracy as commercially available devices. The use of a novel quadriphonic design also facilitated better signal detection through pairwise measures of signal coherence. As highlighted in Chapter 5, integrating knowledge of lion vocal individuality and behaviour with the acoustic localization ability of the CARACAL system has considerable potential to provide an alternative tracking and monitoring method for the species. Figure 6.1 illustrates how the acoustic tools and findings presented in this thesis are interlinked.

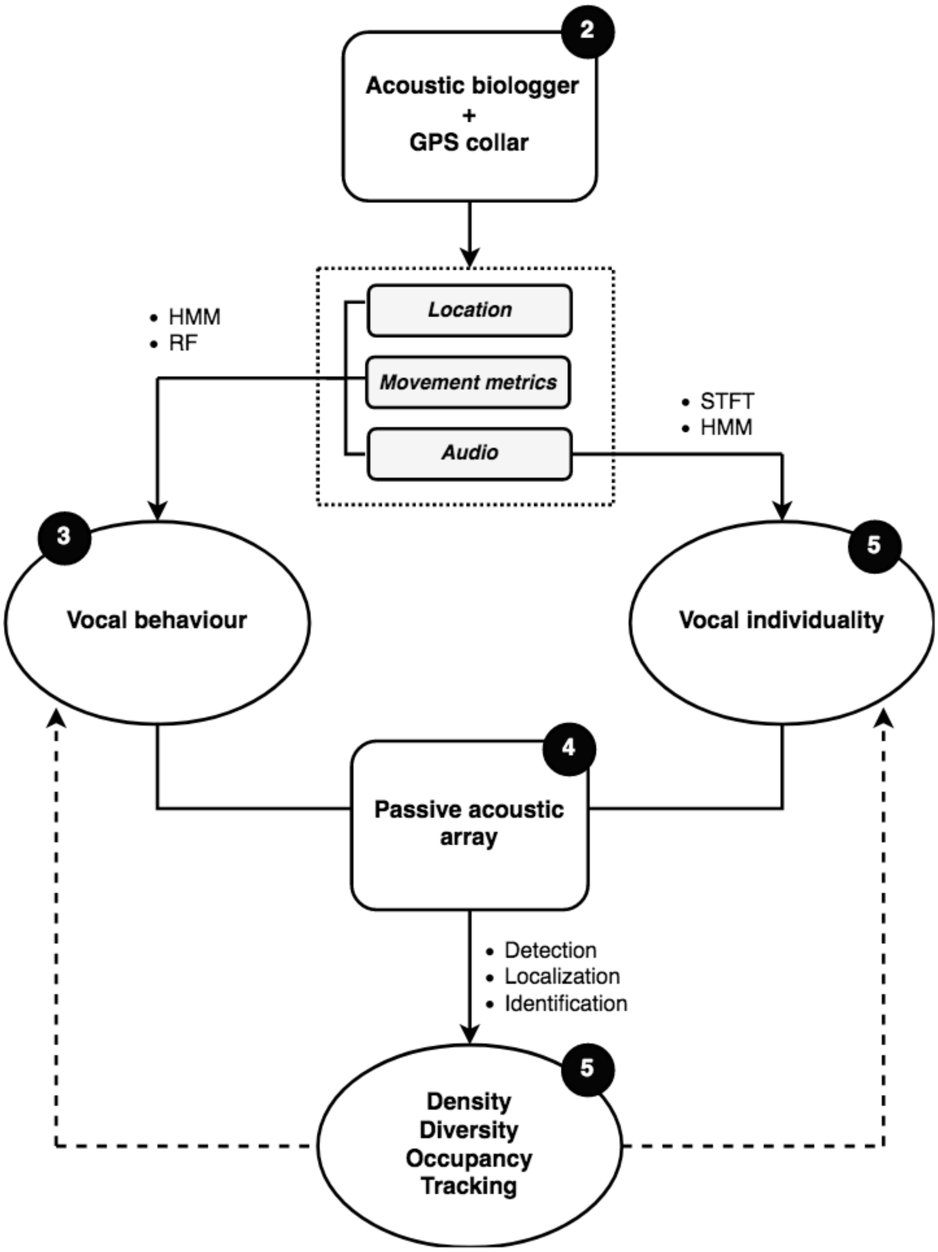

Figure 6.1 A schematic representation illustrating the role of acoustic sensing technology in advancing the understanding of lion vocal behaviour and individuality and its use as a monitoring technique for lion research and conservation.
The numbers in the black circles represent chapter numbers in which the corresponding information is contained. Bullet points represent the methods used to attain the resulting information.

6.2 Animal-borne acoustic sensing

For species capable of carrying biologgers, on-animal audio recording can offer detailed insight into many aspects of animal biology (Couchoux et al., 2015; Insley et al., 2008; Lynch et al., 2013). The audio data obtained from the acoustic biologgers employed in this study was used in two ways: firstly, to provide ground truth information on animal behavioural states for training a behaviour classification algorithm, and secondly, to provide high quality acoustic data on lion vocalizations.

6.2.1 Linking sound with movement metrics

Some of the main challenges associated with on-animal acoustic recording are the high-power consumption and data storage requirements that limit device lifetime. It is therefore impractical to rely exclusively on raw audio recording for long-term (> 1 month) deployments. Consequently, the use of "hybrid" biologgers that combine audio recording with accelerometer and magnetometer measurements allow for the acquisition of shorter periods of ground truth which can be used to construct behaviour prediction models based on long term movement metrics, as demonstrated in Chapter 3.

Watanabe and Takahashi (2013) adopted a similar integrated approach to investigate the foraging behaviour of Adélie Penguins (*Pygoscelis adeliae*) but used on-animal video recording instead of audio to validate prey capture behaviour. Their animal-borne cameras recorded 85-minute videos which were sufficient to identify multiple feeding events. These events were characterized by rapid head movements which could be detected by accelerometers fitted to the head and back of each animal. The corresponding acceleration signals were then used to predict prey capture events after the cameras had stopped functioning.

On-animal video cameras have been used in several studies investigating animal behaviour and have provided valuable insights into feeding ecology and time budgets (Heithaus et al., 2002; Huck and Watson, 2019; Ponganis et al., 2000). In many cases, however, their application is currently limited due to their short recording periods which rarely last longer than 6 hours. For species such as lions, which rest for up to 20 hours a day and may only feed once in a week, video cameras are unlikely to capture the full range of behaviours exhibited by the animal. Audio devices, by comparison, can function continuously for several days and therefore record infrequent behaviours that are rarely observed. Although the use of audio recording is currently preferable for this reason, battery and data storage capacities are likely to increase considerably in the near future and thereby allow researchers to overcome many of the challenges currently limiting the use of on-animal video recording.

Although raw audio recording consumes more power than movement sensors and limits its use in long term deployments, it is important to note that the greatest proportion of the energetic cost is due to saving the raw acoustic data and not actually receiving it. For example, continuous sensing of audio signals consumes approximately 1 mA, whereas storing the data at 44 kHz, 16 bit, uses approximately 3 mA current. Therefore, if specific spectral features can be extracted from sound signals on the device itself, a process which does not incur a major energy penalty, audio can be used as a multimodal sensor for longer term deployments. Furthermore, by incorporating larger batteries, higher capacity micro-SD cards and software that triggers sampling only during activity, the lifetime of an acoustic biologger could be increased significantly.

6.2.2 Linking sound with location

While acoustic and movement data alone may be sufficient to address certain research topics such as time budgets, combining behavioural information with spatial variables is important for investigating the environmental drivers of behavioural preferences. Kill site selection, for example, has been well studied for large carnivores such as lions and cheetahs but has generally involved manually confirming kill site locations by either following individual animals or investigating clusters of GPS points for evidence of a kill (Davidson et al., 2012; Rostro-García et al., 2015). The addition of GPS modules to biologging devices allows for the collection of behavioural data with concurrent location information. Wilson et al. (2013), for example, used a custom-designed collar containing a GPS, accelerometer and gyroscope to explore the locomotion dynamics of hunting cheetahs (*Acinonyx jabatus*) and was able to compare hunting behaviour between different habitat types.

One drawback of relying exclusively on GPS modules to acquire location information is the relatively low temporal resolution of GPS fixes (e.g. hourly fixes as described in Chapter 3) commonly obtained by remote tracking instruments. Although devices can be programmed to increase fix rate, this increases power consumption and therefore reduces battery life. A trade-off must therefore be made between device lifetime and fix interval. An alternative method that can be used to link behavioural data with location involves the use of animal speed and heading (and depth in the case of marine animals) to calculate movement relative to an initial starting position; a process known as 'dead reckoning' (Wilson et al., 2007). The primary advantage of this method is its ability to produce a continuous track of an animal's route of travel without the need for links with external radio transmitters or receivers (e.g. satellites). Dead reckoning can, however, accumulate substantial positional errors that result from inaccuracies in the estimation of animal speed from body acceleration (Bidder et al., 2012, 2015) as well as from drift caused by ocean currents and wind (Wilson et al., 2002). In the case of terrestrial animals, cumulative errors can be reduced by periodically correcting the dead-reckoned track with absolute locations provided by GPS telemetry (Bidder et al., 2012).

In this study, location data was obtained from a commercially available GPS satellite collar to which the biologgers were attached. This approach allowed us to capitalize on an existing platform that provided reliable location information with daily uploads to an internet server. Disadvantages of this method are the expense and lack of flexibility in setting GPS fix rates and times. Furthermore, the biologgers needed to be time synchronized before deployment which introduces additional complexities during animal capture procedures. In future, studies would likely benefit from designs which integrate GPS modules with movement sensors. This can facilitate adaptive GPS sampling that depends on animal activity state (e.g. low fix rate while resting and high fix rate during locomotion) as shown by Markham (2008).

6.2.3 Audio for assessing vocal individuality

Recording animal vocalizations manually from a distance can be extremely difficult particularly for species that are challenging to locate and follow (Pfefferle et al., 2007). As part of this study I attempted to record lion vocalizations from a vehicle using a shotgun microphone and audio recording device. Despite being able to successfully locate vocalizing lions, I was often unable to accurately verify the identity of the caller. Furthermore, my presence often altered lion behaviour and frequently led to individuals moving out of sight. The use of acoustic biologgers is therefore the only feasible method to obtain sufficient replicates of free-ranging lion vocalizations from known individuals. Couchoux et al. (2015) also used miniature, collar-mounted acoustic loggers to record chipmunk (*Tamias striatus*) vocalizations. The authors noted that just 24 hours of on-animal acoustic recording provided more detailed data than the use of a directional microphone over an entire field season.

6.3 Lion vocal behaviour and discrimination

An understanding of a species' vocal behaviour is a fundamental requirement for passive acoustic monitoring (Marques et al., 2013). For many species, these data do not exist, which is one of the main challenges limiting the use of acoustic techniques. In Chapter 3 and 5, we attempted to address this knowledge gap for African lions to offer insights into how the species' vocal behaviour is influenced by environmental factors and how individual identity information is transmitted in the acoustic features of individual animal calls. The data supporting the findings of these studies was obtained from the acoustic biologger described in Chapter 2.

As expected, based on the results of previous studies, lions vocalized mostly at night and increased their rate of vocalization just before dawn (Schaller, 1972; Stander and Stander, 1988). The reason for this pattern has, however, remained untested. Considering that lions rely heavily on vocalizations to advertise ownership of large territories, choosing to call in conditions that maximize calling area, and thereby the chances of detection by conspecifics, is likely to be beneficial (Larom et al., 1997). Our findings supported this theory as lions appeared to prefer vocalizing when atmospheric conditions enhanced signal propagation. While clearly beneficial for lion communication, this behavioural preference is also favourable for acoustic monitoring techniques which are subject to many of the same sound detection limitations (e.g. signal degradation and interference from wind) as lions themselves. Acoustic monitoring systems can also adopt energy-saving strategies that restrict audio recording to hours of the night when lions are most likely to vocalize.

Information on lion spatial preference for vocalization is also particularly pertinent to acoustic monitoring. Lions restrict vocal activity to areas within their home range where the benefits of communication likely outweigh the costs of revealing their location to aggressive competitors. This also means that nomadic individuals are likely to vocalize at considerably reduced rates until successfully acquiring a territory (Grinnell and McComb, 2001). Failure to account for this spatial and social variability in vocal behaviour can lead to biased interpretations of acoustically monitored roars. For example, the absence of vocalizations from an individual may not necessarily indicate its absence from a particular area. Assuming a direct spatial relationship between the locations of vocalizations and space use would likely lead to underestimating actual lion ranging behaviour.

Territorial males also appear to prefer vocalizing repetitively while closer to rivers and water points, most likely as a strategy to deter potential invaders from these valuable territory features. Research on lion habitat selection has also shown that lions actively select areas closer to water where prey are more likely to be located (Davidson et al., 2012; Valeix et al., 2010). Since these areas are used more intensively and are also associated with greater vocal activity, deploying acoustic sensors nearer rivers and water points is likely to result in higher roar detection rates. This would be particularly beneficial for studies relying on mark-recapture methods, for example, where surveys are designed to maximize capture probability as is often the case for camera trap deployments (Larrucea et al., 2007).

In addition to the behavioural adjustments that enable effective long-distance communication, lions have also evolved specialized vocal apparatus capable of producing acoustic signals that propagate over large distances (Weissengruber et al., 2002). Communication is, however, only effective if the receiver is able to extract relevant information from the signal. Caller identity, in particular, is a key feature encoded in the calls of many animal species and is important for influencing the response of the intended receiver (McGregor, 1993). As shown in Chapter 5, lions may convey identity information in the fundamental frequency of their full-throated roars. It is probable that this adaptation evolved in response to the increased attenuation incurred by higher frequency harmonics. The fundamental frequency, by contrast, is likely to suffer the least degradation and thereby carry identity information over greater distances. In order to test these hypotheses, it would first be necessary to investigate the extent to which lions are able to recognise conspecifics by the fundamental frequency alone. This could be done using spectrally modified recordings of known individuals and a cross-modal individual recognition design similar to that used by Gilfillan et al. (2016). If lions can indeed distinguish between conspecifics simply by the information contained in the fundamental frequency contour, the evolution of this trait as an adaptation to long distance communication could be explored using large scale comparative analyses (Harvey and Pagel, 1991). In practice, this might involve examining the degree to which individuality is encoded in the low frequency spectra of vocalizations emitted by other species with large territories that communicate over long distances (e.g. eastern grey wolves (*Canis* *lupus lycaon*)) compared to species with smaller territories and shorter-range vocalizations (e.g. red-bellied lemurs (*Eulemur rubriventer*)).

The existence of individually unique fundamental frequency contours in lion vocal signals can be particularly useful for acoustic monitoring in several ways. Firstly, vocal discrimination of individual lions appears to be possible from large distances allowing deployment of sparse sensor arrays (e.g. 500 – 1000 m between recording stations) which increases area coverage and reduces equipment expenditure. Secondly, acoustic systems can be designed specifically for lions with the sampling frequency reduced to < 1 kHz to focus detection on the bandwidth containing the fundamental frequency. This is likely to reduce power consumption and data storage requirements. Thirdly, wireless transmission of information to a central database would be aided by the small data content of the fundamental frequency contour and thereby enable real-time monitoring of vocal individuals. Ultimately, this knowledge of lion vocal individuality is the key component required to track individual movements and to attain density estimates using acoustic methods.

Although the findings relating to lion vocal behaviour and individuality are valuable for both understanding lion ecology and informing the development of acoustic monitoring methods, it is important to note several limitations of this study. Firstly, no vocalization data was obtained for female lions and therefore the findings and recommendations presented herein are based entirely on territorial males. Although the vocal behaviour of pride females is likely to be similar to that of pride males in many respects (e.g. preferring conditions that maximize signal propagation), further work is necessary to confirm this assumption and to quantify potential differences between the sexes. Secondly, when investigating lion vocal behaviour, roar detection from accelerometer data was only possible while the study animals were stationary. Further research should aim to explore roaring behaviour during active behavioural states. This can potentially be achieved using an acoustic biologger designed to record only roar signals (e.g. by employing an amplitude threshold to trigger recording during loud signals) in order to extend the lifetime of the device. Finally, this thesis did not attempt to address the social factors influencing lion vocal behaviour, such as dynamic interactions (e.g. how does a lion vocally respond to a neighbour's vocalizations?). In future, this could be investigated using the CARACAL system in combination with acoustic biologgers.

6.4 Passive acoustic sensing

Global declines in biodiversity urgently require effective conservation solutions to prevent the ongoing loss of wildlife species (Cardinale et al., 2012). In order to prioritise and adequately address the challenges, knowledge of the status and trends of species populations is vital for informing future conservation policies (Green et al., 2005). Remote sensing methods such as satellite imaging, light detection and ranging (LIDAR), camera trapping and acoustic monitoring are increasingly being used to complement or replace traditional survey approaches that are often invasive and resource intensive (Gibb et al., 2018). Camera trapping, which originated in 1890s with a simple trip wire and flash system, is now an established and highly popular survey tool in the field of ecology (Kucera and Barrett, 2011). Acoustic sensing, by contrast, has not been applied as extensively in terrestrial environments, nor has it experienced the same growth in equipment solutions until recently, partly because of technological costs and constraints (Gibb et al., 2018). Despite its relatively low use, acoustic monitoring has several advantages over camera trapping: Firstly, detection area is larger (depending on the signal strength of an animal’s call). Secondly, all sound-producing animals can be detected irrespective of size, and thirdly, acoustic signals are highly amenable to automated detection (Marques et al., 2013).

The CARACAL system presented in this study was designed to provide an affordable acoustic monitoring platform capable of localizing acoustic signals, including lion roars. The development of this device was motivated by the prohibitive costs of commercially available recorders and the absence of open-source devices capable of acoustic localization.

In contrast to camera traps, long-term, continuous passive acoustic monitoring surveys generate vast quantities of acoustic data which cannot be manually processed. Consequently, an automated processing pipeline is an important component of a PAM system and generally consists of two main stages, namely, signal detection and classification (Gibb et al., 2018). Detection involves identifying sounds of interest located at particular points in time within raw audio recordings and was the focus of the CARACAL processing pipeline. The multi-microphone design of the CARACAL hardware facilitated sound detection through signal coherence which was considerably more effective than detection based on a sound energy threshold. While this design attribute improves precision by reducing false detection of noise such as wind, major challenges still exist with distinguishing between overlapping signals from multiple sources. This is a common issue in the field of bioacoustics and one which will require innovative techniques to overcome (Gibb et al., 2018).

The classification stage of automated signal processing is valuable for categorizing detected signals according to species and individual. Chapter 5 of this thesis demonstrated individual classification of lion roars following manual extraction of the full-throated roar units. It is important to note that a fully automated system would first be required to automatically differentiate between lion vocal signals and those of other species. Although this initial stage was not explicitly tested in this thesis, several studies have demonstrated reasonably accurate acoustic classification of a number of species' vocal signals (Cheng et al., 2012; Heinicke et al., 2015; Sebastián-González et al., 2015). The classification performance is, however, dependent on distinctiveness of the call relative to the surrounding acoustic environment as well as the level of call variation within the species (Choi et al., 2019). As noted in the General Introduction, lion roars are highly conspicuous acoustic signals and are relatively consistent between individuals. While these qualities are likely to facilitate effective initial classification of lion roars, further work is required to develop an appropriate algorithm to fulfil this function. This can be achieved using machine learning techniques, such as the random forest method applied in Chapters 2 and 3.

The localizing performance of the CARACAL system was similar to that of commercial acoustic devices, however, at a fraction of the cost, the system is accessible to projects with limited funding and is also useful for larger surveys requiring long-range acoustic positioning. Localization accuracy was significantly higher within the area bounded by the outermost sensors and also improved when the signal was detected by more than 3 stations. Acoustic surveys would therefore benefit from array designs that aim to maximize animal call detection within the array boundary and from a minimum of 4 stations.

As illustrated in Figure 6.1, the knowledge gained from passive acoustic monitoring can be used to further advance the understanding of animal vocal behaviour and individuality which in turn can be used to adapt acoustic monitoring methods. Ecological systems are inherently dynamic and therefore any long-term acoustic monitoring approach should consider the changes that can occur over time. Individual lions, for example, are unlikely to reside in one particular area for their whole lives; foreign males can force out residents and form new prides while births and deaths can alter pride structure. This inevitably results in the challenge of accurately processing new information (e.g. the call of an unrecognised lion). Current PAM systems are generally limited in this regard as classification algorithms are often trained on a set of known sounds and are therefore unable to classify 'out of set' signals (Spillmann et al., 2017). Future PAM systems could potentially 'learn' new features. For example, the spatial and temporal data associated with vocalizations can be used to determine whether two individual calls originate from two different lions. If the calls are spatially separated and it is impossible for a single lion to occur in both locations in the time between calls then it can be assumed that the vocalizations were emitted from different animals. This logic has already been employed in the field of computer science (Lu et al., 2017).

6.5 Wider application and conservation implications

Acoustic methods have considerable potential to complement traditional monitoring approaches particularly with the recent technological advances that have facilitated hardware and software improvements (Hill et al., 2018; Wilson et al., 2014).

As demonstrated in Chapter 2, acoustic biologging provides an effective means of collecting the data necessary for understanding animal vocal behaviour which is a fundamental requirement for developing passive acoustic monitoring systems. Although the devices used in this study were designed specifically for lions, on-animal acoustic recording can be applied to any species capable of carrying a biologger. Furthermore, the combination of acoustic and movement data can also be used to investigate other aspects of animal behaviour (e.g. locomotion and foraging) which need to be understood in order to develop effective conservation strategies and policies (Buchholz, 2007).

As technology evolves and biologging opportunities increase, it is essential that researchers maintain the ethical standards that seek to minimize the impact of these devices on study animals (Wilmers et al., 2015). Ideally, data should be collected through non-invasive means, but in many cases, this is not possible and therefore the use of animal-borne instruments may be justified. As reported by several publications, particularly those on aquatic and volant species, biologgers and their components can significantly alter animal behaviour and ecology (Barron et al., 2010; Bowlin et al., 2010; Wilson et al., 2004). In order to reduce potential negative effects (e.g. an increase in energy expenditure), researchers often adopt the rule that devices must weigh less than 5% of the animal's body mass. However, with the on-going miniaturization of sensor components, the relative mass of biologgers could be reduced even further as recommended by Portugal and White (2018). Future developments should therefore aim to capitalize on technological advances not only to improve device functionality but to reduce the negative effects on study animals.

The CARACAL system also has wide ranging application. Both the hardware and software are open source and can therefore be further developed and adapted to suit the needs of individual projects. The versatility of the system is exemplified by the case study described in Chapter 4 where vocalizing individuals from three different species were localized. Several other interesting scenarios were detected during test surveys that were not described in the chapter such as lions fighting, brown hyaenas interacting with lions and fish eagles (*Haliaeetus vocifer*) communicating with conspecifics in different locations. Although the CARACAL system would require several improvements (e.g. on-board processing) to enable long-term, autonomous acoustic monitoring, the system can be used in its current form to localize animal calls in shorter surveys (e.g. < 1 month). Indeed, the hardware has already been used to detect and localize the calls of elephants in a separate study.

Perhaps one of the most important insights from this work and that of others who have engaged in the development of technological tools for animal research and conservation is the value of interdisciplinary partnerships. Combining the expertise of biologists, computer scientists and engineers facilitates the creation of innovative tools that can offer incredible insights into animal behaviour and the functioning of the natural environment. Given a biological research challenge (e.g. how to record animal movement and space use continuously at a high temporal resolution) the computer science and engineering disciplines can provide the technical knowledge and resources required to design and manufacture appropriate data recording devices and assist with data processing (e.g. developing machine learning algorithms). Biologists, by comparison, are able to provide insight into species biology (e.g. anatomy and behaviour) that can inform the design process. In addition, biologists act as effective end-users and can offer important feedback that helps drive further technical development and innovation. An important prerequisite to effective collaboration, however, is that each contributor understands the motivations and perspectives of the others to ensure that outputs are beneficial and relevant to all involved (Carey et al., 2019). It is worth highlighting, however, that a common concern in the field of ecology is that the increased use of technology is creating a disconnect between ecologists and their study systems as data can be acquired remotely and automatically and thus reduce the time spent in the field. Wilmers et al. (2015) argue against this and suggest that biologists are still required to spend considerable time and effort in the field collecting data on the environmental covariates which are related to sensor outputs. The authors also maintain that improvements in biologger design results in more species and individuals being equipped with such devices which ultimately enables better data-driven approaches to species conservation.

6.6 Conclusion

The number of free-ranging African lions is declining across much of the continent and thus requires effective monitoring of existing populations to inform and enhance conservation strategies (Bauer et al., 2016). No single technology is likely to provide a simple and immediate solution for the complex challenges faced by wildlife researchers and conservationists. This study has, however, highlighted the value of acoustic methods, in combination with other technologies, for both understanding lion behaviour and monitoring individual movements over time and space. In addition, this work has contributed towards the knowledge of lion vocal behaviour and uncovered a potential mechanism for lion vocal identification, both of which are essential for passive acoustic monitoring. Although further research is still required to establish a fully functional acoustic tracking system for the species, this thesis has presented the first steps towards achieving this. With the on-going technological advancements and the increasing support of the technical sciences, ecologists are likely to derive considerable benefits from tools and techniques of the future that may well provide solutions to many of the challenges associated with contemporary monitoring methods.

6.7 References

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