Acoustically assessing apes:

chimpanzee conservation with passive acoustic monitoring

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List of abbreviations

ALS: acoustic localisation system

aSCR: acoustic spatial capture-recapture

CR: capture-recapture

CT: camera trap

CTCR: camera trap capture-recapture

CTDS: camera trap distance sampling

DS: distance sampling

GAM: generalized additive model

LM: linear model

PAM: passive acoustic monitoring

SCR: spatial capture-recapture

TDOA: time difference of arrival

TOA: time of arrival

Abstract

With one million species at risk of extinction, there is an urgent need to regularly monitor threatened wildlife. In practice this is challenging, especially with wide-ranging, elusive and cryptic species or those that occur at low densities, such as chimpanzees (*Pan troglodytes*). Monitoring is needed to establish conservation actions, but also to assess population trends. For conservationists, key questions concern species distributions and densities. These data must be regularly updated, allowing conservation planners to effectively execute and assess conservation efforts. Conservationists benefit from methods that are time- and cost-efficient and simultaneously provide accurate and precise data. I evaluate passive acoustic monitoring (PAM) as a tool for detecting, localising, and estimating densities of chimpanzees. I compare with results from camera traps (CT), a more common method. I deployed two arrays of acoustic sensors in Issa Valley, Tanzania: one comprising twelve non-GPS-synchronised acoustic sensors across the whole study area for nine months to estimate chimpanzee presence/absence and density. I simultaneously deployed 53 CT for methodological comparison and used spatial capture-recapture (SCR) and distance sampling (DS) methods. Another acoustic array comprised four custom-built GPS synchronised acoustic sensors, deployed for a 3-month period around a single valley (~2km^2), to localise chimpanzees. I found chimpanzee detectability varied over seasons. It is five times faster than an equivalent method using CT. Furthermore, I found that the estimated density of calling chimpanzees with acoustic SCR was lower than density derived from SCR with CT data, but within the 95% CI obtained with DS and CT data. Playback sounds were localisable with 27 ± 21.8m error and chimpanzee calls were localisable within 52m from the location of a researcher following the calling individuals. These results suggest PAM is a promising non-invasive method for chimpanzee monitoring. Despite the current challenges to automate data analysis, improvements of automatic call detection are promising. I anticipate that PAM will become more common in the conservationist’s toolbox for loud calling terrestrial species monitoring such as chimpanzees, gibbons, orangutans, wolves or elephants.

Résumé

Avec un million d'espèces à risque d'extinction, il est urgent de surveiller régulièrement les espèces sauvages menacées. En pratique, c’est cependant un défi, en particulier avec les espèces qui se déplacent à large échelle, difficiles à détecter ou celles qui sont présentes à faible densité, comme les chimpanzés (*Pan troglodytes*). La surveillance est nécessaire pour établir des mesures de conservation, mais aussi pour évaluer les tendances des populations. Pour les conservationnistes, les questions clés concernent la distribution et la densité des espèces. Ces données doivent être régulièrement mises à jour, afin de permettre aux conservationnistes d'exécuter et d'évaluer efficacement les plans d’action pour la conservation. Les conservationnistes bénéficient de méthodes qui sont efficaces en termes de temps et de coûts, et qui fournissent simultanément des données précises et exactes. Dans cette thèse, j'évalue la bioacoustique passive en tant qu'outil pour détecter, localiser et estimer la densité de chimpanzés. Je compare les résultats avec ceux obtenus avec des pièges photographiques, une méthode plus couramment utilisée. J'ai déployé deux réseaux d’enregistreurs audio en Tanzanie, dans la vallée d'Issa : l'un comprenant douze enregistreurs audio - non synchronisés par GPS - dans toute la zone d'étude et pendant neuf mois pour estimer la présence/absence et la densité des chimpanzés. Simultanément, j’ai déployé 53 pièges photographiques pour une comparaison méthodologique et utilisé les méthodes de distance sampling (DS) et spatial capture-recapture (SCR). Un autre réseau acoustique a consisté en quatre enregistreurs audio synchronisés par GPS et fabriqués sur mesure, déployés pendant une période de trois mois autour d'une seule vallée (~2 km^2), pour localiser les chimpanzés. J'ai montré que la détectabilité des chimpanzés variait selon les saisons. C’est cinq fois plus rapide qu'une méthode équivalente utilisant les pièges photographiques. De plus, j'ai montré que la densité de chimpanzés vocalisant estimée avec la méthode de capture-recapture spatiale acoustique était inférieure à la densité dérivée de SCR avec les données de pièges photographiques, mais dans les 95% d’intervalle de confiance obtenus avec la méthode de DS avec les données de pièges photographiques. Les sons préenregistrés et rejoués avec un haut-parleur ont été localisés avec une précision de 27 ± 21.8m et les vocalisations de chimpanzés ont été localisées à moins de 52m de l'endroit où un chercheur suivait les individus qui vocalisaient. Ces résultats suggèrent que la bioacoustique passive est une méthode non invasive prometteuse pour la surveillance des chimpanzés. Malgré les difficultés actuelles pour automatiser l'analyse des données, les améliorations de la détection automatisée des vocalisations sont prometteuses. Je prévois que la bioacoustique passive va devenir de plus en plus utilisée par les conservationnistes pour la surveillance des espèces terrestres qui vocalisent fort comme les chimpanzés, gibbons, orangs-outans, loups ou éléphants.

Declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

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Lastly, I would like to thank all chimpanzees at Issa Valley; thank you for allowing me to observe you in your daily life, but mostly for being quite vocal.

Chapter 1. General introduction

The thesis' overall aim is to assess passive acoustic monitoring (PAM) as a non-invasive method for loud calling terrestrial species monitoring. I focus my study on chimpanzees (*Pan troglodytes*), a highly threatened and charismatic species whose loud calls can travel up to 1km. I evaluate PAM at three levels: detection (presence/absence), density estimation and localisation of calling chimpanzees. This preliminary chapter aims to provide a broader context to the general aspects explored in this thesis, before outlining the thesis structure.

1. The chimpanzee, a species threatened by extinction

Numerous papers and reports increasingly warn about the risk of extinction for one million species and a sixth extinction crisis ongoing, triggered and intensified by anthropogenic disturbance (Koh et al., 2004; Barnosky et al., 2011; Ceballos et al., 2015; Johnson et al., 2017; Díaz et al., 2020). There is an urgent need to curb the biodiversity loss. However, there is much data lacking on species distribution and density. Conservation actions need to be prioritised to monitor and ultimately, mediate species-loss. Conservation planners need to focus efforts on the most diverse or vulnerable species or else those most impacted by intense human activity. They also need to monitor changes in wildlife abundance over time, looking for signs of human impact on behaviour (Kühl et al., 2019), but mostly to evaluate conservation decisions (Junker et al., 2020).

Primates are severely impacted by anthropogenic pressures and about 60% of wild populations are threatened with extinction (Estrada et al., 2017). All great apes (chimpanzee, bonobo – *P. paniscus*, gorilla – *Gorilla gorilla* and *G. beringei*, and orangutan – *Pongo abelii, P. pygmaeus and P. tapanuliensis*) are listed as endangered or critically endangered on the IUCN red list (IUCN, 2020). Chimpanzees live in Africa, with a range of over 2.6 million km^2, from Southern Senegal to western Tanzania and Uganda. They inhabit various habitats, from rainforest to savanna woodland. Chimpanzee populations are globally severely fragmented (Humle et al., 2016). Several studies report the dramatic decline of chimpanzee populations over the past decades (Campbell et al., 2008; Greengrass, 2009; Tranquilli et al., 2012; Junker et al., 2012; Funwi-Gabga et al., 2014; Kühl et al., 2017). In Tanzania, for instance, it is estimated that only 2700 individuals remain, with approximatively 60% found outside protected areas (Moyer et al., 2006). Regular surveys to establish baseline figures and monitor these threatened populations are necessary, especially for these extra-park populations.

Three major threats are responsible for chimpanzee populations decline (e.g. Strindberg et al., 2018). First, chimpanzees face habitat loss and degradation, with a dramatic deterioration of suitable environmental conditions over the recent years, especially for central and western chimpanzees (e.g. Junker et al., 2012; Kühl et al., 2017). The ongoing growing human population in Africa results in the conversion of forests to farmland, or degradation of forest for the purpose of mining, logging, charcoal production and oil extraction (Humle et al., 2016). Second, chimpanzees are threatened by poaching, predominantly for meat and the pet-trade, but also amidst human-primate conflict (Kuehl et al., 2009; McLennan et al., 2012). Lastly, (human-linked) infectious diseases affect chimpanzee populations. Because chimpanzees are genetically similar to humans, they are highly vulnerable to many human-borne diseases (Leendertz et al., 2004; Köndgen et al., 2008; Negrey et al., 2019; Patrono et al., 2020). These threats result in population declines. Rapid monitoring is needed to evaluate the intensity of these threats and establish conservation actions, but also to assess population trends.

For conservationists, the key questions to answer concern chimpanzee distribution and density. These data need to be regularly updated, allowing conservation planners to execute and assess conservation efforts effectively. To answer these questions, we need to be able to reliably detect, localise and estimate density of chimpanzee populations. Several non-invasive monitoring methods have been developed and are available in the primatologist' toolbox.

2. Non-invasive monitoring for chimpanzee conservation

Semi-arboreal and elusive by nature, chimpanzees are difficult to observe in the wild and flee upon contact when not habituated to human presence (Plumptre, 2000). They range over large areas and at low density. Consequently, direct visual study can be a challenge without a lengthy habituation process. Monitoring methods rely mostly on non-invasive and indirect indices. They consist traditionally on genetic material from faeces (Schwartz, Luikart & Waples, 2007; Arandjelovic et al., 2011; Moore & Vigilant, 2014; McCarthy et al., 2015) or sampling of chimpanzee signs, such as nests (Hashimoto, 1995; Kouakou, Boesch & Kuehl, 2009). Weaned chimpanzees build at least one daily nest for night-time sleep, and sometimes another one for day-time rest (Plumptre & Reynolds, 1997; Stewart, Piel & McGrew, 2011). However, these methods present some disadvantages. For instance, genetic samples require costly analyses in time and money (e.g. reagents, lab technicians) and necessitate specialised lab skills. These analyses also present logistical challenges, such as sample transport and export processes. However, new on-site field methods already show promise and suggest a safer future for sample collection, preservation, and extraction (e.g. Gower et al., 2019). Line transects are another traditional means of monitoring wildlife. Transects, however, are labour intensive and estimates of density from nests can be difficult to compare due to inter-observer reliability in finding the nests and in estimating their age. Furthermore, confidence intervals are large due to the challenges with accurate measures of nest production - some chimpanzees build more than one nest a day, and some reuse older nests (Stewart, Piel & McGrew, 2011) - or decay rate that varies between vegetation types and nest heights and a process that is not constant over time (e.g. Walsh & White, 2005; Mathewson et al., 2008).

Primatologists are therefore increasingly turning into new technologies, such as camera traps (CT), portable genomics and drones for their monitoring needs (Fig. 1.1). Over the past decade, these technologies have proven effective in detecting chimpanzee nests (e.g. drones: van Andel et al., 2015) and providing data for detection and occupancy modelling (e.g. CT: Crunchant et al., 2017). Density of chimpanzee populations has also successfully been estimated with CT (Head et al., 2013; Després-Einspenner, Howe, Drapeau, & Kühl, 2017; Cappelle, Després-Einspenner, Howe, Boesch, & Kühl, 2019; Howe, 2019). CT has the advantage of being autonomous, can be remotely deployed for long periods of time and record on a 24h cycle when triggered (e.g. Rovero et al., 2013; Burton et al., 2015). However, its detection range is limited. Drones are also autonomous but operate for short amounts of time, limited by the battery capacity (Wich & Koh, 2018). For assessing habitat or density of chimpanzees, long duration flights are required to capture sufficient ground (Burke et al., 2019). Drones and their required batteries are often prohibitive. To overcome these limitations of visual monitoring, primatologists have begun to use passive acoustic monitoring (Fig. 1.1). However, it is important to stress data collection and analyses, with finding the best balance relative to the needs. For instance, with a line transect the data are in hand after the survey. With drones, CT, and PAM there are large time inputs needed to extract the chimpanzee data from all the images or recordings.

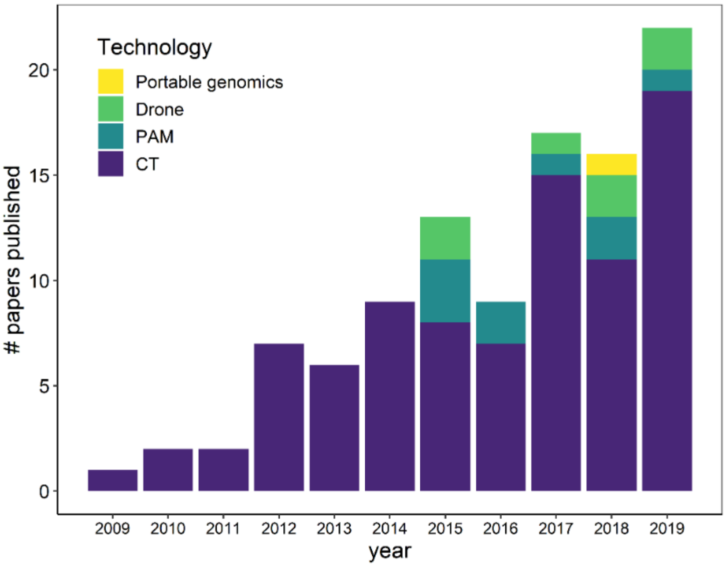

Figure 1.1. Numbers of papers published on primate conservation conducted with new technologies (i.e. portable genomics, drone, passive acoustic monitoring and camera trapping) from 2009 to 2019. Literature search was done on Web of Science with the keywords “primate” or “ape”, with “camera trap”; “drone” or “UAV”; “ARU” or “acoustic sensor” or “passive acoustic monitoring”; “genetics” or “genomics” and “field method”.

3. Conserving chimpanzees with passive acoustic monitoring

Passive acoustic monitoring (PAM) is a method that uses a unit composed of one or several microphones. It has the capability to record wildlife sounds in both marine and terrestrial environments. PAM is applicable to any taxa that produces acoustic signals, including insects, fish, herpetofauna, birds and mammals (Sugai et al., 2019). PAM is non-invasive and especially applicable when visual detection is limited, for instance in dense tropical forests, at night. Because it records sounds remotely, disturbance to primates is minimal. It can be deployed for long periods in the field (months or years) and simultaneously with various units at multiple locations, offering the possibility to record animal calls at large spatiotemporal scales to study e.g. habitat use over areas of multiple square kilometres. However, PAM can be limited in terrestrial environments when conditions are interfering with recordings (i.e. heavy rain or wind), limitation also true for line transects or drones.

While the first system that listened to wildlife sounds was deployed underwater during World War 1 (reviewed in Sousa-lima et al., 2013), recent advances in bioacoustics have expanded the applications of acoustic sensors for terrestrial species, mostly to study bats and birds (Blumstein et al., 2011; Sugai et al., 2019). PAM has rarely been used for terrestrial mammals, despite its great potential for recording wide-ranging and loud calling species, such as wolves (Papin et al., 2018; Kershenbaum, Owens & Waller, 2019) or elephants (Wrege et al., 2012; Hedwig, DeBellis & Wrege, 2018). Chimpanzees, orangutans and gibbons are characterized by long calls that can travel a few hundred meters (up to 1000-3000m) (e.g. Wich & Nunn, 2002), which makes these species ideal candidates for PAM. So far, only a few teams have used PAM for studying apes. Applications ranged from localising Bornean orangutans (Spillmann et al., 2015), whose long calls were localised with a 58m error, to assessing the potential of a chimpanzee buttress drum detector with occupancy modelling (Kalan et al., 2015). Vocal temporal patterns (Piel, 2018) and group territories and spatiotemporal patterns of habitat use (Kalan et al., 2016) have also been studied with PAM. Due to the challenges of other methods to determine the location and density of chimpanzees, it is of interest to investigate under what circumstances PAM allows for localisation and density estimation of chimpanzees.

4. Thesis structure

The thesis focuses on three aspects that are relevant for chimpanzee monitoring: detection, density estimation and localisation (Fig. 1.2). To provide a background, I start with a literature review (**chapter two**): its aim is to review how traditional and more emerging bioacoustic techniques can address species conservation issues, for both marine and terrestrial environments.

- *Detection*. Establishing whether a species is present/absent in an area is often a first and fundamental step in conservation. As mentioned previously, CT is a common monitoring method; however, its detection range is limited, with the necessity of the animal to pass in front of the CT to trigger a detection. In **chapter three**, I conduct a study comparing the efficacy in chimpanzee detection from CT and PAM. With occupancy modelling, I evaluate the efficacy of each method, using the estimated number of sampling days needed to establish chimpanzee absence with 95% probability, as measure of efficacy. I hypothesise that chimpanzee detectability would be higher with PAM compared to CT, given the larger area covered by the acoustic sensors.
- *Density estimation*. Once species presence is confirmed, a natural next parameter to establish is density. Recently, new methods combining passive acoustic monitoring (PAM) and spatial capture-recapture (SCR) models to estimate animal density have been developed (e.g. Stevenson et al., 2015). Call rate is a parameter that allows conservation planners to convert call density into animal density when detecting calls with PAM. In **chapter four**, I investigate chimpanzee call rate during the late dry season by conducting focal follows. I examine the socio-ecological factors that influence call production rate of

savanna woodland chimpanzees, such as vegetation type, behaviour, party size, time of day and presence of swollen female. I evaluate the call rate among the different demographic classes. Estimated call rates allowed me to estimate chimpanzee density from a 3-month PAM deployment and an acoustic spatially capture-recapture (aSCR) model (**chapter five**). I compare estimates from those from SCR and the distance sampling framework from camera trap footage, methods that have been empirically demonstrated as highly accurate.

- *Localisation*. Detecting caller presence via an acoustic localisation system (ALS) can inform on their distribution and social organisation, locating individuals in space and time across their home range. ALS also improves density estimations and can locate chimpanzees at key resources, such as important fruiting trees or at their nesting sites. In **chapter six**, I evaluate a custom-made acoustic sensor array in localising chimpanzees through their landscape. I assess error and precision of the estimated locations by conducting a playback study at known locations. I explore the different ecological parameters such as temperature and wind speed that influence sound propagation and thus localisation error.

To conclude, **chapter seven** summarises the main outcomes of the thesis to demonstrate the potential of PAM not only for the chimpanzee, but also for all loud calling terrestrial species monitoring and conservation. I compare the different methods available for chimpanzee monitoring (i.e. drone, PAM, CT, line transects and genetic sampling) in terms of data collection and analyses to answer questions about chimpanzee distribution, density and threats. I discuss the costs and time needed for each method for estimating chimpanzee density before presenting directions for future research.

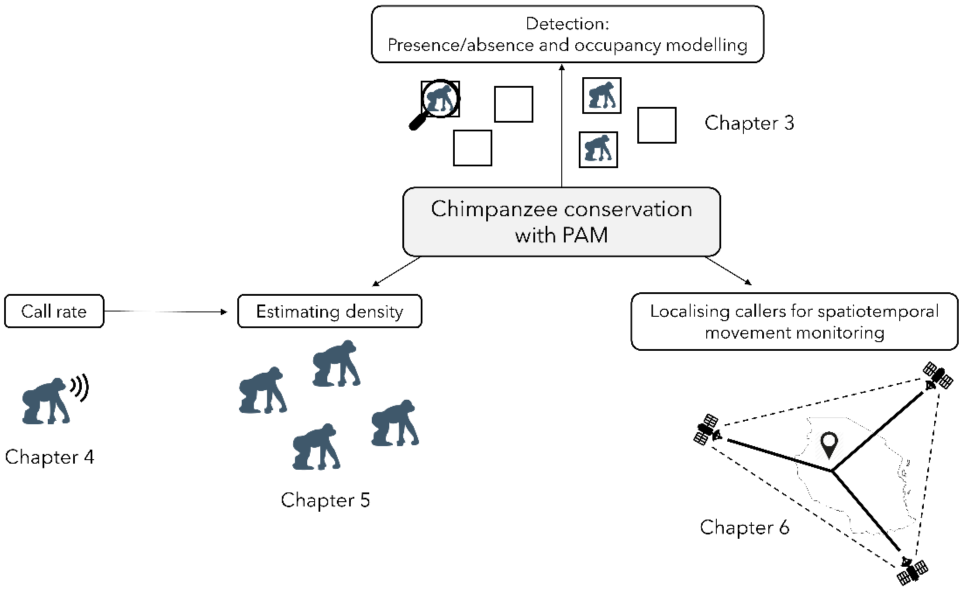

Figure 1.2. Overview of the thesis framework. My research objective is to demonstrate the potential of passive acoustic monitoring (PAM) for detecting, estimating density and localising calling chimpanzees for their conservation.

Chapter 2. Acoustic sensors: a review

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Reference: Crunchant, A. S., Nakka, C. D., Isaacs, J. T., & Piel, A. K. (2021). Acoustic sensors. *Conservation Technology*, 53. DOI:10.1093/oso/9780198850243.003.0004
This chapter was published in August 2021 and has been reformatted to fit the thesis requirements. Footnotes are absent on the published version of the chapter.

Author contribution: ASC and AP led the manuscript writing except part 3 (case study); CDN and JI led the part 3 (case study) writing.

Abstract

Animals share acoustic space to vocally communicate. The employment of passive acoustic monitoring to establish a better understanding of acoustic communities has emerged as an important tool in assessing overall diversity and habitat integrity as well as informing species conservation strategies. The aim of this chapter is to review how traditional and more emerging bioacoustic techniques can address conservation issues. Acoustic data can be used to estimate species occupancy, population abundance and animal density. More broadly, biodiversity can be assessed via acoustic diversity indices, using the number of acoustically conspicuous species. Finally, changes to the local soundscape provide an early-warning of habitat disturbance, including habitat loss and fragmentation. Like other emerging technologies, PAM benefits from inter-disciplinary collaboration between biologists, engineers and bioinformaticians to develop detection algorithms for specific species that reduce time-consuming manual data mining. We describe here different methods to process, visualise and analyse acoustic data, from open source to commercial software. The technological advances in bioacoustics turning heavy, non-portable and expensive hardware and labour and time intensive methods for analysis into new small, movable, affordable and automated systems, make acoustic sensors increasingly popular among conservation biologists for all taxa.

Keywords: vocalisations; spectrogram; ecoacoustics; bioacoustics; PAM; sound; machine learning

1. Introduction

1.1. What questions are we asking?

Animals share acoustic space to vocally communicate. Similar to food, mates, and territory, acoustic space can also be a scarce resource for which animals compete, with callers adjusting spatial, temporal and frequency patterns in response to both abiotic and biotic factors, especially the sounds of sympatric fauna (Araya-Salas et al., 2017). Acoustic sensors offer an important method of monitoring animal behaviour not requiring humans to be in the field with the animals. Moreover when visual detection is limited, as for instance at night, in lush tropical forests, or when weather conditions are poor (e.g. Verfuss et al., 2018), the employment of acoustic sensors is an important tool to reveal and monitor the composition of acoustic communities as well as assess biodiversity, habitat integrity and even threats. More so, as a non-invasive and remote method applicable for any taxa that produces acoustic signals, from insects to fish, herpetofauna to birds and mammals (Sugai et al., 2019), passive acoustic monitoring (PAM), is an increasingly common technique integrated into species conservation (Sugai et al., 2019).

Compared to alternative methods of biomonitoring such as point counts or drones and similarly to camera traps, acoustic sensors can be deployed for long periods in the field (months or years) and simultaneously at multiple locations and because of their large detection range, can monitor places that may be difficult to access by researchers. Moreover, they are non-invasive and require low researcher-hours for deployment compared to alternative devices that demand frequent visits or maintenance. Sensors can also be used in adverse weather conditions (Philpott et al., 2007; Elliott, Dawson & Henderson, 2011). The first device capable of listening to sounds underwater was developed during World War 1, before being used for marine sciences (reviewed in Sousa-lima et al., 2013). Recent advances in bioacoustics have expanded the applications of acoustic sensors for terrestrial species (Blumstein et al., 2011; Kalan et al., 2015; Wrege, Rowland, Keen, & Shiu, 2017). Like with nearly all technology, devices have become more affordable and smaller with technological advances, from where systems began (portable handheld tape recorders) to digital audio recorders and currently, autonomous recorders. However, the non-standardization of monitoring protocols, the labour-intensive acoustic analyses and the limited data curation make PAM a tool that requires careful consideration prior to deployment (Sugai et al., 2019). The increasing inter-disciplinary collaboration between engineers and field ecologists is driving new, affordable and effective biomonitoring methods with reduced size and weight, but increased applicability.

PAM offers a wide variety of applications for the study of wildlife ecology, behaviour, and conservation (Fig. 2.1). It was initially developed for marine species (Marques et al., 2013; Spiesberger & Fristrup, 1990; Tavolga, 2012), before being adopted for birds (e.g. Efford et al., 2009; Bardeli et al., 2010; Leach et al., 2016) and more recently terrestrial species (e.g. reviewed in Blumstein et al., 2011; Huetz & Aubin, 2012; Kalan et al., 2015; Spillmann et al., 2010), insects (Penone et al., 2013) and anurans (e.g. Stevenson et al., 2015). Like with many of the other topics discussed in this volume[1], understanding the relationship between the physical environment, and here, animal acoustic communication, is highly interdisciplinary. That is, data collection (sound production, propagation, measurement) and analyses (machine learning for detection and classification) are largely challenges that physicists and computer scientists are trained to address, whilst biologists tend to focus on animal vocal anatomy, call type, flexibility and behaviour (Erbe et al., 2019).

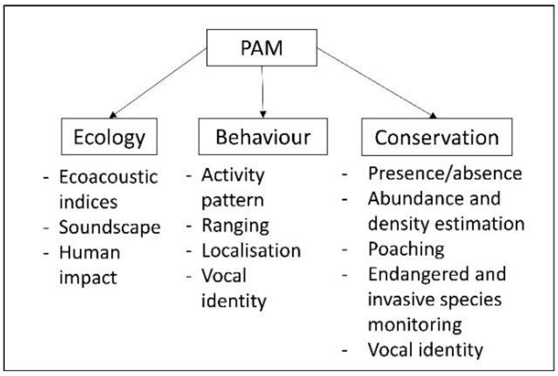

Figure 2.1. Different applications of PAM for ecology, behaviour and conservation

In this chapter, we present the current state of PAM as a tool for conservation biologists, using examples from both terrestrial and marine systems, with a focus on recent developments and applications. Besides PAM, there are other systems that integrate acoustic sensors, namely telemetry and bio-loggers. These systems are often invasive techniques, such as collar-mounted acoustic sensors (e.g. Lynch et al., 2013; Wijers et al., 2018; Yan et al., 2019); we focus instead here on PAM, given its historic and increasing use in conservation. Below, we review how PAM has been used to address related topics across taxonomic groups under each of these themes mentioned above (ecology, behaviour and conservation).

Behaviour

Ranging, territoriality and activity patterns – Acoustic sensors are powerful tools to reveal elements of animal behaviour, especially when subjects cannot be observed visually by researchers. Historically (Watkins & Schevill, 1972) but also more recently (Elliott, Dawson & Henderson, 2011), PAM has been the primary means of revealing cetacean habitat use and behaviour. It is beyond the scope of this chapter to comprehensively review this body of work, but for example, PAM has been used to reveal seasonal and daily temporal movement patterns of harbour porpoises (*Phocoena phocoena*), common (*Delphinus delphis*) and bottlenose dolphins (*Tursiops truncatus*) (Dede et al., 2014), or night-time movements of Yangtze finless porpoises

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[1] This is a reference to the book “Conservation technologies”. Wich, S. & A. Piel (Eds), Oxford University Press.

(*Neophocaena phocaenoides asiaeorientalis*) (Akamatsu et al., 2008), seasonal migrations of mink whales (*Balaenoptera acutorostrata*) (Risch et al., 2014), and simultaneous ranging behaviour of seven adjacent killer whale (*Orcinus orca*) pods (Yurk et al., 2010). It has also been used to study right whale (*Eubalaena glacialis*) use of corridors in urbanised coastal regions (Morano et al., 2012). For the most part, study of marine mammal behaviour using PAM is based on either stationary underwater hydrophones towing or multiple hydrophone arrays behind sea vessels.

There is far less, but nonetheless growing application of PAM to terrestrial species. These studies involve attaching acoustic sensors to stationary locations (e.g. trees usually) and setting recording schedules (i.e. duty cycling, e.g. continuous, 10 minutes every hour, etc. to save battery life and memory). Some of the earliest work assessed wildlife behavioural responses to human activity (see more below). Wrege and colleagues (2010) investigated whether forest elephants (*Loxodonta cyclotis*) avoided areas of higher oil exploration activity in Loango National Park, Gabon. To their surprise, elephants did not, and in fact, neither dynamite blast intensity nor explosion frequency affected elephant presence. In fact, elephant abundance figures followed patterns of other, non-disturbed areas. However, temporal (activity) patterns of behaviour did change in the explored areas, with elephants exhibiting more nocturnal calling behaviour the closer they were to areas of oil exploration (Wrege et al., 2010).

Whilst PAM has rarely been used to assess territoriality, strategic acoustic sensor deployments across territorial boundaries can reveal how vocalisation patterns change with caller location. Forest-dwelling chimpanzees (*Pan troglodytes*) are highly xenophobic and change their behaviour near territorial boundaries. In Tai National Park, Ivory Coast, Kalan and colleagues (2016) used PAM and showed that chimpanzee drumming events were more frequent near territorial boundaries, supporting earlier observational results of vocalisations by Wilson et al. (Wilson, Hauser & Wrangham, 2007). PAM has been used to assess similar questions about vocalisations and territoriality in birds. Male and female wren (*Thryothorus rufalbus*) co-defend territories and were hypothesized to have a territory size and overlap comparable between sexes. Researchers found that both sexes exhibited congruent patterns of singing behaviour within their territory (Osmun & Mennill, 2011). Additional acoustic monitoring of other terrestrial taxa from numerous other groups, including insects, amphibians, and mammals, has provided data on breeding partner coordination in calling, either by overlapping or alternating call elements (e.g. Bryant et al., 2016; Geissmann, 2002). This is also the case for more than 220 species of birds (Mennill et al., 2012). Given the difficulty of not only following wide-ranging species like chimpanzees and elephants, but also monitoring their behaviour at key areas like boundaries, PAM is well poised to reveal location-specific calling patterns.

In species that produce context-specific vocalisations, recording and identifying call types inform on animal activity. For example, chimpanzees (e.g. Crockford & Boesch, 2003), bottlenose dolphins (Janik & Slater, 1998), chipmunks (*Tamias striatus*) (Burke da Silva et al., 1994), humpback whales (*Megaptera novaeangliae*) (Mercado III et al., 2007), short-finned pilot whales (*Globicephala macrorhynchus*) (Jensen et al., 2011), and white-bearded wildebeest

(*Connochaetes taurinus mearnsi*) (Calabrese et al., 2018) exhibit call types that reveal behaviour such as travelling, foraging, greeting, cohesion maintenance, or rutting. Thus, we can remotely infer inter-site and inter-seasonal habitat use across diel phases just by knowing how animals are calling. For example, in bottlenose dolphins, this approach was used to identify areas of higher feeding activity (Elliott, Dawson & Henderson, 2011), whereas in Serengeti wildebeests, call types revealed a highly synchronized reproduction (Calabrese et al., 2018). There are obvious limitations to this employment of PAM, however. Silent individuals go undetected, and so presence/behaviour is not always revealed. Moreover, call types are not always discretely different, instead grading into each other, making the relationship between call type and behaviour inherently difficult to decipher.

Localisation – Using PAM to study more specific social dynamics like sub-group coordination and reunions or territory boundaries requires knowing caller locations, not just caller presence. By localising callers on the landscape through acoustic triangulation (Klimley et al., 2001; Blumstein et al., 2011) we can also reconstruct animal movements if individual identify of callers is known. Acoustic triangulation uses the time difference of arrival of sounds to multiple sensors to produce an estimate of the sound origin. Beside these behaviour purposes, localization also allows to improve algorithms to automatically detect a species by separating animal sounds from background noise but also estimate density (see below) and quantify sound amplitude or directionality (Rhinehart et al., 2020). Initial systems exploited the speed and distance that sounds propagate underwater, with marine vessels toeing hydrophones only centimetres apart (e.g. Filatova et al., 2006; reviewed in Marques et al., 2013). Studies of birds then followed (e.g. Wang et al., 2005a; Mennill et al., 2006). An early prototype system used an eight-microphone cable-based array with sensors placed approximately 75m apart for the study of duetting rufous-and-white wrens (*Thryothorus rufalbus*) (Mennill et al., 2006). This system consistently and accurately localised callers to within 3m. A later prototype with portable and wireless sensors, including GNSS (Global Navigation Satellite System) for time synchronization, showed similar accuracy localisation, as well as offered increased deployment flexibility (Mennill et al., 2012). Location accuracy varies as a function of inter-caller and inter-sensor distance, as well as wind, humidity and vegetation, which impacts the sound transmission and the signal-to-noise ratio, but also sensor synchronization accuracy and recording sample rate (reviewed in Rhinehart et al., 2020).

Ecology

Ecoacoustic indices - Biodiversity assessments can be very labour-intensive and time-consuming, often requiring detailed taxonomic identification of obscure animal species (Sueur et al., 2012). Acoustic approaches to biodiversity, however, have the advantage that they can inform on biodiversity at a community level (group of different species) without species identification and document biodiversity using various acoustic diversity indices (Depraetere et al., 2012). Over 60 indices have been developed to address different types of research questions, such as biodiversity, temporal patterns, and habitat and site effect among others (Buxton et al., 2018b).

However, ecoacoustic (or acoustic ecology) indices are often site-specific (e.g. Gasc et al., 2015; Harris et al., 2016). Moreover, for estimates to be reliable, data should be collected - and indices tested - at a large scale and in reality, sample size is often small. Thus, although generalizing across taxa and ecosystems has not yet been well demonstrated (Buxton et al., 2018b), ecoacoustic indices can be used in longitudinal studies for specific sites. This approach has recently been manifested in soundscape analyses, which include both animal's use of acoustic space and their interactions with all other sources of abiotic and biotic sound sources, including how they partition acoustic space to increase the likelihood of sound transmission to conspecifics (e.g. Ruppé et al., 2015). This field has received increased attention recently, given the increasing global anthropogenic footprint and associated animal vocal and non-vocal responses (behavioural adaptations) to disturbance (Rendell & Gordon, 1999; Brumm et al., 2004; Holt et al., 2015).

Soundscapes – Pijanowski et al.'s (2011a; 2011b) early descriptions of soundscapes integrated biophony (biological sounds), geophony (environmental sounds), and anthrophony (anthropogenic sounds) to characterise the sound environment in a landscape context. They are grounded in the interaction of bioacoustics, landscape ecology, community ecology, and engineering (Gasc et al., 2017). PAM is best placed to document these interactions given the need for continuous recordings of multiple frequencies and often, at times of the day that are not easy to record, for example pre-dawn. In contrast to species-specific PAM studies that are tuned to the frequency of the target vocalisations, soundscape recordings for biodiversity are more general and serve to detect audible signals ranging from 20Hz to 20KHz (Pijanowski et al., 2011). Analyses of entire soundscapes – versus specific sounds – have the potential to allow us to examine the biodiversity and inter-specific dynamics of vocally conspicuous species, especially where communities are disturbed by logging, urban, and agricultural expansion, or energy development (Deichmann et al., 2017). However, extensive preliminary work before the disturbance of a system is needed to have a comparative baseline necessary to estimate any subsequent change (Deichmann et al., 2018).

Historically, questions that sought to understand the complex sound environment focused on birds, which were shown to acoustically partition singing competition by alternating the timing of overlapping frequencies (Cody & Brown, 1969; Popp, Ficken & Reinartz, 1985). In a simulation of the effect that call length would have on this phenomenon, Suzuki et al. (Suzuki, Taylor & Cody, 2012) found that callers with longer songs were least likely to make timing adjustments to avoid overlap, and instead those species with shorter songs modified behaviour to fit into the available soundscape space. Similarly, acoustic niche partitioning has been demonstrated in primates as well. Schneider et al. (2008)examined the calling pattern of Kloss gibbons (*Hylobates klossii*), Mentawai macaques (*Macaca siberu*), pig-tailed langurs (*Simias concolor*), and Mentawai leaf monkeys (*Presbytis potenziani*) in Siberut, SE Asia. All four species vocalised mostly early morning, when background noise is low, but callers showed temporal offsets of calling patterns, likely to reduce acoustic competition.

Human impact – Similar to how acoustic sensors capture entire communities of animal acoustic activity, they also capture the human acoustic element. Human-generated noise can impact the basic ecological functions of a biological community, especially acoustic communication processes (Slabbekoorn & Ripmeester, 2008). The anthropogenic effects of noisy soundscapes have been largely investigated in two domains: the influence of (1) urbanization on birdsong and (2) shipping and natural resource exploration on marine mammals. We discuss each here briefly.

The rapid expansion of urban areas results in a rise in ambient noise levels, generated by ever growing transportation networks and human activities. Early studies showed the impact of anthropogenic sounds on the timing of the dawn chorus (Arroyo-Solís et al., 2013), with those bird species that are least variable in their timing being the most affected. Species richness and species abundance also decline significantly with increasing noise (Laiolo, 2010; Proppe, Sturdy & St. Clair, 2013). A recent study from LaZerte *et al.* (2017) demonstrated that male mountain chickadees (*Poecile gambeli*)adjust songs, calls and chorus composition with increasing ambient and experimental anthropogenic noise. In contrast to calls, songs are longer vocalisations and are more complex in terms of structure and thus, carry more information. In their study, LaZerte *et al.* (2017) showed that males increase the frequency of their calls in noisy areas and also use more songs than calls.

PAM has also been a key method in the evaluation of marine mammal responses to drilling, sonar testing by military vessels, and general movements of commercial shipping (e.g. Dyndo et al., 2015; Pirotta et al., 2014; Wisniewska et al., 2018). Noise created by marine vessels is not isotropic (Arveson & Vendittis, 2000); instead vessel direction, speed, size, cargo type, and weight influence the resulting pattern of underwater disturbance (Erbe et al., 2019). For example, harp seals (*Pagophilus groenlandicus*) reduced the loudness of their calls when travelling near vessels in the Gulf of St. Lawrence, Canada (Terhune, Stewart & Ronald, 1979), while Florida manatees (*Trichechus manatus latirostris*) shift their orientation, depth, travelling speed, or diving behaviour as a response to approaching vessels (Rycyk et al., 2018). The diversity in manatee response behaviour, however, represents the interaction of physics and behaviour as mentioned in above. Initial suggestions that manatees were unable to detect oncoming vessels because of manatee hearing were later unsupported (Gerstein, 2002). Instead, the more likely explanation of these accidents concerns manatee preferences to travel near the ocean surface (where noise levels are low compared to lower depths) and their travelling speed (Gerstein et al., 1999). This example symbolizes the complex interaction between animal, sound, and human behaviour when trying to not only identify the sources of human-wildlife conflict, but also develop conservation strategies. The extensive acoustic frequency and geographic spectrum of data that PAM collects allows researchers to tackle these issues.

Conservation

To provide critical data that reveal changes in species abundance and distribution over time, systematic monitoring is necessary to assess the impacts of management decisions and evaluate wildlife status (Akçakaya et al., 2018; Martin et al., 2018). PAM can inform on abundance, distribution, and wildlife population trends – critical information for conservation scientists.

Occupancy - Occupancy is the proportion of an area used by a species (MacKenzie et al., 2017) but also the study relative to the presence/absence of a species. Occupancy statistical models use detection/non-detection data from multiple visits of a given area to infer the probability of species presence. Occupancy modelling provides a useful tool to assess the population status (i.e. declining, stable or increasing) of any species. It can be applied to numerous marine (e.g. whales: Miller & Miller, 2018) and terrestrial species (e.g. birds: Campos-Cerqueira, Aide, & Jones, 2016; chimpanzees: Kalan et al., 2015). The increased survey coverage of PAM compared to camera trapping sometimes results in better detection rates (Rayment et al., 2018; Enari et al., 2019; Crunchant et al., 2020). However, some species change the frequency of vocalising in response to external contexts, such as human hunting pressure, or vocalizations can be sex-specific and thus, other census methods are preferable in these scenarios. Studies from people acting as sensors to monitor animal calls have revealed that low caller activity may result from human disturbance (e.g. Hicks & Roessingh, 2010; Kone & Refisch, 2007). In these cases, PAM should be complemented with other methods to validate results.

Abundance and density - Species abundance and density estimates are two important measures for species monitoring, especially to evaluate extinction risk and to assess the efficacy of conservation policy and practice. PAM was first used to reveal animal density for marine species (reviewed in Marques et al., 2013; McDonald & Fox, 1999) and only more recently for terrestrial species (Stevenson et al., 2015; Measey et al., 2017; Sebastián-González et al., 2018). Current methods to estimate abundance or density have been adapted from direct (visual) observation methods. They include capture-recapture (CR), distance sampling (DS), and a spatially explicit capture-recapture framework (SECR), reviewed in more detail in Marques et al., (2013) and study examples provided below:

- CR: when individual identification is possible (e.g. Norwegian ortolan - *Emberiza hortulana* abundance estimation with automatic song-type and individual identity recognition; Adi et al., 2010)
- DS: when the distance of the animal from the sensors are known, point transect and cue counting methods can be used (e.g. North Pacific right whale - *Eubalaena japonica* density using passive acoustic cue counting and sound propagation model; Marques et al., 2011)
- SECR: when distances to detected animals are not known but the same sound can be detected and localized across multiple sensors and when individual recognitions is not possible (e.g. ovenbird - *Seiurus aurocapilla* density estimation with multiple four-microphones arrays, Dawson & Efford, 2009; minke whale - *Balaenoptera acutorostrata* density from multiple hydrophones, Marques et al., 2012; Cape peninsula moss frog

Arthroleptella lightfooti density from a six microphones array, Measey et al., 2017, Stevenson et al., 2015).

Call rate - To convert calling patterns to animal abundance if methods are based on acoustic cues, information on call rate is necessary, a parameter that is usually collected during focal follows of individuals. Call rate is enormously complex to quantify, as it changes with caller age or sex class, group size and composition, social context, and environmental surroundings, among others (Pérez-Granados et al., 2019). Knowing how often calls are produced can also reveal aggregation patterns of fission-fusion species for whom party composition is ephemeral. Payne et al. (2003), for example, showed that the rate of three different call types varied predictably with herd size in savanna elephants (*L. africana*) from Amboseli, Kenya. Similar relationships have been shown with porpoises (Wang et al., 2005b) and beaked whales (*Ziphiidae* spp.) (Dimarzio et al., 2008) amongst marine mammals.

Vocal identity – Individual recognition of many species can be achieved with acoustic features of their vocalisations (e.g. giant pandas (*Ailuropoda melanoleuca*) - Charlton et al., 2009; four passerines: Gansu leaf warbler (*Phylloscopus kansuensis*), Chinese leafwarbler (*Phylloscopus yunnanensis*), Hume's warbler (*Phylloscopus humei*) and Chinese bulbul (*Pycnonotus sinensis*) - Cheng, Sun, & Ji, 2010; eagle owl (*Bubo bubo*)- Grava et al., 2008; bottlenose dolpins (*Tursiops truncatus*) Kershenbaum et al., 2013) and these features will play the same role as physical marks (tags, scares, patterns) used in camera trapping for individual identification (Laiolo, 2010; Terry et al., 2005). These acoustic features allow us to study e.g. survival rate based on non-invasive acoustic mark-capture-recapture methods, as for instance with great bittern males (*Botaurus stellaris*) (Gilbert, Tyler & Smith, 2002) or Dupont's lark passerine males (*Chersophilus duponti*) (Vögeli et al., 2008) that have distinctive vocalizations, and also estimate site fidelity with the same principle (Grava et al., 2008). Neural networks used to determine call similarities among killer whales (*Orcinus orca*) have shown that calls from individuals from the same matriline were more similar than those from different matrilines (Nousek et al., 2006). This demonstrates that social affiliations have also an effect on vocal identity. Lastly, and especially important for nearly all conservation scientists, vocal individuality can be integrated into census methods to count individuals within a population (e.g. Hoodless et al., 2008; Terry & McGregor, 2002).

Poaching – The illegal killing of wildlife is a widespread and pervasive threat. In addition to revealing the above parameters of calling behaviour, PAM can also be used as a law enforcement tool to assist conservationists combatting poaching, by localising gunshots, for instance. Over two years, acoustic data have been continuously recorded within Cameroon's Korup National Park. With a gunshot detection algorithm, spatiotemporal gun hunting patterns have been derived, allowing to adapt anti-poaching patrol activities (Astaras et al., 2017). There are multiple platforms that have been field-tested and have shown great promise in this context. CARACAL, a low-cost hardware and system, is able to locate gunshots with an accuracy of less than 35m within an array of seven sensors 500m apart (Wijers et al., 2019). AudioMoth, another low-cost hardware, can detect gunshots up to 500m (Hill et al., 2018). Rainforest Connection (www.rfcx.org) is a non-profit group that transforms old smartphones into autonomous solar-powered acoustic sensors. Sensors are deployed in the rainforest, and sounds of gunshots or chainsaw are picked up, recorded, and sent in real-time to a server in the cloud via a GSM connection. With this system, they are trying to prevent animal poaching by detecting patterns of activity in major roads used by poachers and illegal deforestation operations in rainforests around the world.

Endangered and invasive species monitoring - The use of acoustic sensors to detect and monitor invasive species, such as freshwater drum (*Aplodinotus grunniens*) (Rountree & Juanes, 2017), Red-billed Leiothrix (*Leiothrix lutea*) (Farina, Pieretti & Morganti, 2013) and pest insects (Mankin et al., 2011) is promising to allow control and eventual eradication (Juanes, 2018). Acoustic monitoring reveals the presence of new or cryptic species as well. In the Gulf of Trieste, Italy, visual surveys have been carried out for decades and failed to detect the presence of the cusk-eel (*Ophidion rochei)*, an uncharismatic nocturnal predator species classified as Data Deficient in the IUCN Red List. However, after only ten surveys using hydrophones to assess fish acoustic signals, researchers detected its presence off the coast of the Adriatic Sea (Picciulin et al., 2019).

1.2. Traditional methods and how technologies overcome limitations

Point counts, especially for bird surveys, or dung counts for e.g. elephants (Jones et al., 2012) have long been the established method for collecting data on animal presence and abundance (e.g. Scott et al., 1981; Sedláček et al., 2015). Point counts consist on recording all animals of interest visually or aurally detected during a time period at a given point and certain species-specific radius. But this technique is limited by the need for trained observers (Hobson et al., 2002) and typically restricted in spatiotemporal coverage. One way to overcome spatial limitations is to have multiple observers working simultaneously, as it has been successfully demonstrated in northern yellow-cheeked gibbon (*Nomascus annamensis*) density estimation (Kidney et al., 2016). Call-response surveys, that consist in broadcasting conspecific vocalisations to elicit responses, have been used to monitor different species, such as different waterbird species (pied-billed grebe (*Podilymbus podiceps*), American bittern (*Botaurus lentiginosus*), least bittern (*Ixobrychus exilis*), Virginia rail (*Rallus limicola*), and sora (*Porzana carolina*) (Gibbs & Melvin, 1993)) and coyotes (*Canis latrans*) (Hansen et al., 2015). However, limitations on the accessibility to the survey area exist and bias can manifest when detectability is low. Leach et al. (2016) conducted a direct comparison between point counts and automated acoustic monitoring in an Australian rainforest, and found that point counts detected significantly more species across an elevational gradient. They concluded that ‘quiet’ species (those that did not vocalise but were detected from visual cues) at least partially explained the variation. Nonetheless, they reported no differences in community-level patterns (e.g. turnover in species composition) across elevation from the two methods (Leach et al., 2016).

In the case of larger terrestrial mammals, dung counts have traditionally been used to assess species abundance and distribution (Kuehl et al., 2007; Jones et al., 2012), but like point counts, these can be time intensive and spatially limiting. PAM offers a reliable alternative. Acoustic surveys for land mammals have successfully estimated elephant abundance, with confidence intervals half as wide as traditional dung count methods (Thompson, Schwager & Payne, 2010) and for chimpanzees, revealed their presence across an unusually large home range across seasons (Crunchant et al., 2020). In a comparison of visual and acoustic methods for studying anurans in an Afromontane wetland, visual surveys revealed more species during the day, whilst acoustic methods revealed more at night (Sinsch et al., 2012). Alas, combining methods may inevitably be the ideal solution in these scenarios.

2. PAM: from data collection to data analyses

2.1. Data collection

An acoustic sensor is composed of any sound recorder and a microphone/hydrophone. The choice of the acoustic sensor is made as a function of the different parameters necessary to monitor, such as the species studied and the frequency range of its vocalisations, the environment (marine or terrestrial), the design of the study (study length, area covered, etc.) and the budget available, amongst others. Table 2.1. lists some of the most common bioacoustic sensor manufacturers.

Table 2.1. Principal bioacoustic sensor manufacturers for terrestrial and marine environments (adapted from Browning et al., 2017).

Company	Summary	Species/ habitat	Study example	Price/unit (US$)	Website
AudioMoth (UK)	Low cost and open-source device	Terrestrial, audible range and ultrasonic	Hill et al., 2018	60-75	https://www.openacousticdevices.info/
Chelonia (UK)	C-POD and DeepC-POD	Marine	Brandt, et al., 2011	3800-3900	https://www.chelonia.co.uk/
Dodotronic (UK)	USB, parabolic and analogue microphones ; hydrophones	Terrestrial, marine, audible range and ultrasonic	Kloepper et al., 2016	133-1111	https://www.dodotronic.com/
Elekon (Switzerland)	Bat recorders and detectors	Terrestrial, bats	Weier, et al., 2018	1192-4726	https://www.batlogger.com/en/
Frontier Labs (Australia)	Bioacoustic Audio Recorder, with omnidirectional microphone, integrated GPS unit and sampling rate up to 96kHz.	Terrestrial, audible range	Metcalf et al., 2020	538-740	https://frontierlabs.com.au/
Ocean Instruments (New Zealand)	Self-contained sound recorder	Marine	Lillis et al., 2018	2850-6300	http://www.oceaninstruments.co.nz/
Petterson Elektronik (Sweden)	Ultrasonic bat detectors, ultrasound USB microphones	Terrestrial, bats	Nakano & Mason, 2018	173-4090	https://batsound.com/

Solo (UK)	Open source, low cost, customizable, raspberryPi	Terrestrial, audible range	Whytock & Christie, 2017	108	http://solo-system.github.io/home.html
Titley Scientific (UK)	Bat detectors	Terrestrial, bats	Teets et al., 2019	891-2590	https://www.titley-scientific.com/uk/
Wildlife Acoustics (USA)	Song Meter SM4, SM4Bat, SM Mini, SM Mini Bat, handheld bat detector Echo Meter Touch 2	Terrestrial, audible range and ultrasonic	Hagens et al., 2018	179-899	https://www.wildlifeacoustics.com/

Sounds can be recorded at different sampling rates, which is the number of times per second a sound is sampled, measured in Hertz (Hz). Sensors can cover different spectra, from infrasound (typically sounds below a frequency of 20Hz, e.g. whales, elephants), audible sounds (e.g. birds, mammals) to ultrasound (typically sounds above a frequency of 20kHz, e.g. bats) and recordings depend on the targeted species. The sampling rate must be at least twice as high as the highest frequency of the targeted sound to contain necessary acoustic information (namely Nyquist frequency). Therefore, the sampling rate for ultrasounds is much higher than for audible sounds (that is typically 44.1KHz) and is usually between 200 and 400KHz, which generate bigger files requiring larger data storage.

2.2. Analysis

Historically, acoustic data were analysed by visually sifting through hundreds if not thousands of spectrograms and aurally verifying sounds of interest. A spectrogram is a visual representation of a sound recording in the time-frequency domain. Time is represented on the x axis, frequency on the y axis and the amplitude of the signal shown as colour density (Fig. 2.2). One needs to set the frequency window according to the species of interest and identify patterns corresponding to the targeted call of interest.

This visualisation allows analysts to identify and annotate calls manually or automatically through machine learning based algorithms, themselves based on the acoustic signal itself or on its spectrograms (e.g. Clink et al., 2019; Digby et al., 2013; Helble et al., 2015).

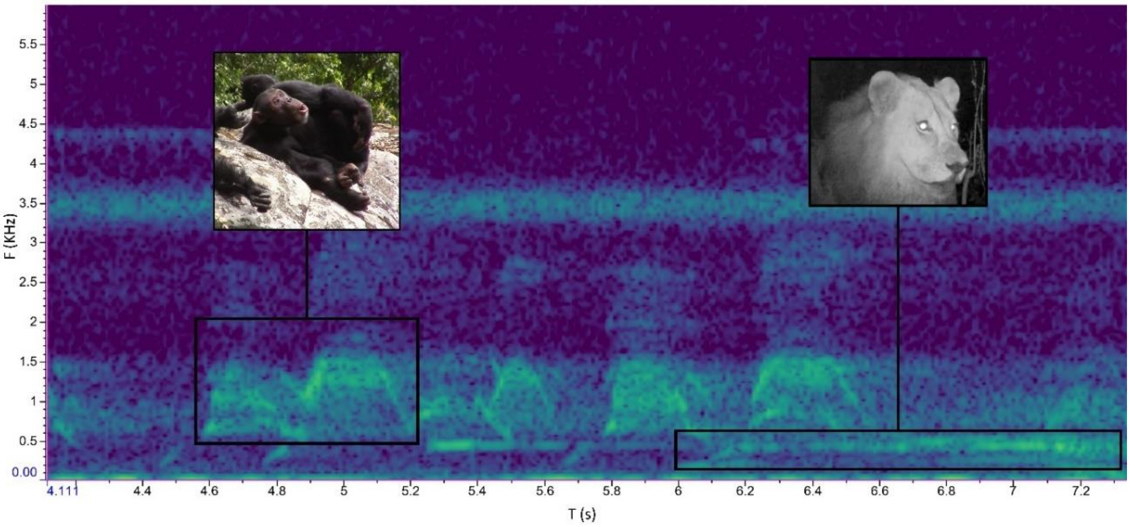

Figure 2.2. Spectrogram of a lion and chimpanzees calling.

Increasingly and because of the growing dataset size, automatic detection is becoming more common. Different pipelines exist to process sound files and create algorithms to detect, classify and thus automate sound identification, based directly on acoustic signal or on the derived spectrogram. These include supervised and unsupervised methods, with thresholding (e.g. Digby et al., 2013), spectrogram cross-correlation (e.g. Aide et al., 2013), random forest (e.g. Ross & Allen, 2014), hidden Markov models (e.g. Enari et al., 2019; Kogan & Margoliash, 1998), convolutional neural networks (e.g. Mac Aodha et al., 2018), support vector machines, and others. Below we describe the design of a chimpanzee detector, using convolutional neural networks, a supervised method without the need of a signal pre-extraction.

Each method has however advantages and disadvantages. For instance, some methods do not require large training datasets but are sensitive to background noise and overlapping signals that will mask the signal of interest (e.g. Digby et al., 2013); some methods do not require training datasets but subsequent identification is necessary (e.g. unsupervised clustering algorithms, Frasier et al., 2016). For a more detailed review on the common methods, see Gibb et al. (2019) and Bianco et al. (2019). While the growing demand and application of artificial intelligence and especially machine learning is applicable to PAM data as well, a major issue with automated detection is the generation of false positives (incorrect identification) and false negatives (failure to identify signals of interest). When the researcher assigns the confidence score that a call has been matched with a known call, the threshold can impact on the false positive and false negative rates. If the threshold is low, for example, the number of false negatives decreases but the number of false positives may also increase. On the contrary, if the threshold is high, the number of false negatives might be high. A high rate of false positives could result in an inflated population size estimate, whilst the opposite could under-estimate the number of individuals in a population, which could impact decision makers. False negatives occur when for instance, the signal is too faint to be recognized, or when the signal-to-noise ratio is low. It can also happen when the signal is masked by other sounds, such as other species (e.g. dawn and dusk choruses), or abiotic noises (wind). This can change seasonally, for example detectability might decrease during times of high rain or wind (e.g. Kalan et al., 2015). Automated detection performance can also vary as a function of site-specific characteristics and quality of recording. Ideally, training sounds are recorded under different conditions and from different locations to improve the generalizability of the detector. A manual step is always necessary to validate or reject the classifications, at least for part of the results as the accuracy of the classifications is not 100% (e.g. Heinicke et al., 2015). We also need to bear in mind that algorithm development is often laborious and complex, requires programming and/or signal-processing expertise, and typically requires a large annotated dataset for training.

Numerous software packages are available for acoustic analyses, from free and open-source software to proprietary ones. Table 2.2 lists some of the most common platforms.

Table 2.2. Software available for analyses (adapted from Browning et al., 2017)

Software	Availability	Summary	Website/Reference
Anabat Insight	Free and paid versions	Bat call detection, annotation, mapping	https://www.titley-scientific.com/
ARBIMON II	Free initially, charges apply for larger quantities of data	Web-based analysis platform: store, visualise, annotate audio recordings; pattern matching detectors; soundscape analyses	https://arbimon.sieve-analytics.com/
AviaNZ	Free, open source	Manual annotation, automated detection	http://www.avianz.net/
Audacity	Free, open source	Multi track audio editor, to listen, visualise, subset and annotate files	https://www.audacityteam.org/
AudioTagger	Free	Listen, visualise, annotate audio files	https://github.com/groakat/AudioTagger
AviSoft	Avisoft Lite (free) Avisoft Pro (license needed)	Visualisation, annotation, spectrogram cross-correlation (find TDOAs), geo-referencing tools and noise analyses	http://www.avisoft.com/
BatScope4	Free	Visualisation, analyse, classification of bat recordings	https://www.wsl.ch/en/services-and-products/software-websites-and-apps/batscope-4.html
CARACAL	Free	Acoustic localization	https://github.com/OpenWild/caracal
CPOD.exe	Free	Analyse data collected by T-PODs and C-PODs	https://www.chelonia.co.uk/cpod_downloads.htm
gibbonR (R package)	Free, open source	Classification, detection and visualization using machine learning	https://github.com/DenaJGibbon/gibbonR-package
iBatsID	Free	Classification of European bat call recordings to genus and species; requires call parameters extracted by SonoBat	http://ibatsid.eu-west-1.elasticbeanstalk.com/
Ishmael	Free	Visualisation, annotations tools, sound localisation and automated call recognition	http://www.bioacoustics.us/ishmael.html

Kaleidoscope	Free trial, license needed	Visualisation, annotation of recordings, automated identification of bats, cluster analysis, noise analysis, batch processing	https://www.wildlifeacoustics.com/products/kaleidoscope-pro
LibROSA (python package)	Free	Visualization	https://librosa.org/librosa/
OpenSoundscape	Free	Preprocessing audio data, machine learning models training, spatial localization of sounds	https://github.com/kitzeslab/opensoundscape
PAMGUARD	Free, open source	Developed for marine mammals, detection, classification, localisation	https://www.pamguard.org/
Pumilio	Free, open source	Web-based management system for ecological recordings, with visualisation and manipulation of sound files	http://ljvillanueva.github.io/pumilio/
Raven	Raven Lite (free), Raven Pro (license needed)	Visualisation, annotation, call detection and spectrogram correlation	https://ravensoundsoftware.com/
scikit-maad (Python package)	Free, open source	Compute ecoacoustic indices	https://github.com/scikit-maad/scikit-maad
Seewave (R package)	Free, open source	Sound analyses and synthesis with acoustic indices calculations	http://rug.mnhn.fr/seewave/
Songscope	Free	Spectrogram visualisation	https://www.wildlifeacoustics.com/download/200-song-scope-software
Sonobat	Proprietary	Visualisation, call detection, parameter extraction and species classification	https://sonobat.com/
SonoChiro	Proprietary	Automated bat identifications	http://sonochiro.biotope.fr/
Soundecology (R package)	Free, open source	Functions to calculate indices for soundscape ecology	https://cran.r-project.org/web/packages/soundecology/
SoundFinder (R package)	Free, open source	Position estimation	(Wilson et al., 2014)
Tadarida	Free	Developing and applying an acoustic classifier	https://github.com/YvesBas
WarbleR (R package)	Free, open source	Spectrogram visualisation, feature extraction, cross-correlation functions, batch processing	https://cran.r-project.org/web/packages/warbleR/index.html

3. Case study: Detecting wild chimpanzees using PAM

With the sixth extinction crisis ongoing (Barnosky et al., 2011; Ceballos et al., 2015; Johnson et al., 2017), one million species are at risk of extinction. For instance, numerous studies report the dramatic and global decline of chimpanzees over the past decades (e.g. Campbell, Kuehl, N'Goran Kouamé, & Boesch, 2008; Junker et al., 2012; Kühl et al., 2017). We need reliable, efficient, and affordable methods to prioritize conservation actions to monitor and ultimately, mediate species-loss. Chimpanzees are elusive and only a few communities are habituated to humans; thus, most chimpanzees are difficult to observe in the wild. Chimpanzees have large ranges for a terrestrial mammal and rely on loud calls to communicate. PAM is therefore a useful way to detect them.

For three months, we deployed a PAM system that enabled localisation of chimpanzee loud calls from the Issa Valley, Tanzania. The acoustic array consisting of four audio recorders has been deployed around the perimeter and on both sides of a single valley known to be an important part of the territory of the Issa chimpanzee community. Each acoustic sensor was composed of a microphone unit integrated with a nano-computer Raspberry Pi (Raspberry Pi 3 Model B Motherboard), a GPS unit and three 10W solar panels and two 44V batteries (Voltaic systems) and was protected in a Pelicase (Pelican 1170 Case) (Fig. 2.3). Sounds were recorded continuously, saved as 1h audio files at 11025 Hz sampling rate in the .flac format and stored in a 64GB SD card. Each sensor was placed at a maximum distance of 500m from each other to maximise the likelihood of triangulation, while simultaneously minimizing the likelihood of missing calls, as calls can carry up to 1km.

Our goal in designing a chimpanzee detector was twofold. First, we needed a system for processing and analysing many hours of existing data recordings. Our second and ultimate goal was to make detections in real-time on the PAM system, thus enabling real-time localization and more efficient use of data storage on these remote devices. Since the detector had to be designed to run on the Raspberry Pi and ultimately perform near-real time inference, it was required to have a low memory footprint. However, the memory constraint of the design could not come at the expense of achieving good classification accuracy.

The detection system was trained with an existing dataset of audio recordings that were recorded at a sampling rate of 11025 Hz, 16-bit depth, and a mono channel. These 1-hour recordings were split into single input audio files with a length of 4 seconds. The raw audio files were then converted to a feature vector[1] consisting of Mel Frequency Cepstral Coefficients[2] (MFCCs) using a Hann window of hop length[3] 512. The windowed signals were then padded[4] with zeros to form consistent vectors of length 2048. This corresponds to a 186 milliseconds recording at the 11025 Hz sampling rate. The 4 second audio clip was converted to 2-dimensional feature vector of size 40 x 87 which represents 40 MFCC channels. By organizing the feature vectors into this image-like representation, we were able to utilize Convolutional Neural Networks[5] (CNNs) which have been well studied in the image detection domain.

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[1] A feature vector is a numerical representation of an object.
[2] MFCCs are a set of representations of the short-term power spectrum of a sound.
[3] The hop length is the number of samples between successive frames.
[4] Zero padding refers to adding zeros to end of a time-domain signal to increase its length.
[5] CNN is a specific class of artificial neural network to analyse data.

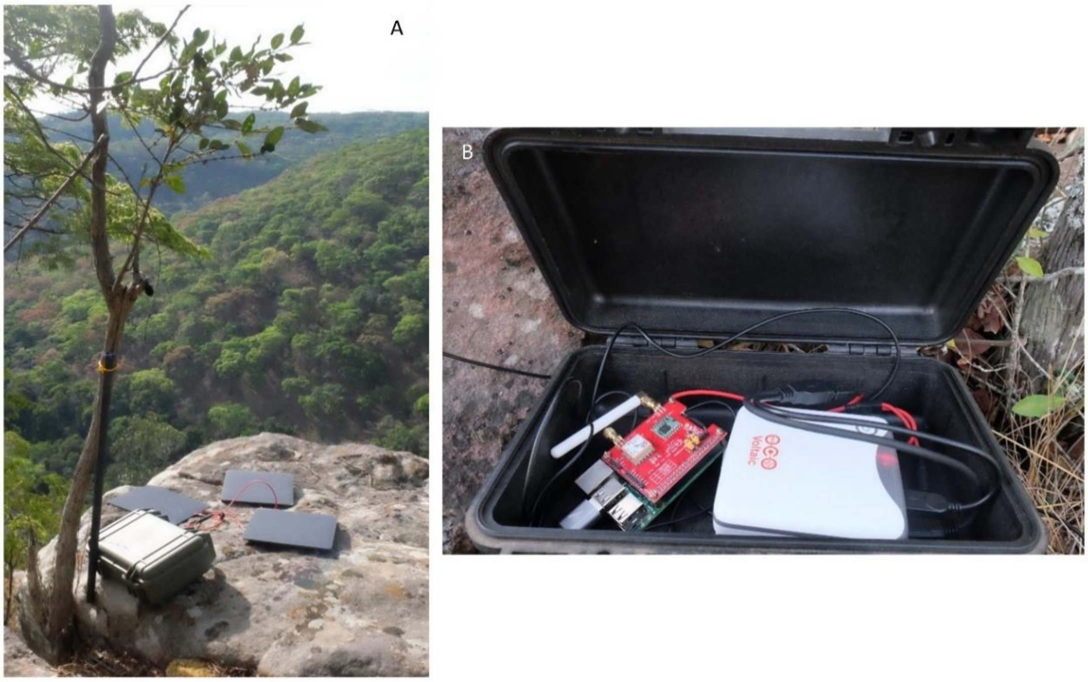

Figure 2.3. Acoustic unit as described in the text. (A) Sensor and three solar panels deployed at the top of a valley, (B) Raspberry Pi 3 model B motherboard with GPS unit and two 44V batteries (Voltaic Systems) protected in a pelicase (Pelican 1170 Case).

The high-level system architecture for the CNN can be seen in Fig. 2.4. The initial feature vector is first passed through a convolutional layer containing 16 filters to produce 16 feature maps[1]. The purpose of this first convolutional layer is to extract simple patterns such as lines. Here, each pixel in each feature map represents the output of a convolutional layer. The second level of the system is another convolutional layer containing 32 filters in order to extract structures of higher complexity. The outputs from this convolutional layer are then passed through a max-pooling[2] layer to produce space invariant, low level features. The purpose of the pooling layer is to reduce the overall size of the representation and therefore reduce the total number of parameters to compute in the network. Next, a fully connected layer is used to obtain the non-linear relationships between these features. This dense layer uses 128 hidden nodes and is followed by a final fully connected layer which gives the probabilities associated with each of the 12 possible classes under consideration. Additionally, the activation function is the Exponential Linear Units (Clevert, Unterthiner & Hochreiter, 2015), and dropout is performed after each max-pooling layer at a rate of 0.3.

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[1] A feature map represents the output of one filter applied to the previous layer.

[2] Max pooling calculates the maximum value in each patch of each feature map to create a downsampled feature map.

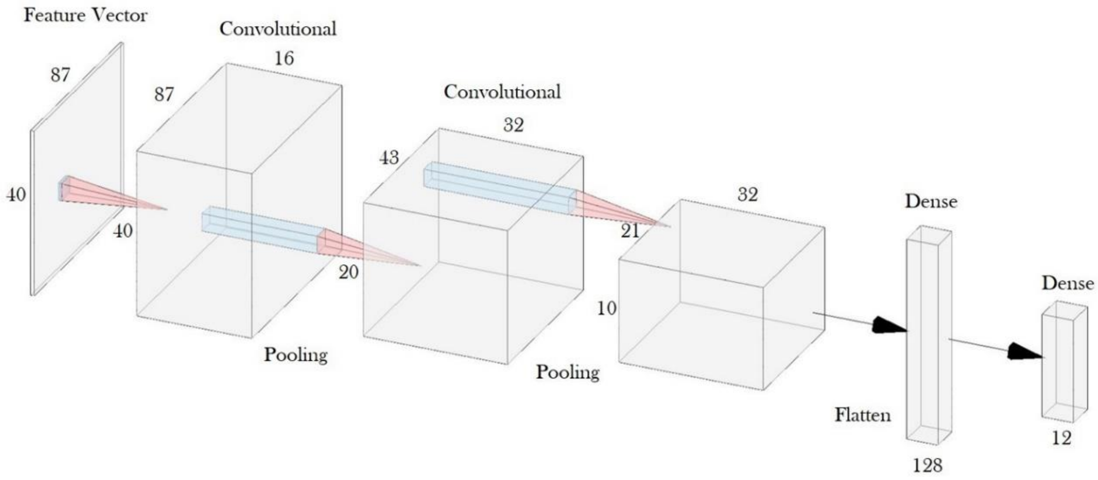

Figure 2.4. Convolutional Neural Network Architecture.

When training and testing a classifier, it is generally better to include more classes than just a single positive (chimpanzee vocalizations) and a single negative (anything but chimpanzee vocalizations). In particular the resulting multiclass classifier is generally more robust to false positives and has improved sensitivity. Ideally, the additional classes would come from sounds commonly heard in the deployment area if such a dataset were readily available. Part of the ongoing work for this study is to build out a such a dataset, but at the time of writing, this dataset is not of sufficient size for use. The proposed multiclass detection system was trained and tested on a dataset using sounds from the Urbansound8K (public acoustic dataset) along with two distinct chimpanzee vocalizations. The resulting 12 possible classes included an air conditioner, car horn, children playing, a dog barking, drilling, an engine idling, a gunshot, a jackhammer, a siren, street music, a chimpanzee shriek, and a chimpanzee pant hoot. This particular dataset was chosen for two reasons. First, as described above, it allows the development of a more robust multiclass classifier. Second, it is a well-studied dataset thus allowing the comparison of performance of the proposed classifier to other benchmarked classifiers on the non-chimpanzee classes as a sanity check.

While accuracy is a very intuitive measure of performance, it is generally not enough to evaluate model performance effectively. Accuracy is simply the ratio of observations that are predicted correctly to the total number of observations. This metric works best when the dataset is mostly balanced, and the classes are evenly distributed. Optimizing purely for accuracy makes the model sensitive and much more prone to detecting falsely labelled examples as positive. False positives are cases the model incorrectly labels as positive that are actually negative. Precision is the ratio of true positive predictions to the total number of positive predictions. Recall is the ratio of true positive predictions to the total number of positive occurrences. To balance out the true positive rate (precision) and sensitivity (recall) together, we use a metric called the F1 score. The F1 score is the harmonic mean of precision and recall, where a score of 1 is considered perfect. The resulting F1 scores for the instances of chimpanzee shrieks and pant hoots were 0.89 and 0.78 respectively which signify accurate and reliable classification results.

The resulting post training size of the model described above was suitable for operation on a Raspberry Pi 3 platform. The neural network described above is designed to have 4 seconds of audio as input to the system. Each 1 second chunk of audio data is appended to the previous 3 seconds to ensure that calls lasting longer than 1 second are detected. If a chimpanzee call is detected above a prescribed probability threshold, the respective audio clip is saved to file on the Raspberry Pi. By only saving audio signals which are predicted to contain useful information the limited storage space of the Raspberry Pi can be more efficiently utilized.

4. Limitations/Constraints

Despite the diverse conservation applications for PAM as an instrument to reveal animal presence and movement, the approach has limitations.

Power limitation – For continuous recordings, PAM is particularly energy consuming and supplying continuous power is challenging. The incorporation of radio-transmission into the system is also energy consuming, as well as on-board detection algorithms. For areas with sufficient sun exposure, sensors can be recharged with solar panels, potentially then offering unlimited deployment durations in terms of energy (Beason, Riesch & Koricheva, 2018; Hill et al., 2018; Sethi et al., 2018), but with a limited period of time due to data storage if files are stored on-board. For areas without sufficient solar exposure, alkaline or rechargeable batteries are options, but those can be costly to import, store, and dispose of properly.

Data storage – Acoustic data generate large datasets, and data storage can be problematic. File size depends on sample rate, number of channels, duration, and file format. Recordings in mono or stereo depends on the study design. Often mono recordings are sufficient but stereo recordings can be useful if one of the microphones fails in the field. If data are stored on the recording devices, researchers must visit sensors regularly (every few weeks or months, depending on the recording schedule and how the audio files are recorded and on which format) to retrieve and download the audio data with final datasets quickly approaching terabytes of audio files. Furthermore, data backup is necessary, and archival storage can be problematic in many countries (uploading speed to cloud, storage cost, storage environment of the data). One way to overcome this problem is to store audio data in compressed file formats without compromising sound quality, such as the lossless format .flac, for instance. Alternatively, some systems transmit data from sensors to a central station via wireless networks, e.g. via a 3G, radio-antenna system, Iridium satellite system or satellite internet, which can also be costly (Aide et al., 2013; Saito et al., 2015; Sethi et al., 2018; Baumgartner et al., 2019) or even lightweight aircraft to receive transmission. However, transmission of raw data is virtually impossible, due to large sizes. If only calls detected with an on-board processor are transmitted, the performance of the detector must be determined *a priori* and additional validation with raw data would not be possible, which can decrease the quality of the data and generate false negatives and false positives errors.

Data processing – As a result of the enormous datasets generated by continuous acoustic recordings, sophisticated, big data processing and analyses are required to post-process (e.g. filter) sounds of interest (Knight et al., 2017). Without automated detection, analyses of PAM data are extremely time-consuming and therefore not advisable for regular monitoring via manual analyses. However, in the past few years, major improvements in automated detection (species-specific identification but also call types for examining vocal repertoire) (Knight et al., 2017) have transformed this process. Such algorithms have been successfully demonstrated to detect many acoustically active taxa, including elephants (Zeppelzauer, Hensman & Stoeger, 2015), bats (Mac Aodha et al., 2018), humpback whales (Helble et al., 2015), sika deer (*Cervus nippon*) and Japanese macaques (*Macaca fuscata*) (Enari et al., 2019), manatees (Castro, Rivera & Camacho, 2015), Diana (*Cercopithecus diana*) and king colobus (*Colobus polykomos*) monkeys (Heinicke et al., 2015) among others. However, for species that exhibit high intra and extra individual variation in acoustic structure, like chimpanzees (Clark & Wrangham, 1993; Riede, Owren & Arcadi, 2004), developing an algorithm is more challenging.

Despite these improvements, manual validation to clean false positives remains compulsory, and involves listening to a sub-sample of pre-identified calls to confirm their identity. This validation is necessary over time and must be done repetitively to ensure against performance decline. Signal degradation and often structural changes to the primary sound are a result of propagation through the environment and vary due to fluctuating environmental variables such as temperature, humidity, and wind, but also the distance and orientation of the caller to the microphone (Schrader & Hammerschmidt, 1997). To compensate for this, intermediate processing steps, such as noise reduction, would help to increase the quality of the recordings and benefit detecting sounds of interest. However, this is costly in time and money for analysis and algorithm development.

Costs – Besides data and power capacity, another principal constraint of acoustic sensors is the large cost of the on-shelf devices and accessories (i.e. microphones, batteries…etc.). For instance, the SM4 from Wildlife Acoustics cost US$849 per unit (www.wildlifeacoustics.com) and requires high capacity batteries (D batteries at 10000mAh) that are expensive (i.e. US$76 for a 4-pack). Custom made units run however much cheaper (see above Table I e.g. Solo or Audiomoth - US$60-108) but can often not be made in mass quantities and risk structural inter-unit variability. Software to analyse the data can also be expensive (e.g. US400$ for a non-profit Raven license or US$680 for Sonobat 4 Universal), which can limit use of PAM as a biomonitoring tool for small NGOs.

5. Social Impact/Privacy

Privacy - Like drones and camera traps, acoustic sensors can reveal information on 3rd parties that threaten personal privacy, especially when sensors are deployed in urban areas. Human voices could be recorded without speaker's knowledge and sensitive information overheard. Currently there is little discussion on the regulation of acoustic sensors, and nothing governmentally instituted (as compared to drones). To mitigate against these concerns, sensor locations could be published on a website for the public to access, including duration, study objectives, and contact information, among other details; however, with that information revealed, sabotage and theft could easily result, complicating how scientists protect privacy without risking the loss of valuable equipment. Another solution could be the inclusion of band filters to remove frequencies with human voices; the trade-off here would be the loss of animal vocalisations that overlap in these frequencies. Data sharing could also be restricted, and not allowed if human voices are heard. More simply, a general warning like with CCTV cameras could be placed on the boundaries of a protected area.

Social impact - Over the last few years citizen science projects have been increasingly used to help collect and analyse large datasets, but also to promote the importance of biodiversity to the general public. Citizen science is a collaborative approach to research projects conducted by amateur and professional scientists, from data collection to data analysis. Some of the most well-known projects involving citizen science include e.g. Chimp&See (www.chimpandsee.org), Snapshot Serengeti (www.snapshotserengeti.org., Swanson et al., 2015), iNaturalist (www.inaturalist.org) and solicit help with images and videos. Citizen science projects with acoustic data are rarer, but some exist. For instance, in Australia, Rowley and colleagues (2019) have developed "FrogID", a database of frog occurrences based on acoustic validation. The platform relies on participants using their smartphones to record frog sounds and submit them for subsequent identification. This has allowed scientists to build a database that includes rare and threatened species, document the decline of native frog species from parts of their range, and detect invasive species. In only one year, over 66000 frog observations have been made, representing 13% of the total number of previous records made in Australia (Rowley et al., 2019).

Similarly, in England, the Norfolk Bat Survey was launched by the British Trust for Ornithology in April 2013, to conduct a large scale survey on bat activity and distribution (Newson, Evans & Gillings, 2015) and also indirectly on bush-crickets (Orthoptera of the family Tettigoniidae) (Newson et al., 2017). Acoustic sensors can be borrowed by the public to record bat calls following a determined protocol (more information can be found on their website – www.batsurvey.org). After two years, the project generated over 600 million audio recordings (Newson, Evans & Gillings, 2015) and after four years 1.9 million bat recordings have been analysed (www.batsurvey.org). The dataset is one of the most extensive datasets in the world for bats. Finally, the large ultrasonic audio dataset collected along road-transects across Europe and labelled by citizen scientists has allowed scientists to use deep learning to detect bat species

(Mac Aodha et al., 2018). However, a large amount of the calls has been misidentified due to the difficulty of recognizing bat calls and the inexperience of some of the citizen scientists.

Similarly, acoustic monitoring and citizen science offer several advantages for assessing insect biodiversity at large spatial and temporal extents (Penone et al., 2013). The authors found that urbanization has a negative effect on average mass of Orthoptera communities. In summary, PAM has both advantages and disadvantages, i.e. extensive audio datasets capture diverse acoustic soundscapes full of biodiversity and human activity, broadly, the increasingly large datasets require machine learning or armies of citizen scientists to help sieve through the noise. We see real potential for societal impact with these citizen science platforms, but also with the broader interest in what especially soundscapes provide. That is, already related sounds are incorporated into mobile phone applications used to calm tension (e.g. “Calm” – Huberty et al., 2019), wake people, or provide background noise. Soundscape from different parts of the world are also made publicly available (e.g., www.naturesoundmap.com, acoustics.safeproject.net), and sometimes in real-time (Sethi et al., 2020).

6. Future directions

As is the case of nearly each technological approach described in this book[1], the ongoing development of new technologies and the increasing inter-disciplinary nature of especially field ecologists, computer scientists, engineers, and bioinformaticians are driving new affordable and effective acoustic biomonitoring methods. We close this chapter with where and how we see the future use of acoustic sensors in conservation science.

Combination of new technologies - Similar to PAM, drones can provide real-time feedback for rapid surveys and offer an aerial perspective. By combining aerial and acoustic technologies, otherwise labour and time intensive species monitoring is being revolutionised by remotely recording sounds with drone-mounted microphones. Drones have already been integrated with acoustic sensors that have captured bat and bird sounds (August & Moore, 2019; Wilson, Barr, & Zagorski, 2017), and there are plans to diversify applications to terrestrial species. The excessive drone noise recorded by mounted sensors was initially an impediment to this work, but new signal processing algorithms and drone architectures that reduce this noise are promising (Hioka et al., 2019).

As stated above, camera traps and acoustics sensors provide complementary information on wildlife behaviour. By combining these two sensor types into a single system, we capture complementary extents of human disturbance on wildlife, study biotic interactions and animal behaviour at multiple scales, and provide a more thorough picture of animal presence, movement, and communication (Buxton et al., 2018a).

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[1] This is a reference to the book “Conservation technologies”. Wich, S. & A. Piel (Eds), Oxford University Press.

AI, real-time monitoring, and edge computing – Given the desire and usefulness of identifying acoustic events in real-time (e.g. gunshots), acoustic monitoring systems are being increasingly developed with on-board signal processing for event detection (e.g. Hill et al., 2018). Klinck et al. (2012) were one of the first to demonstrate this for marine mammals with an underwater vehicle (SeaGlider), equipped with an acoustic sensor and on-board data processing capabilities to passively scan for marine mammals. Methods with edge computing are in development (Sheng et al., 2019). Edge computing, or local processing, is a method consisting of data analysis at or near the source, on edge devices, and thus do not require transmitting large audio data volumes (Sheng et al., 2019). The advantage of on-board processing is the potential to detect in real-time and also record only sounds of interest, in so doing dramatically reducing dataset sizes, e.g. Audiomoth (Hill et al., 2018). The cost, however, is the loss of broader acoustic data that may provide researchers future questions to pursue (e.g. acoustic biodiversity, non-focal species presence, etc.) but also to control for quality of the call detector. The reality is that acoustic datasets can be mined for years to come to examine patterns and metrics that we may not yet realise are important. As always, then, the trade-off of collecting large datasets against the costs to manage them is one that any researcher must carefully consider. New projects looking at providing internet to remote areas, such as the project Loon (Nagpal & Samdani, 2017) and its use of helium balloons launched in the stratosphere are making acoustic real-time monitoring possible worldwide.

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Chapter 3. Listening and watching: do camera traps or acoustic sensors more efficiently detect wild chimpanzees in an open habitat?

Anne-Sophie Crunchant, David Borchers, Hjalmar Kühl & Alex Piel

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This chapter was published in January 2020 and has been reformatted to fit the thesis requirements.
The same dataset has also been used in chapter 5.

Author contribution: ASC, DB, HK, AP conceived the ideas and designed methodology; ASC collected and analysed the data; ASC and AP wrote the manuscript, and all authors contributed critically to the drafts and gave final approval for publication

Abstract

1. With one million animal species at risk of extinction, there is an urgent need to regularly monitor threatened species. However, in practice this is challenging, especially with wide-ranging, elusive and cryptic species or those that occur at low density.
2. Here we compare two non-invasive methods, passive acoustic monitoring (n=12) and camera trapping (n=53), to detect chimpanzees (*Pan troglodytes*) in a savanna-woodland mosaic habitat at the Issa Valley, Tanzania. With occupancy modelling we evaluate the efficacy of each method, using the estimated number of sampling days needed to establish chimpanzee absence with 95% probability, as our measure of efficacy.
3. Passive acoustic monitoring was more efficient than camera trapping in detecting wild chimpanzees. Detectability varied over seasons, likely due to social and ecological factors that influence party size and vocalisation rate. The acoustic method can infer chimpanzee absence with less than ten days of recordings in the field during the late dry season, the period of highest detectability, which was five times faster than the visual method.
4. *Synthesis and applications*: Despite some technical limitations, we demonstrate that passive acoustic monitoring is a powerful tool for species monitoring. Its applicability in evaluating presence/absence, especially but not exclusively for loud call species, such as cetaceans, elephants, gibbons or chimpanzees provides a more efficient way of monitoring populations and inform conservation plans to mediate species-loss.

Keywords: camera traps; chimpanzee; occupancy modelling; passive acoustic monitoring; Tanzania; savanna-woodland mosaic habitat; seasonality; vocalisations

1. Introduction

With the sixth extinction crisis ongoing, triggered and exacerbated by anthropogenic disturbance (Barnosky et al., 2011; Ceballos et al., 2015; Johnson et al., 2017), there is an urgent need to prioritize conservation actions to monitor and ultimately, mediate species-loss. Typically, conservation planners focus efforts on the most diverse or vulnerable species or else those suffering from intense human activity. To provide critical data that reveal patterns of species distribution over time, systematic monitoring is necessary to assess the impacts of management decisions and evaluate wildlife recovery (Akçakaya et al., 2018; Martin et al., 2018). However, in practice, wildlife monitors must overcome numerous challenges, especially when direct observations are nearly impossible, e.g. when studying nocturnal, cryptic, elusive or hunted species that have changed their activity pattern/behaviour. Consequently, innovative biomonitoring methods are revolutionising the way, the speed, and the reliability of providing the necessary data on not only the threats, but also how animals distribute themselves in ever-changing landscapes.

Detecting species presence is the first and fundamental step for population monitoring. Occupancy is the proportion of an area used by a species (MacKenzie et al., 2006). Occupancy statistical models then use detection/non detection data from multiple visits of a given area to infer the probability of species presence. Occupancy modelling provides a useful tool to assess the population status i.e. declining, stable or increasing, of any species and can be applied to numerous species. It has been successfully used with diverse taxa, including tiger (*Panthera tigris*) monitoring (Karanth et al., 2011) and Antarctic sperm whale (*Physeter macrocephalus*) occupancy and diel behaviour (Miller & Miller, 2018). In long-term monitoring programs, occupancy modelling can further reveal the effect of disturbance on animal presence by providing data that reveal landscape-use changes and site colonization and extinction, as well as reveal multi-species interactions as disturbance levels oscillate (Mackenzie et al., 2002; MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). Occupancy modelling allows us to refine species distribution models in conservation planning and adjust policy priorities. Whilst these models offer valuable information on species presence and the probability of occupancy, challenges remain to control for detection bias.

Detection probability is the likelihood to detect a species when it is present. Imperfect detection is a common issue and a challenge for species monitoring (MacKenzie et al., 2002), as it can lead to underestimates of occupancy, e.g. type II errors. Occupancy models account for imperfect detection (MacKenzie et al., 2002), which can arise from a variety of causes, including a sensor's placement (Cusack et al., 2015) and detection zone (i.e. closed forest or open area), habitat characteristics, use of baits (Comer et al., 2018), timing and duration of sampling, or animal density and behaviour (Neilson et al., 2018) among others.

Autonomous methods such as passive acoustic monitoring (PAM) and camera trap (CT) monitoring are two ways to remotely monitor wildlife presence, distribution, and behaviour (Rowcliffe & Carbone, 2008; Burton et al., 2015; Sugai, Silva, Ribeiro Jr, & Llusia, 2019), and both provide data for occupancy models. These methods are non-invasive and for both methods, sensors can be deployed for significantly longer periods (months or years) than time typically used in for example traditional approaches like point count surveys (Alquezar & Machado, 2015). Furthermore, multiple locations that may be difficult to access by researchers can be monitored simultaneously by autonomous recording units. This is particularly useful for detecting species that occur at low density.

CT is widely used among conservationists and researchers to study birds and medium to large mammals (Rovero, Tobler & Sanderson, 2010). Originally, PAM was developed for use with marine mammals (Spiesberger & Fristrup, 1990) and continues to be widely employed for studies of cetacean ranging and abundance (Mellinger, Stafford, Moore, Dziak, & Matsumo, 2007; Sugai, Silva, Ribeirao Jr & Llusia, 2019). However, recent advances in bioacoustics have expanded the applications of acoustic sensors for terrestrial species (Blumstein et al., 2011; Wrege et al., 2017). More recently applications include study of gibbons (*Nomascus gabbrielae*) (Vu & Tran, 2019), and wolves (*Canis lupus*) (Papin et al., 2018), among others. Both methods allow for diverse applications (Burton et al., 2015; Gibb, Browning, Glover-Kapfer, & Jones, 2019; Sugai, Silva, Ribeiro Jr & Llusia, 2019), ranging from revealing occurrence and occupancy (Rovero et al., 2013a; Campos-Cerqueira & Aide, 2016), population size and density (e.g. Marques, Munger, Thomas, Wiggins, & Hildebrand, 2011), demography (e.g. McCarthy et al., 2018), activity patterns (e.g. Oberosler, Groff, Iemma, Pedrini, & Rovero, 2017) and behaviour (e.g. Tsutsumi et al., 2006).

With numerous studies reporting the dramatic, global decline of chimpanzees over the past decades (e.g. Campbell, Kuehl, N'Goran Kouamé, & Boesch, 2008; Junker et al., 2012; Kühl et al., 2017), we need reliable, efficient, and affordable methods to monitor their population status. Like cetaceans, chimpanzees have wide ranges, and rely on loud calls to communicate. Seasonality influences activity patterns, ranging and feeding behaviour of chimpanzees (Doran, 1997), and may consequently influence chimpanzee detectability with CT and PAM. CT studies on chimpanzees have been conducted to study uncommon behaviour, for example stone throwing (Kühl et al., 2016) and crab-hunting (Koops et al., 2019), but also for abundance and density estimation (Després-Einspenner et al., 2017; Cappelle et al., 2019) among others. Only a few studies have employed PAM with chimpanzees; those have focused on group ranging and territory use (Kalan et al., 2015, 2016) and temporal patterns of vocalisations (Piel, 2018).

What conservation planners most need, however, is information on the reliability of these methods for application into understanding chimpanzee presence and distribution. Thus, the primary aim of the study was to compare the efficacy in chimpanzee detection from these two non-invasive methods, namely PAM and CT. Specifically, we had three objectives and for both PAM and CT we sought to: (1) estimate chimpanzee detection probabilities from occupancy modelling; (2) identify the parameters that influence the detectability and more specifically to what extent seasonality plays a role in detectability; and (3) estimate and compare the sampling effort needed to produce precise occupancy estimates and make recommendations for wildlife managers regarding which is the more suitable appropriate method for wildlife surveys. We hypothesized that chimpanzee detectability would be higher with PAM compared to CT, given the larger area covered by the acoustic sensors.

2. Methods

2.1. Study site

The study was conducted between March and December 2018, in the Issa Valley, western Tanzania (Fig. 3.1). The area is comprised of a series of valleys separated by steep mountains and flat plateaus, with an altitudinal gradient ranging from 1050 to 1650 m above sea level. Vegetation is dominated by miombo woodland and also includes grassland, swamp and riverine forest. For analyses, we collapsed these categories into just two: 'open' (woodland, grassland, swamp) and 'closed' (riparian forest). It hosts eight primate and four large carnivore species (spotted hyena, lion, leopard, wild dog), and over 260 species of birds (Moyer et al., 2006). The region is one of the driest and most open habitat inhabited by chimpanzees (Moore, 1992). At the time of data collection, the mean monthly rainfall was 118.4 ± 92mm during the wet season (mid-October to mid-May) and 0.6 ± 0.9mm during the dry season. Mean minimum and maximum temperatures per day were 16.6 ± 1.7°C and 27.7 ± 2°C, respectively for the dry season and 16.9 ± 1°C and 25.7 ± 2.2°C for the wet season. Data points were measured every five minutes by a weather station (HOBO model RX3000, Onset Corp., Bourne, MA) situated near the research station. The study site covers the territory of at least one chimpanzee community.

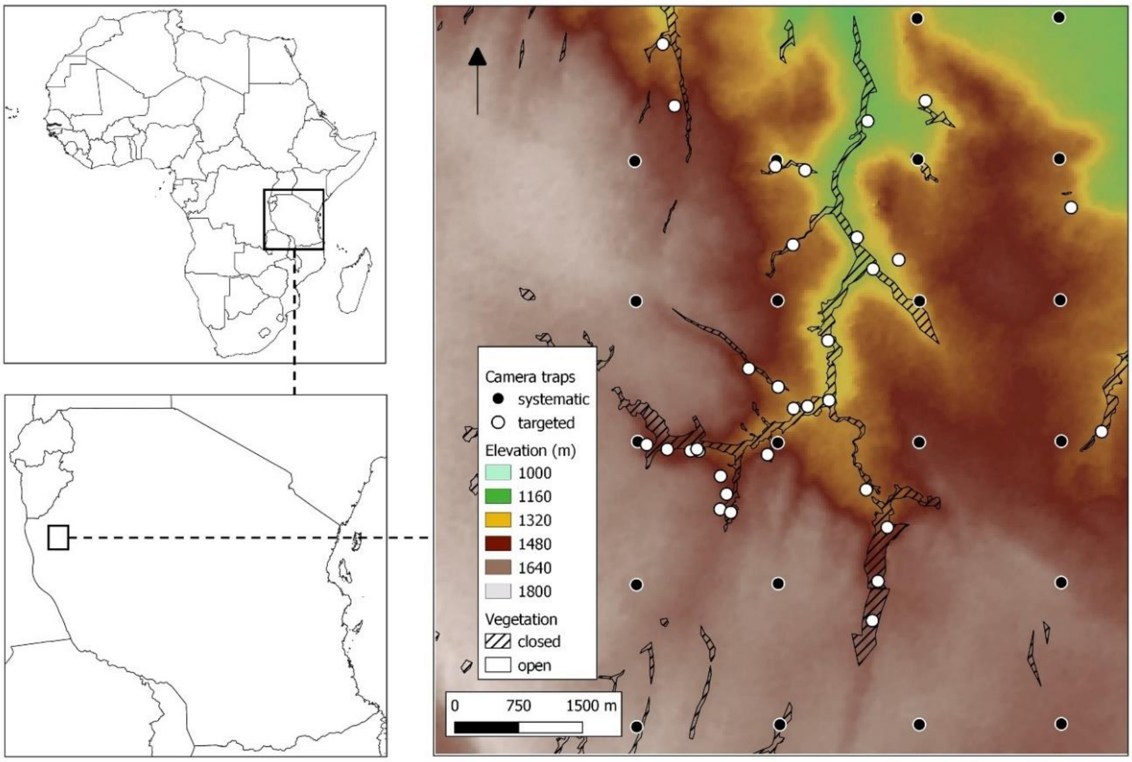

Figure 3.1. Study site and camera trap locations (targeted and systematic placements) in Issa Valley, Western Tanzania.

2.2. Study design

2.2.1. Camera trap deployment

For nine months, we deployed twenty-one camera traps (Bushnell Trophy Cam) in a systematic layout (henceforth ‘systematic’ cameras), in grid cells of 1.67km x 1.67km. We deployed thirty-two additional camera traps (Bushnell Trophy Cam) at targeted locations, i.e. animal paths or termite mounds (seven of them) (henceforth ‘targeted’ cameras, Fig. 3.1). We attached cameras to trees 90cm above the ground and were triggered by movement, which activated a 60s recording, followed by a minimum 1s break before another recording began. For technical reasons, some cameras recorded 15s videos instead of 60s and videos recorded within the same minute have been combined into one video for the analyses. Cameras monitored continuously and were checked once or twice a month to change batteries and SD cards.

2.2.2. PAM deployment

We deployed twelve acoustic sensors (SM2, Wildlife Acoustics) for the same nine-month period that were secured on trees at a height of approximately 1.65m, at the top of the valleys to maximize the chance of recording calls. We recorded sounds at a 16kHz sample rate and 16 bit/s in uncompressed .wav format. We scheduled the sensors to record for 30 minutes of every hour from 6:00 to 19:30 (7h/day) to maximize capturing calls when chimpanzees are the most vocally active. We set up the sensors in three clusters of four sensors/cluster, two sensors on each side of a valley (Fig. 3.2), with inter-sensor distance ~500m to allow for later sound localization. We drew a 500m buffer around each acoustic sensor, corresponding to the area within which a call could reliably be detected (Piel, unpublished data). We rotated the clusters to new locations within the study area every two weeks (four arrays, Fig. 3.2). We replaced batteries and SD cards every two weeks.

We manually processed acoustic recordings by visualizing spectrograms and aurally confirming any detection, with the aid of the acoustic software Raven (Bioacoustics Research Program, 2019). Duplicate detections were controlled for by pooling detections from the four sensors belonging to the same cluster into one detection.

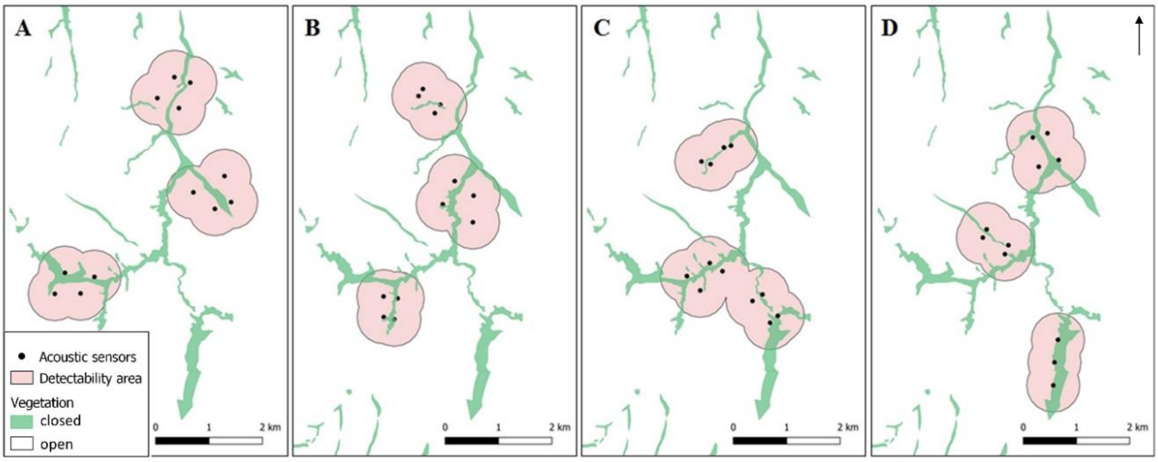

Figure 3.2. Location of acoustic sensors: each set-up (A, B, C, D) remained two weeks before being rotated to another one. Detectability is the area where a call can reach a sensor, defined as a 500m buffer around a sensor.

2.3. Occupancy modelling

2.3.1. Modelling framework

Occupancy modelling estimates two parameters: Ψ, the probability that a species is present within a site, i.e. probability of occupancy, and p, the probability that a species present is detected within a site, i.e., probability of detection (MacKenzie et al., 2006). For a discussion of assumptions, see (MacKenzie et al., 2006; Kalan et al., 2015).

For both datasets, we divided the sampling period into sampling occasions (SO) of eight days each, resulting in 34 and 35 occasions per site, for PAM and CT respectively. Detection histories were compiled into a matrix containing two different values: (0) non detection and (1) detection. When no survey was conducted during a SO (e.g. due to camera or audio recorder malfunctioning or not deployed), a value of NA was assigned. To estimate the occupancy and detection probabilities, we used a single-season model. We applied the “occu” function from the “unmarked” package in R (Fiske & Chandler, 2011).

2.3.2. Covariates

To account for imperfect detection and heterogeneity in occupancy as well as detection probabilities across sampling sites and occasions, we incorporated covariates into the model. To explain the variability in chimpanzee occupancy, we created six vegetation/topography combination categories: A- closed/slope, B- closed/valley, C- closed/plateau, D- open/plateau, E- open/slope and F- open/valley. We did not include site covariates for PAM, as acoustic sensors were only deployed in one type of location.

For the CT dataset, variables that could influence the detectability were the number of camera-trap days a camera was functioning during a SO (henceforth ‘days’), and whether the camera was set-up on a systematic or targeted deployment (henceforth ‘method’). For the PAM dataset, variable that could influence the detectability was the number of 30-min occasions the sensors were recording (henceforth ‘hours’). For both datasets, we included the seasons (early and late wet, early and late dry) as a covariate. We defined the beginning of the dry season as the first week with no rain (i.e. from 16th of May) and the beginning of the wet season the first week with rain (i.e. from 14th October). Camera trap days and acoustic sensor hours covariates were z-transformed to a mean of 0 and standard deviation of 1 before running the models.

2.3.3. Model selection

To determine the factors that best explained chimpanzee detection, we compared all possible combinations of covariates that can influence the detection probability, p. Akaike weights were used to evaluate the weight of evidence for each model and were summed for all models containing each predictor variable. Variables resulting in high summed model weights were considered more important in explaining heterogeneity in detection. For CT we first considered covariates for chimpanzee detectability (p) while keeping occupancy (Ψ) constant and evaluated the best model. We included season, camera placement and days as covariates. Then we evaluated the effect of the vegetation and topography on chimpanzee occupancy. For PAM, we evaluated the effect of seasonality on chimpanzee detectability (p), by evaluating the best model based on the AIC values.

‘occu’ models produce estimates with lower and upper bounds for both occupancy and detection probability on the logit scale. Hence, values were transformed to the original scale using the functions ‘predict’ of the package “Unmarked” (Fiske & Chandler, 2011). To assess goodness-of-fit of the models, we used the parametric bootstrap procedure (MacKenzie & Bailey, 2004) with the function ‘parboot’ from “unmarked” package (Fiske & Chandler, 2011), using 1000 simulations. We found no indication of lack of fit for our best models ($P > 0.05$).

With the estimation of the detection probability (p), it is possible to estimate the necessary number of sampling visits (N) to infer chimpanzee absence (Kéry, 2002). The probability α to not detect a chimpanzee after N visits is: $\alpha = (1-p)^{N}$ (McArdle, 1990; Kéry, 2002).

Thus, for $\alpha=0.05$, corresponding to a confidence level of 95%, the minimum number of sampling visits Nmin is: $\mathrm{Nmin} = \log(0.05)/\log(1-\mathrm{p})$ (Kéry, 2002).

We estimated the number of trap days corresponding, by multiplying Nmin by eight for CT and PAM given that one visit corresponds to eight days.

All analyses were conducted in R studio version 1.2.1335; R Core Team, 2018; available online at: https://www.r-project.org) and maps were created in QGIS version 3.6.2 Noosa; QGIS Development team, 2018; available online at: http://www.qgis.org).

3. Results

3.1. Visual vs acoustic detections

For the total duration of the study, the cameras were functional for 11,342 camera days across 21 systematic CT and 32 targeted CT. It resulted in 3349 chimpanzee videos. 125 videos were recorded on 12 systematic cameras and 3224 on 32 targeted cameras (Table 3.1). The acoustic sensors recorded for 5316 cluster hours (15344 sensors hours). Of the 10632 30-min occasions analysed, at least one detection has been detected in 1024 occasions (9.6%) and detections have been made on all sites surveyed. Calls have been made at each hour of the day with a higher proportion early morning (6am and 7am). Both methods reveal a similar strict pattern of seasonal detection with a peak in detections during the late dry and early wet seasons (Fig. 3.3).

Table 3.1. Summary of the visual and acoustic deployments

	CT		PAM
	systematic	targeted	
Number of sensors	21	32	12
Detection distance/sensor (m)	Max. 29	Max. 29	500
Trap days (per CT or acoustic cluster)	217.1 [147-260]	211.9 [66-280]	68.2 [55-75]
Number of sites with detections (CT or acoustic cluster)	12	32	12
Total detections (videos or 30min audio files)	125	3224	1024
Average trap days with a detection (% per CT or acoustic cluster)	1.94 [0-13.8]	8.33 [0.4-22.1]	38.9 [24.6-52.8]

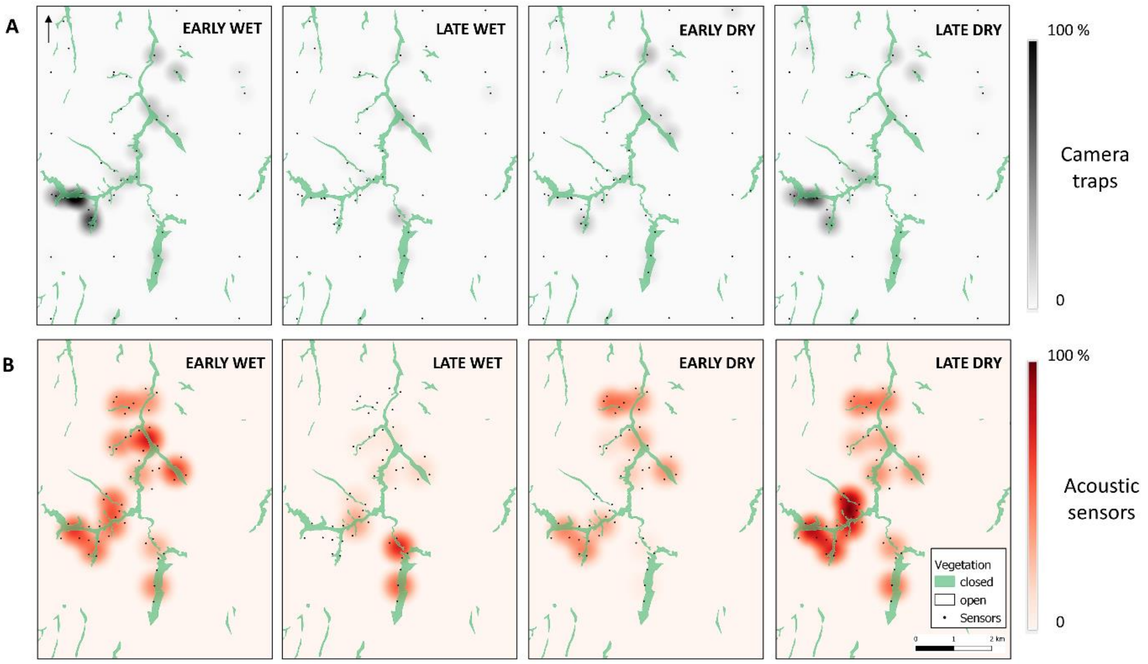

Figure 3.3. Heatmap of chimpanzee detections (proportion of recording days with at least one detection, call or video) for the CT (A) and PAM (B) datasets, in function of the four seasons, early/late wet and early/late dry.

3.2. Factors influencing detectability

The best model to predict chimpanzee detectability for PAM comprised season as a covariate (Table 3.2). The best model to predict chimpanzee detectability for CT comprised all covariates: days, season and camera placement (Table 3.2) and was strongly supported ($\Sigma w > 0.95$; $\Delta AIC < 2$) (Burnham & Anderson, 2004) and ranked higher than the constant model ($\Delta AIC = 148.64$).

Vegetation/topography had no significant effect on chimpanzee occupancy. Detection probabilities were lower during the late wet and early dry seasons and higher during the late dry and early wet seasons (Fig. 3.4). Detection probabilities were higher for the targeted placement compared to the systematic placement. To infer chimpanzee absence with a confidence level of 95%, the number of trap days required was lower for PAM during the late dry and early wet seasons (Fig. 3.5).

Table 3.2. Summary of occupancy modelling for the best models

Models	# Parameters	AIC	Δ	AIC weight
PAM				
p(season+hours) Ψ(.)	6	135.17	0.00	1
p(season) Ψ(.)	5	161.64	26.47	$1.8*10^{-6}$
p(hours) Ψ(.)	3	173.15	37.98	$5.7*10^{-9}$
p(.) Ψ(.)	2	188.68	53.51	$2.4*10^{-12}$
CT				
p(season+method+days) Ψ(vegetation/topography)	12	1507.38	0.00	0.95
p(season+method+days) Ψ(.)	7	1513.33	5.95	0.049

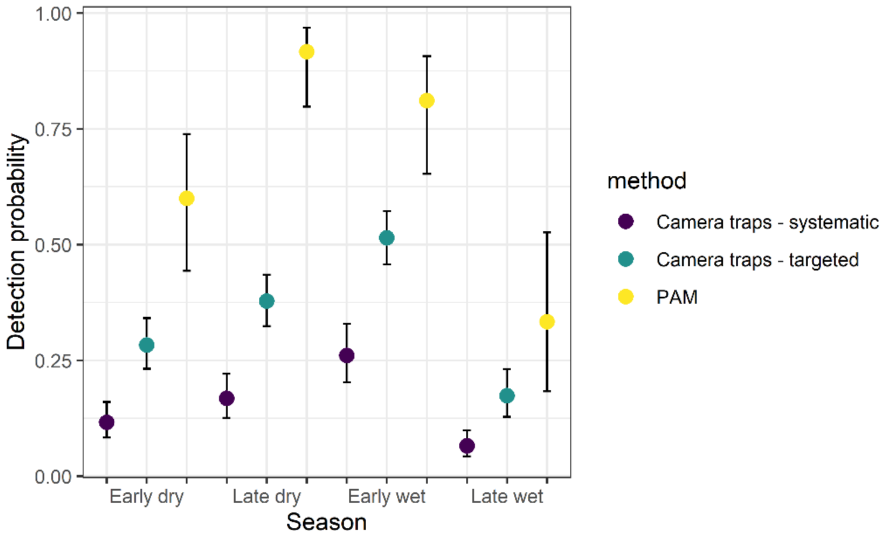

Figure 3.4. Detection probabilities for each method (PAM, systematic and targeted CT) depending on the season. Error bars represent upper and lower bounds.

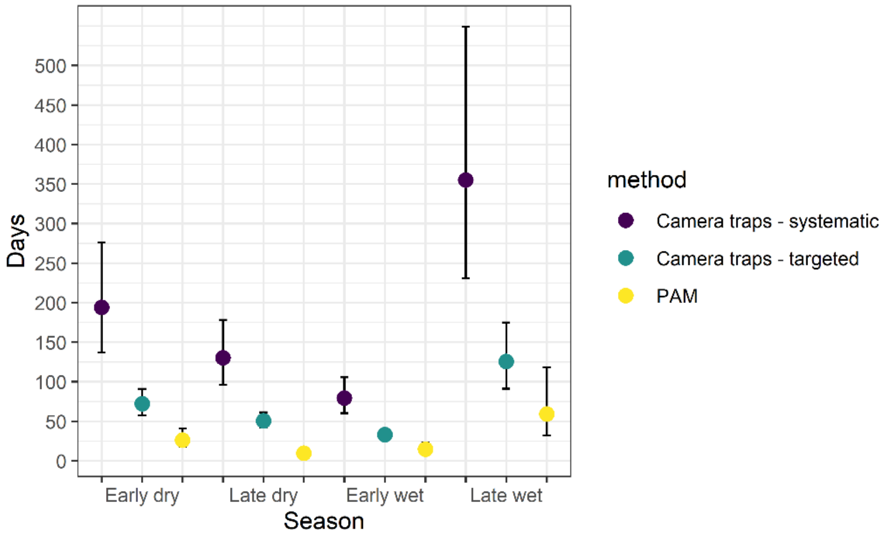

Figure 3.5. Number of trap days necessary to infer chimpanzee absence at a confidence level of 95% in function of seasons and methods. Error bars represent upper and lower bounds.

4. Discussion

CT and PAM methods revealed similar patterns of chimpanzee spatiotemporal distribution, with peaks of detections by both methods occurring in the same valleys in function of the seasons. However, when we compared the deployment duration required of each method to infer chimpanzee absence at a confidence level of 95%, PAM was superior, with only ten and fifteen days needed during the late dry and early wet seasons, respectively. Alternatively, CT required up to five times longer (e.g. 51 and 33 days for the late dry and early wet seasons, respectively, in an area of known for chimpanzee presence – ‘targeted placement’) at the same times of year. Detection probabilities varied as a function of season, with higher vocal and visual detections during the late dry and early wet seasons. We first discuss the efficiency of both methods, explore the ecological and social factors that can explain seasonal variability of detection, and then evaluate the advantages and limitations of these methods.

4.1. Efficacy of PAM and CT in chimpanzee detection

If we define efficacy as the shortest amount of time needed to detect a chimpanzee, PAM was more efficacious and acoustic detection rates were higher. The finding is similar to other studies comparing acoustic and visual methods in detecting southern right whales (*Eubalaena australis*), sika deer (*Cervus nippon*) and Japanese macaques (*Macaca fuscata*) (Rayment et al., 2018; Enari et al., 2019). This is likely due to the detection area with PAM being far larger than with CT, estimated to be up to 7000 times greater than those for CT in the study from Enari et al. (2019).

Detection probabilities were higher on a targeted camera trap placement compared to a random placement, as expected. This suggests that when using the CT method, a pre-survey to find any feeding trees or animal paths will maximise the chance to capture an animal.

4.2. Ecological and social factors influencing detectability

We can assume that acoustic and visual detectability are influenced by party size. Indeed, parties with more chimpanzees call more often (Fedurek, Schel & Slocombe, 2013). Likewise, there is a greater likelihood of chimpanzees being visually recorded on the cameras as party size increases. The variation in detection probabilities across seasons is likely due to seasonal differences in social grouping and ranging patterns. At Issa, for example, mean dry season party size is nearly twice that of the wet season (Piel, unpublished data). In our study, we found higher detectability during the late dry and early wet seasons. Fruit availability itself might not explain party size fluctuation but rather the interaction of food availability and food distribution.

The presence of females showing full swellings is another important factor that influences party size, with parties larger when a swollen female is present (Sakura, 1994; Wallis, 1995; Mitani, Watts & Lwanga, 2010). Furthermore, male chimpanzees become more aggressive when they are in a party with oestrous females (Sobolewski, Brown & Mitani, 2013) and are therefore more vocal (i.e. more vocalisations because fighting) (Fedurek, Donnellan & Slocombe, 2014). At both Issa and Gombe National Park, females show full swellings more often during the late dry season (Gombe: Wallis, 1995; Issa: Piel unpublished data). Consequently, these extrinsic factors may explain the higher detection probability during the late dry season, both by PAM because of the increased calling behaviour and CT, because parties are larger overall.

4.3. Potential applicability to other studies, advantages and limitations

This study confirms the applicability and potential of PAM compared to CT to detect chimpanzees. The methods used here are highly applicable to other loud-calling species, such as elephants (Wrege, Rowland, Keen & Shiu, 2017), gibbons (Kidney et al., 2016), howler monkeys (Aide et al., 2013), and could also be applied to insects or frogs (Aide et al., 2013). Species behaviour plays an important role in detection and should be taken into consideration during study design. For instance, deer detectability will be higher during the rutting season (Enari, Enari, Okuda, Maruyama & Okuda, 2019), just as we might be seeing for chimpanzees as well.

Despite PAM requiring less deployment time to confirm chimpanzee absence in this study, the limitations of the method are significant. In contrast to camera traps that record only when a detection is made, acoustic sensors record all sounds, continuously or on a pre-determined schedule. This generates enormous datasets and sophisticated, big data processing and analyses are required to post-process (e.g. filter) sounds of interest (See below; Knight et al., 2017). Data storage can be problematic as well for both methods. Another challenge is power, with regular visits needed to maintain the system. However, with only a few days required to detect a chimpanzee combined with the development of new low cost sensors that can be recharged with solar panels (e.g. Beason, Riesch, & Koricheva, 2018; Hill et al., 2018; Nazir et al., 2017; Sethi, Ewers, Jones, Orme, & Picinali, 2018), current challenges are already being overcome. Lastly, without automated detection, analyses of PAM and CT data are extremely time-consuming and so not advisable when conducting regular surveys. For instance, in this study with

10 days required for PAM to infer chimpanzee absence, this correspond to 1120min of manual processing (10 (days)*14 (audio files per day) *2 (minutes to process one audio file) *4 (sensors)). In the past few years, major improvements in automated species detection algorithms have transformed the way big data are analysed (e.g. Clink, Crofoot, & Marshall, 2019; Knight et al., 2017; Wrege, Rowland, Keen, & Shiu, 2017). Different methods of machine learning (e.g. neural networks) are available, see the review from Bianco and colleagues (2019) for more details. A manual validation to clean false positives is, however, necessary (e.g. Campos-Cerqueira, Aide, & Jones 2016; Crunchant et al., 2017; Enari, Enari, Okuda, Maruyama & Okuda 2019; Kalan et al., 2015) to control for false positives. With species with high call variabilities, like chimpanzees, developing an algorithm is more challenging but as technology improves rapidly, we can expect the development of a detection algorithm in the near future. Lastly, these two approaches offer complementary information, and methods should be used in accordance with particular objectives. For instance, CT allows for individual identification, necessary to extract information on population abundance (e.g. Després-Einspenner et al., 2017).

Similar to PAM, new technologies such as drones can offer an aerial perspective and provide real-time feedback for rapid surveys (Wich & Koh, 2018). By combining these two promising technologies, otherwise labour and time intensive species monitoring is on the cusp of being revolutionised by remotely recorded sounds with drone-mounted microphones. If the major drawback for using UAV in acoustic biomonitoring is the excessive UAV noise that can mask the targeted sound, new methods are already in progress, such as the development of signal processing algorithms that reduce noise in recording (Hioka et al., 2019).

4.4. Conservation applications

Regular surveys and monitoring are crucial for evaluating conservation efforts aimed at impeding the global decline of great apes and overall biodiversity. Developing an accurate and time-effective method of surveying animals especially in remote areas is critical. Here we demonstrated the usefulness of PAM compared to CT to evaluate the absence of an endangered species. The continuing development of new technologies and the increasing inter-disciplinary collaboration between engineers, field ecologists and bioinformaticians are driving new affordable and effective biomonitoring methods. The dramatic improvements in biomonitoring techniques over the last decade are altering the way we remotely study wildlife distribution by helping to plan surveys (e.g. Hodgson et al., 2018), identify hotspots and prioritize patrols (e.g. Hambrecht, Brown, Piel, & Wich, 2019), and how we monitor the wildlife response to ever-increasing anthropogenic disturbance to their environments (e.g. Buxton, Lendrum, Crooks, & Wittemyer, 2018).

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Data accessibility: The raw presence/absence matrices can be found at: https://doi.org/10.5061/dryad.5dv41ns34. All results reported in this article can be reproduced using these matrices.

Chapter 4. Vocal communication in wild chimpanzees: a call rate study

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Author contribution: ASC, AP conceived the ideas and designed methodology; ASC collected and analysed the data; ASC and AP wrote the manuscript, and all authors contributed critically to the drafts and gave final approval for publication

Abstract

1. Background. Patterns of vocal communication have implications for species conservation: a change in calling behaviour can, for instance, reflect a disturbed habitat. More importantly, call rate is a parameter that allows conservation planners to convert call density into animal density, when detecting calls with a passive acoustic monitoring (PAM) system.
2. Methods. We investigated chimpanzee (*Pan troglodytes schweinfurthii)* call rate during the late dry season in the Issa Valley, western Tanzania by conducting focal follows. We examined the socio-ecological factors that influence call production rate of savanna woodland chimpanzees.
3. Results. We found that sex, proportion of time spent in a vegetation type, proportion of time spent travelling, time of day, party size and swollen parous female presence had a significant effect on the call rate. Call rate differed among the different demographic classes with subadult and adult males vocalising twice as often as the subadult and adult females and three times as often as the juveniles.
4. Applications: The use of PAM and recent statistical developments to estimate animal density is promising but relies on our knowing individual call rate, often not available for many species. With the improvement in automatic call detection, we anticipate that PAM will increasingly be broadly applied to primates but also across taxa, for conservation.

Keywords: fission-fusion, pant hoot, primate, sexual dimorphism, Tanzania, vocalization

1. Introduction

Vocal communication is a means through which senders and receivers exchange information via the production of acoustic signals and is likely influenced by natural and sexual selection (Seyfarth & Cheney, 2003). Vocal signals are widely diversified among taxa, produced by insects, fish, herpetofauna, birds, and mammals to communicate in various social and environmental contexts, from alerting conspecifics to predator presence (e.g. Schel et al. 2013; Vitousek et al. 2007), maintaining bonds (e.g. Fedurek et al. 2013; Wanker et al. 1998), and marking territorial boundaries (e.g. Peek 1972) among others. Similar to food, mates, and territory, acoustic space can also be a scarce resource for which animals compete. Callers must adjust spatial, temporal and frequency patterns in response to both abiotic and biotic factors, especially the sounds of sympatric fauna (Araya-Salas et al., 2017). Widely spaced individuals use long calls to maintain inter-individual contact, which allow them to coordinate movements, especially for socially fluid animals with high fission-fusion dynamics like elephants (*Loxodonta africana)* (e.g. Leighty et al. 2008), spotted hyena (*Crocuta crocuta),* (e.g. Theis et al. 2007), bottlenose dolphins (*Tursiops truncatus)* (Janik & Slater, 1998), beluga whales (*Delphinapterus leucas)* (O'Corry-Crowe et al., 2020), spider monkeys (*Ateles* spp.) (e.g. Spehar and Di Fiore 2013), bonobos (*Pan paniscus)* (e.g. Hohmann and Fruth 1994) and chimpanzees (e.g. Fedurek et al. 2014).

Call rate, the number of calls emitted per unit time per individual, can advertise male quality (Pedroso et al., 2013) and rate changes with caller age and sex class, time of day, group size and composition, social context, and environment, among others (Pérez-Granados et al., 2019). For instance, frog vocalizations are highly sexually different, energetically costly, and are mostly produced by males (Emerson & Boyd, 1999). Dawn and dusk chorusing are common for many species, exploiting low ambient and minimal wind noise levels (Ey & Fischer, 2009). Guereza black and white colobus monkey (*Colobus guereza)* calls are highly contagious and spread from one group to another (Schel & Zuberbühler, 2012). Furthermore, loud calls in baboons advertise male quality, with high-ranking males calling more often (Kitchen et al., 2003; Fischer et al., 2004). Therefore, loud calls serve multiple functions and spatiotemporally shift in predictable ways, which can be reflected in a variation of call rates.

Additionally, vocal communication has implications for species conservation. A change in calling behaviour can reflect a disturbed habitat. Anthropogenic pressure affects call parameters, such as call duration and call frequency, and also the number of calls produced. For instance, a recent study at Los Tuxtlas in Mexico showed that howler monkeys (*Alouatta palliata mexicana*) produced fewer calls when exposed to anthropogenic noise (Cañadas Santiago et al., 2020). There is also evidence that African elephants change the acoustic structure of their alarm calls when threatened by bees or humans (Soltis et al., 2014). LaZerte *et al.* (2017) demonstrated that male mountain chickadees (*Poecile gambeli*) adjust songs, calls, and chorus composition with increasing ambient and (experimental) anthropogenic noise. More importantly, call rate is a parameter that allows conservation planners to convert call density (the number of calls per unit time per unit space) into animal density (i.e.the number of callers per unit space). Acoustic spatial capture-recapture (aSCR) and distance sampling methods can be used to estimate animal density by detecting vocalisations with acoustic sensors (e.g. Marques et al., 2013; Stevenson et al., 2015). This can be particularly useful for cryptic, elusive, wide ranging and not visually detectable species. Using this method, numerous studies have reported abundance and density for various species, such as ovenbirds – *Seiurus aurocapilla* (Dawson & Efford, 2009; Efford, Dawson, & Borchers, 2009), frogs – *A. lighfooti* (Borchers et al., 2015; Stevenson et al., 2015), northern yellow-cheeked gibbons - *Nomascus annamensis* (Kidney et al., 2016). We can convert caller density to population density once we know the call rate (Stevenson et al., 2015). Data on these parameters can be obtained by following individuals and recording call events. Obtaining these values is what motivated the current study. To accurately reflect the call rate of calls that can be detected on acoustic sensors, sometimes deployed hundreds of meters away from the caller for subsequent analyses, we focused only on screams, barks and pant hoots.

Chimpanzees (*P. troglodytes)* are a gregarious species and form small parties that change in size and composition throughout the day. They move through a relatively large territory - e.g. from 7 to 40km^2 for forest dwelling chimpanzees (Newton-Fisher, 2003; Després-Einspenner et al., 2017) and 72 to 90km^2 for savanna dwelling chimpanzees (Samson & Hunt, 2012; Pruetz & Herzog, 2017) and are often hundreds of metres apart. Thus, they must rely on vocal communication to reveal to others information about, for instance, fruiting trees, predator presence, and movement coordination within and between parties. Eckhardt et al. (2015) reported that male chimpanzees from Taï Forest (Ivory Coast) remained out of visual range of conspecifics for almost half of observation time but within auditory range (<1km) for 70% of the time, suggesting chimpanzee vocalisations serve an important function as contact calls between spatially separated individuals. Some of the earliest studies on chimpanzee vocalisations noted an overall sex difference in pant hooting rates in adults, with males calling more than females ago (Marler & Hobbett, 1975, Goodall, 1986), and in some cases, all-female parties calling so rarely to make inter-sex comparisons impossible (Clark & Wrangham, 1994; Arcadi, 1996). Only recently, however, were these observations supported with empirical data from a single community in Tai Forest (Kalan, 2019). Thus, despite a half-century of investigation into chimpanzee vocalisation, much is still not known about call rate, and especially hot it changes between sexes, behavioural contexts, and communities. This intra- and inter-community rate variability has bearing on what value is used for density studies that rely on PAM data, where call rate is a critical parameter (Marques et al., 2013).

The aim of this study was twofold: first, we wanted to estimate the call rate of chimpanzees living in a savanna woodland habitat. Given the known sex differences in chimpanzee acoustic communication, e.g. call rate and acoustic parameters (Kalan, 2019), we calculated the call rate for the following age/sex classes: subadult and adult females, subadult and adult males and male and female juveniles. Second, we investigated socio-ecological factors influencing call rate. We therefore examined the effect of (1) *party size*: we expected chimpanzees to call more often as party size increased due to the chorus effect and contagious calling (Fedurek, Schel & Slocombe, 2013); (2) *presence of a swollen female*: we expected that call rate would be higher when callers were in parties with at least one parous swollen female (Fedurek, Donnellan & Slocombe, 2014); (3) *time of day*: we expected a temporal pattern with chimpanzees calling more often in the morning and late afternoon (e.g. Piel 2018); (4) *vegetation*: chimpanzees seem to spread more when in open area, likely because of higher visibility and we consequently expected chimpanzees to call more often when present in the open vegetation (woodland); (5) *activity*: two important call functions are to indicate fruiting trees and maintain spatial cohesion, especially during travelling, hence we expected that the proportion of time spent travelling or feeding would be positively correlated to the call rate (Clark & Wrangham, 1993; Fedurek, Donnellan & Slocombe, 2014).

2. Methods

2.1. Study site

We collected data for three months during the late dry season, between August and October 2019, in the Issa Valley, western Tanzania (Fig. 4.1). The study area of about 70 km^2 is comprised of a series of valleys separated by steep mountains and flat plateaus, with an altitudinal gradient ranging from 1050 to 1650 m above sea level. Vegetation is dominated by miombo woodland and also includes grassland, swamp and riparian forest. For analyses, we collapsed vegetation categories into ‘open’ (woodland, grassland, swamp) and ‘closed’ (riparian forest), see Fig. 4.1. The region is one of the driest and most open that is inhabited by chimpanzees (Moore 1992) and characterised by two seasons: wet (November to April) and dry (May to October) Annual rainfall averaged 1220mm per annum (range from 930 to 1490 mm from 2009 to 2014) and temperatures ranged from 11°C to 38°C (Piel et al., 2017).

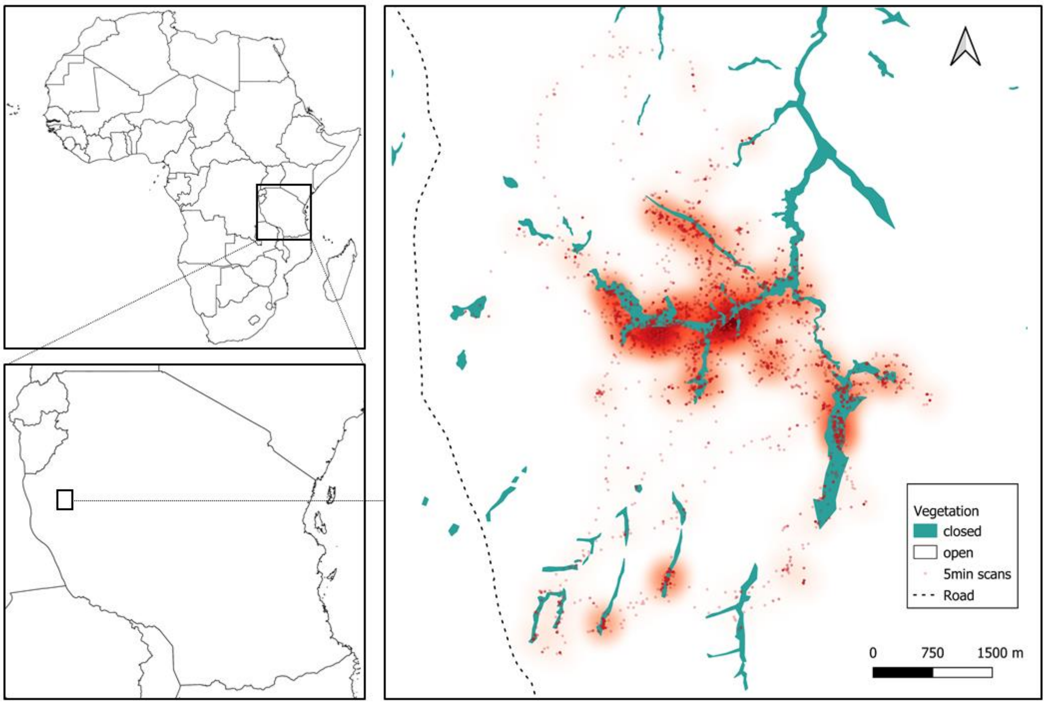

Figure 4.1. Study site in Issa Valley, Western Tanzania and chimpanzee locations during the late dry season from focal follows (7239 5-min scans). Each dot represents the location of an individual and a heatmap shows the preferentially used areas during the study period.

2.2. Study subjects

The study site covers the territory of at least two chimpanzee communities (one habituated community and one or more neighbouring communities). When the study began, the habituated Issa community comprised nine adult females, seven adult males, four subadult males, one subadult female, three juveniles and four infants (Table 4.1). During the study period, one female (AZ) was not yet fully habituated so we have not included data on her, as researcher presence likely influenced her natural behaviour (Crofoot et al., 2010; Nowak et al., 2014). Two individuals (adult female and infant) were killed and a female gave birth during the study period. The habituated community has a home range ≥ 55km^2.

2.3. Data collection

We selected a focal chimpanzee (adult, subadult or juvenile) each morning and tried to follow him/her for the entire day (i.e. from nest to nest). We conducted instantaneous focal animal sampling, with a scan defined as the behaviour of the animal recorded every five minutes, when we collected data on caller location (GPS), behaviour (travelling, feeding, resting, grooming, playing, other), vegetation (open or closed) and party size, defined as the number of juveniles, subadults and adults seen. We further noted all vocal behaviour ad libitum of the focal, including the type of vocalisation (pant grunt, grunt, hoot, pant hoot, bark, scream or combinations of different types (see e.g. Crockford 2019; Goodall 1986 for descriptions of chimpanzee vocalisations). Successive calls were considered as new events when separated by more than one second. We included only vocalisations that involved at least a scream, a pant-hoot or bark in the analyses, to match the calls that can be potentially recorded by an acoustic recorder deployed about 500m away from the caller. We thus excluded grunts and other closed calls that do not propagate far. We included only hours of follow data with at least 10 scans/hour, which corresponds to at least fifty minutes of observation per hour.

2.4. Data analyses

We conducted all analyses in R v.3.6.1 (R Core Team, 2019). For each hour of follow, we determined the proportion of time spent travelling, feeding or other behaviours, in open or closed vegetation by the focal individual. We defined the proportion of time in e.g. open vegetation as the number of scans in which the focal was observed in open vegetation divided by the total number of scans where the focal was in view.

To model the number of calls per hour (call rate, CR) as a function of the covariates, we used a negative binomial distribution GAM with a log link function, that allowed us to account for overdispersion. Fixed covariates were (1) time (T, categorical with 11 levels: from 7am to 6pm), (2) mean hourly party size (PS, continuous), (3) presence of swelling female in the party (PrS, categorical with 2 levels: presence or absence), (4) proportion of time spent feeding (Fe, continuous), (5) proportion of time spent in the closed vs. open habitat (F, continuous), (6) proportion of time spent travelling (Tr, continuous) and (7) age-sex class (AS, categorical with 3 levels: adult-subadult female, adult-subadult male, juvenile). To incorporate the dependency among follows on the same day, we used "individual" as a random intercept and to incorporate the dependency We used the package mgcv (Wood, 2017) to fit the model. We centred and scaled continuous predictors.

We tested predictors for collinearity by calculating variation inflation factors (VIF) using the package car (Fox & Weisberg, 2018) in an equivalent linear model including only the fixed effects from each model fitted with the package MASS (Brian et al., 2020). Multicollinearity was not present (maximum VIF: PS= 1.53). We verified model assumptions by plotting residuals versus fitted values and QQ-plots. We ran a set of models and ranked them by AICc value.

3. Results

In total, we analysed 487 hours of follows on twenty-one chimpanzees (21.2 ± 12.2 hrs per individual, Table 4.1). Call rate varied individually, ranging from an average of 0.24 to 3.41 calls per hour.

Factors influencing the call rate

We did model averaging among models with ΔAICc <2. The significant effects in the best averaged model are age/sex, proportion of time in the forest, proportion of time travelling, time-of-day, presence of swollen female, party size, and the two random intercept terms (individual and date) (Table 4.2).

Results of the GAM revealed that the age-sex class had a significant effect on call rate: overall, Issa chimpanzees exhibited a mean call rate of 1.91 with 95% CI of [1.52 – 2.40] calls per hour for the subadult and adult males, 0.84 with a 95% CI of [0.59 – 1.21] calls per hour for the subadult and adult females, and 0.50 with a 95% CI of [0.24 – 1.05] calls per hour for the juveniles. With 95% confidence, males call between 1.5 and 3.8 times as frequently as females and between 1.3 and 7.9 times as frequently as juveniles. Chimpanzees vocalised significantly more as the proportion of time spent in open vegetation and as the proportion of time spent traveling increased (Table 4.3). The smooth effect of time reveals call rates being highest in the morning decreasing thereafter, before increasing late afternoon (Figure 4.2).

Table 4.1. Summary of the number of focal follow hours per individual and their call rate. Mean call rate, defined as the number of pant-hoots, screams or barks per hour is presented with the individual range in brackets.

Name	Age	Sex	# hrs of follow	Call rate (# calls/hr, min-max)
AZ	Adult	Female	0	NA
BS	Adult	Female	13	0.38 [0-2]
JU	Adult	Female	11	1.73 [0-4]
KL	Adult	Female	5	0.60 [0-2]
KN	Adult	Female	9	2.22 [0-5]
KJ	Adult	Female	14	1.14 [0-3]
MA	Adult	Female	18	1.56 [0-5]
ZA	Adult	Female	17	0.24 [0-2]
KS	Sub-adult	Female	26	0.31 [0-3]
BG	Adult	Male	41	3.41 [0-11]
EL	Adult	Male	23	2.04 [0-8]
IM	Adult	Male	35	2.37 [0-9]
KT	Adult	Male	37	2.65 [0-14]
MY	Adult	Male	33	1.06 [0-6]
SM	Adult	Male	35	2.23 [0-9]
WA	Adult	Male	23	1.48 [0-8]
DH	Sub-adult	Male	25	2.60 [0-7]
MS	Sub-adult	Male	29	1.45 [0-6]
SN	Sub-adult	Male	30	2.90 [0-13]
WG	Sub-adult	Male	30	1.53 [0-8]
MW	Juvenile	Female	5	1.20 [0-2]
KK	Juvenile	Male	28	0.57 [0-5]
BN	Juvenile	Male	0	NA

Table 4.2. Model selection. CR: call rate; AS: age/sex class; PrS: presence swelling female; Fe: proportion of time spent feeding; F: proportion of time spent in closed vegetation; Tr: proportion of time spent travelling; PS: party size; T: time, Fo: follow, D; date.

Model	df	logLiK	AICc	delta	weight
CR ~ AS + PrS + F + Tr + PS + T + Fo	24	-814.710	1681.5	0.00	0.094
CR ~ AS + PrS + F + Tr + PS + T + Fo + D	24	-814.710	1681.5	0.00	0.094
CR ~ AS + PrS + F + Tr + Fo	25	-814.471	1682.4	0.84	0.062
CR ~ AS + PrS + F + Tr + Fo + D	25	-814.471	1682.4	0.84	0.062
CR ~ AS + PrS + Fe + F + Tr + PS + T + Fo	25	-814.078	1682.6	1.09	0.055
CR ~ AS + PrS + Fe + F + Tr + PS + T + Fo + D	25	-814.078	1682.6	1.09	0.055
CR ~ AS + F + Tr + T + Fo	24	-816.013	1683.0	1.50	0.045
CR ~ AS + F + Tr + T + Fo + D	24	-816.013	1683.0	1.50	0.045
CR ~ PrS + F + Tr + T + Fo	26	-813.445	1683.4	1.88	0.037
CR ~ PrS + F + Tr + T + Fo + D	26	-813.445	1683.4	1.88	0.037
CR ~ PrS + Fe + F + Tr + T + Fo	27	-812.771	1684.1	2.54	0.027
CR ~ PrS + Fe + F + Tr + T + Fo + D	27	-812.771	1684.1	2.54	0.027

Table 4.3. Outcome of a GAM investigating the effect of time, age/sex class, presence of swelling female, party size (PS), proportion of time spent in the closed area and proportion of time spent travelling for the averaged best three models.

Predictors	Parameter Estimate			
	Estimate	Std. E.	z value	Pr(>|z|)
Intercept	0.477	0.225	2.115	3.44e-02*
Age/sex class (male)				
Subadult/adult female	-0.864	0.252	3.413	6.43e-04***
juvenile	-1.129	0.456	2.820	4.79e-03**
Closed area (forest)	-0.171	0.063	2.698	6.977e-03*
Swollen parous female presence	0.315	0.141	2.236	2.536e-01*
Party size	0.164	0.734	2.223	2.619e-02*
Travel	0.237	0.059	3.977	1.60e-04***

* = p < 0.05; ** = p < 0.01; *** = p < 0.001.

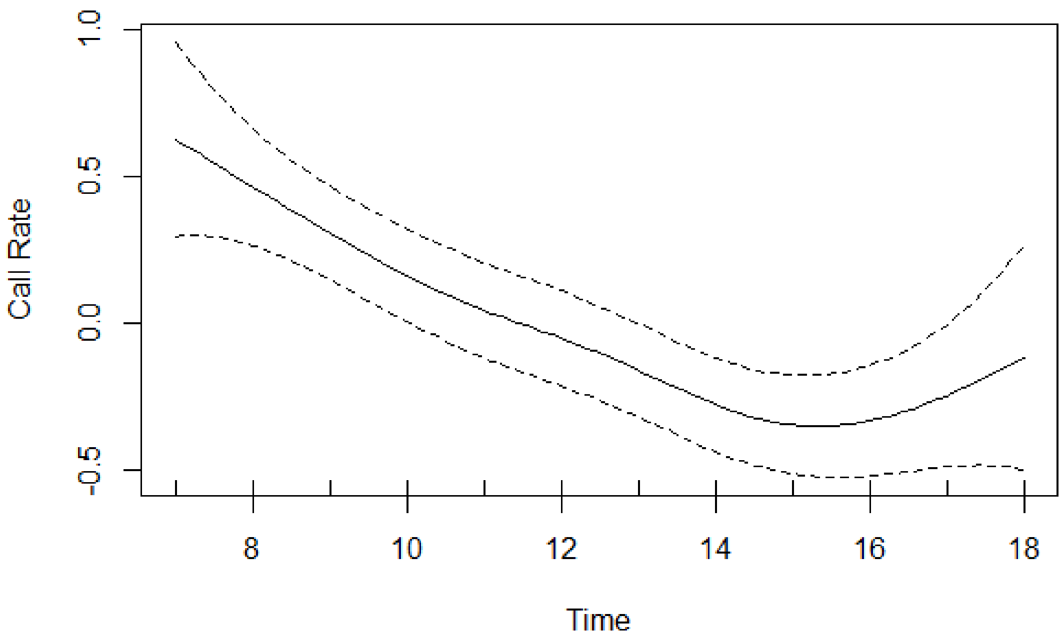

Figure 4.2. Call rate change over the course of the day. Rates were highest in the morning and decreased thereafter, before increasing in the late afternoon.

4. Discussion

In this study, we sought to establish the mean call rate of different demographic classes of wild chimpanzees, as well as examine the socio-ecological factors that influence call production rate. We found that time spent in a specific vegetation type, time spent travelling, time of the day, party size and swollen parous female presence had significant effects on call rate.

4.1. Call rate among demographic classes

Our results confirm early reports on sex differences between adult chimpanzee loud call production (Clark, 1996) and a recent study that subadult and adult male chimpanzees vocalise more than twice as often as subadult and adult females (Kalan, 2019). The sexual dimorphism seems to be even more pronounced for forest than savanna woodland dwelling chimpanzees. At Taï, males produced on average 2.5 ± 1.08 calls per hour and females produced 0.88 ± 0.32 calls per hour (Kalan, 2019), compared to 1.91 ± 0.12 calls per hour for the males and 0.84 ± 0.18 calls per hour for the females at Issa (this study). We propose two explanations for this sexual difference: (1) necessity of maintaining strong bonds and/or (2) sexual selection. Chimpanzees are male-philopatric, where males stay in their natal territory, while females disperse at sexual maturity and migrate to neighbouring communities (e.g. Moore et al. 2015; Nishida 1968). This sex difference in dispersal explains strong male-male relationships (e.g. Mitani 2009). Males tend to develop stronger bonds with other male community members with whom they spend more time, forming a linear dominance hierarchy and developing affiliations and coalitions. East African female chimpanzees, on the contrary, are far less gregarious than males, travel less and spend most of their time alone or with their offspring in their core home range (Wrangham and Smuts 1980).

4.2. Ecological factors

We found that chimpanzees called most at two times of day (morning and evening) and from open (miombo woodland) compared to closed (riparian forest) vegetation. This temporal information is important for conservationists, who can for instance record sounds with PAM systems at these periods to maximise the likelihood of detecting calls and simultaneously limit the number of audio files to analyse. There are ecological and social reasons for these patterns. Temporally, the bimodal pattern that we found in this study is similar to what has been reported previously at Issa (Piel 2018) and elsewhere (e.g. Wilson et al. 2007; Wrangham 1975). Vocalisations allow parties to coordinate movements, notably prior to arrival at their nesting sites (Fischer & Zinner, 2011) or feeding trees (Clark & Wrangham, 1993). Ecologically, callers may exploit ideal sound transmission conditions. The Acoustic Adaptation Hypothesis predicts that animals may adjust their vocal signals to maximize signal transmission and minimize sound degradation, specifically within each environment in which calls occur (Waser & Waser, 1977; Ey & Fischer, 2009; Brown & Waser, 2017). Environmental metrics, such as temperature gradients, humidity and wind, vary with time of day, and can degrade signals, resulting in structural changes to the primary sound (Waser & Brown, 1984). Relatedly, the natural habitat distorts signals as distance from the sound origin increases. Open vegetation, with increased wind-induced noises compared to closed vegetation, can further degrade signals but sounds attenuate faster in closed vegetation because of tree density (Brown & Waser, 2017). If chimpanzees rely more on close contact calls (not included in this study) to maintain party cohesion in closed, rather than open vegetation, the fact that chimpanzees vocalize significantly more often in open vegetation might be explained by their activity, rather than the external environment. Furthermore, the Issa landscape is dominated (>65%) by miombo woodland vegetation, thus it is unsurprising that they vocalize more from open than closed vegetation types. Calls made in open vegetation could serve multiple purposes. First, individuals may spread out more in these areas, given that food sources are more widely distributed here than in closed areas and so calls are functioning to preserve party cohesion. Additional data on inter-individual distance (e.g. party spread) in each vegetation type would help us resolve this. Second, calls travel further in open compared to closed vegetation, with fewer trees to attenuate sound (although see Waser & Brown 2017), so individuals also may be calling to communicate with distantly located parties. Often counter calls are heard from these woodland pant hoots (A. Crunchant, 2019, pers. obs.), but we do not have comparative data from forests.

4.3. Travelling and feeding activities

We evaluated the effect of activity, namely travelling and feeding behaviour, on call production rate. While previous studies have shown that chimpanzees frequently pant-hoot at food sources (Clark and Wrangham 1993; Fedurek et al. 2014; Wrangham 1977), call rate did not change with the proportion of time spent feeding in our study. However, our brief field season took place during the late dry season, when fruit availability is highest (McLester et al., 2019). The abundance of food might reduce competition among individuals and thus depress the need for calling. Furthermore, we did not incorporate which food items were consumed. Fedurek and colleagues (2014) have shown that male chimpanzees were more likely to pant hoot at high-quality food patches and thus we suggest that subsequent studies consider food type consumption during calling bouts.

The number of calls increased as the proportion of time spent travelling increased. It has long been demonstrated that loud calls facilitate fusion events and help regulate grouping dynamics and coordination among community members during travel (e.g. Goodall 1986). In other communities, males travel significantly more after a pant hoot is produced (Mitani & Nishida, 1993) and males are more likely to repeat a call prior to, rather than after, fusion with other males (Fedurek, Donnellan & Slocombe, 2014).

4.4. Party size and presence of parous swollen female

We have shown that call rate was positively related to party size. Coordinating movement with a higher number of individuals requires more communication, especially for decision making and coordinating party fusion (Fischer & Zinner, 2011). Furthermore, a previous study has shown that the number of aggressive events is positively correlated to the number of males in a party (Muller 2002), and thus the number of calls produced during agonistic events (i.e. barks, screams and pant hoots) would likely increase with the number of males in the party.

Finally, the presence of a swollen female in the party did also impact call production rate, as expected. It has indeed been shown that males prefer to mate with parous females and are more involved in male-male competition in their presence because parous females are attractive to males, which exhibit aggressive displays and courtship behaviour during these times (Muller et al. 2006).

4.5. Implications and limitations

Variability in chimpanzee calling is well known, described in nearly every study on the topic; early work attributed variability to age, sex, context, party size, and community, among others (Goodall, 1986; Arcadi & Wrangham, 1993; Arcadi & Wrangham, 1994; Mitani et al., 1992; Mitani et al., 1994). For the most part, these studies reported variability in the context of call function. In the current study, however, we were not interested in call function. Whilst similar to some previous work, we report on context-specific variability, our primary interest is in the implications of call rate variability for conservation studies that rely on PAM to extract animal densities. For example, sex ratio, vegetation types and proportions, and activity budgets vary between communities. Our results here begin to reveal how call rate changes with each of these, which has direct bearing on how its parameterised in density analyses. Specifically, for community that range across more open vegetation – Issa (Tanzania), Fongoli (Senegal), Semliki (Uganda) – call rate should reflect this in density models, varying with sensor location.

Those implications notwithstanding, we are cautious interpreting these results and conclusions should not be generalized to scenarios other than that where data were collected. We sampled over a single and brief 3-month season and recorded only 487 hours of follows (compared to Kalan (2019) who recorded 731.5 hours of follows across 10 months). With food availability, party size and the number of swollen females highest at this time of year (A.Piel, 2021, unpublished data), it is likely that our data are inflated against annual means. More data collected across multiple seasons would resolve this uncertainty and would result in seasonal variation in call production, especially lower call rates in the early wet season when party size declines and fewer females exhibit maximum tumescence. We were also unable to equally balance data collection across the community, with some individuals being followed only 5hrs and some more than 30hrs. This was mostly due to the difficulty of following recently habituated females. Given that the call rate variation between two individuals is likely to be greater than the variation within the same individual, rather than over-sample fewer individuals, we chose to sample more individuals.

4.6. Future directions

Future studies can not only build off these results by adding more data, but also additional predictor variables that may influence chimpanzee call rate. Specifically, further analyses would benefit from evaluating the effect of rank on call rate. For instance, rank has been implicated in influencing call rate in chacma baboons (*Papio cynocephalus ursinus)* (Kitchen et al., 2003), gelada monkeys (*Theropithecus gelada)* (Benitez et al., 2016), orang-utans (*Pongo pygmaeus)* (Mitani, 1985) and also non-primate [fallow bucks (*Dama dama)* (Pitcher et al., 2014)] species, and strongly suggests that vocal communication is influenced by sexual selection. In support of this, multiple studies examining chimpanzee rank and call production reveal a positive relationship between male quality, testosterone, and rank (Clark, 1993; Clark & Wrangham, 1993; Mitani & Nishida, 1993; Fedurek et al., 2016). There is not yet empirical evidence however, demonstrating female preference for male vocalisations.

Moreover, we recommend that subsequent studies include a spatial component. For example, chimpanzees spend the majority of their time in the core of their home range, usually representing about 75–90 % of their total territory (Wilson, Hauser & Wrangham, 2007). When males conduct patrols in high risk areas, e.g. croplands or territorial boundaries, call rate declines significantly (Wilson, Hauser & Wrangham, 2007). Chimpanzees from savanna habitats have far larger home ranges - e.g. ≥ 55km^2 at Issa (C. Giuliano, 2021, unpublished data) or about 90 km^2 at Fongoli (Pruetz & Herzog, 2017) - than forest dwelling chimpanzees – e.g. 7km^2 at Budongo (Newton-Fisher, 2003). Suzuki (1969) proposed that the low density and widely distributed foods in these savanna landscapes may promote more nomadism in savanna than forest chimpanzees and Moore (1992) suggested that the sheer scale of these home ranges may make them indefensible. Forest-dwelling chimpanzees are well known to be highly xenophobic and respond aggressively to members from neighbouring communities (e.g. Goodall 1986; Mitani et al. 2010; Mitani and Watts 2005; Watts and Mitani 2001; Wilson and Wrangham 2003). In contrast to forest dwelling chimpanzees, recent observations at Issa suggest that chimpanzees there may be more tolerant of neighbouring individuals, sharing large parts of their territory with non-community members (pers. obs). Similarly, as mentioned in the introduction, many species modulate their call rate in response to human disturbance - e.g. amphibians (Sun & Narins, 2005), birds (LaZerte, Otter & Slabbekoorn, 2017), and elephants (Soltis et al., 2014). For example, in Bili, northern DRC, chimpanzees call significantly less when they nest near human settlements (Hicks & Roessingh, 2010). The Issa study site lies not far from a human settlement and a road. Despite the fact that snare encounter rates increased with distance from the research station (Piel et al., 2015), the presence of cattle herding is still frequently observed in the area (AC, pers. obs.). We recommend that subsequent work evaluate whether Issa chimpanzees adjust their call rate near areas of increased human presence (e.g. road or cattle herders).

5. Conclusion

Whilst we discussed the inherent importance of biological and social predictors of call rate in wild chimpanzees, this study was primarily motivated by the need to establish call rate to estimate chimpanzee density from passive acoustic monitoring (PAM) and acoustic spatial capture-recapture (aSCR) methods (A. Crunchant, 2021, unpublished data[1]). Chimpanzee call rate is highly sexually dimorphic and like many other chimpanzee behaviours (e.g. Kühl et al. 2019; Whiten et al. 1999) shows community-specific patterns. To estimate an average and unbiased call rate, and consequently an unbiased density estimate, we need to weight values of each age/sex class by the proportion of each demographic class constituting the community. Similar to great ap nest decay and nest production rates, even context-specific call rate is likely to vary between communities. We recommend call rate studies to be conducted in parallel to PAM deployment. Call rates can only be studied in habituated chimpanzees, as follows are necessary to add context to vocalizing behaviour. Comparison of call rates between communities will be instrumental to evaluate how strongly it can affect density estimation from aSCR methods. The use of PAM and SECR to estimate chimpanzee density is promising and with the improvement of automatic call detection, we anticipate that PAM will become more common in the primatologist's toolbox.

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[1] See chapter five.

Chapter 5. Counting calling chimpanzees: density estimation from passive acoustic monitoring and spatial capture-recapture modelling

The dataset from this chapter is the same than in chapter 3.

Abstract:

1. Abundance and density are two important measures to evaluate extinction risk and to assess the efficacy of conservation interventions, policy and practice. Rapid and regular monitoring allows researchers to evaluate population trends and the potential threats to wildlife. In practice, however, monitoring wide-ranging, elusive species, and/or low density animals is difficult. Recently, new methods combining passive acoustic monitoring (PAM) and spatial capture-recapture (SCR) models to estimate animal density have been developed to overcome these challenges.
2. We estimated chimpanzee (*Pan troglodytes)* density from a 3-month PAM deployment and an acoustic spatially capture-recapture (aSCR) model, in a savanna-woodland mosaic habitat at the Issa Valley, western Tanzania. We compared estimates with those from camera trap footage [camera trap capture-recapture (CTCR) and camera trap distance sampling (CTDS)].
3. Our chimpanzee density estimate obtained from aSCR (0.24 ind./km^2) was lower compared to direct observations (0.45 ind./km^2), CTCR (0.56 ind./km^2) and CTDS (0.32 ind./km^2). Despite accounting for the sexual dimorphism in chimpanzee calling behaviour, we suspect that the occurrence of chorusing, where multiple animals vocalise simultaneously, likely contributed to the lower estimate using aSCR. With current methods, counting individuals in a chorus is not yet reliable and counting a group of calls as a single call underestimates the number of individuals.
4. *Synthesis and applications*. We are encouraged by the potential applications of SCR with acoustic data to estimate density of any vocalising animals. With the improvement of automatic call detection, we anticipate that PAM and aSCR will soon become a reliable monitoring method of elusive but especially loud calling species, such as elephants, wolves, gibbons and chimpanzees.

Keywords: call, camera trap, chimpanzee, density, distance sampling, passive acoustic monitoring (PAM), primate, spatial capture-recapture (SCR)

1. Introduction

Abundance and density are two important measures for species monitoring, especially to evaluate extinction risk and to assess the efficacy of conservation interventions, policy and practice. The main approaches to estimating abundance include capture-recapture (CR: e.g. Borchers, Buckland & Zucchini, 2002), distance sampling (DS; e.g. Buckland et al., 2015 and spatial capture-recapture (SCR; e.g. Borchers & Efford, 2008, Borchers & Fewster, 2016) These approaches allow imperfect detections and estimate both detection probabilities and abundance.

CR and SCR methods use traps of various types (e.g. pitfall, camera, hair, etc.) to “capture” individual animals. For conventional CR analysis, the population is sampled multiple times (at least two independent occasions), and any animal caught is marked before being released. The number of animals “recaptured” (marked from a previous occasion) contains information on capture probability and allows abundance to be estimated. Conventional CR methods are non-spatial, in that capture locations are not used. This makes it difficult to estimate density objectively because the data contain no information on how far animals range (Obbard, Howe & Kyle, 2010), and animals that live closer to traps have a higher probability of being detected. With a spatial component, DS overcomes this issue and assumes that the probability of detecting an animal decreases as its distance from the observer increases (Buckland et al., 2001). Perpendicular or radial distances to animals are obtained from line or point transects and allow researchers to estimate a detection function (Buckland et al., 2001). DS has the advantage of not requiring individual identification, however it assumes that all animals with activity centres that are at traps are detected, and this may not be the case. SCR methods combine temporal and spatial components, and use the CR data with data on capture locations to estimate both abundance and density (Borchers & Efford, 2008). These three methods are well established and used across a range of taxa and environments.

Historically, line transects have been the preferred sampling approach for terrestrial mammals (e.g. Plumptre, 2000; Marques et al., 2001). Where transects are not possible, researchers can use acoustic monitoring to detect and monitor vocalising individuals. Acoustic surveys estimate the density of sounds, which can subsequently be converted to animal density given a cue rate. Although in its infancy, the application of SCR to acoustic data represents a promising direction for surveying wide ranging, elusive, or cryptic loud calling species.

Acoustic spatial capture-recapture (aSCR) methods can be used to estimate vocalising animal density. Numerous teams have reported aSCR for various species, such as ovenbirds – *Seiurus aurocapilla* (e.g. Dawson & Efford, 2009), frogs – *A. lighfooti* (e.g. Measey, Stevenson, Scott, Altwegg, & Borchers, 2017), northern yellow-cheeked gibbons - *Nomascus annamensis* - (Kidney et al., 2016) and Minke whales – *Balaenoptera acutorostrata* (Marques et al., 2012). Current methods have been adapted from visual methods and are reviewed in Marques et al. (2013). In contrast to DS, where detection locations are assumed to be estimated without error, aSCR does not assume this. The addition of auxiliary data, such as signal strength (e.g. Dawson & Efford, 2009), time-of-arrival (TOA, requires sensors to be time synchronized) (Stevenson et al., 2015; Measey et al., 2017), estimated angles (Kidney et al., 2016), improve estimation precision (Borchers et al., 2015; Borchers & Fewster, 2016). We can convert estimates of call density to population density using estimates of the proportion of animals that call and the call rate (Stevenson et al., 2015).

Monitoring primate populations is essential, given that 60% of wild populations are threatened with extinction (Estrada et al., 2017). Chimpanzees are listed as endangered by the IUCN, with a global population severely fragmented and in decline (Humle et al., 2016). They are threatened by poaching, habitat loss and degradation, and infectious diseases (Humle et al., 2016; Kühl et al., 2019). Rapid and reliable monitoring are necessary to evaluate the potential threats and population trends.

Semi-arboreal and elusive by nature, chimpanzees are difficult to directly observe in the wild without habituating them to human presence (Plumptre, 2000). Consequently, monitoring methods rely mostly on non-invasive and indirect indices. Several indirect methods have been used historically, and consist of sampling animal signs, like nests (e.g. Hashimoto, 1995) or genetic material from faeces (Waits & Paetkau, 2005). More recent technologies, for instance camera trapping (CT) and passive acoustic monitoring (PAM), have proven effective in detecting chimpanzees and providing data for occupancy modelling (Crunchant, Borchers, Kühl, & Piel, 2020; Crunchant et al., 2017; Kalan et al., 2015), ranging and territoriality (Kalan et al., 2016), and density estimation (Head et al., 2013; Després-Einspenner, Howe, Drapeau, & Kühl, 2017; Cappelle, Després-Einspenner, Howe, Boesch, & Kühl, 2019; Howe, 2019). Chimpanzee is a wide- ranging species, whose calls travel hundreds of meters. Despite PAM offering many advantages, it is not yet widely used for chimpanzee monitoring.

The aim of this study was to compare chimpanzee density calculated from PAM and aSCR with estimates from SCR and DS based on camera trap footage. We explore the factors influencing SCR detection functions and discuss the advantage and limitations of each method, especially as they contribute towards conservation planning. We demonstrate the potential of PAM for estimating abundance and density for any terrestrial, loud calling species and discuss the conservation implications for this emerging census technique.

2. Methods

2.1. Data acquisition

Study site, acoustic and camera trap surveys

We conducted camera trap and acoustic sensor surveys during ten months between March and December 2018, in the Issa valley, western Tanzania. The study site of about 70km^2 is comprised by a series of riverine valleys separated by steep mountains and flat plateaus. Vegetation is dominated by miombo woodland and includes grassland, swamp and riparian forest. For analyses, we collapsed vegetation categories into ‘open’ (woodland, grassland, swamp) and ‘closed’ (riparian forest), see Fig. 5.1. We deployed 53 CTs (Bushnell Trophy Cam): 21 in a systematic layout (1.67x1.67km grid, henceforth ‘systematic’ CT) and 32 at targeted locations (animal paths or termite mounds, henceforth ‘targeted’ CT (Fig. 5.1A). We deployed 12 acoustic sensors (SM2, Wildlife Acoustics), in three clusters of four sensor/cluster, at the tops of valleys (Fig. 5.1B) in miombo woodland trees, attached at 1.65m. We rotated the clusters to new locations within the study area every 2 weeks (four arrays). For more details on the study site, PAM and CT deployments, see chapter three.

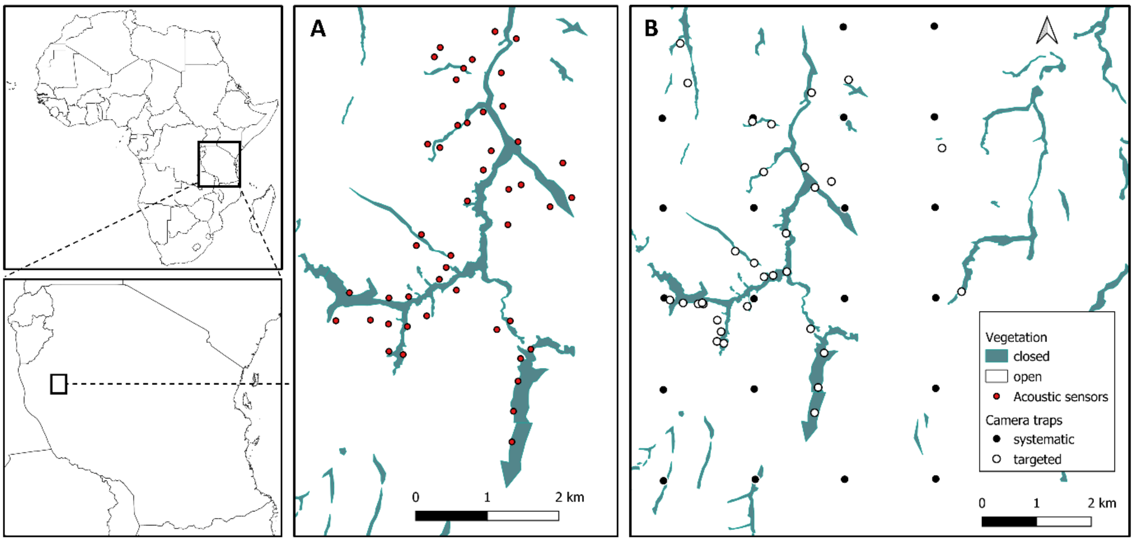

Figure 5.1. PAM (A) and CT (B) deployments in the Issa Valley, Tanzania.

2.2. Data analyses

a) PAM and aSCR

Call extraction and signal strength

Since call rate is likely to vary as a function of season and was known only for a specific season, we analysed a reduced dataset of three months of acoustic data, corresponding to the late dry season (mid-July to mid-October). We manually processed acoustic recordings by inspecting spectrograms and aurally confirming any detection, with the aid of the acoustic software Raven Pro (Bioacoustics Research Program, 2019). Vocalisations that were separated by one second or more were defined to be separate calls. We determined the signal strength of each call and at each sensor by manually drawing a square around the call in the spectrogram. We used the ‘filtered RMS amplitude’ function in Raven to derive the signal strength.

Model

We fitted a multi-session model within the package ‘ascr’ (Stevenson & Borchers, 2017) in R (R Core Team, 2019). A session involved a group of at least two detectors from the same cluster that could potentially detect the same call. The data comprised the detection histories of each call (information about which calls were detected by which detector) and the log-transformed signal strength of each detected call on each detector. We defined a detection as a call visible on the spectrogram. All detections below a threshold signal strength of log(5) were discarded (Stevenson et al., 2015). The SCR models require a mask defined as the surveyed area containing the acoustic sensors and an extended area surrounding them, large enough to ensure that any animals outside this area have a zero, or near-zero probability of being detected during the survey (Efford, 2004; Borchers & Efford, 2008). We defined the mask with a buffer of 3km around each acoustic sensor, given that chimpanzee calls can travel up to 1km.

Density of chimpanzee callers

To convert call density into calling chimpanzee density, we conducted an independent study on chimpanzee call rate during the late dry season (chapter four). To account for the age/sex variability in call rate, we weighted the call rate values of the different demographic classes with the proportion of all juveniles, subadult and adult females and males identified across all CT footage. The weighted mean call rate was 1.23 calls/hr.

b) CT and SCR

Models

Chimpanzees were identified through a combination of facial and bodily characteristics and only observations of identified chimpanzees were included in the models. We ran a set of candidate models using a maximum likelihood approach within the package 'secr' (Efford, 2020) in R. To facilitate comparison with previous studies (e.g. Després-Einspenner et al., 2017), we defined a sampling occasion as one week of deployment. We accounted for variation in sampling effort (i.e. the number of days a CT was active each sampling occasion, from 0 to seven days) with the function 'usage' in all models (Efford, Borchers, & Mowat, 2013). We considered cameras as count detectors, allowing multiple detections per location and per occasion (Efford et al., 2009). We included only one observation per individual, per CT, per day to allow independence between observations. Each individual could then be detected up to seven times per CT during each occasion; the model fits a binomial distribution with a size determined by usage.

Given well-established sex-differences in range-use (Bates & Byrne 2009), we defined the mask using the functions make.mask() and suggest.buffer() in 'secr' derived from the capture history of the subadult and adult males from the combined dataset, using a hazard half-normal detection function, to ensure that the mask was large enough to include the activity centres of all individuals (Borchers & Efford, 2008; Royle & Young, 2008). The mask is represented by a regular grid of points 400m apart.

Factors influencing detectability

The SCR detection function is defined by two parameters: $\lambda 0$, the intercept of the detection function, i.e. the expected number of encounters at its activity centre, which can be interpreted as catchability and σ, the spatial scale, which quantify how far animals range. We investigated the effects of the following factors on $\lambda 0$ and σ:

1) Season: occasion level covariate, four levels – early dry, late dry, early wet, late wet.
2) Sex: two levels – female or male.
3) Design: trap level covariate, two levels – targeted or systematic.

4) Vegetation: trap level covariate, two levels – open (miombo woodland) or closed (forest).
5) Individual heterogeneity, h2, defining a two-point finite mixture distribution. This model implicitly divides the population into two groups with similar detection probabilities for animals within each group, without assigning specific individuals to specific groups (Pledger, 2000; Borchers & Efford, 2008).

We investigated the effects of sex, seasonality, vegetation and h2 on σ, and the effects of design (targeted or systematic CT placement), vegetation and season on λ0. The sex of two juveniles was unknown; we randomly assigned their sex (one male and one female) and we assumed that it would not affect the estimates since they were both seen regularly travelling with their mother.

We did not attempt to investigate the effects of the behavioural responses to initial detection at any CT or at specific CT site (Otis et al., 1978), since 23 out of the 32 targeted CT have been deployed for multiple years prior to this study and chimpanzees no longer exhibit unusual behaviour when captured on film to these cameras (AC pers. obs.).

Model selection

To identify the most parsimonious models, we used AICc, the small-sample corrected version of Akaike's Information Criterion (Hurvich & Tsai, 1989; Burnham & Anderson, 2004). We first built univariate models for λ0 and compared AICc values with the null model of constant parameter value. We selected the covariate that gives the lowest AICc and carried out a stepwise forward selection by adding one covariate at a time, while retaining the ones already selected until there is no decrease in the AICc value. We then built univariate models for σ while keeping the best parameters for λ0 determined previously and carried out a similar forward stepwise model selection.

c) CT and distance sampling

Availability

Chimpanzees are semi-arboreal, spend their nights in tree nests, and stay in one place for part of the day, while resting or feeding. They are thus not detectable by CT all day. To account for this lower detection probability, we estimated the proportion of time when chimpanzees are likely to be detected, by quantifying the level of activity (A, see below) using the Rowcliffe method (Rowcliffe, Kays, Kranstauber, Carbone, & Jansen, 2014) with the R 'activity' package (Rowcliffe, 2019). We defined an event as the first video that included a chimpanzee(s) with the following successive videos removed when the time between the start of videos was less than a minute. Because detections must be independent, we considered each event as a separate detection (rather than each video, for example).

Models and assumptions

To estimate chimpanzee density, we applied the formula from Howe et al. (2017) for CT point transects:

$$\widehat{D} = \frac{\sum_1^K n_k}{\pi w^2 \sum_1^K e_k \widehat{P}_k} \cdot \frac{1}{A}$$

where sampling effort at point k is defined by $e_k = \frac{\theta T_k}{2\pi t}$, with T_k the total sampling time (s) at point k, t the interval chosen between snapshot moments (here, 2s), and ϴ (rad) the central angle of field of view (F.O.V.) of the CT. We used different models of CT (Bushnell trail cameras models #119476, 119678, 119776, 119876) with a F.O.V. of 38 or 45º (www.bushnell.com). w is the truncation distance beyond which any distances are discarded, n_k is the number of observations at point k, $\widehat{P}_k$ is the estimated probability that an animal is detected when in front of the CT between ϴ and w; A is the availability as defined above.

Following Howe et al. (2017), we post-processed videos and measured observation distances between CT and the midpoints of each filmed chimpanzee at 2s intervals. We recorded reference videos by holding distance labels during CT set-ups to measure afterwards observation distances. Animals were assigned to 1-meter distance intervals from 0 to 10m, then to 2-meter distance intervals from 10 to 20m, then to 5-meter distance intervals for distance above 20m. This is because precise distances were more difficult to assess for objects further away from the CT. When the midpoint of a chimpanzee was out of field of view, we discarded the observation. To avoid any potential bias created by researcher presence, we excluded the detections and sampling effort of the 24hrs following any visit (for e.g. maintenance) of a CT. Because an animal attracted by the CT and starring at or inspecting might introduce bias (Buckland et al., 2001), we also discarded all observations where animal behaviour seemed to be influenced by the CT. For comparison with the density estimates derived from aSCR and CTCR, that consider only weaned individuals, we excluded all detections of infants but not their mother.

Chimpanzee density was estimated using Distance 7.3 (Thomas et al., 2010). For further explanations regarding CTDS, see Howe et al., (2017). We considered CTDS models with no adjustment term with half-normal, hazard rate and uniform key functions. We estimated variances from 999 bootstrap resamples of data from the different points. For comparison with CTCR, the region area was defined as the same one than the mask defined for CTCR (i.e. 236km^2). We compared AIC values to select among candidate models.

3. Results

3.1. PAM and aSCR

Call detections and calling chimpanzee density

Over the three-month study period and the 62120 minutes of audio recordings analysed, the sensors recorded 2036 calls. The aSCR model estimated a density of 0.24 chimpanzees per km^2 (Fig. 5.2). The probability to detect a call was half for sounds ~1km from a sensor and a call unlikely to be detected from about 1.75km of a sensor (Fig. 5.3).

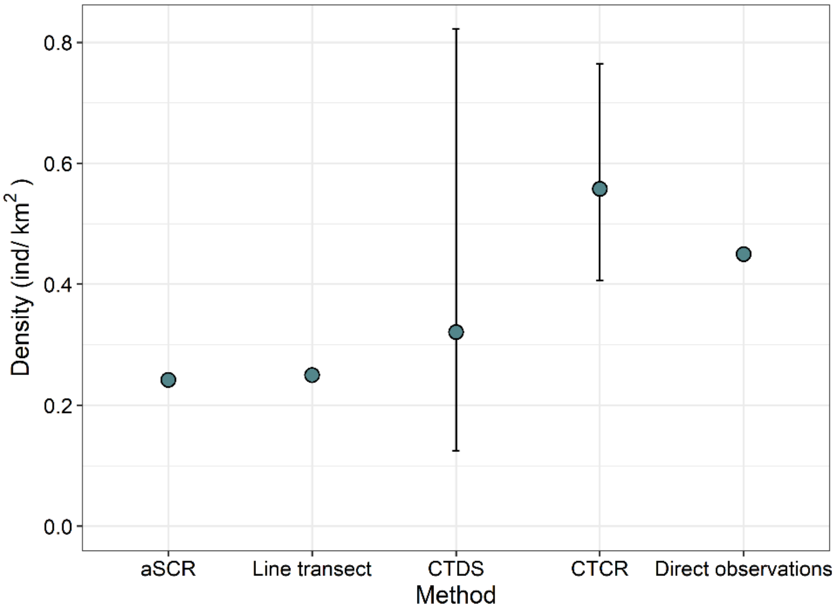

Figure 5.2. Chimpanzee (weaned individuals) density estimates (individuals/km^2) from aSCR, CTDS, and CTCR (this study) and line transect (Piel et al., 2015) methods. Density from direct observations is calculated from the number of weaned chimpanzees in the habituated community (25) divided by the estimated home range (55km^2, Piel, unpublished data). Error bars represent 95% confidence intervals; CI with aSCR has not been estimated, and CI with line transect is too small to be visible on the figure.

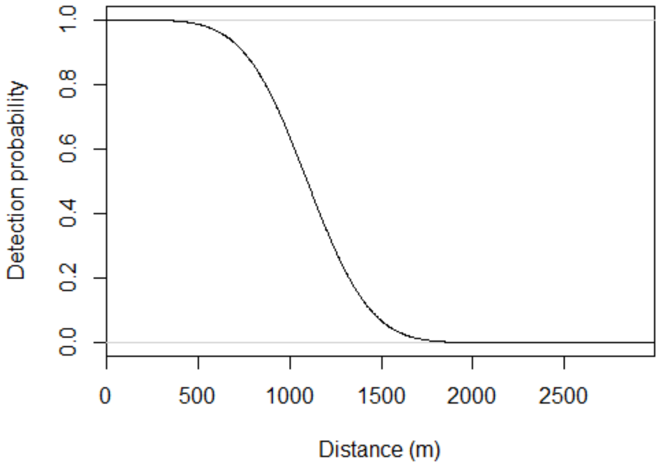

Figure 5.3. Probability to detect a call as a function of distance with the signal strength detection function from the acoustic spatially capture-recapture model.

3.2. CT and SCR

Chimpanzee detections and identifications

A total of 3342 chimpanzee videos were recorded during 280 days of deployment with more than 96% of chimpanzee videos captured on the targeted CT (Table 5.1). The targeted cameras yielded an encounter rate 2.5x higher of identified chimpanzees than with the systematic CT, and more unique individuals were detected and identified (83 unique, weaned individuals). From the combined dataset, 101 unique chimpanzees (88 weaned individuals) were identified in total. 2601 (80.8%) videos with a total of 6880 identified and recaptured chimpanzees came from CT placed at termite mounds.

Table 5.1. Camera trap survey with camera trap effort (trap-days per camera trap), total number of videos containing chimpanzees, number of captured chimpanzees, number of identified chimpanzees, number of unique identified individual (weaned) and mean number of detections per weaned individual for the targeted, systematic and combined layouts.

	Targeted	Systematic	Combined
Trap-days per CT	211.9 [66-280]	217.1 [147-260]	214 [66-280]
Total # of videos recorded	3217	125	3342
Total # of chimpanzees detected	8609	333	8942
Total # of chimpanzees identified	7030 (81.7%)	94 (28.2%)	7124 (79.7%)
Total # of unique individuals	95	51	101
Total # of unique weaned individuals	83	46	88
Mean # of daily recaptures per weaned individual	12.36 [1-83]	1.74 [1-5]	12.57 [1-90]

SCR analyses

The top model that minimized AICc included an effect of the design, season and vegetation on the catchability λ0 and an effect of season, h2, vegetation and sex for σ (Table 5.2). It gives a density of 0.56 chimpanzees per km^2 (Fig. 5.2). The null model ranked last (ΔAICc=1279.2).
λ0 estimated from the best model was $1.06*10^{-2}$. The targeted CTs (λ0=$1.85*10^{-2}$) were seven times more likely to detect chimpanzees than the systematic CT (λ0=$2.63*10^{-3}$). Furthermore, chimpanzees were twice as likely to be recorded on a CT deployed in closed (λ0=$1.53*10^{-2}$) compared to open vegetation (λ0=$5.77*10^{-3}$). Likewise, chimpanzees were almost three times as likely to be caught on a CT during the early wet (λ0= $2.9*10^{-2}$) than during the late dry seasons (λ0=$9.9*10^{-3}$), and more than fifteen times as likely than during the early dry (λ0=$2*10^{-3}$) and late wet (λ0=$1.36*10^{-3}$) seasons.

The estimates of σ were almost 1.5 times higher during the early dry (σ=2046m) and late wet (σ=2158m) seasons than late dry (σ=1468m) and early wet (σ=1291m) seasons. Males travelled slightly more (σ=1871m) than females (σ=1611m), and chimpanzees travelled slightly more in open (σ=1851m) compared to a closed area (σ=1631m).

Table 5.2. Results for the best four SCR models with CT. Covariates are des= design, sea=season, veg=vegetation, h2=individual heterogeneity and sex; Par.=parameters, LL=log likelihood.

Model	Par.	LL	AICc	Δ (AICc)	w (AICc)	Density (ind./km^2)
λ0~des+sea+veg; σ~sea+h2+veg+sex	14	-4630.986	9295.726	0.000	0.6251	0.583 [0.407-0.765]
λ0~des+sea+veg; σ~sea+h2+veg	13	-4633.832	9298.584	2.858	0.1497	0.471 [0.364-0.608]
λ0~des+sea+veg; σ~sea+h2+sex	13	-4634.030	9298.979	3.253	0.1229	0.479 [0.372-0.616]
λ0~des+sea+veg; σ~sea+h2	12	-4635.594	9299.348	3.622	0.1022	0.463 [0.359-0.597]

3.3. CT and distance sampling

Detections and distance observations

Chimpanzees were detected on 11 of the 22 systematic CT. A total of 333 detections of individual chimpanzees (including infants) were made on 125 videos (Table 5.1); we excluded 38 detections of infants, as explained in the method section. 88 (69%) videos came from just three CT locations. We excluded 18 videos because they were recorded within the 24hrs following CT maintenance and 51 distance observations were discarded because we concluded that chimpanzees reacted to the CT (e.g. prolonged staring). Following exploratory analyses, we binned all distances up to 14m into 2m intervals, left truncated at 2m (because of a paucity of data between 0 and 2m) and right truncated at 14m (the detection function shows a heavy tail). This resulted in 1644 distance observations.

Availability for detection

Chimpanzees were active from 5am to 7pm and had two main peaks of activity during the day: one early morning (7-8am) and a second one in the afternoon (4-5pm), as well as a lower peak at 11am (Fig. 5.4). CT detection availability (A) was 0.40 (SE 0.067).

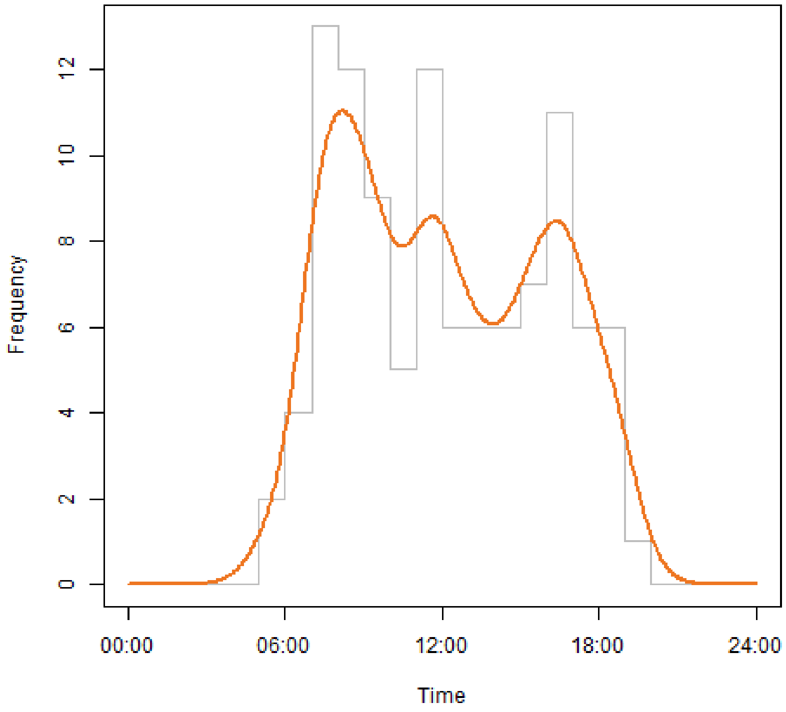

Figure 5.4. Chimpanzee movement activity from CT data. Grey histogram represents observed frequency (i.e. number of events per hour) and orange curve is fitted circular distribution, representing the pattern of relative activity over the day.

Distance sampling analyses

The best density model was derived from the model with a hazard rate key function and no adjustment term (Fig. 5.5, Table 5.3). Due to the non-independence of observations, AIC ranking favour more complex models. The model estimated a density of 0.32 chimpanzees per km^2 and an abundance of 79 unique individuals (Fig. 5.2, Table 5.3). Precision was poor (CV=0.48); 94% of the variance was explained by the encounter rate.

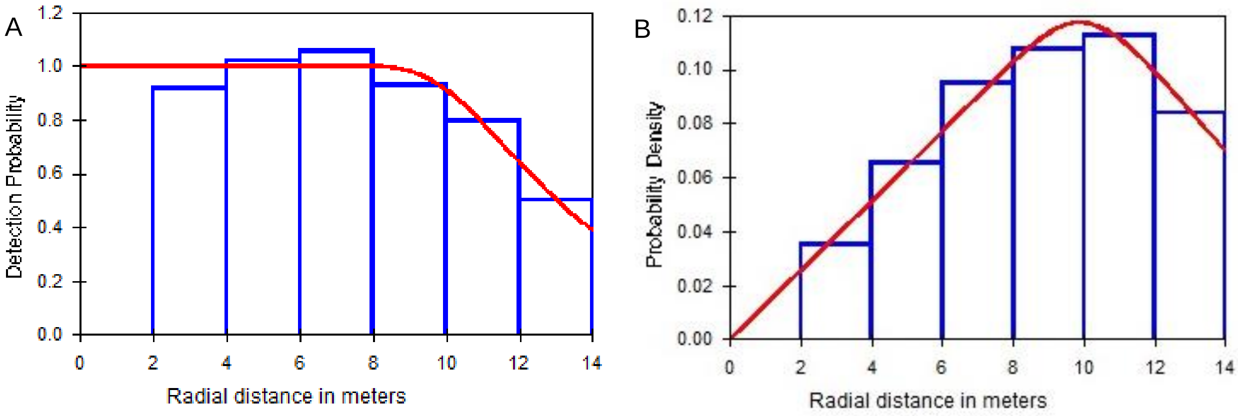

Figure 5.5. Probability to detect a chimpanzee (A) and probability density function (B) as a function of distance with a hazard rate key function and no adjustment terms.

Table 5.3. Density and abundance estimates for the three CTDS models (HR=hazard rate, HN=half normal or U=uniform, without adjustment terms) corrected for the activity pattern and after bootstrapping. Models are ranked with Akaike Information Criterion (AIC) and coefficient of variation (CV) is specified.

Rank	Key function	AIC	Δ AIC	Density (ind./km^2)	Abundance	CV
1	HR	5690.25	0	0.321 [0.125-0.822]	79 [32-198]	0.478
2	HN	5719.08	28.83	0.391 [0.153-1.003]	95.6 [35-263]	0.480
3	U	5811.93	121.69	0.261 [0.102-0.666]	61.1 [17-119]	0.477

4. Discussion

Our study assessed the applicability of an acoustic spatially capture-recapture method for monitoring wild chimpanzees. We have shown that aSCR yielded lower estimates than CTDS and CTCR, ranging from 0.24 to 0.56 chimpanzees per km^2. Compared to CTCR, DS precision was low and has not been estimated for aSCR, since the bootstrap method assumes that chimpanzees are immobile during the acoustic survey. CT catchability ($\lambda 0$) varied with CT study design and vegetation but mostly as a function of season, with a higher $\lambda 0$ during the late dry and early wet seasons. We first discuss advantages and limitations of each method, then explore the factors that can explain the detection heterogeneity with CTCR and finally, evaluate which method is the most adequate given available means, skills and objectives.

4.1. Use of PAM and aSCR to estimate calling chimpanzee density

Chorusing, where multiple animals vocalise simultaneously, might explain the lower density estimate with aSCR. Counting individuals in a chorus is difficult (Torti et al., 2018) and counting a group of calls as a single call underestimates the number of callers, negatively biasing an estimate of individual call density. More work would be needed to estimate the number of callers in a chorus, as has been done with wolf choruses (Passilongo et al., 2015). Furthermore, the acoustic sensors were not time-synchronized and did not allow us to include the time difference of arrival (TDOA) into the model. Adding TDOA information to signal strength to reveal animal location improves estimator precision and decreases bias (Stevenson et al., 2015).

4.2. Use of CT with SCR and DS to estimate chimpanzee density

Only three studies have previously applied CTCR to chimpanzees (Head et al., 2013; Després-Einspenner et al., 2017; Howe, 2019). In an empirical evaluation of CTCR on a habituated chimpanzee community, Després-Einspenner et al. (2017) showed that estimates were highly accurate and precise from targeted and systematic designs. Five CTs deployed for ten months were sufficient to yield accurate estimates (Després-Einspenner et al., 2017; Howe, 2019).

We attempted to estimate the density with CTCR from the systematic design, however, our recaptures were insufficient and yielded high estimates. Howe (2019) recommended at least three detections per animal (DPA); the mean DPA for our systematic design was 1.74 (compared to 12.57 for the combined dataset, Table 5.2). Furthermore, we were able to identify only 28.2% of the chimpanzees detected, vs. 76% in the Tai dataset (Després-Einspenner et al., 2017). Chimpanzees were often walking too far from the CT for us to identify (sometimes more than 15-20m), or else away or perpendicular to the CT, thus impairing identification. In open vegetation, a targeted design would likely improve identifications and estimated accuracy.

Lastly, we want to acknowledge potential violations of CTCR assumptions. The SCR models assume that all individuals are identified correctly. At Issa, an experienced observer made all identifications; given that 96% of detections were of habituated chimpanzees, we are confident these identifications are reliable. However, we acknowledge the possibility of misidentification. The model further assumes the population to be demographically closed (Borchers & Efford, 2008). Given that females giving birth every five to seven years and adolescent females emigrate, we expected minimal violations of this assumption. Lastly, the model assumes independence between detections. Chimpanzees exhibit fission-fusion and are often detected as groups that can lead to an overdispersion of the data. SCR models are robust to moderate level of aggregation (Bischof et al., 2020), but further analyses would confirm the potential bias.

CTDS has only been recently developed (Howe et al., 2017) and to date, just three studies have evaluated the method – all in closed-canopy forests: one on Maxwell's duikers – *Philantomba maxwellii* (Howe et al., 2017), another on chimpanzees – *P. t. verus* (Cappelle et al., 2019), and a third in a multi-species study in Salonga National Park, Democratic Republic of the Congo (Bessone et al., 2020). In contrast to these forest environments, Issa chimpanzees from a savanna-woodland were detected at distances greater than 25m, compared to 12-15m in forests. Similar to Cappelle et al. (2019), the low precision is explained by the encounter rate variation, with most detections occurring at only three CTs. Low precision might be more extreme here given habitat heterogeneity.

CT detection availability is estimated for each survey, as this parameter varies among sites and influences estimates. For instance, we calculated availability to be 0.40 vs. 0.26 at Tai for a 24hr period (Cappelle et al., 2019).

4.3. Ecological factors, design and detection heterogeneity

We evaluated the effects of different parameters on the capture probability with the CTCR method. The probability to detect an individual at its activity centre ($\lambda 0$) was higher during the late dry and early wet seasons and lower during the late wet and early dry seasons. We assume that there is greater likelihood of chimpanzees being recorded on a CT as party size increases. Monthly party size shows pronounced fluctuations across seasons (Giuliano & Piel, unpublished data), with larger parties observed in the late dry and early wet seasons. Furthermore, more than 80% of the videos come from CTs deployed at termite mounds. Termite fishing is a seasonal activity, which increases during the early wet season (Stewart & Piel, 2014). Seasonality also affects σ (spatial scale), with lower values meaning that chimpanzees range less broadly, during the late dry and early wet seasons. Party size is also correlated to food availability, with smaller parties when food availability is low (Giuliano and Piel, unpublished data). As expected, the design of the CT had an effect on $\lambda 0$, with targeted CT yielding three times more detections than systematic CT.

4.4. Comparing estimates: selecting a method and conservation implications

In this study, we compared density estimates from three methods, two of which were empirically evaluated to be highly reliable (CTCR - Després-Einspenner et al., 2017 and CTDS - Cappelle et al., 2019). Chimpanzee density at Issa has previously been estimated from nest counts at 0.25 individuals/km^2 (Piel et al., 2015), nearly identical to what we calculated from aSCR. However, nest counts are known to sometimes underestimate density (Cappelle et al., 2019).

Nowadays, commonly used non-invasive monitoring techniques include CT, PAM, genetics, drones and line or point transects (Plumptre, 2000; Schwartz, Luikart & Waples, 2007; Burton et al., 2015; López & Mulero-Pázmány, 2019; Sugai et al., 2019). We suggest that field practitioners consider four parameters: (1) costs, (2) field and (3) analysis labour and time, and (4) estimate precision. It is beyond the scope of this paper to review advantages and limitations of each monitoring method. However, we present some considerations for conservation managers (Table 5.4). For loud calling species, PAM detects vocalising animals more efficiently and rapidly than CT (chapter three)-, however results may underestimate the true density by not accounting for chorusing behaviour. With the improvement of automatic call detection, we anticipate an increasing and widespread use of PAM and aSCR in censusing and monitoring vocally conspicuous wildlife.

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Table 5.4. Main density estimation and non-invasive monitoring methods used for terrestrial animals.

Density estimation method	Key assumptions	Monitoring method	Advantages	Limitations	Example application studies
DS	- Animals distributed independently from line or point - Animals are always detected - Instantaneous observation process (snapshots): animals detected at their original location - Distances are measured without errors	Direct observations, signs (e.g. nests, dungs, vocalisations with active acoustic monitoring, aerial surveys)	- Low material costs (e.g. binoculars, compass)	- Need estimates of sign production or decay rate, for e.g. dungs or nests - Reliability and consistency between observers - High field labour	- Chimpanzee nests: Kouakou, Boesch & Kuehl, 2009 - Red foxes (Vulpes vulpes): Ruette, Stahl & Albaret, 2003
		CT, vocalisations (PAM)	- Multi-species studies (e.g. songbirds) - Low long-term material costs - PAM more efficient than CT to detect calling species	- Initial costs of CT or acoustic sensors - High analyses time	- Mammals: Bessone et al., 2020 - Birds: Sebastián-González et al., 2018
SCR	- Individuals are identifiable - Some individuals are detected more than once and at more than one location	Genetic samples	- Allow to conduct population viability analyses - High resolution of data - Can address other questions such as diet, parasitism, paternity analyses…	- High analyses time - High analyses costs (reagents, lab technicians…) - Requires specialised lab skills - Logistical challenges: expensive and risky export process but new on-site field methods are on development	- Chimpanzees: McCarthy et al., 2015 - American black bears (Ursus americanus): Howe, Obbard & Kyle, 2013
		CT	- ID (demography: age/sex composition) provides data on decline stage or recovery - Low long-term material costs - Can address other questions e.g. social network	- Initial costs of CT - Require experience skills for ID	- Leopards (Panthera pardus): Hedges et al., 2015 - Jaguars (Panthera once): Silver et al., 2004
		PAM	- Low field labour and time - Low long-term material costs - More efficient to detect calling species than CT	- Initial costs of acoustic sensors - High analyses time when no automated call recognition - Individual ID very difficult for now - Reserved for calling species	- Frog (Arthroleptella lightfooti): Stevenson et al., 2015 - Ovenbirds (Seiurus aurocapilla): Dawson & Efford, 2009

Chapter 6 : Localising wild chimpanzees with passive acoustics

Abstract

1. Localising wildlife contributes in multiple ways to species conservation. Data on animal locations can reveal elements of social behaviour, habitat use, population dynamics and help calculations of density estimation. Acoustic localisation systems (ALS) are a non-invasive method widely used in the marine environment but not well established and rarely employed for terrestrial species.
2. We deployed an acoustic array in a mountainous environment with a heterogeneous vegetation, comprised of four custom-built GPS synchronised acoustic sensors at about 500m intervals in Issa Valley, western Tanzania, covering an area of near 2km^2. Our goal was to assess the precision and error of the estimated locations by conducting playback tests, but also by comparing the estimated locations of wild chimpanzee calls with their true locations obtained in parallel during focal follows. We explored the factors influencing localisation error, such as wind speed and temperature, which fluctuate during the day and are known to affect sound transmission.
3. We localised 282 playback sounds and found that the mean localisation error was 27 ± 21.8m. Localisation was less prone to error and more precise during early mornings (6h30) compared to other periods, when temperatures were low. We furthermore localised 22 chimpanzee calls within 52m of the location of a researcher closely following the calling individuals.
4. We demonstrate that acoustic localisation is a powerful tool for chimpanzee monitoring, with multiple behavioural and conservation applications. Its applicability in studying social dynamics and revealing density estimation among many others, especially but not exclusively for loud calling species, provides an efficient way of monitoring populations and inform conservation plans to mediate species-loss.

Keywords:; acoustic array; ALS; apes; localisation; playback; precision

1. Introduction

Localising animals can help to answer questions related to species conservation. Its application ranges from informing on social behaviour, habitat use, and even revealing population dynamics, to estimate abundance and density (e.g. Blumstein et al., 2011; Rhinehart et al., 2020). Direct visual observations of animals are often difficult because animals can be cryptic, elusive, nocturnal, live in dense vegetation, or range widely. For decades, researchers have relied on animal-borne loggers to remotely track animals (Millspaugh & Marzluff, 2001; Kays et al., 2015). However, this invasive method is controversial. It often requires darting and capturing the targeted animal, which can be a stressful event for the animal, and can affect subsequent behaviour and survival (reviewed in Wilson & McMahon, 2006). Initially restricted to larger animals and offering limited resolution movement data, improvement in loggers have resulted in better location resolution and movement accuracy, and from far smaller devices (Kays et al., 2015). GPS loggers can be expensive and present battery issues, with collars/batteries requiring changing at regular intervals. To overcome this invasiveness and limitations of using GPS loggers, researchers also use acoustic localisation to monitor animals, by exploiting sounds that can travel long distances.

Acoustic localisation uses the time difference of arrival (TDOA) of sounds to multiple (time synchronised) sensors to identify the sound origin location, following triangulation (e.g. Spiesberger & Fristrup, 1990; Blumstein et al., 2011). Despite its ubiquity in marine mammalogy, acoustic localisation system (ALS) work is not as pervasive with birds or terrestrial mammals. In studies applying ALS to birds, researchers synchronised acoustic sensors by deploying thousands of meters of cable (e.g. Mennill et al., 2006; Fitzsimmons et al., 2008) before later developing wireless time-synchronised arrays (e.g. Collier, Kirschel & Taylor, 2010; Mennill et al., 2012). Location error varies as a function of inter-caller and inter-sensor distances; localisation can be limited in terms of applicability for widely spaced callers, as it would require a larger number of sensors. Sound transmission and thus localisation can also be impacted by environmental variables such as high temperature, high wind speed and vegetation – all that can distort acoustic signals and affect the signal-to-noise ratio, where in noisy environments target signals can overlap with other sounds. Lastly, sensor time synchronisation error and recording sample rate can bias the estimation of TDOA and lead to inaccurate localisations (reviewed in Rhinehart et al., 2020).

Initially pioneered in the marine environment, early acoustic localisation systems (ALS) exploited low attenuation characteristics in underwater sound (Spiesberger & Fristrup, 1990; Stafford et al.,1998). Comparatively, fewer ALS deployments in terrestrial systems have been conducted, likely because of obstacles (i.e. trees) that attenuate sounds, but mostly due to technical constraints, such as the difficulty of simultaneously monitoring multiple acoustic sensors. Studies have mainly focused on birds (e.g. Wang et al., 2005; Mennill et al., 2006, 2012; Collier et al., 2010) and recently on some loud calling mammals, such as orangutans (*Pongo pygmaeus wurmbii*) (Spillmann et al., 2015), elephants (*Loxodonta cyclotis*) (Wrege et al., 2017; Hedwig et al., 2018) and wolves (*Canis lupus*) (Papin et al., 2018; Kershenbaum et al., 2019).

The aim of this study was to evaluate a custom-made ALS composed of four GPS time-synchronised acoustic sensors to localise wild chimpanzees (*Pan troglodytes schweinfurthii)* in western Tanzania. Chimpanzees are a wide-ranging species and rely on loud calls that can travel hundreds of meters to coordinate movement (e.g. Uhlenbroek, 1996; Gruber & Zuberbühler, 2013; Fedurek et al., 2014). Our goal was to assess the precision and error of the estimated locations by conducting playback sound experiments, but also by comparing the estimated locations of actual wild chimpanzee calls with the true (ground) locations obtained in parallel with focal follows. We explore the factors influencing the localisation error, such as wind speed and temperature that fluctuate during the day. We hypothesized that higher wind speed would lower localisation error. We demonstrate the potential of ALS for localising any terrestrial, loud calling animals and discuss the behavioural and conservation applications for this emerging census technique with wild chimpanzees.

2. Methods

2.1. Study site

We conducted the 3-month study between August and October 2019, in Issa Valley, western Tanzania. The study site of about 70km^2 is comprised of a series of riverine valleys separated by steep mountains and flat plateaus. Vegetation is dominated by woodland and also includes grassland, swamp and riparian forest. For analyses, we collapsed vegetation categories into ‘open’ (woodland, grassland, swamp) and ‘closed’ (riparian forest). For more information on the study site, see chapter three.

2.2. Acoustic localisation system

We deployed a passive acoustic monitoring (PAM) system that enables localisation of chimpanzee loud calls. The acoustic array consisting of four sensors was deployed on the ground, around the perimeter of a single valley known to be important for the Issa community during the late dry season (AC pers. obs.), when we collected the data. Each audio recorder was comprised of a microphone (USB Lavalier omnidirectional) unit integrated with a nano-computer Raspberry Pi (Raspberry Pi 3 Model B Motherboard); a GPS unit, three 10W solar panels and two 44V batteries and was protected in a Pelicase (Pelican 1170 Case). The recording script averaged sensor locations regularly determined by the GPS unit. Sounds were recorded continuously, saved as 30min audio files at 48kHz sampling rate in .flac format, and stored in a 32GB SD card. Each sensor was placed ~ 500m from each other, to maximise the likelihood of triangulation via detection on multiple sensors, while simultaneously minimizing the likelihood of missing calls. Chimpanzee calls can travel at least 500m, so we estimated that the area covered about 1.9km^2 by drawing a 500m buffer around the sensors. We downloaded and saved audio files to an external hard drive every ten days.

2.3. Localisation precision and error

To quantify the error and precision of the system, we conducted two playback studies: a static test and a walking test. For both tests, playback sounds consisted of a tonal sequence (range 500-1800Hz, Fig. 6.1). This sound sequence was used in place of a pant hoot (the chimpanzee long call – e.g. Goodall, 1986) to minimize disturbance to otherwise xenophobic chimpanzees (Herbinger et al., 2009). We broadcast sounds from 1m above the ground with a FoxPro Fusion portable loudspeaker (FoxPro Inc., Lewiston, PA, USA) at mean peak sound pressure level of 102.4dB (A-weighting), measured at 1m from the speaker with a Sound Pressure Level meter (DL7103 Di-LOG, Manchester, UK). We chose this level to correspond to pant hoots produced by wild individuals (Herbinger et al., 2009). We recorded environmental variables (temperature, wind speed and relative humidity) with a HOBO weather station (model RX3000) deployed near the base station.

The static test consisted of broadcasting repeatedly the tonal sequence at different times of day (6:30, 9:30, 12:30, 15:30, 18:30), fifty consecutive times at a single location, in the geographic centre of the array. The walking test consisted of broadcasting the tonal sequence along line transects, two times each at 30 different locations, sequentially separated by 50m. We recorded GPS locations with a handheld GPS (Garmin Rino750). In both tests, we faced North when broadcasting the tonal sequence.

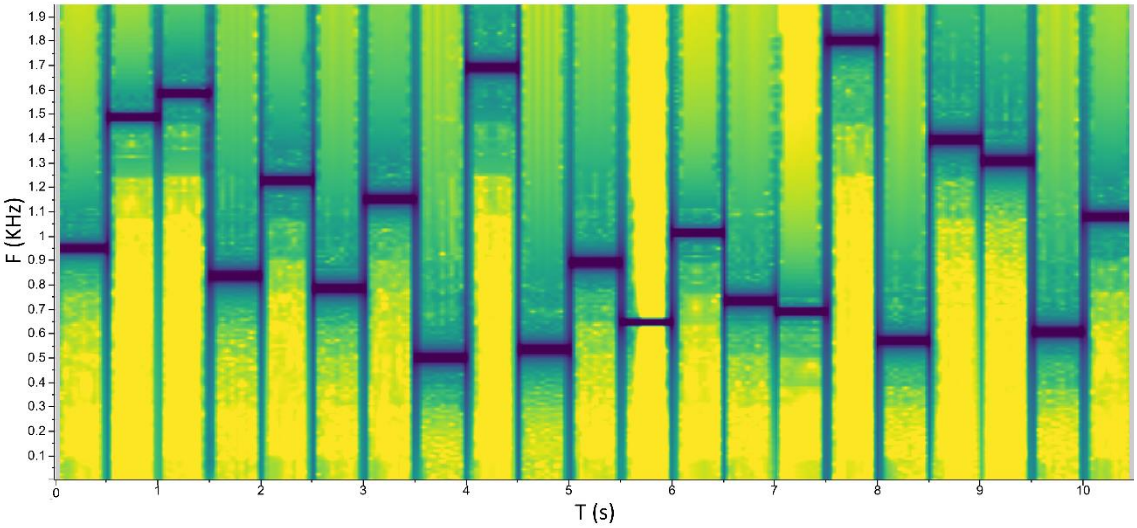

Figure 6.1. Spectrogram of the tonal sequence used for the playback tests (range 500-1800Hz), developed from acoustic parameters of a wild chimpanzee pant hoot by Adam Clark Arcadi).

2.4. Validating the localisation system with calls from wild chimpanzees

To validate the system with calls from wild chimpanzees, we conducted chimpanzee focal follows. We selected a focal chimpanzee (adult, subadult or juvenile) each morning and tried to follow him/her for the entire day. We conducted instantaneous focal sampling (Altmann, 1974) with a scan defined as the behaviour of the animal recorded every five minutes, when we collected among other data the location of the individual (GPS). We further noted all vocal behaviour ad libitum of the focal. We then compared the estimated location (see below) of chimpanzee calls recorded by the sensors with the associated locations of the calling chimpanzees determined during focal follows. The minimal distance between the observer and the chimpanzee was 10 meters to avoid human-chimpanzee disease transmission, and the GPS location was recorded every five minutes with a handheld GPS.

2.5. Time of arrival and sound localisation

The time of arrival (TOA) of the sounds was determined at the sub-second by visualising the spectrogram with the software Raven (Bioacoustics Research Program, 2019). We then estimated the sound localisations with the software SoundFinder (Wilson et al., 2014). The software uses the temperature at the time at which the sound is produced to calculate the sound speed following the formula from Wölfel and McDonough (2009). It estimates the location of the sound source by applying the least-squares solution developed for global positioning systems (Bancroft, 1985), using the time difference of arrival (TDOA), with the TOA of the sensor reached first set to 0. We defined localisation error as the Euclidean distance between estimated and true locations.

2.6. Statistical analyses

We conducted all analyses in R v.3.6.1 (R Core Team, 2019). To model the error of the localisation (E) as a function of the covariates, we used a linear model. Fixed covariates were (1) temperature (T, continuous), wind (W, continuous), number of sensors that detected the sound (S, two levels: 3 or 4 sensors), vegetation type at the sound source (V, two levels: open or closed). We centred continuous predictors.

We tested predictors for collinearity by calculating variation inflation factors (VIF) using the package car (Fox & Weisberg, 2018). Multicollinearity was not present (maximum VIF: W=1.20). We verified model assumptions by plotting residuals versus fitted values and QQ-plots. We ran a set of models and ranked them by AICc value.

3. Results

3.1. Localisation precision and error

At some locations, the TOA at the acoustic sensors was not possible to calculate because the signal-to-noise ratio was too low, or the tonal sequence was only partially recorded. From the 30 locations tested twice on the walking test, we managed to localise 45 of 60 (75%) sounds. From the 250 possible localisations for the static test, we succeeded to localise 249 sounds. SoundFinder calculates an error of the estimated locations, defined as a temporal error. Similar to Papin et al. (2018), to establish a threshold above which the estimated temporal error associated to the estimated location is considered unreliable, we examined the relationship between localisation error (m) and temporal error (ms) (Fig. 6.2). Based on these results, we set the threshold to 200ms, subsequently excluding all estimated locations associated to a temporal error superior to 200ms. This resulted in 238 estimated locations for the static test (Fig. 6.3) and 44 estimated locations for the walking test (Fig. 6.4). The mean error for all localised sounds was 27 ± 21.8m [range 2.03-169.8m, N=282]. Localisation was the least prone to error and most precise at 6h30, the most prone to error at 12h30 and the least precise at 9h30 (Fig. 6.3).

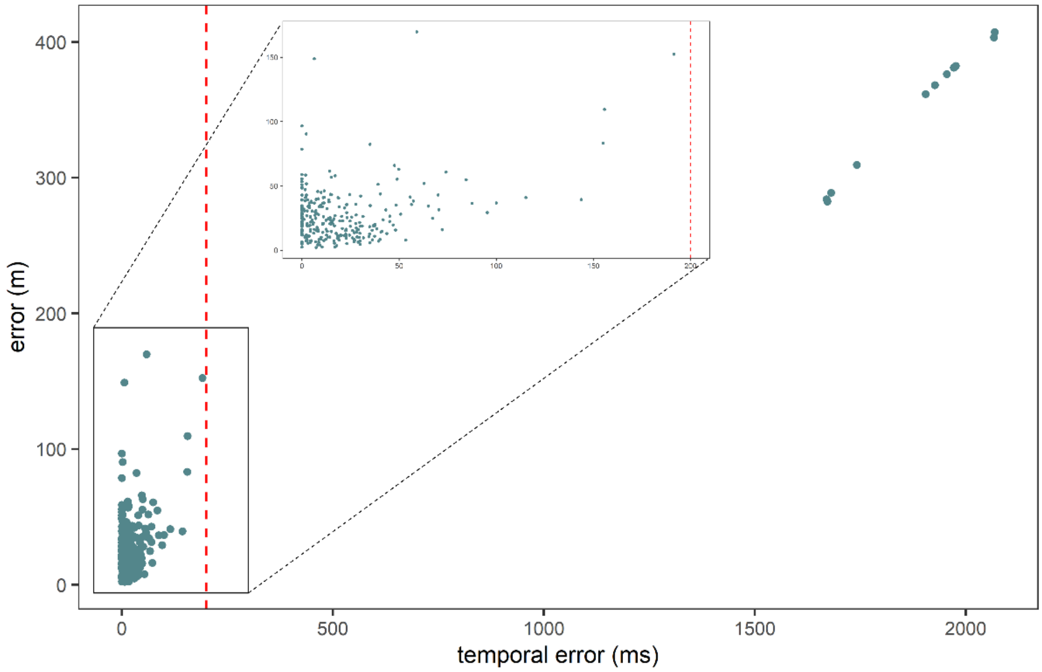

Figure 6.2. Relationship between the temporal errors associated to the estimated localisations from SoundFinder and the errors of the estimated localisations. The red dashed line represents the threshold (200ms) above which the estimated localisation associated to the temporal error is considered unreliable.

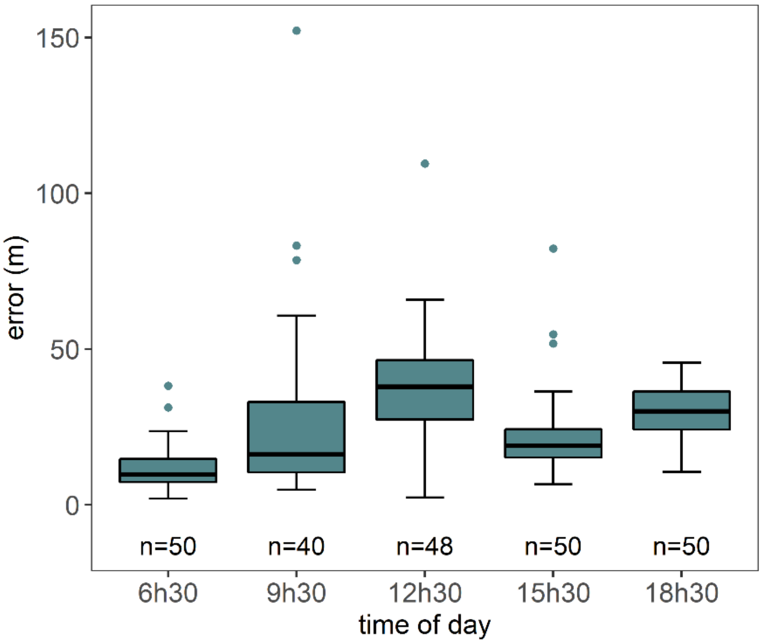

Figure 6.3. Localisation error at different times of day for the static test.

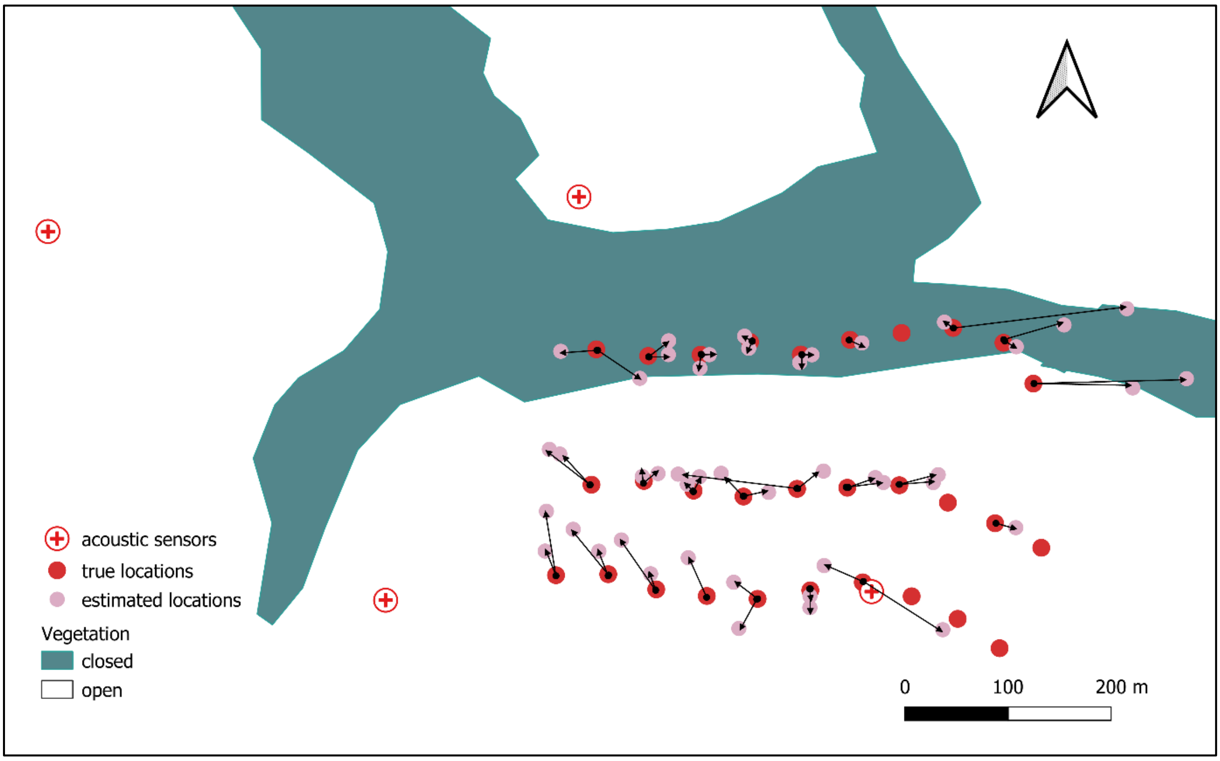

Figure 6.4. Estimated (pink) and actual (red) locations from a (walking) playback test; arrows show link between estimated and actual locations.

3.2. Factors influencing localisation error

We did model averaging among models with ΔAICc <2 (Table 6.1). The significant effects in the best averaged model are temperature, vegetation, and wind (Table 6.2).

Table 6.1. Model selection. E: error; T: temperature; V: vegetation; W: wind; S: sensor

Model	df	logLiK	AICc	delta	weight
E ~ T + V + W	5	-1049.687	2109.6	0.00	0.656
E ~ T + V + W + S	6	-1049.527	2111.4	1.77	0.270
E ~ T + W	4	-1053.335	2114.8	5.22	0.048
E ~ T + W + S	5	-1052.956	2116.1	6.54	0.025

Table 6.2. Outcome of a LM investigating the effect of temperature, vegetation type at the sound source, wind and number of sensors that detected the sound on localisation error for the averaged best two models.

Predictors	Parameter Estimate			
	Estimate	Std. E.	z value	Pr(>|z|)
Intercept	24.477	1.495	16.304	<2e-16***
Temperature	1.488	0.324	4.498	6.9e-06***
Vegetation	18.538	6.9383	2.659	7.83e-03**
Wind	-5.2419	0.999	5.219	2..0e-07***
Sensor	-1.378	2.452	0.558	0.577

* = p < 0.05; ** = p < 0.01; *** = p < 0.001.

3.3. Validating the localisation system with chimpanzee calls

We estimated the locations of 22 chimpanzee calls (Fig. 6.5). The mean error was 51.2 ± 20.6m [range 19.9-96.04m].

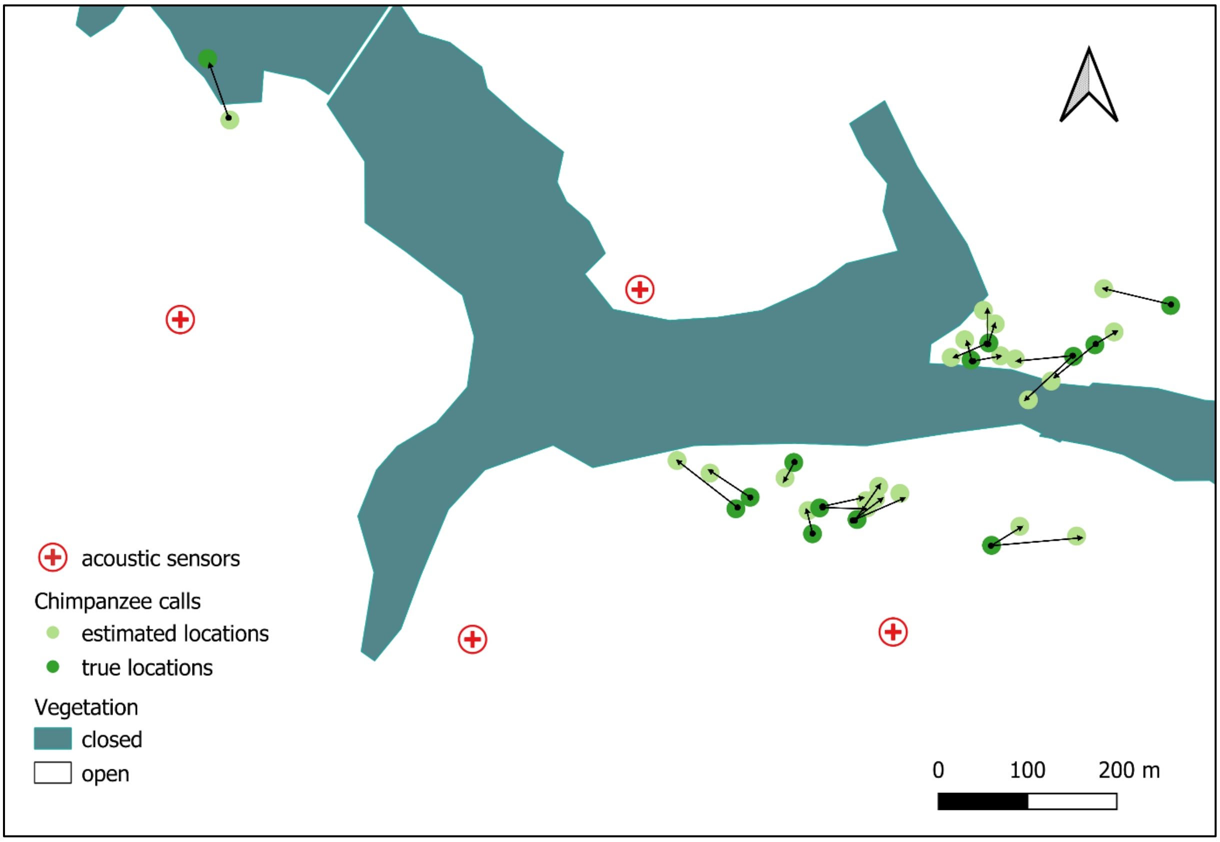

Figure 6.5. Estimated locations by triangulation (light green) of chimpanzees and locations determined with a handheld GPS during parallel focal follows (true locations, dark green); arrows show link between estimated and true locations.

4. Discussion

In this study, we sought to demonstrate, as a proof of concept, that a custom-made acoustic array composed of four sensors could localise chimpanzees. The array enables sound localisation in a difficult mountainous environment with heterogeneous vegetation that makes sound propagation unpredictable. With a playback study, we found that the mean localisation error was 27 ± 21.8m. To empirically validate the system, we also successfully localised wild chimpanzee calls, applying this system under natural conditions. We compare the error of this system with previous ALS for terrestrial species described in the literature. We explore the behavioural and conservation applications of this approach to the study of wild chimpanzees and more broadly other loud calling terrestrial species and conclude with a discussion of the limitations of the current system.

4.1. Error of the localisation system

We found that error of the ALS was similar to those figures reported from other studies targeting terrestrial mammals. These systems covered areas that ranged from a few hundreds to thousands of m^2, reflecting the ranges of the targeted species. Other systems that target birds and frogs localised animals to a much lower error, in some cases below 1m. These arrays were composed of spatially closer acoustic sensors (less than 50m) offering less spatial coverage (Table 6.3).

Environmental variables such as temperature and wind speed influence sound behaviour e.g. sound attenuation (Harris, 1966) and consequently, localisation error. Sound localisations were less prone to error and sounds were more precisely localised in early morning (6h30), when temperature is the lowest. This is the same period when chimpanzees are the most vocally active (e.g. Wilson et al., 2007; Piel, 2018). Inversely, localisation was the most prone to error at 12h30, when temperature is the highest. Wind speed is the highest early morning (6h30 and 9h30) and might thus not be the main factor influencing localisation error, given that precision was the highest at 6h30 but lowest at 9h30, but the result of the influence of a combination of temperature and wind speed.

Table 6.3. Previously described terrestrial acoustic localisation systems and reported error

Target species	Acoustic array	Error	Reference
Cape buffalo *(Syncerus caffer),* chacma baboon *(Papio ursinus)* and spotted hyena *(Crocuta crocuta)*	Four CARACAL stations at 500m intervals	Within 70m	Wijers et al., 2019
Chimpanzee *(Pan troglodytes)*	Four custom-made recorders at 543.7 ±163.8m intervals	27 ± 21.8m	This study
Elephant *(Elephas maximus)*	Four Audio Technica recorders	30m	Dissanayake et al., 2018
Orangutan *(Pongo pygmaeus wurmbii)*	20 SM2 (Wildlife Acoustics) recorders at 500m intervals	58m ± 7.2m	Spillmann et al., 2015
Wolf *(Canis lupus)*	20 SM3 (Wildlife Acoustics) recorders at 1km intervals	167 ± 308m	Papin et al., 2018

Wolf *(Canis lupus)*	Five SM3 (Wildlife Acoustics) at 1-3km intervals	20m	Kershenbaum et al., 2019
Rufous-and-white wren *(Thryothorus rufalbus)*	Eight microphones at 75.2 ±2.6m intervals	2.82 ± 0.26m	Mennill et al., 2006
Antbird *(Formicarius moniliger)*	Eight nodes (each node contains four microphones) at 39m intervals	0.199 ± 0.064m for playbacks and 0.445 ± 0.500m for wild bird songs	Collier et al., 2010
Different bird and frog species	Four SM2 (Wildlife Acoustics) recorders at 25 or 50m intervals	1.87 ± 0.13m	Mennill et al., 2012

4.2. Behavioural applications

Despite over a half century of research into wild chimpanzees (e.g. Pusey et al., 2007; Nakamura et al., 2015; Boesch et al., 2019) and in the deployments of PAM for wildlife in other systems (Spiesberger & Fristrup, 1990; Tavolga, 2012; Marques et al., 2013), only few studies have deployed this tool with wild apes, and only one, besides the current study, evaluated its localisation error (Spillmann et al., 2015). Acoustically localising chimpanzees offers multiple benefits to behavioural study of habituated and unhabituated individuals. First, resulting data can improve our understanding of social dynamics. Similarly to e.g. elephants (*Loxodonta africana)* (e.g. Leighty et al. 2008), spotted hyenas (*Crocuta crocuta),* (e.g. Theis et al. 2007), bottlenose dolphins (*Tursiops truncates)* (Janik & Slater, 1998) chimpanzees are socially fluid animals that exhibit a fission-fusion structure (e.g. Fedurek et al. 2014). They form ephemeral sub-parties that change in size and composition throughout the day. So far, little is known on how chimpanzees coordinate sub-group reunions, more specifically at their nesting sites, and maintain cohesion within the community (e.g. Lehmann & Boesch, 2004). This is especially the case of savanna-mosaic dwelling chimpanzees, who live at a density up to 10 times lower than their forest-dwelling counter-parts - e.g. 0.56 ind./km^2 at Issa, Tanzania (Crunchant et al., unpublished data) vs. 6.8 ind./km^2 at Budongo, Uganda (Newton-Fisher, 2003) - and cover a territory far larger - e.g. ≥ 55 km^2 at Issa, Tanzania (Giuliano, unpublished data) vs. 6.8km^2 at Budongo, Uganda (Newton-Fisher, 2003). Only two studies have attempted multiple, simultaneous focal follows (Uhlenbroek, 1996; Eckhardt et al. 2015), despite our knowledge of the importance of vocalisations for spatially separated callers (e.g. Gruber & Zuberbühler, 2013; Fedurek, Donnellan & Slocombe, 2014). One means of overcoming the logistical demands of multiple follows is by using an ALS, consequently detecting (and potentially monitoring) caller presence in space and time, which has been done in the marine environment. For instance, dolphins (*Delphinus delphis*) can be tracked via their whistles that can propagate over multiple kilometres omnidirectionally (Wiggins et al., 2013). The authors showed with whistle localisation that dolphins were more widely spread and travelled more slowly at the beginning of the night in contrast to daytime and hypothesised that it was associated with foraging behaviour.

To track chimpanzee movements over time, we need caller individual identification. Acoustic detectors of chimpanzee calls are in development (Heinicke et al., 2015). Individual identification remains complicated, however, due to the high intra and inter-caller variability of chimpanzee calls and their large vocal repertoire highly graded (call types are difficult to categorise) (Mitani et al., 1996; Crockford, 2019). Call combinations and the chorusing effect, where multiple individuals vocalise simultaneously add another level of complexity for developing a call detector. Individual identification detectors have been developed for numerous other terrestrial species, such as tigers (*Panthera tigris*) (Ji et al., 2013), orangutans (*Pongo pygmaeus wurmbii*) (Spillmann et al., 2016) and gibbons (*Hylobates muelleri*) (Clink et al., 2018). With new machine learning pipelines, we believe that such an individual identification detector can be developed for chimpanzees as well.

A second behavioural application of ALS is to accelerate the habituation process, one that is especially time-intensive with chimpanzees - e.g. ~ 5-7 years, Taï Forest, Côte d'Ivoire (Bertolani & Boesch, 2008). Historically, researchers attempted to habituate chimpanzees to human presence by provisioning them with food (Wrangham, 1974; Goodall, 1986; Nishida, 2011). However, this method modifies natural behaviour patterns, for instance it induces increased aggression rates and exposes wildlife to disease transmission (Wrangham, 1974; Williamson & Feistner, 2003). Instead of provisioning, to find unhabituated animals, often researchers listen at specific spots (e.g. at the top and junction of different valleys), for chimpanzee loud calls to locate individuals or waiting at key spots such as feeding trees (e.g. Williamson & Feistner, 2003). If researchers had access to chimpanzee caller locations – especially when searching for parties, search efforts efficiency would be dramatically improved. It is nearly impossible to quantify the extent of this improvement, but Sommer et al. (2004) report seeing an individual chimpanzee in average once every 22.8 days during the two first years of habituation at the Gashaka Gumti National Park, Nigeria. Even though chimpanzees could be outside of sensor range, integrating traditional search efforts with an ALS would likely improve search efficiency, especially with (near) real-time data transmission.

4.3. Conservation applications

Density is a critical parameter for species monitoring. New methods combining PAM and spatially explicit capture-recapture (SECR) models have been developed to estimate animal density (e.g. Dawson & Efford, 2009; Efford, Dawson & Borchers, 2009; Stevenson et al., 2015; Measey et al., 2017). The addition of auxiliary data, such as TDOA or signal strength provide more accurate information on the distance between the caller and the acoustic sensor, in turn allowing more precise detection functions and density estimation (Stevenson et al., 2015), and will thus benefit monitoring efforts.

The ALS also enables key resources localisation, such as the presence of chimpanzees at fruiting trees. Chimpanzees produce calls with a different acoustic structure (e.g. peak frequency and call duration) as a function of the food patch size or tree species (Slocombe & Zuberbühler, 2006; Fedurek et al., 2014; Kalan et al., 2015). Being able to locate such feeding trees via the calls produced by chimpanzees will first help providing a broader picture of their feeding ecology and second further aid habituation efforts (see above). Similarly, the ALS will also enable researchers to identify chimpanzee nesting sites. Locating chimpanzees at their nesting sites and thus indirectly locating fresh nests with the ALS will benefit conservation by allowing researchers to collect e.g. fresh faecal samples that can reveal population dynamics (Schwartz et al., 2007) but also for health monitoring (Gilardi et al., 2015), or allowing for nest decay studies.

Finally, poaching and deforestation are the two main threats to great apes. Besides detecting animals, ALS can also indirectly help species conservation by locating poachers via gunshot sounds (e.g. Wijers et al., 2019) or locating illegal logging via chainsaw sounds (e.g. Andrei, 2015). A few platforms have recently been field-tested but are not widely used yet. For instance, CARACAL is a low-cost hardware (~£150 per unit) and software able to extract and localise gunshots at an average error of 33.2m with an array of seven stations composed each of four microphones (Wijers et al., 2019). ALS can thus be used as a law enforcement tool to assist conservationists and prevent animal poaching or deforestation.

4.4. Limitations

There are three primary limitations of the current study. First, we did not consider the GPS error. GPS locations at each sensor were averaged and given that the sensors were stationary, we suspect minimal errors due to the GPS sensors. However, the exact error of the handheld device used to measure ground truth is unknown.

Second, we were not able to capture microhabitat (environmental) variation, which may have affected sound propagation (Röhr & Juncá, 2013; Rodriguez et al., 2014). In the current study, we used the weather data from a centrally-located weather station, >1000m from the nearest sensor. More spatially-explicit weather data would be useful. This is especially important for some variables like wind speed, which is known to vary significantly, especially in valley systems (Lihoreau et al., 2006; Renterghem et al., 2007). Furthermore, we did not evaluate the effect of the caller position, i.e. whether they were terrestrial or arboreal. Previous studies have shown that caller height and the frequency at which they vocalise have an impact on sound transmission. Lower frequencies propagate further when the animal vocalises higher than 1m above the ground, due to an increase of the effective area by reducing the attenuating effect of soft ground (Marten & Marler, 1977; Forrest, 1994; Parris, 2002). Similarly, we did not assess the effect of ambient noise level on localisation error. The TDOA estimation error depends on the signal-noise ratio (SNR) (e.g. Urazghildiiev & Clark, 2013). It has been shown that sound level increases during early evenings (Piel, 2014), which could explain why error was higher at 18h30 compared to 6h30 for similar temperature and relative humidity and higher wind speed early morning. Dawn chorus is a well-studied phenomenon exhibited by multiple species and has been studied especially on birds (reviewed in Gil & Llusia, 2020). Among multiple hypotheses for this behaviour such as advertising territory boundaries and social dynamics, the hypothesis of a better sound transmission at dawn has been evocated (Henwood & Fabrick, 1979) but is controversial (Gil & Llusia, 2020).

Lastly, we conducted manual analyses. TDOA is often estimated by pairwise cross-correlations of the sound waveforms or spectrograms (e.g. Mennill et al., 2006; Harlow et al., 2013; Spillmann et al., 2015). Similar to Papin et al. (2018) and Kershenbaum et al. (2019), we manually estimated TDOA from the spectrograms due to the low SNR of some of the playbacks or chimpanzee calls. If manual analyses allow to decrease the probability of missing a call, they can also be prone to errors. Indeed, TOA needs to be measured very accurately (onset can vary by less than 1ms) and manual measurement can increase localisation error (Rhinehart et al., 2020). Furthermore, such analyses are time intensive.

5. Conclusion

In this study, we have demonstrated the performance of a low-cost custom-made ALS for chimpanzee localisation, one that can also be applied to any loud calling and wide-ranging species. The ALS powered by a solar system can be deployed for long periods (only limited by storage capacity), and the recording script is easily modifiable in Python for e.g. adding a recording schedule, changing the recorded frequency or file length. Like other PAM systems, it allows for the study of conspicuous or even cryptic animals without disturbing them. With recent technological advances, devices are increasingly robust and affordable. Despite the current challenges to automate data analysis, improvements of automatic call detection are promising, and we anticipate that PAM and ALS will become more frequently deployed tools for loud calling terrestrial species monitoring.

Chapter 7: General discussion

Throughout their distribution, chimpanzee (*Pan troglodytes*) populations are increasingly fragmented and in decline (Humle et al., 2016). They are mainly threatened by habitat loss, fragmentation and degradation, poaching and infectious diseases (e.g. Strindberg et al., 2018). Rapid monitoring is needed to evaluate the impact of these threats on population abundance and trends, and to assess the effect of conservation actions. Accurate, precise, and frequent data on chimpanzee distribution and density are crucial data to achieve this. However, chimpanzees occur at low densities – e.g. 0.03-6.8 ind./km^2 (Newton-Fisher, 2003; Moyer et al., 2006) - and range over large territories – up to 90km^2 (Pruetz & Herzog, 2017); monitoring populations is therefore challenging. Conservationists benefit from methods that are time and cost-efficient and simultaneously provide accurate and precise data.

Five main non-invasive methods are available for chimpanzee monitoring: camera trapping (CT), passive acoustic monitoring (PAM), line transects, drone and genetic sampling (Table 7.1). I compare these methods in terms of equipment, field and analyses costs, labour and time required for data collection and analyses, and accuracy and precision. Line transects do not require equipment except binoculars, GNSS devices, measuring tape or range finder to measure distances of nests to transects and compasses. However, data collection is labour and time-intensive; it requires walking often large distances and sometimes through difficult habitats (e.g. dense rainforest, mountains) and to set up satellite camps if study areas are large. PAM, CT and drones are more costly in terms of equipment. However, data processing, i.e. extracting detections (calls, nests, individuals) from audio files, videos or images is time-intensive, as most of the analyses are often conducted manually. Genetic sampling is costly, labour intensive and requires specialised lab skills; but data resolution is high (e.g. identification of relationships between individuals possible). The aim of my PhD was to evaluate PAM as a monitoring tool for chimpanzee detection, density estimation and localisation.

PAM was developed half a century ago and is widely used for marine mammals (Spiesberger & Fristrup, 1990; Tavolga, 2012; Marques et al., 2013). Even though chimpanzees are characterised by long calls that can travel hundreds of meters (Wich & Nunn, 2002), and are thus an ideal candidate for PAM, it has only rarely been used to monitor them. Only two PAM systems have been deployed for chimpanzee monitoring, leading to five studies (Piel, 2014, 2018; Heinicke et al., 2015; Kalan et al., 2015, 2016). In this thesis, I demonstrated that PAM is a promising non-invasive method for monitoring loud calling chimpanzees. I deployed two arrays of acoustic sensors in Issa Valley, western Tanzania: one comprising twelve on-shelf non-GPS-synchronised acoustic recorders (Song Meters 2, Wildlife acoustics) across the whole study area for nine months to estimate chimpanzee presence/absence and density. I simultaneously deployed an array of 53 CT for methodological comparisons. The other acoustic array comprised four custom-built GPS synchronised acoustic recorders, deployed for a 3-month period around a single valley (~2km^2) known to be important for chimpanzees at the time of deployment, to localise chimpanzees. I have shown that chimpanzee detectability varies over seasons and chimpanzee presence is determined in only 10 days of deployment during the late dry season with PAM. This rate was five times faster than an equivalent method using CT. Furthermore, I found that the estimated density of calling chimpanzees with acoustic spatially capture-recapture (aSCR) was lower to those derived from distance sampling and capture-recapture with CT data. The density with aSCR was however within the 95% CI of the estimate from camera trap distance sampling. With a playback experiment (N=282), I showed that sounds can be localised with 27 ± 21.8m accuracy. The localisation was most accurate and precise during early mornings (6h30) compared to other periods, when temperatures were low. Furthermore, 22 chimpanzee calls were localised within 52m from the location of a researcher closely following the calling individuals.

In the remainder of this thesis, I discuss PAM and the results of my thesis within the broader context of the different monitoring methods available for chimpanzee conservation. I compare PAM, CT, drone, line transects and genetic sampling in terms of data collection and analyses to answer questions about chimpanzee distribution, density and threats. I discuss the costs and time needed for each method for estimating chimpanzee density, before exploring some directions for future research.

1. Which questions to answer and how to monitor chimpanzees?

1.1. Chimpanzee distribution

Detecting presence/absence is the first monitoring step for evaluating species distribution. All five monitoring methods available to chimpanzee conservationists allow evaluating animal presence/absence and territory use (Table 7.1). For instance, line transects have been used to identify hotspots of chimpanzee activity and to identify home ranges from nest counts, in Taï National Park Côte d'Ivoire (Kouakou, Boesch & Kuehl, 2011). Two studies have evaluated drones for chimpanzee nest detections. The first one conducted in Gabon evaluated nest detection with a camera on a fixed-wing drone that flew line transects, by comparing detections from aerial images and nests detected by a research team on the ground (van Andel et al., 2015). Nearly half of the ground nests in open forests were detected on the aerial images but only 8% in inland forests. The second study was conducted in Issa Valley (Bonnin et al., 2018). Only 10% of the nest grounds were detected from the air. Aerial nest detection was limited by nest-forest colour contrast. Researchers are also trying to detect animals directly with thermal cameras mounted on drones, exploiting the heat radiated from animals. Although this approach has not been used for chimpanzee detection yet, results from a study on Bornean orangutans in Sabah (Burke et al., 2019) are promising and the method could be extended to chimpanzees. The increasing resolutions of both visual spectrum and thermal infrared cameras on the market will likely lead to more applications with both these methods in the coming years.

Occupancy modelling is a statistical method to estimate the probability of a species to be present in an area, with detection/non-detection data from multiple visits of a given area (MacKenzie et al., 2017). In addition, it is a useful tool to assess population trends (i.e. declining, stable or increasing) over time and at large scale. Prior to this thesis, only two studies have used this statistical tool for chimpanzee monitoring and only with PAM and CT (Kalan et al., 2015; Crunchant et al., 2017). These studies employed occupancy as a means to validate call or face automated detectors. The first one evaluated the potential of a semi-automated buttress drum detector to obtain reliable estimates of chimpanzee occurrence from PAM (Kalan et al., 2015). The authors showed that this approach provided similar results to point transects and has the advantage to require less effort in the field. Similarly, the second one evaluated a face detection algorithm to estimate chimpanzee site use from CT (Crunchant et al., 2017). The semi-automated method greatly sped up data processing and required only 2-4% of the time required for manual analyses. In chapter 3, I compared PAM and CT in terms of chimpanzee detection efficacy, defined as the estimated number of sampling days needed to establish chimpanzee absence with 95% probability the time. Chimpanzee detectability was higher with PAM compared to CT, given the larger area covered by the acoustic sensors, following results from another comparative study with macaques (Enari et al., 2019). The results indicated that short monitoring surveys of only ten days are sufficient to evaluate chimpanzee presence/absence in an area with PAM, which is nearly five times faster than with CT. However, this finding must be contextualised. That is, data stem from a period of high detectability by PAM and CT, which, at Issa, corresponds to the late dry season with high food availability and multiple swollen females. Combined, it is a period when chimpanzees are the most vocally active. Care needs to be also taken when conducting surveys in areas heavily impacted by human presence, where chimpanzee calling behaviour can be affected (Hicks & Roessingh, 2010). Indeed, chimpanzees may remain silent and be undetected although present.

Furthermore, besides just detecting presence/absence, seasonal changes in territory use can be evaluated by monitoring methods. For instance, line transects were conducted over a period of five months in the Kalinzu Forest in Uganda (Furuichi, Hashimoto & Tashiro, 2001). The authors showed that chimpanzees nested in different vegetation types in different fruiting seasons. At Issa, PAM and CT show a similar seasonal variation in chimpanzee territory use, with some areas exploited only during specific parts of the year, likely due to fruit availability and distribution (chapter 3). Because PAM and CT are deployed continuously for long periods of time, they can also reveal temporal and spatial patterns of activity at a finer scale. Level of activity throughout the day can be quantified with CT data which provides insight on when an animal is the most active and thus detectable (Rowcliffe et al., 2014; chapter 5). Chimpanzees have two main peaks of moving activity, between 7 and 8am and between 4 and 5pm, and a smaller one around 11am (chapter 5). Furthermore, hourly peaks of calling revealed a bimodal temporal pattern of chimpanzee calling (chapters three, four, and five). Chimpanzees vocalise mostly early morning and late afternoon, similar to what has been reported at Issa in a previous study with PAM (Piel, 2018) and elsewhere from other communities (e.g. Wilson, Hauser, & Wrangham, 2007; Wrangham, 1975). This information is important for conservation managers, who can for instance schedule recording at these periods to maximise the likelihood of detecting calls and simultaneously limit the number of recording audio files to analyse.

Lastly, CT can localise chimpanzees at some extent, but while the accuracy of each sighting will be very high the opportunity to cover large areas at high resolution is limited due to the limited area coverage of each camera. Drone and line transects allow localising nests but not actual chimpanzee locations throughout the day. PAM allows researchers to accurately and with high-resolution localise chimpanzees over space and time across a large area. Chimpanzees can be localised via their calls with an error under 30m (chapter 6). With the development of an individual call recognition detector, it has the potential to track chimpanzees through their territory and thus, for instance, allow researchers to study social dynamics and have a more comprehensive explanation on how they can coordinate movements through large territories (see below).

1.2. Chimpanzee density

Density is important to evaluate extinction risk and to assess the efficacy of conservation interventions, policy and practice. Three approaches are usually used to estimate density: capture-recapture (CR; Otis, Burham, White, & Anderson, 1978), distance sampling (DS; Buckland et al., 2001) and a spatially capture-recapture framework (SCR; Borchers & Efford, 2008). These approaches allow imperfect detections and estimate detection probabilities that allow practitioners to estimate the density. At present, the aerial images acquired with drones do not allow practitioners to estimate chimpanzee density, because of the low nest detection on those images.

Initially, but still mainly used, surveys conducted to estimate chimpanzee density have relied on nest counts from line transects. Two methods based on distance sampling have been developed: standing-crop nest counts (Tutin & Fernandez, 1984) and marked nest-count (Plumptre & Reynolds, 1997). However, accurate and precise estimates are difficult to derive from standing crop nest counts, due to the necessity of adding correction factors such as nest decay and nest production rates. Nest decay rates depend on external parameters such as vegetation and rainfall (e.g. Kamgang et al., 2020), and decay process is not constant over time (Walsh & White, 2005). Nest production rates are difficult to estimate. Furthermore, these correction factors are site-specific. An additional study must be conducted in parallel to the line transects to estimate these factors.

Genetic sampling is also a widely used method for estimating density. On one hand, it is a very costly method to deploy over large areas (see below), labour and time-intensive (for data collection and data processing) and requires specialised lab skills (Table 7.1). On the other hand, high-resolution data allows researchers to answer specific questions that the other methods cannot. It allows not only individual identification but can also inform on relationships between individuals. For example, male philopatry has for instance been confirmed via genetic analyses in Ugalla, Tanzania (Moore, Langergraber & Vigilant, 2015) and Uganda (McCarthy et al., 2018b). Population connectivity can also be studied with genetic sampling; rivers have for instance been shown to influence the population structure of bonobos (Eriksson et al., 2004).

Table 7.1. Comparison with advantages/disadvantages of non-invasive monitoring methods for chimpanzee distribution and density, and threat evaluations. Grey cases mean that the monitoring method is currently not possible for the research topic associated. + means advantages, - means disadvantages.

Research topic		PAM		CT		Drone		Line transects		Genetic sampling	
Chimpanzee distribution		+	Low field labour and time Low long-term equipment costs High detection range High localisation precision with ALS	+	Low long-term equipment costs Individual ID possible	+	Low long-term equipment costs Training in a few days High detection range	+	Data in hand after survey Low material costs	+	High data resolution Can address other questions (e.g. diet, parasitism…etc.)
		-	Initial equipment cost Time consuming data processing individual ID impossible for now	-	Initial equipment cost Low detection range	-	Initial equipment cost	-	Field labour intensive	-	High analyses time and costs Require specialised lab skills
Chimpanzee density		+	Low field labour and time Low long-term equipment costs High detection range	+	Low long-term equipment costs Individual ID possible			+	Data in hand after survey Low material costs	+	Allow to conduct population viability analyses High data resolution Individual ID, family relationship
		-	Initial equipment cost Time consuming data processing Require call rate No individual ID possible for now	-	Initial equipment cost (need e.g. at least 20 CT for distance sampling) Time consuming data processing Low detection range			-	Field labour intensive Require estimates of sign production and decay rates	-	High analyses time and costs Require specialised lab skills
Threats	Poaching	+	ALS can locate poachers	+	Can locate at some extent poachers Poachers identification	+	Thermal infrared cameras can detect poachers at night Detection of fires	+	Detection of gun shells/snares		
		-	Initial equipment costs	-	Initial equipment costs Risk for the CT to be stolen or broken Privacy and ethics	-	Initial equipment costs Vegetation type can limit performance	-	Field labour intensive		
	Habitat disturbance	+	ALS can locate illegal loggers			+	Landcover classification Changes monitoring	+	Habitat change detection		
		-	Initial equipment costs			-	Initial equipment costs	-	Field labour intensive		
	Diseases			+	Detection of e.g. facial lesions in videos					+	Health monitoring with parasites and viruses found in faecal samples
				-	Initial equipment costs					-	High analyses time and costs Require specialised lab skills

The use of CT to infer chimpanzee density is more recent. Only four studies have employed CT with SCR or DS (Cappelle, Després-Einspenner, Howe, Boesch, & Kühl, 2019; Després-Einspenner, Howe, Drapeau, & Kühl, 2017; Head et al., 2013; Howe, 2019). Després-Einspenner et al., (2017) evaluated SCR with CTs based on a habituated community at Tai Forest, and results showed that density estimate is precise and accurate, and only five CT were sufficient to detect nearly all weaned individuals. Similarly, Cappelle et al., (2019) evaluated DS with CT revealing that density estimate was accurate and less biased than that calculated from line transects. DS has the advantage over SCR that it does not require individual identification (a process that is time-intensive and can be prone to errors) and that the random design required for the method allows for a multi-species study (Bessone et al., 2020). However, the random design with DS is likely the reason for a low precision of the estimated density, with chimpanzees detected on a limited number of CT (Cappelle et al., 2019; chapter 5).

Lastly, acoustic spatial capture-recapture (aSCR) methods from PAM data have recently been developed (e.g. Stevenson et al., 2015). I assessed the possibility of using aSCR and PAM for chimpanzees (chapter 5). Although a promising technique, estimated chimpanzee density from aSCR and PAM is lower compared to the estimates from distance sampling and spatial capture-recapture frameworks with CT data. Estimates can, however, serve as a baseline and comparison over time would allow evaluating of population trends, but see below. One hypothesis that could explain this result is the chorus calling behaviour. Chimpanzees often vocalise simultaneously, and it is complicated to accurately count individuals in a chorus (Torti et al., 2018). Counting such bouts as a single call underestimates the number of individual callers, negatively biasing individual call density estimate. More work would be required regarding how to address the calling behaviour. For instance, one could estimate the number of callers in a chorus through spectrograms. A study on wolf choruses showed that estimations of chorus size with visual inspection by spectrogram were highly correlated with the number of wolves and it was possible to identify up to seven individuals in a chorus of nine wolves (Passilongo et al., 2015). Another limit for this method to be widely used by conservation managers is the necessity of knowing the call rate to convert calling density into animal density. Similar to the nest decay or nest production rates, call rate is likely to vary from site to site and survey-specific studies to evaluate the call rate should therefore be conducted in parallel to the PAM deployment. Rate can only be studied in habituated chimpanzees, however, as focal follows are necessary. Comparison of call rates between field sites with habituated communities will be instrumental to evaluate to what extent call rate varies and evaluate how strongly it can affect density estimation. Finally, calling rates can decrease due to hunting pressure or other disturbance (e.g. Hicks & Roessingh, 2010). Hunting might however not be targeting chimpanzees and thus not impact their density. However, if densities estimated with PAM are being compared over time, one could conclude that density decreases even though populations are stable.

1.3. Evaluation of threat levels

As mentioned in the general introduction (chapter 1), chimpanzees face three main threats: poaching, habitat disturbance and diseases that result in population declines. PAM, drone, camera traps, line transects and genetic sampling can be used to evaluate these threats (Table 7.1).

a) Poaching

Poaching is widespread and occurs at a large scale in landscapes that are covered by dense vegetation, poacher detection is thus challenging (Wich & Koh, 2018). Thermal infrared cameras have been used to detect poachers (Olivares-Mendez et al., 2015); although promising, its application is limited by habitat type. Poachers are unlikely to be detected with this method when in dense forest, as thermal infrared signals do not carry through this vegetation type (Burke et al., 2018). However, poachers can be detected indirectly via human-started camp fires (Burke et al., 2018). Poachers can be detected and identified on CT, but the devices are likely to be stolen or destroyed unless carefully hidden. Furthermore, it raises questions about privacy and ethics, as do also drone and PAM: legality of photographing or recording people without their permission varies across countries but also cultures (e.g. Sandbrook, 2015). Practitioners must ask permission of local authorities and be careful about where to deploy the CT. PAM can be used to detect gunshot sounds and ALS can help locate poachers with an accuracy of less than 35m for gunshot origins from over 1km (e.g. Wijers, Loveridge, Macdonald, & Markham, 2019). A recent study comparing CT and PAM found that CT under-detected hunting activity by 939% (Dobbins et al., 2020).

b) Habitat disturbance

Chimpanzees are highly threatened by habitat loss, fragmentation and degradation (Estrada et al., 2017). Similar to poaching, ALS can locate illegal logging by detecting chainsaw sounds (e.g. Andrei, 2015). Old smartphones are also being transformed into autonomous solar-powered acoustic sensors to record and send in real-time gunshot or chainsaw sounds to a server in the cloud via a GSN connection (Rainforest Connection, www.rfcx.org, accessed 28/10/2020). Alerts can be sent to patrols via text messages, who can verify the presence of illegal loggers or poachers. However, this method would require many sensors to cover a large area and would be a limit for scalability.

Drones have been used to get detailed data on chimpanzee habitat and detailed disturbance can be detected (Koh & Wich, 2012). Orthomosaics can be made and repeated over time to get a high-resolution map of an area to detect change. Furthermore, visual spectrum images allowed researchers to identify 14 chimpanzee food species in Gabon (van Andel et al., 2015). Multispectral cameras will allow for a better tree identification and at a larger scale (Wich & Koh, 2018).

Lastly, CT can be used to identify human-wildlife conflicts and help addressing them. For instance, Krief et al., (2014) showed that chimpanzees in Kibale, Uganda, crop-raided maize plantation during the night to avoid humans and presented little signs of vigilance. Similarly, chimpanzees in Sierra Leone temporally avoid areas when frequented by people (Garriga et al., 2019). These studies can inform on chimpanzee responses to landscape changes and help developing strategies to mitigate human-wildlife conflicts and elaborating conservation actions.

c) Diseases

Health monitoring is important for conservation. Because chimpanzees are genetically similar to humans, they are vulnerable to many human-borne diseases (e.g. Köndgen et al., 2008; Leendertz et al., 2004). Genetic samples can be collected during line transects. As mentioned in chapter 6, the ALS could also help locating the chimpanzees at their nesting site, allowing researchers to collect fresh faecal samples for further genetic analyses. Portable genomics is a new technology that allows for conducting analyses focusing on genomes directly in-situ at field sites. This can speed up the analysis process and limit disadvantages by addressing some issues of exporting process that is increasingly expensive, political sensitive and risky with entire shipments vulnerable to loss or damage when in transit. CT can also be used to identify animals who may have a physically visible disease or being injured. For instance, multiple individuals were seen with severe lesions on CT in Haut Niger National Park, lesions likely due to a pathogen responsible of yawn disease (Mubemba et al., 2020).

2. Comparison of costs and time associated to each monitoring method for a density study

When selecting a monitoring method, practitioners must consider different parameters, such as data collection and analyses costs, and be aware of the different limitations specific to each method. The time needed to conduct a study, from data collection to data analyses is an important parameter to consider when selecting a monitoring method. Indeed, surveys need to be regularly repeated and interval between two surveys is restricted by the time required to conduct the survey and analyse the results. A balance between cost and efficiency must be carefully considered. I present here a comparison of costs and time associated to the different monitoring methods for chimpanzee density estimation (Table 7.2). I take as example the Issa Valley study area of about 60km^2. Even though chimpanzee density estimation from drone surveys is presently not possible, I show this method for comparison with others.

- PAM – I consider a 3-month survey because call rate is likely to vary as a function of season. Similar to the method explained in chapter 5, I consider 12 audio recorders, deployed at top of valleys in three clusters of four sensors spaced by about 500m for a 2-week period before being rotated to new sites (valleys), for a total of 12 sites. The 4AA batteries in each sensor can record up to 215hrs, so would be sufficient to record for 7hr a day for two weeks. I estimate that two days of training would be required to learn how to set up and schedule the sensors, and how to identify calls on spectrogram and extract signal strengths from Raven. Sensors are moved every two weeks, with on day needed to move one cluster (i.e. four sensors), so 18 days would be required in the field to deploy and maintain the system for the study period. I estimate that between 5 and 20min per 30min and per cluster (i.e. four audio files) are required to extract signal strengths of chimpanzee calls, depending on how many calls are detected.

- CT – I consider a 9-month survey with a distance sampling framework. I consider 25 CT deployed in a systematic design with a random origin (do not require a pre-survey to identify e.g. animal paths of fruiting trees). I estimate that two days of training would be required to learn how to set up the camera traps and how to estimate observation distances from CT videos. I estimate that about two days are required to select videos containing chimpanzees from the dataset and about 30min per video to estimate distances of chimpanzees (for instance, 9 months of CT deployment yielded 125 videos containing chimpanzees, chapter 5).
- Line transects – I consider 16 line transects for marked nest counts. These transects (e.g. 1km long) are walked by two persons four times at two weeks interval (Kouakou, Boesch & Kuehl, 2009). I consider that two transects can be walked per day, so 64 days would be required in the field to collect nest count data.
- Drone – I consider 16 1km-long line transects repeated four times at two weeks interval with a basic drone (https://hornbillsurveys.wordpress.com/). I consider that four line transects can be surveyed per day. I estimate it would require 16 days to collect data. Each flight would generate 30 images, so a total of 1920 images. I estimate that data processing would take 4 days (1min/image).
- Genetic sampling – I consider that about 400 samples are required for the analyses. Indeed Arandjelovic & Vigilant (2018) suggest that as a rule-of-thumb, 3-4 times as many samples as the number of expected individuals present in the area should be collected. I consider that about 50 samples can be collected in 8 days (e.g. Brand et al., 2016), so 32 days would be required to collect 400 samples. I consider that one day of training is required to learn how to collect and store samples in the field; training does not include training for lab analyses that require specified skills. I consider that 30 days are required to analyse samples in a lab. I did not include the time needed to export the samples and the costs associated to the export permit are for an exportation from Tanzania to Germany.

For simplification, I consider labour cost (for data collection and analyses) at $50 per working day. Line transect is the least costly method, while genetic sampling is the most prohibitive (three time for expensive than line transects and twice more expensive than PAM, CT and drone). Although PAM, CT and drone have high initial equipment costs, equipment can be reused for further studies, in contrast to genetic sampling where costs are associated to a unique study. The time needed for data acquisition and data processing varies greatly depending on the methods. To be used to regularly monitor animal populations, data processing needs to be easy and relatively fast. PAM is the more time-consuming method because it requires call rate estimation.

Table 7.2. Comparison of costs and time required for data collection and analyses for estimating density with PAM, CT, drone, line transects and genetic sampling for an area of about 60km^2 in Tanzania.

		PAM	CT (distance sampling)	Drone	Line transects (marked nest count)	Genetic sampling
Costs	Data collection	- 12 audio recorders - e.g. Song Meters mini (Wildlife Acoustics, $500/u); 4AA batteries/u (*2 for recharge, $10/4batt.), 32GB SD card/u (*2, $8/u) - Hard drive 2TB (*2 for backup, $60/u) - Handheld GPS (e.g. Garmin eTrex at $200) - Compass ($10) - Field labour (18d *$50 for PAM deployment and maintenance + 70d *$50 for call rate estimation)	- 25 camera traps (e.g. Bushnell trail HD, $140/u; 8AA batteries/u (*2 for recharge, $20/8batt.), 16GB SD card/u (*2, $6/u) - Handheld GPS (e.g. Garmin eTrex at $200) - Hard drive 1TB (*2 for backup, $50/u) - Compass ($10) - Field labour (72d* $50)	- Drone ($3500) - Handheld GPS (e.g. Garmin eTrex at $200) - Field labour (16d* $50 *2) - Hard drive 1TB (*2 for backup, $50/u) - Drone license ($1300)	- Binoculars (~$100, *2) - Handheld GPS (e.g. Garmin eTrex at $200) - Compass ($10) - Measuring tape ($20) - Field labour (64d* $50*2)	- Handheld GPS (e.g. Garmin eTrex at $200) - Compass ($10) - Field labour (32d* $50*2) - Sample export permit ($5/sample) - collecting tube ($0.2/sample) - ethanol for sample preservation ($0.05/tube)
	Data analyses	- Modest processing power computer (~$500) - Software to process audio files (e.g. Raven Pro at $400 for non-profit) - Human labour (70d * $50)	- Modest processing power computer (~$500) - Human labour (10d *$50)	- High processing power computer (~$1500) - Software to process images (~$550) - Human labour (4d *$50)	- Modest processing power computer (~$500) - Human labour (1d *$50)	- Modest processing power computer (~$500) - Lab analyses ($35/sample) - Lab technician (30d *$50)
	Total	~$12110	$9710	$8950	$7380	$21510
Time	Training	2 days	2 days	10 days	2 days	1 day (genetic analyses require lab skills not included here)
	Data collection	18 days (PAM deployment and maintenance) 70 days (call rate estimation)	72 days	16 days	64 days	32 days
	Data analyses	70 days	10 days	4 days	1 day	30 days
	Total	160 days	84 days	30 days	67 days	63 days

3. Directions for future research

3.1. Machine learning and automatization of data processing

Data processing is the main limitation for PAM and CT data, as analyses are mainly done manually which is time intensive (see above). Improvement in pattern recognition with machine learning are promising and can speed up data processing and analyses (e.g. Kühl & Burghardt, 2013). Face or call detectors are, however, generating false detections and a manual verification is often required (e.g. Heinicke et al., 2015; Crunchant et al., 2017). A trade-off between these false detections and time saving must be considered.

Because humans and chimpanzees share similar face properties (Loos & Ernst, 2013), chimpanzee face detection and recognition algorithms have been adapted from those originally developed for humans. At least three chimpanzee face detectors have been developed. An application of a first detector (Loos & Ernst, 2013) has shown that the semi-automated method to estimate site use with CT data greatly sped up data processing and required only 2-4% of the time required for manual analyses (Crunchant et al., 2017). Chimpanzees were mostly detected on videos containing frontal face views. With a deep convolutional neural network (CNN) and a 14-year dataset including 10 million face images from 23 individuals, Schofield et al., (2019) developed an individual face recognition and detector. It allows for identity recognition with a 92.5% accuracy and sex recognition with 96.2% accuracy. These results are promising, and a larger dataset would increase accuracy and applicability. Lastly, another face detector (ChimpFace, https://conservationx.com/project/id/8 - accessed 28/10/2020) is being developed to identify photos on social media and e-commerce websites that are likely linked to trafficking-related activities.

For PAM to become widely used by conservationists, the development of a chimpanzee automated call detector is necessary. Recent studies on other ape species are promising. For instance, a study examining the coding of individual signatures through the vocal repertoire of bonobos (*Pan paniscus*), has shown that the high hoots – the bonobo loud calls (Hohmann & Fruth, 1994) - strongly encode caller identity (Keenan et al., 2020). This study involved 1850 individuals calls from 21 individuals. Another study evaluated a caller recognition procedure in male orangutan (*Pongo pygmaeus wurmbii*) long calls, and a 72.2% correct identification rate was obtained with recordings from an ALS (Spillmann et al., 2016). The authors also showed that automatic individual identification was reliable for calls recorded from orangutans placed at distances up to 420m from the ALS. Lastly, Clink et al. (2018) have applied a semi-automated vocal fingerprinting approach to Bornean gibbon (*H. mulleri*) females monitoring and analysed 376 calls from 33 females. Caller identity was predicted with 99.5% accuracy. By combining focal follows and the ALS, we could record calls with the ALS and match them with the caller identity obtained from focal follows, but also record high quality calls with a shotgun microphone. Without the essential development of an automated call detector, the methods presented in this thesis are likely to remain in the realm of academics and not of conservation managers and small NGOs for example, due to the highly time-consuming data extraction process, currently done manually.

However, with the recent improvements in machine learning and the successful examples with other species, there is still the hope of developing a chimpanzee (individual) call recognition detector in the (near) future.

3.2. Real-time bioacoustic monitoring

As mentioned in chapter six, adding a (real-time) remote data transmission component to the ALS would help many applications, such as accelerating chimpanzee habituation process. In practice, no post-deployment visits would be needed to retrieve data, making the system fully autonomous. A system relying on long-distance radio frequency has been deployed at Issa Valley, Tanzania for chimpanzee monitoring and chimpanzee spatiotemporal vocalisation patterns (Piel, 2014). An open source and low-cost system has also recently been develop for real-time acoustic monitoring (Sethi et al., 2018). It relies on a local mobile network and can operate even under harsh climatic conditions but requires direct sunlight for the solar power system.

In this dissertation, I attempted to develop a real-time transmission system with a radio network. Each acoustic unit was composed of the unit as previously described in chapter 6, along with a radio (Ubiquiti Networks PICOM2-HP PicoStation M2 HP Indoor/Outdoor AirMAX BaseStation). Data from each sensor were transmitted directly to the camp through a relay system supported by a solar panel with battery, a PoE injector (Ubiquiti Thoughswitch TS-8-PRO) and two antennas (Ubiquiti LiteBeam ac 5GHz, one directed to the sensors and one directed to the camp). It has however not been successful, mainly due to a battery issue, and audio files were only sparsely transmitted to the camp. A potential solution would be to add machine learning on the units to record and store only chimpanzee calls to reduce the volume of data to be transmitted (Deniz et al., 2017). However, this would mean that we would not be able to re-analyse the data with new methods (e.g. new call detector) and data would be species-specific. Given the Issa landscape – a mountainous and open habitat - there is, however, a high potential to successfully develop such a system.

3.3. Combination of monitoring methods

Because each monitoring method has its own advantages/disadvantages (Table 7.1) and can offer different information, pairing different methods could help monitoring. Complementary data could be collected on biotic interactions and provide a more accurate image of animal presence and movement (Buxton et al., 2018a). For instance, detection probabilities could be improved when using both PAM and CT for chimpanzee monitoring. In turn, this could potentially improve the accuracy of the density estimate.

3.4. Behavioural studies

Although the aim of the work was to demonstrate PAM as a tool for chimpanzee conservation, acoustically monitoring chimpanzee can also help our understanding of chimpanzee behaviour, and more specifically their social dynamics. PAM and more specifically ALS will allow for simultaneously following multiple individuals in space and time and might reveal how they coordinate. High data resolution will also help to quantify the socio-ecological drivers of group cohesion.

4. Conclusion

The work presented here demonstrates that PAM is a promising non-invasive method for chimpanzee monitoring, allowing for presence detection, density estimation and localisation. It allows for the study of chimpanzees without disturbing them. Results can also be transposed to any loud calling terrestrial species, such as wolves, gibbons, orangutans and elephants. With recent technological advances, devices are increasingly robust and affordable. Open-source devices allow for customisation of e.g. recording schedule and parameters. Some challenges to automate data analysis exist, a limitation similar to CT and drone for instance. However, improvements of automatic call detection are promising, and I anticipate that PAM will become more common in the conservationist’s toolbox for loud calling species monitoring.

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