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

Article

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

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Running headline: Acoustic and visual chimpanzee detectability

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

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, Avgar, Burton, Broadley, & Boutin, 2018) among others.

Autonomous methods such as passive acoustic methods (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 e.g. 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, Rowland, Keen, & Shiu, 2017). More recently applications include study of gibbons (*Nomascus gabbrielae*) (Vu & Tran, 2019), and wolves (*Canis lupus*) (Papin, Pichenot, Guérold, & Germain, 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, Collett, Ricci, Martin, & Spitale, 2013; 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, e.g. stone throwing (Kühl et al., 2016) and crab-hunting (Koops et al., 2019), but also for abundance and density estimation (Després-Einspenner, Howe, Drapeau, & Kühl, 2017; Cappelle, Després-Einspenner, Howe, Boesch, & Kühl, 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.

Method

1) Study site

The study was conducted between March and December 2018, in the Issa Valley, western Tanzania (Fig. 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.

2) Study design

a. 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. 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.

b. 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. 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. 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, 2014). Duplicate detections were controlled for by pooling detections from the four sensors belonging to the same cluster into one detection.

3) Occupancy modelling

a. 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).

b. 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.

c. 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: $\alpha = (1\text{-}p)^{N}$ (McArdle, 1990; Kéry, 2002).

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

Results

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 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).

2) Factors influencing detectability

The best model to predict chimpanzee detectability for PAM comprised season as a covariate (Table 2). The best model to predict chimpanzee detectability for CT comprised all covariates: days, season and camera placement (Table 2) and was strongly supported ($\Sigma w > 0.95$; $\Delta AIC < 2$) (Burnham & Anderson, 2002) 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. 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. 5).

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.

3) 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, Webster, Brough, Jowett, & Dawson, 2018; Enari, Enari, Okuda, Maruyama, & Okuda, 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, Enari, Okuda, Maruyama & Okuda (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) 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 (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, 2002). 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, 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.

5) 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, Kingan, Schmid, McKay, & Stol, 2019).

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: all acoustic and video data are accessible upon request to the authors**.**

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.

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Tables

Table 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]

Table 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

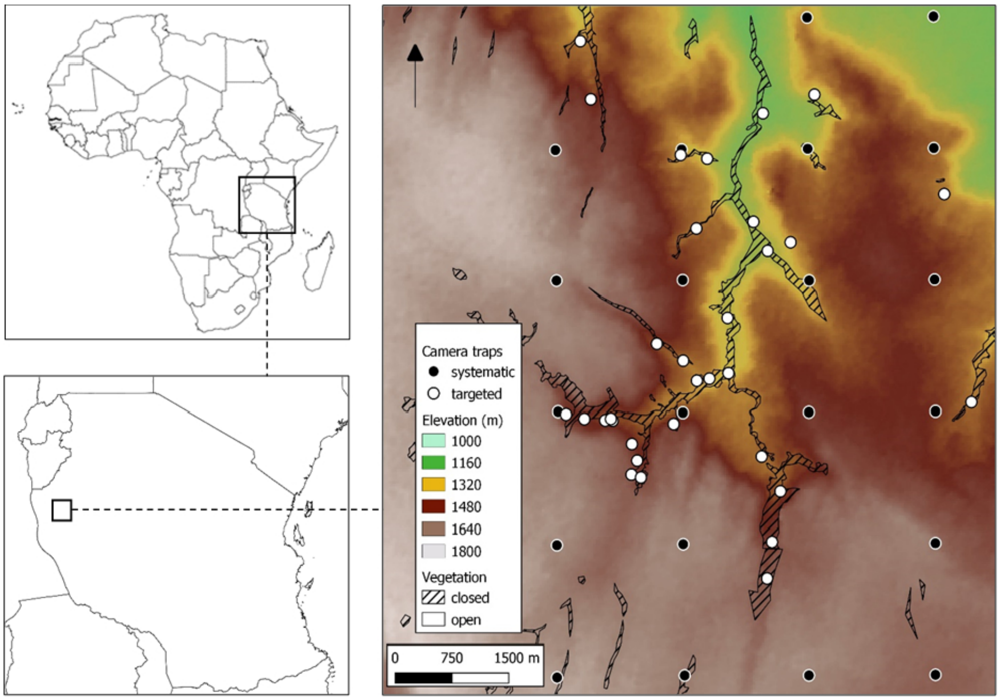

Figure 1: Study site and camera trap locations (targeted and systematic placements) in Issa Valley, Western Tanzania.

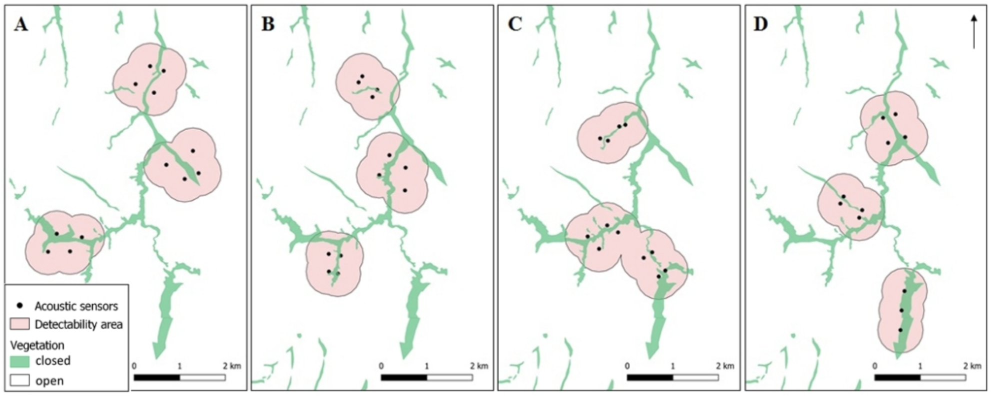

Figure 2: Location of acoustic sensors: each set-up (A, B, C, D) remained two weeks before being rotated to another one. Detectability is the area where a call can reach a sensor, defined as a 500m buffer around a sensor.

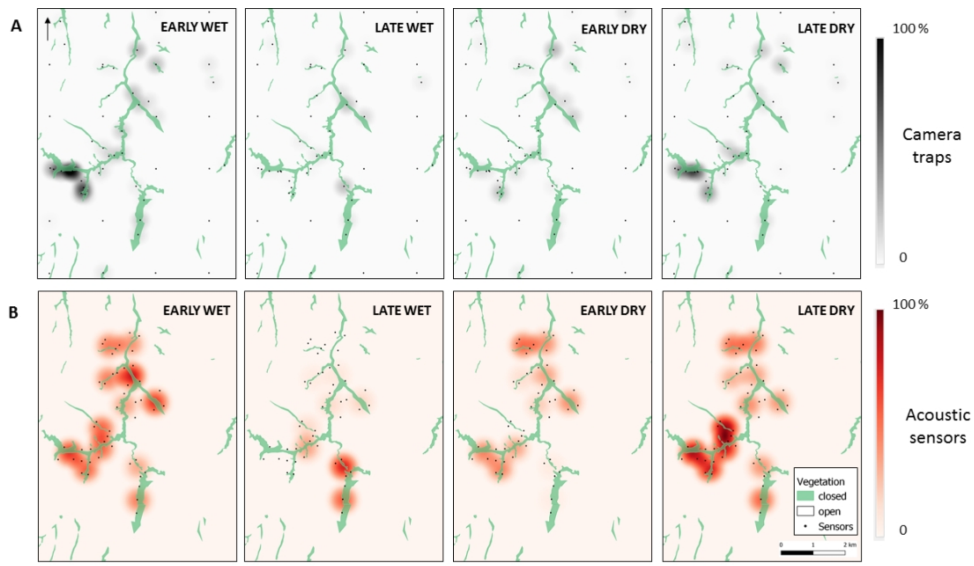

Figure 3: Heatmap of chimpanzee detections (proportion of recording days with at least one detection, call or video) for the CT (A) and PAM (B) datasets, in function of the four seasons, early/late wet and early/late dry.

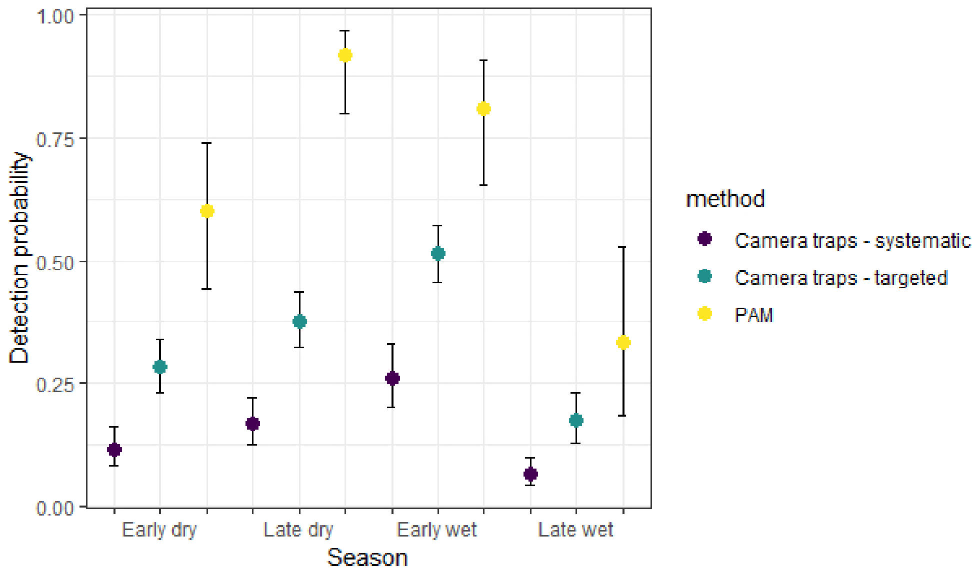

Figure 4: Detection probabilities for each method (PAM, systematic and targeted CT) depending on the season. Error bars represent upper and lower bounds.

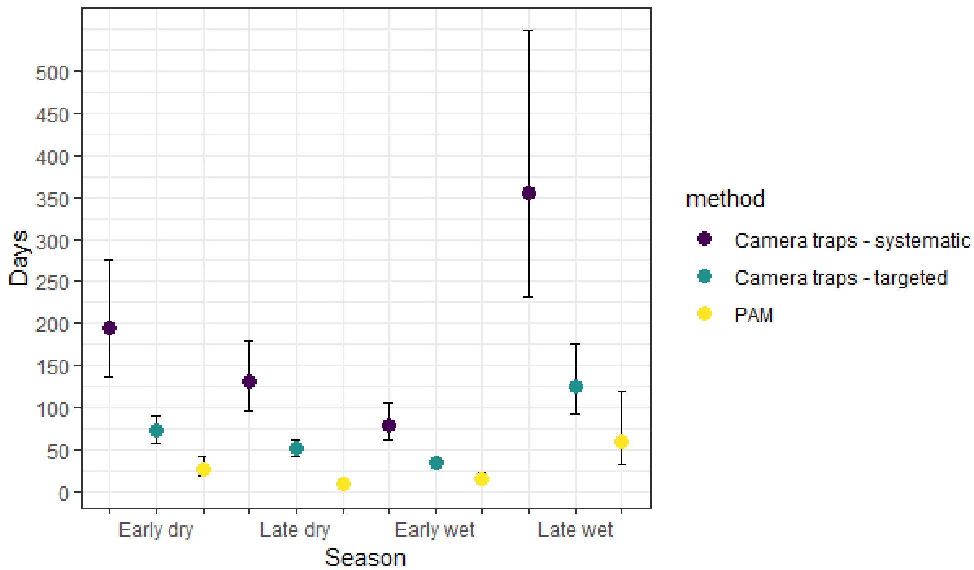

Figure 5: Number of trap days necessary to infer chimpanzee absence at a confidence level of 95% in function of seasons and methods. Error bars represent upper and lower bounds.