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

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Abstract

- 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 vocalization rate. The acoustic method can infer chimpanzee absence with less than 10 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, savannawoodland, mosaic habitat, seasonality, Tanzania, vocalizations

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, for example when studying nocturnal, cryptic, elusive or hunted species that have changed their activity pattern/behaviour. Consequently, innovative biomonitoring methods are revolutionizing 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, that is 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 multispecies interactions as disturbance levels oscillate (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003; Mackenzie et al., 2002). Occupancy modelling allows us to refine species distribution models in conservation planning and adjust policy priorities. While 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, for example 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 monitoring (PAM) and camera trapping (CT) are two ways to remotely monitor wildlife presence, distribution and behaviour (Burton et al., 2015; Rowcliffe & Carbone, 2008; 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.

Camera trap 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 et al., 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 the 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 et al., 2019), ranging from revealing occurrence and occupancy (Campos-Cerqueira & Aide, 2016; Rovero, Collett, Ricci, Martin, & Spitale, 2013), population size and density (e.g. Margues, 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 in 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 (Cappelle, Després-Einspenner, Howe, Boesch, & Kühl, 2019; Després-Einspenner, Howe, Drapeau, & Kühl, 2017) 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 vocalizations (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: (a) estimate chimpanzee detection probabilities from occupancy modelling; (b) identify the parameters that influence the detectability and more specifically to what extent seasonality plays a role in detectability; and (c) estimate and compare the sampling effort needed to produce precise occupancy estimates and make recommendations for wildlife managers regarding which is the 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 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted between March and December 2018, in the Issa Valley, western Tanzania (Figure 1). The area is comprised of a series of valleys separated by steep mountains and flat plateaus, with an altitudinal gradient ranging from 1,050 to 1,650 m a.s.l. 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 primates and four large carnivore species (spotted hyena, lion, leopard and 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 ± 92 mm during the wet season (mid-October to mid-May) and 0.6 ± 0.9 mm during the dry season. Mean minimum and maximum temperatures per day were 16.6 \pm 1.7 and 27.7 \pm 2°C, respectively, for the dry season and 16.9 ± 1 and 25.7 ± 2.2°C for the wet season. Data points were measured every 5 min by a weather station (HOBO model RX3000; Onset Corp.) situated near the research station. The study site covers the territory of at least one chimpanzee community.

2.2 | Study design

2.2.1 | Camera trap deployment

For 9 months, we deployed 21 camera traps (Bushnell Trophy Cam) in a systematic layout (henceforth 'systematic' cameras), in grid cells of $1.67 \text{ km} \times 1.67 \text{ km}$. We deployed 32 additional camera traps (Bushnell Trophy Cam) at targeted locations, that is animal paths or termite mounds (seven of 32; henceforth 'targeted' cameras, Figure 1). We attached cameras to trees 90 cm above the ground and were triggered by movement, which activated a 60 s recording, followed by a minimum 1 s break before another recording began. For technical reasons, some cameras recorded 15 s videos instead of 60 s 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 12 acoustic sensors (SM2, Wildlife Acoustics) for the same 9-month period that were secured on trees at a height of approximately 1.65 m, at the top of the valleys to maximize the chance of recording calls. We recorded sounds at a 16 kHz sample rate and 16 bit/s in uncompressed.wav format. We scheduled the sensors to

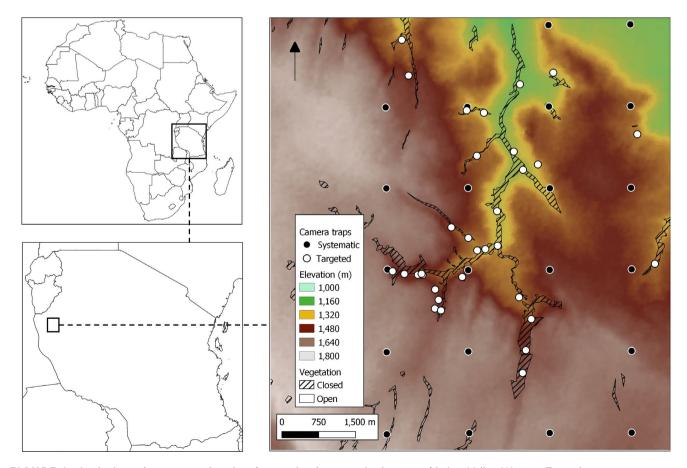


FIGURE 1 Study site and camera trap locations (targeted and systematic placements) in Issa Valley, Western Tanzania

record for 30 min of every hour from 6:00 to 19:30 (7 hr/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 (Figure 2), with inter-sensor distance ~500 m to allow for later sound localization. We drew a 500 m buffer around each acoustic sensor, corresponding to the area within which a call could reliably be detected (A. Piel, unpublished data). We rotated the clusters to new locations within the study area every 2 weeks (four arrays, Figure 2). We replaced batteries and *SD* cards every 2 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.

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, that is the probability of occupancy, and *p*, the probability that a species present is detected within a site, that is the probability of detection (MacKenzie et al., 2006). For a discussion of assumptions, see (Kalan et al., 2015; MacKenzie et al., 2006).

For both datasets, we divided the sampling period into sampling occasions (SOs) of 8 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 16 May) and the beginning of the wet season the first week with rain (i.e. from 14 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

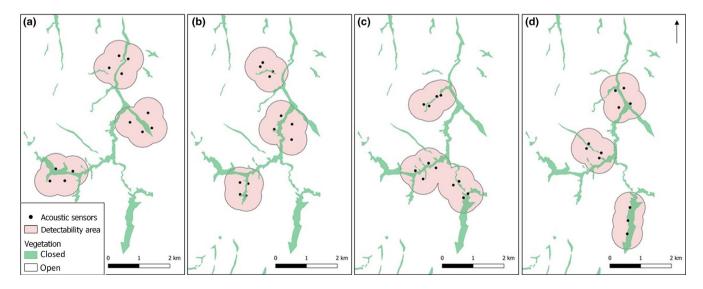


FIGURE 2 Location of acoustic sensors: each set-up (a)–(d) remained 2 weeks before being rotated to another one. Detectability is the area where a call can reach a sensor, defined as a 500 m buffer around a sensor

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 1,000 simulations. We found no indication of lack of fit for our best models (p > .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: $\alpha = (1 - p)^N$ (Kéry, 2002; McArdle, 1990).

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

We estimated the number of trap days corresponding, by multiplying N_{\min} by eight for CT and PAM given that one visit corresponds to 8 days.

All analyses were conducted in R studio version 1.2.1335; R Core Team, 2018) and maps were created in QGIS version 3.6.2 Noosa; QGIS Development Team, 2018).

3 | RESULTS

3.1 | Visual versus 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 3,349 chimpanzee videos. About 125 videos were recorded on 12 systematic cameras and 3,224 on 32 targeted cameras

TABLE 1	Summary of the visua	al and acoustic deployments
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	Systematic	Targeted	PAM
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 30 min audio files)	125	3,224	1,024
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)

Abbreviations: CT, camera trapping; PAM, passive acoustic monitoring.

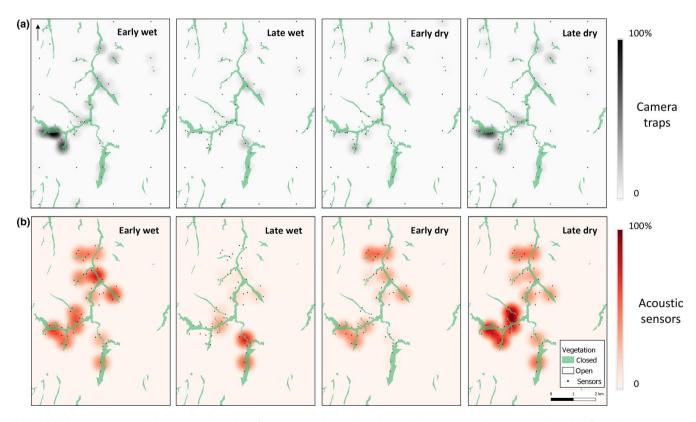


FIGURE 3 Heat map of chimpanzee detections (proportion of recording days with at least one detection, call or video) for the camera trap (a) and passive acoustic method (b) datasets, in function of the four seasons, early/late wet and early/late dry

(Table 1). The acoustic sensors recorded for 5,316 cluster hours (15,344 sensors hours). Of the 10,632 30-min occasions analysed, at least one detection has been detected in 1,024 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 (6 and 7 a.m.). Both methods reveal a similar strict pattern of seasonal

Models	No. parameters	AIC	Δ	AIC weight
PAM				
$p(\text{season} + \text{hours}) \Psi(.)$	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
р(.) Ψ(.)	2	188.68	53.51	2.4×10^{-12}
СТ				
p(season + method + days) Ψ(vegetation/topography)	12	1,507.38	0.00	0.95
$p(\text{season} + \text{method} + \text{days}) \Psi(.)$	7	1,513.33	5.95	0.049

TABLE 2 Summary of occupancy modelling for the best models

Abbreviations: CT, camera trapping; PAM, passive acoustic monitoring.

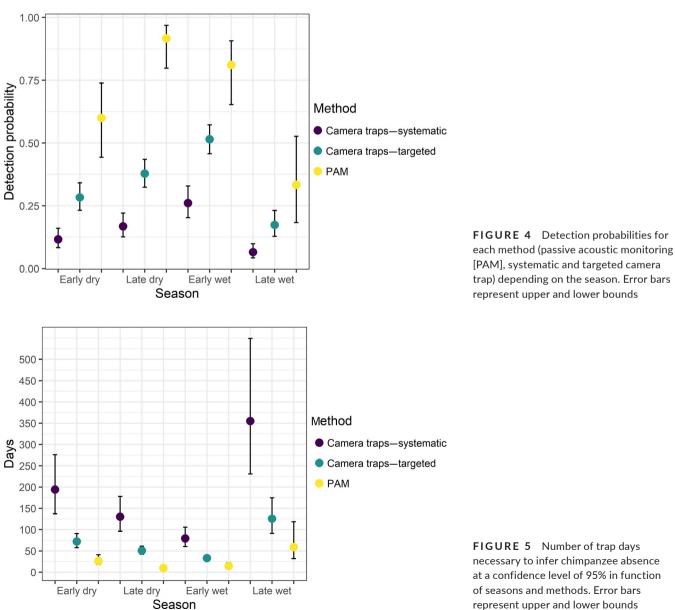


FIGURE 5 Number of trap days necessary to infer chimpanzee absence at a confidence level of 95% in function of seasons and methods. Error bars represent upper and lower bounds

detection with a peak in detections during the late dry and early wet seasons (Figure 3).

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 (Figure 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 (Figure 5).

4 | DISCUSSION

The 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 10 and 15 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* (Enari, Enari, Okuda, Maruyama, & Okuda, 2019; Rayment, Webster, Brough, Jowett, & Dawson, 2018). This is likely due to the detection area with PAM being far larger than with CT, estimated to be up to 7,000 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 maximize 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 (A. 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 (Mitani, Watts, & Lwanga, 2002; Sakura, 1994; Wallis, 1995). 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 vocalizations 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; A. 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 et al., 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 et al., 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 1,120 min of manual processing (10 (days) × 14 (audio files per day) \times 2 (minutes to process one audio file) \times 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 et al., 2017). Different methods of machine learning (e.g. neural networks) are available, see the review from Bianco et al. (2019) for more details. A manual validation to clean false positives is, however, necessary (e.g. Campos-Cerqueira & Aide, 2016; Crunchant et al., 2017; Enari et al., 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 revolutionized 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).

5 | 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 interdisciplinary 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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AUTHORS' CONTRIBUTIONS

A.-S.C., D.B., H.K. and A.P. conceived the ideas and designed methodology; A.-S.C. collected and analysed the data; A.-S.C. and A.P. wrote the manuscript, and all the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The raw presence/absence matrices can be found at Dryad Digital Repository https://doi.org/10.5061/dryad.5dv41ns34 (Crunchant, Borchers, Kühl, & Piel, 2020). All results reported in this article can be reproduced using these matrices.

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REFERENCES

- Aide, T. M., Corrada-Bravo, C., Campos-Cerqueira, M., Milan, C., Vega, G., & Alvarez, R. (2013). Real-time bioacoustics monitoring and automated species identification. *PeerJ*, 1, e103. https://doi.org/10.7717/ peerj.103
- Akçakaya, H. R., Bennett, E. L., Brooks, T. M., Grace, M. K., Heath, A., Hedges, S., ... Young, R. P. (2018). Quantifying species recovery and conservation success to develop an IUCN Green List of Species. *Conservation Biology*, 32(5), 1128–1138. https://doi.org/10.1111/ cobi.13112
- Alquezar, R. D., & Machado, R. B. (2015). Comparisons between autonomous acoustic recordings and avian point counts in open woodland savanna. *The Wilson Journal of Ornithology*, 127(4), 712–723. https:// doi.org/10.1676/14-104.1

- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., ... Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471(7336), 51–57. https://doi. org/10.1038/nature09678
- Beason, R. D., Riesch, R., & Koricheva, J. (2018). AURITA: An affordable, autonomous recording device for acoustic monitoring of audible and ultrasonic frequencies. *Bioacoustics*, 4622, 1–16. https://doi. org/10.1080/09524622.2018.1463293
- Bianco, M. J., Gerstoft, P., Traer, J., Ozanich, E., Roch, M. A., Gannot, S., & Deledalle, C.-A. (2019). Machine learning in acoustics: Theory and applications. Journal of Acoustical Society of America, 1–39. https:// doi.org/10.1121/1.5133944
- Bioacoustics Research Program. (2014). Raven Pro: Interactive sound analysis software (version 1.5). Ithaca, NY: The Cornell Lab of Ornithology.
- Blumstein, D. T., Mennill, D. J., Clemins, P., Girod, L., Yao, K., Patricelli, G., ... Kirschel, A. N. G. (2011). Acoustic monitoring in terrestrial environments using microphone arrays: Applications, technological considerations and prospectus. *Journal of Applied Ecology*, 48(3), 758–767. https://doi.org/10.1111/j.1365-2664.2011.01993.x
- Burnham, K. P., & Anderson, D. (2002). Model selection and multi-model inference. New York, NY: Springer.
- Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., ... Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology, 52(3), 675-685. https://doi. org/10.1111/1365-2664.12432
- Buxton, R. T., Lendrum, P. E., Crooks, K. R., & Wittemyer, G. (2018). Pairing camera traps and acoustic recorders to monitor the ecological impact of human disturbance. *Global Ecology and Conservation*, 16, e00493. https://doi.org/10.1016/j.gecco.2018.e00493
- Campbell, G., Kuehl, H., N'Goran Kouamé, P., & Boesch, C. (2008). Alarming decline of West African chimpanzees in Côte d'Ivoire. Current Biology, 18(19), 903–904. https://doi.org/10.1016/ j.cub.2008.08.015
- Campos-Cerqueira, M., & Aide, T. M. (2016). Improving distribution data of threatened species by combining acoustic monitoring and occupancy modelling. *Methods in Ecology and Evolution*, 7(11), 1340–1348. https://doi.org/10.1111/2041-210X.12599
- Cappelle, N., Després-Einspenner, M.-L., Howe, E. J., Boesch, C., & Kühl, H. S. (2019). Validating camera trap distance sampling for chimpanzees. American Journal of Primatology, https://doi.org/10.1002/ ajp.22962
- Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1(5), e1400253. https://doi.org/10.1126/sciadv.1400253
- Clink, D. J., Crofoot, M. C., & Marshall, A. J. (2019). Application of a semi-automated vocal fingerprinting approach to monitor Bornean gibbon females in an experimentally fragmented landscape in Sabah, Malaysia. *Bioacoustics*, 28(3), 193–209. https://doi.org/10.1080/ 09524622.2018.1426042
- Comer, S., Speldewinde, P., Tiller, C., Clausen, L., Pinder, J., Cowen, S., & Algar, D. (2018). Evaluating the efficacy of a landscape scale feral cat control program using camera traps and occupancy models. *Scientific Reports*, 8(1), 1–9. https://doi.org/10.1038/s41598-018-23495-z
- Crunchant, A. S., Borchers, D., Kühl, H., & Piel, A. (2020). Data from: Listening and watching: Do camera traps or acoustic sensors more efficiently detect wild chimpanzees in an open habitat? *Dryad Digital Repository*, https://doi.org/10.5061/dryad.5dv41ns34
- Crunchant, A.-S., Egerer, M., Loos, A., Burghardt, T., Zuberbühler, K., Corogenes, K., ... Kühl, H. S. (2017). Automated face detection for occurrence and occupancy estimation in chimpanzees. *American Journal* of Primatology, 79(3), 1–12. https://doi.org/10.1002/ajp.22627
- Cusack, J. J., Dickman, A. J., Rowcliffe, J. M., Carbone, C., Macdonald, D. W., & Coulson, T. (2015). Random versus game trail-based camera

trap placement strategy for monitoring terrestrial mammal communities. *PLoS ONE*, 10(5), e0126373. https://doi.org/10.1371/journ al.pone.0126373

- Després-Einspenner, M.-L., Howe, E. J., Drapeau, P., & Kühl, H. S. (2017). An empirical evaluation of camera trapping and spatially explicit capture-recapture models for estimating chimpanzee density. *American Journal of Primatology*, 79, e22647. https://doi.org/10.1002/ajp. 22647
- Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Tai chimpanzees. *International Journal of Primatology*, 18(2), 183–206.
- Enari, H., Enari, H. S., Okuda, K., Maruyama, T., & Okuda, K. N. (2019). An evaluation of the efficiency of passive acoustic monitoring in detecting deer and primates in comparison with camera traps. *Ecological Indicators*, 98(July 2018), 753–762. https://doi.org/10.1016/j.ecolind. 2018.11.062
- Fedurek, P., Donnellan, E., & Slocombe, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology*, 68(8), 1345–1355. https://doi. org/10.1007/s00265-014-1745-4
- Fedurek, P., Schel, A. M., & Slocombe, K. E. (2013). The acoustic structure of chimpanzee pant-hooting facilitates chorusing. *Behavioral Ecology and Sociobiology*, 67(11), 1781–1789. https://doi.org/10.1007/S00 265-0
- Fiske, I. J., & Chandler, R. B. (2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, 43(10), 1–23. https://doi.org/10.18637/jss.v043. i10
- Gibb, R., Browning, E., Glover-Kapfer, P., & Jones, K. E. (2019). Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution*, 10, 169–185. https://doi.org/10.1111/2041-210X.13101
- Hambrecht, L., Brown, R. P., Piel, A. K., & Wich, S. A. (2019). Detecting 'poachers' with drones: Factors influencing the probability of detection with TIR and RGB imaging in miombo woodlands, Tanzania. *Biological Conservation*, 233, 109–117. https://doi.org/10.1016/j. biocon.2019.02.017
- Hill, A. P., Prince, P., Piña Covarrubias, E., Doncaster, C. P., Snaddon, J. L., & Rogers, A. (2018). AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and the environment. *Methods in Ecology and Evolution*, *9*, 1199–1211. https://doi. org/10.1111/2041-210X.12955
- Hioka, Y., Kingan, M., Schmid, G., McKay, R., & Stol, K. A. (2019). Design of an unmanned aerial vehicle mounted system for quiet audio recording. *Applied Acoustics*, 155, 423–427. https://doi.org/10.1016/j. apacoust.2019.06.001
- Hodgson, J. C., Mott, R., Baylis, S. M., Pham, T. T., Wotherspoon, S., Kilpatrick, A. D., ... Koh, L. P. (2018). Drones count wildlife more accurately and precisely than humans. *Methods in Ecology and Evolution*, 9(5), 1160–1167. https://doi.org/10.1111/2041-210X.12974
- Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L., & Wilmshurst, J. M. (2017). Biodiversity losses and conservation responses in the Anthropocene. *Science*, 356(6335), 270–275. https://doi.org/10.1126/science.aam9317
- Junker, J., Blake, S., Boesch, C., Campbell, G., Toit, L. D., Duvall, C., ... Kuehl, H. S. (2012). Recent decline in suitable environmental conditions for African great apes. *Diversity and Distributions*, 18(11), 1077–1091. https://doi.org/10.1111/ddi.12005
- Kalan, A. K., Mundry, R., Wagner, O. J. J., Heinicke, S., Boesch, C., & Kühl, H. S. (2015). Towards the automated detection and occupancy estimation of primates using passive acoustic monitoring. *Ecological Indicators*, 54, 217–226. https://doi.org/10.1016/j.ecolind. 2015.02.023
- Kalan, A. K., Piel, A. K., Mundry, R., Wittig, R. M., Boesch, C., & Kühl, H. S. (2016). Passive acoustic monitoring reveals group

ranging and territory use: A case study of wild chimpanzees (*Pan troglodytes*). *Frontiers in Zoology*, 13(1), 34. https://doi.org/10.1186/s12983-016-0167-8

- Karanth, K. U., Gopalaswamy, A. M., Kumar, N. S., Vaidyanathan, S., Nichols, J. D., & Mackenzie, D. I. (2011). Monitoring carnivore populations at the landscape scale: Occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology*, 48(4), 1048–1056. https:// doi.org/10.1111/j.1365-2664.2011.02002.x
- Kéry, M. (2002). Inferring the absence of a species: A case study of snakes. The Journal of Wildlife Management, 66(2), 330–338.
- Kidney, D., Rawson, B. M., Borchers, D. L., Stevenson, B. C., Marques, T. A., & Thomas, L. (2016). An efficient acoustic density estimation method with human detectors applied to gibbons in Cambodia. *PLoS ONE*, 11(5), e0155066. https://doi.org/10.1371/journal.pone. 0155066
- Knight, E. C., Hannah, K. C., Foley, G. J., Scott, C. D., Brigham, R. M., & Bayne, E. (2017). Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *Avian Conservation and Ecology*, 12(2), 14. https://doi.org/10.5751/ACE-01114-120214
- Koops, K., Wrangham, R. W., Cumberlidge, N., Fitzgerald, M. A., van Leeuwen, K. L., Rothman, J. M., & Matsuzawa, T. (2019). Crabfishing by chimpanzees in the Nimba Mountains, Guinea. *Journal of Human Evolution*, 133, 230–241. https://doi.org/10.1016/j.jhevol. 2019.05.002
- Kühl, H. S., Kalan, A. K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., ... Boesch, C. (2016). Chimpanzee accumulative stone throwing. *Scientific Reports*, 6(November 2015), 1–8. https:// doi.org/10.1038/srep22219
- Kühl, H. S., Sop, T., Williamson, E. A., Mundry, R., Brugière, D., Campbell, G., ... Boesch, C. (2017). The critically endangered western chimpanzee declines by 80%. *American Journal of Primatology*, 79(9), https:// doi.org/10.1002/ajp.22681
- MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. Journal of Agricultural, Biological, and Environmental Statistics, 9(3), 300–318. https://doi.org/10.1198/108571104X3361
- MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, 84(8), 2200–2207. https://doi.org/10.1890/02-3090
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droedge, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2006). Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Burlington, MA: Academic Press.
- Marques, T. A., Munger, L., Thomas, L., Wiggins, S., & Hildebrand, J. A. (2011). Estimating North Pacific right whale Eubalaena japonica density using passive acoustic cue counting. Endangered Species Research, 13(3), 163–172. https://doi.org/10.3354/esr00325
- Martin, T. G., Kehoe, L., Mantyka-Pringle, C., Chades, I., Wilson, S., Bloom, R. G., ... Smith, P. A. (2018). Prioritizing recovery funding to maximize conservation of endangered species. *Conservation Letters*, 11, 1–9. https://doi.org/10.1111/conl.12604
- McArdle, B. H. (1990). When are rare species not there? *Nordic Society Oikos*, 57(2), 276–277. https://doi.org/10.2307/3565950
- McCarthy, M. S., Després-Einspenner, M.-L., Samuni, L., Mundry, R., Lemoine, S., Preis, A., ... Kühl, H. S. (2018). An assessment of the efficacy of camera traps for studying demographic composition and variation in chimpanzees (*Pan troglodytes*). American Journal of Primatology, 80(9), 1-10. https://doi.org/10.1002/ajp.22904
- Mellinger, D., Stafford, K. M., Moore, S. E., Dziak, R. P., & Matsumo, H. (2007). An overview of fixed passive acoustic observation methods

for cetaceans. Oceanography, 20(4), 36–45. https://doi.org/10.5670/ oceanog.2007.03

- Miller, B. S., & Miller, E. J. (2018). The seasonal occupancy and diel behaviour of Antarctic sperm whales revealed by acoustic monitoring. *Scientific Reports*, 8, 1–12. https://doi.org/10.1038/s41598-018-23752-1
- Mitani, J. C., Watts, D. P., & Lwanga, J. S. (2002). Ecological and social correlates of chimpanzee party size and composition. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), *Behavioral diversity in chimpanzees and bonobos* (pp. 102–111). Cambridge: Cambridge University Press. https://doi.org/10.1017/cbo9780511606397.011
- Moore, J. (1992). Savanna chimpanzees. In T. Nishida, P. McGrew, P. Marler, M. Pickford, & F. de Waal (Eds.), *Topics in primatology, vol. 1 human origins* (pp. 99–118). Tokyo: University of Tokyo Press.
- Moyer, D., Plumptre, A. J., Pintea, L., Hernandez-Aguilar, A., Moore, J., Stewart, F., ... Mwangoka, M. (2006). Surveys of chimpanzees and other biodiversity in Western Tanzania. Arlington, VA: United States Fish and Wildlife Service (USFWS).
- Nazir, S., Newey, S., Irvine, R. J., Verdicchio, F., Davidson, P., Fairhurst, G., & Van Der Wal, R. (2017). WiseEye: Next generation expandable and programmable camera trap platform for wildlife research. *PLoS ONE*, 12(1), 1–15. https://doi.org/10.1371/journal.pone.0169758
- Neilson, E. W., Avgar, T., Burton, A. C., Broadley, K., & Boutin, S. (2018). Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere*, 9(1), e02092. https://doi.org/10.1002/ecs2.2092
- Oberosler, V., Groff, C., Iemma, A., Pedrini, P., & Rovero, F. (2017). The influence of human disturbance on occupancy and activity patterns of mammals in the Italian Alps from systematic camera trapping. *Mammalian Biology*, *87*, 50–61. https://doi.org/10.1016/j.mambio.2017.05.005
- Papin, M., Pichenot, J., Guérold, F., & Germain, E. (2018). Acoustic localization at large scales: A promising method for grey wolf monitoring. Frontiers in Zoology, 15, 1–10. https://doi.org/10.1186/ s12983-018-0260-2
- Piel, A. K. (2018). Temporal patterns of chimpanzee loud calls in the Issa Valley, Tanzania: Evidence of nocturnal acoustic behavior in wild chimpanzees. American Journal of Physical Anthropology, 166(3), 530– 540. https://doi.org/10.1002/ajpa.23609
- QGIS Development Team. (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from http:// ggis.org
- R Core Team. (2018). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org
- Rayment, W., Webster, T., Brough, T., Jowett, T., & Dawson, S. (2018). Seen or heard? A comparison of visual and acoustic autonomous monitoring methods for investigating temporal variation in occurrence of southern right whales. *Marine Biology*, 165(1), 12. https:// doi.org/10.1007/s00227-017-3264-0
- Rovero, F., Collett, L., Ricci, S., Martin, E., & Spitale, D. (2013). Distribution, occupancy, and habitat associations of the gray-faced sengi (*Rhynchocyon udzungwensis*) as revealed by camera traps. *Journal of Mammalogy*, 94(4), 792–800. https://doi.org/10.1644/12-mamm-a-235.1
- Rovero, F., Tobler, M., & Sanderson, J. (2010). Camera trapping for inventorying terrestrial vertebrates. In J. Eymann, J. Degreef, C. Hauser, J. C. Monje, Y. Samyn, & D. Vanden Spiegel (Eds.), Manual on field recording techniques and protocols for all taxa biodiversity inventories and monitoring (pp. 100–128). Brussels, Belgium: ABC Taxa.
- Rowcliffe, J. M., & Carbone, C. (2008). Surveys using camera traps: Are we looking to a brighter future? Animal Conservation, 11(3), 185–186. https://doi.org/10.1111/j.1469-1795.2008.00180.x
- Sakura, O. (1994). Factors affecting party size and composition of chimpanzees (Pan troglodytes verus) Bossou, Guinea. International Journal of Primatology, 15(2), 167–183. https://doi.org/10.1007/BF02735272
- Sethi, S. S., Ewers, R. M., Jones, N. S., Orme, C. D. L., & Picinali, L. (2018). Robust, real-time and autonomous monitoring of ecosystems with an

open, low-cost, networked device. *Methods in Ecology and Evolution*, 9(12), 2383–2387. https://doi.org/10.1111/2041-210X.13089

- Sobolewski, M. E., Brown, J. L., & Mitani, J. C. (2013). Female parity, male aggression, and the Challenge Hypothesis in wild chimpanzees. *Primates*, 54(1), 81–88. https://doi.org/10.1007/s10329-012-0332-4
- Spiesberger, J. L., & Fristrup, K. M. (1990). Passive localization of calling animals and sensing of their acoustic environment using acoustic tomography. *The American Naturalist*, 135(1), 107–153. https://doi. org/10.1086/285035
- Sugai, L. S. M., Silva, T. S. F., Ribeiro, J. W. Jr, & Llusia, D. (2019). Terrestrial passive acoustic monitoring: Review and perspectives. *BioScience*, 69(1), 5–11. https://doi.org/10.1093/biosci/biy147
- Tsutsumi, C., Ichikawa, K., Arai, N., Akamatsu, T., Shinke, T., Hara, T., & Adulyanukosol, K. (2006). Feeding behavior of wild dugongs monitored by a passive acoustical method. *The Journal of the Acoustical Society of America*, 120(3), 1356–1360. https://doi.org/10.1121/1.2221529
- Vu, T. T., & Tran, L. M. (2019). An application of autonomous recorders for gibbon monitoring. *International Journal of Primatology*, 2. https://doi. org/10.1007/s10764-018-0073-3

- Wallis, J. (1995). Seasonal influence on reproduction in chimpanzees of Gombe National Park. International Journal of Primatology, 16(3), 435–451. https://doi.org/10.1007/BF02735796
- Wich, S. A., & Koh, L. P. (2018). Conservation drones: Mapping and monitoring biodiversity. Oxford, UK: Oxford University Press.
- Wrege, P. H., Rowland, E. D., Keen, S., & Shiu, Y. (2017). Acoustic monitoring for conservation in tropical forests: Examples from forest elephants. *Methods in Ecology and Evolution*, 8(10), 1292–1301. https:// doi.org/10.1111/2041-210X.12730

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