Exploring the potential of occupancy modelling using passive acoustics in *Coua gigas* and *Coua coquereli*

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ABSTRACT

In highly threatened habitats such as the dry deciduous forests of western Madagascar, it is essential to develop new approaches to detect population changes and evaluate conservation measures. Passive acoustic monitoring (PAM) is such a promising approach. This method has many advantages over conventional methods, such as time efficiency, money savings, and reduced wildlife disturbance. It is especially suitable for studying occupancy and activity patterns of vocalizing species such as birds. Our study analyzed data recorded with autonomous sound recorders in 2018 in Kirindy Forest for the territorial calls of *Coua gigas* and *Coua coquereli*. We modeled occupancy and detection probability for both species in the study area. We also examined activity patterns and found that the peak of vocal activity for *Coua coquereli* is at 700h and for *Coua gigas* at 1100h. To also test the value of PAM in relation to ecological factors we modeled occupancy and included logging status as a site covariate. We detected a positive influence of logging in occupancy of *Coua gigas*. Our study provides guidelines for future occupancy studies using PAM in the two coua species. We conclude that PAM will improve the ecological monitoring of soniferous animals in Madagascar.

RÉSUMÉ

Dans les habitats très menacés tels que les forêts sèches à feuilles caduques de l'ouest de Madagascar, il est essentiel de développer de nouvelles approches pour détecter les changements de population et évaluer les mesures de conservation. La surveillance acoustique passive (PAM) est une approche prometteuse. Cette méthode présente de nombreux avantages par rapport aux méthodes conventionnelles, comme le gain de temps, l'économie d'argent et la réduction des perturbations de la faune. Elle est particulièrement adaptée à l'étude des modèles d'occupation et d'activité des espèces qui vocalisent telles que les oiseaux. Notre étude a analysé les données enregistrées avec des enregistreurs sonores autonomes en 2018 dans la forêt de Kirindy pour les vocalisations territoriales de *Coua gigas* et *Coua coquereli*. Nous avons modélisé l'occupation et la probabilité de détection des deux espèces dans la zone d'étude. Nous avons également examiné les schémas d'activité et constaté que le pic d'activité vocale de *Coua coquereli* se situe à 0700h et celui de *Coua gigas* à 1100h. Pour tester la valeur de la PAM par rapport aux facteurs écologiques, nous avons modélisé l'occupation et inclus le statut d'exploitation forestière en tant que covariable du site. Nous avons détecté une influence positive de l'exploitation forestière sur l'occupation de *Coua gigas*. Notre étude fournit des lignes directrices pour les futures études d'occupation utilisant la PAM pour les deux espèces de coua. Nous concluons que la PAM améliorera le suivi écologique des animaux sonifères à Madagascar.

INTRODUCTION

Due to ongoing declines in biodiversity, there is an increasing need for cost-effective and scalable ecological monitoring approaches (Gibb et al. 2018). Apart from addressing fundamental ecological questions, continuous monitoring of biodiversity and population dynamics in response to climate change and anthropogenic pressure is of fundamental importance in informing conservation planning and assessing the success of conservation measures (Honrado et al. 2016). However, finding a suitable wildlife monitoring approach can be challenging (Pollock et al. 2002). Traditional monitoring methods such as human observations and camera traps are well established in conservation studies (Beaudrot et al. 2019, Plumptre 2000, Besonne et al. 2020). Nevertheless, they also have disadvantages, mainly the high level of experience required and their high costs if conducted regularly (Zwerts et al. 2021). Vocal species, such as birds, are generally easier to detect by hearing than by seeing (Rosenthal and Ryan 2000).

Consequently, passive acoustic monitoring (PAM, Ross et al. 2023) with the usage of autonomous recorder units (ARU) is a
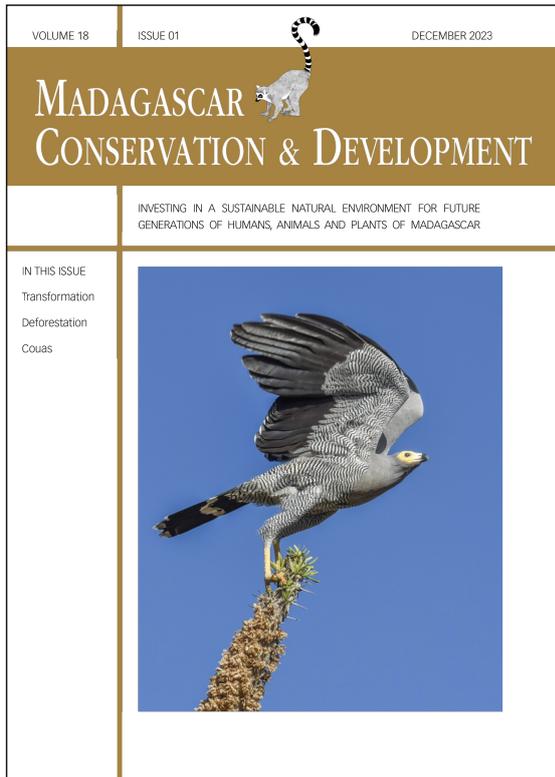
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rapidly growing method to study terrestrial wildlife (Darras et al. 2019). Several studies on bats (Revilla-Matrín et al. 2021), cetaceans (Todd et al. 2020), and primates (Kalan et al. 2015, Markolf et al. 2022) indicate the great potential of passive acoustic monitoring. In addition, many previous studies have demonstrated its effectiveness for bird monitoring (Celis-Murillo et al. 2012, Oppel et al. 2014, Priyadarshani et al. 2018, Pérez-Granados and Schuchmann 2021). It is particularly well suited to study the presence/absence of a species at a site and activity patterns (Mielke and Zuberbühler 2013), as it allows constant recordings over a long period (Sugai et al. 2019). The autonomous recording units can be installed or retrieved at any time, making the investigation more flexible and reducing the disturbance of the studied species by human activities (Zwerts et al. 2021). This allows for studying large areas simultaneously and reduces temporal differences between samples while keeping costs relatively low (Sugai et al. 2019). Therefore, PAM is suitable for investigating the presence of a vocalising species effectively and rapidly in an area and detecting changes in habitat use over time (Zwerts et al. 2021). It consequently provides a reliable method to assess human-induced impacts and the success of conservation measures (Astaras et al. 2020). However, as generating meaningful population estimates based on PAM data requires knowledge of acoustic activity which corresponds to some degree to the ecological activity of a species, preliminary studies of acoustic activity are needed to make ecologically meaningful statements about focal species (Wood and Peery 2022).

Occupancy models are an important approach to model habitat use as they explicitly account for imperfect detection (MacKenzie et al. 2002) to avoid underestimating species' occupancy at a site (MacKenzie et al. 2017). Additionally, they allow analyses of the relationship between occupancy/detection probability and potential model covariates, such as habitat characteristics or environmental conditions (MacKenzie and Bailey 2014). There are still few studies which combine both passive acoustic monitoring, and occupancy models to assess population status (Kalan et al. 2015), as validation of all acoustic recordings is time-consuming and automated species detection algorithms result in a high proportion of false-positive detections (Campos-Cerqueira and Aide 2016). One approach is to use automated species identification to reduce the size of the data set and then eliminate the false positive detections (Zwerts et al. 2021). Especially in biodiversity hotspots or highly threatened habitats, further development of this combined approach and preliminary studies are essential to protect existing populations and conduct biodiversity screenings (Campos-Cerqueira and Aide 2016). Consequently, to efficiently model habitat use and species distribution, incorporating passive acoustic monitoring data in occupancy models are increasingly important (Bailey et al. 2014).

Madagascar is considered one of the top world priorities for species and habitat conservation due to its high rate of endemic species, many of which are threatened due to continued habitat loss (Myers et al. 2000, Brooks et al. 2002, Ralimanana et al. 2022). Over 97% of dry deciduous forests in western Madagascar have been destroyed by human activities, predominantly by slash and burn agriculture, but also by logging (Harper et al. 2007, Waeber et al. 2015, Vieilledent et al. 2018). The areas remaining are often so fragmented that population sizes of nearly all species are declining (Langrand and Wilmé 1997, Ganzhorn et al. 2001, Ralimanana et al. 2022).

The dry deciduous forest in western Madagascar is home to several representatives of an endemic genus of cuckoos, the couas (Rajaonarivelo et al. 2020), including the two study species, Coquerel's coua (*Coua coquereli*) and the largest living member of the genus, the giant coua (*Coua gigas*) (Safford et al. 2020). They belong to the ground-dwelling couas and are mainly distributed in western Madagascar (Chiatante 2021). Previous studies have already addressed the increasing anthropogenic pressure on the microhabitat and behaviour of both birds (Chouteau 2004, 2007, 2009, Chouteau et al. 2004). These studies suggest that the species are sensitive to selective logging and forest loss due to fires.

In Kirindy Forest, their nesting extends from November to April (Chouteau and Pedrono 2009, Safford et al. 2020). Both species are described as apparently monogamous and males of both species are reported to offer food to females during the mating period (Safford et al. 2020, S.N. Razanamahenina pers. comm.). They vocalise intensively during mating period, but their songs are prominent year-round (Safford et al. 2020). The songs of the two species are similar, however the call of *Coua coquereli* is less rasping and higher pitched (Hawkins et al. 2015) and the song frequency of *Coua gigas* is decreasing, while that of *Coua coquereli* remains constant (Figure 1).

Although both species have been listed as least concerned by the International Union for Conservation Nature (IUCN 2016, 2018) some studies demonstrate they can face pressure from human actions to different degrees (Chouteau et al. 2004, Chouteau 2007, 2009). However, despite considerable forest loss around the study area in recent years, camera trap data indicate both species are abundant in Kirindy Forest/CNFEREF (unpublished data). In addition, both species may serve as biological indicators for dry forest conditions (Wilmé 1996) and should therefore occupy an important position in future protection considerations. Thus, understanding their habitat use and diel activity patterns is essential for future investigations and to define conservation priorities (Guisan and Thuiller 2005).

Previous studies of *Coua gigas* and *Coua coquereli* were mainly conducted by using the common method of human observation, such focal animal observations or transects (Chouteau et al. 2004, Chouteau 2007, 2009). These investigations help to understand the behaviour of both species and their ecological niches. Additionally, an efficient approach is needed to monitor population dynamics over several years to support the implementation of appropriate conservation measures. PAM in combination with occupancy modelling, could be such a promising approach.
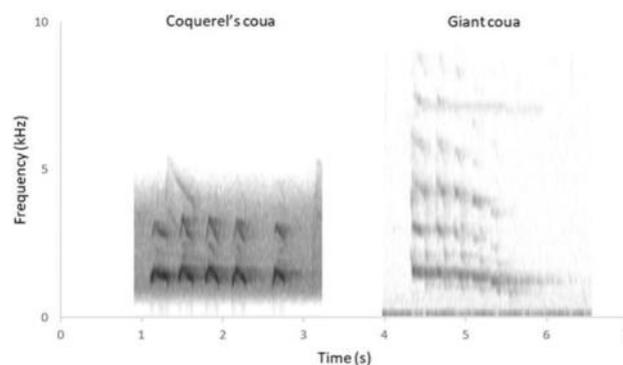
Figure 1. Sound frequency of *Coua coquereli* and *Coua gigas*. Both calls are in a similar frequency range, but while frequencies of *Coua gigas* are descending towards the end of the call, *Coua coquereli* remains at a constant frequency.

Hence, here we have evaluated acoustic data from Kirindy Forest for the presence of *Coua coquereli* and Coua giga calls and modelled occupancy (MacKenzie et al. 2002) for both species to explore whether the PAM approach is suitable for the ecological monitoring of the two species.

METHODOLOGY

STUDY SITE. The study site is located in the forestry concession of the Centre National de Formation et Recherche en Environment et Foresterie (CNFEREF), the Kirindy Forest, in west Madagascar. The site includes three grids with walking trail intersections every 25 m (CS5, CS7 and N5, Figure 2) used for naming the survey sites. Sites vary in their logging status. CS5 and the three most western sites in N5 were selectively logged for certain species (e.g., *Commiphora* spp.) between 1980 and 1990 (Ganzhorn 1995). CS7 is an unlogged forest. The forest in Kirindy is a dry deciduous forest characterised by alternating dry and rainy seasons. The hot wet season is between November and March/April and dry season extends from May to August, with some rain in October and November (Hawkins and Wilmé 1996). The average temperature varies between 20.0°C and 30.3°C and the Kirindy River crosses the study side from east to west.

DATA COLLECTION. We collected acoustic data in from 4 September until 10 October 2018 towards the end of the dry season. Data collection was not specifically aimed at the two coua species but to test the passive acoustic monitoring (PAM) method for monitoring vocally active species within dry forest, including lemurs (Markolf et al. 2022). We evaluated the data with respect to the two coua species. Through PAM with three autonomous recording units (ARU), acoustic data were collected in September and October 2018. The ARUs were placed at a distance of 150m from each other at a height of about 1.5m. An overview of the placement of the recorders is presented in Figure 2. Each ARU recorded for three consecutive days at three adjacent sites, and we then moved them to three new sites, covering nine sites at each grid (CS5, CS7, and N5). One of the ARUs failed during one

Figure 2. Placements of the ARUs in Kirindy Forest and naïve occupancy of both coua species. White circles represent areas without any detections of either of the two species.

recording (CS7-Q11), resulting in data from 26 sites on three consecutive days for each site. The sites were chosen to cover an area as large as possible and at the same time to avoid recording the same sound with more than one recorder. Given that no previous experiences for sound attenuation were available we choose a distance of 150m between ARUs. The ARU split recordings into 10-minute files, but for better processing, we split them into one-minute recordings before they were uploaded to the open-source platform RFCx Arbimon.

DATA PROCESSING. The RFCx Arbimon platform offers a template matching function (https://support.rfcx.org/article/99-what-is-pattern-matching-pm-in-arbimon) we used to identify the territorial song of both coua species in our data set. Template matching is a semi-automatic classification of sound patterns in which the software filters for matches with an example (template) in a data set based on a correlation score. In this case, the template is an image of the frequency spectrogram of couas' territorial song. Besides the template, a correlation score threshold must be chosen, above which the results are automatically defined as matches. The algorithm presents a correlation score for each match, which should indicate how well the result matches the template. To avoid false positives, it is necessary to validate the result visually or by listening to each match, ensuring that the final dataset contains only true positives.

For our occupancy analysis, we first created templates with the typical territorial calls of *Coua gigas* and *Coua coquereli*. We decided to focus only on the territorial song as it is unique for both species. Other calls, such as alarm calls, are highly similar across multiple coua species. Furthermore, we used the data of the early morning hours from 0700h to 1000h for our template matching, as preliminary results showed the highest activity during that time. Next, we created a test template matching analysis to optimise the parameters to be set (maximum matches per recording and per site, threshold). Based on our testing for the occupancy analysis, we then set matches per site as unlimited, set matches per recording to ten, and set the threshold at 0.2 to produce as few false negatives as possible while covering most calls. We repeated this process for both species at all 26 sites. For the analysis of activity patterns, we kept the settings as they were. However, we chose a reference data set of continuous recordings of 48 hours at five sites per species. We chose the sites based on the most verified matches in the occupancy analysis.

ANALYZING OCCUPANCY. For occupancy analysis, we defined survey units as 30-minute periods between 700h and 1000h. It was considered present if the focal species' call was identified at least once within that period. Therefore, we created a 1/0 matrix with 1 representing "present" and 0 representing "not present". We included site logging status as a site covariate for occupancy probability since focal species are presumably sensitive to deforestation.

We used the *Occu* function of the "unmarked" R-package (Fisk and Chandler 2011) to run occupancy models (MacKenzie et al. 2002). The model accounts for imperfect species detection in surveys to determine the probability of true presence or absence at a site (MacKenzie et al. 2002). Otherwise, the species distribution will be underestimated whenever the detection probability is <1. This is done by quantifying detection probability based on our data. For example, if the species is detected at 13 of 26 sites in t =

3 surveys, detection probability is calculated as $p = 1 - (1 - 0.5)^3 = 0.875$ (see MacKenzie et al. 2002 for details). We performed a single-season single species analysis for both species. Single-season assumes all data have been collected within one season, in contrast to multi-season occupancy models. We used the function "backTransform" to estimate true occupancy and detection. Secondly, we run another model, including logging status as a covariate. We tested for the significance of the covariate using a likelihood-ratio test against the null model (no covariate) (Dobson 2018). Model fit was evaluated using the MacKenzie and Bailey (2004) goodness-of-fit test. In the case of a significant impact of logging on occupancy probability, we used the predict function to represent occupancy probability for disturbed (logged) and undisturbed (unlogged) sites.

ESTIMATING FALSE NEGATIVES. To investigate whether a semi-automated species detection software offers an effective alternative to conventional monitoring, we examined whether false negatives created by the automatic detection process lead to deviating results. To get an estimation of the false negatives, we manually looked through the 30-minute recordings that did not confirm the presence of the species after the occupancy analysis. We searched for visual patterns of typical calls and listened to recordings we suspected to contain a call. We considered only those calls that could be detected by visual observation of the frequencies, as distant calls that are audible but not visible are outside the study area or detected by a proximate ARU. We compared the total number of calls per species during the occupancy analysis period and the number of calls not detected by the algorithm, the false negatives. We also estimated the time needed to review all records to evaluate the effort. Additionally, we did all occupancy analyses with a 1/0 matrix that included the false negatives to assess whether occupancy and detection probability changed.

ANALYZING VOCAL ACTIVITY PATTERN. To analyse the diel activity patterns of both coua species, we analysed continuous recordings of 48 hours at five sites per species. We used the "overlap" package to visualise the activity patterns (Meredith and Ridout 2014). It provides function to fit kernel density functions to data on temporal animal activity. The timestamp of each detected vocalization was used as input. We applied a Mises kernel fit for both species separately using the method "densityPlot" as this accounts for circular distributions like a diel circle. We also plotted both activity patterns together using the "overlapPlot" method to visualise activity overlap. The latter fits kernel density functions to two data sets and plots them, shading the area corresponding to the coefficient of overlap.

ANALYSING SURVEY EFFORT. We calculated the cumulative detection probability to recommend efficient sampling periods and durations for future investigations using passive acoustic monitoring. We calculated and plotted cumulative detection probability curves for our total sampling period for each species based on the detection probability of the null model. Cumulative detection probability was calculated using the formula:

$$\text{cumulative detection probability} = 1 - (1 - p_1)(1 - p_2)\ldots(1 - p_n)$$

where p is the detection probability of a survey (30-minute unit), and n is the total number of surveys. The curves show the probability of at least one detection in relation to the effort, quantified as the number of 30-minute surveys.

RESULTS

SINGLE SEASON OCCUPANCY MODELS. The overall occupancy probability of *Coua coquereli* in the study area was 0.59 (SD = 0.15) and the detection probability was 0.18 (SD = 0.04). The model, including logging status (binary, logging and no logging), was not a better fit (χ^2 (1) = 0.622, p = 0.430), indicating that our data do not support a significant effect of logging on the occupancy of *Coua coquereli*. We, therefore, tested the fit of the null model to the data using the goodness-of-fit test. The test resulted in a non-significant p-value of 0.636, indicating that the model provides an adequate fit to the data.

The overall occupancy probability of the single-season model for *Coua gigas* was 0.57 (SD = 0.14) and the detection probability was 0.21 (SD = 0.04) in the studied area. We also tested logging status as a site covariate for the occupancy of *Coua gigas* in a second occupancy model. The likelihood-ratio test indicated that there is a significant difference in occupancy between logged and unlogged sites (χ^2 (1) = 4.144, p < 0.05). We tested goodness-of-fit for this model, which produced a p-value of 0.335, indicating that the model fits the data well. Using the predict function, we plotted the occupancy probability for *Coua gigas* in logged and unlogged sites (Figure 3).

ANALYSIS OF FALSE NEGATIVES. Searching manually for false negatives per 30-minute survey in which pattern matching did not find any matches, took us 3 minutes. For *Coua coquereli*, there were 281 out of the 312 surveys without any matches. This results in an effort of ca. 14 hours. For *Coua gigas*, there were 272 out of 312 surveys without matches; thus, the search for false negatives took ca. 15 hours. This results in a total of ca. 28 hours. We found undetected calls for *Coua coquereli* in four survey intervals and for *Coua gigas* in one interval. Of the total 630 calls of *Coua coquereli* occurring in the considered period, 48 were not found by pattern matching. Thus, 7.6% of the calls were false negatives. For *Coua gigas*, only one of the 292 calls was not detected. This resulted in a rate of 0.3% false negative calls. The occupancy and detection probability for *Coua gigas* remained unchanged at
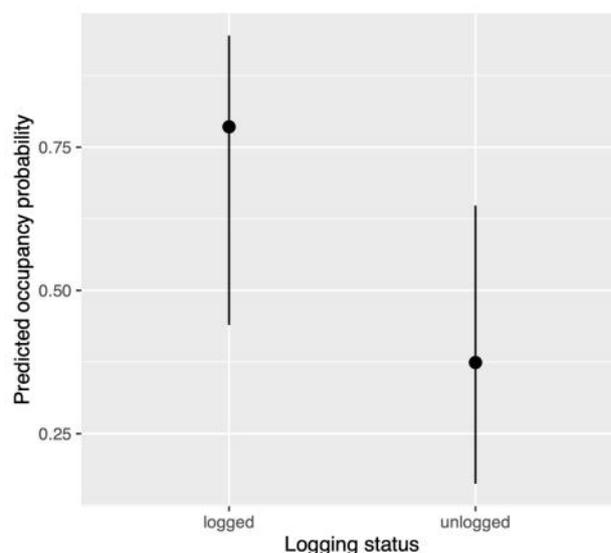
Figure 3. The predicted occupancy probability for *Coua gigas* at logged and unlogged sites. Logged sites are significantly more likely to be occupied by *Coua gigas*, indicating it might benefit from logging.

0.57 (SD = 0.14) and 0.21 (SD = 0.04), even in the occupancy model based on the data including false negatives. Additionally, we ran the occupancy model with logging as site covariate for *Coua gigas* including not detected calls (false negatives). The results were not different from the data excluding the false negatives.

In the analysis for *Coua coquereli*, the overall occupancy probability increased from 0.59 to 0.67 (SD = 0.15), and the detection probability remains unchanged at 0.18 (SD = 0.04).

VOCAL ACTIVITY PATTERN. To analyse the diel activity patterns of both coua species, we additionally analysed continuous recordings of 48 hours at five sites per species with known occurrence. The vocal activity pattern of *Coua coquereli* shows that this species is mostly vocally active from 0500h to 1300h (Figure 4). The highest activity is right after sunrise, around 0700h. It then drops sharply around 0800h and reaches a second peak around 0900h. It flattens again and ceases at 1300h. *Coua coquereli* thus vocalises mainly in the period between sunrise and noon.

Coua gigas' vocal activity starts around 0500h just before sunrise (Figure 4). It then rises until 0700h and flattens around 0800h. It then peaks clearly at 1100h and drops sharply in the following hour. Finally, it has a small rise around 1300h and is at zero from 1500h onwards. *Coua gigas* vocal activity is spread over the period between sunrise and afternoon.

Activity overlap of *Coua coquereli* and *Coua gigas*: Comparing the vocal activities of both species (Figure 4), it can be observed that both species start being vocally active simultaneously. However, *Coua gigas* is active longer, until about 1500h while *Coua coquereli* stops vocalising at 1300h. Activity around sunrise increases in both, but more in *Coua coquereli*. Both activities have a drop at about 800h and rise sharply again thereafter. The peak of *Coua coquereli*'s activity is at 700h, much earlier than that of *Coua gigas* at 1100h.

SURVEY EFFORT. The cumulative detection probability curve for *Coua coquereli* shows the cumulative probability of getting at least one detection as a function of the number of 30-minute surveys if the species is present at the site (Figure 5). After 7 surveys, the cumulative probability of at least one detection is 0.75. The probability of detections still increases and reaches 0.9 after 12 surveys.

The same cumulative detection probability curve was plotted for *Coua gigas* (Figure 6). The cumulative probability of at least one detection is 0.75 after half of the surveys, reaching a probability 0.95 after 12 surveys. Recording twelve 30-minute periods has a very high probability of vocally detecting a *Coua gigas* if it is present in the area.

DISCUSSION

Our study revealed that acoustic data collected within three consecutive days are sufficient to estimate occupancy of *Coua gigas* and *Coua coquereli*. Cumulative detection probability after three days with a total of 12 survey periods was above 0.9. Furthermore, we found both species to be vocally most active from sunrise to 1100h. Logging status had a significant effect on occupancy in *Coua gigas* but not in *Coua coquereli*. False negatives after semi-
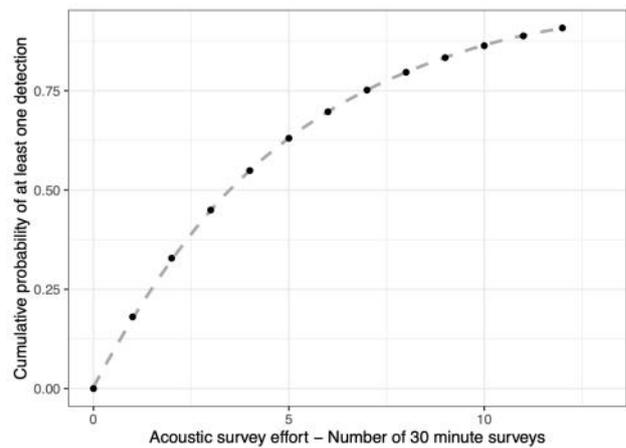
Figure 5. Cumulative detection probability curve for *Coua coquereli*. It shows the cumulative probability of at least one detection depending on the number of 30-minute surveys.
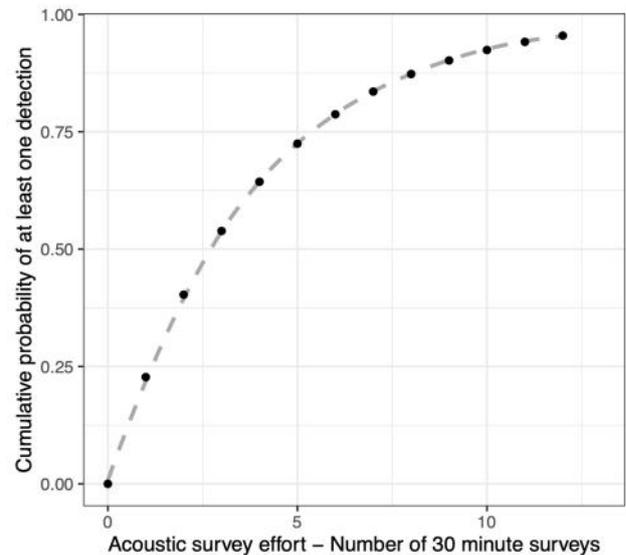
Figure 6. Cumulative detection probability curve for *Coua gigas*. It shows the cumulative probability of at least one detection depending on the number of 30-minute surveys.

Figure 4. Activity overlap of *Coua coquereli* and *Coua gigas*. The density curve for vocal activity of *Coua coquereli* (blue) increases more than that of *Coua gigas* (red). Both species start vocalising shortly before sunrise and stop vocal activity in the afternoon. Sunrise/sunset over the study period is shown in yellow. The gray-colored area shows the activity overlap.

automated analysis were low and had no influence on the result. In the following, we discuss strengths and limitations of our results.

PASSIVE ACOUSTIC MONITORING IS SUITABLE FOR OCCUPANCY STUDIES ON *COUA COQUERELI* AND *COUA GIGAS*. With our research, we demonstrated that passive acoustic monitoring is suitable for monitoring the occupancy of *Coua gigas* and *Coua coquereli* rapidly and effectively. We analysed data using semi-automated species detection software. To our knowledge, there are only few studies on passive acoustic monitoring in bird species in Madagascar. A thesis entitled "Passive Acoustic Monitoring in Ranomafana National Park" studied frugivorous bird species and concluded that the method is suitable for increasing the ecological knowledge of Malagasy bird species (Slingerland 2021). Our results confirm this, as we could model occupancy probability in the overall area using acoustic monitoring data. It is important to stress that the data were not collected to specifically study occupancy in the two coua species, however, they are still suitable for occupancy models. This is especially noteworthy since studies with explicit conservation intent are often planned and funded for certain endangered species (Campos-Cerqueira and Aide 2016). Data collection with passive acoustic monitoring provides an opportunity to examine data for multiple species without necessarily having to conduct data collection for each of those species. This aspect underlines the advantages of passive acoustic monitoring in terms of time-saving and cost-efficiency compared to conventional monitoring methods, which has been confirmed in previous studies (Darras et al. 2019). Occupancy trends and population dynamics of several species can be recorded simultaneously, which is particularly interesting for introducing or evaluating conservation measures. This aspect is especially important in habitats threatened by deforestation and degradation, such as most of the dry deciduous forests of Madagascar inhabiting numerous threatened species.

Previous studies dealing with the ecology of *Coua coquereli* and *Coua gigas* were mainly conducted by Philippe Chouteau. In his methods, he described problems in locating the two species, as they were easily stressed by the presence of the observing researchers (Chouteau 2006, 2009). Passive acoustic monitoring might not be suitable for studying foraging behaviour, but it is superior to studying the occupancy or activity of these two shy cuckoo species in the future.

Noticeably, the detection probability for the 30-minute units is rather small for both species. When compared with an occupancy model that combines all 30-minute intervals in one day and therefore uses 3-hour intervals, the detection probability for *Coua coquereli* is 0.667 (SD = 0.157) and for *Coua gigas* 0.783 (SD = 0.095). This is because the two coua species tend to sing for an enlarged period and are not vocalising for long periods in between. This produces many zeros in the detection matrix. With longer survey units, however, there is the additional problem that the standard error also becomes larger. Therefore, longer study periods of several days are necessary to generalise our findings. Furthermore, the activity pattern of *Coua gigas* shows that the vocal peak is only reached between 1100h and 1200h, which is beyond the time we chose for our study. The two peaks in *Coua coquereli*'s activity are within the period considered.

THE INFLUENCE OF LOGGING ON OCCUPANCY. Our study found no effect of logging on occupancy probability for *Coua coquereli*, but only for *Coua gigas*. Hawkins and Wilmé studied the influence of logging on the bird community in the Kirindy in 1996 (Hawkins and Wilmé 1996). They found that logged areas had significantly more individuals of *Coua coquereli* than unlogged habitats and suggested that the species benefits from increased insect availability associated with new vegetation growth. They also described in their study that vegetation in Kirindy Forest changes depending on the distance to the Kirindy River and that it is also highly dependent on season. In a 2004 study, Chouteau et al. confirmed the findings of Hawkins and Wilmé. They found that *Coua coquereli* is more present in logged areas, whereas the density of *Coua gigas* is greater in unlogged areas (Chouteau et al. 2004). This is contrary to our results. Many reasons can be responsible for this. The strong variation of vegetation in dry deciduous forests already described by Hawkins and Wilmé could be one reason. However, other environmental factors might also be considered. CS5 was logged in 1980 (Ganzhorn et al., 1990) and N5 was partially logged in 1990 (Ganzhorn, 1995). The studies by Hawkins and Wilmé and by Chouteau were conducted more than 19 years ago, and Kirindy Forest has undergone changes since then. It could potentially be that *Coua coquereli* profited primarily from early successional stages and therefore benefited from logging in temporal proximity to it. *Coua gigas* could be benefiting from later successional stages and, therefore more likely occupies logged sites currently. Another factor influencing the habitat use of the two species could be increased hunting pressure by a substantially increasing human population in the area, which is well-known to regularly hunt bird species (Favre 1996, unpublished data). It is certainly interesting that with our study, several studies have now demonstrated a potential benefit for coua species from selective logging. Variation in local occupancy could also be linked to food availability which itself could be linked to variation in forest structure as suggested by Hawkins and Wilmé (1996) who hypothesized *Coua coquereli* could benefit from logging due to increased insect availability in the leaf litter and understorey vegetation. Further studies in this direction are promising regarding ongoing habitat degradation and deforestation in Madagascar. Accordingly, passive acoustic monitoring would be well suited for this purpose.

Chouteau found in his 2006 study that there is seasonal variation in the foraging behaviour of the two coua species (Chouteau 2006). In future passive acoustic monitoring studies, it would be interesting to apply multi-season approaches to examine whether this variation also exists in activity and occupancy. In addition, future studies should examine further site covariates such as distance to Kirindy river or canopy cover. Since *Coua coquereli* and *Coua gigas* are ground-dwelling, vertical vegetation structure should also be considered, for example, by including data on the density of understorey vegetation. To gain further insight into anthropogenic influence, it would also be recommendable to include distance to roads or human settlements. Also, in their 2004 study, Chouteau et al. found that forest fires impact the abundance of both species (Chouteau et al. 2004). They conclude that covariates that differ in their level of disturbance are interesting from a conservational perspective. Unfortunately, with only 26 survey sites, we could not add more site covariates to the occupancy models.

FALSE NEGATIVES HAVE LITTLE EFFECT ON THE RESULTS. Our results show that the proportion of false negatives in the analysis of both species is widely divergent. This can have different reasons. In the analysis using pattern matching, the choice of template is crucial. Consequently, the differences could indicate that we could have chosen a suboptimal template for *Coua coquereli*. More comprehensive preliminary tests with different templates should be performed in further analyses using pattern matching. It should be ensured that the template was also recorded with the same devices as the examined data set. In addition, further sound analyses are needed for the two species. The calls we identified as false negatives were low in volume and could only be heard at 30 times amplification. They were far away, and failed recognition was most likely based on low signal intensity. Further studies on the sound pressure level of the two species would be useful to cover the complete study area and thus to choose the radius around the ARU appropriately. Our evaluation revealed only increased occupancy probability for Coua couquereli when false negatives are considered. This indicates that the occupancy probability is underestimated based on the pattern-matching results. However, the time cost is very high and is contrary to the time efficiency that passive acoustic monitoring offers. In addition, there is no altered result about the influence of logging on *Coua gigas*. We believe, that for the calls used in our study, the effort is not commensurate with the benefit and that reducing false positives through extensive preliminary analyses is more helpful than additional manual verification.

RECOMMENDATIONS FOR FURTHER STUDIES USING PASSIVE ACOUSTIC MONITORING. Above all, we recommend increasing the number of sites to be able to include more ecological covariates. Second, given that our survey-based detection probability was relatively low, further studies based on PAM should therefore consider that the two coua species usually vocalise for a few minutes at a time and then stop for a longer period. Cumulative detection probability for both species was above 0.9 after 12 surveys, translating roughly to recording three consecutive morning periods. These findings are important in order to prevent an unnecessary number of surveys in the future and thus to make acoustic surveys more effective. An approach to calculate the number of monitoring days required for a reliable result can be found in previous studies on PAM in birds (Pérez-Granados et al. 2018) and we recommend to choose intervals longer than 30 minutes and to monitor at least one or two days longer per site. Based on our analysis of activity patterns, we recommend the period between 0600h and 1000h for *Coua coquereli* and between 0800h and 1200h for *Coua gigas*. The visualisation of activity overlap reveals that the time to monitor both species with one single ARU is between 0600h and 1100h.

The vocal activity of *Coua coquereli* drops sharply between the two peaks. During the same time, the activity of *Coua gigas* also decreases, but proportionally less. More comprehensive multi-species occupancy models are essential for understanding this drop. It can be assumed that this decrease in activity is due to interaction with other species not surveyed here. Passive acoustic monitoring would also be an appropriate method for examining influences from multiple species on occupancy, as previous studies have shown that it is suitable for modeling the entire biodiversity (Chalmers et al. 2021). Another reason for the sharp decline in song activity could be that calls of other species dominated that

of the two coua species during this period resulting in a biased outcome. It is therefore important not only to improve data collection via passive acoustic monitoring, but also to improve automatic species detection software. There are studies addressing this problem (Bardeli et al. 2010, Stowell et al. 2019) and for future studies, it is important that high detection rates can be achieved using automatic detection software. This will not only allow faster evaluation of protection measures but also more reliable ecological and behavioural studies can be planned with passive acoustic monitoring.

In addition, to facilitate not only future studies of *Coua coquereli* and *Coua gigas*, but occupancy analyses of birds in general using passive acoustic monitoring instead of classical observations, a comparison of both methods is needed. We cannot conclude whether both approaches provide similar results based on our data. However, previous studies show that appropriately applied autonomous recorder units and a standardised methodology for monitoring via acoustic provide equally precise results (Darras et al. 2018).

Our study benefited from the advantages provided by passive acoustic monitoring. We were able to analyze data for *Coua coquereli* and *Coua gigas* without additional data collection which saved a remarkable amount of time and money which is one of the biggest advantages of passive acoustic monitoring. By collecting acoustic data, the entire vocalising fauna was stored in the long term, creating a bioacoustic time capsule (Sugai and Lluisa 2019) for the dry forest of Kirindy, which could potentially be reevaluated using improved automatic algorithms in the future.

CONCLUSION

Our study showed that a few consecutive days of passive acoustic monitoring provide sufficient data to model occupancy of *Coua gigas* and *Coua coquereli*. Furthermore, our data, although limited to a few weeks in September and October, suggest that acoustic activity of the two bird species is most prominent in the morning hours from sunrise until 1100h. Our research can serve as guideline for designing future passive acoustic monitoring studies to learn more about the ecology of couas, but also about other species of birds in Madagascar.

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