Integrating ecoacoustic monitoring with machine learning to survey black-and-white ruffed lemurs (*Varecia variegata*) in Madagascar's Corridor Forestier d'Ambositra Vondrozo (COFAV)

Running title: Ruffed lemur distribution in the COFAV using ecoacoustic monitoring

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Abstract

Black-and-white ruffed lemurs (*Varecia variegata*) are a Critically Endangered species limited to the fragmented eastern Malagasy rainforests. The importance of their conservation is underscored by their vital seed dispersal and pollinator niches; they are a keystone species and indicator of forest health. Little is known of their distribution in the Corridor Forestier d'Ambositra Vondrozo (COFAV), an important rainforest corridor connecting multiple protected areas. Because of their fragmented and dispersed distribution, we used passive acoustic monitoring to survey ruffed lemurs throughout the COFAV. We deployed autonomous recorders at 30 sites across the COFAV from December 2021 to June 2022. We then implemented a machine learning pipeline by compiling an annotated training data subset of ruffed lemur call presence and absence clips and then training a convolutional neural network to automatically detect these calls in the full dataset (550,000 recording minutes). After validating top model predictions, we used acoustic detections and non-detections with geospatial variables in spatial occupancy models to assess ruffed lemur occurrence across the COFAV. Ruffed lemurs were only detected at 10 of 30 sites, all of which were in the northern COFAV. There appears to be an abrupt delineation in their distribution around a band of deforested land near the middle of the corridor, which may be preventing their southward dispersal. We found that ruffed lemur occupancy was positively influenced by the Normalized Difference Vegetation Index (NDVI), a proxy for vegetation health. This study demonstrates the power of combining different conservation technologies to generate meaningful ecological and conservation insights, and can be generalized to other species.

Keywords

Varecia, ecoacoustics, deep learning, conservation, biodiversity monitoring

Introduction

Lemurs are the most endangered mammalian taxon worldwide, with over 90% of the approximately 120 species threatened with extinction (IUCN RedList; Rakotomanana et al. 2013; Schwitzer et al. 2014). This is in large part due to the rapidly increasing deforestation of Madagascar's forests over the past decades (Vieilledent et al. 2018). In the face of this habitat degradation, up-to-date information about lemur distributions remains scarce. Scalable and efficient monitoring is essential for tracking patterns in lemur populations and informing conservation initiatives. National parks provide critical habitat refugia for lemurs, and as such, most lemur research occurs in such strict protected areas, leaving a gap in our understanding of species' ecology and distribution in habitats outside of national parks (Irwin et al., 2005; Mittermeier et al., 2010; Herrera 2017). Surveys in unprotected areas are therefore vital to gathering up-to-date data on lemur species' distributions and conservation status throughout their known range (Irwin et al., 2005; Raberivony et al., 2015). This is particularly important in the context of ongoing climate change and subsequent range shifts of many species. Protected areas are fixed in landscapes, but as species shift distributions as a result of climate change, it will be important to understand whether the habitat around existing protected areas can support this.

Ruffed lemurs (Genus *Varecia*) are Critically Endangered and limited to fragments of the once-continuous eastern Malagasy rainforests (Louis et al 2020). The conservation of the two ruffed lemur species (*Varecia variegata* and *V. rubra*) is particularly important given their vital seed disperser and pollinator roles; some fruiting trees rely entirely on ruffed lemurs as their sole dispersers (Dew & Wright 1998; Moses & Semple 2011; Wright et al. 2011; Federman et al. 2016). Ruffed lemurs also require pristine rainforest habitat due to their highly-frugivorous, narrow diet (Beeby et al. 2021) and unique reproductive system (e.g., parked litters of infants; Baden et al. 2013; Vasey et al. 2018; Baden 2019). Ruffed lemurs have been found to forego breeding for up to four or more years in disturbed forests (Ratsimbazafy 2003) and are particularly sensitive to fragmentation (Balko 1998; Dehgan 2003). These lemurs are therefore both good indicators taxon for forest health and integral to maintaining forest regeneration (Vasey et al. 2022).

Black-and-white ruffed lemurs (*V. variegata*) are patchily distributed throughout their remaining rainforest range, including a mosaic of forest fragments that make it difficult to simultaneously monitor geographically different populations (Irwin et al. 2005; Louis et al. 2020). An area of the black-and-white ruffed lemur (hereafter 'ruffed lemurs' for concision) range that is under particular threat from anthropogenic pressures is the precariously narrow Corridor Forestier d'Ambositra Vondrozo (COFAV) forest corridor in southeastern Madagascar. The COFAV, protected as a level IV IUCN designation for sustainable extraction (Conservation International, 2014; Gardner et al., 2018; Goodman et al., 2018), connects Ranomafana and Andringitra National Parks and is considered essential for animal populations' genetic diversity, dispersal and long-term sustainability in the region (Goodman et al 2001; Irwin et al 2005; Ramiadantsoa et al 2015; Batist et al. 2023; Mancini et al. 2023). While there have been repeated lemur survey efforts in Ranomafana and Andringitra National Parks (Sterling & Ramaroson 1996; Rasoloarison & Rasolonandrasana 1999; Goodman & Rasolonandrasana 2001; Wright et al. 2012; Herrera 2016), monitoring in the corridor has been extremely limited. Consequently, the distribution of ruffed lemurs and many other endangered animal species throughout this large tract of forest is unclear (see Table 1 for an overview of previous studies). It has been decades since the last multi-species, cross-COFAV surveys were carried out (Goodman et al. 2001; Irwin et al. 2005), and most subsequent studies have been small-scale (Deppe et al. 2007; Rakotonirina et al 2013), focused primarily on other lemur species (Rakotondravony et al. 2004; Delmore et al. 2009), or opportunistic in nature (Batist et al. 2023).

For this reason, there have not been systematic, population-wide censuses of ruffed lemurs; however, emerging conservation technologies allow us to more feasibly undertake such ambitious, yet essential surveys. Passive acoustic monitoring (PAM) is an increasingly popular data collection method in which autonomous audio recorders are deployed across a study area

(Blumstein et al 2011; Gibb et al. 2018) to detect and sample biophony (animal calls), anthropophony (human voices, machinery, etc.) and geophony (rivers, wind, etc.) at large spatial and temporal scales (Sugai et al 2018; Gibb et al 2018). Species-specific call detections can then be used to model the presence, abundance, and range of animal populations. By using autonomous sensors, PAM only requires field personnel during initial deployment and eventual recovery of devices (plus maintenance trips as needed), thereby minimizing disturbance, manual effort, and cost. PAM is a particularly powerful tool because it is able to record different species simultaneously, and yield long-term audio datasets that can be repeatedly analyzed for different purposes (Blumstein et al 2011; Gibb et al 2018; Piel et al. 2021). Studies have shown that PAM can detect animals up to 10x more frequently than camera-trapping due to the 360° nature of microphones and wider detection area (Enari et al 2019; Crunchant et al 2020). Further, PAM has been shown to be just as, if not more efficient than traditional sampling methods, such as transects or in-person observations (Castro et al. 2019; Melo et al. 2021; Hoefer et al. 2023; Batist et al. 2024). PAM is particularly useful in the dense, montane forest habitats of the COFAV because it enables animal detection in areas with limited visibility and arduous topography (Thompson et al 2010; Kalan et al 2015). Moreover, ruffed lemurs emit distinct roar-shriek choruses that make them an ideal species for PAM (Pereira et al 1988; Batist et al 2021).

PAM has been further transformed by the “big data” revolution, artificial intelligence, and the development of highly efficient and potent machine learning (ML) models (Ruff et al. 2021; Dufourq et al. 2022; Stowell 2022; Cauzinille et al. 2024). In these models, a computer “trains” itself by extracting salient features from a set of example recordings (here, spectrograms) and then classifies segments from other test recordings based on their similarity to those features (Stowell 2022). This innovative automated approach eliminates much of the labor-intensive manual processing that has historically been a prohibitive time constraint (Ruff et al. 2021; Stowell 2022). Machine learning models trained to detect species-specific calls can then be used to generate the detection/non-detection matrices required for occupancy models (Campos-

Cerqueira & Aide 2016). Occupancy modeling is a powerful statistical framework used to estimate the probability of a species occurrence in a given area based on diverse environmental covariates (Mackenzie et al. 2002; Bailey et al. 2014; Mackenzie et al., 2017). A suite of occupancy models have been optimized for data from fixed acoustic sensors such that detections from PAM can yield robust ecological, behavioral, and biogeographic insights (Kalan et al. 2015; Campos-Cerqueira & Aide 2016; Hagens et al. 2018; Milchram et al 2020). These models are especially useful with sparse datasets such as those ones yielded by autonomous sensors, as they are able to account for imperfect detection and handle missing data (Mackenzie et al. 2002; Mackenzie et al. 2017).

Despite growing interest in applying integrated PAM and ML pipelines in primatology (Cauzinille et al. 2024), there have been comparatively few studies which have done so with lemurs (but see Markolf et al. 2023; Ravaglia et al. 2023; Batist et al. 2024). By leveraging and integrating the strengths of PAM, ML and occupancy modeling, the goal of this study was to fill critical knowledge gaps on ruffed lemur distribution and habitat use in the COFAV. There has been extensive research in the national parks within the COFAV, but there is a huge dearth of information from the corridors that connect these protected areas. We aimed to assess the current distribution of black-and-white ruffed lemurs in the COFAV of southeastern Madagascar (Figure 1), including identifying the species' southernmost extent. Within this goal, we had three objectives: (1) deploy acoustic recorders at geographically representative sites across the COFAV; (2) use a machine learning model to determine ruffed lemur presence/absence at each site; and (3) assess ruffed lemur occurrence and its relationship with environmental factors in the corridor. In doing this, we aimed to create an integrated PAM-ML-occupancy modeling framework that could also be generalized to other taxa and regions. This information will allow us to identify areas of concern and areas to prioritize within the corridor, so that resources and conservation efforts can be allocated in the most effective ways possible (e.g., increased protection, more patrolling, more funding, etc.). This will be one of the first studies to use PAM with lemurs, will increase the spatial and temporal scope of monitoring efforts in southeast Madagascar, and will make available soundscapes from which additional animal taxa can be assessed. Moreover, although focused on a single lemur species here, the acoustic data generated from this study can be used for other vocal species as well; such is one of the great benefits of permanent monitoring methods such as PAM.

Methods

Ethical Statement

This study was approved by Madagascar National Parks and the Malagasy Directorate of Protected Areas and Ecosystems (permit # - 379/21/MEDD/SG/DGGE/DAPRNE/SCBE.Re and 069/22/MEDD/SG/DGGE/DAPRNE/SCBE.Re). The project was approved by the Institutional Animal Care and Use Committees (IACUC) of Hunter College (#AB-10/22). The research herein adheres to the *American Society of Primatologists*' Principles for the Ethical Treatment of Primates.

Data Collection

The COFAV is a sub-humid forest corridor (200-1900 m elevation) in southeastern Madagascar that is designated as a level IV management area for sustainable extraction (Conservation International, 2014; Gardner et al., 2018; Goodman et al., 2018). Temperatures and rainfall peak in January-February; rainfall drops to its lowest around October while temperatures are at their lowest around June-July. The COFAV runs from Ambositra in the north to Vondrozo in the south ~300 km). It is a narrow corridor, ranging from 2-50 km in width, although the majority of the corridor is <10 km wide (Conservation International, 2016; Goodman et al., 2001). The COFAV connects with the Fandriana-Marolambo corridor to the north and Midongy-Sud National Park in the south, part of a network of corridors that provide vital linkage among many protected areas within the eastern Malagasy forests (Irwin et al., 2000). Forest fragmentation in the COFAV is escalating rapidly as a result of *tavy* (slash-and-burn agriculture), illegal mining, and logging (Goodman et al., 2001; Deppe et al., 2007; Ramiadantsoa et al., 2015).

We deployed passive acoustic recorders at 31 geographically representative sites in the COFAV from November 2021-May 2022 (distance between northernmost and southernmost sites was ~227km; Figure 1). We were unable to recover one device due to a cyclone-induced landslide at the deployment site (Namahoaka), and thus present data from 30 sites (Table 2). We used two types of autonomous recording units (ARUs): 8 Swifts and 26 Audiomoths. We used Energizer Ultimate Lithium AA batteries in the Audiomoths and Energizer Max D batteries in the Swifts. We used SanDisk ExtremePro SD cards in both devices. ARUs continuously recorded sound within the 1-20 kHz range from 5am to 8pm daily (15 hours/per day), parameters that were derived from an earlier pilot study (Batist et al. 2024). ARUs had a sample rate of 48kHz, a gain of 36dB (Swifts) and 30dB (Audiomoths), and recorded in 16-bit mono format. Full parameters are listed in Table S1.

To the best of our ability (given logistical constraints), we deployed recorders at distances of ~3-6km apart to avoid pseudo-replication while also optimizing spatial coverage. This distance was chosen based on existing data on ruffed lemur home range size, spatial ecology, and vocal behavior (Baden et al. 2016; Baden et al. 2020; Batist et al. 2022). Previous research has demonstrated that ruffed lemur roar-shrieks can be detected by ARUs up to (and potentially beyond) distances of 400m (Batist et al. 2024).

General deployment areas in the corridor were chosen *a priori*, though exact locations within each area were determined largely by feasibility and logistical constraints (e.g., impassable rivers, rock cliffs, security concerns). We tried to deploy devices along ridgelines as much as possible to maximize their detection radius. We placed recorders away from trails (at least 100m) for device security and to minimize human voice “bycatch.” Each recorder was placed as high in a tree as was safely possible without climbing it (~2-3m), microphone oriented sidewise, and secured with cable locks. Local guides selected the exact tree for deployment based on their determination of its health and strength. We used cable locks to attach the recorders to the tree trunk.

The recorders collected a total of 9,507 hours of audio; given that we were recording 15 hours per day, this equates to approximately 634 sampling days (Table 2). The mean number of hours (and standard deviation) recorded per Audiomoth was 200.36 ± 38.67 (range: 108.8 - 241.5 hrs) and per Swifts was 618.94 ± 128.31 (range: 462.8 - 778.3 hrs). This corresponds to ~13 recording days per Audiomoth and ~41 recording days per Swift.

Data Analysis – Training dataset development

CHB manually reviewed 10-15 hours of recordings from each site (proportional to the total number of recordings) to use as the training dataset for an acoustic species identification model. This subsampling strategy maximizes the spatial variation within the dataset, exposing the model to examples of potentially site-specific background noise. To increase temporal representation, we used 3-4 hours of files per day across 3 distant days (typically the second day, midpoint-day, and second-to-last day). We also ensured that all surveyed hours of the day were represented and varied across days and sites (e.g., 9:00-12:00 on day 1, 12:00-3:00pm on day 2, etc.). The final training dataset contained 407 hours total (300 from Audiomoths, 107 from Swifts), corresponding to ~4% of the overall dataset.

Call files in the training dataset were digitized into spectrograms and annotated using RavenPro (Cornell University K. Lisa Yang Center) and Arbimon (Rainforest Connection). In Raven, we drew bounding boxes around ruffed lemur roar-shriek calls within a recording and marked these as present (Figure S1). We also used Arbimon's Pattern Matching tool to generate additional presence and absence clips. This tool uses a cross-correlation algorithm that compares audio recordings to a species-specific call template and returns potential matches that are above a user-defined correlation threshold (Figure S2). These clips can then be marked as presence or absence, and become examples of true positives and true negatives in the CNN training dataset.

Finally, to generate more absence training data, we ran "negative" pattern matching, which uses a similar cross-correlation algorithm to find examples of audio clips that are not similar to the call template.

From each presence and absence detection, we extracted spectrogram images representing two seconds of audio time-centered on the detection and spanning 24 kHz (LeBien et al. 2020). We then converted these into mel-frequency using a Hann window of 1024-samples, with 50% segment overlap, and 2048 FFT coefficients per segment (LeBien et al. 2020; *librosa* package-McFee et al., 2015). These presence and absence segments comprised our binary classification dataset. We randomly split these labeled audio files into training (70%) and validation (30%) datasets.

Data Analysis – CNN model training and deployment

We implemented a convolutional neural network (CNN) pipeline, a commonly-used deep learning model that has shown promise with acoustic monitoring data (Stowell 2022; Dufourq et al. 2022; Batist et al. 2024). A CNN uses inputs (training data; here, spectrograms) that are passed through a series of interconnected mathematical-processing layers and condensed into a vector of numerical features that classify the inputs (i.e., lemur call vs none). More details on how CNNs are used for bioacoustic classification tasks can be found in Dufourq et al. (2022) and Batist et al. (2024).

We followed the methodology outlined in Lebien et al. (2020) to develop and implement our CNN model. We implemented the CNN using Keras API in the TensorFlow Python library (Abadi 2016; Gulli & Pal 2017). We used a MobileNetV2 model, pre-trained on the ImageNet dataset, which contains over one million photo images across 1000 classes (Deng et al., 2009). We included only the feature extraction layers of this MobileNetV2, and replaced the ImageNet classification layer by a new layer containing a single node representing the target species (outlined fully in Lebien et al. 2020). We first froze the convolution layers and trained for 15 epochs using a learning rate of 1×10^{-3} . We then unfroze the convolutional layers and trained for an additional 15 epochs using a learning rate of 1×10^{-5}. We used an early stopping strategy where training automatically stops if the monitoring metrics did not improve for 5 consecutive epochs to avoid overfitting. The model parameters were iteratively tuned based on the aforementioned evaluation metrics.

Prediction was performed using a sliding window approach such that predictions were made for every 2-s time-window of each audio recording with no overlap between consecutive frames. To evaluate model performance, we used a suite of standard metrics including false positive rate, recall (how many of the total annotated roar-shrieks did the model find, i.e., sensitivity), accuracy and AUC (area under the curve; Table 3). A confidence level threshold of ≥0.5 was used to infer presence during the model evaluation. There is an inherent trade-off between recall and precision, and we specifically developed the model to optimize recall (at the expense of precision), as the cost of potentially missing a lemur call is high compared to having more false positives. Even if the CNN initially produced a considerable number of false positives, we manually confirmed all positive detections so that occupancy modeling results would be accurate. The final model had low precision due to the imbalanced test dataset, which contained a disproportionately larger number of true negatives compared to true positives. While precision is conventionally reported, it may not be an appropriate performance metric for such imbalanced settings.

After we developed a CNN with sufficient evaluation metric scores (Table 3), we deployed the CNN over the remaining (un-annotated) audio dataset. We then manually validated the top

10 highest-ranked positive (lemur call) model predictions per site and per day. This was done in Arbimon's validation interface (similar to the Pattern Matching page; Figure S2), using filters that ranked the model's prediction score (the model confidence that it was a true positive) by site and day. Because occupancy models only require one presence per day, per site, to count the site 'occupied', it was not necessary to manually check all model predictions. We thus used the top-10 detections per site per day, given the chance that there was a lemur call outside the top 10 highest-ranked detection scores was low.

Data Analysis – Environmental covariates

We used a variety of open-access geospatial layers to assess how different environmental variables (and proxies for them) influence ruffed lemur occupancy. Initially, we evaluated six covariates for inclusion in our occupancy models: i) elevation, ii) forest height, iii) forest cover loss, iv) forest extent, v) normalized difference vegetation index (NDVI), and vi) Impact Observatory's 9-class Land Use and Land Cover imagery.

Elevation (i) data came from the Terra Advanced Spaceborne Thermal Emission and Reflection Radiometer's Global Digital Elevation Model (Version 3), which provides a global digital elevation model at a spatial resolution of 1 arc second (~30m). Forest height (ii) came from the Global Land Analysis and Discover (GLAD) team at the University of Maryland, which integrates NASA's Global Ecosystem Dynamics Investigation lidar forest structure measurements and Landsat analysis-ready data time-series (Potapov et al. 2021). Imagery is from 2020 and at 30m resolution; pixel values are height in meters. Forest cover loss (iii) was developed by the GLAD team via time-series analysis of Landsat images from 2000 through 2022, with 30m resolution (Hansen et al. 2013; Potapov et al. 2022; with version 1.1 update as in https://glad.earthengine.app/view/global-forest-change). Forest cover loss was defined as a change in a pixel from a forest to non-forest state, and encoded as 0 (no loss) or a value from 1-

20 indicating the year of change. Forest extent (iv), also developed by the GLAD team, was derived by attributing pixels with ≥5m forest height in 2020 as 'forest' (as defined by the FAO's FRA).

NDVI (v) was calculated directly from a composite PlanetScope Ortho Scene, which is an 8-band, surface reflectance PlanetScope Scene at 3m resolution. PlanetScope Ortho Scenes are orthorectified and processed to remove distortions caused by terrain. They are radiometrically-, sensor-, and geometrically-corrected products projected to a cartographic map projection. The geometric correction uses fine Digital Elevation Models with a post spacing of 30-90 meters. The composite was derived from daily PSScenes taken from March-May 2022, compiled together to achieve a cloud-free, haze-free composite. The resulting GeoTIFF composite file was resampled at 3 meters and projected into the UTM projection using the WGS84 Datum. Complete information about the corrections and processing can be found in Planet's Product Specification. This image file and associated bands were read into R using the *raster* package (Hijmans et al. 2015), and used to calculate vegetation indices. NDVI was calculated using the formula (NIR – R) / (NIR + R), where NIR is the near-infrared band and R is the red band.

Finally, we used the 2022 Land Use & Land Cover map from Impact Observatory (vi). This is a 9-class layer developed at 10m resolution for the year 2022. The layer is derived from Sentinel-2 10-meter satellite imagery using an AI model to classify land use types.

Of the six layers initially assessed, we excluded two layers from further analysis due to low variation across sites (all sites had the same value except for <5 sites): forest extent and the 9-class Land Use & Land Cover layer.

Because correlated covariates can lead to unreliable model estimates when included in the same model, we assessed pairwise correlations of all environmental variables. All of the habitat covariates had a correlation coefficient <0.6 except for forest cover loss and forest height;

we chose to use forest cover loss in the models as it is showed greater variation between sites. Therefore, we used three environmental covariates in occupancy models: elevation, forest cover loss, and NDVI (Figures S3, S4, and S5 respectively). We normalized all continuous explanatory covariates to have a mean of 0 and a standard deviation of 1.

To incorporate our three selected environmental variables into our model, we used QGIS (v3.30) to create a 400-meter radius buffer around each site (50.27ha total area). We then calculated the mean value of each of the aforementioned spatial variables within the buffer area using the Zonal Statistics tool in QGIS. This tool averages each pixel value for that variable within the buffer area. The buffer distance was chosen as a result of previous knowledge on ruffed lemur home range size, roar-shriek detection distance, and the topography of the area. This buffer area allowed us to capture the site-specific micro-environment to better understand how environmental variables influence species detection and occurrence. The area-averaged values per site were compiled into a matrix along with each site's GPS coordinates.

Data Analysis – Occupancy models

Occupancy modeling is a powerful statistical framework used to estimate the probability of a species occurrence in a given area based on diverse environmental covariates (Mackenzie et al. 2002; Bailey et al. 2014; Mackenzie et al., 2017). There are a suite of occupancy models capable of intaking data from fixed acoustic sensors such that detections from PAM can yield robust ecological, behavioral, and biogeographic insights (Kalan et al. 2015; Campos-Cerqueira & Aide 2016; Hagens et al. 2018; Milchram et al 2020). These models are especially useful with sparse datasets such as those yielded by autonomous sensors, as they are able to account for imperfect detection and handle missing data (Mackenzie et al. 2002; Mackenzie et al. 2017). Occupancy models estimate both occupancy and detection probability. The former refers to the probability of a species being present at a given site (0=absent, 1=present), whereas the latter refers to the probability of detecting a species at a site, given that it is occupied. We used a

Bayesian spatial occupancy model (*spOccupancy* R package), which allows for incorporation of random effects to account for spatial autocorrelation (i.e., the dependency/similarity between neighboring sites; Doser et al. 2022a). We used day as the re-sampling period for each site and generated a detection/non-detection matrix (rows=sites, columns=days) where 1 indicated detection and 0 non-detection of ruffed lemur calls.

In the *spOccupancy* package, the *PGOcc* function fits single-species occupancy models using Markov Chain Monte Carlo (MCMC) and Pólya-Gamma data augmentation (Polson et al 2013; Doser et al. 2022b). Spatial models are fit using the *spPGOcc* function and with Gaussian processes. We first ran a series of non-spatial candidate models to determine which covariates were included in the top models for detection and occupancy probability. The effects of covariates on the occupancy and detection probabilities were modeled on the logit scale. We applied a sequential approach to identify the top-ranked (most parsimonious) candidate model for both the detection and occupancy components (Ribeiro et al. 2022). We first held the occupancy probability constant and fit 9 a priori candidate models for detection probability (Table 4). Then, we held the top-ranked detection model constant and fit 8 candidate models for the occupancy probability (Table 4). We used the covariates from the top-ranked candidate models for detection and occupancy in the final occupancy model. Finally, we compared this full non-spatial model with a model that contained the same detection and occupancy functions but also included a random effect for spatial autocorrelation. Even though the sampling sites were far enough apart to be considered statistically independent, accounting for spatial autocorrelation in occupancy models can improve species prediction and distribution maps (Johnson et al. 2013; Doser et al. 2022a; Ribeiro et al. 2022; Roberts et al. 2023).

We obtained samples from the posterior distribution by running 3 chains, each for 2,500,000 iterations, with a burn-in period of 2,475,000 iterations and thinning by 25. This process resulted in >1,000 posterior samples for each Markov chain. For the spatial model, we used the Nearest Neighbor Gaussian Process with 5 neighbors (other settings set to defaults per Doser et al. 2022a). We checked chains' convergence of models through the effective sample size (n_eff), R-hat value (values <1.1 indicate good convergence; Gelman & Rubin 1992) and by visually inspecting trace plots (Doser et al. 2022b; Ribeiro et al. 2022). We compared candidate models using the Watanabe–Akaike information criterion (wAIC; Watanabe 2010), where smaller values indicate models with better performance. We also used posterior predictive checks to assess model fit using the *ppcOcc* function (Doser et al. 2022b). We checked Bayesian p-values, where values >0.1 indicate an adequate model fit, and drew inferences using a 95% Bayesian credible interval (Doser et al. 2022b).

Results

CNN

After demonstrating good performance on the validation set (Table 3), the CNN model was then deployed on the complete unannotated test set. As previously stated, we developed the CNN to optimize recall, as the cost of potentially missing a ruffed lemur call (and concluding there were no lemurs there) was high. This came at the expense of an increased number of false positives; we therefore manually checked the top 10 positive predictions per site per day (in the test set) to filter out false positives. Using this filter (top 10 per site per day) yielded 5,468 clips from the test set to manually check through Arbimon's validation page. Of these clips, 951 were true positives (17.4%). We detected ruffed lemur calls in 571 of the 506,784 total recorded minutes (0.11%) and at 10 of the 30 sites (33%, Table 5); however, none of these sites were south of the Ambohimahamasina region (Figure 3). The southernmost site that ruffed lemurs were detected was Lovasoa North (Table 5; Figure 1).

Ecological Models

The occupancy models presented good convergence and adequate mixing of MCMC chains given all R-hat statistic values <1.1, effective sample sizes were <4500 and trace plots were sufficient. The Bayesian p-values were between 0.1-0.9 (indicating adequate model fit) but were still small, suggesting results from the model should be interpreted with some caution. Nevertheless, these results document important, if introductory, trends on ruffed lemur occupancy in the COFAV. The detection probability for ruffed lemurs was 0.855 ± 0.034 (95% CRI: 0.784 - 0.916), and the occupancy probability was 0.281 ± 0.118 (95% CRI: 0.080 - 0.530). Occupancy is quite low and is underscored by the fact that ruffed lemurs were only found at sites north of the Ambohimahamasina region (near Lovasoa sampling sites). The top-ranked detection probability model contained NDVI and elevation (Table 4). Detection probability was positively related to NDVI (Figure 4) and negatively related to elevation (Figure S6). This means that ruffed lemurs were more likely to be detected at low elevation sites with high NDVI. The top-ranked occupancy probability model contained only NDVI (Table 4). The model showed that NDVI had a positive effect on ruffed lemur occupancy, meaning that lemurs were more likely to occur in sites with higher NDVI (Figure 4).

Discussion

Our study aimed to assess the current distribution of black-and-white ruffed lemurs in the Corridor Forestier d'Ambositra Vondrozo (COFAV) of southeastern Madagascar, including identifying the species' southernmost extent. We used passive acoustic monitoring to comprehensively and systematically survey 30 sites across the COFAV, from northern RNP to south of Vondrozo. We manually annotated a subset of recordings and ran pattern matching algorithms to develop a training dataset that was used to develop a deep-learning model which automated the detection of ruffed lemur roar-shrieks. The model performed well on our validation dataset, and we were able to deploy it over the full dataset to generate a detection-nondetection matrix for occupancy modeling. Our CNN results showed that ruffed lemurs were only detected in the northern third of the COFAV, with an abrupt cut-off east of Ambohimahamasina (Figure 3).

Previous studies over the past few decades have also failed to detect ruffed lemurs in southern COFAV sites (Rasoloarison & Rasolonandrasana 1999; Sterling & Ramaroson 1996; Goodman et al. 2001; Goodman & Rasolonandrasana 2001; Delmore et al 2009). There is a band of deforestation just east of Ambohimahamasina that nearly bisects the COFAV; this is precisely the cut-off area below which we did not detect ruffed lemurs. This deforested area may prevent ruffed lemurs from moving south, particularly as they are reluctant to come to the ground or cross matrix-type habitat. However, as this deforestation band is likely a recent (past few decades) development, it is still not clear what has historically precluded ruffed lemurs from occurring in the southern COFAV. Moreover, it does not explain why all other diurnal species except ruffed lemurs (Batist et al. 2023) are found there. One possibility is variation in forest quality. The models also showed that NDVI had a positive effect on ruffed lemur occupancy. Southern sampling sites (where ruffed lemurs were not detected) showed lower NDVI values, which potentially indicate lower forest cover or quality.

A previous study examining ruffed lemur landscape genetics and movement ecology found that canopy height and NDVI were significant predictors of gene flow and dispersal (Mancini et al. 2023). Ruffed lemur dispersal was facilitated by tall canopy heights and areas of low NDVI, in contrast to our results in this study (Mancini et al. 2023). However, it is important to note that Mancini et al. (2023) focused on a smaller scale than the present study, with sites encompassing just the area between Sakaroa and Malazamasina. As such, the factors that influence ruffed lemur movement in this specific region may be different from those that affect dispersal across the COFAV (this study). There could also be less variation in NDVI in the northern part of the corridor. This ambiguity in results may be due to the fact that ruffed lemur occurrence is more influenced by floral species composition rather than forest cover as a whole. Previous studies have shown that ruffed lemurs in RNP are selective feeders, focusing on a fairly narrow set of fruiting tree species (Beeby & Baden 2021; Beeby et al. 2023). Furthermore, ruffed lemurs are also selective in choosing nest sites to park their young (Baden 2019; Vasey et al. 2018). Incorporating data from botanical plots and floral inventories, alongside PAM, may help to better disentangle the influences that particular tree species have on ruffed lemur distribution.

An additional mitigating factor potentially influencing these trends is hunting. As ruffed lemurs are one of the larger lemurs taxa, they are frequently targeted for bushmeat hunting and sale into the illegal pet trade (Golden 2009; Borgerson 2015; Schubler et al. 2024). Previous research has shown that in many areas in Madagascar, ruffed lemurs are hunted unsustainably for maintaining stable populations (Golden 2009; Borgerson 2015). If ruffed lemurs were historically in the southern COFAV, hunting may have caused local extirpations of populations which then could not rebound because subsequent deforestation and fragmentation limited re-population from the north (Morelli et al. 2020).

We also found that elevation negatively influenced ruffed lemur detection probability, such that they were less likely to be detected at high elevations (>1000m). Previous research has shown ruffed lemurs typically inhabit low- and mid-altitude forests (Mittermeier et al. 2010). This may also limit ruffed lemur dispersal throughout the COFAV, as much of the forest that remains is at the very tops of cliffs and ridgelines while lowlands have been converted for agriculture. This land conversion may be driving ruffed lemurs to higher elevations, even though they typically favor lowland forests.

Beyond the implications of our occupancy model results, we also showcase the power of acoustic monitoring to survey lemurs at large spatial and temporal scales. As the COFAV does extend and connect with other corridors to the north and south, there are interesting questions that remain on lemur ranging in these corridor transition areas. We did not detect ruffed lemurs at sites in the north of Ranomafana National Park (north of RN25, the road that bisects RNP), but previous accounts have provided anecdotal evidence of hearing individuals. It may be that there are transient (nonresident) ruffed lemur individuals who pass through this region en route to other more hospitable habitats. It is also not clear if these are individuals who have crossed the road (i.e., come from the south) or who have traveled south from forest fragments outside of RNP.

At the opposite end of our sampling, we were only able to sample as far south as Vondrozo, due to safety and security concerns (caused by heightened *dahalo* [bandit] presence). Ruffed lemurs are found in Midongy du Sud National Park, in the far southeast of Madagascar, but it remains unclear how far north they range from Midongy into the unprotected corridors. There is evidence that they were found in some forest fragments north of Midongy about a decade ago (Rakotonirina et al. 2013). Unfortunately, we were not able to sample the area south of Vondrozo so we cannot address this question in the present study.

During the course of this study, two Category 4 cyclones (Batsirai and Emnati) struck the coastline adjacent to the COFAV in February 2021, bringing about extensive devastation to forests and adjacent communities. Due to the escalating impact of climate change and global warming, cyclones in the Indian Ocean basin have grown in intensity and frequency, and their landfall in Madagascar is now occurring further south than previously (Weiskopf et al. 2021). With climate change-induced increases in cyclone frequency and strength, the COFAV faces heightened risks of deforestation, habitat fragmentation, and food insecurity for its inhabitants. Indeed, previous research has suggested that climate change will lead to substantial shifts in species richness and turnover across the protected area network of Madagascar (Coldrey & Turpie 2021). Villagers living around the COFAV reported anecdotes of lemurs ranging further into croplands and matrix habitats immediately after the cyclones; this may be a result of preferred foods and fruit trees being wiped out. Thus, the cyclones may have also influenced lemur distribution in the COFAV; we are in the process of conducting more nuanced analyses to better tease apart this hypothesis. Climate change is driving many species to shift their ranges beyond the protected areas that once served as refuges. Understanding how populations persist in the surrounding landscapes is therefore essential to support these range shifts.

Limitations

We used the environmental variables that were publicly accessible to us, but it is likely that more fine-grained spatial products are necessary to disentangle the drivers of ruffed lemur occupancy (also noted in Irwin et al. 2005; Morelli et al. 2020). Access to high-resolution base imagery and derived geospatial layers remains a concern in remote sensing, but an increasingly large number of new and powerful satellites being launched will hopefully mitigate this issue.

We did not sample sites simultaneously over the seven-month period, as recorders lasted ~2 weeks and logistical constraints made it challenging to visit sites in rapid succession. Further, as the study period did not encompass a full year, this dataset may be overlooking seasonal variation in ruffed lemur range use and calling. The aforementioned cyclones likely also influenced ruffed lemur distribution and ranging behavior given the extensive tree falls, landslides, and floods. We are currently looking in more detail at vocal activity within sites before and after the cyclones to better assess these nuances.

Conclusion

This study has provided the first published survey of black-and-white ruffed lemur distribution and occupancy across the COFAV, including in some previously-unsurveyed areas. The COFAV plays a crucial role in connecting protected areas and sustaining many threatened and endemic species in the region. However, it faces ongoing threats like mining, logging, and climate change (Irwin et al. 2005; Ramiadantsoa et al. 2015). The remaining primary forest in the COFAV is highly fragmented, existing within a mosaic of human-dominated areas and forested landscapes (Goodman et al. 2001; Irwin et al. 2005; Ramiadantsoa et al. 2015; Conservation International 2014; Batist et al. 2023). Urgent conservation measures are needed to protect these important eastern rainforest corridors. As ruffed lemurs are keystone species vital for seed dispersal and pollination, their conservation is of particular importance in the eastern Malagasy rainforests.

There appears to be a strict delineation within the COFAV in the ruffed lemur range that corresponds to a wide band of deforested land just east of Ambohimahamasina. This area could potentially hold great promise for restoration efforts to establish corridors across this matrix that facilitate animal dispersal. Given that the COFAV is designated as level IV for sustainable extraction (Conservation International, 2014; Gardner et al., 2018; Goodman et al., 2018), this would require significant buy-in from local communities. We also found that ruffed lemur occurrence was positively influenced by NDVI which contrasts a previous, smaller-scale, study. There are likely nuances in the effect that environmental variables have on ruffed lemurs at different scales; disentangling these relationships requires further work integrating *in-situ* floral measures with PAM. We hope this project will be a catalyst for more extensive, multi-species PAM in the eastern Malagasy rainforest corridors. The acoustic data generated from this study can be used for other vocal species as well; such is one of the great benefits of permanent monitoring methods such as PAM. More broadly, this passive acoustic monitoring – machine learning – occupancy modeling pipeline shows great promise for future studies and can be generalized to a plethora of other threatened species.

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Conflict of Interest Statement

The authors declare no conflict of interest.

Author Contributions Statement

CHB and ALB conceived and designed the study. CHB, RR, GR and MD carried out data collection. MCC and CHB developed the data analysis workflow. CHB annotated the training dataset and NB implemented the machine learning pipeline. KH assisted in geospatial analyses and JWR supported the occupancy model workflow. CHB and ALB drafted the manuscript, and all authors approved the final version.

Data Availability Statement

Detection data used in the occupancy models are available in the Supplementary materials. The geospatial variables used in the occupancy models are freely available (sources listed in Methods). Audio recordings from this study are archived in Arbimon, and results can be explored through the Arbimon Insights project dashboard. Raw recordings can be requested from the corresponding author.

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Figure 1. Map of southeastern Madagascar showing the deployment sites for this study (November 2021-May 2022) across the COFAV. Generated in QGIS using a Carto basemap. Protected area polygons in green (north to south: Ranomafana National Park, Andringitra National Park, Ivohibe Special Reserve) from UNEP-WCMC World Database on Protected Areas.

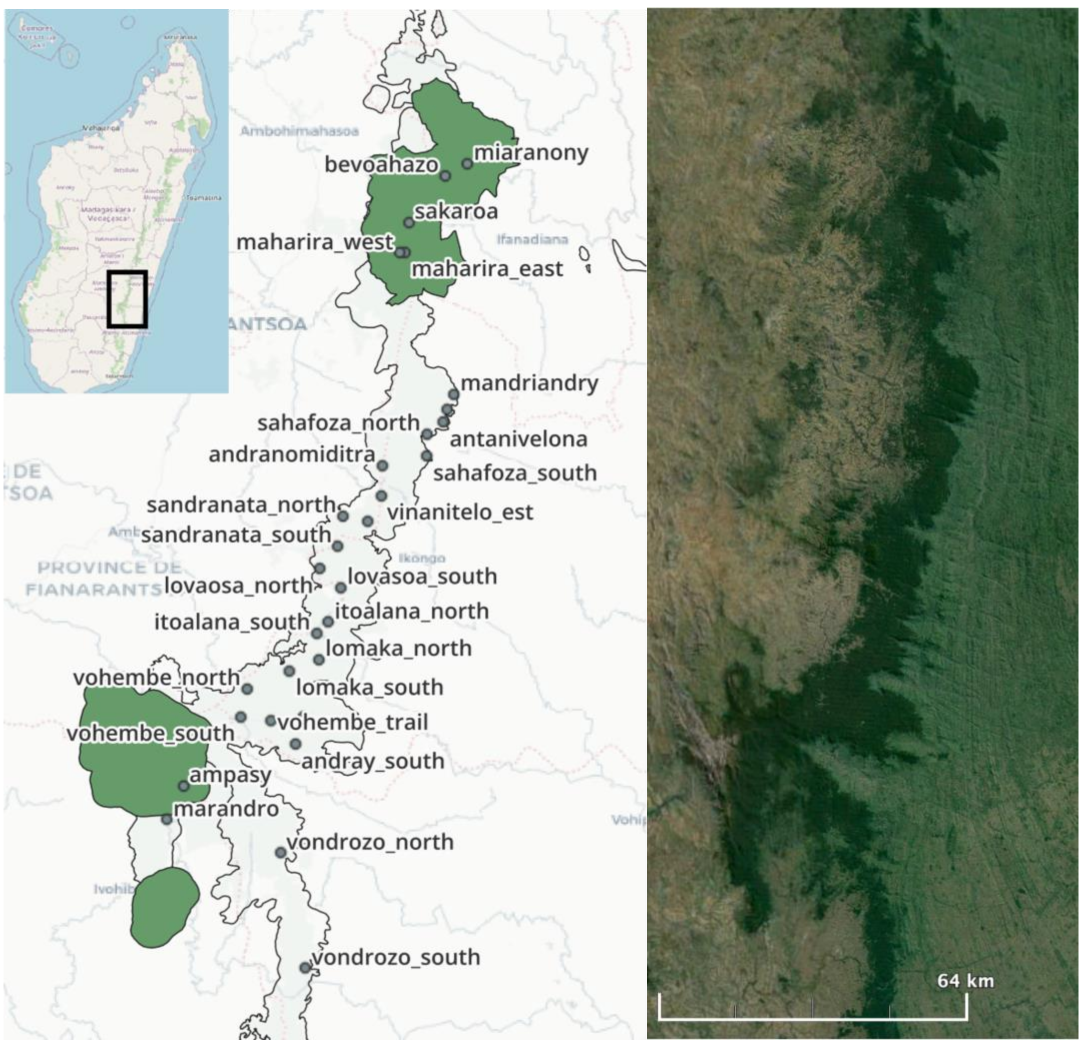

Figure 2. Detection of black-and-white ruffed lemur calls across COFAV sites in this study and compared to previous studies (cropped to the max allowed area per Planet Education program). Circles = current study's sites, triangles = previous studies' sites. White = lemur detected, black = lemur not detected. Background imagery shows NDVI, where darker colors = low NDVI and lighter colors (yellow) = high NDVI.

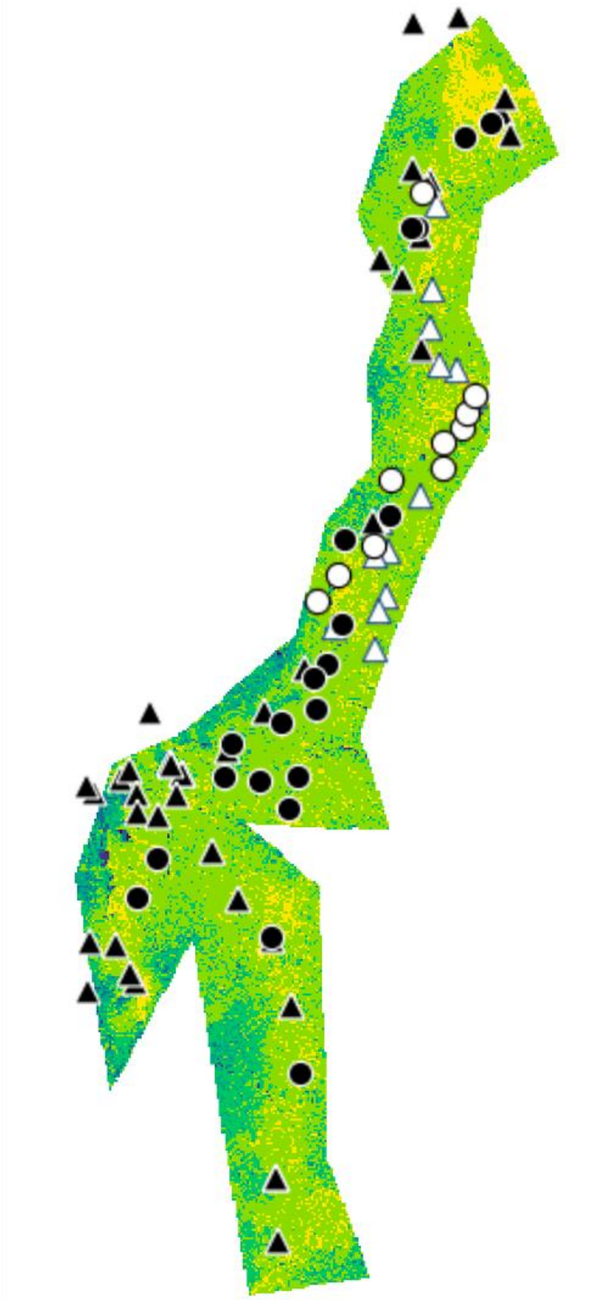

Figure 3. Composite PlanetScope Ortho Scene (8-band surface reflectance PlanetScope Scene) at 3m resolution, derived from daily PSScenes taken from March-May 2022, compiled together (cropped to the max allowed area per Planet Education program). Darker green indicates forested areas. Top call-out is the middle of Ranomafana National Park, where the RN25 highway runs through. Bottom call-out is of the COFAV area immediately east of Ambohimahamasina where there is a band of deforestation that nearly bisects the corridor completely.

Figure 4. Positive relationship between NDVI and both occupancy (top) and detection (bottom) probability for black-and-white ruffed lemurs in the COFAV of Madagascar. The black central lines represent the mean and the shaded areas represent the 95% credibility interval of the posterior sample of the model.

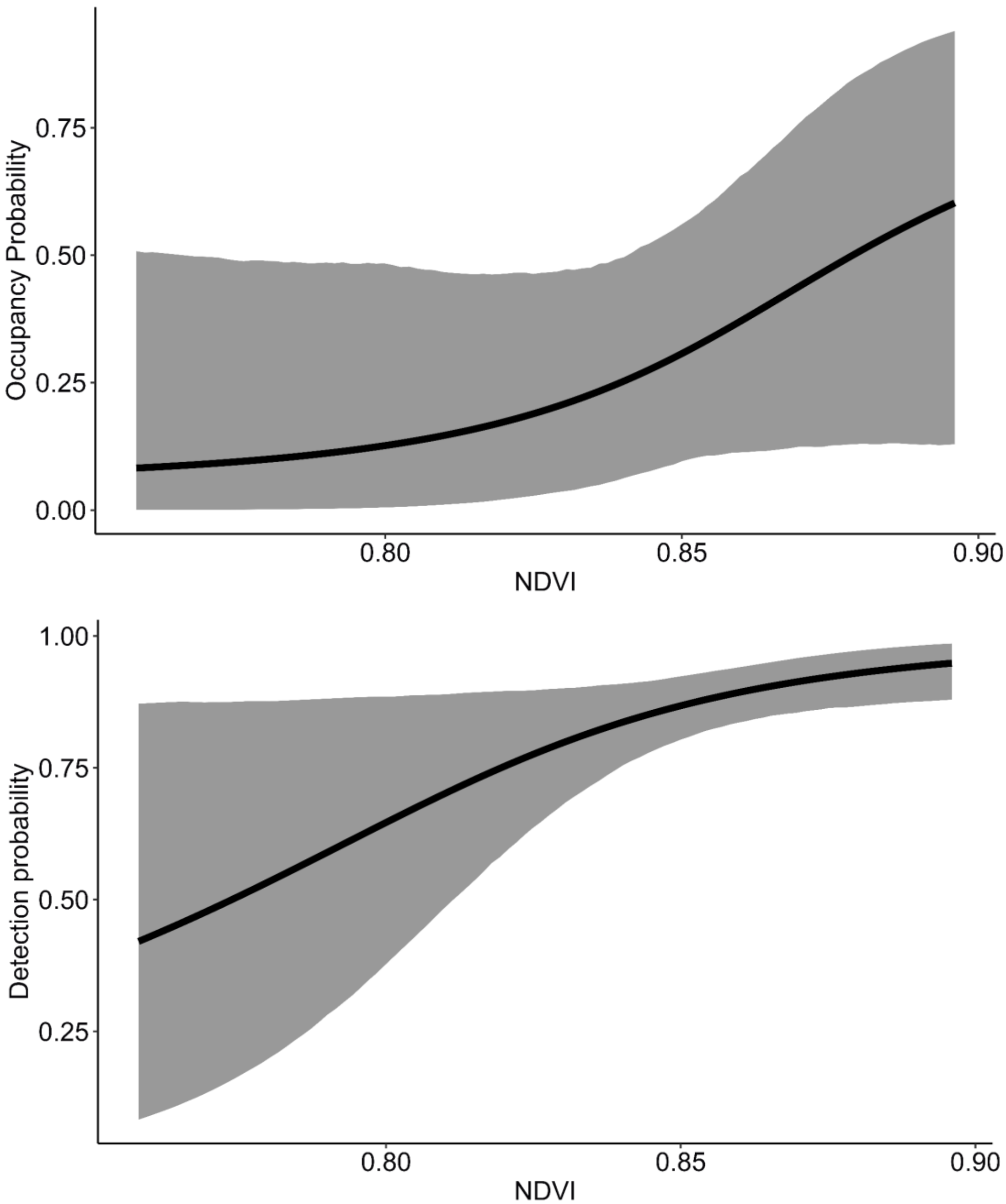

Table 1. Previous *Varecia variegata* sightings in the COFAV. Question marks indicate publications that did not list GPS coordinates. RNP = Ranomafana National Park, ANP = Andringitra National Park; these indicate the site is within park limits.

Reference	Site	Latitude	Longitude	V. variegata detected?
Batist et al. 2023	Namahoaka	-21.136	47.550	yes
Batist et al. 2023	Maharira	-21.331	47.339	no
Batist et al. 2023	Ambalavero	-21.526	47.407	yes
Batist et al. 2023	Mandriandry	-21.579	47.495	yes
Batist et al. 2023	Malazamasina	-21.610	47.481	yes
Batist et al. 2023	Antanivelona	-21.641	47.447	yes
Batist et al. 2023	Sahafoza	-21.653	47.439	yes
Batist et al. 2023	Andranomiditra	-21.717	47.359	no
Batist et al. 2023	Vinanitelo Sud	-21.812	47.337	yes
Batist et al. 2023	Sandranata	-21.84399	47.28106	yes
Batist et al. 2023	Lovasoa	-21.93958	47.28213	yes
Batist et al. 2023	Lomaka	-22.04578	47.17191	no
Batist et al. 2023	Ankarimbelo	-22.175667	47.266361	no
Batist et al. 2023	Vohembe	-22.160	47.135	no
Batist et al. 2023	Ankona	-22.16197	47.09542	no
Batist et al. 2023	Ambarongy	-22.22171	47.02002	no
Batist et al. 2023	Ampasy	-22.29512	47.0047	no
Batist et al. 2023	Marandrano	-22.35357	46.98151	no
Batist et al. 2023	Emma	-22.41654	47.17585	no
Batist et al. 2023	Manasara	-22.62687	47.23049	no
Batist et al. 2023	Vevembe	-22.79161	47.19849	no
Batist et al. 2023	Bemahala	-23.023278	47.202833	no
Dehgan 2003	Fragments east of RNP	?	?	yes (some)
Delmore et al 2009	Ambato Rakanana	-22.1274	47.1102	no
Delmore et al 2009	Andavav' Androngo	-21.9384	47.2753	no
Delmore et al 2009	Ambondro	-22.0017	47.2295	no
Delmore et al 2009	Iharagara	-22.0678	47.1673	no
Delmore et al 2009	Ampasy	-22.2829	47.0871	no
Delmore et al 2009	Ankorabe	-22.3561	47.1270	no
Delmore et al 2009	Ambohitsara	-22.4186	47.1791	no
Delmore et al 2009	Ranomena Masakafatsy	-22.5198	47.2089	no

Deppe et al. 2007	Mandriandry	-21.5833	47.4929	yes
Gaidet 1996	Angodongodona	?	?	yes
Goodman & Rasolonandrasana 2001	Andringitra (1960m)	-22.1712	46.9459	no
Goodman & Rasolonandrasana 2001	Andringitra (1990m)	-22.1578	46.9593	no
Goodman & Rasolonandrasana 2001	Andringitra (1625m)	-22.1942	46.9711	no
Goodman & Rasolonandrasana 2001	Andringitra (1210m)	-22.2228	46.9717	no
Goodman & Rasolonandrasana 2001	Andringitra (810m)	-22.2278	47.0036	no
Goodman & Rasolonandrasana 2001	Andringitra (720m)	-22.2222	47.0247	no
Goodman & Rasolonandrasana 2001	Andringitra (2050m)	-22.1920	46.9045	no
Goodman & Rasolonandrasana 2001	Andringitra (2450m)	-22.1815	46.8933	no
Goodman & Rasolonandrasana 2001	Andringitra I	?	?	no
Goodman & Rasolonandrasana 2001	Andringitra II	?	?	no
Goodman et al. 2001	Andrambovato	-21.5116	47.4100	yes
Goodman et al. 2001	Mandriandry	-21.5917	47.4850	yes
Goodman et al. 2001	Ambahaka	-21.7367	47.4083	yes
Goodman et al. 2001	Vinanitelo	-21.7767	47.3467	yes
Goodman et al. 2001	Ambatambe	-21.8217	47.3583	yes
Goodman et al. 2001	Ankopakopaka	-21.8283	47.3383	yes
Goodman et al 2001	Manombolo I (1300m)	-22.1494	47.0236	no
Goodman et al 2001	Manombolo II (1600m)	-22.1633	47.0417	no
Herrera 2016	Ampatsona	-21.0090	47.3970	no

Herrera 2016	Miaranony	-21.1480	47.5330	no
Herrera 2016	Vohiparara	-21.2350	47.3960	no
Herrera 2016	Maharira	-21.3380	47.4080	no
Irwin et al 2000	Marofotsy	-21.0000	47.4667	no
Irwin et al 2000	Namahoaka	-21.1250	47.5383	no
Mancini et al. 2023	Mandriandry	-21.5850	47.4915	yes
Mancini et al. 2023	Malazamasina	-21.5965	47.4798	yes
Mancini et al. 2023	Madiorano	-21.5434	47.4642	yes
Mancini et al. 2023	Ambodivanana	-21.5356	47.4376	yes
Mancini et al. 2023	Tatamaly	-21.4784	47.4229	yes
Mancini et al. 2023	Tandrokaomby	-21.4198	47.4264	yes
Nicoll & Langrand 1989	Andringitra (ANP)	?	?	yes
Rajaonson et al 2010	Ambendrana	-21.3730	47.3463	no
Rajaonson et al 2010	Amindrabe	-21.4036	47.3799	no
Rajaonson et al. 2010	Ambodiara	-21.9115	47.3914	yes
Rajaonson et al. 2010	Antarehimamy	-21.9331	47.3716	yes
Rajaonson et al. 2010	Antaranjaha	-21.9723	47.3380	yes
Rajaonson et al 2010	Manambolo	-22.0684	46.9910	no
Rakotonirina et al 2013	Fandana	-23.0500	47.2167	no
Rakotonirina et al. 2013	Ambalavero	-23.1500	47.2000	yes
Rakotonirina et al. 2013	Vohitrambo	-23.2893	47.3009	yes
Rasoloarison & Rasolonandrasana 1999	ANP-Ivohibe Corridor (1200m)	-22.4217	46.8983	no
Rasoloarison & Rasolonandrasana 1999	ANP-Ivohibe Corridor (900m)	-22.4267	46.9383	no
Rasoloarison & Rasolonandrasana 1999	Ivohibe (1200m)	-22.4833	46.9684	no
Rasoloarison & Rasolonandrasana 1999	Ivohibe (1575m)	-22.4969	46.8950	no

Rasoloarison & Rasolonandrasana 1999	Ivohibe (900m)	-22.4701	46.9602	no
Sterling & Ramaroson 1996	Andringitra (1625m)	NA	NA	no
Sterling & Ramaroson 1996	Andringitra (1210m)	NA	NA	no
Sterling & Ramaroson 1996	Andringitra (810m)	NA	NA	no
Sterling & Ramaroson 1996	Andringitra (720m)	NA	NA	no
Wright et al. 2012	Valohoaka (RNP)	-21.2970	47.4380	yes
Wright et al. 2012	Vatoharanana (RNP)	-21.2900	47.4333	yes
Wright et al. 2012	Talatakely (RNP)	-21.2612	47.4192	yes

Table 2. GPS coordinates, elevation, and deployment times for each recorder. Dates are in mm/dd/yyyy format.

Site Name	Device #	Latitude	Longitude	Elev. (m)	Start Day/Time	End Day/Time	Total hours recorded
Ampasy	Audiomoth 8	-22.29435	47.00300	877	01/31/2022 13:28	02/16/2022 13:25	240.3
Andranomiditra	Audiomoth 10	-21.71269	47.36344	1203	03/03/2022 09:40	03/14/2022 07:59	163.5
Andray_north	Audiomoth 11	-22.16872	47.21992	972	03/19/2022 10:00	04/04/2022 10:28	240.8
Andray_south	Swift 2	-22.21797	47.20589	997	03/18/2022 09:44	04/15/2022 15:03	711.0
Antanivelona	Audiomoth 3	-21.63311	47.47358	923	12/13/2021 09:01	12/29/2021 05:04	233.7
Bevoahazo	Audiomoth 18	-21.18658	47.47742	1087	01/11/2022 09:53	01/27/2022 06:21	237.3
Itoalana_north	Audiomoth 13	-21.99603	47.26494	990	02/01/2022 09:52	02/15/2022 05:07	202.6
Itoalana_south	Audiomoth 6	-22.01731	47.24444	918	01/31/2022 09:34	02/15/2022 14:45	230.5
Lomaka_north	Audiomoth 20	-22.06500	47.24819	1019	01/29/2022 09:23	02/07/2022 16:50	236.6
Lomaka_south	Audiomoth 16	-22.08572	47.19456	1007	01/28/2022 10:23	02/12/2022 08:15	223.6
Lovaosa_north	Audiomoth 9	-21.89922	47.24981	1410	02/03/2022 09:49	02/16/2022 07:41	192.9
Lovasoa_south	Swift 3	-21.93442	47.28800	1158	02/18/2022 09:03	03/08/2022 18:20	462.8
Maharira_east	Audiomoth 15	-21.32553	47.40428	1217	12/02/2021 05:00	12/17/2021 06:26	241.5
Maharira_west	Audiomoth 4	-21.32561	47.39486	1221	12/02/2021 5:00	12/17/2021 17:41	237.7
Malazamasina	Audiomoth 1	-21.61039	47.48078	1023	12/11/2021 07:48	12/25/2021 05:19	207.3
Mandriandry	Audiomoth 5	-21.58322	47.49294	1060	12/09/2021 13:52	12/25/2021 06:26	232.6
Marandro	Audiomoth 7	-22.35466	46.97229	727	02/08/2022 09:39	02/23/2022 10:59	126.6
Miaranony	Audiomoth 14	-21.16450	47.51739	970	01/09/2022 09:23	01/24/2022 08:14	223.9
Namahoaka[1]	Swift 6	-21.13789	47.55028	1204	01/07/2022 08:55	n/a[1]	n/a
Sahafoza_ north	Swift 5	-21.65561	47.44439	938	12/16/2021 10:53	12/31/2021 15:30	464.9
Sahafoza_ south	Audiomoth 2	-21.69486	47.44375	823	12/15/2021 09:01	01/03/2022 05:24	230.1
Sakaroa	Audiomoth 1	-21.27131	47.41175	1136	05/06/2022 10:32	05/17/2022 12:16	168.7

Sandranata_ north	Swift 7	-21.80436	47.29189	1128	02/25/2022 10:09	04/01/2022 15:57	541.2
Sandranata_ south	Audiomoth 12	-21.85886	47.28206	1183	02/20/2022 11:42	03/03/2022 10:03	163.5
Vinanitelo_est	Audiomoth 17	-21.76753	47.36169	1135	03/01/2022 11:21	03/08/2022 15:16	108.8
Vinanitelo_sud	Audiomoth 22	-21.81369	47.33681	999	02/27/2022 09:05	03/10/2022 08:33	164.7
Vohembe_ north	Swift 4	-22.11811	47.11814	1172	01/24/2022 10:24	02/24/2022 06:56	778.3
Vohembe_ south	Swift 1	-22.16908	47.10658	1078	01/23/2022 10:11	02/22/2022 17:03	714.1
Vohembe_trail	Swift 8	-22.17556	47.16117	989	03/17/2022 09:50	04/12/2022 19:13	660.3
Vondrozo_ north	Audiomoth 10	-22.41514	47.17903	736	05/28/2022 12:38	06/09/2022 05:11	171.4
Vondrozo_ south	Audiomoth 22	-22.62443	47.22335	580	06/16/2022 15:06	06/17/2022 14:43	165.0

[1]*Device lost, no data*

Table 3. CNN evaluation metrics on validation set for *V. variegata* acoustic classifier.

Metric name	**Metric definition**	**Metric value (this model)**
True presence	Positive samples that were correctly classified as positive by a model.	297
False positive	Negative samples that were incorrectly classified as positive by a model.	55474
True absence	Negative samples that were correctly classified as negative by a model.	150244
False negative	Positive samples that were incorrectly classified as negative by a model.	10
False positive rate	Calculated as: FP / FP+TN.	0.270
Precision	Calculated as: TP / TP+FP	0.005
Recall	Also known as sensitivity. Calculated as: TP / TP+FN	0.974
Area under curve (AUC)	Metric that assesses the performance of a binary classification model by measuring the area under its Receiver Operating Characteristic (ROC) curve.	0.967
Accuracy	Measures overall correctness of a model’s predictions. Calculated as: TP+TN / TP+TN+FP+FN.	0.73

Table 4. Candidate models tested for estimating probability of detection and probability of occupancy. wAIC = Watanabe-Akaike Information Criterion. The detection and occupancy models with the lowest WAIC (signifying best model fit) are bolded.

Model	Model formula	WAIC
Detection		
null	~ 1	169
Sampling days	~ days	168
NDVI	~ ndvi	170
Elevation	~ elevation	154
Forest cover loss	~ cover	158
Elevation + Forest cover loss	~ elevation + cover	154
NDVI + Forest cover loss	~ ndvi + cover	159
Elevation + NDVI	**~ elevation + ndvi**	**151**
Full	~ elevation + ndvi + cover	152
Occupancy		
null	~ 1	169
NDVI	**~ ndvi**	**168**
Elevation	~ elevation	171
Forest cover loss	~ cover	172
Elevation + Forest cover loss	~ elevation + cover	173
NDVI + Forest cover loss	~ ndvi + cover	172
Elevation + NDVI	~ elevation + ndvi	170
Full	~ elevation + ndvi + cover	172

Table 5. Black-and-white ruffed lemur call detections across sites (ordered by latitude, most northern to most southern).

Site	Total # of Calls Detected	Detection frequency
Sakaroa	28	0.003
Mandriandry	74	0.005
Malazamasina	53	0.004
Antanivelona	138	0.010
Sahafoza North	78	0.003
Sahafoza South	81	0.006
Andranomiditra	40	0.004
Vinanitelo Sud	34	0.003
Sandranata South	30	0.003
Lovasoa North	15	0.001

Supplementary Materials for the manuscript entitled:
Implementing an ecoacoustic – machine learning – occupancy model pipeline to survey black-and-white ruffed lemurs (Varecia variegata) in Madagascar's Corridor Forestier d'Ambositra Vondrozo (COFAV)

Table S1. Configuration parameters for the 2 types of autonomous recorders used in this study.

	Swifts ('rugged' housing version)	**Audiomoths**
Sample Rate	48kHz	48kHz
Gain	36dB	30dB
Schedule	05:00 - 20:00	05:00 - 20:00
Bandfilter	none	1-20kHz
Sleep/record cycle	continuous	55 seconds recording, 5 seconds sleep
File length	20 minutes	55 seconds
SD card	256GB SanDisk Extreme Pro SD card	128GB SanDisk Extreme Pro micro-SD card
Battery	9 Energizer Max D batteries	3 Energizer Ultimate Lithium AA batteries
Other	n/a	Energy saver mode enabled

Figure S1. Spectrogram of a black-and-white ruffed lemur roar-shriek from active acoustic monitoring using a directional microphone (top) and passive acoustic monitoring using an autonomous recording unit (bottom; roar-shriek outlined in white)

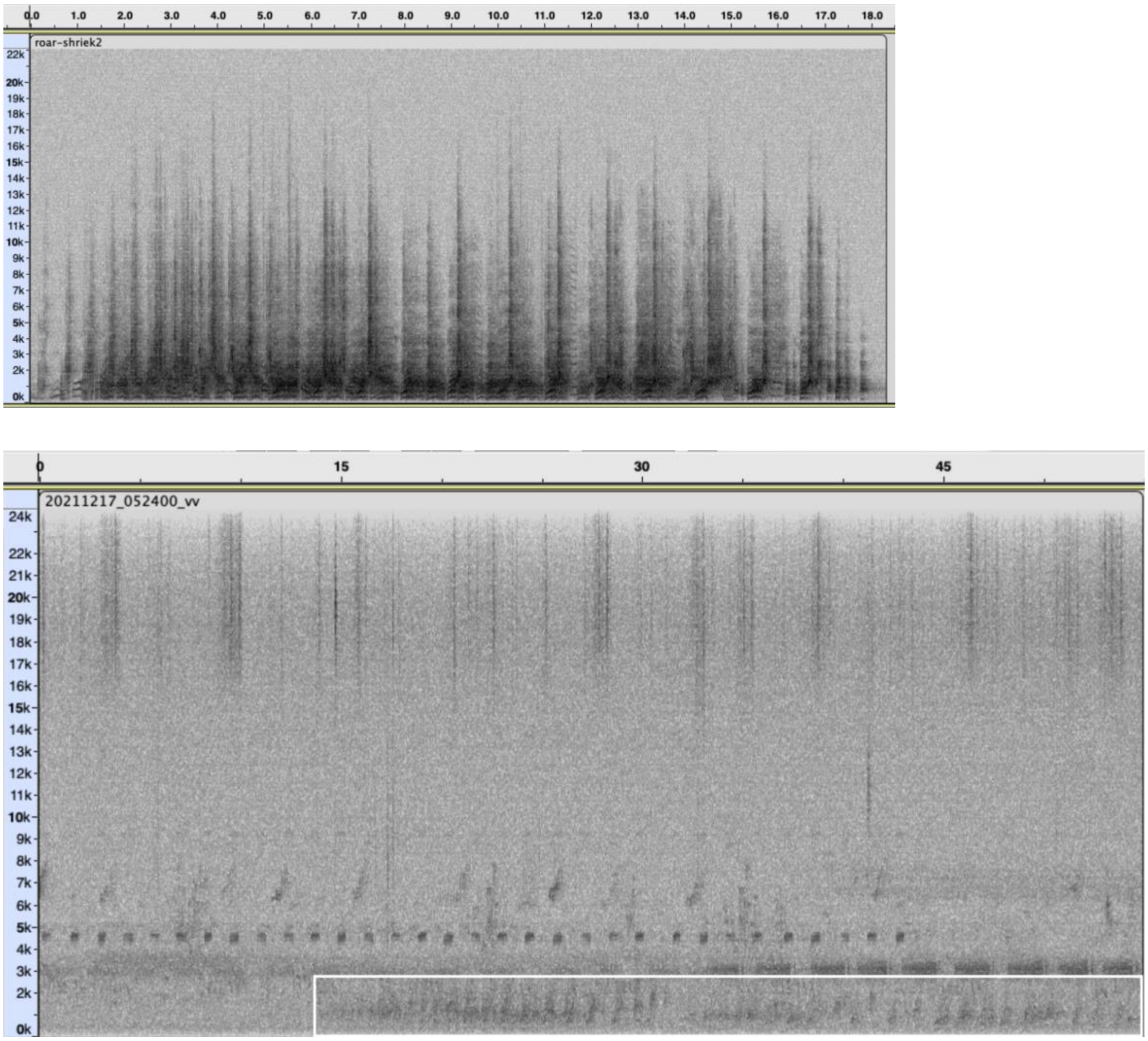

Figure S2. Arbimon validation page for manually checking CNN model predictions

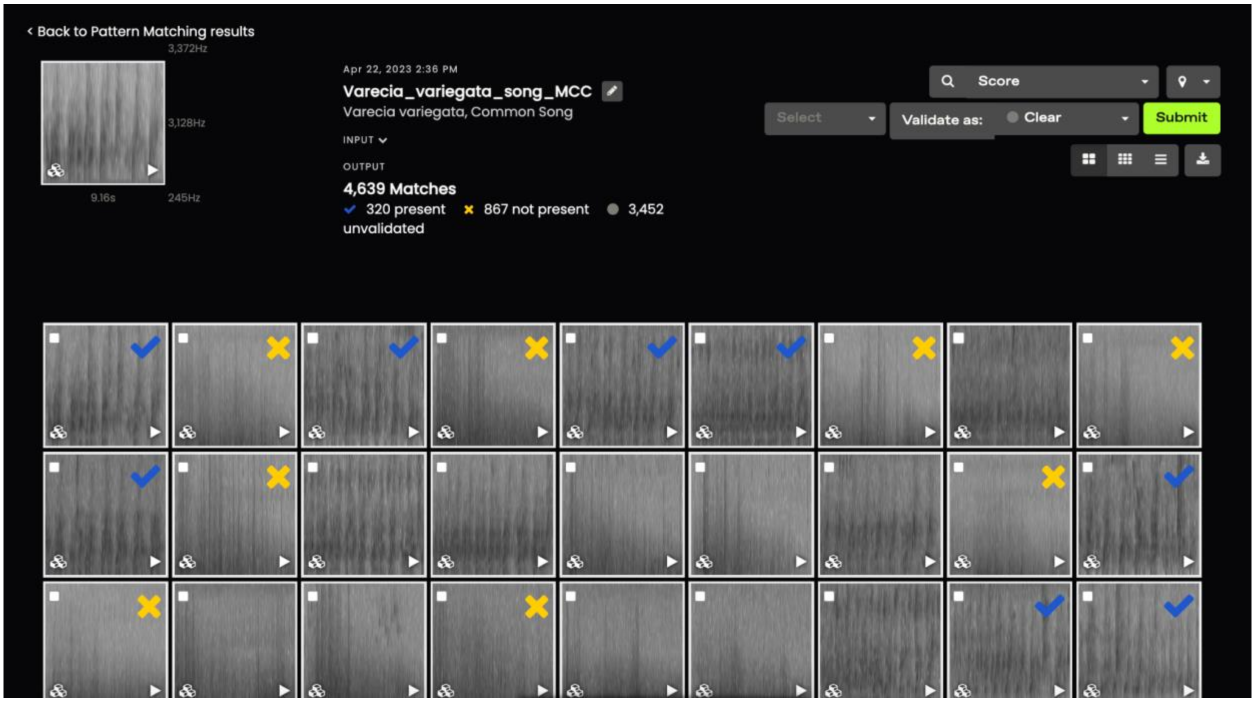

Figure S3. Map of elevation for the study area (lighter colors = higher elevation). From the Terra Advanced Spaceborne Thermal Emission and Reflection Radiometer's Global Digital Elevation Model (Version 3) at ~30m resolution

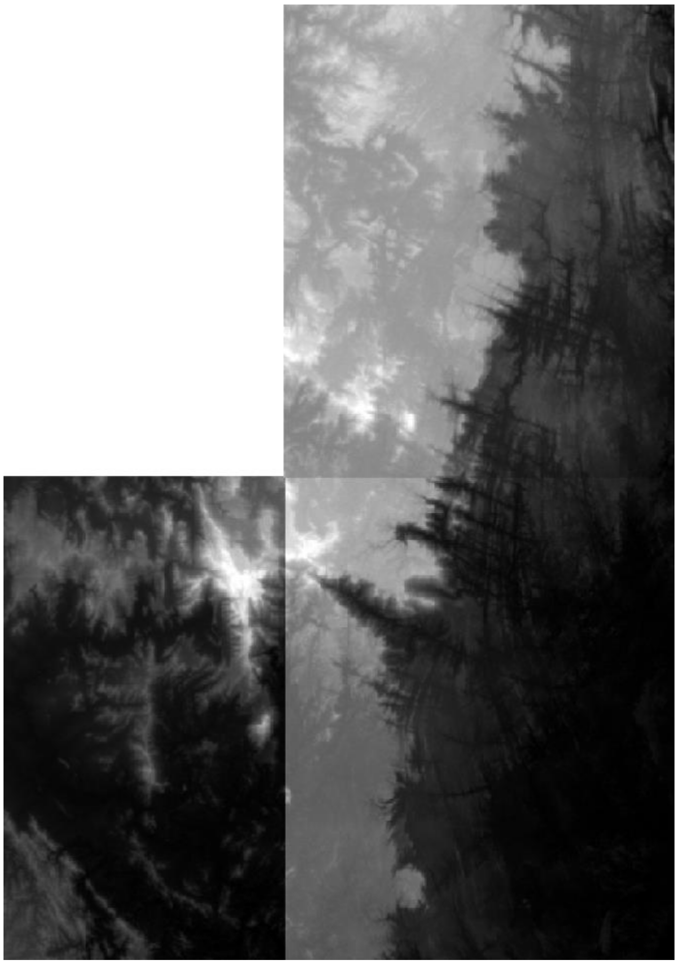

Figure S4. Map of forest cover loss (2000-2022) for the study area. Shades of pink and red indicate forest cover loss. Layer developed by the University of Maryland GLAD team via time-series analysis of Landsat images from 2000 through 2022, with 30m resolution (Hansen et al. 2013; Potapov et al. 2022; with version 1.1 update as in https://glad.earthengine.app/view/global-forest-change).

Figure S5. Map of NDVI in March for the study area. NDVI was calculated directly from a composite PlanetScope Ortho Scene, which is an 8-band, surface reflectance PlanetScope Scene at 3m resolution. The composite was derived from daily PSScenes taken from March-May 2022, compiled together to achieve a cloud-free, haze-free composite. Darker colors = low NDVI and lighter colors (yellow) = high NDVI.

Figure S6. Output of top-ranked detection probability model showing a negative relationship between elevation and detection probability of black-and-white ruffed lemurs in the COFAV.