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RESEARCH ARTICLE

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Singing in the rain! Climate constraints on the occurrence of indri's song

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Abstract

The study of how animals adapt their behaviors depending on weather variables has gained particular significance in the context of climate change. This exploration offers insights into endangered species' potential threats and provides information on the direction to take in conservation activities. In this context, noninvasive, cost-effective, and potentially long-term monitoring systems, such as Passive Acoustic Monitoring (PAM), become particularly appropriate. Our study investigates the relationship between weather variables and the vocal behavior of *Indri indri*, the sole singing lemur species, within Madagascar's Maromizaha New Protected Area. Using PAM, we explore the factors shaping the vocalization patterns of this primate species in response to some environmental factors in their natural habitat. Analysis of an extensive audio data set collected across different years revealed the differential influence of temperature and precipitation on *Indri indri* vocal activity. We found that rainfall negatively influenced the emission of the vocalizations while warmer temperatures correlated with a greater emission of songs. The various environmental factors we considered also affected the timing of vocal emissions, showing the same pattern. Furthermore, our study confirms, once again, the strength of PAM as a valuable tool for studying vocal animal communication quickly, giving us information about long-term behavioral patterns that would be difficult to get in other ways. This research gives us further valuable information about how indris use vocalizations in their environment and how they adjust to environmental changes.

KEYWORDS
bioacoustics, climate, conservation, indri, Madagascar, Maromizaha New Protected Area, Passive Acoustic Monitoring, song

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Abbreviations: AIC, Akaike Inflation Criterion; ARU, automated recording unit; CNN, convolutional neural network; PAM, Passive Acoustic Monitoring; VIF, variation inflation factors; WAV, waveform audio file format.

Claire Raisin, Marco Gamba, Achaz Von Hardenberg, and Cristina Giacoma shared last authorship.

1 | INTRODUCTION

In the face of a rapidly changing climate and escalating environmental challenges, reframing ecological, animal behavior, and conservation studies through the lens of weather events is imperative. Environmental variables such as temperature, nocturnal visibility, and precipitation levels significantly impact animal behaviors (Mandl et al., 2018), including foraging, reproductive behavior, and daily energy expenditure (Brockman & van Schaik, 2005). Notably, these behaviors need to adapt to undergoing changes. The survival of individuals relies on their ability to exhibit behavioral plasticity—the capacity of individuals or populations to alter behaviors in response to environmental conditions (as defined by Hadfield & Strathmann, 1996)—and find a balance between costs and benefits (Evans & Moustakas, 2018). In this global context, studying and monitoring how animals respond to everyday weather events (Beever et al., 2017; Buchholz et al., 2019) are crucial for guiding conservation plans in the face of biodiversity threats posed by climate change and intensifying atmospheric events.

Communication may be subject to some degree of behavioral plasticity: producing a sound is not always beneficial for the signallers as the costs, both ecological (e.g., vulnerability to predation) or social (e.g., vulnerability to receive attack), can be high. Primates are flexible in the production of vocalizations by changing the timing (*Sanguinus oedipus*, cotton-top tamarins, Egnor et al., 2007; *Callithrix jacchus*, common marmoset, Roy et al., 2011) or the amplitude (common marmosets, Brumm et al., 2004; cotton-top tamarins, Roian Egnor & Hauser, 2006) of their vocalizations to avoid overlapping with environmental noises. Moreover, producing vocalizations is highly energetically costly, as has been demonstrated across different taxa, including anurans, insects (Prestwich, 1994; Ryan, 1988), birds (Chappell et al., 1995; Ophir et al., 2010) and mammals (Gillooly & Ophir, 2010; Speakman et al., 1989). In birds, the complexity of vocal emissions is positively correlated with the metabolic rate (Garamszegi et al., 2006), and in nonhuman primates, long-distance calling has been related to energy levels and male vigour (e.g., Kitchen et al., 2003; Sicotte et al., 2007; Whitten, 1982).

We still need more data to properly understand nonhuman primates' acoustic communication energetic demand (Wich & Nunn, 2002; on humans: Russell et al., 1998). Still, different studies underline one trend: nonhuman primates produce more vocalizations in conditions associated with potentially greater energy reserves. Notably, Cowlishaw (1996) found that calling rates increase with fruiting season and when thermoregulation costs are low in gibbons. Indeed, thermoregulation costs are higher in weather conditions such as low temperatures or rainy days and this relation can be particularly strong with lemurs, who often use social behaviors such as sunning and huddling (Donati et al., 2011; Kelley et al., 2016) to keep warm. Also, in support of the link between energy reserves and vocalizations, Kloss's gibbons (*Hylobates klossii*) produce fewer morning calls after rainy nights (Whitten, 1982), and wild black and white ruffed lemurs (*Varecia variegata*) produce fewer calls when there are higher daily rainfall levels (Batist et al., 2022). The black and gold howler monkey (*Alouatta caraya*) displays a distinct seasonal roaring activity peak during the wet season (74.9%, peak activity occurring in November and December), potentially associated with increased flowering and fruit production (Pérez-Granados & Schuchmann, 2021). However, weather variables can have distinct effects on different species. There is not a linear relationship: some species increase vocal production with high temperature (*Nomascus* sp., Coudrat et al., 2015), others decrease production (Kloss's gibbons, Whitten, 1982), and some are not influenced (Central Yunnan black crested gibbon, Fan et al., 2009; Bornean white-bearded gibbon, Cheyne, 2008; coppery titi monkey, Dolotovskaya & Heymann, 2022).

Weather can also influence the time at which nonhuman primates vocalize. A study on Müller's gibbons (*Hylobates muelleri*) in Malaysia found that the amount of rain in the previous 24 h influenced the timing of male solo emissions, explaining 30% of the timing variance. These findings suggest that male solo events are influenced by environmental factors, even in the timing of the emission (Clink et al., 2020), which could be linked to energy expenditure. Clink et al. (2020) also examined illumination levels associated with lunar phases and found no effect on the timing of gibbons' singing. However, lunar phases affect song timing in birds (i.e., singing sooner when there is a full moon; Bruni et al., 2014) and many lemur species, both cathemeral (red-fronted lemur, Donati et al., 2001; red fronted brown lemurs, Donati et al., 1999), and diurnal (ring-tailed lemur, Donati et al., 2013), are influenced by moon phases in their activities.

Indri *(Indri indri)* is the only lemur species to produce songs (Valente et al., 2019, 2022), which it only performs in the form of a duet or chorus (Gamba et al., 2016). Songs are subject to variation during the development of individuals and may vary with the presence of juveniles and subadults within the family social group (De Gregorio et al., 2019, 2021; De Gregorio, Zanoli, et al., 2022). The prevalent daily vocalization among indris is referred to as the "advertisement song," primarily aimed at signaling a group's presence to nearby conspecifics, as documented by Torti et al. (2013), and it is produced by the individuals of the groups in the mornings. Indri is classified as Critically Endangered in the IUCN Red List of Threatened Species (King et al., 2020), and the population decline is attributed to the adverse impacts of habitat loss, hunting, and climate change. Brown and Yoder's (2015) analysis specific to the indri's habitat projected a 39.5% reduction in the species' range from 2000 to 2080 solely due to climate change, without accounting for the impact of deforestation.

Passive Acoustic Monitoring (PAM) can play a pivotal role in informing and guiding conservation efforts, offering the potential for long-term monitoring of both animal populations and the biodiversity of the forest with Automated Recording Units (ARUs) (Ross et al., 2023; Sugai et al., 2019). This is particularly significant for a species like indri, known for producing long-distance songs that can disperse a considerable distance in the forest (up to 2 km, Zanoli et al., 2020). Thanks to indri's frequent and diverse vocalizations, PAM has been demonstrated to be a helpful methodology to monitor the distribution and population density of this species, showing that it is a feasible and accurate technique for collecting information on the group size and individuals (Torti et al., 2018). Insights gained through PAM can contribute significantly to conservation strategies. They aid in understanding behavioral patterns, population dynamics, and habitat utilization for effective long-term management and preservation of indri. This includes accounting for factors such as funding availability, proximity of sleeping sites to study groups, trail conditions, and the degree of habituation of study groups to human presence.

Here, we analyzed recordings obtained from a network of ARUs in the Maromizaha New Protected Area (Madagascar) to explore if and how weather conditions influence the singing behavior of these primates. The findings from this analysis have significant implications, as they provide information potentially crucial for this species' conservation. We show how weather variability affects the probability of indris' songs and, therefore, demonstrate the need to consider the weather when estimating the distribution and density of this species with PAM. Furthermore, this research could play a pivotal role in elucidating variations associated with weather patterns, enriching our knowledge of this species, potentially giving us information on its conservation, and allowing comparisons with other song-producing primate species to understand further the evolution of primate songs (De Gregorio, Carugati, et al., 2022).

We developed and tested two working hypotheses in this study:

1. As rain creates noise in the soundscape and attenuates sound propagation, and colder temperatures, combined with rain, result in higher thermoregulation costs, we predict that individuals would emit fewer vocalizations with unfavorable weather. This would align with the behavioral plasticity hypothesis. Under conditions of less energetic disposition and less probability that songs would exert a strong effect (rain would diminish propagation, hence diminishing the range of the song), the factors would lead to a decrease in the number of indri songs.
2. Our second hypothesis suggests that indris, for similar reasons, postpone their singing due to adverse weather conditions such as rain or low temperatures. Therefore, we anticipate that the timing of song emissions will be delayed on days with inclement weather (or the days following inclement weather) compared to days with favorable weather conditions.

2 | METHOD

2.1 | Ethical note

The noninvasive methods used for the data collection of this study adhere to the American Society of Primatologists (ASP) “Principles for the Ethical Treatment of Non-Human Primates.” Field data collection protocols were reviewed and approved by Madagascar's Ministere de l'Environnement, de l'Ecologie et des Forets on July 1, 2022, under Permit 2022:186/22/MEDD/SG/DGGE/DAPRNE/SCB.Re. Field data collection protocols were also approved by GERP (Groupe d'Etude et de Recherche sur les Primates de Madagascar), the association overseeing research in the Maromizaha New Protected Area.

2.2 | Acoustic data collection

We conducted this study in the Maromizaha New Protected Area in eastern Madagascar (coordinates 18° 56′ 49″ S and 48° 27′ 33″ E, Figure 1). A tropical climate with distinct seasons characterizes the area: a cool season from May to September and a warm season from October to April (Randrianarison et al., 2002). The study site covers 2150 hectares within the Ankeniheny-Zahamena Corridor, a large protected forest biome.

Data collection spanned from July 15, 2019 to September 04, 2019 and from August 02, 2022 to November 26, 2022, with a temporal stop in the data collection due to the COVID-19 pandemic. We employed three types of autonomous recorders: AudioMoth recorders (LabMaker), Song Meter SM4 recorders (Wildlife Acoustics Inc.), and Song Meter Micro recorders (Wildlife Acoustics Inc.). In 2019, we obtained the recordings from AudioMoth recorders, placed at 10 sites within the Maromizaha forest. By 2022, additional recorders were installed, resulting in a total of 18 AudioMoth recorders, 3 Song Meter Micro recorders, and 2 Song Meter SM4 recorders (that rotated over two different locations) (Figure 2).

We deployed autonomous recording units (ARUs) across a 390 ha area, attached to trees approximately 1.5 m above the ground, recording day and night during the study period. We deployed the recorders at the center of different group territories (Bonadonna et al., 2020; De Gregorio et al., 2021). We left the ARUs for 10–14 days before returning to check the correct functioning of the units and change batteries (AA rechargeable batteries with 2800 mah) and SD cards (32 GB SD with speed up to 100 MB/s) if needed. To ensure comprehensive coverage, the sampling schedule involved recording 10 min every 30 min throughout the day, resulting in 48 daily recordings. We saved the audio recordings across all locations as 600-s-long Waveform Audio File Format (WAV) files with a sample rate of 48 kHz, 16-bit resolution, and a gain setting of 18db for Wildlife Acoustics device and Med Gain for AudioMoth.

We obtained climatic information from two different weather stations (both HOBO USB Micro Station Data Logger) to complement the acoustic data: for the first part of the data collection (2019) the first weather station was located at the Petite Bellevue (18°58′47″ S and 48°28′0″ E) and from 2022 the second weather station was located at the Maromizaha Multipurpose Centre, at the center of the recording array (18°58′34″ S and 48°27′53″ E). The weather stations collected temperature (in degrees Celsius, collected for 24 h a day, each hour), and the rainfall (in millimeters, collected for 24 h a day, each hour). Our first weather data collection covers the period from April 20, 2018 to September 04, 2019, while the second data collection goes from August 01, 2022 to July 13, 2023. We have 190 days of data collection for which both PAM data and climatic information are available, with a total of 67,381 WAV files (873,810 min). All continuous outcome and predictor variables were scaled before model selection.

FIGURE 1 Map of Madagascar and the position of Maromizaha New Protected Area inside the protected biome of Ankeniheny-Zahamena Corridor.

2.3 | Automated detection of indri songs

We detected the songs by Indris using an established automated detection algorithm, as Ravaglia et al. (2023) detailed. This machine learning algorithm had been created and rigorously tested before, thereby enabling the accurate identification of indri songs within the audio recordings. The algorithm's architecture and parameters were preserved from the referenced study to maintain consistency and comparability in our analysis.

The algorithm incorporates a series of advanced techniques, including spectrogram conversion using Praat (Boersma & Weenink, 2024; version 6.1.52), feature extraction based on the third-octave band system, and convolutional neural network (CNN) architecture. Initially, each audio recording was converted into a spectrogram using Praat, with a frequency range optimized to capture the fundamental frequency (f0) and first harmonics of indri songs. Visual inspection of individual spectrograms was followed by manual labeling recordings containing indri songs. The algorithm then

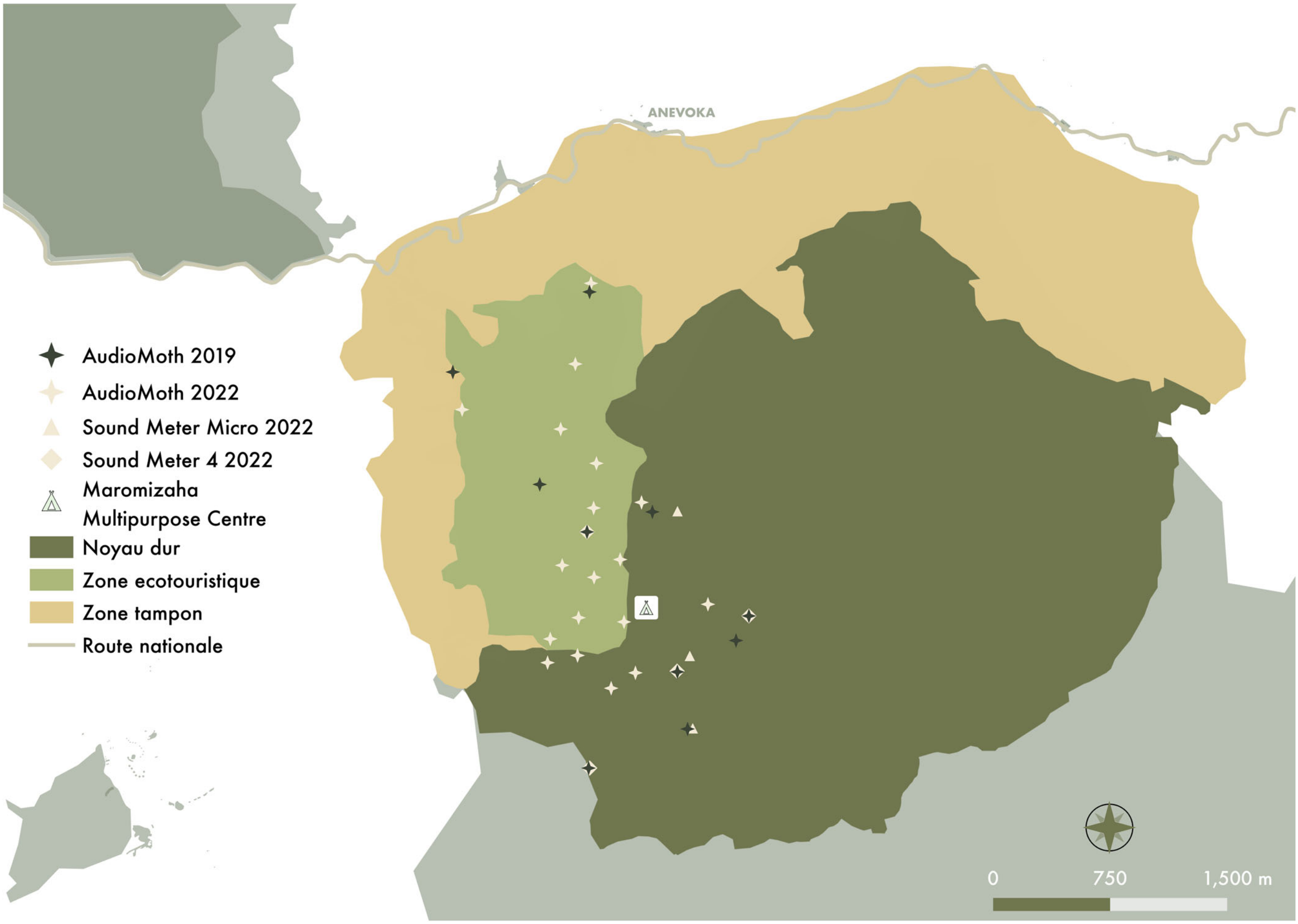

FIGURE 2 Map of Maromizaha New Protected Area and disposition of the automated recording units in 2019 and 2022.

extracted acoustic features from these labeled recordings, decomposing the spectrum into one-third-octave bands to quantify the acoustic environment. A key aspect of the algorithm was data augmentation, which addressed class imbalance issues by slicing and rearranging spectrogram images to create novel training examples. This process enhanced the algorithm's ability to generalize and detect indri songs accurately across different recording conditions and environments. The CNN architecture underwent modifications and fine-tuning of hyperparameters to optimize performance. Notably, including the hour of the day and week of the year as additional input features improved song detection accuracy. Transfer learning was employed to adapt the algorithm to new data sets, further enhancing its versatility and effectiveness.

2.4 | Statistical analysis

We used a Generalized Linear Mixed Model (GLMM, *lme4* package, Bates et al., 2015) in R (R Core Team 2023; version 3.4.3) and formulated a series of models to test our hypothesis. For all the models, we assessed collinearity among predictors by calculating variance inflation factors (VIFs) using the vif package (Lin et al., 2011). Collinearity was ruled out based on standard linear models, excluding the random effects (max. VIF = 2.3). Initially, we examined the nonrandom association of indri-calling events with environmental predictors using two methods. First, we assessed the effect of environmental variables on whether or not indri produced songs. In our data set, we determined the presence/absence of indri song (family = binomial) for each acoustic recording unit (ARU) on each day, resulting in one data point per ARU per day. Second, we focused on modeling the count of indri songs (family = Poisson) throughout the day. In the second case, we treated any detection of a song by at least one recorder within a specific hour as a single occurrence and counted the number of hour ranges in which there was a song. We examined data in this way as multiple recorders operated simultaneously. This could result in some overlap between devices for the calls detected, and we did not have information regarding individual or group identities to confirm duplicates. As a result, we did not use the total count of calls as a response variable. For each method, the model included the mean temperature, the rainfall during the day, rainfall the preceding night and year as fixed effects, and the identity of the ARU and the date as random effects. Finally, we employed a Linear Mixed Model (LMM, lme4 package, Bates et al., 2015) to explore whether the start times of songs, quantified as minutes from

TABLE 1 List of response and predictor variables used in this work.

Response variables	Description	Mean and SD	Range
Indri song event	Binary variable: If indri song was detected (1) or not (0) in that day, by that ARU	~	~
Indri songs count	N. of songs emitted during the day (i.e., sum of the binary variables for each hour range composing the day: If at least one indri song was detected (1) or not (0) by any ARU in each hour range)	4.2 ± 3.7	0–14
Song starting time	Minutes relative to nautical dawn from the hour of the song	480.4 ± 158.1	−269.9 to 1251

Predictor variables	Description	Mean and SD	Range
Temperature	Daily mean temperature (C°, mean on 24 h starting from 06:00)	16.7 ± 2.3	11.1–21.6
Rain	Total precipitation (mm/24 h) taken at 06:00	1.2 ± 3.1	0.0–23.8
Overnight rain	Precipitation (mm) of rain from 18:00–06:00 the night preceding the songs	0.4 ± 1.5	0.0–19.0
Year	Variable indicating year of data collection	~	~
Lunar cycle	Categorical variable indicating whether the moon was full, waning, waxing or new	~	~
Random effect			
Recorder	The location and device which recorded the soundscape containing the song	~	~
Date	The date of the recording	~	~

nautical dawn, changed based on environmental factors. For all three investigations, we used the environmental variables as predictors as outlined in Table 1, except for the "lunar phase," which we exclusively used for the timing investigation. We derived nautical dawn information using the *suncalc* R package (Thieurmel & Elmarhraoui, 2019) and added lunar phase information using the R package *lunar* (Lazaridis, 2022). We define "night" as the period between 18:00 (6:00 p.m.) and 06:00 (6:00 a.m.) in Madagascar. We chose this timeframe based on the region's average times for sunset and sunrise.

We utilized the Akaike Information Criterion (AIC) for model selection (Akaike, 1973). We chose the model with the lowest AIC as the best-fitting model. We also considered the model showing the second lowest AIC if it presented a delta AIC ≤ 2, thus indicating substantial statistical support (Burnham & Anderson, 2002).

3 | RESULTS

3.1 | Influence of environmental variables on indri song events

The model which considered the mean temperature and rain outperformed the other models, as indicated by its lower AIC values and higher model weights (Supporting Information S1: Table SU1), highlighting the robustness of its predictive power. The mean temperature showed a positive influence (estimate = 0.615; se = 0.076) (Figure 3a), as overnight rain (estimate = 0.113, se = 0.065) and year (estimate = 0.599, se = 0.165) while the daily precipitation showed a negative influence (estimate = −0.178; se = 0.068) (Figure 3b) on the detected songs. The second best-fitting model showed the effect of rain (estimate = −0.218; se = 0.085), temperature (estimate = 0.589; se = 0.076), year (estimate = 0.539; se = 0.168) and the interaction between rain and temperature (estimate = −0.140; se = 0.083). Speaking of odds, the first model revealed a significant association-a 1°C increase in temperature is linked to a 31.3% increase in the odds of singing. While not statistically significant, there is an intriguing trend where a 1 mm increase in overnight rain might lead to a 6.8% increase in the odds of singing for each additional unit of overnight rain. This finding warrants further investigation. In contrast, each 1 mm increase in daily precipitation corresponds to a 5% decrease in the odds of singing for each additional unit of daily rain. The second model showed a 19.6% decrease in the odds of singing for each additional mm of daily rain and an 80.2% increase for each additional temperature unit.

3.2 | Influence of environmental variables on indri-singing events (count)

For the models including the number of indri-calling events as dependent variables the best-fitting model, according to AIC comparison (for Supporting Information S1: Table SU2), included the mean temperature (estimate = 0.182; se = 0.075) (Figure 4a), rain (estimate = −0.190; se = 0.087) (Figure 4b), overnight rain

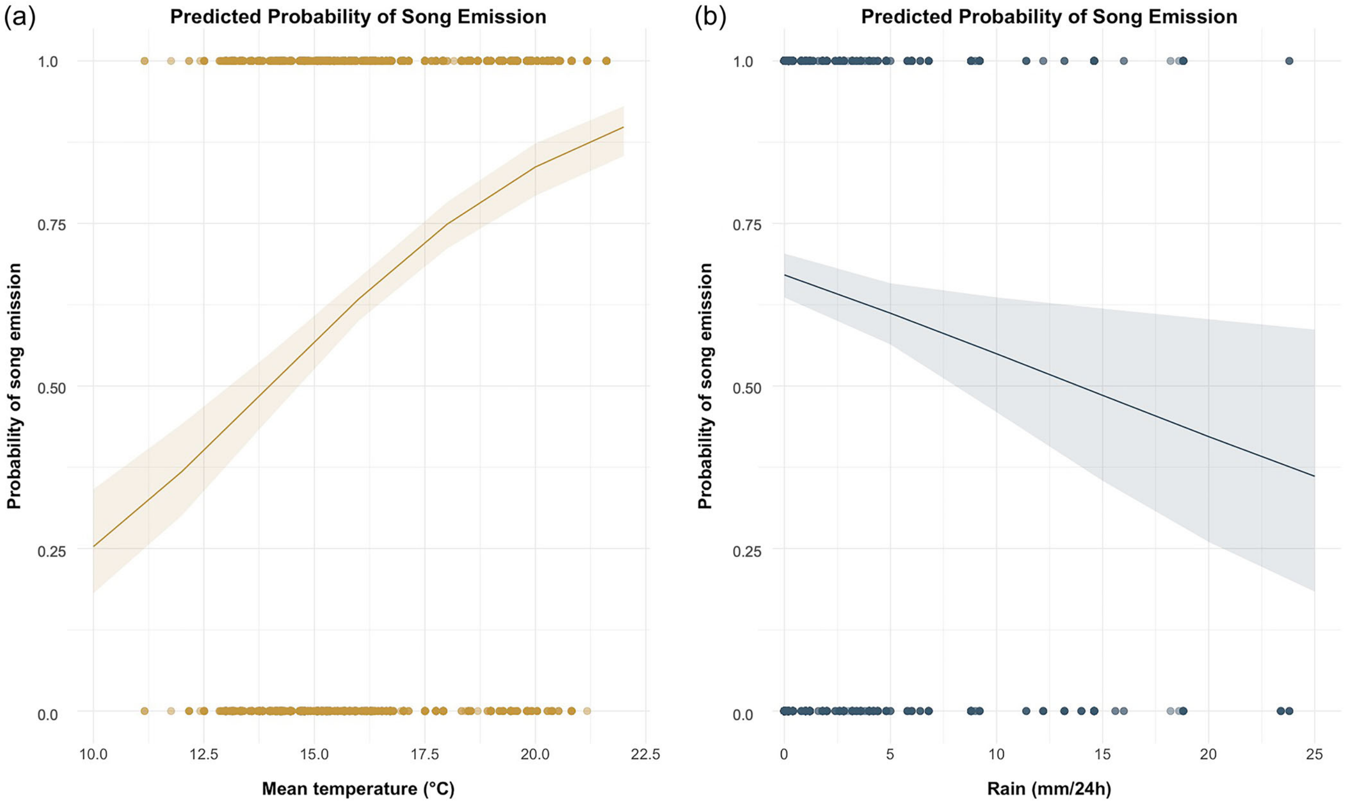

FIGURE 3 Effected plot showing the predicted probability of song emission taken from the GLMM looking at the effect of temperature (°C, a); and rain (mm/24 h, b). Shaded areas indicate confidence intervals.

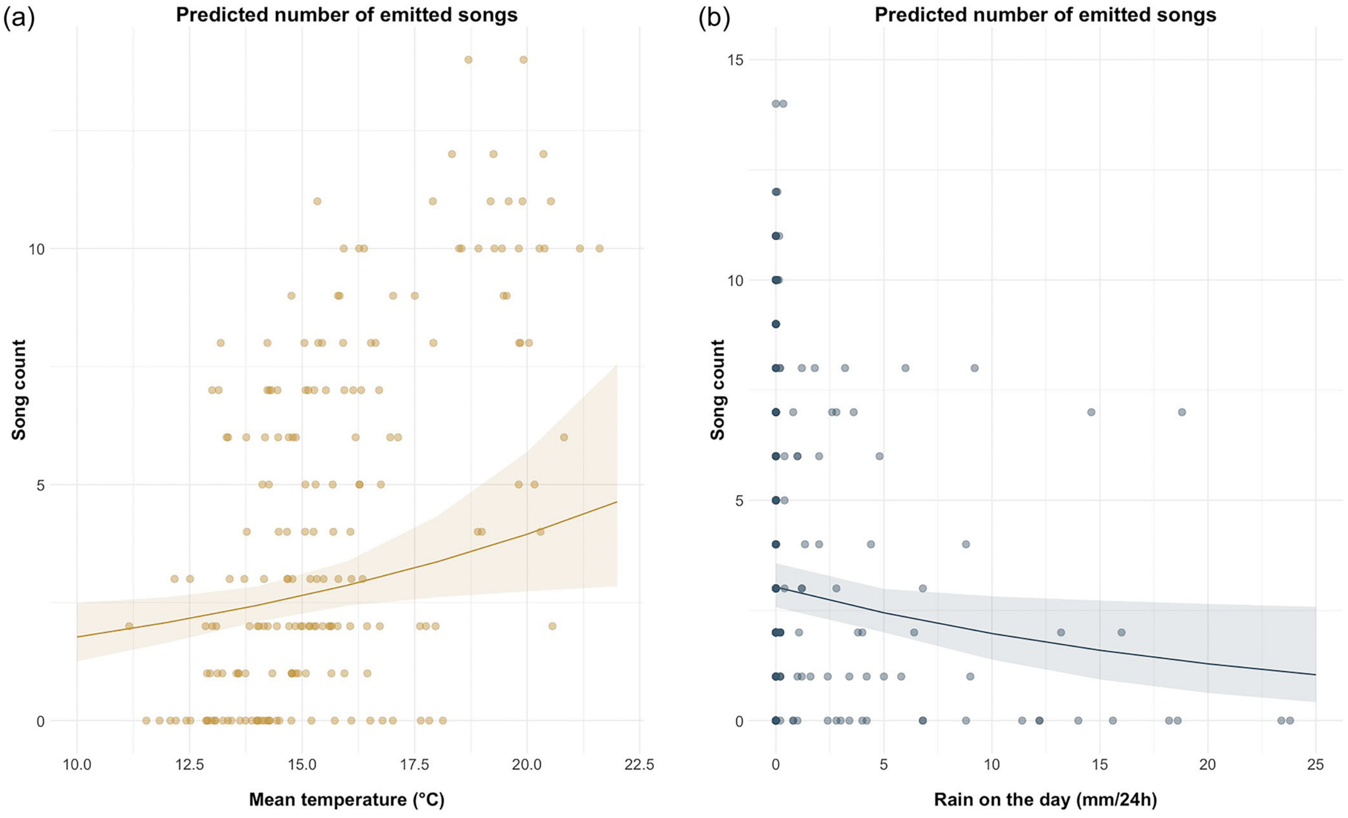

FIGURE 4 Effected plot showing the predicted number of songs emitted taken from the GLMM looking at the effect of temperature (°C, a) and rain (mm/24 h, b). Shaded areas indicate confidence intervals.

(estimate = −0.409; se = 0.179), year (estimate = 0.888; se = 0.129) and the interaction between overnight rain and temperature (estimate = −0.389; se = 0.159). Speaking of odds, the model revealed a significant association a 1°C increase in temperature is linked to a 29.7% increase in the odds of detections, while each 1 mm increase in rain corresponds to a 2.9% decrease.

3.3 | Influence of environmental variables on song timing

Among the models on song timing, the best-fitting model, according to AIC comparison (for Supporting Information S1: Table SU3), included the temperature (estimate = 0.091; se = 0.017) and rain (estimate = 0.033; se = 0.014). The second best-fitting model included the temperature (estimate = 0.086; se = 0.018), rain (estimate = 0.004; se = 0.037) and the interaction between them (estimate = − 0.023; se = 0.027).

We narrowed our analysis to focus specifically on morning calls, establishing a time constraint encompassing 92% of our song data set, equivalent to 581.7 min after dawn or the period before 14:00 (Figure 5). Our hypothesis that the positive correlation between temperature and song timing could be attributed to afternoon songs driving this choice, which, based on our field experience, are predominantly observed out of the reproductive period, when temperatures are notably warm.

When the data set is centered on morning observations, the best-fitting models' results appear to support our hypothesis (Supporting Information S1: Table SU4). Notably, the best-fitting model incorporates only rainfall as a significant factor (estimate = 0.011; se = 0.004).

4 | DISCUSSION

This study conducted an in-depth exploration of the relationship between environmental factors and the singing behavior of *Indri indri* within the Maromizaha New Protected Area in Madagascar. Our

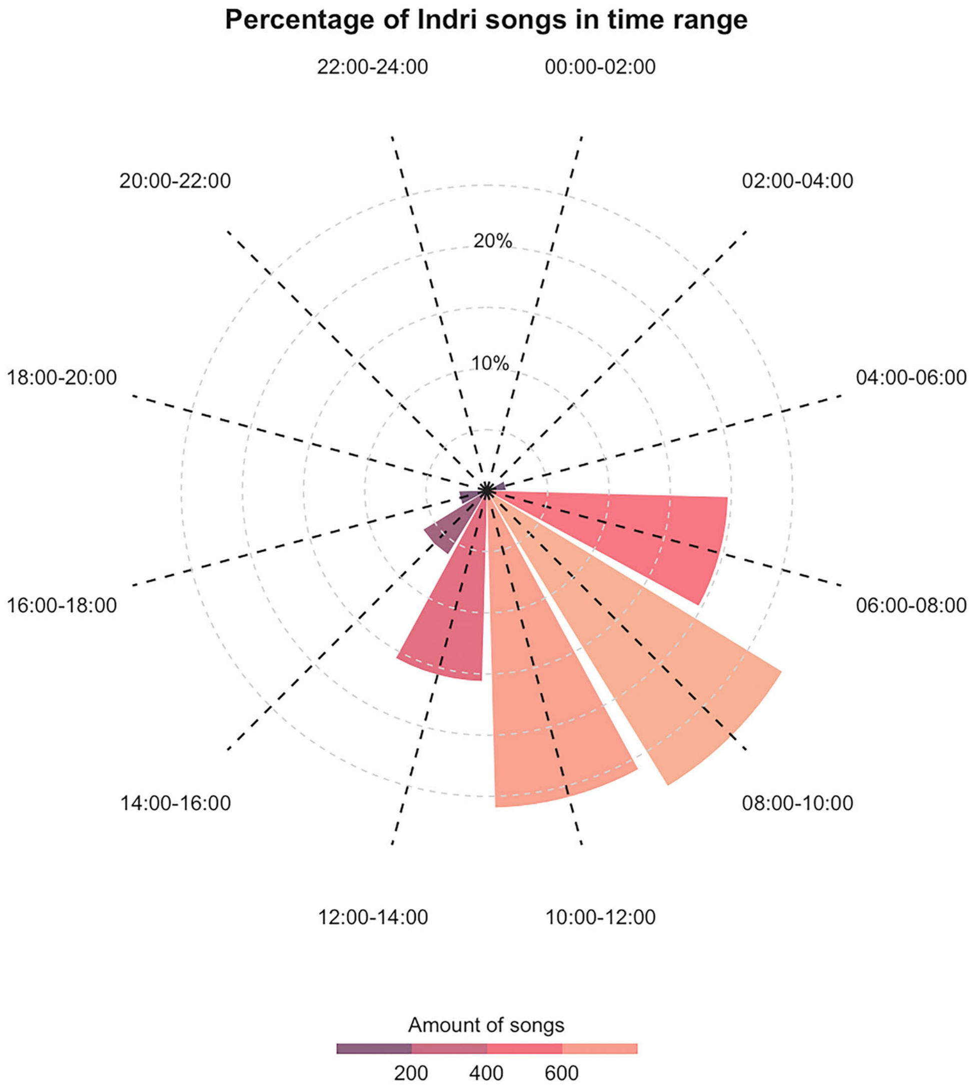

FIGURE 5 The number and percentage of songs produced by the indris in different time ranges. The dotted gray lines represent the percentage of the songs in that time range for the total number of songs detected. Colors denote different numbers of songs.

primary aim was to unravel the factors affecting the vocalization patterns of the indris. One of the most noteworthy findings of our study is that temperature and rainfall affect the production of the indris' songs, which supports our initial hypotheses. Our research revealed a relationship between rainfall and vocal activity. Indeed, while temperature positively affects song production, indris sang less on rainy days, showing a critical effect of the interaction between rain and temperature.

In nonhuman primates, vocal activity may depend on environmental and physiological factors associated with the callers' body temperature and energy levels (i.e., after a cold night, animals may need to replenish their energy reserves and prioritize finding food over other activities; Whitten, 1982). When considering both the presence or absence of songs or the songs' count, the interaction between rain or overnight rain and temperature was significant in our study: higher temperatures mitigated the negative effect of rain on indri songs. Our results are in agreement with findings on Bornean white-bearded gibbons (Cheyne, 2008), Mueller's Bornean gibbons (Clink et al., 2020), guereza colobus monkeys (Schel & Zuberbühler (2012), and black and gold howler monkeys (Pérez-Granados & Schuchmann, 2021). In adverse weather conditions, singing can be energetically costly, as suggested by previous studies considering low temperatures and rainy nights (Cowlishaw, 1996; Whitten, 1982). Similarly to our findings in the indris, Carolina wrens (*Thryothorus ludovicianus*) sang more on days when the ambient temperature was higher, which may be due to a trade-off between singing behavior and time allocated to foraging (Strain & Mumme, 1988). Birds may likely spend more time feeding on colder days, thus singing less to limit energy expenditure.

In line with the idea that overnight rain constrains energy expenditure, we also found that the rain on the preceding night negatively affected the number of songs given but not the overall occurrence of the song. Thus, we can hypothesize that the indris may sing once after a cold rainy night, but then they barely move from their singing point and do not need to advertise their position later on. However, we cannot rule out an effect of sound propagation on the probability of the songs being recorded by a particular device, and further data on sound attenuation across different weather conditions in tropical rainforests is needed (Fricke, 1984; Marten & Marler, 1977).

We found an effect of temperature and rainfall concerning the timing of song emission. This result agrees with findings in Kloss's gibbons duets (*Hylobates klossii*; Clink et al., 2020) and agile gibbons (*Hylobates albibarbis*, Cheyne, 2008). Even if the indris show a consistent time window for song emission (Figure 5, but also Ravaglia et al., 2023), the timing of the songs is shifted later in the day if it rains more and the temperature is higher. Our data accurately evaluate the timing of morning calls, with a maximum estimation delay of 20 min, in relation to environmental factors. From a statistical perspective, it appears that calls are detected earlier in the morning when the weather is cooler and drier. Still, when we focussed only on mornings, we found, as expected from the above results, that rainfall influences the timing of song emission (i.e., when it rains more, indris emit songs later). Our findings corroborate the idea that songs play a critical role in advertising the presence of the indris in a particular area of their territory (Bonadonna et al., 2014, 2017). The indris' song emission does not strictly correlate with the presence in a particular zone (Bonadonna et al., 2020). Still, it primarily relates to the amount of activity and movement, which may be dramatically influenced by temperature and rainfall. We know that overnight rain can significantly impact the weather the next day. It can create more cloud cover in the early morning, keeping temperatures cooler by blocking the sun's rays (Sun et al., 2000). However, the increase in moisture can trap more longwave radiation, leading to warmer conditions in temperate environments (Zhao et al., 2018). This is unlikely to happen in the rainforest, where humidity is always high, and it makes sense that overnight rains do not affect activity and behavior later in the day.

Lunar phases do not significantly affect the indris' singing behavior. While limited research exists on the impact of moonlight on primate vocalization, Reyes et al. (2021) conducted a study on two gibbon species (*Hylobates moloch* and *Hylobates pileatus*), demonstrating that higher lunar illumination correlated with more overnight activity. Future research may investigate a connection between lunar phases and singing behavior, disentangling the role of seasonality.

PAM, in combination with weather stations, can be critical to understanding how activity and singing are related and essential for conservation efforts. This study confirms that PAM can be crucial in studying animal behaviors beyond monitoring species' distribution, presence, and density. Quantifying and understanding behavior can help understand and act upon their ecology and ensure lemur conservation.

Our study focused on a limited timeframe in the Maromizaha New Protected Area during the dry season. We acknowledge that other factors may come into play when analyzing data from a whole year, especially considering the severity of weather conditions that can be found during the wet season in this geographic area due to cyclones. This study is of significant importance because it examines how this critically endangered species responds to average seasonal weather and provides a tool to aid in conserving this species in the face of intensifying weather conditions worldwide driven by climate change.

AUTHOR CONTRIBUTIONS

Valeria Ferrario: Conceptualization (equal); data curation (equal); formal analysis (equal); methodology (equal); visualization (equal); writing—original draft (equal); writing—review and editing (equal). **Teresa Raimondi**: Formal analysis (equal); methodology (equal); writing—review and editing (equal). **Chiara De Gregorio**: Writing—review and editing (equal). **Filippo Carugati**: Writing—review and editing (equal). **Walter Cristiano**: Writing—review and editing (equal). **Rebecca N. Lewis**: Writing—review and editing (equal). **Daria Valente**: Writing—review and editing (equal). **Leah J. Williams**: Writing—review and editing (equal). **Claire Raisin**: Supervision (equal); writing—review and editing (equal). **Marco Gamba**: Conceptualization (equal); methodology (equal); supervision (equal); writing—original draft (equal); writing—review and editing (equal). **Achaz Von**

Hardenberg: Supervision (equal); writing—review and editing (equal). **Cristina Giacoma**: Supervision (equal); writing—review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available, together with the R code we used for the analysis, in a GitHub repository that can be found in the Supporting Information of the paper.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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