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Environmental drivers of calling activity in the critically endangered lemur leaf frog, *Agalychnis lemur* (Hylidae: Phyllomedusinae)

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Tropical frog species are known to exhibit high sensitivity to weather regime alterations, which leaves them vulnerable to ongoing climate change. This challenge is exacerbated by limited knowledge of species-specific responses to environmental change. We integrated passive acoustic monitoring and automatic signal detection to investigate the environmental underpinnings of calling activity of the critically endangered lemur leaf frog, *Agalychnis lemur*. We combined template-based detection with machine learning mitigation of false positives to infer the calling activity of a lemur leaf frog population across 18 months. We used directed acyclic graphs to determine the covariates needed to infer causal relationships between environmental variables and calling activity. Our findings revealed that daily temperature has a strong direct positive effect on calling activity, with additional indirect effects mediated by relative humidity. Moreover, higher activity of the lemur leaf frog was triggered by increasing humidity independently of temperature, and by accumulated rainfall within the preceding 24 h and by decreased moonlight. This study provides insights into the complex interplay of environmental factors for determining calling activity in frogs. Our findings underscore the potential of passive acoustic monitoring for elucidating frog population activity and its responses to environmental changes, which can be valuable for understudied species in the context of climate change.

This article is part of the theme issue 'Acoustic monitoring for tropical ecology and conservation'.

1. Introduction

The alarming trend of population declines and extinctions among amphibian species worldwide presents a significant challenge for their conservation efforts, further exacerbated by the limited knowledge of species-specific susceptibilities to environmental change [1,2]. Nearly 60% of the world's threatened amphibian species are found in the Neotropics, of these, 92% face elevated levels of habitat loss and one-third are distributed in areas with low levels of rainfall and humidity [3]. As ectothermic organisms, amphibians rely on environmental cues to regulate most physiological processes and behaviours [4,5]. In this scenario, short-term variations in weather or environmental factors can significantly impact amphibian performance, affecting reproductive success and making them especially vulnerable to human-induced environmental changes (i.e. habitat fragmentation) that alter microclimates with direct consequences for population dynamics [6–8]. Therefore, developing strategies to mitigate these impacts and implementing research tools enabling cost-efficient monitoring of endangered species are essential in addressing amphibian conservation challenges and safeguarding their ecosystems [9–11].

For animals whose communication and reproductive interactions largely rely on acoustic signals, as is the case of amphibians, passive acoustic monitoring (hereafter PAM) methods can be used to register vocal activity over extensive temporal and/or spatial scales [12,13]. PAM methods allow researchers to gather high-resolution data on calling activity, which can be influenced by several environmental variables [14]. This tool is particularly valuable in conservation efforts, as PAM can help quantify behavioural responses to environmental changes, assess the acoustics of little known or rarely seen species and thus identify priority conservation areas [15–17]. By integrating PAM with traditional ecological methods, scientists can improve their capacity to understand population dynamics in changing environments [18,19].

One of the main advantages of PAM is its capacity to generate large amounts of acoustic recordings [18]. This provides more precise answers to questions about activity patterns by offering continuous and systematic data [13,20]. However, the analysis of acoustic datasets has traditionally relied on human observers to visually identify acoustic signals in spectrograms [21]. Data curation under this approach is therefore subjective and time consuming, a problem that is only amplified in data-rich PAM studies [21]. Automated detection approaches of acoustic signals allow solving of many of these issues, as they are in principle verifiable, reproducible and can handle large amounts of acoustic data [14,18]. Thus, the combination of PAM and automated detection pipelines can offer a robust and efficient approach for the monitoring of highly vocal species [22,23].

Environmental factors can affect the vocal activity of frogs in diverse ways. First, rising evapotranspiration increases the likelihood of rainfall, which in turn increases relative humidity [24]. High relative humidity can support a higher rate of calling activity by reducing desiccation risk [7]. Second, higher ambient temperature decreases relative humidity, as warmer air holds more moisture. Calling activity can therefore be negatively affected by a rise in local temperature [25]. By contrast, temperature directly influences metabolic rates in ectotherms, potentially increasing vocalization rate and energy expenditure in frogs [5,26–28]. Therefore, temperature may also directly intensify calling activity [29].

In addition, rainfall can strongly influence calling activity, and its effect can vary across temporal scales [10]. Preceding rainfall boosts relative humidity through evaporation, positively impacting calling activity [30]. Both daytime and night-time rainfall contribute to increased humidity, further promoting calling behaviour. However, rainfall also lowers local temperatures, affecting frog calling activity through the metabolic processes described above. Moreover, it is known that heavy rains can dampen sound quality, potentially leading to decreased calling rates if frogs need to invest more energy for producing louder calls that can be detected by conspecifics [31]. Similarly, moonlight can affect calling activity because the lunar synodic cycle (i.e. the transition from one new moon to the next new moon) changes the brightness of lunar light that can be perceived by animals [32]. Most frog species are nocturnal and are at risk of visually oriented predators [33]. This predation risk is maximized during nights of high moon illumination that facilitate visual predators to locate their prey.

In this work, we quantified the calling activity of the critically endangered lemur leaf frog, *Agalychnis lemur* over an 18 month period aiming to understand the effect of weather and moonlight variations on the calling behaviour of this species. We used graphical causal modelling in a directed acyclic graph (DAG) for depicting the array of potential causal pathways in the system [34]. This approach allowed us to explicitly represent our hypotheses of the causal relationships between environmental factors and calling activity and to derive the models to statistically evaluate these relationships [34,35]. Our results provide valuable insights into the climatic underpinnings of reproductive behaviour in an endangered and poorly known species and demonstrate the effectiveness of bioacoustic approaches for understanding key aspects of the species biology in a context of growing threats to biodiversity.

2. Methods

(a) Study species

The lemur leaf frog is an arboreal nocturnal species distributed in tropical rainforests of Costa Rica, Panama and Colombia from 440 to 1600 m.a.s.l. [36]. The species is currently restricted to a few populations across the Talamanca Mountain Range in Costa Rica and western Panama, and it is classified as critically endangered, with deforestation, chytridiomycosis infection and habitat loss as its main threats [37–39]. Its call consists of a short single note with a duration of 200–290 ms and a dominant frequency that ranges from 2272 to 2520 Hz [36]. We focused on the advertisement call because of its mating role, which makes it a proxy for breeding activity.

(b) Study site and weather data collection

We conducted the study at Veragua Rainforest (9.924819° N, −83.191206° W; 420 m.a.s.l.), a 13.7 km² private reserve in the Central Caribbean region of Costa Rica, situated on the northern edge of the Matama Mountains within the Talamanca Mountain Range. This reserve falls within the Basal Tropical Wet Forest life zone (200–600 m.a.s.l.) as described by Holdridge [40], and features a mix of mature forest, secondary vegetation at various stages of regeneration, open areas and dirt roads [41].

Data were collected in an area with five experimental ponds established in 2012 (length 200 cm, width 150 cm, depth 50 cm) as a habitat restoration programme that aimed to serve as *in situ* breeding sites for the different frog species inhabiting the area and where the species was previously detected [41]. We obtained weather data from a station located 300 m from the study site. While a degree of microclimatic differences probably exists at this spatial scale, we note that the weather station was located within the same patch of continuous rainforest as the study site and at a height above ground (8 m) at which these arboreal frogs are commonly found. The station registered temperature (°C), relative air humidity (%) and rainfall (mm) every minute. From these data we estimated the average values for each 15 min recording interval (see the detailed description below) and the accumulated rainfall during the 48 and 24 h previous to each sampling event. We obtained the moonlight intensity during those periods using the R package *LunaR* [42] which was used to estimate the percentage of lunar illumination per night based on the site's geographical location and the date of recording.

(c) Acoustic monitoring and call recognition

We recorded the advertisement calls of the lemur leaf frog through passive acoustic monitoring using the SM4 digital sound recorder [43]. These were placed at a height of 2 m above the ground, with a distance of 7 m between the device and the experimental ponds.

The sampling period spanned 18 months, from July 2019 to February 2021. We set the recorder to collect acoustic data daily from 18.00 to 5.00 h the following morning, coinciding with the expected reproductive activity of nocturnal species like the lemur frog [44]. The equipment was programmed to record for 15 min every 20 min (with a 5 min resting period), resulting in three 15 min samples per hour. Recordings were stored in WAV stereo format at a sampling rate of 44.1 kHz and a 16-bit amplitude resolution. Afterwards we split each recording into 5 min clips and resampled at 10 kHz to enhance computational performance during further analysis.

We used a template detector model in the R package *ohun* (v. 1.0.1) [45,46] to automatically detect advertisement calls of the lemur leaf frog in our recordings. The automatic detector was trained with recordings used in this study and from others recorded at an additional site that hosts another population of the lemur leaf frog in order to improve detection performance [41]. We selected a subset of recordings to be used as the training dataset, using stratified random sampling to ensure a balanced representation across months, weeks, hours and 4 h sampling periods. Then, two recordings were randomly chosen from each level of a full factorial combination of these factors.

The resulting training dataset consisted of 467 recordings. We annotated all visually identifiable lemur leaf frog calls on the Fourier spectrograms of these recordings using the RAVEN software [47], noting the start and end times and frequency range of each call. These annotations were then imported into R [46] using the *Rraven* package [48] and processed in the package *warbleR* [49] to ensure precise time and frequency positioning of the signals.

The template-based detection routine identifies sounds similar to template sounds using spectrographic cross-correlation. Therefore, detection performance usually varies among templates. We evaluated three acoustic templates in order to select the template with the best performance. We selected a set of templates that represented the structural diversity of calls. For this the *warbleR* package was used to measure 23 spectral features (related to the distribution of power in time and frequency; see the electronic supplementary material, table S1) representing the acoustic structure of the manually annotated calls. We selected three candidate templates: two were calls with parameters closest to the mean duration and mean frequency, respectively, and the third was the call closest to the mean of the first component from a principal component analysis (PCA) on z-transformed acoustic features.

We trained the template-based detection routine on the annotated recordings, serving as a reference dataset for evaluating its performance. We identified as signals of interest those sounds in which correlation with the template surpasses a predefined threshold. The three candidate templates were tested across 20 correlation thresholds ranging from 0.1 to 0.9. The template with the best performance was determined based on recall and precision metrics. Recall measures the ability to identify signals of interest, while precision indicates the routine's ability to exclude non-target sounds [50]. Hence, an efficient detection routine should maximize recall and precision, and this criteria used to guide correlation threshold selection. However, as low precision can be mitigated in further analysis (see below), we favoured a threshold that improved recall performance despite having a poor performance in precision.

After applying the selected correlation threshold for defining detections, we implemented a machine learning approach to mitigate incorrect detections [51]. For this secondary filter, we trained a supervised random forest (RF) classification model [52] using the R package *ranger* [53]. The RF model identified the lemur leaf frog calls based on acoustic features, measuring the same spectral features used for selecting templates in addition to statistical descriptors of Mel-frequency cepstral coefficients (MFCCs) using *warbleR*.

Cepstral coefficients represent perceptually relevant features as they are derived from spectral bands that resemble sound representation in animal auditory systems and have been widely used in human speech recognition and increasingly in non-human animals [54–58]. We measured 25 cepstra on 10 warped spectral bands, analysing the minimum, maximum, mean, median, skewness, kurtosis and variance of each MFCC, along with the mean and variance of their first and second derivatives. The RF model was trained with 1000 trees and mtry (number of features considered for splitting trees) of 13 variables. The out-of-bag error (OOB) was used to evaluate classification performance.

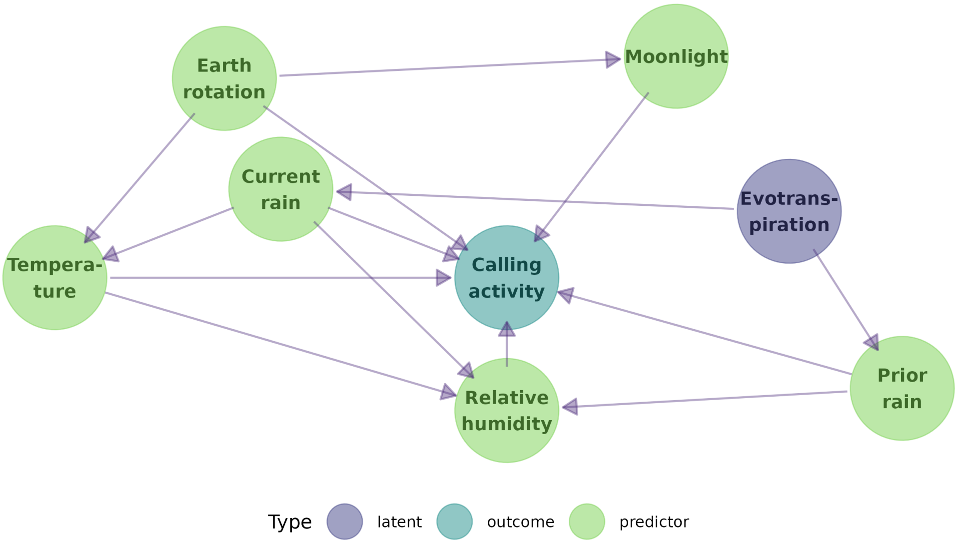

Figure 1. Directed acyclic graph (DAG) illustrating the hypothesized causal pathways between environmental variables (temperature, rainfall, relative humidity and moonlight) and the calling activity of the lemur leaf frog. Our DAG includes two types of variables: observed variables which were measured in the field, such as 'temperature' and 'relative humidity' and a latent variable, evapotranspiration, which was not measured. The stage of Earth's rotation is represented in our data as a continuous value between 0 and 24 h.

(d) Causal modelling

Environmental factors which may influence the calling activity of the lemur leaf frog are part of a complex system in which factors are also causally related to each other ([34]; figure 1). Causal models can help to understand these complex systems by explicitly stating relationships among variables [35]. In this study, we used DAGs to determine which variables should be included or excluded in order to estimate causal effects of interest without introducing bias (figure 1; [34]).

We were interested in the effects of temperature, rainfall, relative humidity and night illumination on frog calling activity. Our DAG hypothesizes that the effect of temperature can be direct, via effects on frog metabolism, or indirect by affecting relative humidity (figure 1). Rainfall was expected to affect calling activity through two time frames: 'current rainfall' which refers to the cumulative rainfall during the hour before a sampling event and 'prior rainfall' which represents the precipitation during previous days (figure 1). Current rainfall was expected to have a positive effect on frog calling activity by increasing relative humidity and a negative effect through a decrease in temperature (figure 1). Prior rainfall might increase activity by expanding breeding micro-habitats (e.g. ponds) and by increasing relative humidity (figure 1). Prior rainfall was represented by two variables that measured the 24 h cumulative rainfall in two different periods: on the day prior to each sampling unit, and 2 days prior to each sampling unit. The two prior rainfall variables were modelled in separate analyses in order to determine the most relevant period for calling activity. We then estimated the direct effects of relative humidity and nocturnal light on frog calling activity.

Our DAG depicts additional causal relationships that are not of particular interest in this study but inform our variable selection process required for unbiased estimation of the causal effects. First, by controlling sunlight hours, the earth's rotation may influence calling activity both directly, and indirectly, via effects on temperature. The Earth's rotation also interacts with the moon's rotation and thus influences nocturnal illumination. The Earth's rotation was modelled as the time of the day for statistical analyses. Similarly, evapotranspiration represents the total water loss to the atmosphere preceding cloud formation and eventual rainfall and thus also influences relative humidity. In our DAG, evapotranspiration is an unmeasured (latent) variable that affects both current rainfall and prior rainfall.

(e) Statistical analyses

For each predictor, we determined the set of variables (i.e. adjustment set) that allow for the asymptotic estimation of unbiased causal direct and total effects on call rate, using the R package *daggity* [59]. Direct effects represent the predictor's effect on the response that is not mediated by any other variable, while total effects take into account both direct effects and those mediated by other variables. The difference between the two effects provides evidence of the mediated (indirect) effects.

Variables in the adjustment sets were used as predictors in regression analyses. Regressions were fitted for each environmental variable (temperature, relative humidity, current rainfall, prior rainfall and moon illumination) using Bayesian generalized linear models in the R package *brms* [60]. The models accounted for temporal autocorrelation (i.e. the dependency among observations close to each other in time) using an autoregressive moving average correlation structure, with time of the day (discretized in 1 h periods) as the grouping variable. We modelled calling activity as a rate of calls per hour using a negative binomial distribution with a logarithmic link function. All predictor variables were zero-centred and transformed to unit variance.

When several adjustment sets existed for modelling a predictor's effect, the posterior distribution of the correspondent models were averaged, weighted by their predictive performance using a stacking leave-one-out cross-validation approach [61].

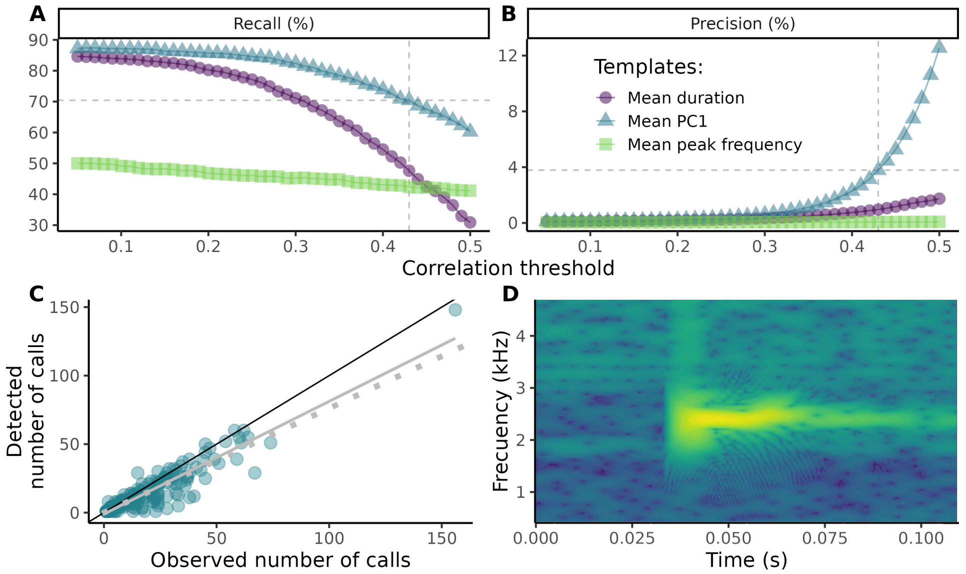

Figure 2. (A) Recall and (B) precision across increasing correlation threshold values for the three acoustic templates in the detection procedure. We selected template calls as those closer to the mean value of three acoustic features: duration, peak frequency and the first vector from a PCA summarizing several spectro-temporal features. Dashed grey lines show the selected correlation threshold (0.43) and correspondent recall (A) or precision (B) value. (C) Scatterplot showing the number of calls observed on each 5 min clip used for training and those found by our detection procedure (template detector + random forest mitigation of false positives). The black line is the 1 : 1 diagonal. The solid grey line shows the best fit line from a linear regression on the entire data (slope: 0.82) while the dotted grey line shows the best fit line when excluding the outlier (slope: 0.76). (D) Spectrogram of the lemur leaf frog call.

Effect size estimates were transformed into percentage of change to facilitate interpretation and are presented as medians of posterior distributions and 95% uncertainty intervals (UI). Parameters in which intervals did not include zero were regarded as affecting the calling rate. Models were run for 10 000 iterations, following a warm-up of 10 000 iterations on four Markov chain Monte Carlo chains. For all parameters, the effective sample size was maintained at or above 4000. We plotted the trace and distribution of posterior estimates for all chains for visual evaluation of model performance. In order to assess the independence of the posterior samples, we also inspected the autocorrelation of successive sampled values and estimated the potential scale reduction factors for checking model convergence (kept below 1.01 for all parameter estimates).

3. Results

Across the entire sampling period, from which we examined a total of 370 718 calls in 1707 h of recording, we recorded an average of 27 vocalizations h^{-1}. The vocalization of the lemur leaf frog consists of a single, non-frequency modulated call with amplitude modulation, emitted by males from the leaves and branches of vegetation surrounding swamps and other similar lentic environments, at heights ranging from 30 cm to 1.5 m. The call is tonal, with the amplitude peak typically located at the beginning of the call duration, depicting a triangular-shaped call in the spectrogram. The frequency bands exhibit no significant modulation throughout the call duration.

The performance of the acoustic templates (mean peak frequency, mean duration and mean PCA1) for detecting the lemur leaf frog calls varied importantly according to the performance metrics recall and precision (figure 2). The mean PCA1 was chosen to be used as the template in subsequent analysis given its positive balance between the two performance metrics (70.4% recall and 3.7% precision with a 0.43 correlation threshold). After RF mitigation of false positives (OOB error rate of 0.88%), we obtained a 67% recall and 91% precision. The observed number of calls on the 5 min clips in the training dataset and the number of calls found by our detection procedure were highly correlated (Pearson correlation score: 0.92; 0.89 after removing the outlier).

For the accumulated rainfall during the 24 h prior to sampling, we found a positive direct effect (effect size: 10%; UI: 5.8–14.7%; figure 3) and total effect (effect size: 9.1%; UI: 5.2–13.6%; figure 3) on calling activity, whereas accumulated rainfall during the day 48 h before sampling did not have a detectable influence on calling (direct effect: 0.62%; UI: −2.9 to 4.1%; total effect: 0.54%; UI: −3.3 to 4.4%). Therefore, results hereafter are based on models using prior 24 h accumulated rainfall whenever prior rainfall was included in the adjustment set for other effect estimates. Temperature had the largest positive direct effect on calling rate (effect size: 77%; UI: 65.1–92.5%; figure 3), followed by relative humidity (effect size: 37.0% 27.0–47.0%; figure 3), while moonlight showed a negative direct effect (effect size: −12.0%; UI: −17.1 to 6.2%; figure 3). We did not find a detectable direct effect of current rainfall on calling activity (effect size: 3.6%; UI: −0.01 to 7.9%). Total effect sizes were similar to direct effect sizes for all predictors (24 h prior rainfall: (9.1%; UI: 5.1–13.5%); 48 h prior rainfall: 0.54% (−3.2 to 4.4%); moonlight: −9.6% (−15.6 to 3.9%); current rainfall: 3.6% (−3.3 to 3.5%); figure 3) except for temperature (36.1% (29.4–43.4%); figure 3).

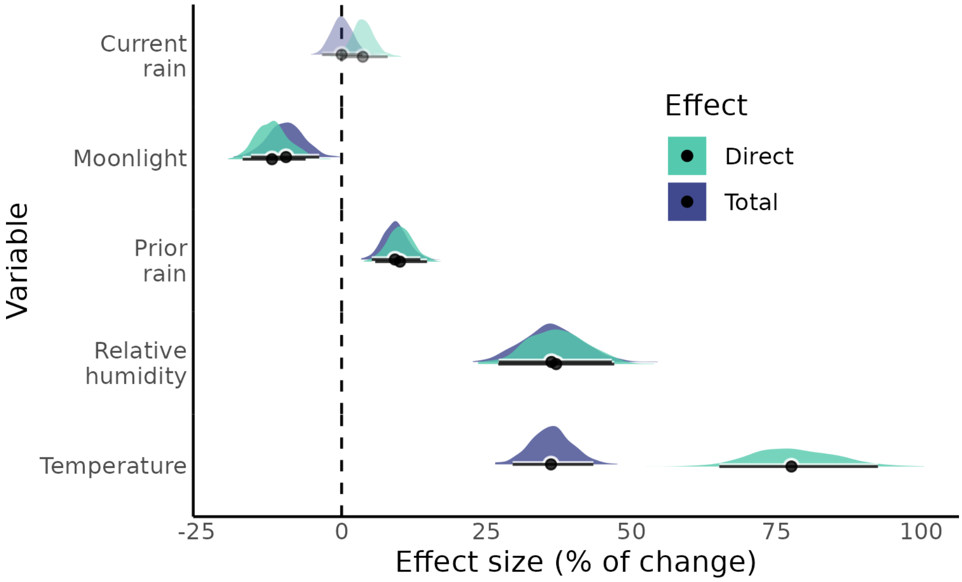

Figure 3. Posterior distribution of direct (green) and total (purple) effect sizes of environmental factors on the calling activity of the lemur leaf frog. Posterior values were transformed into percentage change to facilitate interpretation. Dots and error bars show the median and 95% uncertainty intervals of the distributions. Solid colour distributions correspond to effect sizes in which uncertainty intervals do not include zero. 'Prior rain' accounts for the 24 h period before sampling calling activity.

4. Discussion

In this study, we aimed to untangle the causal effects of several environmental variables on the calling activity of the lemur leaf frog, using PAM combined with an automatic detection technique. We provide quantitative evidence of the way in which environmental variation shapes calling activity. We found that calling activity is mainly triggered by the increase in temperature and relative humidity, as well as by the rainfall accumulated during the day before, although this effect is only moderate. On the contrary, the calling rate of this species decreases during luminous nights and, in general, is not affected by current rainfall. More broadly, our results demonstrate the potential of monitoring efforts that passively collect information in a continuous and systematic manner, to gain insights into the ecological drivers of reproductive behaviour in natural populations.

The precision of our automated detection procedure allowed us to accurately infer variation in call activity. Despite having a moderate performance for detecting individual calls (67% recall), our approach succeeded in predicting call activity in 5 min intervals with high accuracy (figure 2C). The applied routine for call detection is relatively simple compared to recently developed deep learning approaches [14]. However, RF, the algorithm used for mitigating incorrect detections, stands as a highly robust machine learning classification method [62]. Overall our results demonstrate that traditional bioacoustic methods can be boosted by combining them with classification approaches that are already familiar to ecologists in order to drastically improve automated detection in PAM studies.

The lemur leaf frog is a prolonged breeder [63]. This strategy is characterized by linking their energy allocation to advertisement calling, which are influenced by local environmental cues [9,64,65]. Our results indicate that the calling activity of lemurl leaf frogs responds to environmental conditions on a short timescale, especially temperature and humidity, whereas prior environmental conditions such as those of cumulative rainfall from previous days are less relevant. Importantly, variation in calling rate may indicate changes in the number of frogs that attend the chorus, the calling rate of individual males, or both. The goal of this and other PAM studies is ultimately to use calling rate as a proxy of reproductive activity, to which both chorus attendance and individual calling rate probably contribute [44,66–68]. Thus, future studies that integrate PAM with direct observations of calling and reproductive behaviour can probe into the adequacy of PAM data as a proxy, given this potential caveat.

Temperature had a direct positive effect on calling activity (figure 3), as expected if calling activity responds to a general increase in metabolic rate [27]. Temperature was also expected to have a negative effect on calling activity, mediated by a reduction in relative humidity. The total effect of temperature on calling activity was substantially smaller than its direct effect estimate, suggesting a negative indirect effect through relative humidity (figure 1). Thus, while our data support this dual mechanism, the net effect of temperature on calling activity was positive.

The skin of arboreal leaf frogs is particularly resistant to evaporative water loss [69–71], which may allow them to tolerate relatively dry conditions, compared to other frogs, and exhibit an overall positive response to high temperatures [29]. It is plausible, however, that in the face of climate change, frogs will be exposed to a wider range of temperatures, in which the relationship between temperature and calling rate is unlikely to remain unaltered [25,27]. Thus, the indirect negative effect of temperature may be amplified by global warming, while the direct positive effect on calling rate may not [30,72]. While in the current temperature ranges warmer conditions seem to favour reproductive activity, our finding of two opposing effects of temperature on calling activity suggests a possible mechanism for the effect of total temperature to be reduced or even change direction with climate change [73].

Our findings that temperature and relative humidity have the largest effects on the calling activity of the lemur leaf frog are also consistent with previous studies in other tropical frogs [10,25,30,74–76]. Frog vocal activity is probably maximized at a temperature that is high enough to promote calling but that does not reduce humidity to the point of risking desiccation or where a large input of water, such as heavy rainfall during day time, is available to maintain a humid environment [27,77]. In our study site, the relative humidity was 90% on average, which probably enables a relatively continuous year-round calling activity of lentic breeders like the lemur leaf frog [76].

Our findings show that rainfall affected the acoustic activity of lemur leaf frogs, but interestingly, these effects seem to vary across temporal scales. A rainy period of a few days or even hours can elicit migration to reproductive areas, in species that depend on temporary ponds to reproduce, particularly for explosive breeders [63]. Lemur leaf frogs reproduce in both temporary and permanent pools [78]. In addition, adult frogs are often observed resting during the day near this permanent water resource, suggesting that they can quickly relocate to the reproductive sites when necessary. Consistently, we found that rainfall accumulated during the prior 24 h influenced the calling activity of the lemur leaf frog, but effects from 48 h prior rainfall were undetectable. Alternatively, the total effect of prior rainfall could be because of an increase in relative humidity in the coming night. However, the similarity between total and direct effects for prior rainfall suggests little indirect effects through mediator variables. Our results are therefore consistent with a direct but short-term effect of prior rainfall on calling activity.

Calling activity is thought to be influenced by lunar light in some species, but not others [36,78–80]. The lemur leaf frog seems to exhibit lunar phobia, with activity peaking during the darker evenings. Other species such as *Engystomops pustulosus*, *Boana albopunctata* and *Rana dalmatina* present greater calling activity on illuminated nights [33,80,81]. This behaviour is associated with species that rely on visual communication to reproduce and to identify potential predators [32]. Future research assessing the moon's influence using other more direct measures of reproductive activity, such as the occurrence of amplexus and the number of egg masses laid per night [81] could help disentangle the influence of environmental light on amphibian reproductive behaviour.

Our study makes two significant contributions to a growing literature on the acoustic responses of tropical frogs to environmental variation (e.g. [30,65,82,83]). First, we build on an explicit causal framework (figure 1) to obtain unbiased estimates of environmental effects on the calling activity of the lemur leaf frog. Our causal model provides a foundation for future work contrasting acoustic responses from species that differ in their physiological sensitivities to abiotic stressors, such as rising temperatures and reduced humidity. Second, our PAM approach, coupled with automated call detection, enabled the quantification of these acoustic responses at a high temporal resolution and over a relatively long time period of uninterrupted sampling. Such an approach is crucial for building a nuanced understanding of the effects of the abiotic environment on frog calling activity [44,67]. Thus, our results imply that conservation actions in response to climatic changes will benefit from integrating PAM and automated call detection over longer timescales.

Protecting habitats with suitable environmental conditions is essential for the remaining populations of the lemur leaf frog. Given that weather variables impact the calling behaviour and associated reproductive activity in this species, we recommend the implementation of conservation strategies that consider monitoring of microclimatic factors, including humidity, temperature and regular rainfall to optimize their effectiveness. Conservation efforts attempting to recreate climatic conditions at small spatial scales might help to mitigate the impact of climate change by providing suitable environmental conditions and therefore prevent local extinctions [84]. In this regard, passive acoustic protocols emerge as key tools to generate behaviour data to inform such conservation efforts but also to evaluate the response of managed populations in a timely, objective and low-cost manner. With our protocol, we provide a baseline for phenological studies that aim for greater temporal precision and thus can document population dynamics in a context of climate uncertainty.

Ethics. This study was approved by the institutional ethics committee of the School of Biology of the University of Costa Rica under the supervision of Dr. Marcelo Araya Salas and Dr. Beatriz Willink.

Data accessibility. The data and code that support the findings of this study have been shared as supplementary materials [85].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. F.C.: conceptualization, data curation, formal analysis, project administration; B.W.: conceptualization, formal analysis, methodology, software, supervision, writing - original draft, writing - review and editing; J.E.-C.: conceptualization, data curation, investigation, writing - original draft; W.C.-A.: conceptualization, writing - review and editing; D.S.-S.: methodology; J.A.S.-Z.: conceptualization; M.A.-S.: conceptualization, data curation, formal analysis, investigation, project administration, validation, writing - original draft, writing - review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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