1 **Environmental drivers of calling activity in the endangered species Lemur Leaf frog 1**

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16 **Keywords:** Causal modeling, Hylidae, Bayesian models, temperature, relative humidity, bioacoustics.

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18 **Abstract** Tropical frog species are known to exhibit high sensitivity to weather regime alterations, which leaves them vulnerable **2**

19 to ongoing climate change. This challenge is exacerbated by limited knowledge of species-specific responses to environmental

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20 change. We integrated passive acoustic monitoring and automatic signal detection to investigate the calling activity of the

21 Critically Endangered tree-frog, *Agalychnis lemur*. We combined template-based detection with machine learning mitigation

22 of false positives to infer the calling activity of a lemur leaf frog population across 18 months. We used directed acyclic

23 graphs (DAGs) to determine the covariates needed to infer causal relations between environmental variables and calling

24 activity. Our findings revealed that daily temperature has a strong direct positive effect on calling activity, with additional

25 indirect effects mediated by relative humidity. Moreover, higher activity of lemur leaf frog was triggered by increasing

26 humidity independent of temperature, higher accumulated rainfall within the preceding 24 hours, and decreases in moonlight.

27 This study provides unique insight into the complex interplay of environmental factors for determining calling activity in

28 frogs. Our findings underscore the potential of passive acoustic monitoring for elucidating frog population activity and its

29 responses to environmental changes, which can be valuable for understudied species in the context of climate change.

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31 1. Introduction

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32 The alarming trend of population declines and extinctions among amphibian species worldwide presents a significant challenge

33 for their conservation efforts [[1](#_bookmark0)]. This challenge is exacerbated by limited knowledge of species-specific susceptibilities to

34 environmental change. Nearly 60% of the world’s threatened amphibian species are found in the Neotropics, where 92%

35 face elevated levels of habitat loss and a third suffer from reduced rainfall and humidity [[2](#_bookmark1)]. Moreover, over 11% of all

36 amphibian species are classified as data deficient, hindering effective conservation strategies [[2](#_bookmark1)]. As ectothermic organisms,

37 amphibians rely on environmental cues to regulate most physiological processes and behaviours [[3](#_bookmark2)]. Short-term variations in

38 weather or environmental factors can significantly impact reproductive success, rendering amphibians vulnerable to human-

39 induced environmental changes that alter microclimates, with consequences for population dynamics [[4](#_bookmark3)–[6](#_bookmark5)]. Therefore, developing

40 strategies to mitigate these impacts and implementing research tools enabling cost-efficient monitoring of critical species are

41 crucial steps in addressing amphibian conservation challenges and safeguarding their ecosystems [[7](#_bookmark6)–[9](#_bookmark8)]. For animals whose

42 communication and reproductive interactions largely rely on acoustic signals, as is the case of amphibians, passive acoustic

43 monitoring (hereafter PAM) methods can be used to register vocal activity over extensive temporal and/or spatial scales [[10](#_bookmark9),[11](#_bookmark10)].

44 These relatively novel technologies provide a non-invasive method that is particularly promising for generating key information

45 on threatened, understudied anuran species. Such approaches are increasingly used for documenting population changes in

46 frogs [[12](#_bookmark11)]. However, their analysis often rely on human observers which suffers from limited standardization, and make data

47 curation time consuming and subjective [[13](#_bookmark12)]. Automated detection approaches of acoustic signals allow to solve many of these

48 issues, as they are in principle verifiable, reproducible and can handle large amounts of acoustic data [[12](#_bookmark11)]. Thus, the combination

49 of PAM and automated detection pipelines can offer a robust and efficient approach for the monitoring of highly vocal species [[14](#_bookmark13)].

50 Environmental factors can affect the vocal activity of frogs in diverse ways. First, rising evapotranspiration increases the likelihood

51 of rainfall, which in turn increases relative humidity [[15](#_bookmark14)]. High relative humidity can support a higher rate of calling activity by

52 reducing desiccation risk [[5](#_bookmark4)]. Second, higher ambient temperature decreases relative humidity, as warmer air holds more moisture.

53 Calling activity can therefore be negatively affected by a rise in local temperature [[16](#_bookmark15)]. In contrast, temperature directly influences

54 metabolic rates in ectotherms, potentially increasing vocalization rate and energy expenditure in frogs [[3](#_bookmark2),[17](#_bookmark16)–[19](#_bookmark18)]. Therefore,

55 temperature may also directly intensify calling activity [[20](#_bookmark19)]. In addition, rainfall can strongly influence calling activity and its

56 effect can vary across temporal scales [[8](#_bookmark7)]. Preceding rainfall boosts relative humidity through evaporation, positively impacting

57 calling activity [[21](#_bookmark20)]. Both daytime and nighttime rainfall contribute to increased humidity, further promoting calling behaviour.

58 However, rainfall also lowers local temperatures, affecting frog calling activity through the metabolic processes described above.

59 Moreover, it is known that heavy rains can dampen sound quality, potentially leading to decreased calling rates if frogs need to

60 invest more energy for producing louder calls that can be detected by conspecifics [[22](#_bookmark21)]. Similarly, moonlight can affect calling

61 activity because the lunar synodic cycle (i.e. the transition full from new moon to the next new moon) changes the brightness of

62 lunar light that can be perceived by animals [[23](#_bookmark22)]. Most frog species are nocturnal and are at risk of visually oriented predators [[24](#_bookmark23)].

63 This predation risk is maximized during nights of high moon illumination that facilitate visual predators to locate their prey. In

64 this work, we quantified the calling activity of the critically endangered lemur leaf frog (*Agalychnis lemur*) over an 18-month period

65 aiming to understand the effect of weather and moonlight fluctuations on the calling behaviour of this species. We used graphical **4**

66 causal modeling in a directed acyclic graph (DAG) for depicting the array of potential causal pathways in the system [[25](#_bookmark24)]. This

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67 approach allowed us to explicitly represent our hypotheses of the causal relationships between environmental factors and calling

68 activity and to derive the models to statistically evaluate these relationships [[25](#_bookmark24),[26](#_bookmark25)]. Our results provide valuable insights about the

69 climatic underpinnings of reproductive behaviour in an endangered and poorly known species and demonstrates the effectiveness

70 of bioacoustics approaches for understanding key aspects of the species biology in a context of growing threats to biodiversity.

71 2. Materials and Methods

72 (a) Study Species

73 The lemur leaf frog is an arboreal nocturnal frog historically distributed in tropical rain forests of Costa Rica, Panama

74 and Colombia from 440 to 1600 masl [[27](#_bookmark26),[28](#_bookmark27)]. Currently restricted to few populations in the Talamanca Mountain Range in

75 Costa Rica and the Caribbean slope of the Chiriqui province in Panama, considered critically endangered, with deforestation,

76 chytridiomycosis infection, and habitat loss as its main threats [[29](#_bookmark28)–[31](#_bookmark29)]. In captivity, the lemur leaf frogs produce three types of

77 vocalizations: an advertisement call, an encounter call, and a release call [[32](#_bookmark30),[33](#_bookmark31)]. The advertisement call consists of a very short

78 “tick” repeated every 25 s, used as a mating vocalization broadcasted during the breeding season as well as communicating

79 territory occupancy among males [[33](#_bookmark31),[34](#_bookmark32)]. We focused on the advertisement call because of its mating role, which makes it a proxy

80 for breeding activity.

81 (b) Study site and weather data collection

82 We conducted the study at Veragua Rainforest (9.924819°N, -83.191206°W; 420 masl), a 13.7 km² private reserve in the Central

83 Caribbean region of Costa Rica, situated on the northern edge of the Matama Mountains within the Talamanca Mountain Range.

84 This reserve falls within the Basal Tropical Wet Forest life zone (200–600 m a.s.l.) as described by Holdridge [[35](#_bookmark33)]. The area features

85 a mix of mature forest, secondary vegetation at various stages of regeneration, open areas, and dirt roads [[36](#_bookmark34)]. Located at the

86 closest point of the Talamanca Mountain Range to the Caribbean Sea, it is part of the buffer zones of La Amistad International

87 Park, a UNESCO World Heritage Site. Data was collected in an area with 5 experimental ponds established in 2012 (length 200

88 cm, width 150 cm, depth 50 cm) as a habitat restoration program that aimed to serve as in situ breeding sites for the different frog

89 species inhabiting the area, and where the species was previously detected [[36](#_bookmark34)]. We obtained weather data from a station located

90 300 m from the study site. The station registered temperature (°C), relative air humidity (%), and rainfall (mm) every minute.

91 From this data we estimated the average values for each 15 min recording interval (see the detailed description below) and the

92 accumulated rainfall during the 48 and 24 hour previous to each sampling event. We obtained the moonlight intensity during

93 those periods using the R package LunaR [[37](#_bookmark35)] which was used to estimate the percentage of lunar illumination per night based

94 on the site’s geographic location and the date of recording.

95 (c) Acoustic monitoring and call recognition **5**

96 We recorded the advertisement calls of the lemur leaf frog through passive acoustic monitoring using the SM4 digital sound

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97 recorder [[38](#_bookmark36)]. The sampling period spanned 18 months, from July 2019 to February 2021, . We set the recorder to collect acoustic

98 data daily from 18:00 to 5:00 the following morning, coinciding with the expected reproductive activity of nocturnal species like

99 the Lemur frog (ADD REF). The equipment was programmed to record for 15 minutes every 20 minutes (with a 5-minute resting

100 period), resulting in three 15-minute samples per hour. Recordings were stored in WAV stereo format at a sampling rate of 44.1

101 kHz and a 16-bit amplitude resolution. Afterwards we split each recording into five minute clips and resampled at 10 kHz to

102 enhance computational performance during further analysis. We used a template detector model in the R package ohun [[39](#_bookmark37)]

103 to automatically detect advertisement calls of the lemur leaf frog in our recordings. The automatic detector was trained with

104 recordings used in this study and from others recorded at an additional site that hosts another population of the lemur leaf frog

105 in order to improve detection performance. We selected a subset of recordings to be used as the training data set, using stratified

106 random sampling for ensuring a balanced representation across months, weeks, hours and 4 hour sampling periods. Then, two

107 recordings were randomly chosen from each level of a full factorial combination of these factors. The resulting training data

108 set consisted of 467 recordings. We annotated all visually identifiable lemur leaf frog calls on the Fourier spectrograms of these

109 recordings using the Raven software [[40](#_bookmark38)], noting the start and end times and frequency range of each call. These annotations

110 were then imported into R [[41](#_bookmark39)] using the Rraven package [[42](#_bookmark40)] and processed in the package warbleR [[43](#_bookmark41)] to ensure precise time

111 and frequency positioning of the signals. The template-based detection routine identifies sounds similar to template sounds using

112 spectrographic cross-correlation. Therefore, detection performance usually varies among templates. We evaluated three acoustic

113 templates in order to select the template with the best performance. We selected a set of templates that represented the structural

114 diversity of calls. For this the warbleR package was used to measure 23 spectral features (related to the distribution of power in

115 time and frequency) representing the acoustic structure of the manually annotated calls. We selected three candidate templates:

116 two were calls with parameters closest to the mean duration and mean frequency respectively, and the third was the call closest to

117 the mean of the first component from a Principal Component Analysis (PCA) on z-transformed acoustic features. We trained the

118 template-based detection routine on the annotated recordings, serving as a reference dataset for evaluating its performance. We

119 identified as signals of interest those sounds in which correlation with the template surpasses a predefined threshold. The three

120 candidate templates were tested across 20 correlation thresholds ranging from 0.1 to 0.9. The template with the best performance

121 was determined based on recall and precision metrics. Recall measures the ability to identify signals of interest, while precision

122 indicates the routine’s ability to exclude non-target sounds [[44](#_bookmark42)]. Hence, an efficient detection routine should maximize recall

123 and precision, and this criterion is used to guide correlation threshold selection. However, as low precision can be mitigated

124 in further analysis (see below) we favored a threshold that improved recall performance despite having a poor performance in

125 precision. After applying the selected correlation threshold for defining detections we implemented a machine learning approach

126 to mitigate incorrect detections [[45](#_bookmark43)]. For this secondary filter we trained a supervised random forest classification model (RF) [[46](#_bookmark44)]

127 using the R package ranger [[47](#_bookmark45)]. The RF model identified the lemur leaf frog calls based on acoustic features, measuring the

128 same spectral features used for selecting templates in addition to statistical descriptors of Mel-frequency cepstral coefficients

129 (MFCCs) using warbleR. Cepstral coefficients represent perceptually relevant features as they are derived from spectral bands

130 that resemble sound representation in animal auditory systems, and have been widely used in human speech recognition and

131 increasingly in non-human animals [[48](#_bookmark46)–[52](#_bookmark47)]. We measured 25 cepstra on 10 warped spectral bands, analyzing the minimum, **6**

132 maximum, mean, median, skewness, kurtosis, and variance of each MFCC, along with the mean and variance of their first and

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133 second derivatives. The RF model was trained with 1000 trees and mtry (number of features considered for splitting trees) of 13

134 variables. The out-of-bag error (OOB) was used to evaluate classification performance.

135 (d) Causal modeling

136 Environmental factors which may influence the calling activity of the lemur leaf frog are part of a complex system, in which

137 factors are also causally related to each other. Causal models can help to understand these complex systems by explicitly stating

138 relationships among variables. Here, we used directed acyclic graphs (DAGs) to identify the set of variables that must and must

139 not be taken into account to estimate causal effects of interest without bias (Fig. 1., [[25](#_bookmark24)]). We were interested in the effects of

140 temperature, rainfall relative humidity and night illumination on frog calling activity. Our DAG hypothesizes that the effect of

141 temperature can be direct, via effects on frog metabolism, or indirect by affecting relative humidity (Fig. 1). Rainfall was expected

142 to affect calling activity through two time frames: “current rainfall” which refers to the cumulative rainfall during the hour

143 before a sampling event and “prior rainfall” which represents the precipitation during previous days (Fig. 1). Current rainfall

144 was expected to have a positive effect on frog calling activity by increasing relative humidity and a negative effect through a

145 decrease in temperature (Fig. 1). Prior rainfall might increase activity by expanding breeding micro-habitats (e.g. ponds) and by

146 increasing relative humidity (Fig. 1). Prior rainfall was represented by two variables that measured the 24 hour cumulative rainfall

147 on two different periods: on the day prior to each sampling unit, and two days prior to each sampling unit. The two prior rainfall

148 variables were modeled in separate analyses in order to determine the most relevant period for calling activity. We then estimated

149 the direct effects of relative humidity and nocturnal light on frog calling activity. Our DAG depicts additional causal relationships

150 that are not of particular interest in this study, but inform our variable selection process required for unbiased estimation of the

151 causal effects. First, by controlling sunlight hours, the earth’s rotation may influence calling activity both directly, and indirectly,

152 via effects on temperature. Earth rotation also interacts with the Moon’s rotation and thus influences nocturnal illumination.

153 Earth rotation was modeled as the time of the day for statistical analyses. Similarly, evapotranspiration represents the total water

154 loss to the atmosphere preceding cloud formation and eventual rainfall, and thus also influences relative humidity. In our DAG,

155 evapotranspiration is an unmeasured (latent) variable that affects both current rainfall and prior rainfall.

156 (e) Statistical analyses

157 For each predictor, we determined the set of variables (i.e. adjustment set) that allow for the asymptotic estimation of unbiased

158 causal direct and total effects on call rate, using the R package daggity [[53](#_bookmark48)]. Direct effects represent the predictor’s effect on the

159 response that is not mediated by any other variable while total effects take into account both direct effects and those mediated

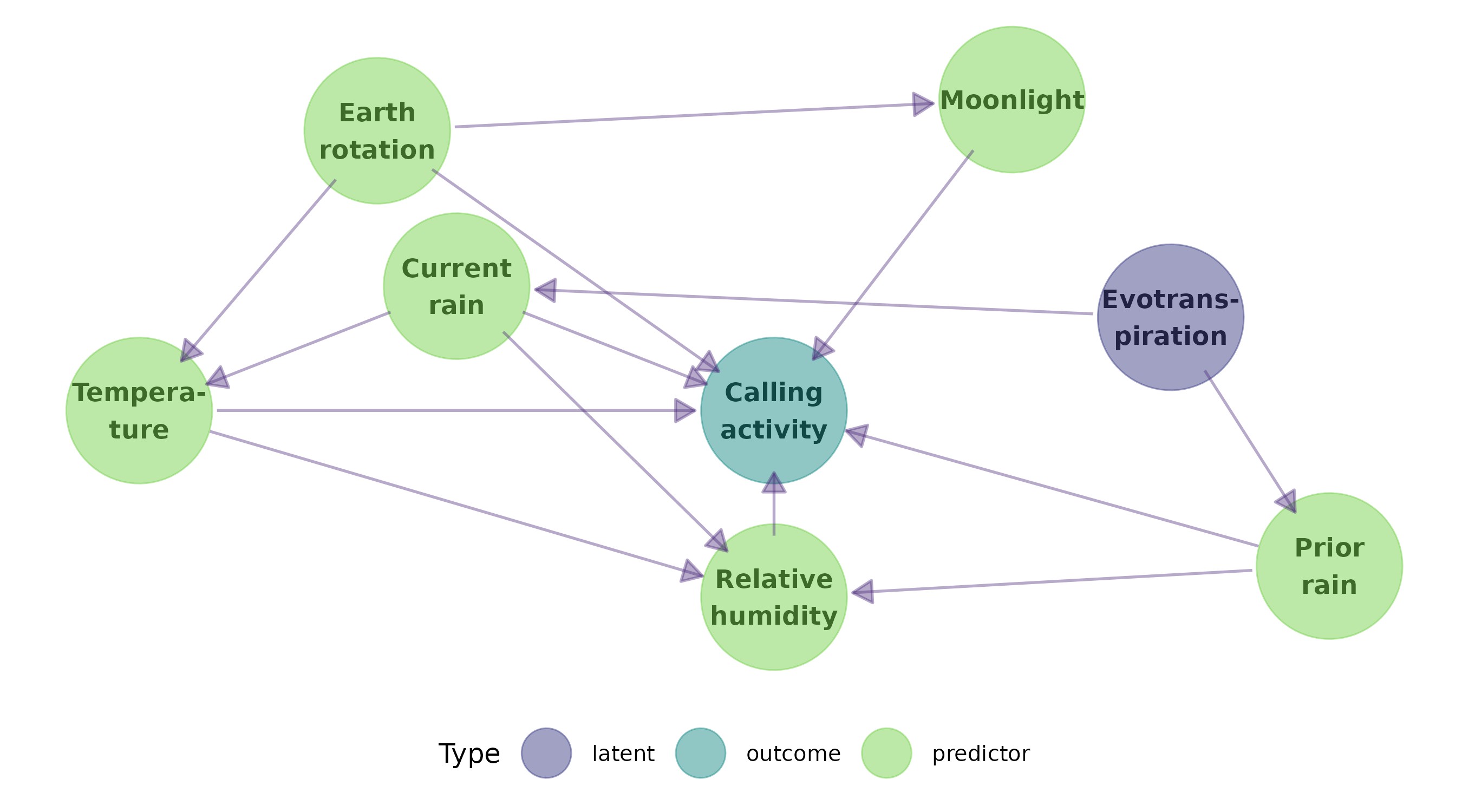
160 by other variables. The difference between the two effects provides evidence of the mediated (indirect) effects. Variables in

161 the adjustment sets were used as predictors in regression analyses. Regressions were fitted for each environmental variable

162 (temperature, relative humidity, current rainfall, prior rainfall and moon illumination) using Bayesian generalized linear models

163 in the R package brms [[54](#_bookmark49)]. The models accounted for temporal autocorrelation (i.e., the dependency among observations close

164 to each other in time) using an Autoregressive Moving Average (ARMA) correlation structure, with time of the day (discretized

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**Figure 1.** Directed acyclic graph (DAG) depicting the hypothesized causal pathways between environmental variables and the calling activity of 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 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 hours.

165 in one hour periods) as the grouping variable. We modeled calling activity as a rate of calls per hour using a negative binomial

166 distribution with a logarithmic link function. All predictor variables were zero-centered and transformed to unit variance. When

167 several adjustment sets existed for modeling a predictor’s effect, the posterior distribution of the correspondent models were

168 averaged, weighted by their predictive performance using a stacking leave-one-out cross validation approach [[55](#_bookmark50)]. Effect size

169 estimates were transformed into percentage of change to facilitate interpretation and are presented as medians of posterior

170 distributions and 95% uncertainty intervals (UI). Parameters in which intervals did not include zero were regarded as affecting

171 calling rate. Models were run for 10,000 iterations, following a warm-up of 10,000 iterations on four MCMC chains. For all

172 parameters, the effective sample size was maintained at or above 4000. We plotted the trace and distribution of posterior estimates

173 for all chains for visual evaluation of model performance. In order to assess the independence of the posterior samples, we also

174 inspected the autocorrelation of successive sampled values and estimated the potential scale reduction factors for checking model

175 convergence (kept below 1.01 for all parameter estimates).

176 3. Results

177 We examined a total of 370,718 calls of the lemur leaf frog in 1707 hours of recording. The vocalization consists of a single, non-

178 frequency modulated call with amplitude modulation, emitted by males from the leaves and branches of vegetation surrounding

179 swamps and other similar lentic environments. The call is tonal, with the amplitude peak typically located at the beginning of

180 the call duration, depicting a triangular-shaped call in the spectrogram. The frequency bands exhibit no significant modulation

181 throughout the call duration. Across the entire sampling period, we recorded an average of 27 vocalizations of lemur leaf frog per

182 hour. The performance of the acoustic templates (mean peak frequency, mean duration and mean PCA1) for detecting the lemur **8**

183 leaf frog calls varied importantly according to the performance metrics recall and precision (Fig. 2). The mean PCA1 was chosen

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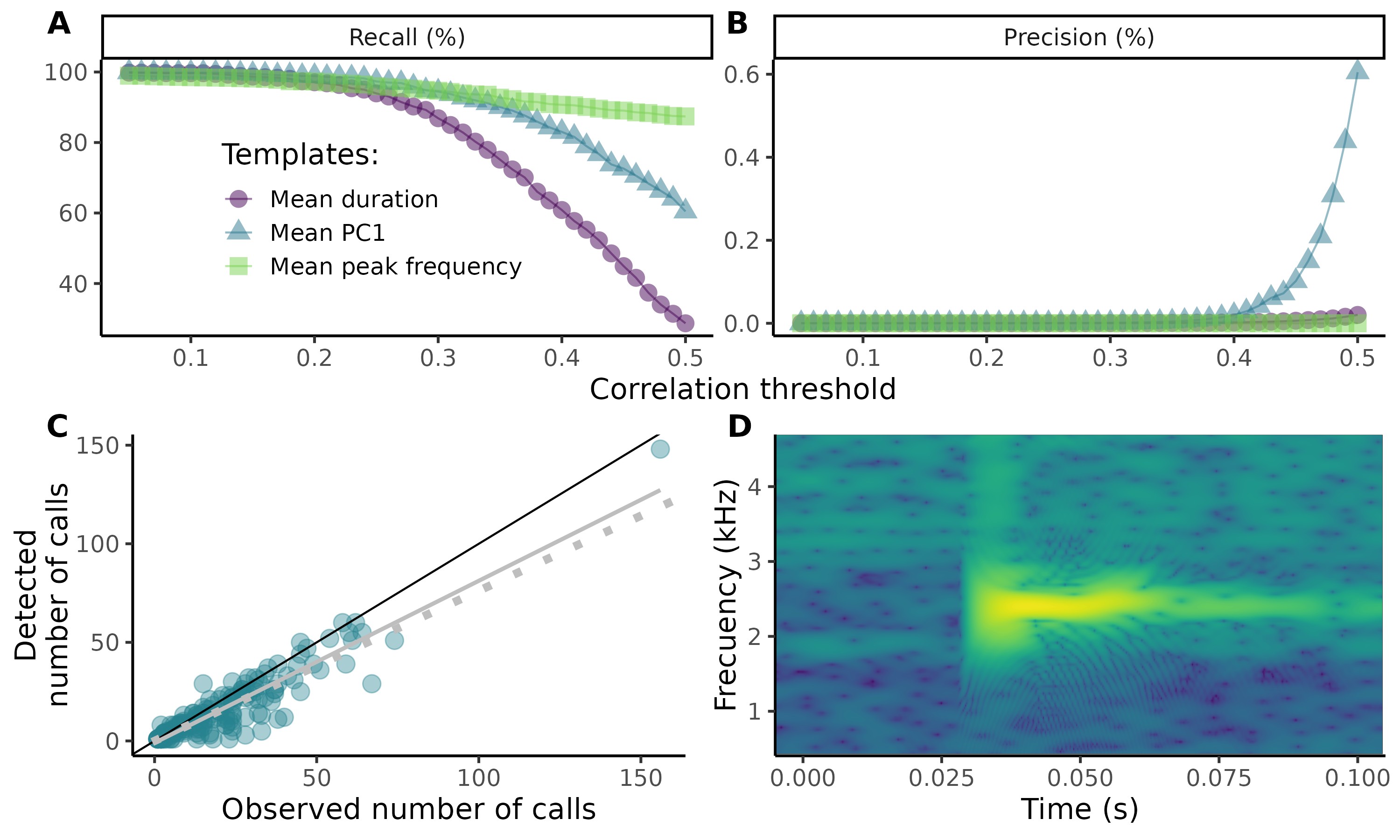
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184 to be used as the template in subsequent analysis given its positive balance between the two performance metrics (70.4% recall

185 and 3.7% precision with a 0.43 correlation threshold). After RF mitigation of false positives (OOB error rate of 0.88%) we obtained

186 a 67% recall and 91% precision. The observed number of calls on the 5-min clips in the training data set and the number of calls

187 found by our detection procedure were highly correlated (Pearson correlation score: 0.92; 0.89 after removing outlier).



**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 gray 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 gray line shows the best fit line from a linear regression on the entire data (slope: 0.82) while the dotted gray line shows the best fit line when excluding the outlier (slope: 0.76). D) Spectrogram of a Lemur frog call.

188 For the accumulated rainfall during the 24 hour prior to sampling we found a positive direct effect (effect size: 10% UI: 5.8% –

189 14.7%; Fig. 3) and total effect (effect size: 9.1% UI: 5.2% – 13.6%; Fig. 3), on calling activity, whereas accumulated rainfall during

190 the day 48 hour before sampling did not have a detectable influence on calling (direct effect: 0.62% UI:-2.9% – 4.1%; total effect:

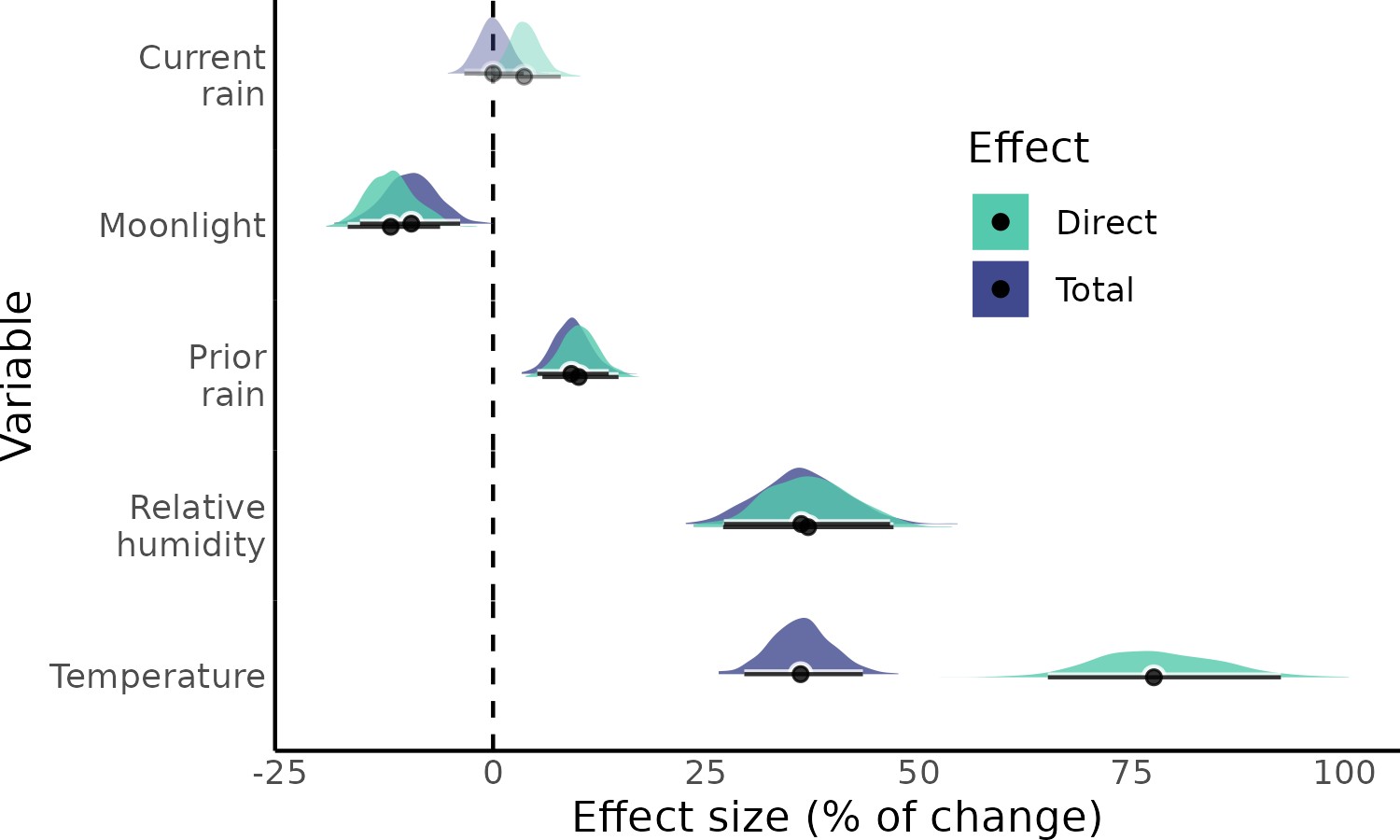
191 0.54% UI:-3.3% – 4.4%). Therefore, results hereafter are based on models using prior 24 hour accumulated rainfall whenever prior

192 rainfall was included in the adjustment set for other effect estimates. Temperature has the largest positive direct effect on calling

193 rate (effect size: 77% UI:65.1% - 92.5%; Fig. 3), followed by relative humidity (effect size: 37.0% (27.0% - 47.0%; Fig. 3), while

194 moonlight showed a negative direct effect (effect size: -12.0% UI:-17.1% – -6.2%; Fig. 3). We did not found a detectable direct effect

195 of current rainfall on calling activity (effect size: 3.6% UI:-0.0% – 7.9%). Total effects sizes were similar to direct effects sizes for all 196 predictors (24 hour prior rainfall: 9.1% (Ui: 5.1% – 13.5%); 48 hour prior rainfall: 0.54% (-3.2% – 4.4%): moonlight: -9.6% (-15.6% – 197 -3.9%); current rainfall: 3.6% (-3.3% – 3.5%); Fig. 3) except for temperature (36.1% (29.4% – 43.4%); Fig. 3).

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**Figure 3.** Posterior distribution of direct (green) and total (purple) effect sizes of environmental factors on the calling activity of 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 color distributions correspond to effect sizes in which uncertainty intervals do not include zero. “Prior rain” accounts for the 24 hour period before sampling calling activity.

198 4. DISCUSSION

199 In this study, we aimed to untangle the causal effects of several environmental variables on the calling activity of the lemur leaf

200 frog, using passive acoustic monitoring. We provide quantitative evidence of the way in which environmental variation shapes

201 calling activity. We found that calling activity is mainly triggered by the increase in temperature and relative humidity, as well as

202 by the rainfall accumulated during the day before, although this effect is only moderate. Contrary, the calling rate of this species

203 falls during luminous nights but in general is not affected by current rainfall. More broadly, our results demonstrate the potential

204 of monitoring efforts that passively collect information in a continuous and systematic manner, to gain insights into the ecological

205 drivers of reproductive behaviour in natural populations. The precision of our automated detection procedure allowed us to

206 accurately infer the variation in call activity. Despite having a moderate performance for detecting individual calls (67% recall),

207 our approach succeeded in predicting call activity in 5 min intervals with high accuracy (Fig. 2-C). The applied routine for call

208 detection is relatively simple compared to recently developed deep learning approaches. However, Random Forest, the algorithm

209 used for mitigating incorrect detections, stands as a highly robust machine learning classification method [[56](#_bookmark51)]. Overall our results

210 demonstrate that traditional bioacoustic methods can be boosted by combining them with classification approaches that are

211 already familiar to ecologists in order to drastically improve automated detection in PAM studies. The lemur leaf frog, like other

212 species of Leaf Frogs (subfamily Phyllomedusinae), has been classified as a prolonged breeder [[57](#_bookmark52)]. This strategy is characterized

213 by linking their energy allocation to advertisement calling, based on local environmental cues [[7](#_bookmark6),[58](#_bookmark53),[59](#_bookmark54)]. Our results indicate that

214 the calling activity of lemur leaf frogs respond to environmental conditions in a small time scale, especially temperature and

215 humidity, whereas prior environmental conditions such as those of cumulative rainfall from previous days are less relevant.

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Temperature had a direct positive effect on calling activity (Fig. 3), as expected if calling activity responds to a general increase in metabolic rate [[18](#_bookmark17)]. 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 (Fig. 1). Thus, while our data supports 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 [[60](#_bookmark55)–[62](#_bookmark56)], which may allow them to tolerate relatively dry conditions, compared to other frogs, and exhibit an overall positive response to high temperatures [[20](#_bookmark19)]. It is plausible, however, that in 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 [[18](#_bookmark17),[63](#_bookmark57)]. Thus, the indirect negative effect of temperature may be amplified by global warming while the direct positive effect on calling rate may not [[21](#_bookmark20),[64](#_bookmark58)]. While in the current temperature ranges warmer conditions seem to favor 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 [[65](#_bookmark59)]. 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 [[8](#_bookmark7),[21](#_bookmark20),[63](#_bookmark57),[66](#_bookmark60)–[68](#_bookmark61)]. Frog vocal activity is likely 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 [[18](#_bookmark17),[69](#_bookmark62)]. In our study site, the relative humidity was 90% on average, which likely enables a relatively continuous year-round calling activity of the lemur leaf frog [[68](#_bookmark61)]. As expected, rainfall impacts 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 [[57](#_bookmark52)]. Lemur leaf frogs reproduce in both temporary and permanent pools v [[70](#_bookmark63)]. The artificial ponds where the present study was conducted do not dry up and are therefore a constant breeding resource. In addition, adult frogs are often seen resting during daytime in close proximity to this permanent water resource (F. C. personal observation), suggesting that movements towards the reproductive sites can be accomplished at a short notice. Consistently, we found that rainfall accumulated during the prior 24 hour influenced the calling activity of the lemur leaf frog, but effects from 48 hour prior rainfall were undetectable. Alternatively, the total effect of prior rainfall could be owed to an increase in relative humidity in the coming night. However, the similarity between total and direct effects for prior rainfall suggest 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 [[23](#_bookmark22),[71](#_bookmark64),[72](#_bookmark65)]. 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 [[24](#_bookmark23),[72](#_bookmark65),[73](#_bookmark66)]. This behaviour is associated with species that rely on visual communication to reproduce and to

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identify potential predators [[23](#_bookmark22)]. 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 [[73](#_bookmark66)] could help disentangle the influence of environmental light on amphibian reproductive behaviour. Our analyses support with robust quantitative evidence the widely assumed but rarely tested relationship between weather variables and frog calling activity [[59](#_bookmark54),[74](#_bookmark67)]. Current computational tools and monitoring methods allowed us to confirm and expand previous evidence on the role of environmental factors that influence the advertisement calling behaviour of anurans [[32](#_bookmark30)]. These approaches also enable studies at a higher temporal resolution and

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over longer time periods of uninterrupted sampling, which can contribute to building a more nuanced understanding of the effects of the abiotic environment on calling activity. This detailed perspective can also be used to predict the potential response of frog populations under plausible scenarios of climatic change and its associated implications in conservation. 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 considering 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 [[75](#_bookmark68)]. In this regard, passive acoustic protocols emerge as key tools to generate behaviourally 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.

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264 5. Acknowledgements

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265 We are grateful to the Veragua Foundation for providing us with research funding to conduct this study as part of our efforts to

266 increase research related to tropical endangered species. We also express our thanks to Leo, a local indigenous person who helped

267 gather the bioacoustic data from Cerro Chimú. Without Leo, it would have been impossible to collect this data. Special thanks

268 to the University of Costa Rica team, Jimena Víquez and Elena Cantero, for their essential contributions during the annotation

269 phase. Both dedicated countless hours of hard work to analyze the 467 recordings. We also thank Professor Gerardo Ávalos and

270 to Adrián García Rodríguez for his manuscript recommendations. WCA thanks ANPCYT (PICT 346/2019, 59/2021), CONICET

271 (PIP2800), FAPESP (2018/15425-0, 2021/10639-5), and the Mohamed Bin Zayed Species Conservation Fund (Project 242534066).

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