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# Sunlight Sonata: Contrasting the Roles of Solar Ultraviolet Radiation and Temperature on the Calling Behavior of a Diurnal Forest-specialist Frog

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Diurnal animals are frequently exposed to solar ultraviolet radiation (UV) during their daily activities, which can lead to DNA damage and other physiological challenges. To counteract these effects, they have evolved complex DNA repair mechanisms. The high energetic cost of DNA repair creates a trade-off with behavior, potentially constraining energetically demanding activities like anuran calling under harmful UV exposure. We tested hypotheses on how natural heterogeneity in the abiotic environment – particularly in the UV radiation – influences the calling behavior of *Crossodactylus schmidti*, a diurnal forest-specialist frog found in preserved neotropical streams. To gather data on male calling behavior, we used passive acoustic monitoring of a well-studied population, using a set of recorders and data loggers that measured short- and long-term cumulative doses of UVA and UVB, air temperature, light intensity and cloud cover during the austral summer. To investigate associations between the abiotic variables and proxies of calling behavior (occurrence, number, and duration of calls), we used a model selection approach based on generalized linear mixed models followed by model averaging of the best-supported models. We found that: 1) the *probability of recording males in calling behavior* decreased with increasing mean air temperature and cumulative UVB dose but increased with short-term (15-minute) UVB exposure; 2) the *number of calls* emitted by males decreased with increasing mean air temperature but increased with cumulative UVB dose; and 3) *call duration* decreased with increasing mean air temperature but increased with cumulative UVB dose at calling sites. Short- and long-term doses of UVA, on the other hand, did not influence any proxy of calling behavior. Our findings show that higher temperatures in months of peak calling activity consistently reduce calling behavior, while UVB exposure has more complex effects. Together, these results underscore the need to consider both thermal and ultraviolet components of sunlight when assessing how anurans respond behaviorally to abiotic heterogeneity under ongoing environmental and climatic changes.

**Keywords:** Air Temperature, *Crossodactylus*, Environmental Heterogeneity, Hylodidae, Reproductive Behavior, Solar Ultraviolet Radiation

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## BACKGROUND

Diurnal animals have evolved under exposure to solar ultraviolet radiation (UV). The two spectra of UV radiation that reach the Earth's surface are UVA, which has longer and less energetic wavelengths (315-400 nm), and UVB, of shorter and more energetic wavelengths (280-315 nm) (Frederick et al. 1989). UVB is more dangerous to organisms because of a higher absorbance by the DNA molecule, while UVA has a lower absorbance and requires a longer exposure time to generate similar damage relative to UVB (Hamzavi and Lui 2005; Markovitsi et al. 2010; Schuch et al. 2017). The consequences of exposure to UV on organisms—which include genetic, physiological, and behavioral effects—are therefore wavelength-dependent and dose-dependent (reviewed in Londero et al. 2019). For example, the negative effects of UVB on echinoderm embryo development increase with exposure time (Lesser and Barry 2003), fish mortality increases with accumulated UVB irradiance, and prolonged exposure to UVA causes skin lesions (Zagarese and Williamson 2001; Kouwenberg et al. 1999). However, animals such as anurans and other vertebrates have evolved adaptive responses to UV radiation exposure (reviewed in Cockell and Blaustein 2001), including biochemical mechanisms to repair UV-induced DNA damage (Lamare et al. 2006; Dong et al. 2007; Kienzler et al. 2013; Cortat et al. 2013) and the capacity to benefit from low doses of UVB light for metabolic regulation, such as in vitamin D synthesis (Neer 1975; Xue and Fleet 2009; Hohman et al. 2011).

Animals typically concentrate their active periods at specific times of the day as strategies to cope with the environment's temporal variation in abiotic factors (Daan 1981). Nonetheless, diurnal animals that remain active for prolonged times, or when UV radiation is most intense, may be exposed to UV radiation that exceeds their physiological optimum and induces DNA damage. Photoproducts such as Cyclobutane pyrimidine dimers and [6-4] pyrimidine-pyrimidone can disrupt homeostasis by causing mutations and impairing cellular functions (Schuch and Menck, 2010). In fact, even small doses of UV radiation are genotoxic at the cellular level and can cause DNA damage (Schuch et al. 2017; Yagura et al. 2017; Londero et al. 2019). In vertebrates, the DNA repair mechanism counteracts this damage, but because the mechanism is physiologically costly, it can limit energy allocation in certain behaviors (García-Huidobro et al. 2017; Pulgar et al. 2017). For example, an energetic trade-off between behavior and physiology due to exposure to harmful UV radiation can be discerned through a focused examination of anuran calling behavior.

Amphibian studies provide insightful findings on the influence of UV exposure on animal behavior, as these organisms lack protective skin appendages, and their eggs, lacking shells, are highly susceptible to environmental variations (Blaustein and Belden 2003). For example, adult frogs exposed to a minor increase in daily UV dose reduce their investment in locomotion and in selection and use of calling sites (Blaustein et al. 2000; Kats et al. 2012), whereas tadpoles are more susceptible to predation and less capable of foraging under UV exposure (Kats et al. 2000; Londero et al. 2017; Martins et al. 2021). Forest-specialist diurnal amphibians are expected to be more vulnerable to UV effects than open-habitat species due to their lower concentration of melanin in the skin (Blaustein and Belden 2003), which acts as a protective barrier for the UV spectrum (reviewed in Brenner and Hearing 2008). However, studies examining how UV heterogeneity influences the behavior of diurnal amphibians in forest streams are scarce and mostly limited to laboratory conditions (see Kats et al. 2012; Schuch et al. 2015). This gap is particularly striking because most amphibians are nocturnal and thus rarely exposed to solar UV radiation, making diurnal lineages especially valuable for understanding behavioral responses to UV.

Here we aimed to answer the following question: how does the abiotic environment modulate male frogs' calling behavior in forest streams? We used *Crossodactylus schmidti*, a diurnal forest-specialist frog found in preserved neotropical streams, as a study species. Unlike most amphibians, which avoid sunlight, *C. schmidti* is active throughout the day under natural and varying levels of UV exposure, making it an exceptional model to assess how solar radiation influences animal behavior in the field. The ecology and behavior of *C. schmidti* offer a unique opportunity to investigate, in natural settings, how heterogeneity in the abiotic environment modulates the behavior of diurnal amphibians in forest streams. Males of *C. schmidti* compete for and defend territories in the stream bed, emitting acoustic, visual and multimodal signals during contests (Caldart et al. 2014 2022), from sunrise to sunset, throughout the year (Caldart et al. 2016).

In this study, we deployed data loggers in a stream to monitor ultraviolet radiation, air temperature, and luminosity for extended periods, while audio equipment simultaneously recorded the calling behavior of males of *C. schmidti*. We then tested two hypotheses on how abiotic factors correlate with calling behavior: (1) high UV doses at male calling sites are associated with a lower *probability of recording males in calling behavior*; and (2) the investment of males in calling behavior (i.e., in *number* and *duration of calls*) decreases with increasing UV incidence in calling sites. Overall, we expect UVB to have stronger impacts on male calling behavior than UVA, as it is more readily absorbed by DNA, causes faster damage, and demands more energy for repair.

## MATERIAL AND METHODS

### Study Area

The study was carried out at Turvo State Park, located in the municipality of Derrubadas, northwest of Rio Grande do Sul, Brazil (27°13'57.61"S, 53°51'4.82"O), on the border with Argentina. The park vegetation is semi-deciduous Atlantic Forest and covers an area of 17,491 ha (SEMA 2005). The local climate is subtropical humid, characterized by temperatures above 22°C in January and minimum temperature close to -3°C in July (Alvares et al. 2013). The annual mean precipitation is 1,787 mm, with rainfall evenly distributed throughout the year. Summer occurs in December–March and winter in June–September (Maluf 2000).

### Data Sampling

The data were collected from December 2019 to January 2020, the warmer months that correspond to the austral summer, in which there is a high proportion of sexually mature adults of *Crossodactylus schmidti* in the study area and male calling behavior peaks (Caldart et al. 2016). As individuals of this species are not regularly distributed between and within streams due to spatial variation in the availability of calling and breeding sites, we visited streams beforehand to select a stream having active males in high density to conduct the study (see Caldart et al. 2016). We chose a first-order stream that presents an extensive canopy cover (27°14'01.7"S 53°57'52.9"W). Along the stream we established three fixed sites with confirmed occurrence of males, in which we deployed data loggers and conducted passive acoustic monitoring (Fig. 1). The monitoring sites were separated from each other by at least 50 m, which is a sufficient distance to assure acoustic independence in a forest-lotic habitat (Caldart et al. 2016; see Statistical Analysis section, Fig. 1B).

At each site we used passive acoustic monitoring to record the vocalizations emitted by males between 07:00 and 18:00 h, for 19 days, using a pair of Sony ICD-PX312 digital recorders (following Acevedo and Villanueva-Rivera 2006; Blumstein et al. 2011) positioned in opposite stream banks and at 40 cm from the streambed (*i.e.*, the calling sites, Fig. 1C). The audio recordings were combined into a stereo file using PluralEyes 4 software (Red Giant). The first five minutes at every 15-minute time interval (time hereafter) were analyzed using the software Audition (Adobe Audition CC 2018). From the stereo files we then obtained the following data for each time interval analyzed, at each site and day of monitoring: 1) either the *occurrence or the absence of individuals in calling behavior*, 2) the *total number of calls* emitted by all males, and 3) the *mean duration of the calls* emitted by all males. In the analysis of the recordings, we considered only advertisement calls because it is a call frequently emitted by males throughout the day (Caldart et al. 2016), is higher pitched, louder, and has higher inter-individual temporal segregation in emission than other calls known for the species (Caldart et al. 2011).

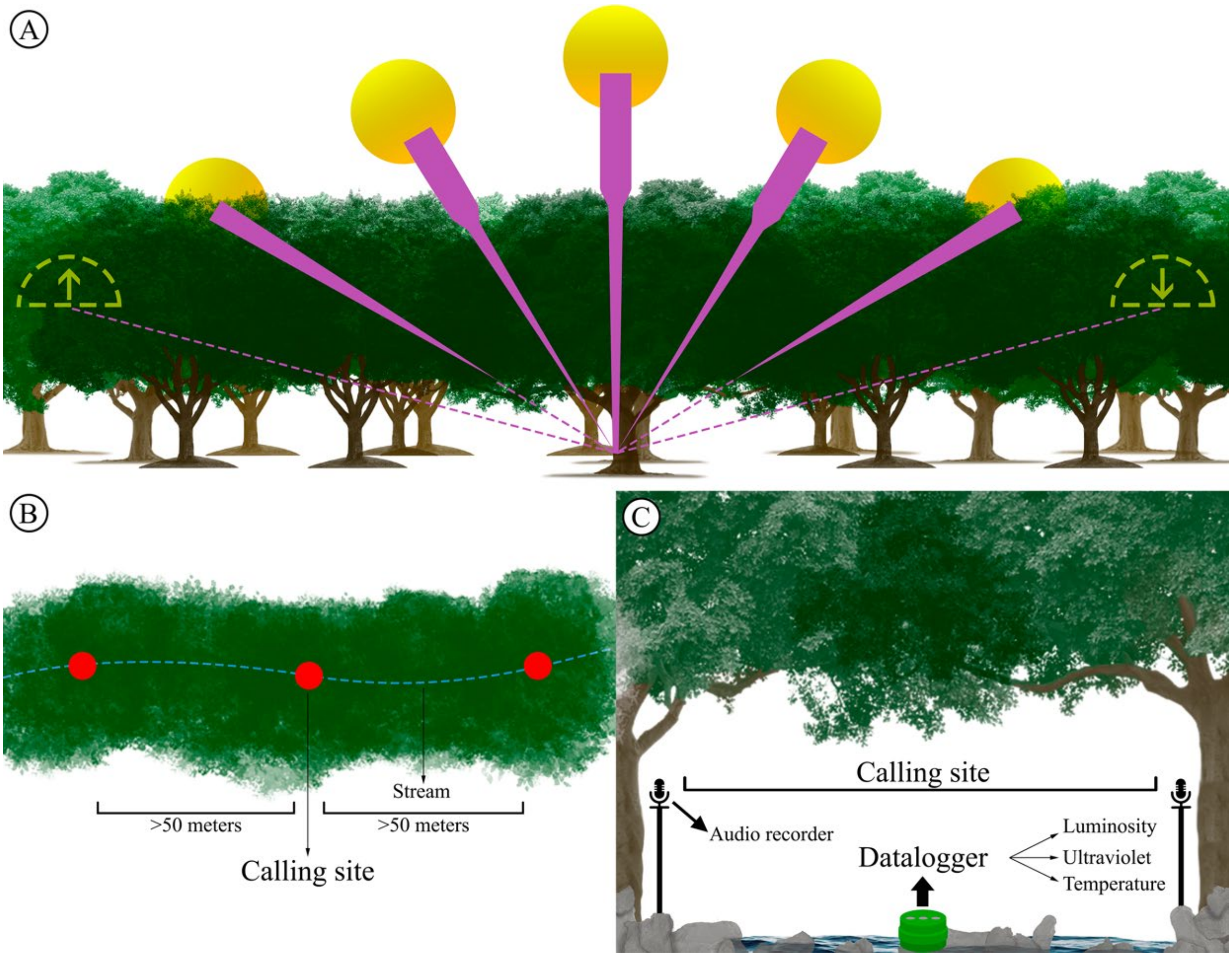

**Fig. 1.** Schematic representation of data collection. (A) Purple arrows and dashed lines denote the incidence of ultraviolet radiation (UVB and UVA) varying according to the solar angle and canopy cover from 07:00 to 18:00 h, which is the whole time interval between sunrise (up arrow) and sunset (down arrow). (B) Distribution of the three fixed points of acoustic monitoring (red-filled circles) along the stream (blue dashed line), showing the minimum distance between them. (C) Example of the centralized positioning of the datalogger and opposed placement of audio recording equipment in the fixed sampling points.

Simultaneously with the acoustic monitoring at each of the three fixed sites we measured the incidence of solar UVB ($kJ/m^2$) and UVA ($kJ/m^2$) radiation, luminosity, and air temperature with data loggers we built. Each data logger has a battery and a secure digital card for data recording that allows monitoring for at least 45 days without recharging or changing the battery. The device is registered and under confidentiality in the Instituto Nacional da Propriedade Industrial (INPI, Brazil) under the number BR 10 2021 005008 0 (see validation test in Supplemental material S1). We obtained the following data from the data loggers for each 15 min time interval, at each site and day of monitoring: the 15 minutes ultraviolet dose of UVA and UVB, and the cumulative (from

07:00 h) ultraviolet dose of UVA and UVB. The daily dose in a clear sky day for UVB in the fixed sampled sites ranged from 0.02 kJ/m² to 0.45 kJ/m², while for UVA ranged from 3.36 kJ/m² to 104.59 kJ/m². This dose is equivalent to 2.69% and 6.06% of the daily dose in a clear sky day out of the forest, in the same period and latitude (see Supplemental material S2 for more details on the profiles of UV incidence in the fixed samples sites). Because the calling behavior of diurnal frogs, including *C. schmidti*, is often correlated with abiotic factors including luminosity and temperature (Caldart et al. 2016; Hatano et al. 2002; Van Sluys and Guido-Castro 2011), we also obtained from the data loggers the mean air temperature and the mean light intensity for each 15 min time interval at each site and day of monitoring.

Finally, because there is a relationship between cloud cover and UV radiation incidence, we obtained the cloud cover data from the Instituto Nacional de Pesquisas Espaciais (INPE, Brazil) for the same period as for the previous variables. These measures are based on an index of cloud coverage derived from the corrected reflectance values obtained in satellite imagery (Souza et al. 2013).

## Statistical Analyses

To test the predictions of our hypotheses we used as response variables the 1) *occurrence of calling behavior*, the 2) *number of calls emitted*, and the 3) *mean duration of calls*. The first variable was used as a proxy of calling behavior (i.e., whether males are acoustically active or not), whereas the other two variables were used as proxies of calling investment (i.e., how much males invest in call frequency and duration). We used data from the period of 07:00 to 18:00 h (Fig. 1A), as *C. schmidti* has a diurnal activity spanning from sunrise to sunset (Caldart et al. 2016). For each response variable we used a four-step analysis protocol that was the most suitable considering the intrinsic characteristics of our data, which contained autocorrelated observations collected through a passive acoustic monitoring method, several covariates, and random terms of different structures.

In the first step we fitted a global (full) Generalized Linear Mixed Model (GLMM) to the original dataset to establish a baseline model that captures the relationship between the response variable and the predictor variables. We considered different combinations of response variables, error distributions and link functions (see Supplemental material S3) in the package *glmmTMB* v. 1.1.8 (Brooks et al. 2017). To control the variation in the response variables among sites, days, and time, we fitted these variables as random factors. The random factor time was fitted as a first order autoregressive term (AR1), that relates the observation at the current time, *t*, to the observation at the previous time, *t-1* (see Larsen et al. 2021). The model also accounted for the fact that observations close in time within the same date group may be more correlated than observations further apart in time or in different date groups (i.e., ar1(time+0|date) in R notation).

In the second step we performed bootstrap resampling to assess the stability and variability of the global model, using the package *lme4* v. 1.1.37 (Bates et al. 2015). Random resampling with replacement of the original model estimates were computed and repeated through 1000 iterations, and the stability of the model estimates were assessed comparing the curves shapes, median values and quantile ranges of original and bootstrap estimates in Kernel density estimation plots (see Supplemental materials S4-S6). Bootstrap resampling helps in understanding how stable the estimates from the global model are and provides a distribution of parameter estimates that reflects the variability in the data (Davison and Hinkley 1997).

In the third step we performed a model selection approach (model dredging) upon the global model to explore alternative models that may better explain the variability in the data. Finally, in the fourth step we used a model averaging procedure to obtain a consolidated estimate by combining the subset of models with $\Delta$AIC < 2 obtained in step 3, as implemented in the *MuMIn* package v.1.48.11 (Bartón 2025). Model averaging considers the uncertainty associated with model selection by assigning weights to each model's predictions and combining them to obtain a final estimate, providing a more robust estimate by considering multiple candidate models (Symonds and Moussalli 2011). To ensure comparability across models with different response distributions (binomial, gamma, and gaussian) and correlation structures, we quantified model fit using the pseudo-$R^2$ metric, computed as the squared Pearson correlation between observed and predicted values (Nakagawa and Schielzeth 2013).

In the model designed to examine the hypothesis that high UV doses at male calling sites correlate with a lower probability of males engaging in calling behavior, we introduced the response variable *occurrence of calling behavior*. This variable adopts binary values (0 or 1), where 0 represents the absence of male vocalizations during a specified time interval, and 1 indicates the presence of vocalizations, regardless of the number of males or the frequency of calls emitted. The predictor variables were the time correspondent values of cloud cover, mean luminosity, mean air temperature, 15-minute dose of UVA, 15-minute cumulative dose of UVB, cumulative dose of UVA (from 07:00 h to the observation at the current time, *t*) and cumulative dose of UVB (from 07:00 h to *t*).

In the models built to test the hypothesis that the calling investment decreases with increasing UV incidence at calling sites, we entered the *number of calls emitted* and the *duration of calls* as response variables. The number of calls emitted, and the duration of calls, represent the total and the mean observed values within each time interval, respectively. Predictor variables were the same as in the first model. These models included only non-zero values in the response variable (i.e., only active males) as we were interested in exploring further the association between UV and the calling investment of individuals that remained acoustically active. For all models, the cloud cover was the only predictor entered as an interaction term with 15-minute dose of UVA, 15-minute dose of UVB, mean light intensity, and mean air temperature, because cloud cover can affect these variables in different ways. For example, cloud cover can either act as a major barrier to UV after the ozone layer or can diffuse the UV in the environment when there is a greater number of water particles in the air (Frederick et al. 1989).

Finally, to evaluate whether the *number of calls* and the mean *call duration* differed among periods of the day (*i.e.*, morning hours, midday hours and afternoon hours), we fitted generalized linear mixed-effects models (GLMMs) using the *glmmTMB* v. 1.1.8 (Brooks et al. 2017). In both models, the period of the day (either 07:00–10:45 h, 11:00–13:45 h or 14:00–17:45 h) was included as a categorical fixed effect. To account for the non-independence of observations taken at the same sites and on the same dates, we included random intercepts for site and date in both models. As in the previous models, the random factor time was fitted as a first order autoregressive term (AR1), that relates the observation at the current time, *t*, to the observation at the previous time, *t-1* (see Larsen et al. 2021), and the model accounted for correlation between observations close in time within the same date (*i.e.*, ar1(time+0|date) in R notation). Estimated marginal means (EMMs) and pairwise contrasts among periods of the day were obtained using the *emmeans* package v 1.11.2.8 (Lenth and Piaskowski 2025) with Tukey's correction for multiple comparisons.

Rainfall and air humidity were not included in the models because previous work on the same population showed no effect of air humidity on daily calling activity and demonstrated that accumulated rainfall influences calling behavior only at monthly, but not daily, temporal scales (Caldart et al. 2016). Furthermore, *C. schmidti* males occupy permanent lotic environments with consistently high ambient humidity and, as a result, males do not experience meaningful humidity gradients during daily calling activity (Caldart et al. 2016). In all models, the continuous predictors were standardized and centered to zero to produce comparable effect sizes (Schielzeth 2010). When fitting a model, we used the variance inflation factor (VIF) to analyze the magnitude of multicollinearity of model terms using the package Performance (Lüdecke et al. 2021), and kept in models only the predictors that presented VIF < 4 with other predictors (a VIF value > 5 indicates a problematic amount of collinearity of a given predictor with other predictors; James et al. 2013). Finally, after fitting a model we tested its goodness of fit, the significance of the dispersion parameter (to check for under- or over-dispersion), and the presence or absence of zero-inflation, when applicable, using package *DHARMa* version 0.4.7 (Hartig 2022). Diagnostic plots and diagnostic tests for all models are presented in Supplemental materials S4-S6. All statistical analyses were performed in R version 4.1.2 (R Core Team 2022).

## RESULTS

The 19 days of passive acoustic monitoring totaled 484 hours and 15 minutes of recordings, of which 193 hours and 45 minutes (40.1% of total recording time) included males exhibiting calling activity. The occurrence of calling activity was more common during the morning hours (53.1% of total morning time intervals analyzed), intermediate at midday hours (42.6%), and lower in the afternoon hours (25%; Fig. 2A).

The best-supported models ($\Delta AIC_c < 2$) to explain the occurrence of male calling behavior contained three models with $\Delta AIC_c$ weights ($w_i$) varying from 0.52 to 0.24 (Table 1). The best-ranked model included air temperature, 15-minute dose of UVB, and cumulative dose of UVB as predictors ($\Delta AIC_c$ $w_i = 0.52$). The other two models included air temperature, 15-minute dose of UVB, cumulative dose of UVB, and cumulative dose of UVA ($\Delta AIC_c$ $w_i = 0.24$), and air temperature, 15-minute dose of UVB, cumulative dose of UVB, and cloud cover ($\Delta AIC_c$ $w_i = 0.24$), respectively. Model-averaged parameter estimates that do not overlap zero (Table 2) were air temperature (-0.215, S.E = 0.067, CI = -0.347 to -0.083), cumulative dose of UVB (-0.289, S.E = 0.073, CI = -0.433 to -0.146), and 15-minute dose of UVB (0.128, S.E = 0.044, CI = 0.042 to 0.214). Thus, the probability of recording males in calling behavior decreased with mean air temperature and cumulative dose of UVB but increased with 15-minute dose of UVB (Fig. 3). Both the best model and the averaged model showed equally moderate predictive performance (Pearson's pseudo-$R^2 = 0.35$) and were consistent in the direction and magnitude of the effects (Supplemental material S4).

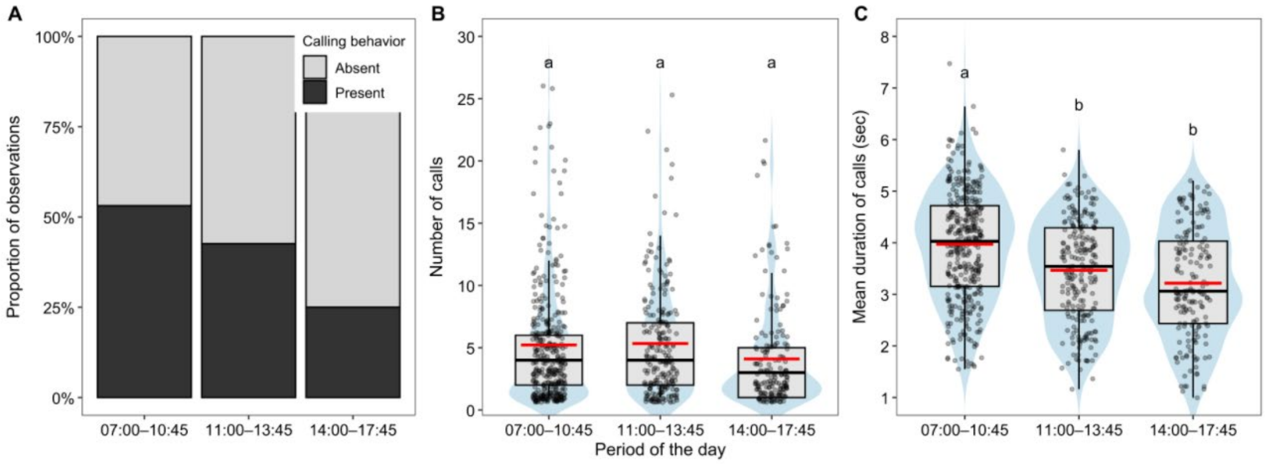

**Fig. 2.** Temporal patterns of the calling behavior of *Crossodactylus schmidti* males during three periods of the day (07:00 to 18:00 h): morning hours (07:00 to 10:45 h), midday hours (11:00 to 13:45 h) and afternoon hours (14:00 to 17:45 h). Bars in (A) show the proportion of occurrence or absence of calling behavior (n = 1936 successive time intervals), box plots in (B) show the number of calls emitted (n = 775 time intervals), and in (C) show the duration of calls (n = 775 time intervals) emitted by *Crossodactylus schmidti* males. The red horizontal bar inside box plots indicates the mean value, while different letters above box plots indicate significant post-hoc differences between periods by the Tukey HSD test ($p < 0.05$).

**Table 1.** List of best-supported models ($\Delta AIC_c < 2.0$) to fit the observed data about the effect of short- and long-term cumulative doses of UVA and UVB, air temperature, light intensity and cloud cover on different proxies of calling behavior of *Crossodactylus schmidti* males. Best-ranked models are indicated in boldface. The full model and a null model including only random terms are presented for each response variable for comparison

| Response variable | Rank | Candidate model | $AIC_c$ | $\Delta AIC_c$ | *k* | $w_i$ |
|---|---|---|---|---|---|---|
| *Occurrence of calling behavior* | 1 | **Mean air temperature + 15 min dose of UVB + Cumulative dose of UVB** | **2230.4** | **0.0** | **8** | **0.52** |
| | 2 | Mean air temperature + Cumulative dose of UVA + 15 min dose of UVB + Cumulative dose of UVB | 2231.9 | 1.5 | 9 | 0.24 |
| | 3 | Cloud cover + Mean air temperature + 15 min dose of UVB + Cumulative dose of UVB | 2231.9 | 1.6 | 9 | 0.24 |
| | full | 15 min dose of UVA * Cloud cover + 15 min dose of UVB * Cloud cover + Cumulative dose of UVA + Cumulative dose of UVB + Mean light intensity * Cloud cover + Mean air temperature * Cloud cover | 2241.3 | 11.0 | 16 | 0.002 |
| | null | 1 + (1 \| site) + (1 \| date) + AR1(time + 0 \| date) | 2266.9 | 36.5 | 5 | <0.001 |
| *Number of calls* | 1 | **Mean air temperature + Mean light intensity + Cumulative dose of UVB** | **3811.7** | **0.0** | **9** | **0.26** |
| | 2 | Mean air temperature + Mean light intensity + Cumulative dose of UVA | 3812.4 | 0.7 | 10 | 0.18 |
| | 3 | Mean air temperature + Mean light intensity + 15 min dose of UVA | 3812.6 | 0.9 | 10 | 0.17 |
| | 4 | Mean air temperature + Mean light intensity + 15 min dose of UVA + Cumulative dose of UVA + Cumulative dose of UVB | 3812.8 | 1.1 | 11 | 0.15 |
| | 5 | Mean air temperature + 15 min dose of UVA + Cumulative dose of UVB | 3813.1 | 1.4 | 9 | 0.13 |
| | 6 | Mean air temperature + 15 min dose of UVA + Cumulative dose of UVA + Cumulative dose of UVB | 3813.3 | 1.6 | 10 | 0.12 |
| | full | 15 min dose of UVA * Cloud cover + 15 min dose of UVB * Cloud cover + Cumulative dose of UVA + Cumulative dose of UVB + Mean light intensity * Cloud cover + Mean air temperature * Cloud cover | 3821.8 | 10 | 17 | 0.002 |
| | null | 1 + (1 \| site) + (1 \| date) + AR1(time + 0 \| date) | 3825.3 | 13.5 | 6 | <0.001 |
| *Mean duration of calls* | 1 | **Mean air temperature + Cumulative dose of UVB** | **2090.2** | **0.0** | **8** | **0.21** |
| | 2 | Cloud cover + Mean air temperature + Cumulative dose of UVB | 2090.9 | 0.7 | 9 | 0.15 |
| | 3 | Mean air temperature + 15 min dose of UVA + Cumulative dose of UVB | 2091.3 | 1.2 | 9 | 0.12 |
| | 4 | Cloud cover * Mean air temperature + Cumulative dose of UVB | 2091.3 | 1.2 | 10 | 0.12 |
| | 5 | Mean air temperature + 15 min dose of UVB + Cumulative dose of UVB | 2092.0 | 1.8 | 9 | 0.09 |
| | 6 | Mean air temperature + 15 min dose of UVA + 15 min dose of UVB | 2092.1 | 1.9 | 10 | 0.08 |
| | 7 | Mean air temperature + Mean light intensity + Cumulative dose of UVB | 2092.1 | 1.9 | 9 | 0.08 |
| | 8 | Cloud cover + Mean air temperature + 15 min dose of UVA + Cumulative dose of UVB | 2092.1 | 1.9 | 10 | 0.08 |
| | 9 | Mean air temperature + Cumulative dose of UVA + Cumulative dose of UVB | 2092.1 | 2.0 | 9 | 0.08 |
| | null | 1 + (1 \| site) + (1 \| date) + AR1(time + 0 \| date) | 2096.1 | 6.0 | 6 | 0.01 |
| | full | 15 min dose of UVA * Cloud cover + 15 min dose of UVB * Cloud cover + Cumulative dose of UVA + Cumulative dose of UVB + Mean light intensity * Cloud cover + Mean air temperature * Cloud cover | 2103.2 | 13.0 | 17 | <0.001 |

Note: Models are ranked by increasing order of their $\Delta AIC_c$ values. All models included the same random-effects structure: (1|site) + (1|date) + AR1(time | date). k = number of parameters, $\Delta AIC_c$ = difference between the $AIC_c$ value of each model and the $AIC_c$ value of the best-ranked model, and $w_i$ = $AIC_c$ weight of each model. The symbol + indicates an additive effect between variables, and the symbol * indicates an interaction between variables.

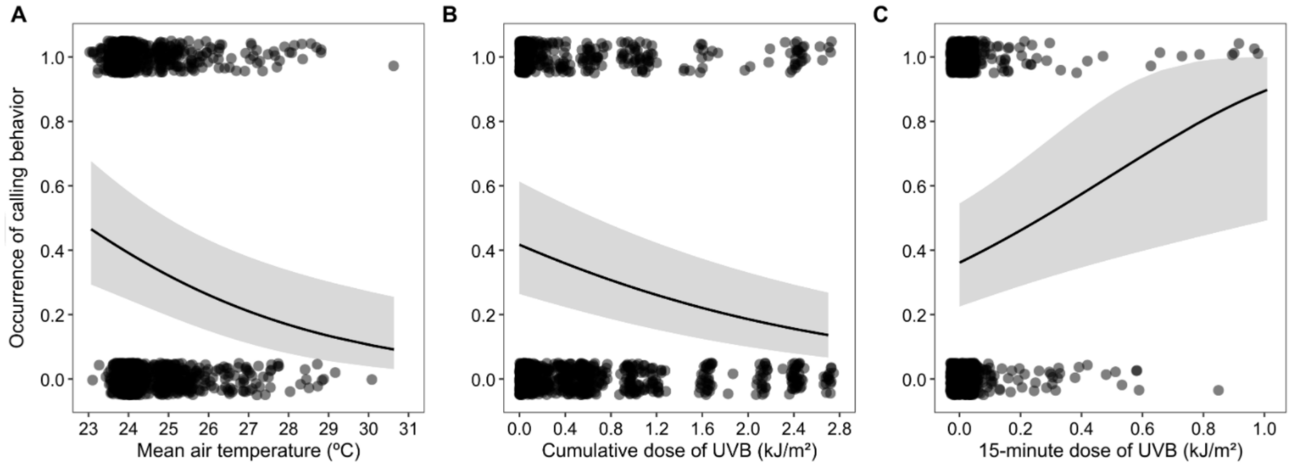

**Fig. 3.** Association between air temperature (A), cumulative dose of UVB (B), and 15-minutes dose of UVB (C) on the occurrence (probability) of calling behavior of *Crossodactylus schmidti* males. The thick line represents the mean value predicted by the best-ranked model ($\Delta AIC_c$ $w_i$ = 0.52), and the gray area indicates the 95% confidence interval. Each dot represents data from successive time intervals (n = 1936) of passive acoustic sampling from 07:00 to 18:00 h, adjusted in the GLMMs for temporal autocorrelation. Dots are shown with a small amount of jitter for clearer visualization of superimposed data points.

The number of calls emitted by males was highly variable during the day (mean 5.31 ± 4.98 calls; range = 1 - 42), with no difference between morning (5.24 ± 0.74 sec), midday (5.39 ± 0.53 sec) and afternoon hours (4.23 ± 0.87 sec; Fig. 2B). The best-supported models to explain the number of calls emitted contained six models with $\Delta AIC_c$ weights ($w_i$) varying from 0.26 to 0.12, all of which contained air temperature and cumulative dose of UVB as predictors (Table 1). The best-ranked model included air temperature, luminosity, and cumulative dose of UVB ($\Delta AIC_c$ $w_i$ = 0.26). Model-averaged parameter estimates that do not overlap zero (Table 2) were air temperature (-0.182, S.E = 0.043, CI = -0.267 to -0.097), and cumulative dose of UVB (0.107, S.E = 0.051, CI = 0.006 to 0.207). Thus, the number of calls emitted by males decreased with mean air temperature but increased with cumulative dose of UVB (Fig. 4). Both the best model and the averaged model showed equally good predictive performance (Pearson's pseudo-$R^2$ = 0.49) and were consistent in the direction and magnitude of the effects (Supplemental material S5).

**Table 2.** Summary of model-averaged coefficients combining the subset of best-supported models ($\Delta AIC_c < 2$) to fit the observed data about the effect of short- and long-term cumulative doses of UVA and UVB, air temperature, light intensity and cloud cover on different proxies of calling behavior of *Crossodactylus schmidti* males. SE = standard error; 95% CI = 95% confidence interval

| Variable | Estimate | SE | 95%CI |
|---|---|---|---|
| Occurrence of calling behavior | | | |
| Intercept | -0.778 | 0.286 | -1.339 to -0.218 |
| Mean air temperature | -0.215 | 0.067 | -0.347 to -0.083 |
| 15 min dose of UVB | 0.128 | 0.044 | 0.042 to 0.214 |
| Cumulative dose of UVB | -0.289 | 0.073 | -0.433 to -0.146 |
| Cumulative dose of UVA | -0.015 | 0.050 | -0.231 to 0.107 |
| Cloud cover | -0.007 | 0.026 | -0.121 to 0.059 |
| Number of calls | | | |
| Intercept | 1.397 | 0.194 | 1.017 to 1778 |
| Mean air temperature | -0.182 | 0.043 | -0.267 to -0.097 |
| Mean light intensity | 0.075 | 0.062 | -0.004 to 0.202 |
| Cumulative dose of UVB | 0.107 | 0.051 | 0.006 to 0.207 |
| Cumulative dose of UVA | -0.029 | 0.047 | -0.164 to 0.034 |
| 15 min dose of UVA | 0.028 | 0.037 | -0.021 to 0.122 |
| Mean duration of calls | | | |
| Intercept | 3.603 | 0.286 | 3.043 to 4164 |
| Mean air temperature | -0.138 | 0.049 | -0.234 to -0.043 |
| Cumulative dose of UVB | 0.104 | 0.052 | 0.001 to 0.207 |
| Cloud cover | -0.014 | 0.028 | -0.107 to 0.026 |
| Cloud cover * Mean air temperature | -0.006 | 0.021 | -0.126 to 0.027 |
| 15 min dose of UVA | 0.012 | 0.029 | -0.039 to 0.124 |
| 15 min dose of UVB | -0.006 | 0.022 | -0.120 to 0.052 |
| Mean light intensity | -0.002 | 0.018 | -0.139 to 0.095 |
| Cumulative dose of UVA | 0.001 | 0.018 | -0.101to 0.136 |

Note: Estimates correspond to full model-averaged coefficients across the subset of best-supported models ($\Delta AIC_c < 2$; Table 1), with model weights incorporated in the averaging process.

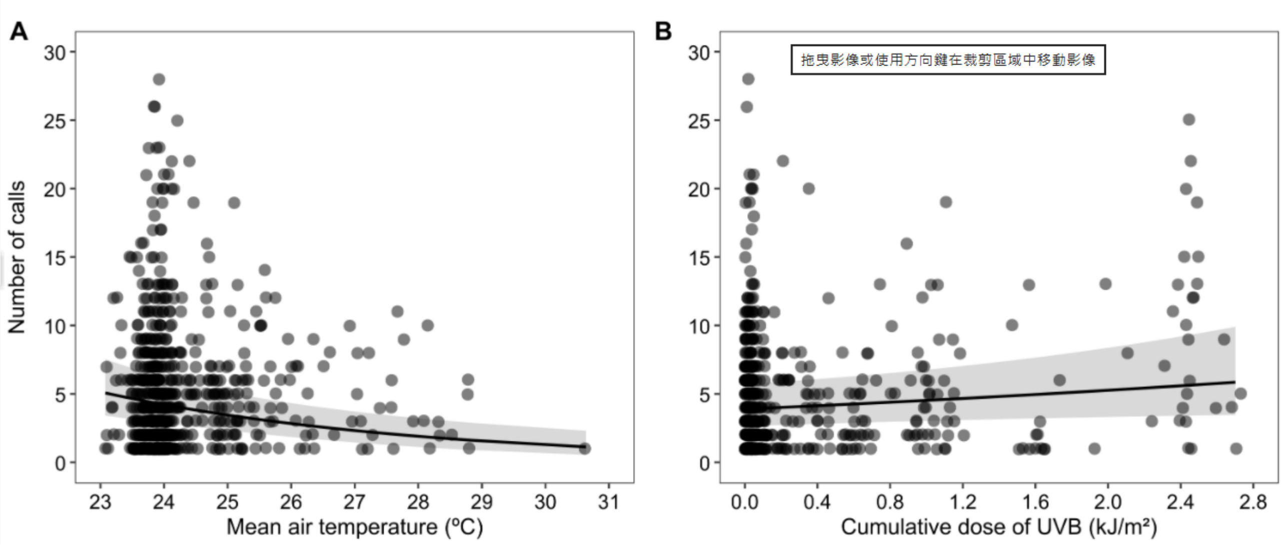

**Fig. 4.** Association between air temperature (A) and cumulative dose of UVB (B) on the number of calls emitted by *Crossodactylus schmidti* males. The thick line represents the mean value predicted by the best-ranked model ($\Delta AICc\ w_i = 0.26$), and the gray area indicates the 95% confidence interval. Each dot represents data from successive time intervals (n = 775) of passive acoustic

sampling from 07:00 to 18:00 h, adjusted in the GLMMs for temporal autocorrelation. Dots are shown with a small amount of jitter for clearer visualization of superimposed data points.

The mean duration of the advertisement calls emitted by males during the day was quite variable (mean 3.65 ± 1.16 sec, range = 0.996 - 9.852). However, the mean duration of calls was longer during the morning hours (3.95 ± 0.21 sec), intermediate at midday hours (3.47 ± 0.12 sec), and lower in the afternoon hours (3.22 ± 0.13 sec; Fig. 2C). The best-supported models to explain the duration of the calls emitted by males contained nine models with $\Delta AIC_c$ weights ($w_i$) varying from 0.21 to 0.08, all of which contained air temperature and cumulative dose of UVB (Table 1). The best-ranked model included only air temperature and cumulative dose of UVB as predictors ($\Delta AIC_c$ $w_i$ = 0.21). Model-averaged parameter estimates that do not overlap zero (Table 2) were air temperature (-0.138, S.E = 0.049, CI = -0.234 to -0.043), and cumulative dose of UVB (0.104, S.E = 0.052, CI = 0.001 to 0.207). Thus, the duration of calls emitted by males decreased with mean air temperature but increased with cumulative dose of UVB (Fig. 5). Both the best model and the averaged models showed good predictive performance (Pearson's pseudo-$R^2$ = 0.52 and 0.53, respectively) and were consistent in the direction and magnitude of the effects (Supplemental material S6).

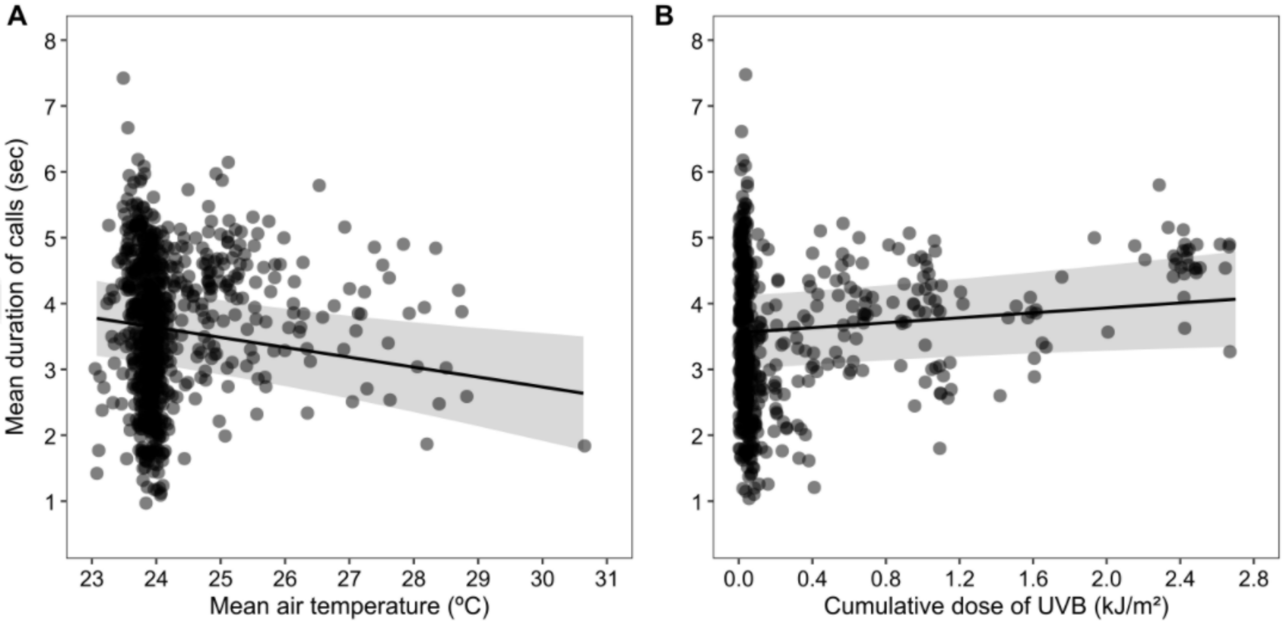

**Fig. 5.** Association between air Temperature (A) and cumulative dose of UVB (B) on the duration of calls emitted by *Crossodactylus schmidti* males. The thick line represents the mean value

predicted by the best-ranked model (ΔAICc $w_i = 0.21$), and the gray area indicates the 95% confidence interval. Each dot represents data from successive time intervals (n = 775) of passive acoustic sampling from 07:00 to 18:00 h, adjusted in the GLMMs for temporal autocorrelation. Dots are shown with a small amount of jitter for clearer visualization of superimposed data points.

## DISCUSSION

In this study we tested the association between the abiotic environment and the calling behavior of *Crossodactylus schmidti*, a diurnal stream-breeding frog from the Neotropics. We predicted that high doses of UV reaching calling sites are associated with a reduced *probability of males engaging in calling behavior*. We also predicted that the investment of males in calling behavior (i.e., *number* and *duration of calls*) decreases with increasing UV incidence. Overall, we expected UVB to impact male calling behavior more than UVA due to its higher DNA absorption, faster damage, and greater energy demand for repair. We found that both best-ranked and average models consistently included air temperature and long-term cumulative UVB dose as variables influencing calling behavior, with cumulative UVB effects varying in direction and magnitude across response variables. In what follows we discuss how these results support some predictions of the hypotheses tested, and we also discuss the relevance of unexpected results regarding positive associations between UVB and male calling behavior.

Higher air temperatures at calling sites were associated with a *lower probability of recording males in calling behavior*, as well as *shorter* and *less frequent calls*. This result agrees with well-established evidence that temperature influences anuran activity (Wells and Schwartz 2007), as daily minimum and mean temperatures often correlate positively with calling, whereas high maximum temperatures and large daily fluctuations tend to suppress it (Ospina and Villanueva-Rivera 2013; Santos et al. 2020). The association between temperature and activity reflects the basking behavior of ectotherms (Sinsch 1989; Snyder and Hammerson 1993; Centeno et al. 2015), as several diurnal species use sunlight for thermoregulation but face increasing evaporative water loss that limits activity at higher temperatures (Hatano et al. 2002; Lingnau and Bastos 2007;

Ospina and Villanueva-Rivera 2013). Although this pattern is well documented, its confirmation under natural conditions is relevant in the context of concurrent solar exposure during warmer summer days, highlighting the importance of considering not only thermal but also ultraviolet components of sunlight when evaluating behavioral responses of anurans to increasing trends of environmental and climatic change.

Higher cumulative UVB doses at calling sites (but not UVA) were associated with a lower *probability of recording males in calling behavior*. We predicted that cumulative UVB exposure throughout the day would negatively correlate with male calling behavior, as harmful UVB doses have high genotoxic potential, leading to mutations or even cell death (Londero et al. 2019; Lundsgaard et al. 2020). At such harmful UVB doses a costly molecular mechanism is triggered to repair DNA damage (Sancar and Tang 1993; Friedberg 2003; Iyama and Wilson 2013). Since DNA damage is proportional to UVB exposure, high doses may lead to energy deficits due to the costly repair process, affecting motor, immune, and metabolic functions (Blaustein et al. 2000; Belden and Blaustein 2002; Alemanni et al. 2003; Santos et al. 2018). Although photorepair mechanisms operate on a timescale of a few femtoseconds (Kao et al. 2007), the associated energetic cost may impose a trade-off between physiological maintenance and behavioral investment (García-Huidobro et al. 2017; Pulgar et al. 2017). In anurans, calling behavior requires substantial energy, as it involves the contraction of large muscle groups relative to total body mass (Prestwich 1994; Ophir et al. 2010). Thus, under high UVB exposure, males may cease calling if they are unable to meet both the energetic demands of vocalization and the metabolic costs of DNA repair. In *C. schmidti*, males establish and defend territories in forest streams by emitting advertisement calls throughout the daytime (Caldart et al. 2016). Consequently, ceasing calling behavior increases opportunity costs, as males failing to vocalize may lose mating opportunities and territorial control (Wells 1977; Wells and Schwartz 2007). The observed decrease in calling probability with increasing cumulative UVB exposure aligns with our prediction and suggests a direct link between harmful UVB doses and behavioral constraints in this diurnal anuran species inhabiting preserved forest streams.

The 15-minute doses of UVB (*i.e.*, a minor dose relative to cumulative UVB) were associated with an increased *probability of recording males in calling behavior*, and the total cumulative UVB dose incident on calling sites were associated with *longer* and *more frequent calls*.

These results contradict our initial prediction that higher UVB exposure would be associated with reduced calling behavior and investment. Our data shows a pattern in which the number and duration of calls increase along the cumulative UVB gradient; however, this pattern is accompanied by a reduction in both the number of observations and data variance at higher UVB doses. This suggests that only a subset of males can sustain calling activity under high UVB exposure. This interpretation aligns with our finding that the overall probability of calling behavior decreases as cumulative UVB exposure increases, suggesting a selective process favoring individuals with greater tolerance to UVB-induced stress. In ectothermic species, basking behavior serves not only thermoregulatory purposes but also facilitates vitamin D production (Ferguson et al. 2003) as ultraviolet B radiation plays a key role in vitamin D synthesis in vertebrates (Antwis and Browne 2009; Bouillon and Suda 2014). Vitamin D plays a critical role in calcium metabolism and muscle function, which are important for sustained calling activity. However, prolonged UVB exposure also imposes metabolic costs (Michaels and Preziosi 2013; Londero et al. 2019; Lundsgaard et al. 2020), including increased energy expenditure for DNA repair mechanisms and potential oxidative stress (Blaustein et al. 2000; Belden and Blaustein 2002; Alemanni et al. 2003; Santos et al. 2018).

Taken together, the observed pattern may suggest a potential trade-off in which males in superior physiological condition are better able to tolerate and potentially benefit from UVB exposure. Body size and energy reserves might also contribute to this pattern, since larger individuals have greater lung capacity for sustaining longer calls (Wells and Schwartz 2007; Ophir et al. 2010) and tend to possess higher lipid reserves (Simpson 1992; Scott et al. 2007). Therefore, it is plausible that males in better body condition—those with greater energy reserves and/or enhanced UVB tolerance—could be overrepresented among individuals calling under high UVB exposure. We emphasize, however, that our interpretation should be viewed with caution. Controlled manipulations of UVB exposure, combined with physiological measurements of male subjects, are needed to test this hypothesis and to evaluate whether the pattern truly reflects condition-dependent tolerance to UVB. Additionally, alternative explanations, including unmeasured environmental factors, social dynamics, or individual hormonal variation, may also contribute to the pattern observed.

## CONCLUSIONS

We investigated associations between the abiotic environment and the calling behavior of *Crossodactylus schmidti*, a diurnal frog that inhabits preserved forest streams. We found that males are less likely to engage in calling behavior during periods of higher temperatures and higher cumulative UVB doses. These results emphasize that both thermal and ultraviolet components of sunlight must be considered when evaluating how anurans respond behaviorally to ongoing environmental and climatic changes. However, contrary to our predictions about the associations between UV exposure and calling investment, males emitted longer and more frequent calls at higher cumulative UVB doses, although fewer males did so. These findings suggest that UVB may play a role in selecting high-quality males, a possibility that warrants further experimental investigation. In addition to bringing new possibilities of research about the role of UV radiation on the calling behavior of anurans, our results showcase how heterogeneity in the abiotic environment can have contrasting behavioral effects in diurnal anurans in forest streams, organisms to which our understanding of the UV effects on behavior is still incipient.

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**Authors' contributions:** AAM, MBS, and APS conceived the study and designed the methodology; AAM and MBS developed and built the datalogger; AAM collected and organized the data with MBS under supervision of VMC; NJS provided access to cloud cover data and logistical support; VMC analyzed the data and prepared the figures; AAM wrote the first draft, and all authors revised and approved the final manuscript.

**Competing interests:** The authors declare no competing interests.

**Availability of data and materials:** All data and materials will be made available upon request.

**Consent for publication:** All authors consent to publication.

**Ethics approval and consent to participate:** This study was conducted under collection license 64137-1 issued by SEMA-RS. No individuals were captured, marked, or held in captivity, and minimal disturbance occurred due to the passive nature of data collection.

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