

Sunlight and diel behaviors promote coexistence of frogs through temporal acoustic partitioning

Running title: Sunlight and behaviors promote coexistence

Authors: Bryan H. Juarez^{1,2*}, Yuren Sun^{1,3*}, Trevor Hebert⁴, Elizabeth A. Hadly^{1,2,4}

Co-first authors*.

¹Department of Biology; Stanford University; Stanford, California 94305, USA.

²Department of Earth System Science; Stanford University; Stanford, California 94305, USA.

³Department of Computer Science; Stanford University; Stanford, California 94305, USA.

⁴Jasper Ridge Biological Preserve, Stanford University; Stanford, California 94305, USA.

Corresponding Author Email: bryanhjuarez@gmail.com

ORCIDs: Juarez: 0000-0002-5474-596X, Sun: 0009-0004-2196-2070, Hadly: 0000-0002-8227-8967

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Abstract

Understanding how species coexist is one of the main goals in ecology. While many have documented how species coexist in nature, there is much interspecific and spatial heterogeneity in which resources are partitioned and in the contributing environmental factors. Overall, we lack a general understanding of how stable coexistence is maintained for particular groups of organisms. Thus, we studied how climate relates to temporal acoustic partitioning in two frog species, *Pseudacris sierra* and *Anaxyrus boreas* at Jasper Ridge Biological Preserve - 'Ootchamin 'Ooyakma in Woodside, USA. We predicted that *P. sierra* prefers cooler temperatures, greater humidity, less wind, and less ultraviolet radiation relative to *A. boreas*. We collected climatic data and a total 1,380 hours of audio from 3PM to 1AM from January to June of 2022. We then trained a convolutional neural network model to identify our study species with 97.63% testing accuracy and manually estimated the model's precision and true positive and false negative rates which showed adequate statistical properties. Next, we used a zero-inflated generalized linear mixed model to determine the climatic factors influencing overall and relative amphibian activity at Jasper Ridge. We found warmer temperatures and less wind were associated with overall calling activity, while only UV index affected the relative call abundance of *P. sierra* and *A. boreas*. *P. sierra* was unaffected by UV index while *A. boreas* calling activity showed a positive relationship with UV index. These results indicate sunlight and diel activity (diurnality and nocturnality) are the primary drivers of temporal acoustic partitioning in this system. We also describe how interspecific male-male competition and wind may result in signal interference which indirectly reduces sexual conflict by limiting access to conspecific females, increasing female fitness in a frequency-dependent fashion, thus promoting coexistence. Finally, we discuss the importance of noise and light pollution in relation to species coexistence in urban environments and describe several ways to improve signal-to-noise ratios for machine learning applications.

Introduction

Persistence and extinction are two possible outcomes of species interactions over short time scales (Hastings, 2010, 2001). Historically, the competitive exclusion principle laid the foundation for the more general theory of limiting similarity that posits some maximal overlap in resource use before extinction becomes inevitable (Abrams, 1983; Gause and Witt, 1935; MacArthur and Levins, 1967). The latter transition happened alongside a shift in how we might quantify ecological similarity among species, from complete niche overlap to shared limiting resources (DeBach and Sundby, 1963; Gause and Witt, 1935; MacArthur, 1984; Schoener, 1974). The sharing of limited resources may promote species coexistence and happens through a process called resource partitioning (Roughgarden, 1976). Resource partitioning happens when populations or species use resources such that the net costs associated with competition for resources are reduced (Schoener, 1974; Toft, 1985). Many types of biotic and abiotic resources are partitioned in nature such as food and habitat (Pianka, 1975), foraging or breeding sites (Beaulieu and Sockman, 2012; Linnebjerg et al., 2013; Wiens et al., 2014), and even the soundscape (Chhaya et al., 2021). Resource partitioning happens through selection for reduced shared resource use and can involve density-dependent effects, ecological differentiation, or reproductive interference (Gómez-Llano et al., 2021; Gröning and Hochkirch, 2008; Roughgarden, 1976). Overall, resource partitioning is thought to promote coexistence among similar species.

Coexistence can result from the partitioning of shared resources across many dimensions and scales. Partitioning of resources across the dimension of time has perhaps received the most attention (Adams and Thibault, 2006; Kronfeld-Schor and Dayan, 2003; Lima and Magnusson, 1998; Pianka, 1975). For example, mesopredators in the Mediterranean partition prey resources relative to time of day (Ferreiro-Arias et al., 2021). Resource partitioning across time can also occur at larger or smaller scales. For example, birds partition food resources differently across seasons and this was possibly explained by increased competition when bird abundances were high (Beaulieu and Sockman, 2012). Similarly, organisms may partition resources across different spatial scales ranging from small microhabitat (~1 m) scale to large regional (~100 km)

scales (Jones et al., 2015; Prado et al., 2005; Traba et al., 2015). Lastly, animals that communicate through sound might also partition the spectral properties of the noises they produce, such as calling frequency (Bignotte-Giró et al., 2019; Perkins et al., 2017). An ideal model system for studying resource partitioning and coexistence in nature should be abundant, widespread, ecologically and taxonomically diverse, and exhibit many types of resource partitioning.

Anuran amphibians are an ideal model system for studying resource partitioning in natural habitats. First, anuran amphibians are an ecologically diverse group with >7,700 species with a near circumglobal distribution (AmphibiaWeb, 2024). Their ecological diversity allows us to study resource partitioning in a variety of abiotic and biotic contexts. Second, frogs reproduce year-round or seasonally and use loud calls to attract mates during the breeding season (Duellman and Trueb, 1994). This allows easy detection of reproductive activity in nature (relative to organisms in which sound is not used to attract mates). Third, anuran reproduction is generally tied to water and temperature which allows us to investigate the role of climate in how organisms partition resources. Reproduction often involves breeding migrations to water sources where dense freshwater aggregations are formed to find mates (Duellman and Trueb, 1994; Kopp and Eterovick, 2006). Frogs compete for all kinds of resources during the breeding season including food, mates, calling sites, and the soundscape. Anurans also split resources in many ways including temporal (Kopp and Eterovick, 2006; Lima and Magnusson, 1998; Littlejohn and Martin, 1969; Llusia et al., 2013; Lötters et al., 2004; Lüddecke et al., 2000; Prado et al., 2005; Wood et al., 2023), spatial (Bignotte-Giró et al., 2019; Kopp and Eterovick, 2006; Llusia et al., 2013; Lötters et al., 2004; Lüddecke et al., 2000; Prado et al., 2005; Wood et al., 2023), and spectral partitioning of resources (Allen-Ankins and Schwarzkopf, 2022; Bignotte-Giró et al., 2019; Lötters et al., 2004; Lüddecke et al., 2000; Villanueva-Rivera, 2014). While amphibian activity and reproduction depend on water and is inherently tied to the climate, relatively fewer studies have described how the environment affects resource partitioning in amphibians. Some studies have found that rainfall and temperature affect temporal and spatial partitioning of resources in frogs (Kopp and Eterovick, 2006; Llusia et al., 2013; Prado et al., 2005). However, learning more about how climate might influence activity

and reproduction is necessary for understanding the mechanisms by which resource partitioning promotes coexistence.

The general purpose of this study is to understand how climate influences the calling activity of amphibians at a local preserve. Jasper Ridge Biological Preserve - 'Ootchamin 'Ooyakma is located on the ancestral lands of the Muwekma Ohlone Tribe in Woodside, California, USA and is home to two very common species of frogs. These include the Pacific chorus frog *Pseudacris regilla* and the California toad *Anaxyrus boreas halophilus*. *P. regilla* reproduces from January to July while *A. boreas* can reproduce from February to July, but the exact breeding periods vary by population (Leonard, 1993). Reproduction is aquatic in both species (Lannoo, 2005; Weitzel and Panik, 1993). Across its range, *P. regilla* breeds when water temperatures are at least 5–15°C (Lannoo, 2005), but the same is not known in *A. boreas*. *P. regilla* is nocturnal (Leonard, 1993) while *A. boreas* is primarily diurnal (Smits, 1984). *P. regilla* also tends to call most often on warm nights with little wind (Brenowitz and Rose, 1999). The calling frequency of *P. regilla* includes 1–4 kHz while *A. boreas* calls at a frequency of 1–8 kHz (Awbrey, 1972; Vélez and Guajardo, 2021). Lastly, both species share very similar diets consisting primarily of arthropods and snails; *P. regilla* is 25–48 mm long at sexual maturity while mature *A. boreas* is 56–125 mm in length (Lannoo, 2005). Little is known about how these two species coexist in nature, especially during the breeding season, when they often share the same water sources used for reproduction.

Here, we test the hypothesis that climate influences the calling activity of amphibians at Jasper Ridge Biological Preserve - 'Ootchamin 'Ooyakma. There is very little rainfall at this site throughout most of the year and frogs have access to a permanent lake. This implies rainfall plays a small role in amphibian activity at our study site. Instead, humidity might have an effect on amphibian activity since greater air humidity limits evaporative water loss and desiccation risk (Duellman and Trueb, 1994). Desiccation risk and water loss may also result from prolonged or increased exposure to fast winds or shortwave solar radiation, which can also lead to cellular damage (Kearney et al., 2013; Licht and Grant, 1997; Tracy, 1976). Alternatively, it is possible wind does not have a strong drying effect but instead makes it difficult for amphibians to hear each other's calls (Trowbridge and Litzgus, 2022). Specifically, we predict warmer

temperatures, greater humidity, less wind, and less ultraviolet radiation is associated with greater amphibian activity. We also predict *P. regilla* prefers cooler temperatures, greater humidity, less wind, and less ultraviolet radiation relative to *A. boreas*. In addition, we explore how time of day is related to *P. regilla* and *A. boreas* activity. This study is important because amphibians are an ideal system for understanding resource partitioning and coexistence in similar organisms. But, we lack a detailed understanding of how climate affects reproductive activity across the diversity of anuran amphibians and their local environments.

Methods

Study Site

Jasper Ridge Biological Preserve - 'Ootchamin 'Ooyakma is a 1193 acre (483 hectares) natural area in the eastern foothills of the Santa Cruz Mountains in Woodside, California, USA. The preserve falls within the 48 square mile (19 hectares) San Francisquito Creek watershed. Jasper Ridge is owned and managed by Stanford University for research and educational purposes. Public access to Jasper Ridge is limited to guided tours. Jasper Ridge Biological Preserve - 'Ootchamin 'Ooyakma and Stanford University are on the ancestral lands of the Muwekma Ohlone Tribe.

Prior to its inception in 1973, Jasper Ridge's lands were used for grazing and recreation. The preserve includes the 16-acre (6.5 hectares) Searsville Reservoir, formed in 1891 by the construction of Searsville Dam. Since then, the reservoir has lost 90% of its water storage capacity to sedimentation. The buildup of sediments has also contributed to the creation of marshland and willow forest at the southern end of the reservoir that provide habitat for many species of plants and animals, both native and non-native. Elevation at the preserve ranges from 61.6–211.5 meters. Jasper Ridge has a Mediterranean climate with a mean annual temperature of 14.3°C and an average precipitation of 652 millimeters per year, with most rain falling in winter.

Data collection

We used a Davis Instruments cabled Vantage Pro2 Plus installed in 2013 to collect climate data. The weather station is located at Latitude 37.405408°, Longitude

-122.241506° (Fig. 1). The station has an anemometer, and temperature, humidity, and UV sensors. We used the latter to collect data on temperature, relative humidity, wind run (km of wind passing over an area), and UV index. The temperature sensor type is a PN junction silicon diode accurate to $\pm 0.5^\circ\text{F}$ ($\pm 0.3^\circ\text{C}$) mounted 2m above the ground. The relative humidity sensor type film capacitor element is accurate to $\pm 2\%$. The anemometer was mounted on a pole 10m above the ground and is a solid-state magnetic sensor accurate to ± 2 mph (2 kts, 3.2 km/h, 0.9 m/s) or $\pm 5\%$, whichever is greater. Observations were recorded automatically every 5 minutes. We also collected sunset times for each date using the suncalc library v. 0.5.1 (Thieurmel and Elmarhraoui, 2022) and R v. 4.2.1 (R Core Team 2022).

We collected 1,380 hours of audio from 3PM to 1AM every day from January to June of 2020 at the southern edge of Searsville Reservoir at Jasper Ridge (Fig. 1). Jasper Ridge has operated an environmental microphone and public live audio stream from the western shore of Searsville Reservoir since 2013. The microphone is located near open water, marsh, oak woodland and grassland habitat. Many species of birds, amphibians, and insects can be heard throughout the year. The audio was collected using a Barix Instreamer analog-to-digital encoder (BARIX Technology, Oakdale, Minnesota, USA), sampling at 44 KHz, which uses an outdoor electret microphone with a low noise MOSFET pre-amplifier.

Machine Learning Model Training

We trained a Convolutional Neural Network (CNN) model, VGG-19 (Simonyan and Zisserman, 2014), with TensorFlow (Abadi et al., 2016) to detect frog occurrences from audio recordings. The model was trained for classification of 6 classes including the two most common frog species *Pseudacris sierra* and *Anaxyrus boreas*, the relatively rarer American bullfrog (*Rana catesbeiana*), two currently threatened/endangered species (Lannoo, 2005) whose range includes Jasper Ridge (*Rana boylei* and *Rana draytonii*), and a background noise class. Generally, the model outputs predicted classification probabilities for each class based on spectrogram images of the audio.

We trained the model using transfer learning and external audio sources for each sound class. Transfer learning utilizes data that could be more easily retrieved from a related data domain to pre-train the model and was designed to reduce the impact of having a small training dataset (Weiss et al., 2016). We used transfer learning and pre-trained the model using ImageNet (Deng et al., 2009) to better extract features from the input spectrograms. We converted audio data to spectrograms of equal dimensions ($3 \times 224 \times 224 = 150,528$ dimensions), following the sample dimensions of ImageNet. We trained the model to optimize cross-entropy loss which means the model generalized best to spectrogram patterns; additional details are found in the Supplementary Material. We obtained the audio data used for training from three sources including California Herps , AmphibiaWeb (AmphibiaWeb, 2023), and samples collected by Axel Kwet, Rafael Márquez, and Eduardo Alfredo Sanabria found on FonoZoo (FonoZoo, 2023). Prior to training, we cut spectrograms to 1-second intervals, since shorter intervals drastically reduced model accuracy, and we excluded sounds above 2,500 Hz to minimize different types of misclassifications. We describe the full details of data pre-processing in the Supplementary Material. The dataset included 134–388 samples per class which we randomly separated into 80% training, 10% validation, and 10% testing sets. Since data augmentation achieved a testing accuracy of ~85%, while down-sampling produced the best model achieving 97.63% testing accuracy, we trained the model on the dataset after down-sampling by randomly selecting 134 samples per class. We used the same pre-processing scheme as used for our final model to analyze the raw audio from Jasper Ridge. The class with the highest probability was regarded as the predicted class for each time segment.

Machine Learning Model Evaluation

We tested the model predictions based on two approaches with stratified sampling and compared them with manual classifications made by ear. First, we approximated the true positive rate for *A. boreas*, *P. sierra*, and the background noise categories. We did this by randomly sampling 10 positive predictions or the maximum number of predictions we had, whichever is larger, for each interval of 0.1 across the confidence range (0–1). Second, since the latter exhibited high true positive rates, we

assessed statistical precision and false negative rates for the classification model. Precision is the percent of true positive predictions relative to all positive predictions. We estimated precision and false negative rates for our use cases across classification category, month, hour, and classification probability. To do this, we randomly sampled 60 positive predictions per month for *A. boreas*, *P. sierra*, and the background noise category. Within the 60 samples, 10 predictions were randomly sampled for each hour for each month. For example, for each species, we randomly sampled 10 positive predictions that were from 18:00 to 18:59 on any day in January. We sampled separately for predictions above and below 95% classification probability for *A. boreas* and *P. sierra*.

Data Analysis

To explore the factors driving amphibian activity at Jasper Ridge, we only analyzed occurrence classifications made with >95% confidence. Since our dataset spans daylight savings time, we standardized all data to a common scale by subtracting an hour from all observations occurring on or after 13 March 2022. The resulting overlapping times before and after 13 March 2022 included the range of 4PM to 11PM.

We performed an exploratory linear discriminants analysis to determine how *P. sierra* and *A. boreas* activity might differ across date and time. We first separated the observations into 60% training and 40% testing sets. Then, we trained the linear discriminants model and used it to classify the testing set using the MASS library v. 7.3-57 (Venables and Ripley, 2002). We evaluated the model by estimating the intra- and interclass true positive rates for the training and testing sets.

We fit two separate models to test our hypothesis that climate influences the calling activity of amphibians at Jasper Ridge. First, we fit a zero-inflated negative binomial mixed model using the NBZIMM library v 1.0 in R (Yi 2020; Zhang and Yi, 2020). We fit the model by regressing counts against temperature, humidity, wind run, and UV index with species as a random effect and a continuous autoregressive correlation structure to account for time-dependence resulting from taking repeated samples (Box et al., 2015). Models with zero-inflation account for the abundance of 0's typically associated with count data (Zhang and Yi, 2020). Biologically, accounting for

zero-inflation is ideal since we expect different processes to control the lack of amphibian activity versus different levels of activity on days when amphibians are active. For example, reproductive calling activity in amphibians is typically described as depending on minimum temperature or rainfall thresholds but different levels of temperature and rainfall (or other climatic variables) can have differential effects on activity after breeding activity is commenced (Duellman and Trueb, 1994; Prado et al., 2005). Additionally, negative binomial models are general models used to account expected residual variance for ‘typical’ and overdispersed count data (O’Hara and Kotze, 2010; Zhang and Yi, 2020). Second, we fit the same model as above except this time we used date as a random effect and included interactions between species and each climatic variable. In summary, the first model tells us how we may expect climate to influence the activity of any amphibians at Jasper Ridge, whereas the second model tells us how climate is related to differences in activity between *P. sierra* and *A. boreas*.

Results

Overall, the classification model exhibited a testing accuracy of 97.63% and displayed good statistical properties. We found approximate true positive rates of 1.0 for high probability (>0.9) classifications of *P. sierra* and *A. boreas* (Table 1). Additionally, we found high classification precision for *P. sierra* (Fig. 2) and *A. boreas* (Fig. 3) particularly in evening and early afternoon hours, respectively. Lower classification precision for *P. sierra* in the early afternoons and *A. boreas* in the evenings reflected greater false positive rates during those times. We also found false negative rates as high as 48% (during the hours 9–10PM during March 2022) for *P. sierra* and generally low rates for *A. boreas* regardless of hour and month (Fig. 4). However, the overwhelming majority of false negatives occurred because we could hear the distinctive call of *P. sierra* in the far background during high (evening) activity periods, and these happened during the middle of the Spring breeding season (AmphibiaWeb, 2022). We report 34,685 identifications of *P. sierra* 1,820 identifications of *A. boreas* with >95% classification probability. We used the latter high-probability identifications in all downstream analyses.

We found date and time together to reliably classify *P. sierra* but not *A. boreas*. In the testing set, date and time classify *P. sierra* with 99.45% accuracy and *A. boreas* with only 68.58% accuracy. The interclass classification accuracy for the training set was 99.45%. Similarly, for the testing set, the model classified *P. sierra* with an accuracy of 99.42% accuracy and *A. boreas* with 66.29% accuracy. The interclass classification accuracy for the testing set was 99.42%, showing the trained model generalized well to new observations. Interestingly, the sunset line seemed visually parallel to the first linear discriminant function (Fig. 5a). Generally, *P. sierra* is only calling after sunset while *A. boreas* mainly calls before sunset and occasionally active after sunset. *A. boreas* most actively called from mid-April to mid-May at Jasper Ridge, while *P. sierra* exhibited the most calling during mid-February, mid-March, and roughly during the same period as *A. boreas* too. We show the raw data for three biologically important variables (based on our analyses) including temperature, wind run, and UV index in Fig. 5b–d.

We determined temperature, wind, and ultraviolet radiation all influence amphibian activity at Jasper Ridge. In appearances, warmer temperatures are associated with greater activity of both *P. sierra* and *A. boreas* (Fig. 5b). However, it is difficult to visually distinguish how wind might relate to amphibian activity (Fig. 5c). When determining the day-to-day factors affecting amphibian activity (Table 2), we found that greater numbers of calls are associated with warmer temperatures ($t = 2.63$, $p < 0.01$) and less wind ($t = -2.19$, $p < 0.03$). We visualized these effects by plotting generalized least squares fitted values against temperature and wind (Fig. 6). Neither humidity nor UV index were related to calling activity ($p > 0.80$). While temperature and wind were important factors in determining overall activity, neither was an important variable determining the relative call abundance of *P. sierra* and *A. boreas*. After accounting for the effects of other variables, only the UV index seemed to be an important determinant of the relative activity of both species (Fig. 5d; Table 3; $t = -10.10$, $p < 0.001$). The latter result is associated with increasing *A. boreas* activity on days with more UV radiation and no statistically significant effect of UV on *P. sierra* (Fig. 7).

Discussion

Overall, the results suggest temperature, wind, and UV index are important environmental controls on amphibian calling during reproduction. Additionally, the coexistence of *P. sierra* and *A. boreas* at Jasper Ridge is promoted through temporal acoustic partitioning associated with solar activity (UV index) and interspecific differences in diel behavior (diurnality vs. nocturnality).

Amphibian reproduction at Jasper Ridge depends on temperature and wind

We found substantial evidence that climate influences the calling activity of amphibians at Jasper Ridge. As predicted, warmer temperatures and less wind are associated with greater amphibian activity. Our results support the common findings that higher temperatures are typically associated with increased activity (Duellman and Trueb, 1994). Our results are also consistent with a recent study in northern California, USA investigating how *P. sierra* coexists with the Yosemite toad *Anaxyrus canorus* (Wood *et al.*, 2023), in which the authors did not identify any calls on days with minimum daily temperatures as low as 2.8–6.5°C and high winds. While humidity and UV index did not influence overall amphibian activity in this study, our findings indicate that either 1) wind prohibits frogs from hearing each other, and/or 2) wind is the predominant driving force of evaporative water loss of amphibians at Jasper Ridge during the sampled study period and can result in much more rapid dehydration than low humidity or high UV conditions.

Contrary to our findings, one meta-analysis reported the importance of rain and overall lack of an effect of temperature on amphibian abundance (Ficetola and Maiorano, 2016). Importantly, several studies report great spatial and interspecific heterogeneity in the factors affecting amphibian reproduction (Ficetola and Maiorano, 2016; Ge *et al.*, 2015; While and Uller, 2014). Few ecologists would be surprised that amphibian reproduction may exhibit great spatial heterogeneity since different factors might be important in different contexts. In this study, we reasoned that rainfall was not important for amphibian reproduction at Jasper Ridge since the area receives almost no rainfall during the sampled days (95th percentile = 0.225 mm rain) and since amphibians have direct access to water from a permanent lake found at the study site

used for shelter and reproduction. Many areas of ecology would benefit from determining why interspecific heterogeneity in results happens and this is necessary to disentangle true biological processes from potential methodological and statistical artifacts (e.g. heterogeneity in which variables are measured and controlled for across studies). The need to account for potential methodological artifacts has been discussed by many authors, specifically in the area of amphibian conservation (Beebee and Griffiths, 2005; Blaustein and Kiesecker, 2002; Ficetola, 2015).

Sun and diel activity drive acoustic partitioning and species coexistence

While UV index was not associated with overall calling activity at Jasper Ridge, it did play a unique role in the ecology of both species. In this study, days with higher UV indices were associated with greater *A. boreas* activity, but not higher *P. sierra* activity. This finding is consistent with a study that argues photoperiod might be more important than temperature and rainfall in determining amphibian breeding activity (Canavero and Arim, 2009). In fact, when we removed UV index from our model, temperature took its place in giving the apparent result that the animals are tracking temperature. The latter result is apparent from the raw data, since the early and late evenings are quite different in temperature, relative to when species are calling (Fig. 5b). Others have also argued (in mammals) that the importance of photoperiod over temperature in relation to temporal partitioning of resources has been overlooked (Bennie et al., 2014). Links between diel behaviors and temporal resource partitioning have also been reported in mammals and simulation studies (Barros et al., 2024; Gao et al., 2020; Monterroso et al., 2014; Vieira and Paise, 2011). Photoperiod and diel behaviors seem to be the main driving force promoting coexistence of *P. sierra* and *A. boreas* at Jasper Ridge through acoustic partitioning of the soundscape.

The mechanism by which photoperiod and diel behaviors promote coexistence might involve asymmetrical interspecific male-male competition. *A. boreas* can sometimes be found calling after sunset (Fig. 5a) and, while much rarer, some *P. sierra* individuals sometimes call before sunset at Jasper Ridge. The latter is reflected by the performance of the linear discriminant analysis since, unlike *P. sierra*, *A. boreas* cannot easily be classified using a strict date-time cutoff. Furthermore, these findings are

similar to a report that *P. sierra* and *A. canorus* sharply switch the relative abundance of calls they make in response to time of day: the relative number of *P. sierra* calls increased between the hours of 4 and 9PM during May/June 2021 (Figure 3 in Wood et al., 2023). This asymmetry in one species calling when the second tends to call might reflect the fact that *A. boreas*' calling frequency includes and is wider than the calling frequency of *P. sierra* (Awbrey, 1972; Vélez and Guajardo, 2021). This is similar to asymmetric calling patterns found in frogs and cicadas where one species does not call if the other is calling (Endo and Osawa, 2018; Littlejohn and Martin, 1969). The latter may be a common occurrence where rather than interfere with one another's calling, species simply shift their calling times (Lüddecke et al., 2000; Schwartz and Bee, 2013; but see Allen-Ankins and Schwarzkopf, 2022; Villanueva-Rivera, 2014). Following a recent review of how reproductive interactions may promote coexistence (Gómez-Llano et al., 2021), we argue that interspecific and possibly asymmetrical male-male competition for the soundscape and interference from wind promotes coexistence in this system. This is consistent with the argument that acoustic interference from males of another species and wind can indirectly reduce sexual conflict by limiting access to conspecific females and this can increase female fitness in a frequency-dependent fashion (Gómez-Llano et al., 2021). Whether this is true in *P. sierra* and *A. boreas* remains to be seen, but amphibians make an excellent study system to investigate how sexual conflict and biological interactions may promote species coexistence.

Whether temporal acoustic partitioning is the main or sole driver of coexistence of frogs at Jasper Ridge remains to be seen. Differential diel activity seems to be an important mechanism allowing for acoustic partitioning in animals that produce sounds. However, partitioning of other resources such as food (Beaulieu and Sockman, 2012), egg deposition sites, or shelter might play a greater role in promoting species coexistence than acoustic partitioning in this system. For example, trophic resource use was found to be an important driver of coexistence in mammals, alongside temporal partitioning of activity periods (Barros et al., 2024). Additionally, the acoustic niche space (the soundscape) is not completely independent of time and space. For example, the intensity of competition at local scales might change over time, as days get longer or shorter, in response to ecological change (Chhaya et al., 2021), or in complex ways

(Lima and Magnusson, 1998). Shifting competitive intensity over time implies the degree to which acoustic partitioning contributes to coexistence also changes over time. Rather than compete, populations or species might diverge in calling periods (at the hour or month scale) and this makes acoustic partitioning a potential driver or reinforcer of the speciation process in sound-producing organisms. Our interpretations highlight circadian hormones as potential molecular mechanisms by which acoustic partitioning, species coexistence, and temporal divergence in breeding periods occur.

Improving machine learning models to combat anthropogenic effects

We expect the acoustics of communities to change in response to ecological change due to natural processes and anthropogenic effects (Chhaya et al., 2021). In the context of this study, noise and light pollution associated with continued urbanization seem likely to shift natural ecological processes at Jasper Ridge (Bennie et al., 2014; Monterroso et al., 2014; Schwartz and Bee, 2013). As discussed, the amphibians at Jasper Ridge depend on hearing each other and calling at the right hour for effective communication and reproduction. Jasper Ridge is a large gated preserve and our study site is about 0.5–1 km away from the nearest urban noise and light sources, meaning noise and light from urban sources are unlikely to have impacted our results. However, continued modification of the areas surrounding the preserve could potentially and negatively impact efficient communication and circadian activity of the frogs at Jasper Ridge, disrupting the processes enabling species coexistence. It is possible *P. sierra* and *A. boreas* could shift the frequency of their calls to avoid the consequences of urbanization, but it is unclear how often this occurs in nature and the extent to which frequency shifting reduces acoustic interference is limited (Perkins et al., 2017; Schwartz and Bee, 2013). As others have pointed out, improving the methods we use to identify animal sounds in nature and using this knowledge to understand the links between circadian rhythms, resource partitioning, and anthropogenic change is an urgent need (Frey et al., 2017; Monterroso et al., 2014).

Passive acoustic monitoring and automated detection algorithms show much promise in our quest to predict and mitigate negative anthropogenic effects (Allen-Ankins and Schwarzkopf, 2022; Bridges et al., 2000; Brodie et al., 2020; Frey et

al., 2017; Kahl et al., 2021). Most automated detection algorithms use machine learning methods and while they have already led to many important insights, there are also many important areas of development that remain to be explored in detail. For example, ambient noise remains a challenging factor to account for (Kahl et al., 2021). In this study, we accounted for ambient noise by training our model to recognize ambient sound, such as wind hitting the microphone which initially resulted in many incorrect classifications. For this reason, we champion and continue others' efforts to perform rigorous statistical evaluation of classifications obtained from machine learning algorithms (Brodie et al., 2020; Kahl et al., 2021). Future endeavors might seek to systematically identify and provide samples of the types of background sounds we may expect across many types of habitats, regions, and time of day.

An alternative to reduce the effect of noise would be to increase the signal-to-noise ratio of sampled data (Digby et al., 2013). We may increase the signal-to-noise ratio by using appropriate noise filters (de Cheveigné and Nelken, 2019) or perhaps by improving the way we train our models. Data augmentation is a necessary part of model training whereby we improve the effective sample size of our training set by resampling the data in different ways (Chlap et al., 2021). We may increase the signal-to-noise ratio of our datasets by improving the quality of the signals we analyze and to ecologists, this means training the model to recognize as much natural variation in target sounds as possible. For example, target sounds may vary in relation to sound attenuation (Royle, 2018), body size (Ryan and Brenowitz, 1985), calling plasticity (Allen-Ankins and Schwarzkopf, 2022; Vélez and Guajardo, 2021), frequency shifting (Perkins et al., 2017; Schwartz and Bee, 2013), and the presence of other sounds including other targets or background noises. Future studies might seek to use data augmentation to expand the training set to account for as many expected sources of variation we predict are present in our system.

Conclusion

We found strong evidence that warmer temperatures and less wind result in more amphibian calling activity at Jasper Ridge while relative activity between species depended on sunlight and diel behaviors. We argue that male-male competition and

associated reproductive interactions is the mechanism promoting coexistence in our system. Thus, we conclude that photoperiods and diel behaviors can be just as important as temperature and precipitation in the context of promoting reproductive activity and coexistence in amphibians. Finally, we discuss how continued urbanization can lead to increased noise and light pollution which can have detrimental effects on species coexistence in sound-producing organisms.

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Tables

Table 1. The estimated true positive rate of the classification model. Categories include *Pseudacris sierra*, *Anaxyrus boreas*, and background noise. We sampled all categories each 0.1 interval throughout the confidence range, left inclusive and right exclusive, from 0.1–1. There were no positive predictions with confidence below 0.1. True positive rates above 0.9 are in bold.

Confidence Interval	<i>A. boreas</i>	<i>P. sierra</i>	Background noise
0.1–0.2	0.0	0.0	1.0
0.2–0.3	0.1	0.3	0.8
0.3–0.4	0.2	0.8	0.3

0.4–0.5	0.4	0.7	0.3
0.5–0.6	0.5	1.0	0.5
0.6–0.7	0.9	1.0	0.4
0.7–0.8	0.7	0.9	0.2
0.8–0.9	0.8	1.0	0.9
0.9–1	1.0	1.0	0.9

Table 2. Environmental effects on amphibian activity at Jasper Ridge. Summary table is based on a zero-inflated generalized linear mixed model. β = regression coefficient. Std. Error = standard error. DF = degrees of freedom. t = t-statistic. RH is relative humidity. Rows with significant effects ($p < 0.05$) are in bold.

Term	β (unit)	Std. Error	DF	t	p-value
Intercept	3.27 (Count)	1.28	280	2.56	0.01
Temperature	0.07 (Count °C⁻¹)	0.03	280	2.63	0.01
Humidity	0.00 (Count RH ⁻¹)	0.01	280	0.25	0.80
Wind Run	-0.54 (Count km⁻¹)	0.25	280	-2.19	0.03
UV index	-0.22 (Count UV Index ⁻¹)	1.28	280	-0.17	0.86

Table 3. Environmental effects on the relative activity of *Pseudacris sierra* and *Anaxyrus boreas* at Jasper Ridge. Summary table is based on a zero-inflated generalized linear mixed model. β = regression coefficient. Std. Error = standard error. DF = degrees of freedom. t = t-statistic. RH is relative humidity. Rows with significant effects ($p < 0.05$) are in bold.

Term	β (unit)	Std. Error	DF	<i>t</i>	p-value
Intercept	0.27 (Count)	1.17	138	0.23	0.82
<i>P. sierra</i>	7.09 (Count)	1.19	138	5.96	0.00
Temperature	-0.03 (Count °C ⁻¹)	0.04	138	-0.63	0.53
Humidity	0.01 (Count RH ⁻¹)	0.01	138	0.74	0.46
Wind Run	-0.73 (Count km ⁻¹)	0.58	138	-1.25	0.21
UV index	10.37 (Count UV Index⁻¹)	1.45	138	7.20	0.00
<i>P. sierra:</i> Temperature	-0.02 (Count °C ⁻¹)	0.04	138	-0.47	0.64
<i>P. sierra:</i> Humidity	-0.02 (Count RH ⁻¹)	0.01	138	-1.79	0.08
<i>P. sierra:</i> Wind Run	0.43 (Count km ⁻¹)	0.58	138	0.75	0.46
<i>P. sierra:</i> UV index	-14.65 (Count UV Index⁻¹)	1.45	138	-10.10	0.00

Figures

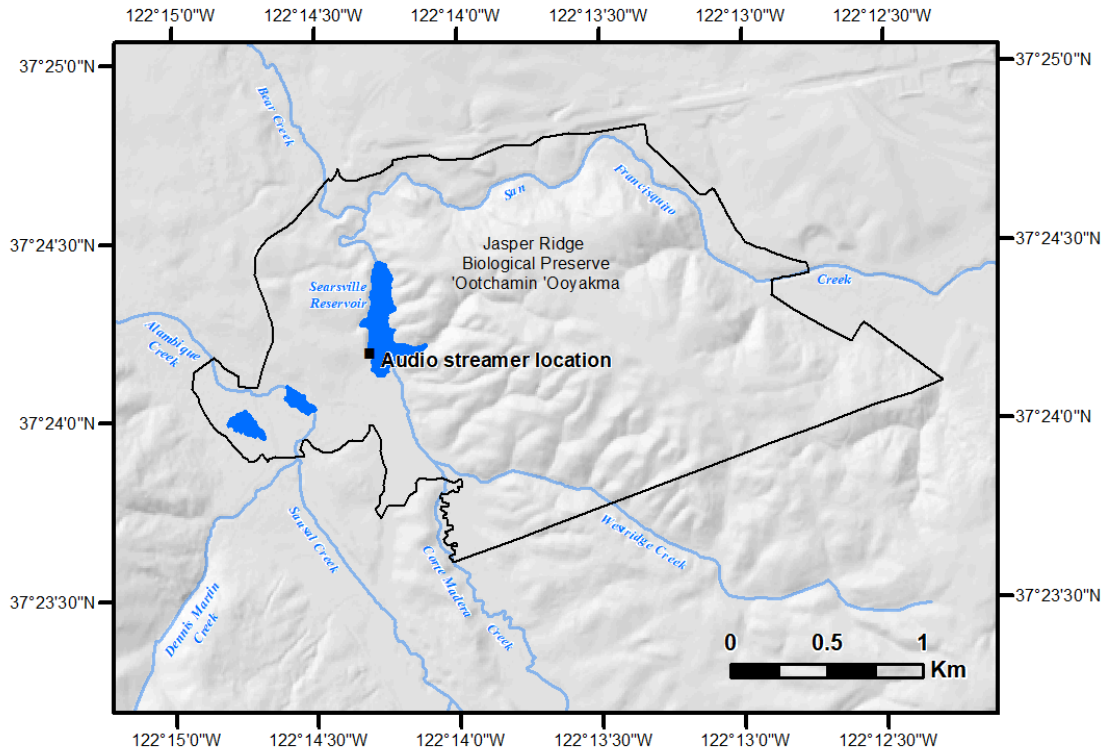


Figure 1. Audio streamer location at Jasper Ridge Biological Preserve - 'Ootchamin 'Ooyakma. Jasper Ridge Biological Preserve - 'Ootchamin 'Ooyakma is located on the ancestral lands of the Muwekma Ohlone Tribe in Woodside, California, USA. The audio streamer was placed at the edge of Searsville Reservoir (16-acre = 6.5 hectares), formed in 1891 by the construction of Searsville Dam.

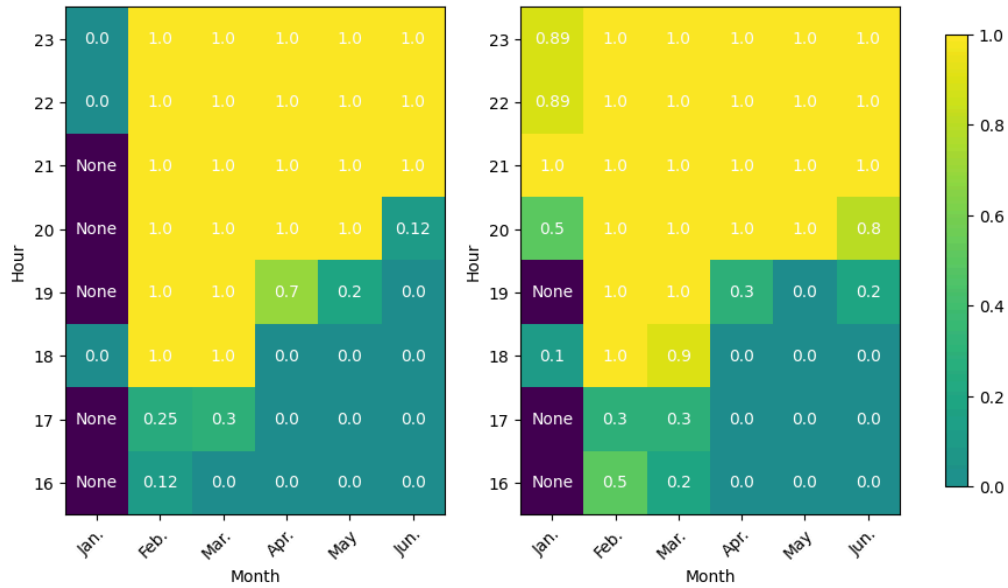


Figure 2. The estimated precision for the classification model based on month and time for *Pseudacris sierra*. Estimates include positive predictions with confidence at or above 0.95 (left) and below 0.95 (right). “None” means that there are no samples in the corresponding hour and month. The numbers represent the estimated precision in the corresponding hour and month.

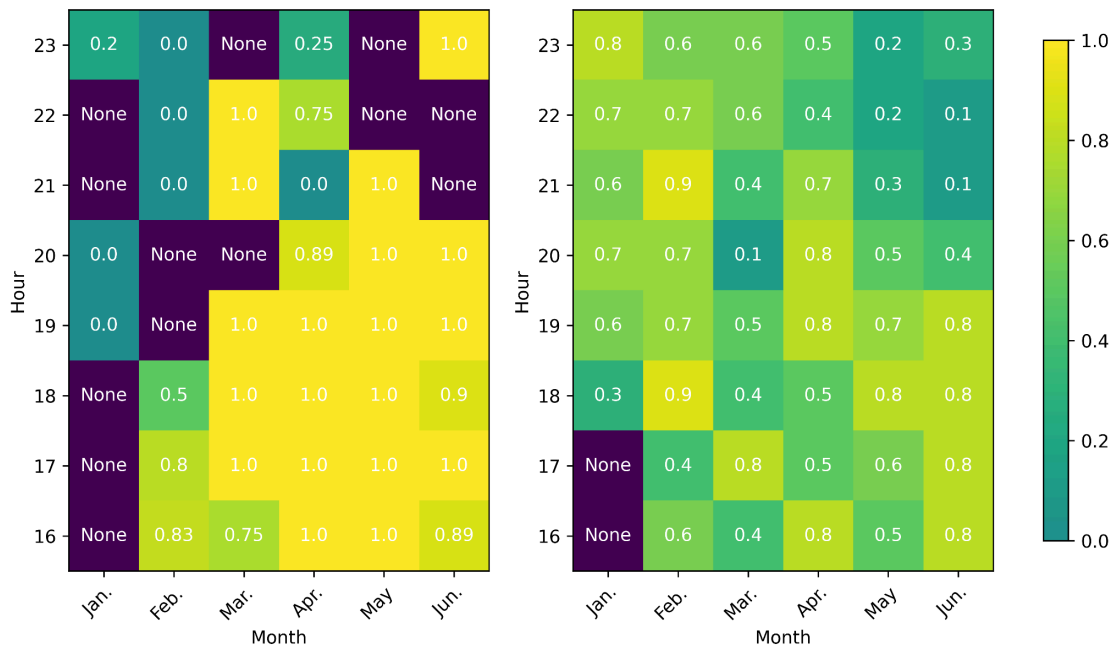


Figure 3. The estimated precision for the classification model based on month and time for *Anaxyrus boreas*. Estimates come from positive predictions with

confidence at or above 0.95 (left) and below 0.95 (right). “None” means that there are no samples in the corresponding hour and month. The numbers represent the estimated precision in the corresponding hour and month.

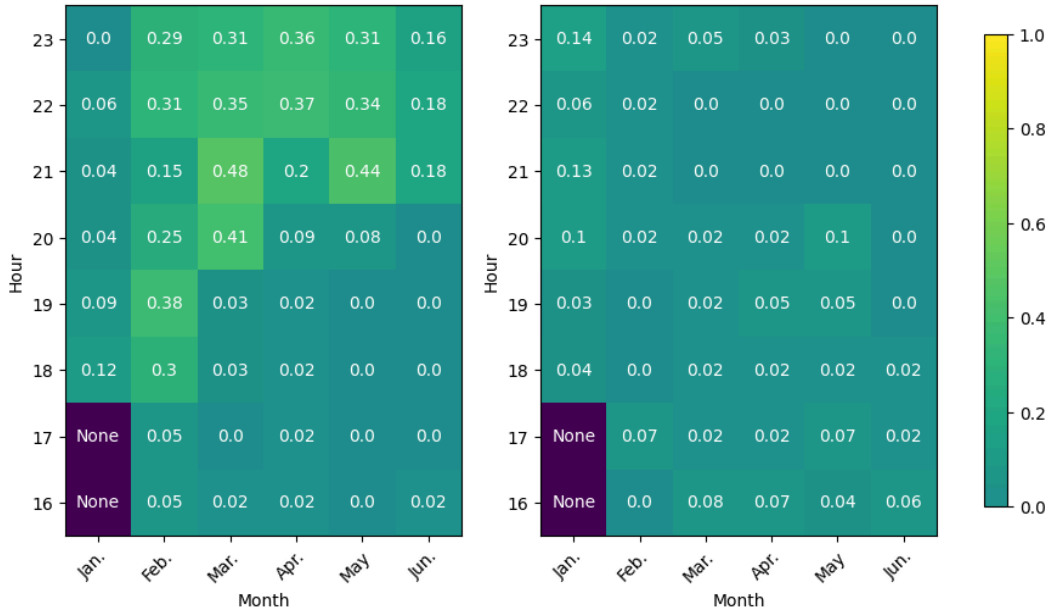


Figure 4. Estimated false negative rates for the model based on month and time for *Pseudacris sierra* (left) and *Anaxyrus boreas* (right). “None” means that there are no samples in the corresponding hour and month. The numbers represent the estimated false negative rates in the corresponding hour and month.

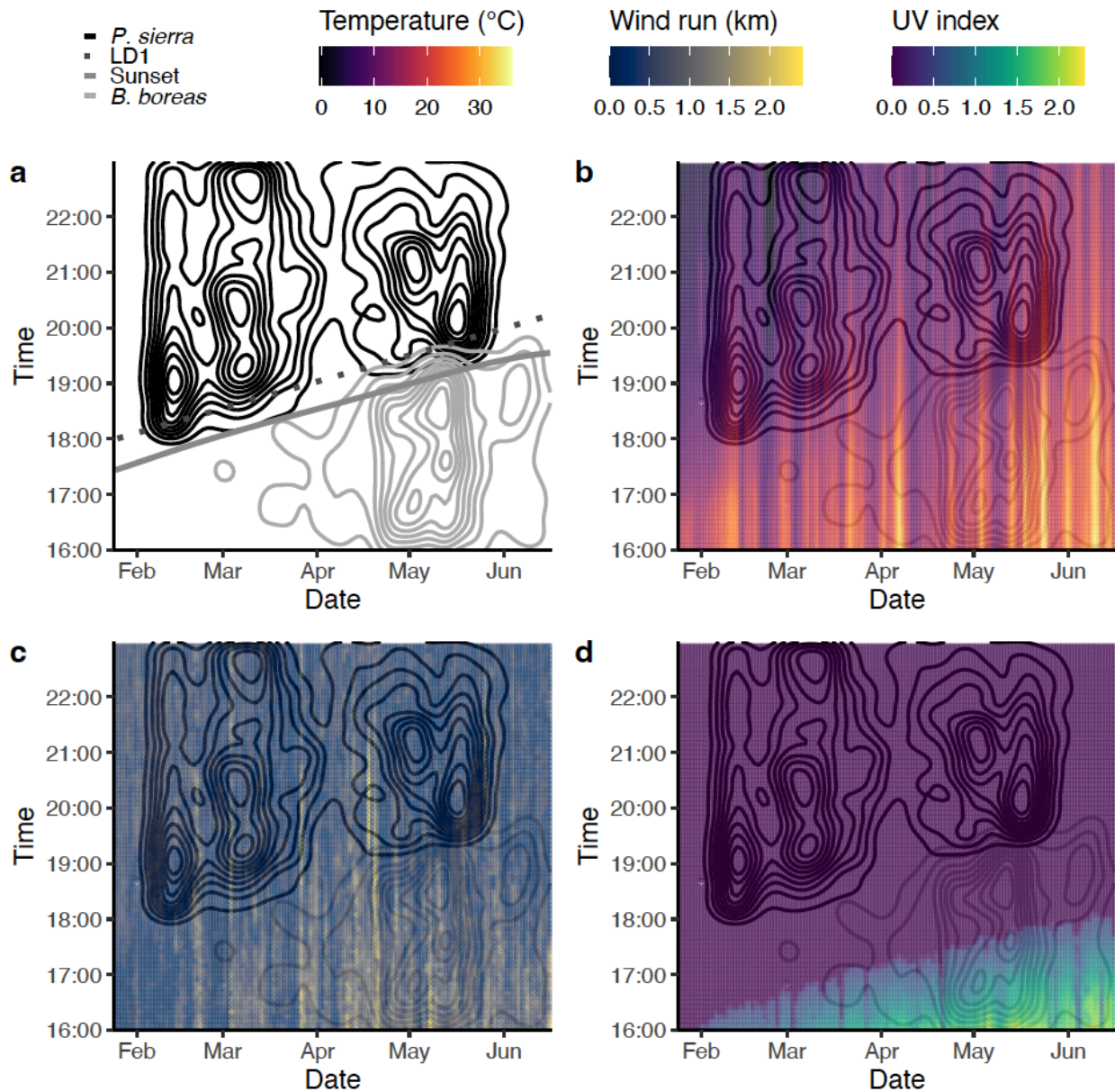


Figure 5. Distributions of *Pseudacris sierra*, *Anaxyrus boreas*, temperature, wind run, and UV index throughout the sampling period from January–June 2022.

Contour lines correspond to deciles for *P. sierra* in black and *A. boreas* in gray. a) the distribution of each species relative to the first linear discriminant (LD1, based on an exploratory analysis including only date and time) and sunset. LD1 is a darker grad dotted line, sunset is a solid line shown in a relatively lighter shade of gray. b) the distribution of temperature at the sampled location. c) the distribution of wind run at the sampled location. d) the distribution of UV index at the sampled location.

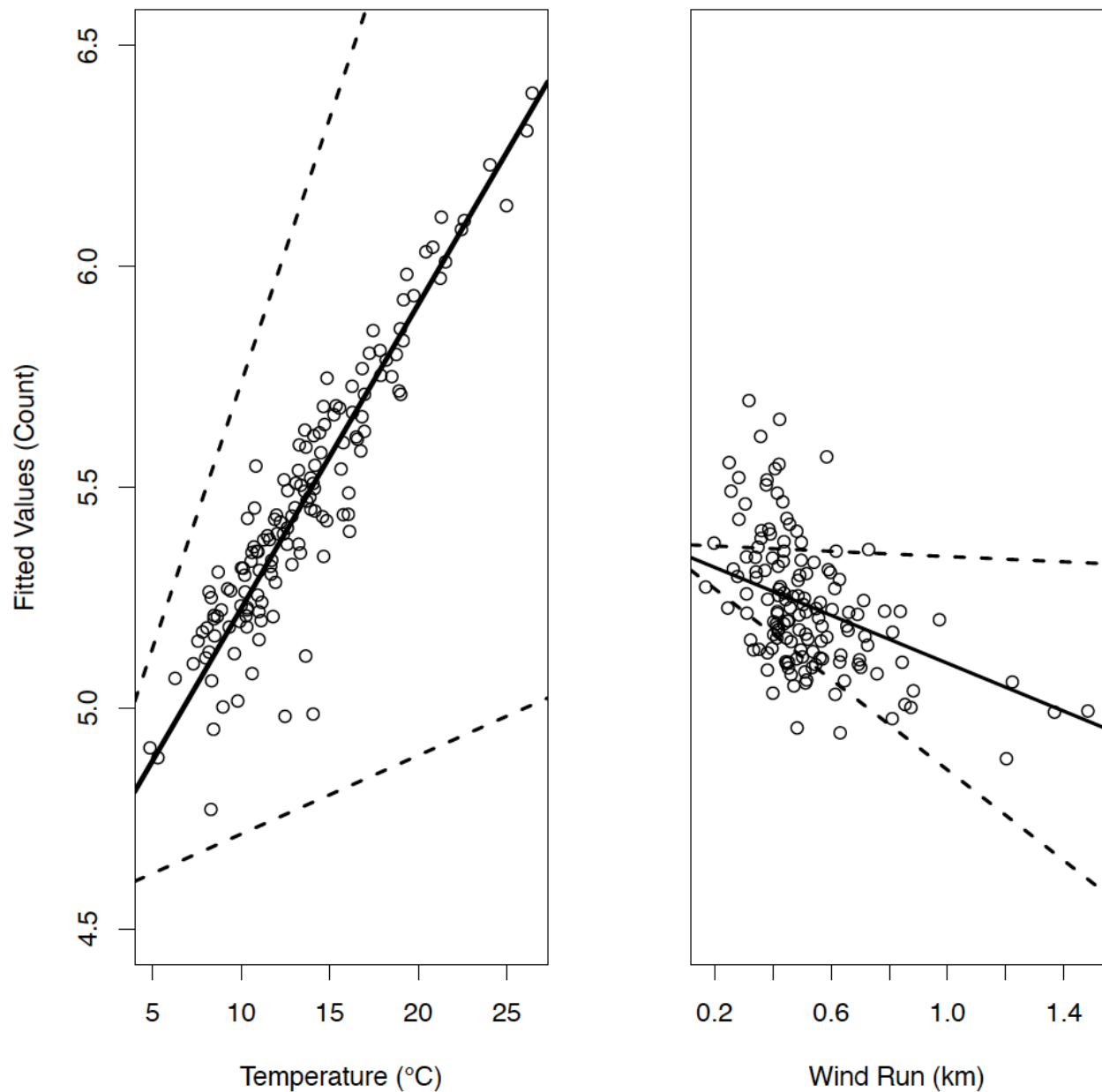


Figure 6. Generalized least squares fitted values for the marginal effects of temperature and wind run on amphibian activity. The fitted values shown correspond to *P. sierra*. Since we used species as a random effect in this model, the fitted values for *A. boreas* are identical but with a lower fitted intercept (4.75 and 1.79, respectively). The latter is indicative of the greater relative activity of *P. sierra*. Dashed lines are the 95% confidence interval for the estimated slope. Both trends are statistically significant ($p < 0.05$).

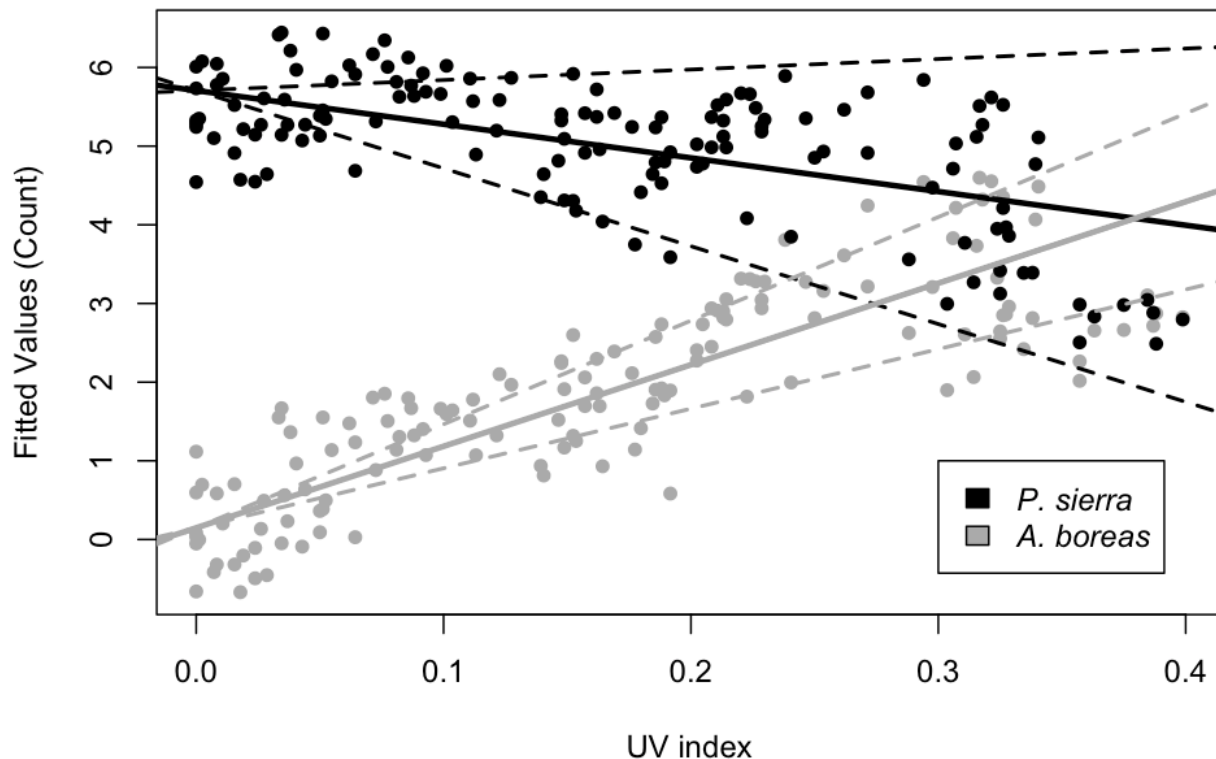


Figure 7. Generalized least squares fitted values for the marginal effect of UV index on the relative activity of *Pseudacris sierra* and *Anaxyrus boreas*. Dashed lines are the 95% confidence interval for the estimated slope. Only the relationship for *A. boreas* is statistically significant ($p < 0.01$).

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Supplementary Material

Pre-Processing

We selected 12-minute recordings, one 1-minute recording per month in the mornings in 2021, with no frogs occurring as background noises from Jasper Ridge audios. To prepare the training dataset, we labeled the start and end times of each occurrence of frogs with Raven Pro (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology, 2023). Then, we plotted the spectrogram of audio recordings with the SciPy (Virtanen et al., 2020) `signal.spectrogram` function, setting the length of each segment (`nperseg`) to 512, the length of the FFT used (`nfft`) to 512, and the number of points to overlap between segments (`noverlap`) to 256 to retrieve better resolution. When chopping the spectrogram based on the start and end times from the labels, we only kept the spectrogram under 2500Hz to avoid impacts from bird calls. As most of the frog calls that we considered are shorter than 1 second and to ensure that we have enough data, we cut spectrograms longer than 1 second into shorter ones with at most 1-second length and posit spectrograms shorter than 1 second in the middle of the sampled spectrogram image. Doing so also reduced mis-predictions of the group calling for *Pseudacris sierra* as background noises.

After sampling, our dataset was imbalanced with 266 samples for *Anaxyrus boreas*, 134 samples for *Pseudacris sierra*, 141 samples for *Rana boylei*, 388 samples for *Rana catesbeiana*, 199 samples for *Rana draytonii*, and 326 samples for background noises.

Model Training

We fine-tuned the model by using the VGG-19 model without the fully-connected layers at the end and adding one flatten layer, two pairs of a dense layer with ReLU activation and a dropout layer, and a final softmax layer. To comply with the transfer learning requirements, the spectrogram samples were resized to 224 pixels * 224 pixels and repeated two more times to generate the 3-channel image representing images with RGB colors with NumPy (Harris et al., 2020) and OpenCV (Bradski, 2000), resulting in the size of 3 * 224 * 224 for each sample.

The model was trained by optimizing cross-entropy loss with the Adam optimizer. Through grid search, we found that using 0.5 dropout rate, 32 batch size, 1e-5 (0.00001) learning rate, and TensorFlow's default exponential learning rate decay would produce the highest testing accuracy. We trained the model until the validation loss was not decreasing for 10 continuous epochs to incorporate fluctuations due to randomness. Throughout the whole training process, we stored the model with the lowest validation loss, indicating that the model is generalized best to spectrogram patterns, and used it as our final model.

To train the neural network model, the training dataset was used to update the model parameters during the training process. The validation dataset was used to determine whether to stop training or not. More specifically, we stop the training process when the validation loss does not decrease, which indicates that the model is no longer improving and generalizing. Finally, the testing dataset was used to evaluate the model. Therefore, we randomly selected 134 samples, the sample size of the class with the smallest number of samples, for each class.

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