Linking Anuran Occupancy and Relative Habitat Use to Environmental and Hydrological Variables in Arizona Wilderness Area Streams

by

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ABSTRACT

Riparian ecosystems comprise less than 2% of the landscape in the arid western U.S. yet provide habitat and resources to over half of arid-land wildlife species, including a broad diversity of anurans (frogs and toads). I surveyed anurans using passive acoustic monitoring to capture spring advertisement calls in wilderness area tributaries of the Verde River, Arizona, USA. In the spring and summer of 2021 and 2022, 13-29 autonomous recording units (ARUs) were deployed along perennial, intermittent, and ephemeral reaches across eight headwater streams. I characterized stream reaches based on the percent of pool, riffle, run, and side channel habitat within 100 meters of each ARU. I quantified substrate, discharge at 95% exceedance probability, flow width, and canopy cover at each site. To relate anuran occupancy and relative habitat use to environmental and hydrological variables, I evaluated acoustic data using single-species occupancy and Royle-Nichols and N-mixture (relative habitat use) models. Four species were detected in this study: canyon treefrog (*Hyla arenicolor*), red-spotted toad (*Anaxyrus punctatus*), Woodhouse's toad (*Anaxyrus woodhousii*), and non-native American bullfrog (*Lithobates catesbeianus*), with canyon treefrog being the most ubiquitous species observed. Occupancy of canyon treefrog was greater at perennial and intermittent sites compared to ephemeral sites, and presence of pool was the most important driver of canyon treefrog occupancy and relative habitat use. Notably, this study did not detect several species with historical records in the middle Verde River watershed, including Arizona toad (*Anaxyrus microscaphus*) and Northern leopard frog (*Lithobates pipiens*). Given climate change-related flow declines and intensifying demands for water in the Southwest, maintaining stream flows that provide consistent and suitable hydroregimes for anuran breeding and larval development is of increasing importance. Determining habitat use and flow regimes necessary to support anuran populations can aid in prioritization of conservation actions related to water management and predict how changes in water availability may impact stream-breeding anurans.

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INTRODUCTION

Freshwater ecosystems contribute disproportionately to ecological diversity and are among the most globally imperiled land types (Naiman et al., 1993; Wallace et al., 2010). Although a fraction of the total landscape, riparian corridors support a high diversity of species and ecological processes forming complex linkages between terrestrial and aquatic ecosystems (Naiman et al., 1993; Gregory et al., 1991). The scarcity of these biodiverse ecosystems is especially apparent in the southwestern United States (hereafter, Southwest), where riparian areas comprise less than 2% of the total land area (Knopf et al., 1988; Ffolliott & DeBano, 2003). Southwestern streams create conspicuous vegetated green belts across an arid landscape, and the transition between aquatic and terrestrial habitats tends to be abrupt (Knopf et al., 1988; Ffolliott & DeBano, 2003). The environmental gradients and diverse habitat mosaics in riparian areas support high productivity and animal biodiversity (Naiman et al., 2005), particularly herpetofauna. Within U.S. portions of the Mojave, Sonoran, and Chihuahuan Deserts, nearly 60% of herpetofauna use riparian areas in a significant way during their life cycles, and over half of these species are riparian obligates only capable of natural establishment in riparian areas (Lowe, 1989). Despite this, relatively few studies describe riparian herpetofaunal communities in the Southwest (Gori, et al., 2014).

Disrupted natural flow regimes can negatively impact biodiversity via habitat alteration and loss of stream connectivity to floodplains (Bunn & Arthington, 2002). For example, greater amphibian richness and abundance have been found with increasing distance downstream from dams, likely due to altered flow regimes reducing breeding area (Guzy et al., 2018; Eskew et al., 2012). Most streams globally are regulated for hydropower, flood protection, and to supply water for municipal consumption, agriculture, and industry (Benke, 1990). In addition to diversions and dams, groundwater withdrawals can reduce stream flow as groundwater discharge contributes significantly to stream flow volume (Barlow & Leake, 2012). Surface water and groundwater are linked such that surface water recharges underlying aquifers when it seeps into the ground, and groundwater discharge supplies streams with base flow. Groundwater-surface water exchange maintains base flows in perennial streams during dry periods (Naiman et al. 2005). However, groundwater pumping can dewater stream reaches if prolonged withdrawals occur, effectively converting perennial reaches into intermittent or ephemeral ones (Goodrich et al., 2018). Perennial streams tend to support greater herpetofaunal diversity than intermittent ones (Welsh Jr et al., 2005). Since 94% of streams in Arizona are intermittent or ephemeral (Goodrich et al., 2018), reduction of existing year-round flows will be especially consequential to the biodiversity supported by perennial habitat.

Riparian areas can be delineated by distinct soil and vegetation communities that require high soil moisture, but vary widely in form and function based on complex hydrological and geomorphic processes (Ffolliott & DeBano, 2003; Naiman et al. 2005). The availability of surface and groundwater largely determines the types of vegetation communities in riparian areas. In the Southwest, middle elevation streams are lined by broad-leaved trees, including Goodding's willow (*Salix gooddingii*), Fremont cottonwood (*Populus fremontii),* and velvet ash (*Fraxinus velutina)* (Stromberg et al., 1996; Holycross et al., 2022). Riparian vegetation communities shift in predictable ways in response to deepening groundwater (Stromberg et al., 2007), where willow-cottonwood dominated forests transition to upland xero-riparian shrub communities with reduced plant diversity. Loss of native pioneer trees (cottonwoods and willows) could impact wildlife communities, as native riparian gallery forests create structurally complex habitats used by many taxa (Patten, 1998). Further, when streams are hydrologically connected to their floodplains, they maintain diverse trophic connections between aquatic and terrestrial food webs (Baruch et al., 2021). Native riparian forests support diverse arthropod, avian, and herpetofaunal communities. For example, bird diversity, species richness, and abundance are positively associated with wetland indicator species like cottonwood, willow, and Arizona sycamore (*Platanus wrightii*) (Merritt & Bateman, 2012), and stream reaches with intact woody riparian vegetation support higher invertebrate diversity than those unbuffered by vegetation (Popescu et al., 2021). Amphibian abundance responds positively to sites with closed-canopies and associated leaf litter and shading (deMaynadier & Hunter, 1999; Rudolph & Dickson, 1990).

In addition to riparian areas with native gallery forests, Southwest riparian areas with high habitat heterogeneity support greater herpetofaunal richness and abundance (Bateman & Riddle, 2020; Bateman & Merritt, 2020). Complexity in habitat structure can result from variability in canopy cover, substrate type, and plant species richness (Bateman & Merritt, 2020). Geomorphic processes interacting with riparian vegetation help shape stream morphology and can create diverse habitat structures. Vegetation and large woody debris interact with stream flow to create complex lateral habitats like side channels and eddies (Gregory, 1991), which provide habitat for aquatic biota. For example, there is a positive relationship between juvenile cutthroat trout abundance and area of low-velocity lateral habitat like stream margins, backwaters, and isolated pools

(Moore & Gregory, 1988). Another example from Manenti et al. (2009) found that shallow, highly heterogeneous streams surrounded by woodlands best predicted the distribution of salamander larvae. The influences of landscape and local environmental factors on amphibian distribution have been less studied in lotic versus lentic systems (Manenti et al., 2009), so examining the links between stream-breeding amphibians and riparian habitat features merits additional focus.

Most amphibians exhibit biphasic life cycles, with an aquatic larval stage followed by a metamorphosis into more terrestrial juvenile and adult life stages (Fig. 1). Water-dependencies make amphibians especially vulnerable to changes in water availability and climate change (Griffis-Kyle et al., 2018). Amphibians are declining globally, and anurans (frogs and toads) are among the most threatened taxonomic groups worldwide (Luedtke et al., 2023; Stuart et al., 2004). There is no single cause for amphibian decline, but rather many causal factors, including land-use changes, disease, non-native species, habitat degradation, environmental pollutants, collection, and climate change (Green, 2005). Anurans are particularly imperiled in the western USA, where, after land use change, non-native species constitute the greatest driver of amphibian declines. Introduced species such as invasive fishes, American bullfrog (*Lithobates catesbeianus*), and northern crayfish (*Faxonius virilis*) pose a greater threat to western amphibians compared to non-western species (Bradford, 2005). Non-native species can harm native amphibians via predation, competition, hybridization, and introduction of disease (Bucciarelli et al., 2014). Among western anurans, members of the family Ranidae represent the most adversely affected taxa and suffer high extirpation rates.

According to Bradford (2005), the majority of ranids are classified as in “major decline,” indicating definite downward trends in population numbers.

In Arizona, all native ranids have experienced population declines (Sartorius & Rosen, 2000). One such ranid, Lowland leopard frog (*Lithobates yavapaiensis),* is an Arizona state protected species that has been extirpated from much of its historical range; significant populations remain only in Arizona west and south of the Mogollon Rim (Sartorius & Rosen, 2000). Chiricahua leopard frog (*L. chiricahuensis)* is a state protected and federally threatened ranid that has been extirpated from the majority of its range (U.S. Fish and Wildlife Service, 2007). Other Arizona stream-breeding amphibians include canyon treefrog (*Hyla arenicolor*), Woodhouse’s toad (*Anaxyrus woodhousii),* red-spotted toad (*Anaxyrus punctatus*), Arizona treefrog *(H. wrightorum),* Northern leopard frog (*L. pipiens*), and Arizona toad *(A. microscaphus),* which is a candidate species for listing under the Endangered Species Act (USFWS, 2015). These species require water throughout their aquatic larval stages, but vary in their water-dependencies as adults. For example, lowland leopard frogs are rarely found far from water (Wallace et al., 2010), whereas canyon treefrogs can retreat to rocky talus far from water for days at a time (Holycross et al., 2022). The breeding requirements and male advertisement calling windows of anurans vary widely. For instance, Northern leopard frogs breed from April through July in ponds, lakes, cattle tanks, and streams (Rorabaugh, 2005). The more terrestrial red-spotted toad breeds from March through June in streams and from June through September in rain-filled pools or tinajas (Sullivan, 2005a).

Biologists survey amphibians using a variety of active field methods, including visual encounter surveys (Fuller et al., 2011; Mac Nally et al., 2017), call surveys

(Knutson et al., 1999; Mac Nally et al., 2017; Forzley et al., 2021), pitfall trapping (Hannon et al., 2002), and mark-recapture (Nelson & Graves, 2004). Passive survey methods using eDNA (Svenningsen et al., 2022) or acoustic recording devices (Corn et al., 2000; MacLaren et al., 2018) can also be applied to amphibians. Male anurans consistently vocalize during the breeding season through loud, species-specific advertisement calls, making passive acoustic monitoring an effective means of determining anuran species richness (Corn et al., 2000) and breeding phenology (Larsen et al., 2021). Regardless of the survey method, scale should be considered when studying amphibian habitat selection. It can be beneficial to assess environmental variables across a range of scales, from landscape level to finer-scale. Third-order characteristics are habitat features used by individuals or social groups within a home range (Johnson, 1980). Mazerolle and Villard (1999) found that patch-scale variables (i.e., third-order habitat characteristics) were important in explaining amphibian abundance in nearly every study they considered in their review.

The objective of this research is to employ passive acoustic monitoring to relate hydrological and habitat features to occupancy and/or relative habitat use (hereafter “use”) of anuran species in Verde River headwater streams. Specifically, I seek to investigate the following research questions: 1) what anuran species are vocalizing (i.e., breeding) in Verde River Basin wilderness area streams, and what is the timing and magnitude of vocal activity? 2) what hydrological and environmental variables are associated with perennial, intermittent, and ephemeral stream reaches? and 3) which variables best predict anuran use? I predict that streams will vary in environmental characteristics, anurans will use perennial reaches more than intermittent and ephemeral reaches, and third-order habitat elements related to stream flow regime, like side channel and canopy cover, will be important predictors of anuran use. By linking anuran use to specific riparian and hydrological variables, natural resource managers can determine the flow regimes (i.e., magnitude, frequency, duration, and timing of extreme high flows and low flows) (Poff et al., 2007) necessary to create and maintain the habitat features selected for by breeding amphibians.

METHODS

Study Area

I surveyed for anurans along eight headwater streams in the Verde River Basin in central Arizona, USA (Yavapai and Coconino Counties, UTM Zone 12 N) (Fig. 2). The streams flow through five federally-designated wilderness areas (Sycamore Canyon, Red Rock-Secret Mountain, Munds Mountain, Wet Beaver, and West Clear Creek Wildernesses) on land managed by Coconino, Prescott, and Tonto National Forests. In the USA, *wilderness area* refers to a large, legally-designated tract of "undeveloped Federal land retaining its primeval character and influence, without permanent improvements or human habitation, which is protected and managed so as to preserve its natural conditions" (Wilderness Act, 1964). Federal wilderness designation protects the land surrounding vast portions of the Verde's major tributaries, though groundwater pumping threatens these riparian ecosystems. Some 10,000 points of groundwater pumping in the Verde River watershed (D. Merritt, personal communication, May 15, 2023) have reduced groundwater storage and average base flows of the Verde River and its tributaries (Blasch et al. 2006). These declines are most observable in developed areas, where the majority of groundwater pumping for municipal use occurs. At the Verde River stream-flow gaging station near Camp Verde, Arizona, the average winter base flow declined by approximately 2,000 acre-feet per year from 1993 to 2003 (Blasch et al. 2006).

The study area is contained within the Arizona Department of Water Resources "Verde Valley subbasin" of the middle Verde River watershed (Blasch et al., 2006; Garner et al., 2013). Surrounding biotic communities range from semidesert grassland and interior chaparral to Great Basin conifer woodland and Petran montane conifer forest. The area is characterized by a semiarid to arid climate with cool-wet winters, hot-dry summers, and hot-wet monsoon seasons from July to September. Mean annual temperatures and precipitations vary throughout the region, where elevation, slope, and canyon geomorphology influence microclimates (Blasch et al. 2006). At Beaver Creek Ranger Station near Wet Beaver Wilderness, the mean minimum and maximum temperatures are 8.0 °C and 24.8 °C, respectively, and the mean annual precipitation is 38.6 cm (Western Regional Climate Center, 2006). Peak runoff in the watershed occurs in March due to winter frontal storms and spring snowmelt (Ellis et al., 2008). Study streams include Wet Beaver Creek, Dry Beaver Creek, West Clear Creek, Dry Creek, Spring Creek, Sterling Canyon Creek, Sycamore Creek, and West Fork of Oak Creek (Fig. 2).

I located sites across perennial, intermittent, and ephemeral stream reaches to achieve a gradient of baseflow (Fig. 3). Streams were categorized based on designations from the National Hydrography Dataset (U.S. Geological Survey, 2019), U.S. Forest

Service expertise (H. Klingel & D. Merritt, personal communication, April 13, 2023), and the following stream type definitions (USEPA, 2015):

> *Perennial*: A stream or portion of a stream that flows year-round, is considered a permanent stream, and for which base flow is maintained by groundwater discharge to the streambed due to the groundwater elevation adjacent to the stream typically being higher than the elevation of the streambed.
>
> *Intermittent*: A stream where portions flow continuously only at certain times of the year, for example when it receives water from a spring, groundwater source or from a surface source, such as melting snow (i.e., seasonal). At low flow there may be dry segments alternating with flowing segments.
>
> *Ephemeral*: A stream or portion of a stream which flows briefly in direct response to precipitation in the immediate vicinity, and whose channel is at all times above the groundwater reservoir.

Elevations of stream reaches ranged from 1085 m at lower Sycamore Creek to 1827 m at upper West Clear Creek.

Passive acoustic monitoring

To detect anurans, 13 and 29 autonomous recording units (ARUs) were deployed in 2021 and 2022 (Table A1, A2), respectively, along perennial, intermittent, and ephemeral tributaries in the Verde River Basin. Call surveys have been shown to detect anuran species similarly or more frequently than dip net or funnel trap surveys (Buech & Egeland, 2002). However, short, in-field call surveys are prone to temporal biases, and can lead to underestimations of population sizes (Digby et al., 2013; Bas et al., 2008). ARUs and automated acoustic data analyses produce similar results to field surveys, thus offering an efficient alternative to traditional call surveys (Digby et al., 2013).

I used Song Meter SM2 and SM4 recording units (Wildlife Acoustics, Maynard, Massachusetts, USA) equipped with one omnidirectional microphone and set to record in mono-L at a sample rate of 24000 Hz in uncompressed WAV format. In 2021, 13 ARUs (all SM4s) were deployed in late March or mid-May along five streams. Deployment periods in 2021 were variable, with some ARUs recording into October. In 2022, 29 ARUs (seven SM2s and 22 SM4s) were deployed from mid-March to early June along eight streams. ARUs were deployed at 12 of the 2021 sampling locations and at 17 additional sites. All but five ARUs were deployed on or before 15 March 2022, with all 29 ARUs recording by 23 March 2022. ARUs were removed between 8 and 29 June 2022. Considering ARU maintenance and data processing time constraints, I focused on collecting data from mid-March to early June 2022 to capture spring breeding activity of anurans rather than monsoon-driven activity.

ARUs were fastened to riparian trees approximately 1-2 meters above the ground and met the following placement criteria: 1) a minimum distance of 250 meters between sampling sites, consistent with the distance used by Ribeiro Jr. et al. (2018) for site independence in amphibian communities and the range of ARUs (Digby et al., 2013), 2) intermittent and ephemeral sites were at least 500 meters from perennial water, and 3) sites were co-located whenever possible with U.S. Forest Service hydrological and climatic instruments and/or ASU/Arizona Game and Fish Department amphibian visual encounter surveys. Sites varied in their proximity to trails and day-use areas, and ranged from highly trafficked by humans to extremely remote. This, in addition to variable stream flow regimes and biotic communities, resulted in distinct acoustic environments with varying degrees of abiotic, biotic, and anthropogenic background noise across sites.

ARUs were programmed to record on a daily schedule coinciding with peak anuran calling periods (i.e., early evening and shortly after sunset; Corn et al., 2011). ARUs recorded continuously beginning one hour before sunrise/sunset to 1 hour after sunrise/sunset and for one five-minute interval per hour overnight. Local time (UTC-7), latitude and longitude settings, and the built-in “sunrise/set” solar calculation type were used to schedule recordings relative to sunset.

Field-collected environmental variables

I collected 15 site-level environmental variables in May and June 2022 (Table 1). At each of the 29 sites, I established a 100-meter transect parallel to the stream with the ARU as the midpoint. I quantified stream subunits by recording wetted channel subunit (pool, riffle, or run) at 21 points, or every 5 meters, along the transect. If the main channel was not wetted at a survey point, I recorded that intercept as “dry.” I calculated the percentages of pool, riffle, and run per transect by summing the number of points classified as a given stream subunit, dividing by 21, and multiplying by 100. Using the same method, I separately quantified wetted side channel, as side channel occurs independently of pools, riffles, or runs. I further classified side channel into three categories: 1) “connected side arm,” which is connected by surface water to the main channel, 2) “isolated pool,” which is not connected by surface water to the main channel, and 3) “bedrock pool,” which is an isolated pool on bedrock substrate that may or may not be connected by overspill from the main channel. Along the transect, I calculated mean elevation, mean width of wetted channel, and mean canopy cover by averaging measurements taken at 3 locations – at the ARU and upper and lower ends of the transect.

Canopy cover was recorded using a spherical densiometer by averaging readings from each cardinal direction. I used a laser range finder to record flow width and a Garmin handheld GPS to record elevation. At the same 3 locations along the transect, I established a 1-meter diameter plot to measure substrate composition. Within each circle, I made visual estimates of percent substrate by bedrock, boulder (>256 mm diameter), cobble (65–255 mm diameter), pebble (2–64 mm diameter), sand (0.125-1 mm diameter), and silt (<0.125 mm diameter). Substrate grain size classifications were based on the Wentworth scale (Wentworth, 1922). Percent substrate was estimated using the following cover classes: 0 = not present; 1 = less than 1%; 2 = 1–5%; 3 = 5–25%; 4 = 25–50%; 5 = 50–75%; 6 = 75–95%; and 7 = 95–100% (Sprague & Bateman, 2018). For analyses, I converted cover class values to the midpoint of each percentage range (Table A3) and averaged the values from 3 plots per site.

Remotely sensed variables

I evaluated two landscape-level variables using remotely-sensed data (Table 2). Normalized difference vegetation index (NDVI) quantifies vegetation greenness, indicating plant productivity. I gathered all available Modis 250-meter resolution satellite imagery (Didan, 2015) from within the study period, resulting in six images from 6 March 2022 to 9 June 2022. Each ARU occupied a unique cell in the Modis imagery, ensuring unique NDVI values at each site. NDVI values were extracted using the stars (Pebesma & Bivand, 2023) and terra (Hijmans, 2023) packages in R v4.3.0 (R core team, 2021). To measure distance to perennial water, I used Google Earth Pro’s linear measurement tool to calculate the distance from each ARU to the nearest perennial water via the most direct overland route. Perennial sites received a value of zero. One intermittent site at upper Wet Beaver Creek was placed < 500 m from perennial water. Thus, it was treated as a perennial site resulting in a non-zero average distance to perennial water across perennial sites.

Hydrologic variables

I used discharge in cubic feet per second (cfs) at 95% exceedance probability to quantify low flow conditions at 13 stream reaches (Table 1). This value indicates the discharge that is equaled or exceeded 95% of the time based on flow records and represents discharge at low flows. Exceedance probabilities were calculated from 2022 flow duration curves (T. Wible, personal communication, June 26, 2023) generated from U.S. Forest Service instream water level recorders (Onset HOBO U20 fresh-water pressure transducers) that recorded stream discharge at 15-minute intervals for 12 months. Instream flows were monitored at 13 reaches total (nine perennial, one intermittent, and 3 ephemeral reaches). Discharge at 95% exceedance probability values calculated from flow records at gauged stream reaches were applied to surrounding acoustic monitoring sites if determined by partner hydrologists to have similar flows. All stream reaches had water level recorders except Sterling Canyon Creek (RR4), an ephemeral tributary of Dry Creek in Red-Rock Secret Mountain Wilderness. At this site, I used 17.37% of the Dry Creek values to reflect the percentage of the total watershed draining to the Dry Creek pressure transducer that is comprised by Sterling Canyon (T. Wible, personal communication, June 27, 2023).

Acoustic data processing

I used Kaleidoscope Pro software v5.5.0 (Wildlife Acoustics, Maynard, Massachusetts, USA) to automate acoustic data processing and determine anuran detection/non-detection and activity levels across sites. Kaleidoscope Pro’s cluster analysis function groups like detections based on similarity of acoustic signature, with each cluster theoretically representing a distinct species. The user can then manually name and “tune” clusters to remove detections that do not represent the target species; this creates a “classifier” through which additional data can be run. I built species-specific classifiers for seven target species (canyon treefrog, Woodhouse’s toad, red-spotted toad, American bullfrog, Arizona toad, Chiricahua leopard frog, and lowland leopard frog). Arizona treefrog was excluded because the species breeds during monsoon season and occurs primarily above the Mogollon Rim (Holycross et al., 2022). Classifiers were trained using high-quality (i.e., high signal to noise ratio) recordings of the target species from the dataset. I ensured training data included a variety of anthropogenic, abiotic, and biotic noises to facilitate the training of the classifier to exclude non-target sounds. If the dataset lacked a sufficient number (>50) of clear calls without overlapping conspecific calls or background noise, I incorporated media from Macaulay Library of Sound (The Cornell Lab of Ornithology, Ithaca, NY), the Arizona Game and Fish Department (AZGFD), and/or Davidson (1996) (Table A4). I used calls recorded in or near the Verde River watershed whenever possible. All recordings received from Macaulay Library (The Cornell Lab of Ornithology, Ithaca, NY) and AZGFD were recorded within Arizona.

To build species-specific classifiers, I created a “training data” folder containing recordings with target calls from the dataset and/or outside media sources. Each “training data” folder also contained the same subset of each site’s recordings from throughout the study period to represent the span of acoustic environments across space and time. I scanned recordings using Kaleidoscope Pro’s cluster analysis function with parameters tuned to best detect the target species (Table A5). Once parameters were tuned to produce satisfactory cluster results, I manually identified and renamed a subset of high-quality target species calls in the output file. I then reran the edited cluster file on the training data, and tuned results by validating high-quality target calls and renaming incorrectly identified detections as “noise.” Low-quality target calls (i.e., overlapping, low amplitude, highly masked, etc.) were not labeled as the target species, but were made blank so as not to influence other clusters. Once the edited cluster file returned satisfactory results from the training data, I ran data from each site through the newly created classifier. I set “max distance from cluster center to include outputs in cluster.csv” to the maximum of 2.0 to increase the chances of finding rarely vocalizing species and reduce false negatives. If a species was ubiquitous at a site (i.e., canyon treefrog), I adjusted the max distance to between 1.0 and 1.5 to reduce false positives. Results from each site included named target species detections, if present, in the first cluster, followed by subsequent clusters retaining their default names. Many non-target sounds were found in the target species clusters, necessitating validation of output files.

Software validation

Although a powerful tool for automating signal detection, Kaleidoscope Pro is prone to error in the form of false positives, i.e., false identifications, and false negatives, i.e., missed detections (Knight et al., 2017). To account for this, I visually and/or auditorily validated output files. I sorted output files by date, then by cluster name (i.e., “Top1Match”) in Kaleidoscope Pro, and scrolled through detections beginning on the first date of each two-week occasion (the time bin used for subsequent modeling) until a target species vocalization was visually and/or auditorily confirmed in the viewing window. If the entire occasions’ detections contained no target species calls, the occasion received a “0,” or non-detection. To further verify Kaleidoscope Pro’s ability to detect rare species, I visually scanned the entire acoustic dataset from one lower West Clear Creek site (WCC3). I did not detect any additional species upon this manual review, and detection results remained similar with the exception of several weak (i.e., low signal to noise ratio) *H. arenicolor* calls detected seven days earlier than Kaleidoscope Pro’s first detection of that species.

Several sites returned abnormally few detections in Kaleidoscope Pro’s cluster analysis, which I attributed to high stream noise decreasing signal to noise ratios below the software’s detectability threshold. Applying noise reduction tools to the data using several audio editing software, including iZotope RX10 Advanced v10.4.0.1926 (iZotope Inc., 2022) and Audacity(R) v 3.2.5 (Audacity Team, 2021), did not significantly improve detection yields. To remedy this, I manually reviewed six additional high-noise sites by visually scanning spectrograms in Kaleidoscope Pro and recording the date and level of anuran activity. High-noise sites were located at lower West Clear Creek (WCC 1, 2, 5) and Wet Beaver Creek (WB 1, 4, 7).

Quantifying call activity

I classified anuran activity levels using a standardized amphibian call index from the North American Amphibian Monitoring Program (NAAMP) (Weir & Mossman, 2005). This index categorizes call intensity on a scale of no activity to full chorus as follows: 0 = no calling; 1 = individuals can be distinguished, no overlap; 2 = individuals can be distinguished, some overlap; and 3 = full chorus, calls are continuous and overlapping. To quantify the maximum daily call activity for each species, I sorted output files by date, then by cluster name (i.e., “Top1Match” in Kaleidoscope Pro), and scrolled through each date’s detections until the maximum call index detected on that day was observed. If the truncated view surrounding a detection contained activity levels less than the maximum value of 3, I expanded the viewing window to visually scan the entire recording for potentially higher activity levels. If the entire date’s detections contained no target species calls, the date received a “0.”

Statistical Analyses

Principal Component Analysis

I conducted a principal component analysis (PCA) to summarize habitat structure at each site by reducing 14 continuous site and landscape-level environmental variables into fewer uncorrelated variables. PCA is a data dimensionality reduction tool that projects data onto axes, called principal components (PCs), which maximize the variance on the fewest possible PCs (Lever et al., 2017). Each successive axis explains less variance than the one prior, such that the first axis (PC1) contains the largest percentage of variance in the dataset. I used eigenvalues, or the variance explained by each PC

(Holland, 2021), of greater than one when determining the number of meaningful PCs to examine in further modeling (Kaiser, 1960). Relative magnitude of loading values (positive or negative) were used to interpret the contribution of variables to each PC, as was a correlation matrix (Table A6). I evaluated the Pearson correlation among all continuous variables and used the standard value of $r > 0.6$ as the threshold for highly correlated variables. I conducted PCAs using the MASS package (Venables & Ripley, 2002) in program R v4.3.0 (R core team, 2021), and all variables were scaled to unit variance. Because PCA is not well suited for datasets containing many zero values, I excluded variables for which > 40% of values were zero (*sensu* Sprague & Bateman, 2018).

Comparison of means

I used one-way Analyses of Variance (ANOVAs) and Tukey’s post hoc tests to compare means of environmental variables and principal components across perennial, intermittent, and ephemeral streams. Non-parametric Kruskal-Wallis and Mann-Whitney U post hoc tests were used when assumptions of normality and homoscedasticity were not met. All comparisons of means and post hoc tests were conducted in program R v4.3.0 (R core team, 2021).

Occupancy modeling

I used a single-species, single-season occupancy modeling framework to link the detection or non-detection of anurans to environmental variables. Occupancy modeling can estimate species presence in a defined area without the cost and effort of determining actual abundance. It instead models a binary state variable to estimate the proportion of area occupied while factoring in imperfect detection of a species (MacKenzie & Nichols, 2004). Occupancy modeling evaluates the influence of covariates on estimates of two parameters: 1) occupancy probability (Ψ), or the probability of a site being used by the target species, and 2) detection probability (p), or the probability of detecting a species given its presence. Repeated sampling of a site is required to estimate detection probability. I simulated repeat site visits, or "occasions," by binning acoustic data into six, two-week intervals spanning the study period (Table A7). Input files for occupancy modeling are formatted into binary detection/non-detection (1/0), reflecting whether the target species was detected during a given occasion or not. Occupancy modeling accommodates missing detection data, denoted by "NA" in the unmarked package (v1.2.5; Fiske & Chandler, 2011). Nine out of 29 sites lacked detection data from one or more occasions due to gaps in the acoustic dataset. If acoustic data were missing from greater than or equal to seven days across an occasion, the entire occasion received an "NA." However, if a species was detected during an occasion, the occasion received a "1" regardless of missing data. Model results were ranked using small sample size corrected Akaike's Information Criterion (AICc) model selection methods to determine model fit (Burnham & Anderson, 2002). I first ranked all combinations of time varying covariates on detection probability compared to the intercept-only model. If the top model included covariates on detection probability, that covariate or combination of covariates was included in all subsequent models evaluating occupancy. I then evaluated all possible combinations of meaningful PCs as site covariates, and I ranked them with Akaike Information Criteria corrected for small sample size (AICc) to determine model fit. A model was considered informative if it outranked the intercept-only model and had a ΔAICc value < 2.0 (Burnham & Anderson, 2002). Occupancy modeling was performed in program R (v4.3.0; R core team, 2021) using the unmarked package (v1.2.5; Fiske & Chandler, 2011). While 2021 data contributed to the species inventory, call activity level, and call phenology analyses, the data loss and variability in ARU deployment periods made the 2021 dataset ill-suited for statistical modeling. Thus, I used the more robust 2022 dataset for all occupancy and relative habitat use modeling.

Royle-Nichols Modeling

I used Royle-Nichols (RN) modeling to estimate the relative habitat use of anurans across sites. Like occupancy models, RN models require repeated detection/non-detection data to estimate the proportion of sites occupied. Since the probability of detecting a species relates to its abundance, RN models link a species-specific detection probability to the underlying distribution of abundance to estimate the relative abundance of a species across sites (Royle & Nichols, 2003). Thus, one can estimate the relative use of a site rather than binary detected/non-detected as in occupancy modeling. RN models estimate two parameters: 1) Lambda (λ), or the Poisson intensity parameter measuring abundance, and 2) a species-specific detection probability (r), which remains constant across individuals within a species. I took a conservative approach and interpreted RN abundance estimates as measures of relative habitat use rather than absolute abundance (Nakashima, 2020). I evaluated all possible combinations of meaningful PCs as site covariates, and I ranked them with Akaike Information Criteria corrected for small sample size (AICc) to determine model fit. A model was considered informative if it outranked the intercept-only model and had a ΔAICc value < 2.0 (Burnham & Anderson, 2002). All RN modeling was performed in program R (v4.3.0; R core team, 2021) using the unmarked package (v1.2.5; Fiske & Chandler, 2011).

N-Mixture Modeling

In addition to RN models, I estimated anuran relative habitat use using N-Mixture modeling, which uses counts of animals across sites and occasions to estimate relative abundance (Royle, 2004a). N-mixture models estimate two parameters: 1) Lambda (λ), or the Poisson intensity parameter measuring abundance, and 2) detection probability (p), or the probability of detecting a species given its presence. Although counts of individual animals cannot be accurately obtained from acoustic data, N-mixture models have been applied to amphibian call index data (Hutto & Barrett, 2022). The relationship between call indices and anuran abundance is not well-defined (Weir et al., 2005). However, several modeling approaches have been proposed for using anuran call index data to estimate abundance (Royle, 2004b; Royle & Link, 2005). Studies have linked anuran call index values to mark-recapture population estimates in green frogs (*Lithobates clamitans*) (Nelson & Graves, 2004). Further, a positive linear relationship exists between call index and the number of wood frog (*Rana sylvatica*) egg masses present in ponds (Stevens & Paszkowski, 2004). As the aim is not to evaluate absolute population size but rather heterogeneity in habitat use across sites, I interpreted N-mixture results conservatively as relative habitat use (Nakashima, 2020) and believe call index is a reliable proxy for count data given the objectives.

For each occasion, I recorded the observed maximum call index for each species. As with occupancy models, I evaluated all combinations of time varying covariates for detection probability compared to the intercept-only model and ranked them according to their differences in the Akaike Information Criterion adjusted for small sample size (AICc). If the top model included covariates on detection probability, that covariate or combination of covariates was included in all subsequent models evaluating relative habitat use. I evaluated each distribution option (Poisson, negative binomial, and zero-inflated Poisson) for intercept-only and global models and ranked them using AICc. I then evaluated all possible combinations of meaningful PCs as site covariates using the most supported distribution option. A model was considered informative if it outranked the intercept-only model and had a ΔAICc value < 2.0 (Burnham & Anderson, 2002). All modeling was performed in program R (v4.3.0; R core team, 2021) using the unmarked package (v1.2.5; Fiske & Chandler, 2011). RN and N-mixture models were only applied to species for which adequate detection data were obtained.

Detection covariates

In occupancy and N-mixture models, I incorporated time-varying covariates to evaluate how detection probabilities varied across occasion in response to daily minimum air temperature, daily precipitation, and noise level (Table 2). I evaluated the Pearson correlation among all covariates and used the standard value of $r > 0.6$ as the threshold for highly correlated variables (Table A8). Daily minimum air temperature and precipitation at 1-kilometer resolution were acquired from Daymet (Thornton et al., 2022). I calculated mean minimum daily temperature and mean daily precipitation for each site per occasion by averaging daily values across the six occasion periods.

To quantify stream noise level, I used the SoundMeter X app v12.0.12 (Faber Acoustical, 2023) on an iPhone SE to record equivalent continuous sound levels (Leq) across sites and occasions. For each site, I analyzed the first ten seconds of the 00:00 (midnight) recording on the first, last, and midpoint dates of the six occasions (Settings: A-weighted Leq; averaging time: infinity; auto stop time: 10 secs). I then averaged the three readings to obtain one Leq(A) value per site per occasion. Recordings were played back using Kaleidoscope Pro software (Wildlife Acoustics, Maynard, Massachusetts, USA) from MacBook Air speakers at the highest volume with the receiving iPhone placed a standard distance of 10 cm from the speakers. Because higher frequency sounds (i.e., insect choruses) outside the frequency range of target anurans did not hinder Kaleidoscope Pro's ability to detect them, I excluded frequencies above this range. I placed a low pass filter (0-3 kHz) on recordings to isolate only the frequency range I analyzed when searching for target anurans. As a result, noise values do not reflect absolute sound levels, but rather relative interfering background noise across sites. The aim was to quantify continuous stream noise; thus, if an animal was vocalizing in the selected 10-second clip, I moved to the next 10-seconds until a recording was relatively free of intermittent biotic noise.

RESULTS

Four anuran species were detected across two study years, including canyon treefrog, Woodhouse's toad, red-spotted toad, and non-native American bullfrog (Table

3). Canyon treefrog was the most ubiquitous species detected at approximately 75% of sites sampled in 2022. Non-native American bullfrog was detected at four sites, all in lower Sycamore Creek, in 2022. The next most detected native species was red-spotted toad, which was found across two years at two intermittent sites on Dry Beaver Creek and one ephemeral site on Dry Creek. Woodhouse's toad was detected in 2022 at one lower Sycamore Creek site.

The 2021 acoustic dataset spanned from late March to mid-October and ranged from 19 to 202 days of data per site (average = 102 days of data, n = 11 sites; Table A1). Due to flooding, wildfire, and/or equipment failure, portions of the 2021 data were lost or unusable. The 2022 dataset spanned from late February to late June and ranged from 49 to 115 days of data per site (average = 91 days of data, n = 29 sites; Table A2). Battery failure and SD card corruption contributed to some data loss in 2022.

Call phenology

Canyon treefrog

Spring calling commenced both years at Sycamore Creek, the lowest elevation system in the study area. The earliest call detected in 2022 was canyon treefrog on 18 March, followed by the first full chorus of canyon treefrog on 25 March at the same system. Maximum activity for canyon treefrog across all sites remained at full chorus levels from 23 April through the end of the study period, 8 June 2022 (Fig. 4). Call activity continued until 21 June, however sample size diminished with ARU removal beginning 8 June. Canyon treefrog call phenology followed similar patterns in 2021. Though several ARUs remained deployed through late June in both 2021 and 2022, canyon treefrog full chorusing (level three activity) ceased beginning in mid-June in both years. In 2021, ARUs remained active into late summer and early fall at some sites, revealing canyon treefrog call activity throughout July and August. These activity spikes, likely driven by monsoon rain events, remained at or below level two calling. The latest call detected of any species was canyon treefrog on 17 August 2021 at Dry Beaver Creek.

Woodhouse's toad

Woodhouse's toad was detected at only one site on lower Sycamore Creek. Activity began as early as 14 April 2022 (Fig. 4), and level one activity continued nearly uninterrupted from 16 May to 21 June. Call activity for this species never surpassed level one.

Red-spotted toad

In 2021, red-spotted toad was first detected on 4 June at Dry Creek and last detected on 7 August at Dry Beaver Creek (Fig. 4). Intermittent Dry Beaver Creek lacked any activity in May and June 2021; only monsoon driven red-spotted toad activity was detected beginning in late July at these sites. In 2022, red-spotted toad was first detected on 3 May at Dry Beaver Creek, where level one activity continued sporadically until ARUs stopped recording on 10 May. No activity was detected after ARUs resumed recording from 2-17 June 2022, so activity likely ceased between mid-May and early-June upon drying of the reach.

American bullfrog

American bullfrog began calling latest of all species, with the first call detected on 2 May 2022 at Sycamore Creek (Fig. 4). Activity remained mostly at level 1 with the exception of one day on which overlapping calls of multiple individuals were observed. American bullfrog activity continued until 21 June 2022 when loggers were removed from Sycamore Creek.

Environmental variability across stream types

Perennial, intermittent, and ephemeral sites (n = 21, 2, 6, respectively) differed by several environmental variables (Table 4), including mean canopy cover and distance to perennial water. Discharge at 95% exceedance probability (i.e., low flow conditions) differed between gauged perennial sites (n = 9) and gauged ephemeral sites (n = 3), and predictably decreased across stream types (3.2, 1.1, and 0.07 cfs at perennial, intermittent, and ephemeral sites, respectively). Mean canopy cover was 71.5, 51.4 and 40.1% at perennial, intermittent, and ephemeral sites, respectively. The mean wetted flow width for perennial sites was 10.3 m.

Principal Component Analysis

A PCA reduced 14 continuous environmental variables to four significant components, explaining 76% of the cumulative variance (Table 5). Principal component (PC) 1 represented an elevation gradient, with flow width and sand loading highly on the negative end of the axis and elevation on the positive end. Thus, sites with low PC1 scores were low elevation, sandy, and with big waters, as found at lower Sycamore Creek. PC2 represented vegetative cover and was driven by NDVI and canopy cover

(Fig. 6). PC3 represented substrate and included percent pebble, cobble, discharge at 95% exceedance probability (i.e., low flow conditions), and boulder. PC4 included percent pool and canopy cover variance, though it was largely driven by pool.

Variability in principal component scores across stream types

I tested for differences in mean PC scores across perennial, intermittent, and ephemeral stream sites (Fig. 5), as PCs explain more variation than any one variable alone. Mean PC1 (elevation gradient) scores differed significantly between perennial and ephemeral sites (ANOVA: $F_{2, 26} = 6.23$, $p < 0.01$). Mean PC2 (vegetative cover) scores for perennial sites differed significantly from intermittent and ephemeral sites (ANOVA: $F_{2, 26} = 9.16$, $p < 0.001$). Mean PC4 (pool) scores differed significantly between perennial and ephemeral sites (Kruskal-Wallis: $X^2_2 = 13.45$, $p = 0.001$).

Occupancy

Estimates of occupancy and detection probabilities for three anurans ranged from 0.04 to 0.77 and 0.28 to 0.56, respectively (Table 6). Most anuran species were rarely detected, with the exception of canyon treefrog ($\Psi = 0.77$, SE = 0.08); therefore, all subsequent models evaluating occupancy and relative habitat use focused on this species. Estimates for occupancy of canyon treefrog at ephemeral, intermittent, and perennial sites were 0.34 (SE = 0.19), 1.00 (SE= 0.00), and 0.87 (0.08), respectively (Fig. 7).

Occupancy models including the time-varying covariate “mean daily precipitation” were most supported based on AICc ranking (Table 7), so subsequent models included this variable as a covariate on detection probability. Canyon treefrog detection probability exhibited a negative relationship with mean daily precipitation (β = -0.96, SE = 0.21; Table 7, Fig. A2).

Canyon treefrog occupancy related negatively to PC4 (pool) (Table 8; Fig. 8). Subsequent top models included PC2 (vegetative cover; Fig. 6), PC3 (substrate), and PC1 (elevation gradient). However, a negative relationship with PC4 (i.e., higher occupancy at sites with high percent pool and canopy cover variance) largely drove model results, as the variable was present in every model with ΔAICc < 2.0 and its 95% confidence intervals did not overlap zero in any model.

Relative habitat use (RN models)

PC4 (pool) demonstrated a consistent relationship with relative habitat use for canyon treefrog (Table 9; Fig 9). PC4 was present in every model with ΔAICc < 2.0 and 95% confidence intervals did not overlap zero in any model, indicating a positive relationship between relative habitat use and sites with high percent pool and canopy cover variance.

Relative habitat use (N-mixture models)

A zero-inflated Poisson distribution was most supported based on model ranking and was used for all subsequent N-mixture modeling (Table A9). N-mixture models including a combination of the time-varying covariates mean daily precipitation, mean daily minimum air temperature, and mean equivalent continuous sound level were most supported based on AICc ranking (Table 10), so subsequent models included these variables as covariates on detection probability. Canyon treefrog detection probability exhibited negative relationships with mean daily precipitation (β = -0.82, SE = 0.13) and mean equivalent continuous sound level (β = -0.54, SE = 0.13) and a positive relationship with mean daily minimum air temperature (β = 0.28, SE = 0.11) when detection covariates were evaluated independently of each other (Table 10). In both occupancy and N-mixture models, mean daily minimum air temperature exhibited a sign flip when modeled in combination with mean daily precipitation (Table 10). Mean daily precipitation was slightly correlated with mean daily minimum air temperature (r = 0.48) and highly correlated with mean equivalent continuous sound level (r = 0.77) in occasion one only (Table A8).

N-mixture relative habitat use estimates exhibited similarities to RN and occupancy model results in that PC4 (pool) was present in all top models (Table 11). The top ranked N-mixture model contained only PC4, demonstrating a positive relationship between relative habitat use and presence of pools (Fig.10).

DISCUSSION

This study provides a comparison of anuran use of riparian areas across a gradient of stream flows and contributes to the understanding of how anuran breeding phenology and use may respond to the dewatering of scarce perennial habitats in arid-land systems. The most important findings included increased canyon treefrog occupancy and relative habitat use in response to pools. Canyon treefrog occupancy of perennial sites was over 150% higher than occupancy of ephemeral sites. Intermittent sites were most similar to perennial sites in terms of occupancy and habitat structure but differed in species composition and consistency of anuran use throughout the study period. These results affirm the importance of perennial reaches for stream-breeding anurans and emphasize the threat of hydrological alteration to Southwestern amphibians (Mims et al., 2020).

This study detected lower than expected anuran diversity, with three native and one non-native anuran species detected. This species composition is consistent with results from ASU/AZGFD visual encounter surveys conducted within the same study period and area (Montgomery, 2023). Canyon treefrog was the most commonly observed species, with an occupancy estimate of 77% across all sites. The ubiquity of this species throughout the study area was unsurprising, as suitable canyon treefrog habitat comprised a majority of the monitoring sites. Canyon treefrog habitat consists of deep, rocky canyons along intermittent and perennial streams, where adults are associated with large boulders, cliffs, and rocky outcrops (Painter, 2005). I detected minimal or no canyon treefrog activity at several lower elevation perennial sites (lower Sycamore and West Clear Creeks), which could be attributed to wider floodplains, increased distance to canyon walls, and associated lack of suitable vertical rocky surfaces for perching and refuge. Due to its moisture requirements and dependence on specific geologic features, canyon treefrog exhibits high climate change vulnerability compared to other Southwestern amphibian species (Griffis-Kyle et al., 2018). As climate change is projected to reduce moisture availability across much of the canyon treefrog’s range (Griffis-Kyle et al., 2018), maintaining the perenniality of canyon-bound streams of the Verde River watershed may be of increasing importance for the conservation of this species.

Habitat characteristics related to percent pool and canopy cover variance (PC4) were the most important predictor of canyon treefrog occupancy and relative habitat use across three modeling approaches. Neither Royle-Nichols nor N-mixture modeling revealed unique patterns in anuran use compared to occupancy modeling. However, the inclusion of all three modeling types in this study provides additional certainty that the presence of pools, and to a lesser degree variable canopy cover, are important drivers of canyon treefrog use. Since occupancy modeling assumptions are easier to meet than N-mixture modeling assumptions and N-mixture models can be unreliable (Ward et al., 2017), future studies may consider only evaluating occupancy to reduce time spent determining maximum call index values. Occupancy models and N-mixture models did reveal differences in the influence of covariates on canyon treefrog detection probabilities. In occupancy models, only mean daily precipitation was in the top model. In N-mixture models, the combination of all three detection covariates (mean daily precipitation, mean daily minimum air temperature, and mean equivalent continuous sound level) improved model fit. In both occupancy and N-mixture modeling, mean daily minimum air temperature and mean daily precipitation were negatively correlated with detection probability when modeled together. However, when mean daily minimum air temperature was modeled independently, it exhibited a positive relationship with detection probability. This sign flip is likely the result of a slight collinearity (Friedman & Wall, 2005) between mean daily precipitation and mean daily minimum air temperature. A positive relationship between daily minimum air temperature and canyon treefrog detection probability was expected, as anuran breeding activity is positively correlated with air temperature for many species (Tevis Jr, 1966; Saenz et al., 2006).

Models results indicate percent cover of pool as the main driver of canyon treefrog occupancy and relative habitat use. Pools are generally loosely defined as slower-moving regions of water compared to shallower, faster-moving, and more turbulent riffles and faster-moving, non-turbulent runs (Gordon, 1992; Hauer & Lamberti, 1996). Selection of breeding habitat consisting of slow-moving, shallow waters along stream margins or in semi-isolated side pools has been documented for canyon treefrog (Wylie, 1981). Upon dewatering, isolated pools persist longer than other channel units (Capone & Kushlan, 1991), and this persistence could further contribute to their predictive power regarding anuran use. Canyon treefrog exhibited higher occupancy at perennial versus ephemeral sites, and perennial sites had higher mean stream discharge at 95% exceedance probability (i.e., low flow conditions) than ephemeral ones. As desiccation has been implicated in the loss of larval life stages (Kissel et al., 2019) and many stream-breeding amphibian species have larval development periods lasting more than 30 days (Painter, 2005; Sullivan, 2005b), persistence of low flows during periods of larval development is likely key to reproductive success.

This study suggests that slow-moving pools are a third-order habitat element crucial for breeding and possible larval development. Since woody debris influences the formation of pools (Gregory et al., 1991), canopy cover and the presence of riparian gallery forest may contribute heavily to the creation and maintenance of regions of slower-moving water and diverse lateral habitat. Model results indicate canopy cover variance as a secondary driver of canyon treefrog use. This aligns with past work indicating habitat heterogeneity, including variability in canopy cover, as an important driver of amphibian abundance (Bateman & Merritt, 2020). Rate of anuran larval development is temperature dependent (Álvarez & Nicieza, 2002) and closed riparian canopies reduce air and water temperatures (Roth et al., 2010). Areas of sun and shade created by canopy cover variability may facilitate the acceleration of metamorphosis while providing benefits of canopy cover and associated leaf litter (Rudolph & Dickson, 1990). Wallace et al. (2010) found that plunge pools inhabited by lowland leopard frog had higher canopy cover (mean 10.9%) than uninhabited pools, and Montgomery (2023) reported higher canopy cover at Arizona toad occupied sites (mean 75.2%) versus random sites. Although mean canopy covers were higher at anuran occupied sites in both of these cases, mean covers between approximately 10 and 75% suggest that some amount of openness is selected for by these species. Habitat heterogeneity also confers refugia (Pearsons et al., 1992), which lowland leopard frogs have shown preference for in pool habitats (Wallace et al., 2010).

At intermittent sites, canyon treefrog exhibited 100% occupancy in 2022, though it did not call consistently across study years. Intermittent Dry Beaver Creek lacked anuran activity in May and June 2021, but in 2022, activity commenced in early April and May for canyon treefrog and red-spotted toad, respectively. This discrepancy in May calling activity between years suggests that spring breeding at intermittent sites may be more dependent on antecedent precipitation (i.e., winter precipitation and associated spring runoff) compared to perennial reaches (Moidu et al., 2023). Importantly, this study included only two intermittent sites representing a single stream (Dry Beaver Creek), so call phenology and occupancy results may be more representative of Dry Beaver Creek than intermittent streams more broadly. Future work should emphasize intermittent stream flows as they relate to anuran breeding phenology across multiple years.

Some species not detected in this study include Arizona toad and leopard frog species. The rim form of Chiricahua leopard frog has been known to inhabit higher elevation headwaters of the Verde River, and Global Biodiversity Information Facility (GBIF) records exist for lowland and Northern leopard frogs in Verde River headwater streams (Sredl, 1997; F. Albuquerque, personal communication, September 8, 2023). Arizona toad was found historically along the Verde River and its tributaries, though many historic localities (prior to 1990) are no longer occupied (Sullivan, 1993). The absence of Arizona toad in this and another study (Montgomery, 2023) provides evidence that the species may be extirpated from Verde River tributaries below the Mogollon Rim (personal communication, M. O'Neill, Feb. 22, 2022). Arizona toad was observed at various localities along the mainstem Verde River and the mouths of Wet Beaver and West Clear Creeks in 1990-91 (Sullivan, 1993). Woodhouse's toad was found along Wet Beaver Creek between 1990-91 and outside the wilderness area on lower West Clear Creek in 2022 (Montgomery, 2023). Woodhouse's toad can hybridize with Arizona toad and has displaced populations of the latter species at a number of historic localities in the middle Verde River watershed (Sullivan, 1993), which may partially explain the lack of Arizona toad observations in this study.

This study provides an assessment of American bullfrog presence in rarely surveyed wilderness areas streams. Non-native American bullfrog was observed only at lower Sycamore Creek, though numerous GBIF records exist for the species on the mainstem Verde River and headwater streams outside of wilderness area boundaries (F. Albuquerque, personal communication, September 8, 2023). Allospecific overlap between American bullfrog and Woodhouse's toad at the lowest elevation site on Sycamore Creek conforms with known habitat preferences for the species, particularly given the site's situation alongside a large pool. Woodhouse's toad is associated with low elevation, larger riparian corridors and prefers standing water and pools for breeding (Sullivan, 2005b). American bullfrog reproduction is restricted to permanent water, and adults are usually found along deep, calm waters (Holycross et al., 2022). As this introduced species has been implicated in the decline and displacement of Chiricahua and lowland leopard frogs and federally threatened Mexican gartersnakes (*Thamnophis eques*) in Arizona (Hossack et al., 2023; Schwalbe & Rosen, 1988), continued monitoring of populations, particularly where they overlap with rare and threatened herpetofaunal species, is essential. Although introduced Northern crayfish (*Faxonius virilis*) were not quantified in this study, it is worth noting the species' ubiquity throughout several of the study reaches. Like American bullfrog, Northern crayfish negatively impact native amphibians and have contributed to declines in native ranid populations in Arizona (Witte et al., 2008). Both Woodhouse's toad and American bullfrog were relatively rarely detected, with occupancy estimates of 4 and 12%, respectively. Detectability could be influenced by the timing of this study, as ARUs did not record past June in 2022. In 2021, a wildfire and historic flooding led to the loss of the majority of acoustic data from Sycamore Creek, which likely explains the lack of detections of these two species in that year. ARU site selection could also indirectly impact detectability for all species, since, with the exception of several extremely remote sites, the study sites were distributed across relatively accessible parts of the wildernesses.

Variables representing wetted side channel (i.e., connected side arm, isolated pool, and bedrock pool) were rarely recorded on the survey transects. The resulting high percentages of zero values necessitated the removal of these variables from the PCA, so the predicted relationship between canyon treefrog use and the presence of side channel could not be evaluated in this study. However, field observations of eggs and tadpoles in side channels on perennial study reaches suggest usage of these habitats by breeding anurans, and this association is supported for several species in the literature. For example, Bateman et al. (2008) documented prolific breeding by Woodhouse's toad and Great Plains toad (*Anaxyrus cognatus*) in response to spring overbank floods that created off-channel aquatic habitat. Miller (2010) found ephemeral pools located in overflow channels to be the most productive breeding habitats for Woodhouse's toad and Great Basin spadefoot (*Spea intermontana*) in semi-arid riparian areas. Passive acoustic monitoring allows for the assessment of species presence at a site scale. While site characteristics were related to anuran use in this study, active survey methods may be better suited for determining breeding habitat use at finer scales (i.e., via visual encounter of larval stages in third-order habitats like side channels or pools). Finally, it is important to note that the detection of calling males does not necessarily translate to successful anuran recruitment (Mac Nally et al., 2017). Other indicators of reproductive success, such as presence of metamorphs, should also be evaluated.

Management Implications

The Verde River supplies a large percentage of the surface water delivered to the Phoenix metropolitan area for municipal and agricultural use. With 36% of Phoenix-area water coming from the Salt-Verde watershed via the Salt River Project (Rushforth et al., 2020), maintaining Verde River flows benefits downstream users. Further, demands on regional water sources will only intensify as human populations increase throughout most of the Verde Valley (Blair, 2021). Compounding growing municipal water needs, climate change is increasing temperatures and temperature-driven river flow reductions and aridification in the Western U.S. are unequivocal (Overpeck & Udall, 2020). Combined with likely climate change-driven declines in precipitation in the region, runoff from the Verde River system will almost certainly decrease in the coming decades (Ellis et al., 2008). Climate change and associated dewatering of wetlands have already reduced amphibian richness and abundance in the arid western U.S. (McMenamin et al., 2008). Given climate change-related flow declines and intensifying demands for water in the Southwest, stream flows that maintain consistent and suitable hydroregimes (i.e., water duration, timing, frequency, and depth) (Greenberg et al., 2017) required for anuran breeding and larval development are at risk. The Verde River and its tributaries have historically provided habitat for at least ten native anuran species according to GBIF records (F. Albuquerque, personal communication, September 8, 2023). This study provides evidence that anuran richness may already have declined from historical levels in the middle Verde River watershed. Thus, protecting Verde wilderness area instream flows is increasingly important, and the consequences of anthropogenic water development in the Verde River watershed should be carefully considered moving forward.

Table 1. Field-collected variables from 29 acoustic monitoring sites along tributaries in the middle Verde River watershed, Arizona, USA. At each site, a 100-m transect was established parallel to the stream channel and centered by the ARU. Elevation, flow width, canopy cover, and substrate were measured at the ARU and either end of the transect (i.e., 50 meters up and downstream from the ARU). Stream subunits and presence of side channel were recorded every 5 meters along the same transect. All variables with < 40% zeros were included in principal component analyses to be modeled as site covariates. Field data was collected in May and June 2022.

Variable	Method/Description	Unit	Scale
Elevation	Mean elevation recorded at 3 points/transect	m	100-m transect
Flow width	Mean width of flow recorded at 3 points/transect	m	100-m transect
Flow width variance	Variance of flow width	m squared	100-m transect
Canopy cover	Mean canopy cover (measured with spherical densiometer by averaging readings from 4 cardinal directions) from 3 plots/transect	%	100-m transect
Canopy cover variance	Variance of canopy cover	% squared	100-m transect
Substrate	Mean percent substrate type based on Wentworth scale (boulder, cobble, pebble, sand, silt, bedrock) from 3 plots/transect	%	3 x 1m plots on 100-m transect
Stream subunit	Percent cover of stream subunit (riffle, run, pool) recorded at 21 points/transect	%	100-m transect
Side channel	Percent cover of side channel (connected side arm, isolated pool, bedrock pool) recorded at 21 points/transect	%	100-m transect
Discharge at 95% exceedance probability	Calculated discharge at 95% exceedance probability (i.e., low flow conditions) generated from 2022 flow records recorded by instream pressure transducers	cfs	Stream reach

Table 2. Remotely-sensed variables and/or time-varying covariates collected at various scales from the middle Verde River watershed, Arizona, USA. NDVI was included in principal component analyses to be modeled as a site covariate. Minimum air temperature, precipitation, and noise level were included as time-varying covariates on detection in occupancy and N-mixture modeling.

Variable	Method/Description	Unit	Scale	Source
NDVI	Mean NDVI from six satellite images taken Mar to Jun 2022		250-m	Modis satellite imagery gathered with NASA's Earthdata Search
NDVI variance	Variance of NDVI		250-m	Modis satellite imagery gathered with NASA's Earthdata Search
Distance to water	Overland distance from ARU to nearest perennial water measured with Google Earth Pro linear measurement tool	m	Landscape-level	Google Earth Pro
Minimum air temperature	Daily minimum 2 m air temperature	º C	1-km	Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 4 R1
Precipitation	Daily total precipitation (sum of all forms of precipitation converted to water-equivalent depth)	mm	1-km	Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 4 R1
Noise level	Mean A-weighted equivalent continuous sound level (LeqA) from three 10-sec readings per occasion	dB(A)	Site-level	Calculated using SoundMeter X app by Faber Acoustical

Table 3. Summary of the number of independent acoustic monitoring sites anuran species were detected at in 2021 (n = 11) and 2022 (n = 29) along tributaries of the middle Verde River watershed, Arizona, USA. The total number of sites detected is the sum of unique site detections across the two study years. Independent monitoring sites were ≥ 250 m apart.

Species	# sites detected 2021	# sites detected 2022	Total # sites detected
Canyon treefrog	7	22	23
Woodhouse's toad	0	1	1
Red-spotted toad	2	2	3
American bullfrog	0	4	4

Table 4. Mean (±SE) of environmental variables collected at perennial, intermittent, and ephemeral wilderness stream reaches in the middle Verde River watershed, Arizona, USA. Tukey's post hoc results of a one-factor ANOVA are denoted by superscripts for variables that differed significantly across stream types (variables with different letters are significantly different). Non-parametric Kruskal-Wallis and Mann-Whitney U post hoc tests were used when assumptions of normality and homoscedasticity were not met. Hydrological variables for which dry sites received a value of zero were excluded from statistical testing. Asterisks denote variables that were excluded from the PCA for having > 40% zero values.

	Perennial	**Intermittent**	**Ephemeral**	**ANOVA/Kruskal-Wallis (α = 0.05)**
Variable	*n = 21*	*n = 2*	*n = 6*	*n = 29*
Elevation (m)	1319.0 (57.2)	1235.5 (29.5)	1372.3 (69.7)	F(2,26) = 0.28, p = 0.76
Canopy cover (%)	71.5 (3.9)^{a}	51.4 (5.3)^{ab}	40.1 (9.7)^{b}	F(2,26) = 6.24, p = **0.006**
Canopy cover variance (%^{2})	503.6 (126.3)	1959.1 (370.7)	584.3 (206.1)	X^2(2) = 4.90, p = 0.09
Boulder (%)	24.6 (5.3)	77.5 (13.3)	20.2 (5.4)	X^2(2) = 4.77, p = 0.09
Cobble (%)	18.1 (3.5)	58.5 (4.2)	16.7 (4.6)	X^2(2) = 5.16, p = 0.08
Pebble (%)	14.9 (3.8)	38.4 (7.5)	14.1 (7.0)	X^2(2) = 2.99, p = 0.22
Sand (%)	53.3 (7.7)	24.5 (16.3)	41.8 (8.2)	F(2,26) = 0.74, p = 0.49
Silt (%)	20.9 (5.5)	35.8 (5.0)	53.1 (17.5)	F(2,26) = 3.06, p = 0.06
Bedrock (%)*	11.6 (4.9)	0.0 (0.0)	7.5 (5.4)	X^2(2) = 0.77, p = 0.68
NDVI	0.40 (0.02)	0.37 (0.03)	0.38 (0.03)	F(2,26) = 0.20, p = 0.82
Distance to water (m)*	6.4 (6.2)^{a}	9590.5 (491.5)^{b}	5190.3 (2014.4)^{b}	X^2(2) = 23.41, p < **0.001**
Discharge at 95% exceedance probability (cfs)†	3.2 (1.3)^{a}	—	0.07 (0.05)^{b}	W = 0, p < **0.01**
Flow width (m)	10.3 (0.79)	0.0 (0.0)	0.0 (0.0)	—
Flow width variance (m^2)	21.3 (7.51)	0.0 (0.0)	0.0 (0.0)	—
Riffle (%)	0.3 (0.04)	0.0 (0.0)	0.0 (0.0)	—
Run (%)*	0.2 (0.05)	0.0 (0.0)	0.0 (0.0)	—
Pool (%)	0.5 (0.07)	0.0 (0.0)	0.0 (0.0)	—
Side arm (%)*	0.2 (0.05)	0.0 (0.0)	0.0 (0.0)	—
Isolated pool (%)*	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	—
Bedrock pool (%)*	0.01 (0.01)	0.0 (0.0)	0.0 (0.0)	—

† Pressure transducers recorded stream flow at 9 perennial, 1 intermittent, and 3 ephemeral sites. Means of discharge at 95% exceedance probability were compared with a Mann-Whitney U test between perennial (n = 9) and ephemeral (n = 3) sites.

Table 5. Principal component analysis (PCA) loading values for the four principal components (PCs) used in analyses. Variables with the highest loading for each component (> 0.35) are in bold. The percent variance explained by each PC is reported, with four PCs explaining 76% of the cumulative variance among sites (n = 29) along wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Site-level variables were collected in May and June 2022. Variables with > 40% zero values were excluded from the PCA.

	Elevation gradient (PC1)	Vegetative cover (PC2)	Substrate (PC3)	Pool (PC4)
Elevation	**0.35**	0.33	0.08	-0.13
Flow width	**-0.38**	0.31	-0.02	-0.19
Sand	**-0.38**	-0.20	0.04	0.06
Canopy cover	-0.02	**0.48**	-0.29	-0.08
NDVI	0.27	**0.43**	-0.09	0.04
Boulder	0.26	-0.14	**-0.37**	-0.31
Cobble	0.20	-0.11	**-0.42**	-0.32
Pebble	0.00	-0.17	**-0.55**	0.06
Discharge at 95% EP	-0.30	0.07	**-0.41**	0.11
Canopy cover variance	0.07	-0.34	0.02	**-0.42**
Pool	-0.16	0.26	0.26	**-0.64**
Flow width variance	-0.29	0.08	-0.17	-0.07
Silt	0.33	0.18	-0.02	0.32
Riffle	-0.31	0.26	-0.15	0.13
Eigenvalue	2.09	1.66	1.55	1.03
% explained variance	0.31	0.20	0.17	0.08
% cumulative variance	0.31	0.51	0.68	0.76

Table 6. Summary of the total number of sites species were detected at in 2022 (n=29 sites) and intercept-only model occupancy and detection probabilities (real estimates and standard errors (se)) for anurans observed along wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Red-spotted toad estimates are excluded because the intercept-only model did not converge due to small sample size. Anuran observations were derived from acoustic data collected in March to June 2022.

		Occupancy		Detection probability	
Species	# sites detected	Estimate	se	Estimate	se
Canyon treefrog	22	0.77	0.08	0.56	0.05
Woodhouse's toad	1	0.04	0.03	0.49	0.22
Red-spotted toad	2	NA	NA	NA	NA
American bullfrog	4	0.12	0.07	0.28	0.13

Table 7. Occupancy model results for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Parameters include detection probability (p) and occupancy probability (Ψ). Models include the y-intercept only (1; no variables) and all combinations of time-varying covariates on detection probability: mean daily precipitation (prcp), mean daily minimum air temperature (tmin), and mean equivalent continuous sound level (leq). Table results include the number of terms in the model (K), AIC value, delta AIC (ΔAIC), model weight (wt), and beta estimates for each variable, followed by the associated standard error (se). Dark gray shading indicates the variable is highly informative (95% confidence interval does not overlap zero).

Model	K	AIC	ΔAIC	wt	prcp	se	tmin	se	leq	se
p(prcp) Ψ(1)	3	181.51	0.00	0.43	-0.96	0.21				
p(prcp + tmin) Ψ(1)	4	182.21	0.70	0.30	-1.13	0.26	-0.28	0.25		
p(prcp + leq) Ψ(1)	4	183.47	1.96	0.16	-0.95	0.22			-0.04	0.22
p(prcp + tmin +leq) Ψ(1)	5	184.15	2.64	0.11	-1.12	0.27	-0.28	0.25	-0.05	0.22
p(tmin) Ψ(1)	3	202.94	21.43	0.00			0.38	0.19		
p(tmin +leq) Ψ(1)	4	203.31	21.80	0.00			0.33	0.19	-0.25	0.20
p(leq) Ψ(1)	3	204.38	22.87	0.00					-0.32	0.19
p(1) Ψ(1)	2	205.27	23.76	0.00						

Table 8. Occupancy model results for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Parameters include detection probability (p) and occupancy probability (Ψ). Models include the y-intercept only (1; no variables) and all combinations of the time-varying covariate on detection probability mean daily precipitation (prcp) and variables PC1 through 4. Table results include the number of terms in the model (K), AIC value, delta AIC (ΔAIC), model weight (wt), and beta estimates for each variable, followed by the associated standard error (se). Models where ΔAIC > 2.0 were omitted, with the exception of the global and intercept-only models. Gray shading indicates the variable is highly informative (95% confidence interval does not overlap zero).

Model	K	AIC	ΔAIC	wt	PC1	se	PC2	se	PC3	se	PC4	se
p(prcp) Ψ(PC4)	4	175.80	0.00	0.31							-1.60	0.74
p(prcp) Ψ(PC2 + PC4)	5	177.00	1.14	0.18			0.53	0.60			-1.54	0.69
p(prcp) Ψ(PC3 + PC4)	5	177.60	1.81	0.13					0.24	0.55	-1.63	0.75
p(prcp) Ψ(PC1 + PC4)	5	177.80	2.00	0.11	0.03	0.56					-1.61	0.77
p(prcp) Ψ(PC1 + PC2 + PC3 + PC4)	7	180.50	4.72	0.03	-0.01	0.59	0.61	0.63	0.36	0.59	-1.63	0.75
p(prcp) Ψ(1)	3	181.50	5.69	0.02								
p(1) Ψ(1)	2	205.30	29.44	0.00								

Table 9. Royle-Nichols model results for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Parameters include species specific detection probability (r) and relative habitat use (λ). Models include the y-intercept only (1; no variables) and all combinations of the variables PC1 through PC4. Table results include the number of terms in the model (K), AIC value, delta AIC (ΔAIC), model weight (wt), and beta estimates for each variable, followed by the associated standard error (se). Models where ΔAIC > 2.0 were omitted, with the exception of the global and intercept-only models. Gray shading indicates the variable is highly informative (95% confidence interval does not overlap zero).

Model	K	AIC	ΔAIC	wt	PC1	se	PC2	se	PC3	se	PC4	se
r(1) λ(PC4)	3	193.50	0.00	0.27							-0.51	0.18
r(1) λ(PC3 + PC4)	4	194.30	0.81	0.18					0.14	0.13	-0.53	0.18
r(1) λ(PC1 + PC4)	4	194.80	1.32	0.14	-0.07	0.08					-0.52	0.18
r(1) λ(PC2 + PC4)	4	195.20	1.74	0.11			0.05	0.10			-0.50	0.18
r(1) λ(PC1 + PC2 + PC3 + PC4)	6	197.70	4.23	0.03	-0.06	0.08	0.05	0.11	0.12	0.13	-0.52	0.19
r(1) λ(1)	2	199.50	6.04	0.01								

Table 10. N-mixture model results for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Parameters include detection probability (p) and relative habitat use (λ). Models include the y-intercept only (1; no variables) and all combinations of time-varying covariates on detection probability: mean daily precipitation (prcp), mean daily minimum air temperature (tmin), and mean equivalent continuous sound level (leq). Table results include the number of terms in the model (K), AIC value, delta AIC (ΔAIC), model weight (wt), and beta estimates for each variable, followed by the associated standard error (se). Dark gray shading indicates the variable is highly informative (95% confidence interval does not overlap zero); light gray shading indicates the variable is moderately informative (85% confidence interval does not overlap zero).

Model	K	AIC	ΔAIC	wt	prcp	se	tmin	se	leq	se
p(prcp + tmin +leq) λ(1)	5	400.90	0.00	0.36	-0.87	0.16	-0.22	0.14	-0.27	0.16
p(prcp + leq) λ(1)	4	401.50	0.64	0.26	-0.75	0.14			-0.28	0.16
p(prcp + tmin) λ(1)	4	401.80	0.94	0.22	-0.94	0.16	-0.22	0.14		
p(prcp) λ(1)	3	402.50	1.66	0.16	-0.82	0.13				
p(tmin +leq) λ(1)	4	435.70	34.79	0.00			0.21	0.11	-0.50	0.13
p(leq) λ(1)	3	437.50	36.63	0.00					-0.54	0.13
p(tmin) λ(1)	3	448.00	47.09	0.00			0.28	0.11		
p(1) λ(1)	2	453.70	52.81	0.00						

Table 11. N-mixture model results for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Parameters include detection probability (p) and relative habitat use (λ). Models include the y-intercept only (1; no variables) and all combinations of the time-varying covariates on detection probability mean daily precipitation (prcp), minimum daily temperature (tmin), and noise level (leq) and variables PC1 through PC4. Table results include the number of terms in the model (K), AIC value, delta AIC (ΔAIC), model weight (wt), and beta estimates for each variable, followed by the associated standard error (se). Models where ΔAIC > 2.0 were omitted, with the exception of the global and intercept-only models. Gray shading indicates the variable is highly informative (95% confidence interval does not overlap zero).

Model	K	AIC	ΔAIC	wt	PC1	se	PC2	se	PC3	se	PC4	se
p(prcp +tmin + leq) λ(PC4)	6	387.89	0.00	0.37							-0.46	0.13
p(prcp +tmin + leq) λ(PC2 + PC4)	7	389.39	1.49	0.18			0.09	0.12			-0.46	0.13
p(prcp +tmin + leq) λ(PC3 + PC4)	7	389.77	1.88	0.15					0.04	0.13	-0.46	0.13
p(prcp +tmin + leq) λ(PC1+ PC4)	7	389.89	2.00	0.14	0.00	0.12					-0.46	0.13
p(prcp +tmin + leq) λ(PC1 + PC2 + PC3 + PC4)	9	393.30	5.41	0.03	0.00	0.13	0.08	0.12	0.04	0.13	-0.46	0.13
p(prcp +tmin + leq) λ(1)	5	398.20	10.31	0.00								

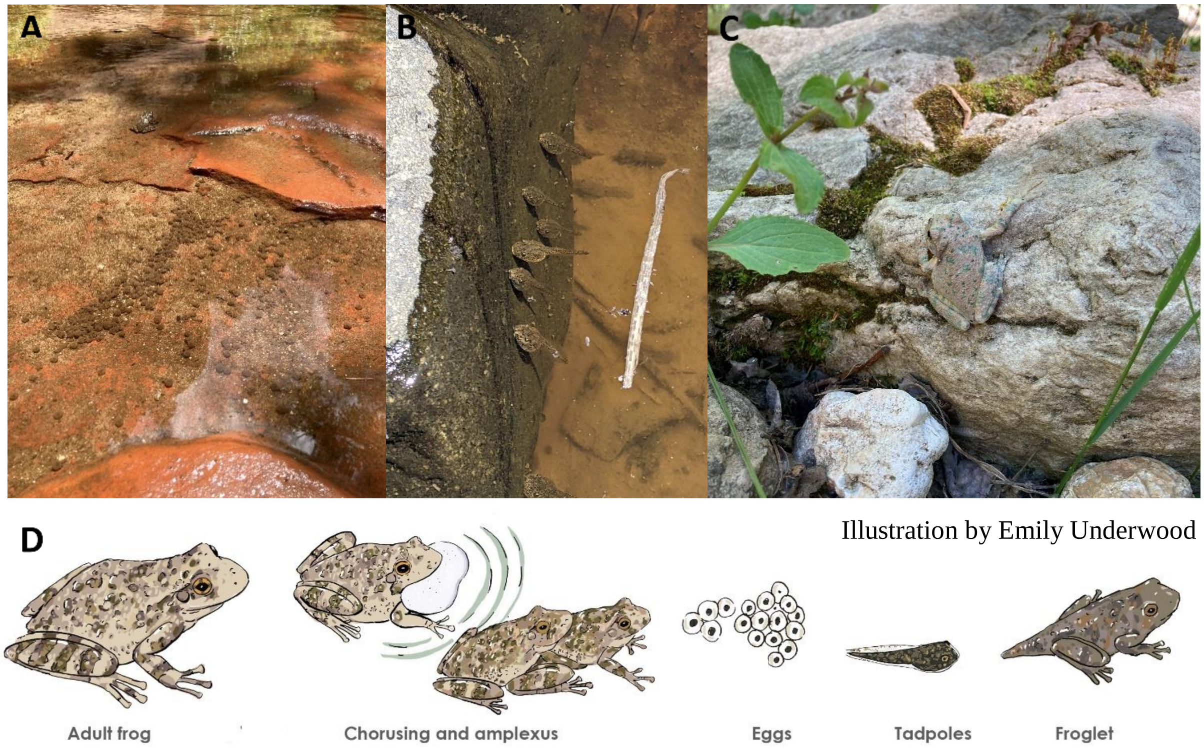
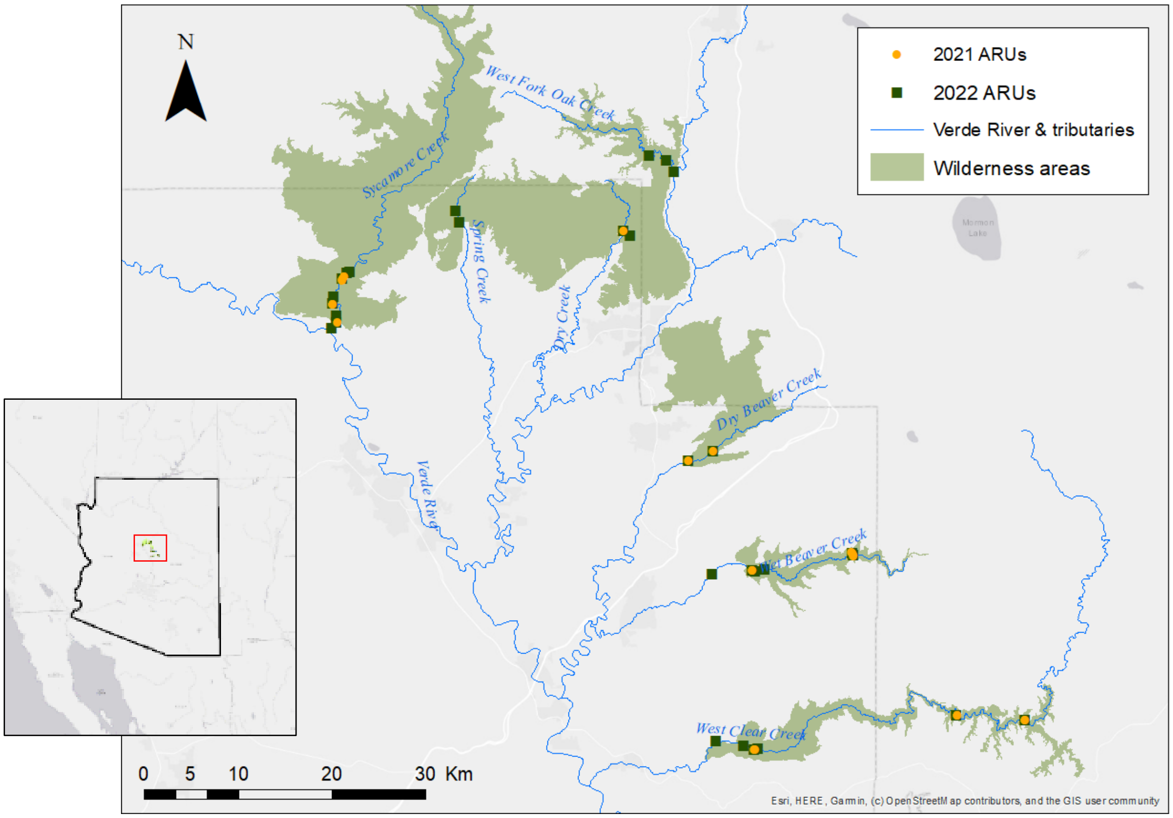


Illustration by Emily Underwood

Figure 1. Canyon treefrog (*Hyla arenicolor*) eggs (A), tadpoles (B), and adult life stages (C). Adult males produce advertisement calls in spring and during summer monsoon rains. After spawning, eggs hatch in roughly two weeks and tadpoles metamorphose in 45-75 days (D).



Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Figure 2. The study area encompasses five wilderness areas in the middle Verde River watershed, Arizona, USA. In 2021 and 2022, autonomous recording units were placed along tributaries of the Verde River, including Sycamore Creek (Sycamore Canyon Wilderness), Spring Creek, Dry Creek, and West Fork of Oak Creek (Red Rock-Secret Mountain Wilderness), Dry Beaver Creek (Munds Mountain Wilderness), Wet Beaver Creek (Wet Beaver Wilderness), and West Clear Creek (West Clear Creek Wilderness).

Figure 3. Perennial, intermittent, and ephemeral reaches in the middle Verde River watershed, Arizona, USA. From left to right, a perennial reach at West Clear Creek, an intermittent reach at Dry Beaver Creek, and an ephemeral reach at Sycamore Creek.

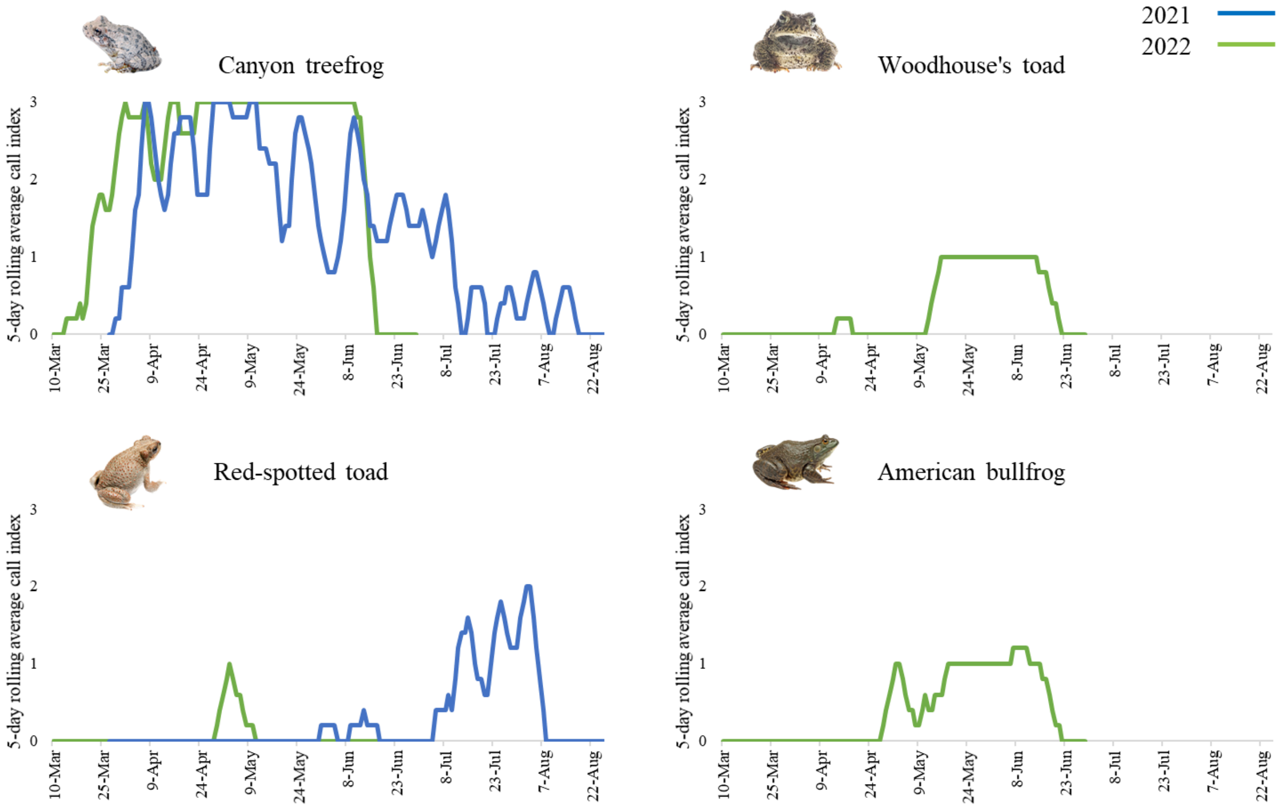


Figure 4. Maximum call index values in 2021 and 2022 of four anuran species in the middle Verde River watershed, Arizona, USA. Activity is plotted as a 5-day rolling average of maximum activity per day using a standard call index: 0 = no calling; 1 = individuals can be distinguished, no overlap; 2 = individuals can be distinguished, some overlap; and 3 = full chorus, calls are continuous and overlapping.

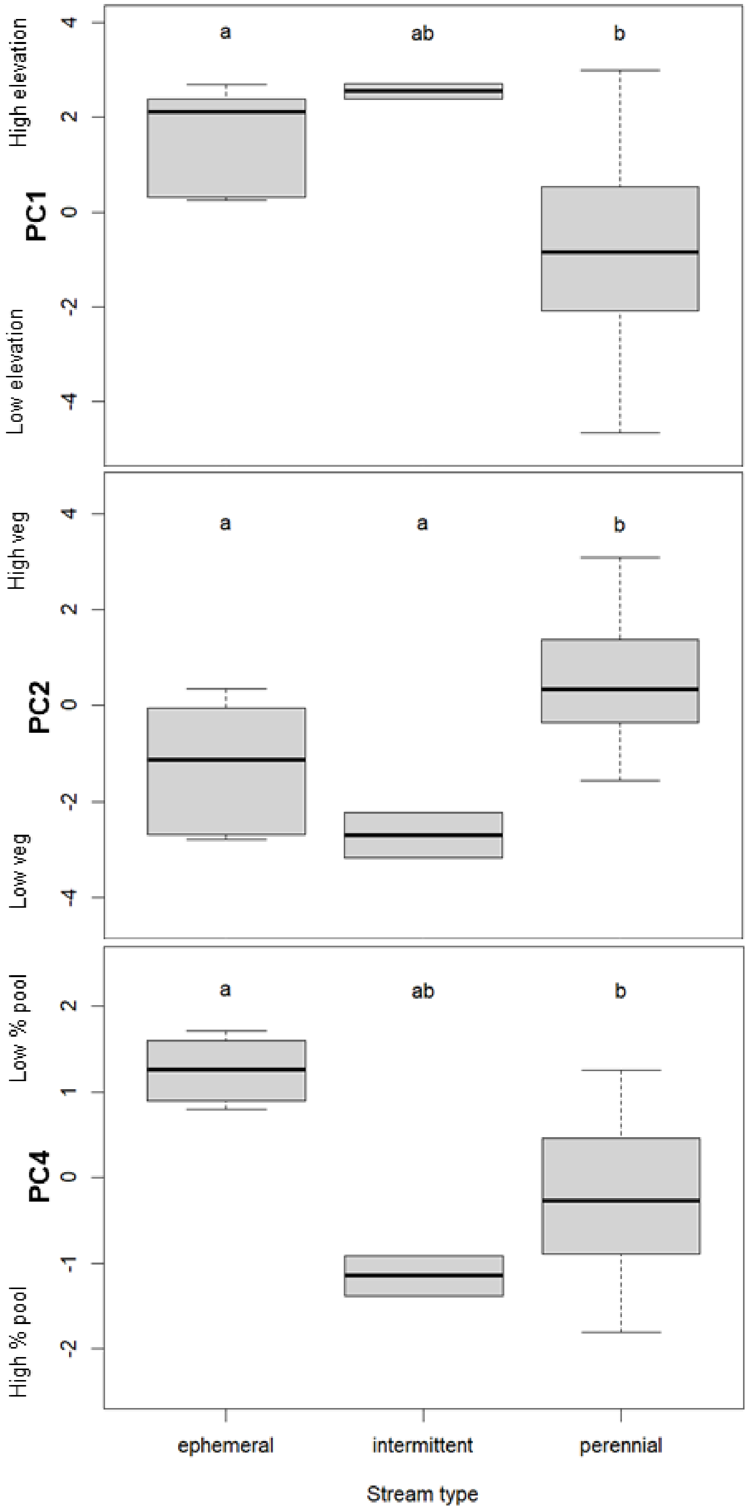


Figure 5. Results of comparison of means of principal components by stream type. Tukey's post hoc results of a one-factor ANOVA are shown in box plots above for PCs that differed significantly across stream type, from top to bottom: PC1, PC2, and PC4 (stream types with different letters are significantly different). Non-parametric Kruskal-Wallis and Mann-Whitney post hoc tests were used when assumptions of normality and homoscedasticity were not met. PCA reduced environmental and hydrological variables collected at perennial, intermittent, and ephemeral stream reaches in wilderness areas of the middle Verde River watershed, Arizona, USA.

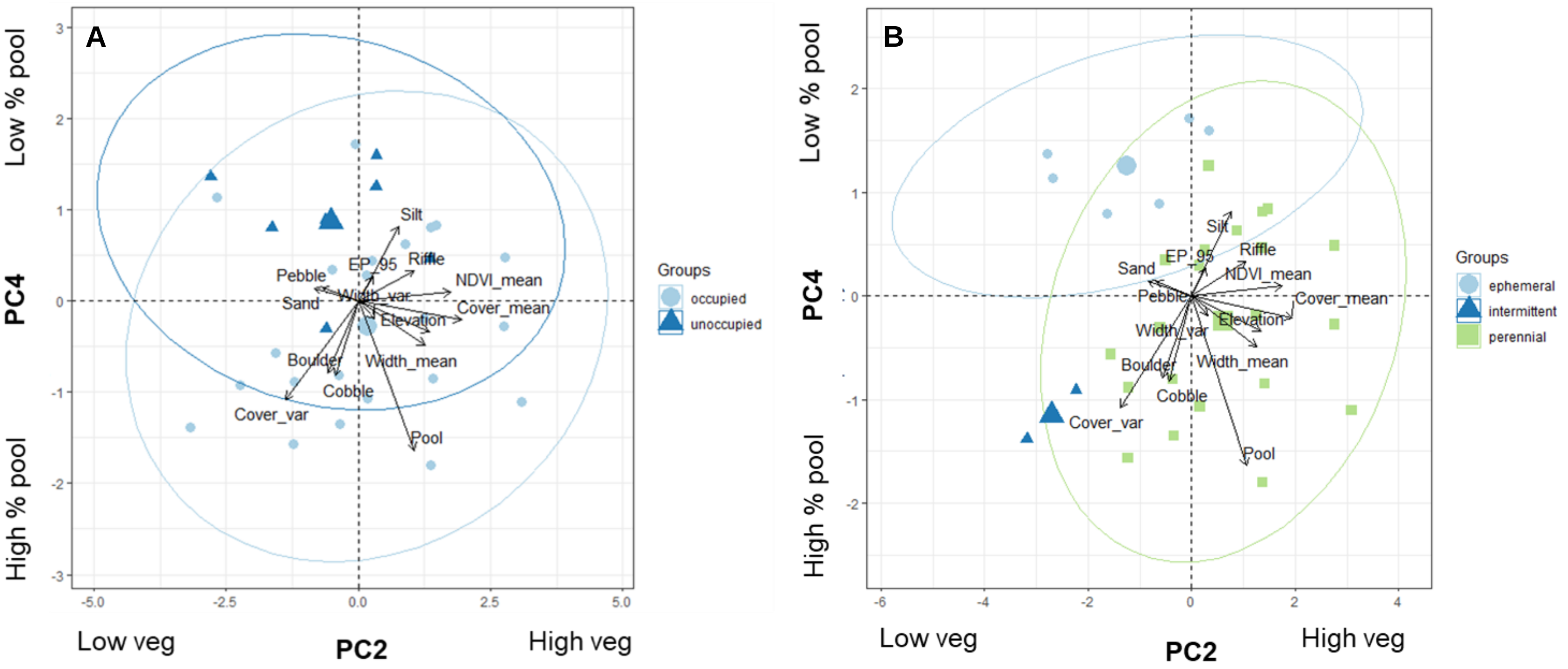


Figure 6. PC2 vs. PC4 biplots for anuran monitoring sites along wilderness area tributaries in the middle Verde River watershed, Arizona, USA. Sites are categorized by canyon treefrog occupancy (A) and stream type (B). Axes are labeled with the variables that define each PC. Stream types include ephemeral, intermittent, and perennial reaches (n=6, 2, 21).

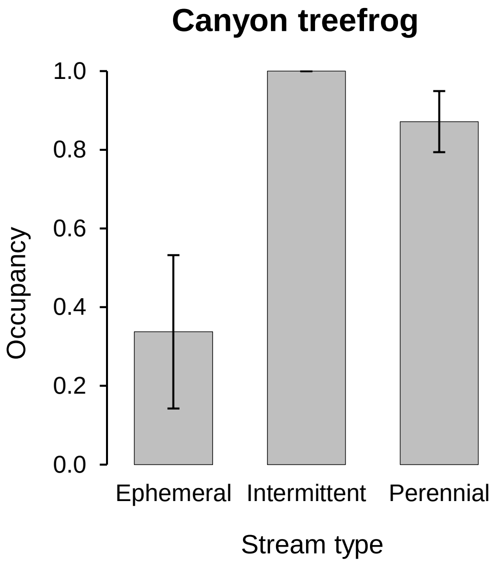


Figure 7. Occupancy probability (with ±1 standard error) across three stream types for canyon treefrog during March to June 2022 along wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Stream types include ephemeral, intermittent, and perennial reaches (n=6, 2, 21).

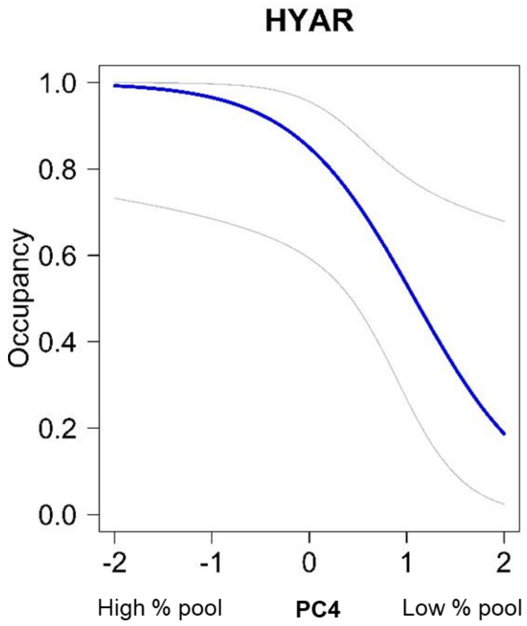


Figure 8. Predicted relationship for occupancy (with 95% confidence intervals) in response to PC4 for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA.

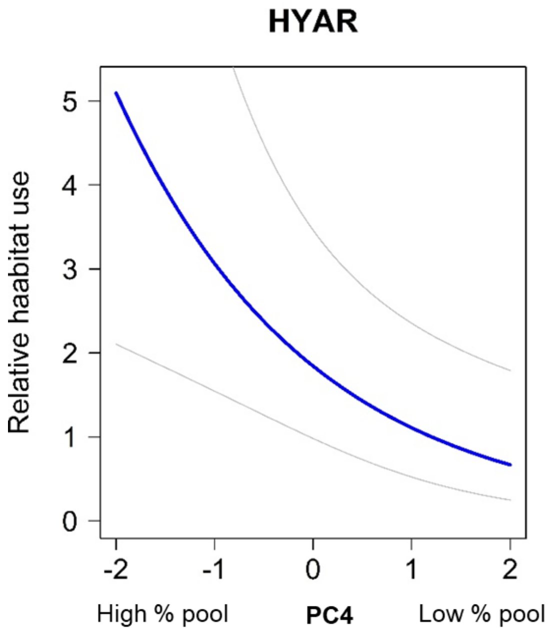


Figure 9. Royle-Nichols model predicted relationship for relative habitat use (with 95% confidence intervals) in response to PC4 for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA.

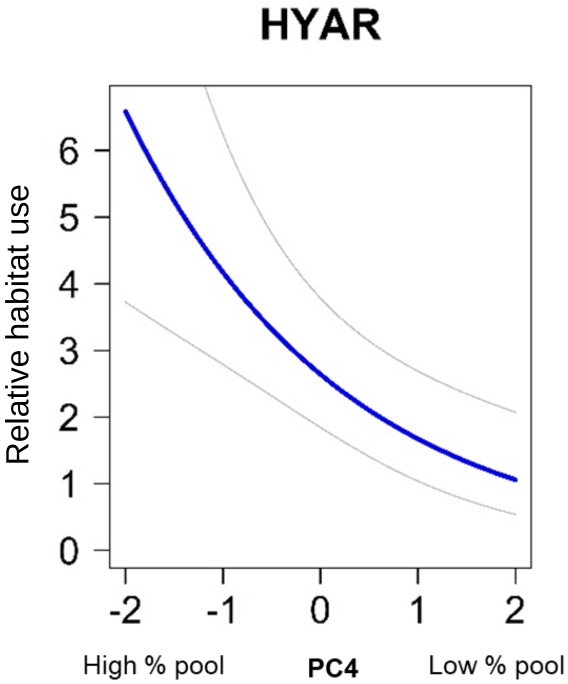


Figure 10. N-mixture model predicted relationship for relative habitat use (with 95% confidence intervals) in response to PC4 for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA.

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APPENDIX A

ADDITIONAL TABLES

Table A1. Acoustic monitoring site locations (Zone 12S, Datum NAD83) in 2021 (n=13 sites total, 11 sites with data), dates of data collected, and causes of data loss. Acoustic data were collected from March to October 2021 at sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA.

Site	Stream	Wilderness area	Stream designation	Easting	Northing	Start	End	Days of data	Weeks of data	Cause of data loss
MM1	Dry Beaver Creek	Munds Mountain	intermittent	432946	3846742	5-May	23-Aug	110	15.7	
MM2	Dry Beaver Creek	Munds Mountain	intermittent	435095	3847544	6-May	3-Jun	28	4.0	
RR1	Dry Creek	Red Rock-Secret Mountain	ephemeral	427441	3866769	5-May	1-Sep	119	17.0	
SC1	Sycamore Creek	Sycamore Canyon	perennial	402762	3862847	22-Mar	12-Jun	82	11.7	wildfire/flood
SC-AC3/AC4	Sycamore Creek	Sycamore Canyon	ephemeral	402927	3863032	22-Mar	6-Jun	76	10.9	wildfire/flood
SC5	Sycamore Creek	Sycamore Canyon	perennial	401940	3660691	24-Mar	12-Apr	19	2.7	wildfire/flood
SC7	Sycamore Creek	Sycamore Canyon	perennial	402262	3839075	NA	NA	0	0	wildfire/flood
WB1	Wet Beaver Creek	Wet Beaver	perennial	438492	3837116	24-Mar	12-Oct	202	28.9	high noise
WB3	Wet Beaver Creek	Wet Beaver	perennial	447347	3838375	8-Jun	5-Aug	58	8.3	
WB5	Wet Beaver Creek	Wet Beaver	perennial	447224	3838556	NA	NA	0	0	unknown
WCC1	West Clear Creek	West Clear Creek	perennial	438556	3821468	27-Mar	6-Sep	163	23.3	high noise
WCC4	West Clear Creek	West Clear Creek	perennial	456351	3824371	11-May	5-Oct	147	21.0	
WCC6	West Clear Creek	West Clear Creek	perennial	462386	3873847	12-May	8-Sep	119	17.0	

Table A2. Acoustic monitoring site locations (Zone 12S, Datum NAD83) from 2022 (n=29), dates of data collected, and causes of data loss. Sites were manually reviewed if Kaleidoscope Pro produced an abnormally low number of detections, attributed to high stream noise. Acoustic data were collected from March to June 2022 at sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA.

Site	Stream	Wilderness area	Stream designation	Easting	Northing	Start	End	2nd Start	2nd End	Days of data	Weeks of data	Cause of data loss	Manually reviewed
SYC1	Sycamore Creek	Sycamore Canyon	perennial	402762	3862847	27-Feb	16-Jun			109	15.6		
SYC2	Sycamore Creek	Sycamore Canyon	perennial	401976	3861284	27-Feb	16-Jun			109	15.6		
SYC3	Sycamore Creek	Sycamore Canyon	ephemeral	403419	3863474	27-Feb	20-Jun			113	16.1		
SYC4	Sycamore Creek	Sycamore Canyon	ephemeral	403208	3863334	27-Feb	15-Mar	4-Apr	16-Jun	89	12.7	battery failure	
SYC5	Sycamore Creek	Sycamore Canyon	perennial	401940	3660691	27-Feb	12-Jun			105	15.0		
SYC6	Sycamore Creek	Sycamore Canyon	perennial	402226	3859619	27-Feb	22-Jun			115	16.4		
SYC7	Sycamore Creek	Sycamore Canyon	perennial	402262	3839075	27-Feb	22-Jun			115	16.4		
SYC8	Sycamore Creek	Sycamore Canyon	perennial	401792	3858581	8-Mar	22-Jun			106	15.1		
RR1	Dry Creek	Red Rock-Secret Mountain	ephemeral	427441	3866769	14-Mar	23-Jun			101	14.4		
RR2	Spring Creek	Red Rock-Secret Mountain	ephemeral	413081	3867671	14-Mar	1-Jun			79	11.3	battery failure	
RR3	Spring Creek	Red Rock-Secret Mountain	ephemeral	412735	3868655	14-Mar	31-May			78	11.1	battery failure	
RR4	Sterling Canyon Creek	Red Rock-Secret Mountain	ephemeral	427966	3866408	23-Mar	23-Jun			92	13.1		
WFOC1	West Fork of Oak Creek	Red Rock-Secret Mountain	perennial	431895	3871921	11-Mar	17-Jun			98	14.0		
WFOC2	West Fork of Oak Creek	Red Rock-Secret Mountain	perennial	431889	3871929	11-Mar	17-Jun			98	14.0		
WFOC3	West Fork of Oak Creek	Red Rock-Secret Mountain	perennial	429708	3873369	10-Mar	17-Jun			99	14.1		
WB1	Wet Beaver Creek	Wet Beaver	perennial	438492	3837116	8-Mar	15-Jun			99	14.1		X
WB2	Wet Beaver Creek	Wet Beaver	perennial	438750	3837025	9-Mar	15-Jun			98	14.0		
WB3	Wet Beaver Creek	Wet Beaver	perennial	447347	3838375	13-Mar	1-May			49	7.0	battery failure	
WB4	Wet Beaver Creek	Wet Beaver	perennial	434978	3836848	14-Apr	15-Jun			62	8.9	SD card corruption	X
WB5	Wet Beaver Creek	Wet Beaver	perennial	447224	3838556	12-Mar	8-Jun			88	12.6		
WB7	Wet Beaver Creek	Wet Beaver	perennial	439545	3837206	8-Mar	15-Jun			99	14.1		X
WCC1	West Clear Creek	West Clear Creek	perennial	438556	3821468	21-Mar	28-Apr	25-May	15-Jun	59	8.4	battery failure	X
WCC2	West Clear Creek	West Clear Creek	perennial	438891	3821520	21-Mar	12-May	24-May	15-Jun	74	10.6	battery failure	X
WCC3	West Clear Creek	West Clear Creek	perennial	435192	3822239	10-Mar	15-Jun			97	13.9		
WCC4	West Clear Creek	West Clear Creek	perennial	456351	3824371	15-Mar	29-Jun			106	15.1		
WCC5	West Clear Creek	West Clear Creek	perennial	437585	3821818	16-Mar	15-Jun			91	13.0		X
WCC6	West Clear Creek	West Clear Creek	perennial	462386	3873847	15-Mar	14-Jun			91	13.0		
MM1	Dry Beaver Creek	Munds Mountain	intermittent	432946	3846742	15-Mar	13-May	2-Jun	17-Jun	74	10.6	battery failure	
MM2	Dry Beaver Creek	Munds Mountain	intermittent	435095	3847544	21-Mar	11-May	2-Jun	10-Jun	59	8.4	battery failure	

Table A3. Cover classes used to visually estimate percent cover of substrate at sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Midpoints of each cover range were used in analyses.

Cover class	Percent cover range	Midpoint conversion
0	0%, not present	0.0
1	< 1%	0.5
2	1–5%	3.0
3	5–25%	15.0
4	25–50%	37.5
5	50–75%	62.5
6	75–95%	85.0
7	95–100%	97.5

Table A4. Audio recordings used to train species-specific anuran classifiers. Data were obtained from the Macaulay Library of the Cornell Lab of Ornithology, the Arizona Game and Fish Department (AZGFD) courtesy of A. Owens, and *Frog and Toad Calls of the Rocky Mountains* (Davidson, 1996). Classifiers were used to process acoustic data collected in 2021 and 2022 at sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA.

Species	Recording ID	Source
Arizona Toad	ML124447	Macaulay
	ML124446	Macaulay
	ML124444	Macaulay
	ML124437	Macaulay
	ML124436	Macaulay
	ML122786	Macaulay
	ML124427	Macaulay
		Davidson, 1996
Lowland leopard frog	ML125885	Macaulay
		Davidson, 1996
Chiricahua leopard frog		Owens, AZGFD
		Davidson, 1996
Woodhouse's toad		Davidson, 1996
Red-spotted toad		Davidson, 1996

Table A5. Parameter settings used for species-specific classifiers built in Kaleidoscope Pro software. Classifiers were used to process acoustic data collected in 2021 and 2022 at sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA.

Parameter	Canyon treefrog	Red-spotted toad	Woodhouse's toad	Arizona toad	American bullfrog	Chiricahua leopard frog	Lowland leopard frog
FFT window (ms)	5.33	5.33	5.33	10.67	10.67	10.67	5.33
Max distance from cluster center to include outputs in cluster.csv	1.0-2.0	2.0	2.0	2.0	2.0	2.0	2.0
Max states	12	12	12	12	12	8	12
Max distance to cluster center for building clusters	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Max clusters	500	500	500	500	500	500	500
Frequency minimum (Hz)	315	1700	1050	1050	135	0	1200
Frequency maximum (Hz)	850	2300	1650	1300	450	3000	1500
Min length of detection (s)	0.3	1	1	3	0.3	0.1	0.2
Max length of detection (s)	7.5	20	3	7	1	3.5	7
Max inter-syllable gap (s)	0.025	0.05	0.05	0.35	0.35	0.35	0.8

Table A6. Correlation matrix containing Pearson correlation values among 14 continuous variables. The standard value of r > 0.6 was used as the threshold for highly correlated variables, indicated by bolding. Site-level variables were collected in May and June 2022 at anuran monitoring sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Variables with > 40% zero values were excluded from analyses.

	Elevation	Flow width	Flow width variance	Canopy cover	Canopy cover variance	Boulder	Cobble	Pebble	Sand	Silt	Riffle	Pool	NDVI
Elevation	—												
Flow width	-0.30	—											
Flow width variance	-0.28	0.53	—										
Canopy cover	0.25	0.45	0.13	—									
Canopy cover variance	-0.11	-0.26	-0.07	-0.39	—								
Boulder	0.17	-0.47	-0.32	0.14	0.23	—							
Cobble	0.22	-0.34	-0.11	0.14	0.15	**0.63**	—						
Pebble	-0.24	-0.11	0.28	0.09	0.08	0.45	0.51	—					
Sand	**-0.72**	0.39	0.42	-0.21	0.02	-0.37	-0.25	-0.03	—				
Silt	**0.64**	-0.43	-0.30	0.20	-0.04	0.09	0.20	-0.05	-0.53	—			
Riffle	-0.27	**0.75**	0.34	0.45	-0.26	-0.30	-0.23	0.00	0.28	-0.34	—		
Pool	0.13	0.57	0.20	0.20	-0.10	-0.32	-0.23	-0.44	0.12	-0.27	0.09	—	
NDVI	**0.79**	-0.10	-0.15	0.57	-0.24	0.22	0.10	-0.03	**-0.67**	0.59	-0.07	0.00	—
Discharge 95% EP	-0.49	0.55	0.51	0.38	-0.16	-0.07	0.08	0.47	0.47	-0.26	0.56	-0.02	-0.19

Table A7. Start and end dates of modeling occasions. Acoustic data were collected from March to June 2022 at sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Data was divided into 2-week bins to simulate site revisits for occupancy, RN, and N-mixture modeling.

Occasion	Start Date	End Date
1	3/15/2022	3/28/2022
2	3/29/2022	4/11/2022
3	4/12/2022	4/25/2022
4	4/26/2022	5/10/2022
5	5/11/2022	5/25/2022
6	5/26/2022	6/8/2022

Table A8. Correlation matrix containing Pearson correlation values among 3 continuous time-varying detection covariates. The standard value of r > 0.6 was used as the threshold for highly correlated variables, indicated by bolding. Time-varying detection covariates include mean daily precipitation (Prcp), mean daily minimum air temperature (Tmin), and mean equivalent continuous sound level (Leq). Mean daily precipitation was zero for all sites on occasions three to six, resulting in NAs for those occasions.

	Occasion 1		Occasion 2		Occasion 3		Occasion 4		Occasion 5		Occasion 6	
	Prcp	Tmin	Prcp	Tmin	Prcp	Tmin	Prcp	Tmin	Prcp	Tmin	Prcp	Tmin
Prcp	−		−		−		−		−		−	
Tmin	-0.48	−	-0.23	−	NA	−	NA	−	NA	−	NA	−
Leq	**0.77**	-0.31	-0.17	-0.04	NA	-0.01	NA	-0.03	NA	0.04	NA	0.12

Table A9. N-mixture model results for canyon treefrog during March to June 2022 at wilderness area tributaries of the middle Verde River watershed, Arizona, USA. Parameters include detection probability (p) and relative habitat use (λ). Models include the y-intercept only (1; no variables) and global models (detection covariates mean daily precipitation, mean daily minimum air temperature, and mean equivalent continuous sound level, and landscape covariates PC1 through PC4) for each distribution option: Poisson (P), Negative Binomial (NB), and Zero Inflated-Poisson (ZIP). Table results include the number of terms in the model (K), AIC value, delta AIC (ΔAIC), and model weight (wt).

Model	K	AIC	ΔAIC	wt
ZIP_global	10	396.28	0.00	0.46
NB_global	10	397.17	0.88	0.29
P_global	9	397.47	1.19	0.25
NB_p(1) λ(1)	3	432.16	35.88	0.00
ZIP_p(1) λ(1)	3	436.17	39.89	0.00
P_p(1) λ(1)	2	453.69	57.41	0.00

APPENDIX B
ADDITIONAL FIGURES

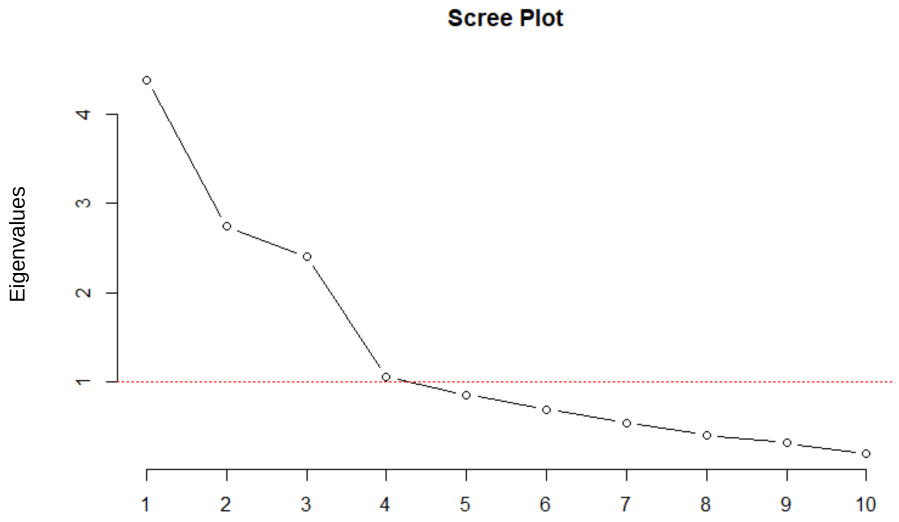

Figure A1. Scree plot with eigenvalues of first ten principal components (PCs) generated by PCA including all variables with < 40% zeros at all sites (n=29). PCs with eigenvalues >1 (above the dashed red line) were included in analyses. Variables were collected at sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA

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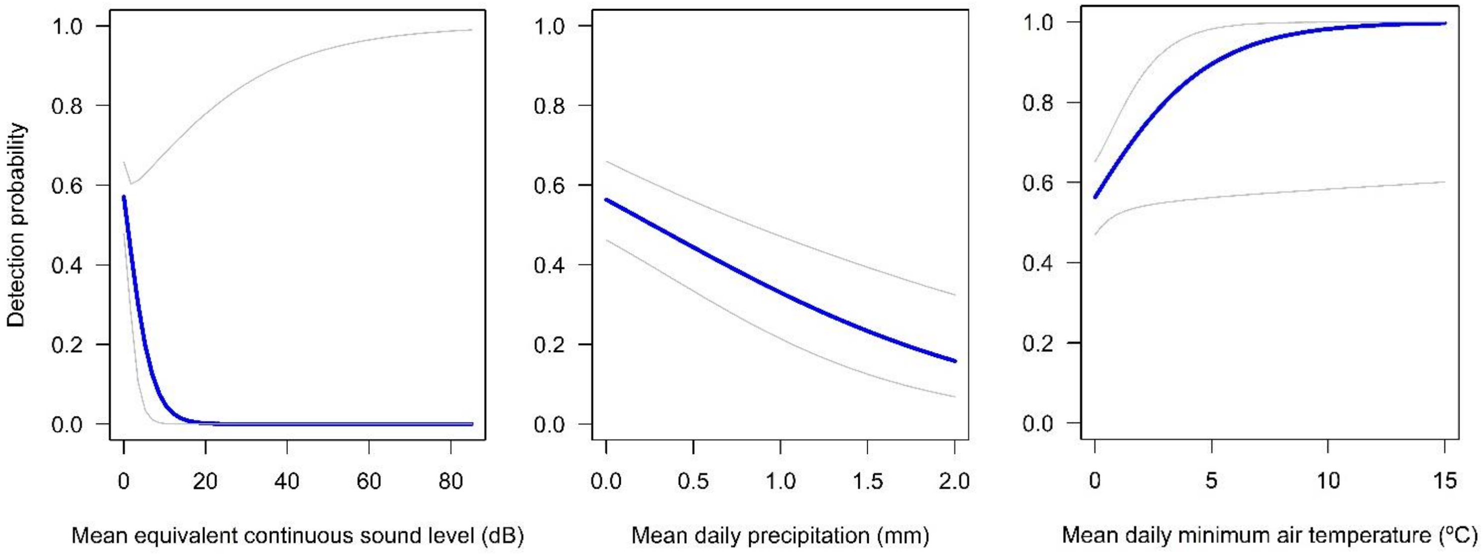

Figure A2. Predicted relationships (with 95% confidence intervals) between canyon treefrog detection probabilities and time varying covariates: from left to right, mean equivalent continuous sound level, mean daily precipitation, and mean daily minimum air temperature. Detection probabilities were derived from occupancy modeling for canyon treefrog from March to June 2022 at acoustic monitoring sites located along wilderness area tributaries of the middle Verde River watershed, Arizona, USA.