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Thermal Traits of Anurans Database for the Southeastern United States (TRAD): A Database of Thermal Trait Values for 40 Anuran Species

Traci P. DuBose¹, Victorjose Catalan¹, Chloe E. Moore¹, Vincent R. Farallo², Abigail L. Benson³, Jessica L. Dade¹, William A. Hopkins⁴, and Meryl C. Mims¹

Thermal traits, or how an animal responds to changing temperatures, impacts species persistence and thus biodiversity. Trait databases, as repositories of consolidated, measured organismal attributes, allow researchers to link study species with specific trait values, enabling comparisons within and among species. Trait databases also help lay the groundwork to build mechanistic linkages between organisms and the environment. However, missing or hidden physiological trait data preclude building mechanistic estimates of climate change vulnerability for many species. Thus, physiologically focused trait databases present an opportunity to consolidate data and enable species-specific or multispecies, mechanistic evaluations of climate change vulnerability. Here, we present TRAD: thermal traits of anurans database for the southeastern United States, a database of thermal trait values related to physiological thermoregulation (critical thermal minima and maxima, preferred temperature), behavioral thermoregulation (activity period, retreat emergence temperature, basking temperature, minimum and maximum foraging temperatures), and body mass for 37 anuran species found within the southeastern United States. In total, TRAD contains 858 reported trait values for 37 of 40 species found in the region from 267 peer-reviewed papers, dissertations, or theses and is easily linked with trait data available in ATraitU, an ecological trait database for anurans in the United States. TRAD contains trait values for multiple life stages and a summation of interspecific adult trait values. Availability of trait data varied widely among traits and species. Estimates of mass were the most common trait values reported, with values available for 32 species. Behavioral trait values comprised 23% of our database, with activity period available for 34 species. We found the most trait values for Cope's Gray Treefrog (*Dryophytes chrysoscelis*), with at least one trait value for eight traits in the database. Conversely, species in the genus *Pseudacris* generally had the fewest trait values available. Species with the largest geographic range sizes also had the greatest coverage of data across traits ($\rho = 0.75$, $P < 0.001$). TRAD can aid studies of anuran response to changing temperatures, physiological niche space and limitations, and potential drivers of anuran geographic range limits, influencing our understanding of other ecological and evolutionary patterns and processes and enabling multispecies comparisons of potential risk and resilience in the face of climate change.

THERMAL traits describe components of an organism's ability to respond to changing abiotic conditions to maintain homeostasis, including physiological tolerance or behavioral amelioration of extreme temperatures. Thermal traits contribute to species divergence (Cadena et al., 2012; Teske et al., 2019), range limits (Díaz-Ricaurte et al., 2020), and persistence (Morley et al., 2019), informing our fundamental understanding of biodiversity (Chown et al., 2004). Thermal traits also inform our understanding of species climate change vulnerability (Huey et al., 2012; Foden et al., 2013; Pacifici et al., 2015). Specifically, trait values that relate to the maintenance of internal body temperature are used to parameterize biophysical and dynamic energy budget models, which use mass balance equations and physiological limits to translate microclimate parameters to specific performance metrics such as body temperature, activity levels, and reproductive output (Peterman and Gade, 2017; Kearney and Porter, 2020). These models ultimately help produce and refine predictions about the impact of climate change on species persistence at local and

range-wide extents. Computerized biophysical models can be computationally expensive and parameter rich, depending on model resolution and complexity, making their application to some species difficult due to lack of data (Williams et al., 2008; Pacifici et al., 2015; Buckley et al., 2018).

Trait databases compile information about species traits into one place to help answer questions that span many taxonomic groups and large geographical areas and can help identify understudied taxa and traits (Tyler et al., 2012; Farley et al., 2018; Martini et al., 2021). Because traits transcend species identity to create a common currency that describes an organism's response to the environment (McGill et al., 2006; Webb et al., 2010), trait databases can be used to help answer fundamental ecological and evolutionary questions. For example, trait databases have contributed to our understanding of community assembly (Cadotte et al., 2013) and niche conservatism (Anderson and Wiens, 2017; Moreira et al., 2021). Trait databases have informed ecosystem and species conservation research as well (e.g., river flow alteration changes community

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Table 1. Nine thermal traits targeted in our literature search, a brief definition, the keywords used to search for values for each trait, and the resulting number of species with at least one value for that trait (trait coverage). We used the keywords in species keyword pairs (e.g., "*Pseudacris fouquettei*" thermal tolerance, "*Pseudacris fouquettei*" thermal maximum, and "*Pseudacris fouquettei*" critical thermal maximum separately for the critical thermal maximum trait for *P. fouquettei*) to search Web of Science (2022) and Google Scholar (2022) beginning 1 September 2020 until 5 July 2022. *, as in bask*, is used as a wildcard symbol when conducting a literature search. Full definition of the traits can be found in the methods of this manuscript.

Trait name	Trait definition	Keywords	Trait coverage
Preferred temperature	preferred temperature, which the individual attempts to behaviorally regulate to	preferred temperature, Tpref, thermal preference	22
Critical thermal maximum	maximum physiological temperature limit, which estimates an individual's biological death	CTmax, critical thermal maximum, upper lethal temperatures	19
Critical thermal minimum	minimum physiological temperature limit, which estimates an individual's biological death	CTmin, critical thermal minimum, lower lethal temperatures	13
Mass	estimation of body size, preferably wet weight	mass	31
Activity	part of the day an individual is active: diurnal, nocturnal, crepuscular	activity, behavior	34
Emergence temperature	temperature at which an individual emerges from retreats	Tmerge, temperature emergence, spring emergence, temperature migration	28
Basking temperature	temperature at which an individual basks	Tbask, bask* temperature, perch temperature	3
Maximum foraging temperature	maximum temperature at which foraging occurs	maximum foraging temperature, maximum predation temperature, maximum feeding temperature	4
Minimum foraging temperature	minimum temperature at which foraging occurs	minimum foraging temperature, minimum predation temperature, minimum feeding temperature	4

life history composition; Mims and Olden, 2013). Although trait databases have been leveraged to conduct climate change vulnerability assessments (Williams et al., 2008; Foden et al., 2013; Lertzman-Lepofsky et al., 2020; Bartelt et al., 2022), multispecies comparisons of vulnerability often do not include estimates of physiological sensitivity due to the real or presumed absence of trait data, even though the potential improvement in assessment precision is well recognized (Griffis-Kyle, 2016).

Anurans, ectothermic animals with a variety of thermoregulatory adaptations (Navas et al., 2016), have often experienced population declines across the United States (Stuart et al., 2004; Grant et al., 2016). Anuran traits can be found in global trait databases that contain diet, life history traits, and activity information (Oliveira et al., 2017) or thermal limits (Bennett et al., 2018; Pottier et al., 2022); these databases have varying levels of transparency to the source of trait information, varying levels of completeness, and are often trait focused, leading to some species being missed during database compilation. As calls for multispecies comparisons of vulnerability increase, the need to include more species and incorporate mechanistic linkages between the environment and biological responses (Foden et al., 2019; Briscoe et al., 2022) underscores the need for trait databases that carefully and explicitly link trait values with their sources. A trait database of anuran thermal trait values allows us to identify data gaps and eases the inclusion of this taxon in multi-species ecological and evolutionary investigations.

We present TRAD: thermal traits of anurans database for the southeastern United States (DuBose et al., 2023), which includes nine traits that are directly or indirectly related to anurans' response to changing temperatures for 40 anuran species native to a biodiversity hotspot, the southeastern United States (Noss et al., 2015), and it is the result of extensive and comprehensive searching of published resources. TRAD supplements the ATraiU database (Moore et al., 2021),

which has habitat, trophic, morphological, and life history trait data for 106 anuran species found within the United States (US). In this manuscript, for each trait, we report the number of species with at least one trait value reported (trait coverage); for each species, we report the number of traits with at least one trait value reported (trait completeness, *sensu* Etard et al., 2020). We explore variation in trait completeness among families and genera and investigate whether trait completeness is correlated with anuran area of occupancy. Species with larger range sizes typically have higher trait completeness, likely because of increased occurrence at study sites (Etard et al., 2020). By collating thermal trait values, we hope to aid other researchers in assessing variation in anuran physiology in a biodiversity hotspot that is likely to continue to experience multiple, interacting threats to anuran biodiversity due to global climate change effects.

MATERIALS AND METHODS

Trait selection and description.—We identified nine traits that are related to an animal's response to temperature (referred to as thermal traits; Table 1). We chose traits that are commonly used to parameterize the biophysical model NicheMapR, which uses mass-balance equations to estimate how solar radiation, air temperature, and soil temperature interact to affect the body temperature of a model ectotherm (Peterman and Gade, 2017; Kearney and Porter, 2020). Although mass, emergence temperature, and activity period are not strictly thermal traits (Taylor et al., 2021), they are directly related to an animal's response to temperature, and these traits are expected to change due to direct and indirect effects of climate change (Sheridan et al., 2018; Levy et al., 2019).

Physiological traits included a species' preferred temperature, critical thermal maximum, and critical thermal minimum. These traits are related to physical and metabolic processes that alter an animal's thermoregulation. Preferred temperature

Table 2. Evidence categories that describe the type of methodology used to determine the reported trait value for eight thermal traits. The type of evidence category ranks the methodology from A to C and reflects the precision with which that methodology reflects that trait value (earlier letters reflect better precision between the methodology and true trait). The *n* trait values column reports the number of unique trait values categorized as that type of evidence. Evidence type was not assessed for the activity trait and categories are identical for maximum and minimum foraging temperatures.

Trait	Methodology	Type of evidence category	<i>n</i> trait values
Preferred temperature	Experimentally selected substrate temperature in temperature gradient	A	74
	Mean recorded body temperature	B	44
	Selected substrate temperature in habitat use study	C	5
Critical thermal maximum	Lethal temperature or (for eggs) no development	A	16
	Loss of movement/righting reflex	B	137
	Highest recorded body temperature	C	1
Critical thermal minimum	Lethal temperature	A	32
	Loss of movement/righting reflex	B	13
	Lowest recorded body temperature	C	3
Mass	Collected from field population	A	254
	Maximum known mass	B	3
	Collected from captive population	C	91
Emergence temperature	Observed emergence from dormancy	A	25
	Lowest recorded temperature for calling/breeding	B	54
	Lowest recorded body temperature	C	1
Basking temperature	Experimentally measured	A	2
	Estimated from field observations	B	2
Maximum and minimum foraging temperature	Experimentally controlled	A	7
	Field observed, foraging inferred outside burrow	B	4

is the body temperature to which the species regulates and is often closely associated with optimal performance temperatures (Angilletta et al., 2002). Both critical thermal maximum and critical thermal minimum describe physiological limits and estimate the temperature at which an individual loses coordinated movement ability (i.e., biological death; Lutterschmidt and Hutchison, 1997).

Mass estimates the size of the animal, which can alter an animal's heat conservation through their surface area to volume ratio and microclimatic experience (Kearney et al., 2021). Although mass is typically considered an emergent property between species' trophic traits and the environment, macroecological patterns in adult anuran body size suggest that anurans leverage their thermoregulatory abilities to reach larger sizes in low energy areas, allowing them to conserve heat in low temperatures (Olalla-Tárraga and Rodríguez, 2007). As a result, anurans of different sizes could have different thermal traits and needs. In this database, we recorded any available mass estimates for different life stages; mean mass was reported across all life stages with the exception of three maximum adult mass values (Table 2).

Behavioral traits included activity period, retreat emergence temperature, basking temperature, and foraging temperature limits. These traits aid thermoregulation by allowing animals to select times and habitats that meet their physiological needs. The activity period describes when the animal prefers to be active on the landscape each day. Activity is phylogenetically conserved (Anderson and Wiens, 2017) and can potentially reduce an animal's exposure to extreme temperatures (Hutchison and Dupré, 1992). Anurans generally cease surface activity in the winter and withstand extreme winter temperatures by seeking hibernacula, overwintering within deep water, or

using freeze tolerance (Pinder et al., 1992). A species' emergence temperature describes the environmental temperature at which an animal annually initiates surface activity after winter dormancy (Green et al., 2016). Basking temperature is the environmental temperature at which an animal begins basking to quickly increase its temperature and improve metabolic performance; however, basking may also increase the rate of water loss and risk of dehydration (Freed, 1980; Muths and Corn, 1997). Although few studies have investigated the benefits of the behavior, basking behavior has been documented in both toads (Bufonidae) and treefrogs (Hylidae; Wells, 2010). Foraging maximum and minimum temperature describes the range of environmental temperatures within which an animal is foraging on the landscape. Species foraging temperature limits likely differ based on species' predation risk, energy loss to thermoregulation, and energy gained through foraging (Putnam and Bennett, 1981).

Species selection and compilation of thermal trait data.—We took a species-centric approach to search the literature for thermal trait data. We used a combination of US state agency species lists and International Union for the Conservation of Nature (IUCN) range maps to identify all anurans native to Alabama, Florida, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia comprising the southeastern United States (Fig. 1; International Union for Conservation of Nature, 2017). We excluded Collinses' Mountain Chorus Frog (*Pseudacris collinsorum*) because it was recently described as distinct from the Mountain Chorus Frog (*Pseudacris brachyphona*; Ospina et al., 2020). Species names were standardized using the Global Biodiversity Information Facility (GBIF) Backbone Taxonomy (GBIF Secretariat, 2019). For the trilling chorus frog complex (*Pseudacris* spp.) and North

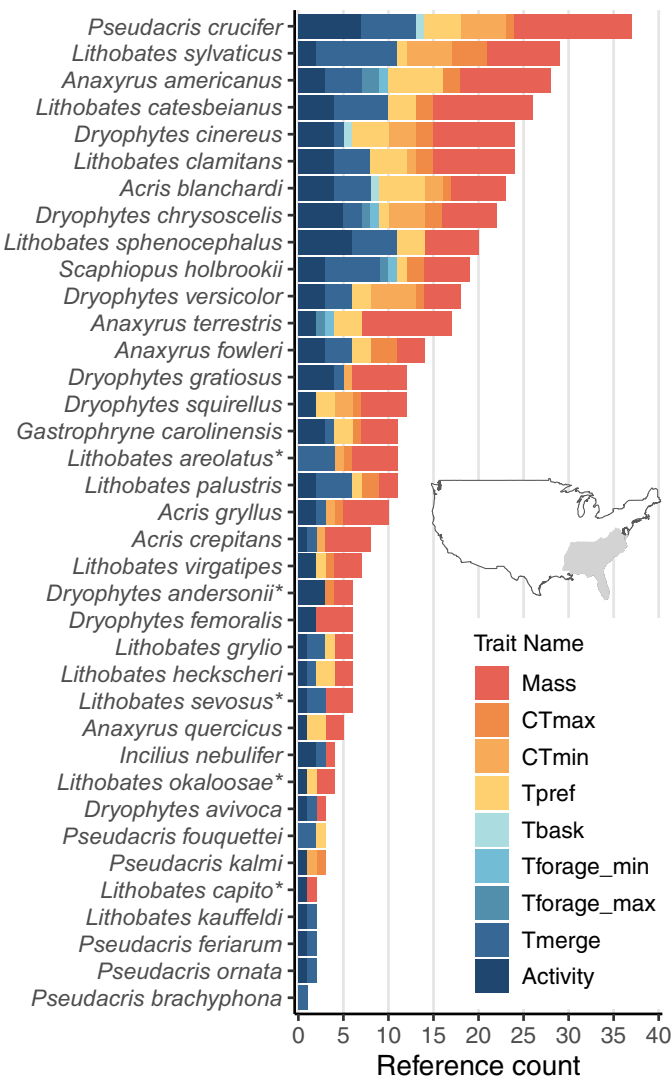


Fig. 1. Counts of adult thermal trait values found within the literature for 37 species of frogs and toads (anurans) within the southeastern United States. Species *Pseudacris brimleyi*, *Pseudacris nigrita*, and *Pseudacris ocularis* are not shown due to no trait values reported. States indicated in gray in the inset map of the conterminous United States are considered the southeastern United States for this database. Trait Name is ordered based on type of trait: warm colored traits are mass and physiological traits, and cool colored traits are behavioral traits. Physiological traits include critical thermal maximum (CTmax), critical thermal minimum (CTmin), and Tpref (preferred temperature). Behavioral traits include basking temperature (Tbas), foraging temperature limits (Tforage_min and Tforage_max), emergence temperature (Tmerge), and activity. An * indicates a species of conservation concern. Conservation status, as defined by the International Union for the Conservation of Nature Red List, was determined on 15 August 2020 (International Union for Conservation of Nature, 2017).

American cricket frogs (*Acris* spp.), we updated species names according to the study location using distributions outlined in Lemmon et al. (2007) and Gamble et al. (2008), respectively. As a result, the traits identified as Western Chorus Frog (*Pseudacris triseriata*) were reassigned to other species, and the Western Chorus Frog was removed from the focal species list. For each species, we used the Integrated Taxonomic Information System (ITIS) to ensure taxonomic synonyms were included in our search for trait values (ITIS, 2021).

We collected thermal traits described for each taxon found within Hutchison and Dupré (1992), Rome et al. (1992), Wells (2010), and *Herpetological Review* (2017). We also built species keyword pairs (e.g., “*Pseudacris fouquettei*” critical thermal maximum) and searched Web of Science’s (2022) Core Collection using species keyword searches for all available sources; species’ literature searches began 1 September 2020 and concluded 5 July 2022 (Table 1). If the Web of Science search returned no records, we searched Google Scholar (2022) with the species keyword pair. Once sources were identified, we screened sources’ abstracts for any mention of thermal traits. This method identified peer-reviewed articles, dissertations, and theses as sources from which we transcribed reported trait information.

From each source, we recorded the species, trait value reported (e.g., mean mass), life stage, sex, study location, trait value variation (e.g., standard deviation of mass), and acclimation temperature, if available. Because there are many ways to measure and describe animals’ thermal traits (Lutterschmidt and Hutchison, 1997; Navas et al., 2021; Taylor et al., 2021), we categorized the methodology used to identify a trait value as the “type of evidence” (Table 2). Type of evidence could be the physiological endpoint used to quantify a trait, the type of experiment used to describe a trait, or the type of observation. Evidence type categorization reflects precision ranked A–C for most to least precise and aims to help database users make informed decisions about trait value inclusion based on how the values were originally measured. For trait data that were reported graphically without a numerical description, we used WebPlotDigitizer to digitize any plots (Rohatgi, 2021). When trait values were reported from a different source (e.g., for comparison among species within a discussion), we incorporated trait values from the original source following the same methodology described here. Overall, our process retains intra-specific trait data when available, allowing multiple trait values recorded for a single trait for a given species.

We conducted quality control measures to reduce transcription errors when recording traits found in the literature. Each trait value was checked by two separate authors. After data compilation, we checked the database for formatting errors (e.g., typing errors such as taxon name misspellings). For numeric traits (all except Activity), we identified trait values that were more than 2.5 standard deviations away from the mean at the family, genus, and species level to identify potential errors at levels of organization that might have different means and standard deviations. These flagged trait values were double checked; if the value was correctly reported, we made no change. Overall, 32 continuous trait values (4.2%) were flagged as outliers, and one value was corrected. No traits were imputed for this database.

We then summarized intraspecific trait data for interspecific comparisons. For categorical activity data, we summed the number of sources that indicate a species’ diel activity type. For continuous traits, if the trait is a minimum trait (i.e., critical thermal minimum, emergence temperature, minimum foraging temperature), we retained the minimum trait data point across all references. If the trait is a maximum trait (i.e., critical thermal maximum, maximum foraging temperature), we retained the maximum trait data point across all references. For all other traits (i.e., mass, thermal preference), we calculated the mean across all references. The TRAD database can be found at DuBose et al. (2023) and the Open Traits Network, a decentralized network of trait databases that follow open science principles (Gallagher et al., 2020).

Quantifying temporal, taxonomic, and trait-based patterns in TRAD.—We reported the number of unique trait values (intraspecific trait values), the number of sources, and the journal with the most sources for the TRAD database. We investigated whether the publication of physiological trait data has increased or decreased through time using a Mann-Kendall test, which tests for a monotonic trend in the number of unique species and trait combinations (R Core Team, 2020; McLeod, 2022). We quantify the matrix completion of the database for adult traits as a percent of the 360 trait values possible (9 traits for 40 species). To further quantify database completion, we calculated trait coverage as the number of species (maximum = 40) that had at least one value for the trait in question and trait completeness as the number of traits (maximum = 9) that had at least one value for the species in question. Total trait coverage and trait completeness are reported as a percentage, but trait-specific trait coverage and species-specific trait completeness are reported as either n species or n trait values, respectively. We report median and interquartile range (IQR) trait coverage and trait completeness for the TRAD database for adult or unknown life stages. We also report median trait coverage and trait completeness for all five life stages: eggs/embryos, tadpoles, metamorphs (intermediate life stages between tadpole and juvenile), juveniles, and adults.

We also investigated taxonomic and trait-based data gaps in thermal trait availability. We evaluated differences in rank mean trait completeness among genera and families using a Kruskal-Wallis rank sum test and Dunn's test to evaluate significant differences among groups ($\alpha = 0.05$; Dunn, 1964; Dinno, 2017). To investigate whether species' range size is correlated with trait availability, we tested whether area of occurrence was correlated with number of recorded adult trait values and trait values for all life stages for each species using a Spearman's rho correlation. We used previously calculated estimates of area of occurrence for most species (DuBose et al., 2022a, 2022b). Briefly, species' point occurrences from data repositories of museum records, survey results, and community/citizen science efforts (HerpMapper, 2019; GBIF.org, 2021a, 2021b) were filtered to remove geographically, climatically, and taxonomically uncertain points and used to identify U.S. Geological Survey (USGS) 12-digit hydrologic unit code (HUC12) watershed sub-basin boundaries that contained at least one point occurrence (U.S. Geological Survey, 2020; DuBose et al., 2022a). The areas of occupied USGS HUC12 watershed sub-basin boundaries were then summed to produce an estimate of the area of occupancy (as a proxy for range size) for each species. When no point occurrences were available for the species (i.e., Dusky Gopher Frog *Lithobates sevosus*), we substituted the IUCN extant range for point occurrences, identified USGS HUC12 sub-basin boundaries that contain the range, and summed the areas of those boundaries (International Union for Conservation of Nature, 2017). All data summarization and analyses were completed in R with the aid of R packages *googlesheets4* and *googledrive* (D'Agostino McGowan and Bryan, 2020; R Core Team, 2020; Bryan, 2021), and plots were created with *ggplot2* (Wickham, 2016).

RESULTS

In total, we found 858 reported trait values for thermal traits from 267 sources, with most sources published in *Herpetological Review* ($n = 47$). The publication of thermal trait data has been increasing since 1945 (Mann-Kendall tau = 0.4, $P <$

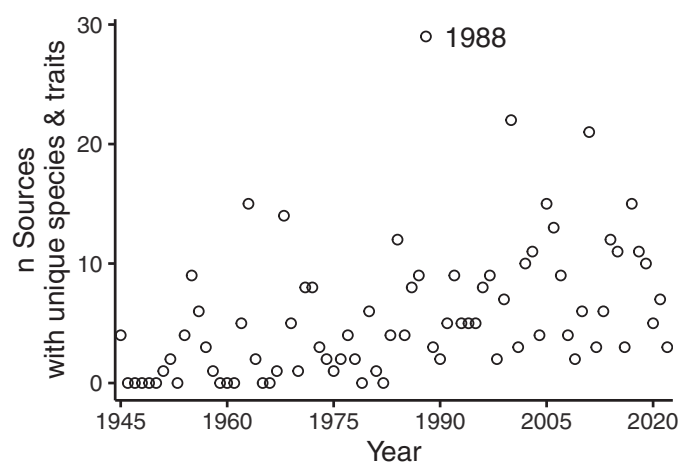


Fig. 2. Species' thermal trait data, measured as sources with unique species and trait combinations (points), have increased since 1945.

0.001; Fig. 2), with the highest amount of species trait data published in 1988 ($n = 29$). Mass estimates accounted for 40.5% of all trait values, physiological traits were 37.9% of all trait values, and behavioral trait values were 21.7% of all trait values. Methodology consistent with the top evidence category (A) accounted for 47.8% of trait values; however, most trait values for critical thermal maximum (88.9%), emergence temperature (67.5%), and basking temperature (50%) were associated with a lower evidence category (B; Table 2).

Our database had a 43.9% matrix completion, 47.5% median trait coverage, and 44% median trait completeness. For the adult life stage, traits had a median trait coverage of 19 of 40 species (IQR = 24 species). Although mass was the most reported trait value (348 trait values for 31 species), activity had the highest trait coverage, with activity estimates available for 34 species. Trait values for basking temperature were available for only three species (Green Treefrog [*Dryophytes cinereus*]; Spring Peeper [*Pseudacris crucifer*]; and Blanchard's Cricket Frog [*Acris blanchardi*]), making it the trait with the lowest trait coverage (Table 1).

The availability of trait data varied greatly between species (Fig. 1), with *Pseudacris crucifer* having the highest number of values reported in the database ($n = 37$ traits from unique sources). Across all species, the median trait completeness was four of nine traits (IQR = 2 traits). Cope's Gray Treefrog had the highest trait completeness for adults, with eight of nine traits having at least one recorded trait value. We found no trait values for three species of chorus frogs (Brimley's Chorus Frog [*Pseudacris brimleyi*]; Southern Chorus Frog [*Pseudacris nigrita*]; and Little Grass Frog [*Pseudacris ocularis*]), and we found values for only one trait for the Mountain Chorus Frog (*P. brachyphona*; emergence temperature; Fig. 1).

Adult trait values were most often reported within the literature ($n = 455$), although the life stage was not clearly stated for 74 trait values. The remaining trait values were reported for tadpoles ($n = 223$), metamorphs ($n = 52$), juveniles ($n = 31$), and eggs ($n = 23$). Sixteen species had reported trait values for the tadpole life stage, with critical thermal maximum and mass trait values being the most common (94 and 71 trait values, respectively). When considering trait completeness across all life stages, American Toad (*Anaxyrus americanus*) had the highest number ($n = 15$) of unique trait and life stage combinations.

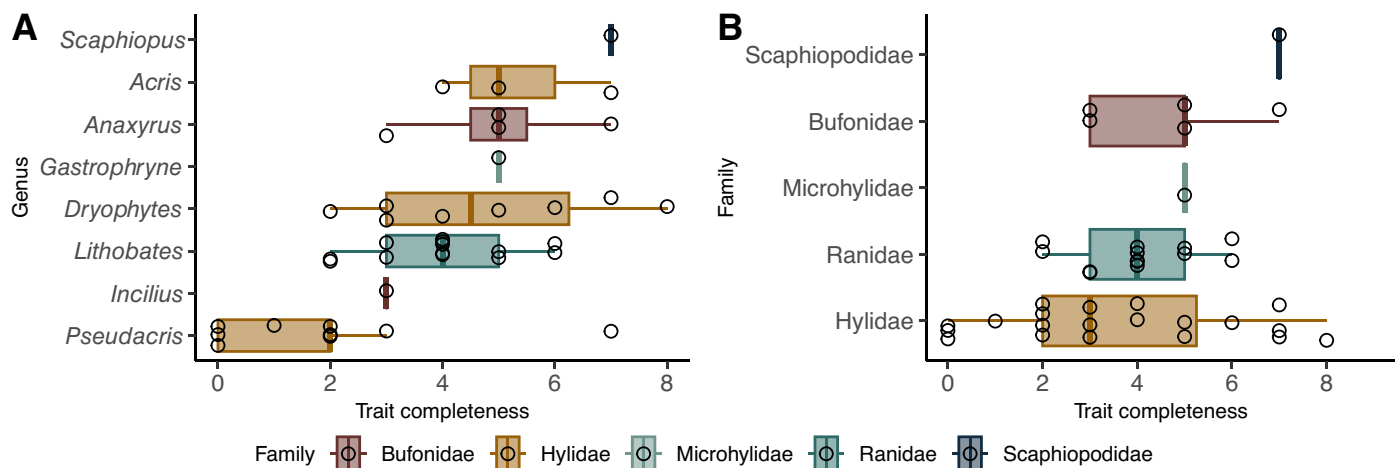


Fig. 3. Adult trait completeness, or number of traits with at least one trait value in the literature, varies among and within anuran genera (A) and families (B). Each y-axis is ordered by the group with the highest trait completion to group with the lowest trait completion. Points represent individual species. Boxplots indicate standard delineations of median, 25th, and 75th percentiles, and lines indicate the lesser of largest or smallest values or 1.5 times the interquartile range.

We found both taxonomic and trait-based differences in trait availability within TRAD. Anuran genera varied in their species' trait completeness (Kruskal-Wallis $H_7 = 14.8$, $P = 0.038$; Fig. 3). The genus *Scaphiopus*, of which only one species is within our study region (*Scaphiopus holbrookii*), had the highest trait completeness. The genus *Pseudacris* had the lowest median trait completeness (2 traits, $n = 9$ species), despite having the species with the most trait values in the database (*P. crucifer*; Fig. 2). Differences between genera's rank mean trait completion were not statistically significant ($P > 0.10$) after Bonferroni correction. Among families, Scaphiopodidae had the highest median trait completeness (7 traits, $n = 1$ species) and Hylidae had the lowest median trait completeness per species (3 traits, $n = 20$ species), but rank mean trait completeness was not statistically different among families ($H_4 = 3.8$, $P = 0.44$). Species that had higher areas of occurrence often had higher trait completeness (Fig. 4; $\rho = 0.74$, $P < 0.001$ for adults, $\rho = 0.79$, $P < 0.001$ for all life stages).

DISCUSSION

The TRAD database provides a data reservoir for thermal trait data that extends the anuran ecological trait data stored in ATraIU (Moore et al., 2021) and complements other physiological trait databases by providing information about behavioral thermoregulation traits (e.g., emergence temperature; Anderson and Wiens, 2017; Bennett et al., 2018). By compiling TRAD, we identified gaps in anuran thermal trait data, which allows researchers to optimize future data collection by targeting species and traits that are understudied. For example, basking and foraging traits could be used to investigate how temperature shifts might impact frog foraging behavior but are not available for most species. Critical thermal maximum values could be a potentially better predictor of species' mortality from increased temperature than local climatic values that also exhibit intraspecific variation (Cicchino et al., 2023). Studying the thermal traits of species of *Pseudacris* could fill in data gaps and improve estimates of the genus's thermal sensitivity. By identifying gaps in this trait database, we hope to enable researchers to balance uncertainties in scientific knowledge with costs associated with further trait collection when

investigating species thermal ecology and climate change vulnerability.

Data gaps for some species and traits might be due to different permitting needs. Field and laboratory studies require collecting permits and animal care and use (e.g., American Association for Laboratory Animal Science [IACUC]) approvals, and measurement of some thermal traits can be physiologically stressful to test animals, which is not ideal for species of conservation concern (Camacho and Rusch, 2017; Taylor et al., 2021). Some thermal traits are more difficult to collect than others: some can be estimated using agar models (Ortega-Chinchilla et al., 2022), some can be measured in the field, and others ideally are measured on laboratory-acclimated animals (Taylor et al., 2021). Therefore, alternative techniques or improvements to current techniques to reduce harm to test animals may help improve availability of trait data (Taylor et al., 2021).

When it is infeasible or unethical to measure trait values (i.e., species of conservation concern), researchers can identify surrogate species that are ecologically similar (i.e., have similar trait values) using trait dissimilarity matrices calculated from existing trait databases (Pracheil et al., 2016). Precision of trait imputation, which can also complete trait matrices with missing trait data by incorporating trait covariance among a hierarchical structure (i.e., a phylogeny or taxonomy), increases with trait data availability (Penone et al., 2014; Johnson et al., 2021). By compiling available trait data, TRAD aids future traits-based research and eases the incorporation of rare, newly described, or understudied species into comparative analyses (like species of *Pseudacris*, many of which were described in 2007 after 73% of values were already recorded [Lemmon et al., 2007]).

Trait-related and taxonomic biases are common in trait databases (González-Suárez et al., 2012; Violle et al., 2015; Etard et al., 2020) and affect the results of comparative analyses (Freckleton, 2009). For example, correlations among range size and trait data availability have potentially skewed our understanding of the relationship between species' traits and extinction risk by missing part of the trait gradient; incomplete trait data for mammals that have small ranges have potentially caused us to overestimate the negative relationship between range size and extinction risk (González-Suárez et al., 2012; Fig. 4). For anurans, species' range size and climate niche

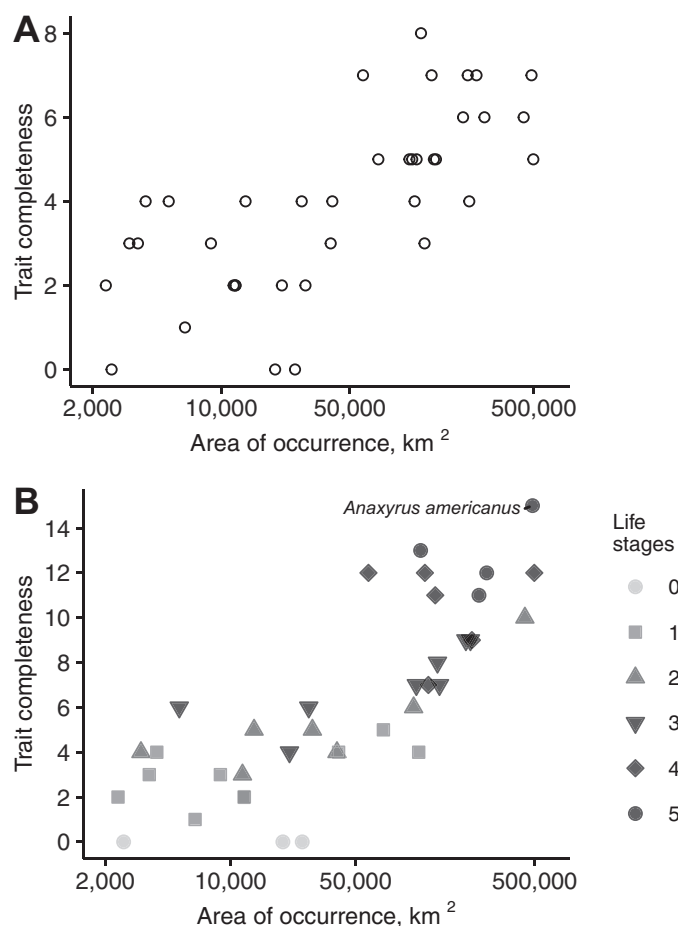


Fig. 4. The number of traits with at least one trait value in the literature (trait completeness) increases with range size for adults (A) and for all life stages (B) for 37 anurans native to the southeastern United States. Maximum trait completeness is 9 for adults and 22 for all life stages. Each point represents a species that has at least one trait value in the TRAD database, with the symbol and shade in (B) representing the total number of life stages (egg/embryo, tadpole, metamorph, juvenile, and adults) with trait data.

breadth have been used to quantify extinction risk and climate change sensitivity (Foden et al., 2013; Griffis-Kyle et al., 2018; DuBose et al., 2022a). Multi-species comparisons of climate change sensitivity based on thermal traits need to carefully consider the species inclusion criteria or how to deal with missing trait data, because species with smaller ranges or within the genera *Psuedacris* are less likely to have the trait data necessary for their inclusion in the comparison, despite a propensity for higher sensitivity to climate change (DuBose et al., 2022a).

Given climate change is altering water availability (Reid et al., 2019) and hydration affects an animal's thermoregulation (Anderson and Andrade, 2017; Bovo et al., 2018), understanding how species vary in their water conservation traits will aid in the identification of at-risk species. Although our database does not fill the critical knowledge gap in anuran water conservation trait values, TRAD can be used to identify study species for investigations on how water availability and temperature interact to impact animal fitness.

Interspecific comparisons of thermal traits can inform conservation, ecological, and evolutionary research by revealing differences among species' sensitivity to abiotic change

(Hoffmann et al., 2021), illuminating drivers of community assembly (Wong et al., 2022) and quantifying the evolutionary importance of thermal tolerance (Bennett et al., 2021). Trait databases remove a barrier to trait-based research by collating trait values from the literature and providing transparency regarding the original source and categorical methodology. By collating trait values for 9 thermal traits and 40 species, the TRAD database improves the availability of existing thermal trait data for species native to the southeastern United States. The TRAD database can be leveraged to conduct interspecific comparisons of vulnerability to temperature change, physiological niche space and limitations, and drivers of geographic range limits, among other ecological and evolutionary patterns and processes, for anurans native to the southeastern US.

DATA ACCESSIBILITY

Associated U.S. Geological Survey (USGS) data release (DuBose et al., 2023) is available at <https://doi.org/10.5066/P9HZFHSR>. Code used to compile the database files and for this manuscript is archived at <https://github.com/TraciPopejoy/AnuransMnMs/tree/main/ATraiU%202.0/code>. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

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LITERATURE CITED

- Anderson, R. C. O., and D. V. Andrade. 2017. Trading heat and hops for water: dehydration effects on locomotor performance, thermal limits, and thermoregulatory behavior of a terrestrial toad. *Ecology and Evolution* 7:9066–9075.
- Anderson, S. R., and J. J. Wiens. 2017. Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. *Evolution* 71:1944–1959.
- Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27:249–268.
- Bartelt, P. E., P. E. Thornton, and R. W. Klaver. 2022. Modelling physiological costs to assess impacts of climate change on amphibians in Yellowstone National Park, U.S. A. *Ecological Indicators* 135:108575.
- Bennett, J. M., P. Calosi, S. Clusella-Trullas, B. Martínez, J. Sunday, A. C. Algar, M. B. Araújo, B. A. Hawkins, S. Keith, I. Kühn, C. Rahbek, L. Rodríguez, A. Singer, F. Villalobos ... I. Morales-Castilla. 2018. GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Scientific Data* 5:180022.

- Bennett, J. M., J. Sunday, P. Calosi, F. Villalobos, B. Martínez, R. Molina-Venegas, M. B. Araújo, A. C. Algar, S. Clusella-Trullas, B. A. Hawkins, S. A. Keith, I. Kühn, C. Rahbek, L. Rodríguez ... M. Á. Olalla-Tárraga. 2021. The evolution of critical thermal limits of life on Earth. *Nature Communications* 12:1198.
- Bovo, R. P., C. A. Navas, M. Tejedo, S. E. S. Valença, and S. F. Gouveia. 2018. Ecophysiology of amphibians: information for best mechanistic models. *Diversity* 10:118.
- Briscoe, N. J., S. D. Morris, P. D. Mathewson, L. B. Buckley, M. Jusup, O. Levy, I. M. D. Maclean, S. Pincebourde, E. A. Riddell, J. A. Roberts, R. Schouten, M. W. Sears, and M. R. Kearney. 2022. Mechanistic forecasts of species responses to climate change: the promise of biophysical ecology. *Global Change Biology* 29:1451–1470.
- Bryan, J. 2021. googlesheets4: access google sheets using the sheets API V4. Version 1.0.0. <https://CRAN.R-project.org/package=googlesheets4>
- Buckley, L. B., A. F. Cannistra, and A. John. 2018. Leveraging organismal biology to forecast the effects of climate change. *Integrative and Comparative Biology* 58:38–51.
- Cadena, C. D., K. H. Kozak, J. P. Gómez, J. L. Parra, C. M. McCain, R. C. K. Bowie, A. C. Carnaval, C. Moritz, C. Rahbek, T. E. Roberts, N. J. Sanders, C. J. Schneider, J. VanDerWal, K. R. Zamudio, and C. H. Graham. 2012. Latitude, elevational climatic zonation and speciation in New World vertebrates. *Proceedings of the Royal Society B: Biological Sciences* 279:194–201.
- Cadotte, M., C. H. Albert, and S. C. Walker. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters* 16:1234–1244.
- Camacho, A., and T. W. Rusch. 2017. Methods and pitfalls of measuring thermal preference and tolerance in lizards. *Journal of Thermal Biology* 68:63–72.
- Chown, S. L., K. J. Gaston, and D. Robinson. 2004. Macro-physiology: large-scale patterns in physiological traits and their ecological implications. *Functional Ecology* 18:159–167.
- Cicchino, A. S., C. K. Ghalambor, and W. C. Funk. 2023. Linking critical thermal maximum to mortality from thermal stress in a cold-water frog. *Biology Letters* 19:20230106.
- D'Agostino McGowan, L., and J. Bryan. 2020. googledrive: an interface to Google Drive. Version 2.0.0. <https://CRAN.R-project.org/package=googledrive>
- Díaz-Ricaurte, J. C., F. C. Serrano, E. C. Guevara-Molina, C. Araújo, and M. Martins. 2020. Does behavioral thermal tolerance predict distribution pattern and habitat use in two sympatric Neotropical frogs? *PLoS ONE* 15:e0239485.
- Dinno, A. 2017. dunn.test: Dunn's test of multiple comparisons using rank sums. Version 1.3.5. <https://CRAN.R-project.org/package=dunn.test>
- DuBose, T. P., V. Catalan, C. E. Moore, V. R. Farallo, A. L. Benson, J. L. Dade, W. A. Hopkins, and M. C. Mims. 2023. TRAD: thermal traits of anurans database for the Southeastern United States. U.S. Geological Survey data release. DOI: <https://doi.org/10.5066/P9HZFHRS>
- DuBose, T. P., C. E. Moore, S. Silknetter, A. L. Benson, T. Alexander, G. O'Malley, and M. C. Mims. 2022a. Mismatch between conservation status and climate change sensitivity leaves some anurans in the United States unprotected. *Biological Conservation* 277:109866.
- DuBose, T. P., C. E. Moore, S. Silknetter, A. L. Benson, T. Alexander, G. O'Malley, and M. C. Mims. 2022b. Rarity and climate sensitivity index and components of 90 species of frogs and toads native to the conterminous United States. U.S. Geological Survey data release. DOI: <https://doi.org/10.5066/P9U56Z7W>
- Dunn, O. J. 1964. Multiple comparisons using rank sums. *Technometrics* 6:241–252.
- Etard, A., S. Morrill, and T. Newbold. 2020. Global gaps in trait data for terrestrial vertebrates. *Global Ecology and Biogeography* 29:2143–2158.
- Farley, S. S., A. Dawson, S. J. Goring, and J. W. Williams. 2018. Situating ecology as a big-data science: current advances, challenges, and solutions. *BioScience* 68:563–576.
- Foden, W. B., S. H. M. Butchart, S. N. Stuart, J.-C. Vié, H. R. Akçakaya, A. Angulo, L. M. DeVantier, A. Gutsche, E. Turak, L. Cao, S. D. Donner, V. Katariya, R. Bernard, R. A. Holland ... G. M. Mace. 2013. Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PLoS ONE* 8:e65427.
- Foden, W. B., B. E. Young, H. R. Akçakaya, R. A. Garcia, A. A. Hoffmann, B. A. Stein, C. D. Thomas, C. J. Wheatley, D. Bickford, J. A. Carr, D. G. Hole, T. G. Martin, M. Pacifici, J. W. Pearce-Higgins ... B. Huntley. 2019. Climate change vulnerability assessment of species. *WIREs Climate Change* 10:e551.
- Freckleton, R. P. 2009. The seven deadly sins of comparative analysis. *Journal of Evolutionary Biology* 22:1367–1375.
- Freed, A. N. 1980. An adaptive advantage of basking behavior in an anuran amphibian. *Physiological Zoology* 53:433–444.
- Gallagher, R. V., D. S. Falster, B. S. Maitner, R. Salguero-Gomez, V. Vandvik, W. D. Pearse, F. D. Schneider, J. Kattge, J. H. Poelen, J. S. Madin, M. J. Ankenbrand, C. Penone, X. Feng, V. M. Adams ... B. J. Enquist. 2020. Open science principles for accelerating trait-based science across the tree of life. *Nature Ecology & Evolution* 4:294–303.
- Gamble, T., P. B. Berendzen, H. B. Shaffer, D. E. Starkey, and A. M. Simons. 2008. Species limits and phylogeography of North American cricket frogs (*Acris*: Hylidae). *Molecular Phylogenetics and Evolution* 48:112–125.
- GBIF Secretariat. 2019. GBIF Backbone Taxonomy Checklist dataset.
- GBIF.org. 2021a. GBIF Occurrence Download. DOI: <https://doi.org/10.15468/dl.urd7d5>
- GBIF.org. 2021b. GBIF Occurrence Download. DOI: <https://doi.org/10.15468/dl.bd4w8b>
- González-Suárez, M., P. M. Lucas, and E. Revilla. 2012. Biases in comparative analyses of extinction risk: mind the gap. *Journal of Animal Ecology* 81:1211–1222.
- Google Scholar. 2022. Google Scholar. <https://scholar.google.com> (accessed 5 July 2022).
- Grant, E. H. C., D. A. W. Miller, B. R. Schmidt, M. J. Adams, S. M. Amburgey, T. Chambert, S. S. Cruickshank, R. N. Fisher, D. M. Green, B. R. Hossack, P. T. J. Johnson, M. B. Joseph, T. A. G. Rittenhouse, M. E. Ryan ... E. Muths. 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Scientific Reports* 6: 25625.
- Green, T., E. Das, and D. M. Green. 2016. Springtime emergence of overwintering toads, *Anaxyrus fowleri*, in relation to environmental factors. *Copeia* 104:393–401.
- Griffis-Kyle, K. L. 2016. Physiology and ecology to inform climate adaptation strategies for desert amphibians. *Herpetological Conservation and Biology* 11:563–582.

- Griffis-Kyle, K. L., K. Mougey, M. Vanlandeghem, S. Swain, and J. C. Drake. 2018. Comparison of climate vulnerability among desert herpetofauna. *Biological Conservation* 225:164–175.
- Herpetological Review. 2017. *Herpetological Review* issues from 1967 to 2017, all open access complete editions. <https://ssarherps.org/publications/herpetological-review/>
- HerpMapper. 2019. HerpMapper—a global herp atlas and data hub. <https://www.herpMapper.org> (accessed 01 December 2019).
- Hoffmann, E. P., K. L. Cavanough, and N. J. Mitchell. 2021. Low desiccation and thermal tolerance constrains a terrestrial amphibian to a rare and disappearing microclimate niche. *Conservation Physiology* 9:coab027.
- Huey, R. B., M. R. Kearney, A. Krockenberger, J. A. M. Holtum, M. Jess, and S. E. Williams. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:1665–1679.
- Hutchison, V. H., and R. K. Dupré. 1992. Thermoregulation, p. 206–249. *In: Environmental Physiology of the Amphibians*. M. E. Feder and W. W. Burggren (eds.). University of Chicago Press, Chicago.
- International Union for Conservation of Nature. 2017. The IUCN Red List of Threatened Species version 3. <https://www.iucnredlist.org> (accessed 08 July 2020).
- ITIS. 2021. Integrated Taxonomic Information System. <https://www.itis.gov/> (accessed 01 December 2022).
- Johnson, T. F., N. J. B. Isaac, A. Paviolo, and M. González-Suárez. 2021. Handling missing values in trait data. *Global Ecology and Biogeography* 30:51–62.
- Kearney, M. R., and W. P. Porter. 2020. NicheMapR—an R package for biophysical modelling: the ectotherm and dynamic energy budget models. *Ecography* 43:85–96.
- Kearney, M. R., W. P. Porter, and R. B. Huey. 2021. Modelling the joint effects of body size and microclimate on heat budgets and foraging opportunities of ectotherms. *Methods in Ecology and Evolution* 12:458–467.
- Lemmon, E. M., A. R. Lemmon, J. T. Collins, J. A. Lee-Yaw, and D. C. Cannatella. 2007. Phylogeny-based delimitation of species boundaries and contact zones in the trilling chorus frogs (*Pseudacris*). *Molecular Phylogenetics and Evolution* 44:1068–1082.
- Lertzman-Lepofsky, G. F., A. M. Kissel, B. Sinervo, and W. J. Palen. 2020. Water loss and temperature interact to compound amphibian vulnerability to climate change. *Global Change Biology* 26:4868–4879.
- Levy, O., T. Dayan, W. P. Porter, and N. Kronfeld-Schor. 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecological Monographs* 89:e01334.
- Lutterschmidt, W. I., and V. H. Hutchison. 1997. The critical thermal maximum: history and critique. *Canadian Journal of Zoology* 75:1561–1574.
- Martini, S., F. Larras, A. Boyé, E. Faure, N. Aberle, P. Archambault, L. Bacouillard, B. E. Beisner, L. Bittner, E. Castella, M. Danger, O. Gauthier, L. Karp-Boss, F. Lombard ... S.-D. Ayata. 2021. Functional trait-based approaches as a common framework for aquatic ecologists. *Limnology and Oceanography* 66:965–994.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21:178–185.
- McLeod, A. I. 2022. Kendall: Kendall rank correlation and Mann-Kendall trend test. Version 2.2.1. <https://CRAN.R-project.org/package=Kendall>
- Mims, M. C., and J. D. Olden. 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biology* 58:50–62.
- Moore, C. E., J. S. Helmann, Y. Chen, S. M. St. Amour, M. A. Hallmark, L. E. Hughes, N. Wax, and M. C. Mims. 2021. Anuran traits of the United States (ATraIU): a database for anuran traits-based conservation, management, and research. *Ecology* 102:e03261.
- Moreira, M. O., Y.-F. Qu, and J. J. Wiens. 2021. Large-scale evolution of body temperatures in land vertebrates. *Evolution Letters* 5:484–494.
- Morley, S. A., L. S. Peck, J. M. Sunday, S. Heiser, and A. E. Bates. 2019. Physiological acclimation and persistence of ectothermic species under extreme heat events. *Global Ecology and Biogeography* 28:1018–1037.
- Muths, E., and P. S. Corn. 1997. Basking by adult boreal toads (*Bufo boreas boreas*) during the breeding season. *Journal of Herpetology* 31:426–428.
- Navas, C. A., F. R. Gomes, and E. A. D. Domenico. 2016. Physiological ecology and conservation of anuran amphibians, p. 155–188. *In: Amphibian and Reptile Adaptations to the Environment: Interplay between Physiology and Behavior*. D. V. de Andrade, C. R. Bevier, and J. E. de Carvalho (eds.). CRC Press, Boca Raton, Florida.
- Navas, C. A., S. F. Gouveia, J. J. Solano-Iguarán, M. A. Vidal, and L. D. Bacigalupe. 2021. Amphibian responses in experimental thermal gradients: concepts and limits for inference. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 254:110576.
- Noss, R. F., W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, and R. K. Peet. 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Diversity and Distributions* 21:236–244.
- Olalla-Tárraga, M. Á., and M. Á. Rodríguez. 2007. Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. *Global Ecology and Biogeography* 16: 606–617.
- Oliveira, B. F., V. A. São-Pedro, G. Santos-Barrera, C. Penone, and G. C. Costa. 2017. AmphiBIO, a global database for amphibian ecological traits. *Science Data* 4:170123.
- Ortega-Chinchilla, J. E., L. C. Cabanzo-Olarte, R. Vaz, F. Lamadrid-Feris, C. R. Bevier, and C. A. Navas. 2022. Behavioral models of hydrothermal regulation in anurans: a field study in the Atlantic Forest, Brazil. *Biotropica* 55:329–338.
- Ospina, O. E., L. Tieu, J. J. Apodaca, and E. M. Lemmon. 2020. Hidden diversity in the mountain chorus frog (*Pseudacris brachyphona*) and the diagnosis of a new species of chorus frog in the southeastern United States. *Copeia* 108:778–795.
- Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R. Scheffers, D. G. Hole, T. G. Martin, H. R. Akçakaya, R. T. Corlett, B. Huntly, D. Bickford, J. A. Carr ... C. Rondinini. 2015. Assessing species vulnerability to climate change. *Nature Climate Change* 5:215–224.
- Penone, C., A. D. Davidson, K. T. Shoemaker, M. Di Marco, C. Rondinini, T. M. Brooks, B. E. Young, C. H. Graham, and G. C. Costa. 2014. Imputation of missing

- data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution* 5:961–970.
- Peterman, W. E., and M. Gade.** 2017. The importance of assessing parameter sensitivity when using biophysical models: a case study using plethodontid salamanders. *Population Ecology* 59:275–286.
- Pinder, A. W., K. B. Storey, and G. R. Ultsch.** 1992. Estivation and hibernation, p. 250–274. *In: Environmental Physiology of the Amphibians*. University of Chicago Press, Chicago.
- Pottier, P., H. Lin, R. R. Y. Oh, P. Pollo, A. N. Rivera-Villanueva, J. O. Valdebenito, Y. Yang, T. Amano, S. Burke, S. M. Drobniak, and S. Nakagawa.** 2022. A comprehensive database of amphibian heat tolerance. *Scientific Data* 9:600.
- Pracheil, B., R. McManamay, M. Bevelhimer, C. DeRolph, and G. Čada.** 2016. A traits-based approach for prioritizing species for monitoring and surrogacy selection. *Endangered Species Research* 31:243–258.
- Putnam, R. W., and A. F. Bennett.** 1981. Thermal dependence of behavioural performance of anuran amphibians. *Animal Behaviour* 29:502–509.
- R Core Team.** 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Version 4.1.1. <https://www.R-project.org/>
- Reid, A. J., A. K. Carlson, I. F. Creed, E. J. Eliason, P. A. Gell, P. T. J. Johnson, K. A. Kidd, T. J. MacCormack, J. D. Olden, S. J. Ormerod, J. P. Smol, W. W. Taylor, K. Tockner, J. C. Vermaire ... S. J. Cooke.** 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews* 94:849–873.
- Rohatgi, A.** 2021. WebPlotDigitizer. Version 4.5. <https://automeris.io/WebPlotDigitizer> (accessed 05 July 2022).
- Rome, L. C., E. D. Stevens, and H. B. John-Alder.** 1992. The influence of temperature and thermal acclimation on physiological function, p. 183–205. *In: Environmental Physiology of the Amphibians*. M. E. Feder and W. W. Burggren (eds.). University of Chicago Press, Chicago.
- Sheridan, J. A., N. M. Caruso, J. J. Apodaca, and L. J. Rissler.** 2018. Shifts in frog size and phenology: testing predictions of climate change on a widespread anuran using data from prior to rapid climate warming. *Ecology and Evolution* 8:1316–1327.
- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller.** 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- Taylor, E. N., L. M. Diele-Viegas, E. J. Gangloff, J. M. Hall, B. Halpern, M. D. Massey, D. Rödder, N. Rollinson, S. Spears, B. Sun, and R. S. Telemeco.** 2021. The thermal ecology and physiology of reptiles and amphibians: a user's guide. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 335:13–44.
- Teske, P. R., J. Sandoval-Castillo, T. R. Golla, A. Emami-Khoyi, M. Tine, S. von der Heyden, and L. B. Beheregaray.** 2019. Thermal selection as a driver of marine ecological speciation. *Proceedings of the Royal Society B: Biological Sciences* 286:20182023.
- Tyler, E. H. M., P. J. Somerfield, E. V. Berghe, J. Bremner, E. Jackson, O. Langmead, M. L. D. Palomares, and T. J. Webb.** 2012. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. *Global Ecology and Biogeography* 21:922–934.
- U.S. Geological Survey.** 2020. National Watershed Boundary Dataset (ver. USGS National Watershed Boundary Dataset in FileGDB 10.1 format (published 20200701). <https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products> (accessed 14 July 2020).
- Violle, C., B. Borge, and P. Choler.** 2015. Trait databases: misuses and precautions. *Journal of Vegetation Science* 26:826–827.
- Web of Science.** 2022. Web of Science Core Collection. May 26, 2022 release. <https://webofscience.help.clarivate.com/Content/wos-core-collection/wos-core-collection.htm> (accessed 5 July 2022).
- Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff.** 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* 13:267–283.
- Wells, K. D.** 2010. *The Ecology and Behavior of Amphibians*. University of Chicago Press, Chicago.
- Wickham, H.** 2016. ggplot2: elegant graphics for data analysis. Version 3.3.5. <https://ggplot2.tidyverse.org>
- Williams, S. E., L. P. Shoo, J. L. Isaac, A. A. Hoffmann, and G. Langham.** 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology* 6:e325.
- Wong, M. K. L., R. H. Lee, C.-M. Leong, O. T. Lewis, and B. Guénard.** 2022. Trait-mediated competition drives an ant invasion and alters functional diversity. *Proceedings of the Royal Society B: Biological Sciences* 289:20220504.