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Body Size Is Related to Temperature Preference in *Hyla chrysoscelis* Tadpoles

DANIELLE R. KIRSCH,[1,2,5] SHAWNA FIX,[1] JON M. DAVENPORT,[3] KRISTEN K. CECALA,[4] AND JOSHUA R. ENNEN[1]

[1] *Tennessee Aquarium Conservation Institute, 175 Baylor School Road, Chattanooga, Tennessee, 37405, USA*
[2] *Department of Integrative Biology, Oklahoma State University, 501 Life Sciences West, Stillwater, Oklahoma, 74078, USA*
[3] *Department of Biology, Appalachian State University, 572 Rivers Street, Boone, North Carolina, 28607, USA*
[4] *Department of Biology, Sewanee: The University of the South, 735 University Avenue, Sewanee, Tennessee, 37375, USA*

ABSTRACT.—**Temperature plays a critical role in growth and development of anurans. Here, we investigated thermal preference of tadpoles from a wide-ranging anuran, *Hyla chrysoscelis*, by establishing an *ex situ* thermal gradient in a laboratory setting. We collected 64 tadpoles with a mean (±SD) body length of 12.2 ± 2.1 mm (range, 7–15 mm). Mean temperature preference of tadpoles ranged from 12.9 to 30.0°C, and we found a positive relationship between temperature preference and body length. Although body length is only one component of amphibian development, its apparent link with temperature preference is an exciting area for further research in this species as well as other species. Furthermore, given the broad distribution of *H. chrysoscelis*, there is an opportunity to investigate how thermal preferences could limit population edges and how populations may respond to shifts in environmental temperatures.**

Many organisms have adapted successfully to long-term temperature fluctuations, but when temperatures shift quickly, these same organisms often rely instead on behavioral responses as a means of acclimation. For aquatic ectotherms, conduction and convection with the surrounding water are the primary means by which they manipulate their body temperature (Reynolds and Casterlin, 1979). They are capable of moving through their environment to select areas in the water with the most optimal temperature (Hutchison and Dupré, 1992). However, temperature fluctuations tend to be rather minimal in aquatic environments because of water's high specific heat, thereby limiting the range of temperatures these organisms can realistically access (Hillman et al., 2009). This limitation in aquatic thermal range is important given that body temperatures for aquatic ectotherms rarely differ from the surrounding water by more than 2°C (Spotila et al., 1992). Understanding the temperatures that individuals select at different times in life can help illuminate their thermal needs at a particular age or developmental stage as well as how those needs may be impacted by rapidly shifting global temperatures. Improved knowledge of temperature selection shifts throughout ontogeny can also increase the accuracy and utility of species distribution models, as survivability can vary with body size (Riddell et al., 2018; Gouveia et al., 2019).

Temperature preference is of particular interest to species with complex life histories, such as amphibians and aquatic insects. Temperature preference for some anuran species can shift as tadpoles progress through development, with individuals in later developmental stages showing preference for warmer temperatures than those at earlier stages (Floyd, 1984; Dupré and Petranka, 1985). For example, both *Rana* (*Lithobates*) *catesbeiana* and *Rhinella marina* tadpoles exhibit a preference for higher temperatures at later developmental stages (Hutchison and Hill, 1978; Floyd, 1984; Dupré et al., 1986). *Pseudacris triseriata* tadpoles do not show distinct temperature preferences earlier in development, but from stage 36 onward, they show a preference for warmer temperatures (Dupré and Petranka, 1985). However, there are some species of anurans—for example, *Rana boylii*—that exhibit no difference in temperature selection at the various life-history stages (Catenazzi and Kupferberg, 2013).

Larval amphibians, in general, balance growth and metamorphosis, depending on a variety of environmental conditions, by using the release of particular hormones to stimulate and inhibit responses (Wilbur and Collins, 1973; Werner, 1986; Hillman et al., 2009). In addition, *Rana arvalis* tadpoles exposed to increased temperatures demonstrated shorter larval periods and larger masses at metamorphosis (Richter-Boix et al., 2015), providing evidence that temperature can interact with other drivers, such as hormones, to alter the rate of growth, metamorphosis, or both. In tadpoles, selection of lower temperatures typically leads to a slower rate of development (Smith-Gill and Berven, 1979), likely the result of decreased metabolism, whereas selection of higher temperatures has been shown to increase growth and developmental rate (Hutchison and Hill, 1978; Wu et al., 2007). The ability for tadpoles to influence their developmental rate is critical for survival, especially to escape stressors, such as predation and pond drying (Wilbur, 1997). In addition, swimming performance increases with temperature in *Limnodynastes peronii* tadpoles (Niehaus et al., 2011), so the selection for higher temperatures could also maximize the ability of tadpoles to escape predation with improved locomotor performance.

Here, we address the temperature preference of tadpoles of a broadly distributed anuran species, *Hyla chrysoscelis* (Cope, 1880) (Cope's Gray Treefrog). We hypothesized that temperature preference would increase for *H. chrysoscelis* tadpoles at larger body sizes to maximize the rate of metamorphosis and emergence as metamorphs, a trend similar to that seen in other North American anurans (Hutchison and Hill, 1978; Floyd, 1984; Dupré and Petranka, 1985; Dupré et al., 1986).

MATERIALS AND METHODS

Study Site and Focal Species.—The distribution of *H. chrysoscelis* extends from the coastal plain of the southeastern United States northward through the most of the midwestern and northeastern states on into Canada (Cline, 2005). *H. chrysoscelis* typically breeds between April and July, depending on the location (Cline, 2005). Individual clutches contain 30–45 eggs, and the larval

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[5] Corresponding author. E-mail: danielle.kirsch@okstate.edu

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period (egg to metamorphosis) is usually 45–65 d, which depends upon the thermal regime of the location (Cline, 2005; Mitchell and Pague, 2014). We collected *H. chrysoscelis* tadpoles at various development stages on 4–5 June 2018 ($n = 48$) and 10 July 2018 ($n = 16$). We collected all individuals from an artificial wetland and concrete retention pool at the Tennessee Aquarium Conservation Institute (TNACI), Chattanooga, Tennessee (35°04′29″N, −85°20′13″W). We did not collect water quality or temperature data of the collection site. TNACI is located in the temperate zone of the ridge and valley physiographic province in Tennessee. The site is adjacent to the impounded Tennessee River (Nickajack Reservoir) at an elevation of 200 m a.s.l. Once collected, all individuals acclimated to room temperature (22.8°C) in a laboratory at TNACI for a minimum of 1 h, and we recorded body length (in millimeters) and wet mass (in grams). Tadpoles were measured for length by using a ruler attached to the inside of a plastic container (118 ml [16 oz]). This container held enough water to cover the ruler and individual tadpoles, which minimized tadpole time spent out of the water. Next, the tadpoles were blotted dry before recording their mass. The entire measurement process used standardized approaches so that handling was minimal and consistent between all individuals, lasting ∼1–2 min per tadpole from start to finish. To our knowledge, no individuals were adversely affected by the measurement process.

Temperature Preference Experiment.—We set up a temperature preference trial following Strickland et al. (2016). Sixteen aluminum rain gutters (150 cm × 10 cm) were arranged around a blind that was used to minimize behavioral disturbance of tadpoles caused by the presence of the observer. Each trough was situated with the lengthwise dimension perpendicular to the blind so that the observer could see the entire water space and tadpole. We filled each gutter with 2 cm of refrigerated, dechlorinated water. Water depths of maximum 2.5 cm have been used to reduce convection in similar experimental setups (Herreid and Kinney, 1967). We created a horizontal thermal gradient by placing one end of each gutter on a hot plate (low temperature setting) and the other end on ice. The hot plate was situated near the blind, whereas the ice bath was situated at the far end. In addition, we placed a handful of ice in the cold end of each gutter to speed up the cooling process and removed it before tadpole placement in the gutters. Because we only had 16 gutters, we conducted four separate trials and gave the individual trials a unique identifier (i.e., trial number). We conducted several of these trials on different dates. At the start of trials, the thermal gradient (mean ± SD) was from 13.2 ± 4.0°C to 25.9 ± 3.1°C at each extreme. At the end of trials, the thermal gradient was from 17.7 ± 1.8°C to 28.6 ± 3.3°C. Trials were conducted between 1000 and 1600 h on each given day.

We placed one tadpole in the center of each trough and allowed 15 min of acclimation before starting the trial. Temperature readings were taken every 15 min for 1 h by using an infrared thermometer (LaserGrip 774, Etekcity) for a total of four temperature readings per individual. Although distance from the target can affect infrared thermometer accuracy, we tested our thermometer and noted that temperature readings from 20 to 164 cm away differed on average by 0.1°C, which we deemed an adequate level of accuracy because the resolution of the thermometer was 0.1°C. Each temperature reading was collected at the body of the tadpole to provide an accurate reading of the temperature selected by the tadpole at that point in time. After the completion of each trial, we returned tadpoles to the artificial wetland surrounding the retention pool to ensure we did not recapture and test the same individual multiple times. All descriptive statistics represent means and SDs.

Analyses.—We used a linear mixed-effects model (package lme4; Bates et al., 2015) to analyze the relationship between tadpole body length and temperature preference. Given that body length and tadpole mass were correlated ($r^2 = 0.834$; $F_{1,62} = 312.32$, $P < 0.001$), we only analyzed body length as an explanatory variable, rather than both body length and mass. We averaged the four recorded temperatures for each individual to calculate their average temperature preference during the trial. Because all gutters were not oriented in the same direction with respect to the room, and not all trials were conducted on the same day, we wanted to control for the possibility that gutter orientation or trial date affected tadpole behavior. For these reasons, the gutter and trial date were tested in as well as the date a trial was conducted were included as random effects. We tested the residuals of the linear model with a Shapiro–Wilks test to ensure we met assumptions of normality. We used Satterthwaite's method, applied using the package lmerTest (Kuznetsova et al., 2017), to calculate df and p values for our model. We calculated conditional r^2 for our model using the function *rsquared* from the R package piecewiseSEM (Nakagawa and Schielzeth, 2013; Lefcheck, 2016). All analyses were conducted in R software (R Core Team, 2018). Raw data can be found in Appendix 1.

RESULTS

The body length of tadpoles was 12.2 ± 2.1 mm (range, 7–15 mm). Tadpoles had average temperature selections ranging from 12.9 to 30.0°C. Our model explained 13.05% of the variance, and we found a significant, positive relationship ($F_{1,62} = 9.454$, $P = 0.0031$, $\beta = 1.0606 \pm 0.3449$ [mean ± SE]) between body length and mean temperature preference (Fig. 1).

DISCUSSION

Temperature plays an integral role in anuran life cycles, wherein it can influence both metabolic (Wu et al., 2007) and developmental (Smith-Gill and Berven, 1979; Goldstein et al., 2017) rates, which contribute to the maturation of tadpoles into adults. Our study demonstrates that preferred temperature increases as body size increases in *H. chrysoscelis* tadpoles. This pattern is similar to that found in several other anuran tadpoles (Hutchison and Hill, 1978; Floyd, 1984; Dupré and Petranka, 1985; Dupré et al., 1986).

There are two main hypotheses to explain the positive relationship between tadpole body size and temperature preference: (1) escape from environmental pressures and (2) escape from ecological pressures. Seeking out warmer temperatures later in development could be an attempt to increase the rate of development, as tadpoles at later stages of development are in a more vulnerable state (Dupré and Petranka, 1985). From an environmental perspective, this vulnerability is often the result of environmental factors, such as pond drying (Wellborn et al., 1996; Wilbur, 1997), that will lead to mortality if tadpoles cannot escape the deteriorating environment in time. Selecting warmer temperatures generally increases the rate at which development proceeds, thus enabling tadpoles to emerge from their aquatic habitats to avoid desiccation (Newman, 1992).

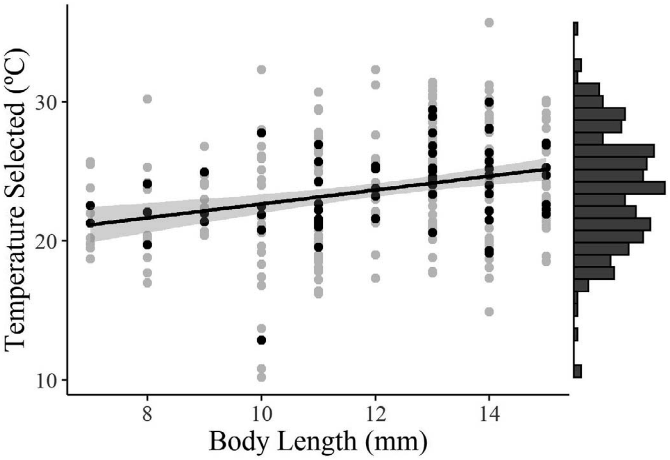

FIG. 1. Positive relationship between average temperature selected (Celsius) by individual *H. chrysoscelis* tadpoles and their body length (conditional $r^2 = 0.1305$, $F_{1,62} = 9.454$, $P = 0.0031$, $\beta = 1.0606 \pm 0.3449$ [mean ± SE]). Gray represents individual temperature measurements, and black represents average temperature selection calculations for each individual. The regression line is shown with a 95% confidence interval. The histogram on the right margin shows the frequency with which tadpoles selected different temperatures.

In an ecological sense, increased temperatures can also enable tadpoles to escape ecological pressures, such as predation and competition. Selection of warmer temperatures may decrease the threat of predation by either increasing locomotion of the tadpoles (Niehaus et al., 2011) or by enabling them to metamorphose and leave the pond sooner (Wilbur, 1997). Dupré and Petranka (1985) discuss that the correlation between thermal preference and body size of tadpoles might also spatially segregate size classes and minimize competition and cannibalism in aquatic habitats, although cannibalism is not known in *H. chrysoscelis*. Differences in thermal preference may even contribute to interspecific niche partitioning, allowing multiple species to coexist in a given habitat by exploiting different temperature regimes.

Although our study demonstrates a relationship between preferred temperature and body size in *H. chrysoscelis* tadpoles, it is narrow in scale as it focuses on a single population in the southern third of its North American range. The tadpoles used in our study were from an artificial wetland and retention pond, which might not mimic a natural thermal regime. Temperature preferences may vary among anuran populations due to local thermal adaptations (Drakulić et al., 2017). Therefore, our results might represent a local thermal adaptation to artificial habitats that might differ if compared with thermal preferences of tadpoles from natural habitats. Because of its cosmopolitan distribution in North America, temperature preference of *H. chrysoscelis* could vary considerably among populations depending on local climates, and future studies should investigate temperature preference of *H. chrysoscelis* at a larger scale.

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Appendix 1. Raw data for temperature preference experiment. Column titles correspond to tadpole ID (ID), gutter ID (Trough), date (Date) and time (Time) trial was conducted, trial number (Trial), body length in millimeters (BL), mass in grams (Mass), first recorded temperature in Celsius (T1), second recorded temperature (T2), third recorded temperature (T3), final recorded temperature (T4), and calculated average temperature (Avg temp).

ID	Trough	Date	Time	Trial	BL	Mass	T1	T2	T3	T4	Avg temp
1	A1	2018-06-04	10:05	1	11	0.49	25.5	24.9	26.6	30.7	26.925
2	D4	2018-06-04	10:05	1	15	1.15	23.2	23	23.9	18.9	22.25
3	C1	2018-06-04	10:05	1	12	0.6	31.2	19	17.3	27.6	23.775
4	D2	2018-06-04	10:05	1	15	1	30.1	23.9	24.9	29.2	27.025
5	A2	2018-06-04	10:05	1	13	0.68	21.9	20.7	24.4	29.4	24.1
6	A3	2018-06-04	10:05	1	15	0.98	21.7	21.1	22.3	22.6	21.925
7	B3	2018-06-04	10:05	1	14	0.88	19.7	26	17.3	25.6	22.15
8	C3	2018-06-04	10:05	1	10	0.44	16.8	10.2	10.8	13.7	12.875
9	D3	2018-06-04	10:05	1	13	0.87	28.5	23.5	24.1	24	25.025
10	C4	2018-06-04	10:05	1	11	0.73	20.2	20.4	19.8	17.8	19.55
11	A4	2018-06-04	10:05	1	12	0.74	21.3	21.4	21.6	22.1	21.6
12	C2	2018-06-04	10:05	1	14	1	28.7	24.9	26.6	18.7	24.725
13	B2	2018-06-04	10:05	1	9	0.31	20.4	20.5	24.1	20.5	21.375
14	D1	2018-06-04	10:05	1	13	0.68	31.1	28.5	30.3	21.2	27.775
15	B4	2018-06-04	10:05	1	12	0.55	24.2	23	22	32.3	25.375
16	B1	2018-06-04	10:05	1	13	0.8	22.5	17.8	26.7	26.4	23.35
17	B2	2018-06-04	14:55	2	14	0.75	19.2	19.2	18.1	20	19.125
18	C1	2018-06-04	14:55	2	15	1	29.9	28.7	28.1	20.9	26.9
19	C4	2018-06-04	14:55	2	13	0.59	20.1	20.7	20.7	20.9	20.6
20	A1	2018-06-04	14:55	2	13	0.68	23	23	25.8	24.3	24.025
21	D2	2018-06-04	14:55	2	12	0.56	21.6	22.1	23.5	25.7	23.225
22	D3	2018-06-04	14:55	2	15	0.94	22.9	23.1	22.7	21.7	22.6
23	C2	2018-06-04	14:55	2	13	0.78	29.8	28.5	21.4	17.7	24.35
24	B4	2018-06-04	14:55	2	14	0.67	27.9	26.6	28.8	28.8	28.025
25	A4	2018-06-04	14:55	2	12	0.51	25.2	24.2	25.9	25.4	25.175
26	C3	2018-06-04	14:55	2	14	0.8	31.2	23.3	29.7	35.7	29.975
27	D1	2018-06-04	14:55	2	14	0.68	23.6	23.9	24.2	29.1	25.2
28	D4	2018-06-04	14:55	2	13	0.71	21.1	25.6	25.7	28.1	25.125
29	A2	2018-06-04	14:55	2	14	0.65	25.2	30.2	22.2	27.8	26.35
30	A3	2018-06-04	14:55	2	11	0.53	20.8	21.5	21.3	20.9	21.125
31	B3	2018-06-04	14:55	2	14	0.9	23.7	23.8	24	24.5	24
32	B1	2018-06-04	14:55	2	11	0.45	20.9	24.9	24.9	26.3	24.25
33	A3	2018-06-05	14:55	3	13	0.74	26.8	26.6	24.7	27.1	26.3
34	D4	2018-06-05	14:55	3	14	0.63	18.1	19.1	19.7	20.2	19.275
35	B2	2018-06-05	14:55	3	14	0.64	24.5	25.9	26.4	26.1	25.725
36	D3	2018-06-05	14:55	3	14	0.86	23	25	24.6	20.9	23.375
37	C1	2018-06-05	14:55	3	13	0.72	28.5	29.2	29.5	30.5	29.425
38	C2	2018-06-05	14:55	3	15	0.91	26.9	26.4	18.5	27	24.7
39	A1	2018-06-05	14:55	3	13	0.64	24.8	22.5	26.4	23.3	24.25
40	B3	2018-06-05	14:55	3	14	0.75	25.2	28.5	28.8	29.9	28.1
41	A4	2018-06-05	14:55	3	15	0.82	24.2	21.4	26.6	28.8	25.25
42	D2	2018-06-05	14:55	3	10	0.35	19.6	20.6	21.2	21.7	20.775
43	B1	2018-06-05	14:55	3	14	0.82	19.4	14.9	20.9	30.8	21.5
44	A2	2018-06-05	14:55	3	13	0.81	26.4	25.4	28.1	27.4	26.825
45	C3	2018-06-05	14:55	3	13	0.7	25.2	23.5	23.1	26.5	24.575
46	B4	2018-06-05	14:55	3	9	0.24	20.7	21.9	22.4	23	22
47	C4	2018-06-05	14:55	3	13	0.71	27.3	18.8	26.7	28.1	25.225
48	D1	2018-07-10	13:25	3	13	0.52	28.8	24.7	31.4	30.8	28.925
49	B2	2018-07-10	13:25	4	8	0.11	23.9	17	17.7	20.2	19.7
50	D1	2018-07-10	13:25	4	7	0.09	22	23.8	19.8	19.5	21.275
51	A4	2018-07-10	13:25	4	8	0.14	30.2	25.3	18.8	22.1	24.1
52	B1	2018-07-10	13:25	4	9	0.18	24.7	24.2	26.8	24	24.925
53	C3	2018-07-10	13:25	4	7	0.1	20.2	18.7	25.5	25.7	22.525
54	B4	2018-07-10	13:25	4	11	0.3	29.5	18.7	16.2	19.7	21.025
55	A1	2018-07-10	13:25	4	11	0.35	19.8	22.3	22.2	26.3	22.65
56	B3	2018-07-10	13:25	4	10	0.21	28	32.3	24	26.8	27.775
57	D4	2018-07-10	13:25	4	8	0.15	23.7	19.9	24.2	20.4	22.05
58	A3	2018-07-10	13:25	4	11	0.29	27.5	29.4	27.4	18.5	25.7
59	C1	2018-07-10	13:25	4	10	0.24	17.4	25.1	19.2	25.9	21.9
60	D2	2018-07-10	13:25	4	10	0.22	21.1	18.3	24.4	26.1	22.475
61	D3	2018-07-10	13:25	4	11	0.25	17.2	21.4	19.9	27.8	21.575
62	C2	2018-07-10	13:25	4	11	0.22	25	20.4	25.4	18	22.2
63	A2	2018-07-10	13:25	4	11	0.28	18.8	18.1	24.3	24.2	21.35
64	C4	2018-07-10	13:25	4	11	0.33	16.4	27	26.5	19	22.225