REVISTA DE
Biología Tropical

Impact of daily variable temperatures in life-history traits of tropical anurans

Manuel Hernando Bernal-Bautista, Jorge Luis Turriago-González & Francisco Antonio Villa-Navarro

Departamento de Biología, Universidad del Tolima, Calle 42 Barrio Santa Helena, Ibagué, Colombia; mhbernal@ut.edu.co, jlturriagog@ut.edu.co, favilla@ut.edu.co

Received 15-II-2016. Corrected 20-VII-2016. Accepted 22-VII-2016.

Abstract: Anuran embryos and tadpoles are daily exposed to wide thermal variations in their ponds, with maximum temperatures at midday. The aim of this research was to study the impact of three daily variable thermal environments (with maximum experimental temperatures between 10:00 and 16:00 hours), on the survival, developmental time and body size of metamorphs of four tropical anuran species from lowland habitats in Colombia. A total of 50 embryos (Gosner stage ten) to metamorphosis (Gosner stage 46) of *Rhinella humboldti*, *Hypsiboas crepitans* and *Engystomops pustulosus* were exposed to each one of the three daily variable temperature treatments: high temperature (mean = 27.5 °C; maximum temperature = 34 ± 1 °C; range = 23-35 °C), medium temperature (25.5 °C; 29 ± 1 °C; 23-30 °C), and low temperature (24 °C; 24 ± 1 °C; 23-25 °C). For the other species, *Espadarana prosoblepon,* 40 embryos to metamorphosis were exposed to each one of the following thermal treatments: high temperature (mean = 22 °C; maximum temperature = 25 ± 1 °C; range = 18-26 °C), medium temperature (20.5 °C; 22 ± 1 °C; 18-23 °C), and low temperature (19 °C; 19 ± 1 °C; 18-20 °C). For all species, the thermal variable environment with the highest temperature showed the greatest accumulated survival, reduced significantly the developmental time from embryos to metamorphs, and the snout-vent-length of metamorphs. Therefore, under field conditions where ponds are exposed to thermally variable environments, the highest temperatures may promote a decrease in the period of time to metamorphosis, and a positive increase for the anuran survival; nevertheless, extreme temperatures were also found in the microhabitat of the species studied, higher than their upper thermal limits reported, which suggest a vulnerable situation for them and other tropical anurans from similar habitats. Rev. Biol. Trop. 65 (1): 55-63. Epub 2017 March 01.

Key words: anuran, development, growth, tadpole, variable temperature.

The effect of constant temperatures on life-history traits in amphibians has been long known, but less so under variable temperature environments. Studies incorporating thermal variations may represent more natural field conditions, since temperature fluctuations are typical of most of the shallow and ephemeral pools where tadpoles live in. Despite the remarkable plasticity of amphibians through the embryonic and larval periods (Álvarez, & Nicieza, 2002; Moore, 1939), environmental temperature is well documented as one of the most predominant abiotic factor to influence the anuran development and growth (Atkinson, 1996; Bradford, 1990; Kern, Cramp, & Franklin, 2015; Smith-Gill, & Berven, 1979). Growth is the trajectory of increase in the somatic mass owned by the uptake, transformation and allocation of materials, while development is the trajectory of differentiation from a fertilized egg or some later stage to its adulthood, which is regulated by gene-by-environment interactions (Zuo, Moses, West, Hou, & Brown, 2011). Temperature has differential effects on larval growth and development, with differentiation decreasing at low temperatures but growth keeps on progressing until temperatures eventually become too low (Smith-Gill, & Berven, 1979). As a consequence, anuran growth tends to get prolonged larval periods at low temperatures and higher stage-specific growth than those growing in warmer conditions (Morrison, & Hero, 2003). The differential effect of temperature on development and growth may be explained by the enzymatic kinetic reactions (Ultsch, Bradford, & Freda, 1999), which is faster for the differentiation rate than for the growth rate (Smith-Gill, & Berven, 1979). Additionally, because temperature exerts a greater effect on the differentiation than on the growth rate (Gomez-Mestre et al., 2010), and the growth rate functionally depends upon the differentiation rate whereas the contrary does not (Berven, & Gill, 1983). Temperature can also interact with an individual's genome to affect the developmental time, body shape, body size, and mass at metamorphosis (Arrighi et al., 2013), although the genetic contribution tends to be masked by some differences resulting from the variation of the environmental conditions (Morrison, & Hero, 2003).

Daily temperature fluctuations on amphibians have also shown to induce a variation in traits associated with fitness, such as an increase in the developmental rate, tadpole body length and jumping performance in *Limnodynastes peronii* (Niehaus, Wilson, & Franklin, 2006), a positive increase in individual performance and development in *Triturus alpestris* (Meřaková, & Gvoždík, 2009), and to cause embryos to hatch at a younger developmental stage and longer snout-vent-length in *Bombina orientalis* (Kaplan, & Phillips, 2006). However, there is a lack of studies on the possible effects of thermally variable environments on life-history traits in amphibians, particularly in tropical anurans, which are important to define the thermal reaction norms for different species and to quantify the anuran vulnerability to global warming under more real variable conditions in nature (Paaijmans et al., 2013). Therefore, we examined the effect of three daily variable temperatures on the expression of several life-history traits in four tropical anuran species from Colombia, *Rhinella humboldti, Hypsiboas crepitans*, *Engystomops pustulosus* and *Espadarana prosoblepon,* that inhabit water bodies susceptible to large daily variations in the thermal environment. We studied these species as they are typical of the tropical dry forest, which is one of the most threatened ecosystems in the study region, the Tolima department, in Colombia and the Neotropics (Pizano, Cabrera, & Garcia, 2014; Portillo-Quintero, & Sánchez-Azofeifa, 2010). Specifically, we evaluated the larval survival, and the larval development time and body length at the end of metamorphosis, due to the strong influence that have on adult fitness (Altwegg, & Reyer, 2003). We were particularly interested in knowing whether the high temperatures, in the daily variable thermal environments, would have a greater effect on the life-history traits assessed, than the medium and low experimental temperatures.

MATERIALS AND METHODS

Study species: We studied four anuran species from different places in the department of Tolima, Colombia. *R. humboldti* (Gallardo, 1965), from Ibagué city (4°27' N - 75°14' W, 1 200 m altitude, mean temperature = 23.2 °C, annual precipitation = 1 691 mm); *H. crepitans* (Wied-Neuwied, 1824), from Ibagué city and Potrerillo locality (4°14' N - 74°58' W, 430 m altitude, mean temperature = 28.01 °C, annual precipitation = 1 234 mm); and *E. pustulosus* (Cope, 1864), from Potrerillo locality. These species are explosive breeders during the rain events, which share temporal shallow ponds with other anurans, where their embryos and tadpoles are exposed to daily temperature variations. The other study species was *E. prosoblepon* (Boettger, 1892), from Falan municipality (5°07' N - 74°58' W, 1 150 m altitude, mean temperature = 25.7 °C, annual precipitation = 2 165 mm), which lays its eggs on leaves overhanging streams where they develop, and then the tadpoles drop into the water to complete their metamorphosis. Although *E. prosoblepon* inhabits shaded places in forests, embryos and tadpoles are frequently exposed to wide environmental temperatures due to anthropogenic deforestation.

Microhabitat temperatures for embryos and tadpoles of *R. humboldti*, *H. crepitans* and *E. pustulosus* were registered on the water surface of ponds (Fig. 1A) and underwater (about 10 cm depth) (Fig. 1B), and for *E. prosoblepon* embryos and tadpoles on the leaves of ferns (air temperature) (Fig. 1C) and underwater of streams (about 10 cm depth) (Fig. 1D), respectively. These data were collected with several MicroLite 16 L data loggers (Contoocook, NH, USA), programmed to obtain temperatures for every hour from September to December 2012, during the breeding season. This information was used to make the thermal profiles of the study species.

Experimental treatments: A total of 25 embryos in gastrula stage, Gosner stage ten (Gosner, 1960), for each species of *R. humboldti*, *H. crepitans* and *E. pustulosus,* and 20 embryos of *E. prosoblepon,* were randomly allocated in each one of two aquariums that were exposed to three daily thermal environments [25 embryos (20 embryos for *E. prosoblepon*) x 4 species x 2 replicates (aquariums) x 3 thermal treatments], following an experimental design approximately similar to that described in Niehaus et al. (2006), and Arrighi et al. (2013). The three daily thermal environments for *R. humboldti*, *H. crepitans* and *E. pustulosus* were: 1) high temperature: mean = 27.5 °C, maximum = 34 ± 1 °C, range = 23-35 °C; 2) medium temperature: mean = 25.5 °C, maximum = 29 ± 1 °C, range = 23-30 °C; 3) low temperature: mean = 24 °C, maximum = 24 ± 1 °C, range = 23-25 °C. Specifically, for *E. prosoblepon* the three daily thermal variable environments were: 1) high temperature: mean = 22 °C, maximum = 25 ± 1 °C, range = 18-26 °C; 2) medium temperature: mean = 20.5 °C, maximum = 22 ± 1 °C, range = 18-23 °C; 3) low temperature: mean = 19 °C, maximum = 19 ± 1 °C, range = 18-20 °C. We chose these three thermal treatments as they may be found in the habitat of the species studied here and are below the lethal embryonic and tadpole temperatures (Bernal, & Lynch, 2013; Turriago, Parra, & Bernal, 2015).

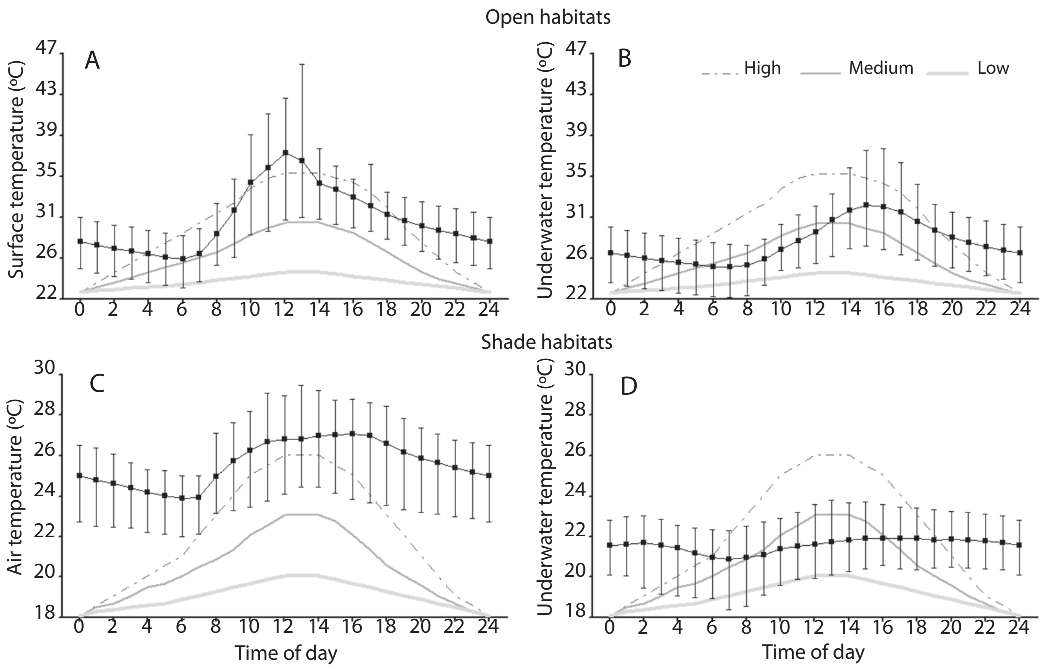

Fig. 1. Profiles of daily environmental temperatures (black lines) and three thermal treatments (curved lines) experienced by embryos and tadpoles of *R. humboldti, H. crepitans, E. pustulosus* (A, B), and *E. prosoblepon* (C, D). The squares indicate the mean temperatures and the lines the minimum and maximum value.

The thermally variable environments were built with heaters (Hopar® H-938) used to increase the water temperature of the aquariums and to maintain the maximum experimental temperatures for about six hours, from 10:00 to 16:00 hours. Then, the heaters were switched off to allow the water to cool down overnight. We used similar heaters for each thermal treatment and the water temperature in the aquariums was continually monitored with digital thermometers (HTC-2, range: -50 °C - 50 °C ± 1 °C).

For this study, we collected several egg masses (of the different species) in early mornings of variable days during the rainy season, between September 2012 and March 2013. The egg masses were taken to the experimental site, the Herpetology laboratory at the University of Tolima, Ibagué, at an environmental temperature around 23 °C for *R. humboldti*, *H. crepitans* and *E. pustulosus,* and in an acclimatized room for *E. prosoblepon* (19 ± 1 °C). The aquatic embryos were placed directly in the aquariums (33 x 28 x 13 cm), whereas arboreal embryos of *E. prosoblepon* were initially located on wet towels in small petri dishes (51 mm) until they reached the stage 25, then the tadpoles were transferred to the aquariums. All the aquariums contained 8 L of previously declorinated tap water, 1 cm base layer of soil and sand, five small stones (150 g approximately) and four macrophytes (*Pistia stratiotes*), so as to simulate some natural conditions for these species. A fine screen nylon cloth (0.5 mm mesh) was also laced at the bottom of the aquariums to facilitate the subsequent checking of embryos and tadpoles. The tadpoles were fed with 0.2 g of fish food once every day and water quality was maintained by regular manual removal (using a small net) of uneaten food and a partial (50 %) (every eight days) and total renewal (every 24 days) of water. A photoperiod of approximately 12 hour light/12 hour darkness was set throughout the experiment.

The survival, development and growth from embryos (Gosner stage ten) to metamorphosis (Gosner stage 46) were the life-history traits evaluated in this study. The survival was analyzed on the accumulated number of animals that reached the metamorphosis in the three thermally variable environments, using a generalized linear model (GLM) with a binomial probability distribution and logit link function (logistic regression). We tested the effects of the species, thermal treatments, aquariums and interactions. The developmental time, from embryos to metamorphs, was recorded in days at the three experimental temperatures, while the growth was assessed by digital measurements of the snout-vent-length for each metamorph, from photos processed with ImageJ software (http://rsbweb.nih.gov/ij/) after checking for scaling artifacts. The developmental time and snout-vent-length were independently analyzed with linear models (LM) testing the effects of the species, thermal treatments, aquariums and their interactions. We did not show the statistical results neither for the aquariums, since they never had a significant effect on all the life-history traits evaluated, nor for the species, due to the remarkable differences in the development and growth, which were statistically significant in all cases. We used the Tukey's post-hoc test to compare the effects of the thermal treatments. All statistical analyses were conducted in SPSS Statistic 19.0 (SPSS Inc., Chicago, Illinois).

The protocols for this research were approved by the Bioethics Committee of the Tolima University (permit number: 2.3-193, May 14, 2012).

RESULTS

The accumulated survival of metamorphs increased significantly at the highest experimental variable temperature, followed by the medium and then the lowest temperatures (GLM: Wald $X^2 = 45.9$, $P = 0.000$). This trend was similar in all four species (Fig. 2). Pairwise comparisons among the three thermal treatments showed significant differences in all cases (high-medium, $P = 0.00$; high-low, $P = 0.00$; medium-low, $P = 0.001$).

High daily temperature variations significantly decreased the developmental time from

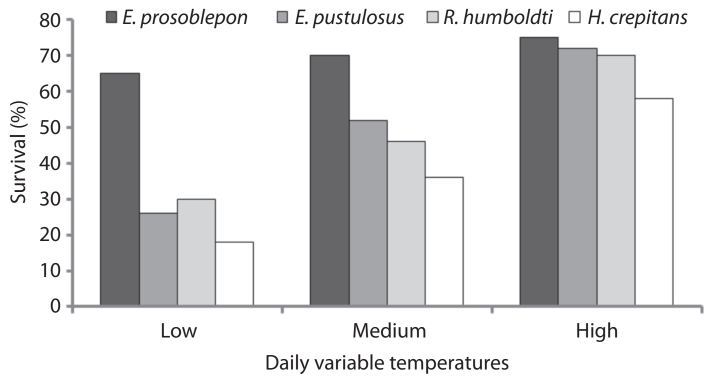

Fig. 2. Accumulated survival for metamorphs of the four study species raised from embryos under three daily variable temperatures.

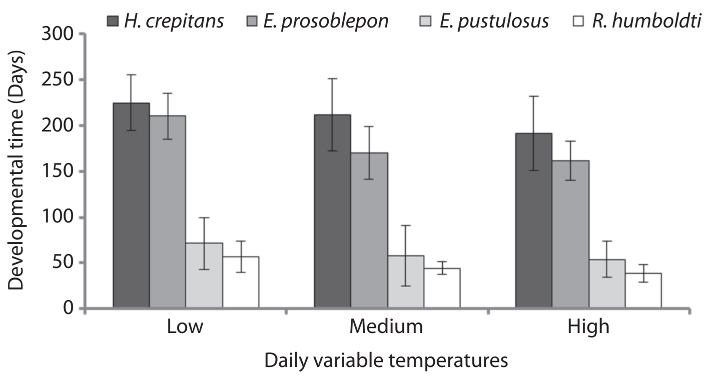

Fig. 3. Mean of developmental time for metamorphs of the four study species raised from embryos under three daily variable temperatures. Bars represent the standard deviation.

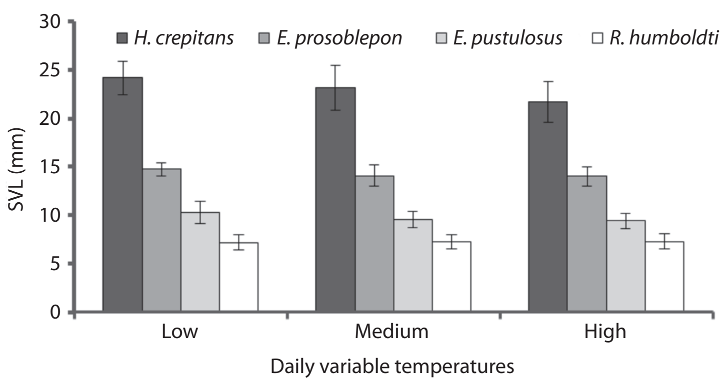

Fig. 4. Mean of snout-vent-length (SVL) for surviving metamorphs of the four study species raised from embryos under three daily variable temperatures. Bars represent the standard deviation.

embryos to metamorphs (LM: F = 26.85, P = 0.00), which was observed in all species (Fig. 3). This difference was statistically significant between the high and low thermal treatments (Tukey: P = 0.000), high and medium (Tukey: P = 0.003), and medium and low treatments (Tukey: P = 0.000). Finally, high daily temperature variation also significantly decreased the snout-vent-length of metamorphs (LM: F = 9.34, P = 0.001) (Fig. 4), although the Tukey's post-hoc tests only indicated a significant difference between the high and low temperatures (P = 0.004).

DISCUSSION

Environmental temperature determines, at a large extent, the larval body size and length of larval period, which in turn are directly related to survival (Alford, 1999; Sibly, & Atkinson, 1994). Then, the greatest survival that we found at the highest temperatures in the daily variable thermal environments, could be explained by the faster-growing tadpoles that metamorphosed early and consequently experienced lower cumulative mortalities. On the contrary, when exposed to lower experimental temperatures, metamorphs were larger, and tadpoles showed a slower growth, which is a typical response in amphibian larvae (Berven, & Gill, 1983; Smith-Gill, & Berven, 1979). Overall, these results were similar to those found in larval anurans raised in constant temperatures (Atkinson, 1996; Laugen, Laurila, & Merila, 2003), nevertheless, the effects of a constant environment does not always equal those of a fluctuating environment at the same mean temperature, according to the Jensen's inequality (Ruel, & Ayres, 1999). Ecologically, high temperature variations may promote a decrease in time to metamorphose and an increase in the anuran survival, when ephemeral ponds are overheated during the pond drying, as is the case for the temporal breeding study species *R. humboldti, E. pustulosus* and *H. crepitans*, and less for *E. prosoblepon*.

We found out that daily differences among the three thermally variable environments were enough to observe changes in the development and growth of all species. However, we are not confident if these responses were the consequence of the daily mean temperatures, the maximum thermal treatments, from 10:00 to 16:00 hours, the daily temperature ranges, or from a combined effect of all these regimens. We did not experimentally separated these three thermal conditions, as they co-occur in nature for the study species, which are more remarkable for those from open habitats, and we wanted to study these simultaneous daily thermal variations on some life-history traits in anurans, as opposed to other experiments that test the effects of daily temperature fluctuations, at a same experimental mean, with respect to constant temperatures (Arrighi et al., 2013; Kaplan, & Phillips, 2006; Kern et al., 2015; Meňaková, & Gvoždík, 2009; Niehaus et al., 2006).

Global warming has increased not only the mean and variance (Bozinovic et al., 2011) of the environmental temperatures, but also the frequency of extremely high temperatures (Easterling et al., 2000). Amphibians, on the other hand, are highly susceptible to temperature variations in their environments (Deutsch et al., 2008), and especially tropical ectotherms have relatively narrow thermal tolerances and the optimal temperatures are only a few degrees below the upper limits (Bozinovic et al., 2011). So, tropical amphibians may be particularly vulnerable to climate warning (Tewksbury, Huey, & Deutsch, 2008). This assertion can be confirmed with our field data, as we found extreme environmental temperatures higher than 42 °C in the habitats of *R. humboldti*, *H. crepitans* and *E. pustulosus*, which are 100 % lethal for their embryos (*R. humboldti* = 38.7 °C, *H. crepitans* = 36.9 °C, *E. pustulosus* = 37.4 °C, *E. prosoblepon* = 27.0 °C) and tadpoles (*R. humboldti* = 40.7 °C, *H. crepitans* = 40.0 °C, *E. pustulosus* = 40.6 °C, *E. prosoblepon* = 32.98) (Turriago, Parra, & Bernal, 2015). Since other anurans are exposed to environmental temperatures very similar to the study species, particularly those from lowlands and ephemeral ponds, these results suggest a vulnerable situation for many tropical anurans.

In conclusion, we found out that differences in the daily variable thermal environment did have a significant effect on the anuran life-history traits studied, with the highest experimental temperatures decreasing the accumulated mortality, the time to reach the metamorphosis and the snout-vent-length of metamorphs.

TABLE 1
Survival, developmental time and growth (snout-vent-length of metamorphs) of four tropical anuran species, exposed from embryos to metamorphs to three daily variable thermal environments

Species	Temperature treatments	N	Survival (%)	Developmental time (days)	Snout-Vent-Length (mm)
E. prosoblepon	Low	40	65	210.27±25.33	14.75 ±0.66
	Medium	40	70	170.36±28.66	14.08±1.12
	High	40	75	161.07±21.33	14.01±0.99
E. pustulosus	Low	50	26	71.38±28.11	10.28±1.13
	Medium	50	52	57.88±32.85	9.55±0.80
	High	50	72	54.11±19.58	9.42±0.77
R. humboldti	Low	50	30	56.53±17.02	7.19±0.78
	Medium	50	46	44.04±6.92	7.28±0.74
	High	50	70	38.60±9.33	7.30±0.81
H. crepitans	Low	50	18	225±30.74	24.17±1.73
	Medium	50	36	212±39.65	23.16±2.28
	High	50	58	191.55±40.37	21.68±2.06

N = Number of individuals exposed.

Thus, these results demonstrate that, within the thermal limits, high temperatures in thermally variable environments would be favorable for anuran survival, especially for those species that breed in temporary ponds. However, our field data also recorded temperatures higher than the upper thermal tolerances reported for the species studied, showing a vulnerable situation for them and other tropical anurans from similar environments.

ACKNOWLEDGMENTS

This research was supported by Fondo de Investigaciones de la Universidad del Tolima (Project number 370112). Collection permit was obtained from Corporación Autónoma Regional del Tolima, CORTOLIMA, resolution number 2046, June 13, 2012. We thank Liliana Marcela Henao for her valuable contribution to the lab experiments and the anonymous reviewers for their constructive comments which helped to improve the manuscript.

SUPPORTING INFORMATION

The data on the accumulated survival, the developmental time and growth of the four species exposed to the three daily thermal variable environments are shown in table 1.

RESUMEN

Impacto de las variaciones de la temperatura diaria en caracteres de historias de vida de los anuros tropicales. Los embriones y renacuajos de anuros están expuestos diariamente a amplias variaciones térmicas en sus estanques, con temperaturas máximas al mediodía. El objetivo de esta investigación fue estudiar el impacto de tres ambientes térmicos diariamente variables, con temperaturas máximas experimentales entre las 10:00 y las 16:00 horas, sobre la supervivencia, tiempo de desarrollo y tamaño corporal de metamorfos de cuatro especies de anuros tropicales de hábitat de tierras bajas de Colombia. 50 embriones (estadio de Gosner diez) hasta la metamorfosis (estadio de Gosner 46) de *Rhinella humboldti*, *Hypsiboas crepitans* y *Engystomops pustulosus* fueron expuestos a cada uno de tres tratamientos de temperatura variable diariamente: temperatura alta (promedio = 27.5 °C; temperatura máxima = 34 ± 1 °C; rango = 23-35 °C), temperatura media (25.5 °C; 29 ± 1 °C; 23-30 °C), y temperatura baja (24 °C; 24 ± 1 °C; 23-25 ºC). Para la otra especie de estudio, *Espadarana prosoblepon,* 40 embriones hasta la metamorfosis fueron expuestos a cada uno de los siguientes tratamientos térmicos: temperatura alta (promedio = 22 °C; temperatura máxima = 25 ± 1 °C; rango = 18-26 °C), temperatura media (20.5 °C; 22 ± 1 °C; 18-23 °C), y temperatura baja (19 °C; 19 ± 1 °C; 18-20 °C). Para todas las especies, los ambientes térmicos variables con las temperaturas más altas tuvieron la mayor supervivencia acumulada, redujeron significativamente el tiempo de desarrollo

de los embriones a metamorfos y la longitud hocico-cloaca de los metamorfos. Por lo tanto, bajo condiciones de campo donde las charcas están expuestas a ambientes térmicamente variables, las temperaturas más altas pueden promover una disminución en el tiempo de la metamorfosis y un aumento positivo para la supervivencia de los anuros; sin embargo, también se encontraron temperaturas extremas en los microhábitats de las especies estudiadas, más altas que sus límites térmicos máximos reportados, lo que sugiere una situación vulnerable para estas especies y otros anuros tropicales con hábitat similares.

Palabras clave: anura, crecimiento, desarrollo, renacuajo, temperatura variable.

REFERENCES

Alford, R. A. (1999). Ecology: Resource Use, Competition and Predation. In R. W. McDiarmid & R. Altig (Eds.), *Tadpoles: The Biology of Anuran Larvae* (pp. 240-278). Chicago: The University of Chicago Press.

Álvarez, D., & Nicieza, G. (2002). Effects of temperature and food quality on anuran larval growth and metamorphosis. *Functional Ecology, 16*, 640-648.

Altwegg, R., & Reyer, H. (2003). Patterns of natural selection on size at metamorphosis in water frogs. *Evolution, 57*, 872-882.

Arrighi, J. M., Lencer, E. S., Jukar, A., Park, D., Phillips, P. C., & Kaplan, R. H. (2013). Daily temperature fluctuations unpredictably influence developmental rate and morphology at a critical early larval stage in a frog. *BMC Ecology*, *13*(1), 18. doi: http://dx.doi.org/10.1186/1472-6785-13-18

Atkinson, D. (1996). Ectotherm life-history responses to developmental temperature. In I. A. Johnston & A. F. Bennett (Eds.), *Animals and Temperature*. *Phenotypic and Evolutionary Adaptation* (pp. 183-204). Cambridge: Cambridge University Press.

Bernal, M. H., & Lynch, J. D. (2013). Thermal tolerance in anuran embryos with different reproductive modes: Relationship to altitude. *The Scientific World Journal,* doi: http://dx.doi.org/10.1155/2013/183212

Berven, K. A., & Gill, D. E. (1983). Interpreting geographic variation in life-history traits. *American Zoologist, 23,* 85-97.

Boettger, O. (1892). *Katalog der Batrachier-Sammlung im Museum der Senckenbergischen Naturforschenden Gesellshaft in Frankfurt am Main.* Frankfurt, Deutschland: Gebrüder Knauer.

Bozinovic, F., Bastias, D. A., Boher, F., Clavijo-Baquet, S., Estay, S. A., & Angilletta, M. J. (2011). The mean and variance of environmental temperature interact to determine physiological tolerance and fitness. *Physiological and Biochemical Zoology, 84,* 543-552.

Bradford, D. F. (1990). Incubation time and rate of embryonic development in amphibians: the influence of ovum size, temperature, and reproductive mode. *Physiological Zoology, 63,* 1157-1180.

Cope, E. D. (1864). Contributions to the herpetology of tropical America. *Proceedings of the Academy of Natural Sciences of Philadelphia, 16*, 166-181.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences, 105*, 6668-6672.

Easterling, D. R., Meehl, G. A., Parmesan. C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: observations, modelling, and impacts. *Science, 289,* 2068-2074.

Gallardo, J. M. (1965). The species *Bufo granulosus* Spix (Salientia: Bufonidae) and its geographic variation. *Bulletin of the Museum of Comparative Zoology*, *134*, 107-138.

Gomez-Mestre, I., Saccoccio, V. L., Iijima, T., Collins, E. M., Rosenthal, G. G., & Warkentin, K. M. (2010). The shape of things to come: linking developmental plasticity to post-metamorphic morphology in anurans. *Journal of Evolutionary Biology, 23*, 1364-1373.

Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica, 16,* 183-190.

Kaplan, R. H., & Phillips, P. C. (2006). Ecological and developmental context of natural selection: maternal effects and thermally induced plasticity in the frog *Bombina orientalis*. *Evolution, 60,* 142-156.

Kern, P., Cramp, R. L., & Franklin, C. E. (2015). Physiological responses of ectotherms to daily temperature variation. *Journal of Experimental Biology*, *218*, 3068-3076.

Laugen, A. T., Laurila, A., & Merila, J. (2003). Latitudinal and temperature-dependent variation in embryonic development and growth in *Rana temporaria. Oecologia, 135,* 548-554.

Meřaková, E., & Gvoždík, L. (2009). Thermal acclimation of swimming performance in newt larvae: the influence of diel temperature fluctuations during embryogenesis. *Functional Ecology, 23,* 989-995.

Moore, J. A. (1939). Temperature tolerance and rates of development in the eggs of amphibia. *Ecology, 20*, 459-478.

Morrison, C., & Hero, J. M. (2003). Geographic variation in life-history characteristics of amphibians: a review. *Journal of Animal Ecology*, *72*, 270-279.

Niehaus, A. C., Wilson, R. S., & Franklin, C. E. (2006). Short and long-term consequences of thermal variation in the larval environment of anurans. *Journal of Animal Ecology, 75,* 686-692.

Paaijmans, K. P., Heinig, R. I., Seliga, R. A., Blanford, J. I., Blanford, S., Murdock, C. C., & Thomas, M. B. (2013). Temperature variation makes ectotherms more sensitive to climate change. *Global Change Biology, 19,* 2373-2380.

Pizano, C., Cabrera, M., & García, H. (2014). Bosque seco tropical en Colombia: Generalidades y Contexto. In C. Pizano & H. García (Eds.), *El Bosque Seco Tropical en Colombia* (pp. 36-47) Colombia: Ediprint Ltda.

Portillo-Quintero, C. A., & Sánchez-Azofeifa, G. A. (2010). Extend and Conservation of tropical dry forest in the Americas. *Biological Conservation*, *143*, 144-155.

Ruel, J. J., & Ayres, M. P. (1999). Jensen's inequality predicts effects of environmental variation. *Perspectives, 14*, 361-366.

Sibly, R. M., & Atkinson, D. (1994). How rearing temperature affects optimal adult size in ectotherms. *Functional Ecology, 8*, 486-493.

Smith-Gill, S. J., & Berven, K. A. (1979). Predicting amphibian metamorphosis. *American Naturalist, 113,* 563-585.

Tewksbury, J. J., Huey, R. B., & Deutsch, C. A. (2008). Putting the heat on tropical animals. *Science, 320,* 1296-1297.

Turriago, J. L., Parra, C. A., & Bernal, M. H. (2015). Upper thermal tolerance in anuran embryos and tadpoles at constant and variable peak temperatures. *Canadian Journal of Zoology*, *93*, 267-272.

Ultsch, G. R., Bradford, D. F., & Freda, F. (1999). Physiology: Coping with the Environment. In R. W. McDiarmid & R. Altig (Eds.), *Tadpoles: The Biology of Anuran Larvae* (pp. 189-214). Chicago: The University of Chicago Press.

Wied-Neuwied, M .A. P. & Prinz, Z. (1824). *Abbildungen zur Naturgeschichte Brasiliens. Heft 7.* Weimar, Deutschland: au Bureau d'Industrie.

Zuo, W., Moses, M. E., West, G. B., Hou, C., & Brown, J. H. (2011). A general model for effects of temperature on ectotherm ontogenetic growth and development. *Proceedings of the Royal Society of London B: Biological Sciences, 279*(1734), 1840-1846.