

Upper thermal tolerances and vulnerability to global warming in a Brazilian Caatinga fish *Astyanax bimaculatus* (Linnaeus, 1758) population

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Abstract Global warming is predicted to increase both average temperatures and the frequency and duration of heat waves. Tropical ectotherms, particularly those living in warm environments are more prone to receive heat impacts. Then, it is crucial to identify those populations already exposed to high temperatures that may be at risk of decimation by ongoing warming. We assessed heating risk in a population of the fish species *Astyanax bimaculatus*, inhabiting hot pools in intermittent streams in the Brazilian Caatinga ecoregion. We experimentally examined the upper thermal tolerance (CT_{max}), and provided estimates of warming tolerance (WT), as the difference between CT_{max} and micro-environmental peak temperatures (T_{max}). Two CT_{max} estimates ranged between 37.6 and 40.6°C, whereas pond T_{max} ranged between 34.6 and 41.3°C. This determines very narrow, even negative WTs, for these extreme heated *A. bimaculatus* populations, which ultimately may determine their local extinction in the coming decades.

Abstract in Portuguese is available with online material. Prevê-se que o aquecimento global aumente tanto as temperaturas médias como a frequência e duração das ondas de calor. Ectotérmicos tropicais, principalmente aqueles que habitam ambientes temperados, estão mais expostos a impactos térmicos. Portanto, identificar populações que já estão expostas a temperaturas altas o suficiente para serem ameaçadas pelo aquecimento atual é crucial. O risco de exposição a altas temperaturas foi estabelecido na espécie de peixe *Astyanax bimaculatus*, que habita poças quentes nos rios intermitentes presentes na ecorregião conhecida como Caatinga. A tolerância térmica superior (CT_{max}) foi aferida experimentalmente e apresentamos medidas de tolerância térmica (WT), definida como a diferença entre a CT_{max} e as temperaturas máximas registradas na escala microambiental (T_{max}). Duas estimativas de CT_{max} ficaram entre 37,6°C e 40,6°C, enquanto o T_{max} das poças variou entre 34,6°C e 41,3°C. Isso determina valores muito estreitos, e até mesmo negativos, de WTs para a população de *A. bimaculatus* estudada, o que pode vir a determinar sua extinção em décadas futuras.

Key words: climate change, CT_{max} , thermal risk, tropical fish, warming tolerance.

INTRODUCTION

Global warming is predicted to increase both average temperatures and the frequency and duration of heat waves for the late 21st century (IPCC 2013). Especially intense will be the biotic consequences expected on tropical and subtropical ectotherms because they are already living closer to their physiological thermal limits (Huey et al. 2012; Campos et al. 2021). Within the tropical and subtropical areas, some special biomes and particular microhabitats such as open forest and semi-arid biomes are currently suffering high temperatures and their biological communities may be candidates to

suffer increased heat impacts (Duarte et al. 2012). Thus, a better knowledge of the more challenging thermal conditions a species has to face, will aid to recognize which are the geographical warm edges where species are at risk of population decimation by ongoing warming. Special concern may be noted for tropical fish communities inhabiting temporary and intermittent streams and rivers (Trape 2009). These aquatic environments, due to the high capacity and conductivity of water, drastically restrict the range of accessible thermal microhabitats (Huey et al. 2012) and then fishes are diminishing the potential for thermoregulation and then their upper thermal limits would closely adjust to their experienced temperatures. This probably forces fishes to evolve increased thermal tolerances and plasticity in order to face extreme temperatures when trapped in

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shallow and desiccating water in tropical environments (Vinagre et al. 2016).

Neotropical fish communities from semi-arid environments such as the Caatinga biome in NE Brazil are poor in species richness although most of them are strict endemics (Rosa et al. 2003). The hydrology of Caatinga streams is conditioned by a highly unpredictable spatio-temporal pattern in rainfall with a high level of evapotranspiration determining highly intermittency with the extremes of flooding and total absence of water flow (Maltchik & Medeiros 2006a). This absence of water flow will restrain fishes to live in ponds with different levels of permanency and extension and thus under highly stressful conditions of low oxygen levels, high conductivity and, especially, high mean and peak temperatures that may reach over 35°C (Maltchik & Medeiros 2006b).

The two spot Astyanax, *Astyanax bimaculatus* (Linnaeus, 1758), is a fish species ranging from Panama to Argentina that occurs in a variety of habitats, including ones that already have very variable flow and temperature conditions that are likely to be exacerbated by ongoing climatic change (Froese & Pauly 2021). It is a common inhabitant of tropical semi-arid waters, being exposed to high environmental temperatures, up to 33°C in northern Venezuela (Chung 2000), between 30 and 37°C in an intermittent river pond in the Caatinga of NE Brazil (Maltchik & Medeiros 2006b), and reaching 35°C in subtropical streams heated by thermal springs in the Yungas of northwestern Argentina (Menni et al. 1998). Although this warm habitat preferences, *A. bimaculatus* exhibits a moderate thermal tolerance (38.6°C) when acclimated to 25°C (Menni et al. 1998), much lower than most heat-specialized fishes that may reach values high over 40°C (Comte & Olden 2017). This relatively low thermal tolerance may determine risky thermal safety margins, <2–4°C, which put this species at thermal risk due to warming in the present and near future.

The goal of this study is to assess thermal vulnerability in a Brazilian Caatinga population of *A. bimaculatus*, inhabiting pools in intermittent streams, particularly during the dry season, which may peak high temperatures (Maltchik & Medeiros 2006b). To do that, we estimated their upper thermal tolerances (CT_{max}), and warming tolerances ($WT = CT_{max} - \text{maximum environmental temperature } (T_{max})$) (*sensu* Duarte et al. 2012).

METHODS

Field collection and thermal regimen

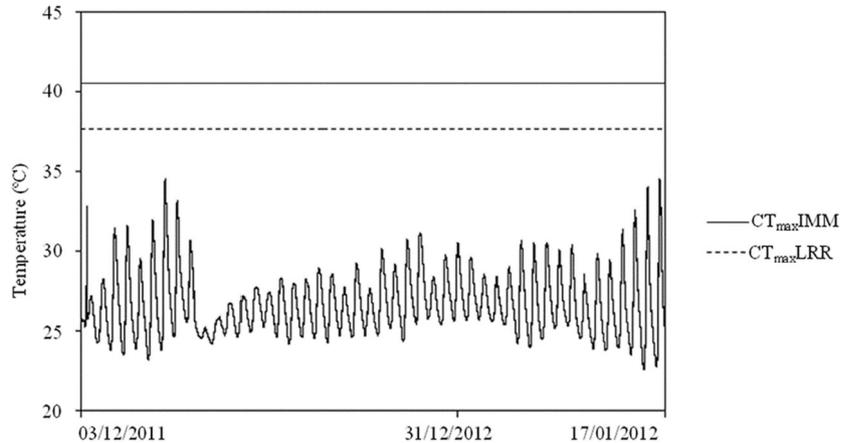
We conducted two field samplings, 2nd–3rd December 2011 and 4th–5th May 2014, in four pools located in the dry bed of two ephemeral streams, Córrego da Goiabeira and

Córrego da Garapa at the National Forest Contendas do Sinacorá, FLONA reserve, state of Bahia, Brazil, (13°55′19.94″S, 41°6′53.27″O, 356 m above sea level). These streams only flow after heavy rainfalls, maintaining water intermittently in waterholes that generally are ephemeral with a few weeks of hydroperiod, or, temporary, lasting for several months during the rainy season (November–February). Only in exceptionally rainy years, they may hold water even during the dry season (March–October) (IBAMA 2006). This reserve is within the Caatinga biome with a semiarid climate (BSwh, Köppen classification) with a mean annual temperature of 23.5°C and an average yearly rainfall of 596 mm but with extreme variability (0.0–1054.7 mm) (IBAMA 2006). In order to estimate thermal variation in water temperature, we deployed dataloggers (Hobo Pendant) at the bottom of each pond (10–40 cm maximum depth) that recorded temperature each 15 min, from 2 December 2011 to 22 April 2012. We estimated: overall mean water temperature (T_{mean}) and the mean of daily maximum (T_{max}) and minimum (T_{min}) temperatures and the absolute maximum temperature (Absolute T_{max}), for each site. In addition, we took water temperatures in one of the sampled ponds (C4) on 5 May 2014 at 11.15 hours and 12.15 hours with a Miller and Weber quick reading thermometer to the 0.1°C. *A. bimaculatus* was sampled by dip netting each pond, being only found at C4 pond during the 2014 sampling.

Experimental analyses of upper thermal tolerance (CT_{max})

All captured individuals were adults, as inferred from their body length, although their sex was not determined, and were transported to the Laboratory of Vertebrates of the Universidade Estadual de Santa Cruz (UESC, Ilhéus, Bahia, Brazil), where they were pooled and kept for 3 days at 20°C in a glass aquarium containing ca. 12 L of dechlorinated tap water. This acclimation temperature was lower than the mean temperature experienced for the species at the sampled location (see below), but we select that value for comparative purposes, because 20°C is the median acclimation temperature for most studies of thermal tolerances in fishes (Fig. 1, in Comte & Olden 2017). The lag period of controlled thermal acclimation was chosen because full CT_{max} accrual is reached after 2–3 days of transfer to a contrasting temperature in fishes (Fangue et al. 2014). Oxygen was provided to the aquarium by an air pump, water was not changed during the whole period and fish were fed with tadpoles *ad libitum*. Upper thermal tolerances CT_{max} were obtained following Hutchison's dynamic method (Lutterschmidt & Hutchison 1997), in which each animal was exposed to a constant heating rate of $\Delta T = 1.0^\circ\text{C min}^{-1}$ (initial temperature 20°C) until an end point is attained. Each fish was tested in individual plastic glasses (0.5 L) and water was heated employing an Agimatic-N magnetic stirrer with heater (Selecta, Barcelona, Spain). Two sublethal and consecutive end-point temperatures, usually employed to estimate upper thermal tolerances in fishes (Beitinger et al. 2000), were recorded with a Miller and Weber quick-recording thermometer, to the nearest 0.1°C. (i) Loss of righting response (CT_{maxLRR}), temperature at which individuals

Fig. 1. Thermal profile for the sampled pool C4, based in thermal records from 2011 to 2012. Horizontal lines represent CT_{\max}^{LRR} and CT_{\max}^{IMM} values (see text for details) for *Astyanax bimaculatus*.



were not able to keep an upright position, although they are able to swim; and (ii) temperature at which fish showed total immobility, and failed to respond to external stimuli by prodding five consecutive hits applied every 2 s with a wooden stick (CT_{\max}^{IMM}). The latter endpoint usually occurs only a few degrees above the LRR, and then measures a more severe thermal stress (Beitinger & Lutterschmidt 2011). After CT_{\max}^{IMM} was determined, tested fish were immediately transferred to the pre-heating water temperature (20°C) to allow recovery. After 24 h, they were weighed (Radwag AS220/c/2 analytical balance, ± 0.0001 g). Each individual was tested only once, and no mortality occurred because of the CT_{\max} procedures. Statistics for *A. bimaculatus* were expressed as mean \pm 1 SD.

RESULTS

Thermal variation in the four sampled pools appears in Table 1. CT_{\max} values were between 37 and 41°C

(Table 2). The thermal profile of the sampling pond C4 during 2011–2012 is shown in Figure 1, CT_{\max}^{LRR} and CT_{\max}^{IMM} values. WT were low ($\leq 6.62^\circ\text{C}$) and even they may be negative when considering the maximal water temperatures recorded in the area (Table 1). Mass was unrelated to any of the measures of thermal tolerance (Spearman rank correlation, $P \geq 0.181$).

DISCUSSION

Astyanax bimaculatus is a dominant species representing even 20% of the total fish communities from the semi-arid Caatinga wetlands in NE of Brazil (Medeiros et al. 2006) and in other hot subtropical environments heated by hot springs (Menni et al. 1998). Its relatively moderate upper thermal tolerances may help in their ability to colonize

Table 1. Thermal analyses of the studied pools, located in the dry bed of two ephemeral streams, Córrego da Goiabeira and Córrego da Garapa at the National Forest Contendas do Sincorá, FLONA reserve, state of Bahia, Brazil, based in data-logger recordings, considering only flooded period during the period 2 December 2011–22 April 2012, (mean (standard error), thermal range)

Pools	Flooded period sampling days and dates	T_{\max}	T_{\min}	T_{mean}	$T_{\max}^{\text{absolute}}$ (°C)
C4	47	29.86°C (0.31°C)	24.50°C (0.12°C)	26.73°C (0.09°C)	34.58
	03.12.2011–17.01.2012	25.61–34.58°C	22.33–25.80°C	24.90–28.13°C	
	5th May 2014	33.50°C			
C3	44	31.52°C (0.66°C)	24.36°C (0.16°C)	27.12°C (0.16°C)	41.34
	03.12.2011–09.01.2012 (1st drying)	25.22–41.34°C	21.66–25.71°C	24.77–28.63°C	
	15.01.2012–23.01.12 (2nd drying)				
C2	44	28.17°C (0.34°C)	24.56°C (0.16°C)	26.23°C (0.12°C)	37.93
	02.12.2011–06.12.2011 (1st drying)	24.06–37.93°C	21.47–26.19°C	23.22–27.79°C	
	12.12.2011–24.01.2012 (2nd drying)				
C1	98	24.65°C (0.21°C)	22.99°C (0.11°C)	23.72°C (0.13°C)	33.43
	02.12.2011–10.12.2011 (1st drying)	22.81–33.43°C	20.61–27.76°C	21.95–29.96°C	
	12.12.2011–11.03.2012 (2nd drying)				

$T_{\max}^{\text{absolute}}$, absolute maximum temperature, for each pool; T_{\max} , mean of daily maximum temperatures; T_{mean} , overall mean water temperature; T_{\min} , mean of daily minimum temperatures.

Water maximum temperatures on 5 May 2014 for C4 pond were obtained with a Miller and Weber quick reading thermometer. *Astyanax bimaculatus* was only found at the C4 pond during the 2014 sampling.

Table 2. Estimates of CT_{max} ($CT_{max}LRR$ and $CT_{max}IMM$) for *Astyanax bimaculatus* (mean (standard error, SE), estimated at an acclimation temperature of 20°C

Variables	Mean (SE; range) (°C)
$CT_{max}LRR$	37.67 (0.58; 34.5 to 39.4)
$CT_{max}IMM$	40.58 (0.10; 40.1 to 41.2)
$WT_{LRR} TMAX C4$	3.09 (0.59; -0.08 to 4.81)
$WT_{IMM} TMAX C4$	6.00 (0.11; 5.52 to 6.62)
$WT_{LRR} TMAX AREA$	-3.67 (-6.84 to -1.94)
$WT_{IMM} TMAX AREA$	-0.76 (-1.24 to 0.11)

Warming Tolerances (WT's) (°C) ($CT_{max} - T_{max}$) were calculated using both estimates of CT_{max} ($CT_{max}LRR$ and $CT_{max}IMM$), $WTLRR$ and $WTIMM$, respectively, and, likewise, considering two different T_{max} 's; maximum temperature of pond C4 (34.58°C) ($WTTMAX C4$) and maximum temperature of the four ponds sampled in 2011–2012 (41.34°C) ($WTTMAX AREA$). Those negative WT's values in bold suggest that fish are able to suffer acute heat impacts at the present, once water temperature in the field are equal or exceeded the estimated upper thermal tolerances.

upstream tributaries, which suffer high uncertainty of drying and are exposed to high peak temperatures (Medeiros et al. 2006). However, their warming tolerance is low, in agreement with current evidence showing that upper tolerances in ectotherms from low latitudes are close to the current maximal experienced temperatures. This is especially so in hotter microenvironments such as forest canopy in ants (Leahy et al. 2022) or in open sunlit temporary ponds in aquatic subtropical amphibian tadpoles (Duarte et al. 2012; Sanabria et al. 2021). Recently, Campos et al. (2021) have reported decreased warming tolerances for low-latitude South American freshwater fishes that would be at high risk of suffering heat impacts. Because our CT_{max} estimates were obtained at a relatively low temperature (20°C), compared to the mean recorded field temperatures ranging between 25 and 27°C (Table 1), it is possible that we have underestimated their warming tolerances. *A. bimaculatus* has been reported to show beneficial thermal acclimation (Chung 2000) reaching up to 41.4°C when acclimated to 34°C (Menni et al. 1998). If our studied Caatinga population also shows this acclimation ability, its warming tolerance would become greater. However, other environmental stressors such as hypoxia occurring in *A. bimaculatus* environments (Menni et al. 1998; Maltchik & Medeiros 2006b) may reduce heat tolerance because the oxygen dependence of thermal tolerances (Verberk et al. 2016; Jung et al. 2020). During the pre-assays period, fishes were kept and acclimated to normoxic conditions (constant oxygen supplied). This could increase the ability to resist higher temperatures for individuals sampled in potentially more

hypoxic environments, especially at night (Díaz & Breitenburg 2011). In addition, we obtained our CT_{max} estimates in short-lasting assays, by employing a fast heating rate (1°C/min). Because CT_{max} are sensitive to the instrumental rate of heating (Rezende et al. 2011), longer and more ecologically realistic thermal tolerance assays at slow rates, they may decrease upper thermal tolerances (Mora & Maya 2006), thus reducing the warming tolerances. Further studies are required to examine the potential for thermal acclimation and the role of other stressors such as hypoxia in the expression of upper thermal tolerances for this extreme heated *A. bimaculatus* population, which ultimately may determine its local extinction in the coming decades.

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AUTHOR CONTRIBUTIONS

Andrés Egea-Serrano: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); resources (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Maiara C. Alves:** Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – original draft (equal). **Mirco Solé:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal). **Miguel Tejedo:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); methodology

(equal); resources (equal); supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

REFERENCES

- Beitinger T. L., Bennet W. A. & Mccauley R. W. (2000) Temperature tolerances of north American freshwater fishes exposed to dynamic changes in temperature. *Environ. Biol. Fishes* **58**, 237–75.
- Beitinger T. L. & Lutterschmidt W. I. (2011) Measures of thermal tolerance. In: *Encyclopedia of Fish Physiology* (ed A. P. Farrell) pp. 1695–702. Academic Press, San Diego.
- Campos D. F., Amanajás R. D., Almeida-Val V. M. F. & Val A. L. (2021) Climate vulnerability of south American freshwater fish: Thermal tolerance and acclimation. *J. Exp. Zool. A Ecol. Integr. Physiol.* **335**, 723–34.
- Chung K. S. (2000) Heat resistance and thermal acclimation rate in tropical tetra *Astyanax bimaculatus* of Venezuela. *Environ. Biol. Fishes* **57**, 459–63.
- Comte L. & Olden J. D. (2017) Evolutionary and environmental determinants of freshwater fish thermal tolerance and plasticity. *Glob Change Biol.* **23**, 728–36.
- Díaz R. J. & Breitenburg D. L. (2011) The expanding hypoxic environment. In: *Encyclopedia of Fish Physiology* (ed A. P. Farrell) pp. 1746–50. Academic Press, San Diego.
- Duarte H., Tejedo M., Katzenberger M. *et al.* (2012) Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. *Glob. Chang. Biol.* **18**, 412–21.
- Fangue N. A., Wunderly M. A., Dabruzzi T. F. & Bennett W. A. (2014) Asymmetric thermal acclimation responses allow sheepshead minnow *Cyprinodon variegatus* to cope with rapidly changing temperatures. *Physiol. Biochem. Zool.* **87**, 805–16.
- Froese R. & Pauly D., eds (2021) *FishBase*. World Wide Web Electronic Publication. Retrieved from www.fishbase.org, version (06/2021). Accessed 27 May 2022.
- Huey R. B., Kearney M. R., Krockenberger A., Holtum J. A. M., Jess M. & Williams S. E. (2012) Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology, and adaptation. *Philos. Trans. R. Soc. B* **367**, 1665–79.
- IBAMA (2006) *Plano de Manejo da Floresta Nacional Contendas do Sincorá, Volume I. Informações gerais sobre a Floresta Nacional*. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, Brasília.
- IPCC (2013) *Climate change 2013: the physical science basis. Working Group I Contribution to the 5th IPCC Assessment Report-Changes to the Underlying Scientific/* Technical Assessment. Retrieved from <http://www.ipcc.ch/report/ar5/wg1/#.UlbtvqK-2Sp>. Accessed 27 May 2022.
- Jung E. H., Brix K. V., Richards J. G., Val A. L. & Brauner C. J. (2020) Reduced hypoxia tolerance and survival at elevated temperatures may limit the ability of Amazonian fishes to survive in a warming world. *Sci. Total Environ.* **748**, 141349.
- Leahy L., Scheffers B. R., Williams S. E. & Andersen A. N. (2022) Arboreality drives heat tolerance while elevation drives cold tolerance in tropical rainforest ants. *Ecology* **103**, e03549.
- Lutterschmidt W. I. & Hutchison V. H. (1997) The critical thermal maximum: history and critique. *Can. J. Zool.* **75**, 1561–74.
- Maltchik L. & Medeiros E. S. F. (2006a) Conservation importance of semi-arid streams in North-Eastern Brazil: implications of hydrological disturbance and species diversity. *Aquat. Conserv.* **16**, 665–77.
- Maltchik L. & Medeiros E. S. F. (2006b) Diversidade, estabilidade e atividade reprodutiva de peixes em uma poça fluvial permanente no leito de um riacho efêmero, Riacho Avelós, Paraíba, Brasil. *Rev. Biol. Ciên. Terra Suplemento Especial* **1**, 20–8.
- Medeiros E. S. F., Ramos R. T. C., Ramos T. P. A. & Silva M. J. (2006) Spatial variation in reservoir fish assemblages along semi-arid intermittent river, Curimatau River, northeastern Brazil. *Rev. Biol. Ciên. Terra Suplemento Especial* **1**, 29–39.
- Menni R. C., Miquelarena A. M. & Gómez S. E. (1998) Fish and limnology of a thermal water environment in subtropical South America. *Environ. Biol. Fishes* **51**, 265–83.
- Mora C. & Maya M. F. (2006) Effect of the rate of temperature increase of the dynamic method on the heat tolerance of fishes. *J. Therm. Biol.* **31**, 337–41.
- Rezende E. L., Tejedo M. & Santos M. (2011) Estimating the adaptive potential of critical thermal limits: methodological problems and evolutionary implications. *Funct. Ecol.* **25**, 111–21.
- Rosa R. S., Menezes N. A., Britski H. A., Costa W. J. W. M. & Groth F. (2003) Diversidade, padrões de distribuição e conservação dos peixes da Caatinga. In: *Ecologia e Conservação da Caatinga* (eds I. R. Leal, M. Tabarelli & J. M. Cardoso da Silva) pp. 135–80. Universidade Federal de Pernambuco, Recife.
- Sanabria E. A., González E., Quiroga L. B. & Tejedo M. (2021) Vulnerability to warming in a desert amphibian tadpole community: the role of interpopulational variation. *J. Zool.* **313**, 283–96.
- Trape S. (2009) Impact of climate change on the relict tropical fish fauna of Central Sahara: threat for the survival of Adrar mountains fishes, Mauritania. *PLoS One* **4**, e4400.
- Verberk W. C. E. P., Overgaard J., Ern R. *et al.* (2016) Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **192**, 64–78.
- Vinagre C., Leal I., Mendonça V. *et al.* (2016) Vulnerability to climate warming and acclimation capacity of tropical and temperate coastal organisms. *Ecol. Indic.* **62**, 317–27.