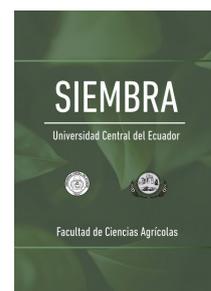


Ecophysiological observations on the body temperatures of the anurans *Dendropsophus bifurcus*, *Rhinella marina*, and *Scinax ruber* from upper basin Amazon in northeastern Ecuador

Observaciones ecofisiológicas sobre las temperaturas de cuerpo de los anuros *Dendropsophus bifurcus*, *Rhinella marina* y *Scinax ruber* de la Cuenca Amazónica Alta en el noreste de Ecuador



Marco A. Altamirano-Benavides^{1,2}, Guillermo A. Woolrich-Piña³

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¹ Universidad Central del Ecuador, Facultad de Ciencias Agrícolas. Jerónimo Leiton y Gato Sobral S/N. Ciudadela Universitaria. C. P. 170521. Quito, Pichincha, Ecuador.

✉ aaltamirano@uce.edu.ec

🌐 <https://orcid.org/0000-0002-3082-8103>

² Universidad Iberoamericana del Ecuador. Dirección de Investigación. Av. 9 de Octubre N25-12 y Colón. Quito, Ecuador.

✉ maltamirano@unibe.edu.ec

³ Tecnológico Nacional de México, Campus Zacapoaxtla. División de Biología, Subdirección de Investigación y Posgrado, Laboratorio de Zoología y Ecofisiología. Carretera Acuaco-Zacapoaxtla km. 8, Col. Totoltepec, Zacapoaxtla. C. P. 73680. Puebla, México.

✉ gwoolrich@live.itsz.edu.mx

🌐 <https://orcid.org/0000-0002-3421-7246>



*Corresponding author:
aaltamirano@uce.edu.ec

Abstract

Ectothermic inhabitants of tropical forests are subjected to constant environmental temperatures, which determine their passive thermoregulatory strategies. We observe these trends during the summer of 2017, in the anurans *Dendropsophus bifurcus*, *Rhinella marina*, and *Scinax ruber*, in a tropical rainforest from the Upper Amazon Basin of Ecuador. *D. bifurcus* and *S. ruber* showed a tendency to tigmothermy, whereas *R. marina* presented tendencies towards heliothermy. Body temperatures (T_b s) did not differ between *D. bifurcus* and *R. marina*, but *S. ruber* presented a lower T_b . Our results suggest that thermal environment is influencing different thermoregulatory strategies as tigmothermy and heliothermy of frogs and toads distributed in tropical environments at low elevation.

Keywords: Amazon, anurans, field body temperatures, thermoconformers, thermoregulation

Resumen

Los ectotermos que habitan los bosques tropicales están sujetos a temperaturas ambientales constantes, lo cual determina que sus estrategias termoregulatorias sean pasivas. Estas tendencias termoregulatorias fueron observadas durante el verano del 2017 en los anuros *Dendropsophus bifurcus*, *Rhinella marina* y *Scinax ruber*, en un bosque tropical de la cuenca amazónica alta del Ecuador. Una tendencia a la tigmotermia se presentó en *D. bifurcus* y *S. ruber*, mientras que *R. marina* presentó tendencia hacia la heliotermia. Las temperaturas de cuerpo (T_b s) no difirieron entre *D. bifurcus* y *R. marina*, pero *S. ruber* mostró una baja T_b . Nuestros resultados sugieren que el ambiente termal influencia las diferentes estrategias termoregulatorias como la tigmotermia y la heliotermia en ranas y sapos distribuidos en ambientes tropicales de baja elevación.

Palabras clave: Amazonía, anuros, temperaturas de cuerpo en campo, termoconformistas, termoregulación.

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1. Introduction

Body temperature (T_b) is a critical ecophysiological variable affecting the performance of ectotherms because intrinsic aspects of ecology, behavior and physiology are sensitive to T_b (Huey, 1982; Huey & Stevenson, 1979), including reproduction (Adolph & Porter, 1993), foraging (Ayers & Shine, 1997), growth (Kingsolver & Woods, 1997), locomotion (Ojanguren & Braña, 2000), and courtship (Navas & Bevier, 2001).

Ectotherms can exhibit heliothermy or tigmothermy, obtaining energy by direct exposure to the sun or by direct contact with the substrate, respectively (Garrick, 2008). Tigmothermy has been recognized for species living in tropical rainforests and nocturnal species (Belliere & Carrascal, 2002). For species living in forests, there is a thermal refuge on the effect of the surrounding climate, creating particular microclimate conditions (higher relative humidity and lower temperatures respect to open habitats that allows avoid overheating and dehydration (Gaudio et al., 2017). Thus, some tropical forest ectotherms appear to be relatively passive with respect to environmental temperatures and behave as thermoconformers (Huey & Webster, 1976; Kohlsdorf & Navas, 2006).

The Western Amazon basin (Ecuador, Perú, and Colombia) has the higher diversity of amphibian (Frost, 2023; Vigle, 2008). Near of the Ecuadorian Amazon there are published studies on herpetofauna for several locations. Duellman (1978), showed that the herpetofauna of Santa Cecilia, on the Río Aguarico, Province of Napo, is composed of 173 species; Lescure and Gasc (1986) compared the spatial distribution between assemblages of lizards and anurans along the Río Putumayo and Ampiyacu (Perú), Igaraparana (Colombia), and Santa Cecilia Ecuador); Almendáriz (1987) reported 101 species of amphibians and reptiles of the Province of Pastaza (Ecuador); Duellman and Mendelson (1995) reported 68 amphibian and 46 reptile species north of the Department of Loreto in the Amazonian Perú. Izquierdo et al. (2000) found 34 amphibian and 27 reptile species in the Province of Sucumbios (Ecuador); however, data on the thermal biology of ectotherms in this region are insufficient. We explored the basic thermal biology of three frogs and their ecological implications in northeastern Ecuador. We describe here below the relationships among T_b and microenvironmental temperatures (e.g., Huey & Slatkin, 1976).

2. Materials and Methods

2.1 Study area

Fieldwork was carried out on July 16th and 17th, 2017, in the surroundings of the Juri-Juri Kawsay Amazon Scientific Station, located in the Protected Forest of Oglán Alto, Arajuno Canton, province of Pastaza, Ecuador (77.688583°N, 01.324152°W, Datum WGS84, elevation 604 m) (Figure 1). The local vegetation is premontane pluvial forest characterized by emergent trees (e.g., *Ceiba pentandra*, *Pachira insignis*, *Ficus perisiana*, and *Otoba parviflora*, among others); as well as abundant mosses and liverworts in the leaves and branches of the arboreal and shrubby vegetation (Cerón Martínez et al., 2007). Mean annual temperature is 18-24 °C, and annual precipitation ranges between 4,000 and 8,000 mm per year (Cerón Martínez et al., 2007).

2.2 Study species

Dendropsophus bifurcus (Figure 2-A) is distributed from the northwestern part of the Amazon Basin in Colombia, Ecuador and northern Perú (Jungfer et al., 2010). The native range of *Rhinella marina* (Figure 2-B) extends from the East Andes to Central Amazonia (Acevedo et al., 2016) although they have established populations in Australia, Eastern Asia and several islands of the Caribbean and the Pacific, as the result of translocations by humans (Lever, 2001); *Scinax ruber* (Figure 2-C) is widely distributed throughout the Guianas and Amazonia (Fouquet et al., 2007).

2.3 Body temperature

We collected 11 *D. bifurcus*, 17 *R. marina*, and 37 *S. ruber* (listening and following the direction of their songs, or through direct search in potential microhabitats: e.g. along water reservoirs, on stems, leaves, leaf litter, and logs, principally), by hand from 1,800 to 2,300 h (all individuals were active at the time of capture).

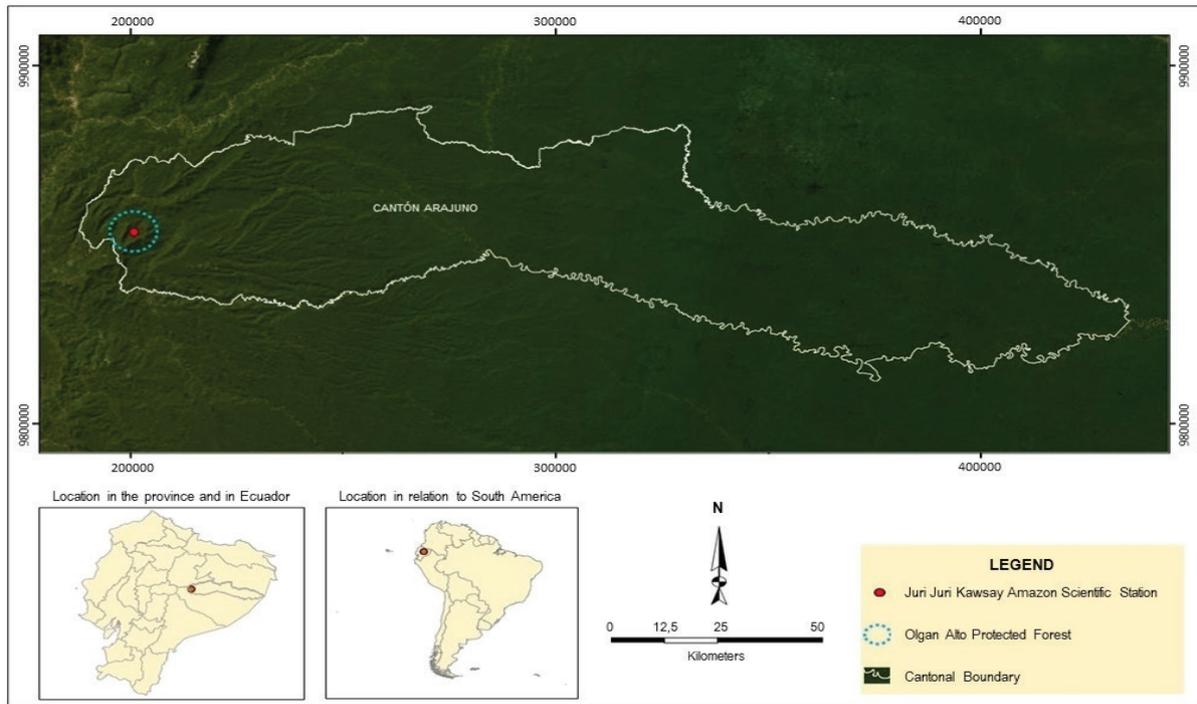


Figure 1. Map of study area.



Figure 2. Study species.

Immediately upon capture, we measured body temperature (T_b), holding tightly on the tarsi to carefully insert a thermocouple into the vent. Air temperature (T_a) was recorded by placing the thermocouple 1 cm above substrate where the individual was first seen, and substrate temperature (T_s) was measured touching the substrate where individual first observed to the nearest 0.1°C with a thermocouple type K connected to quick-reading digital thermometer (Fluke 51-II®). T_b , T_a , and T_s were recorded during the first 5 seconds of the thermometer reading. On both days, the frogs and toads collection preceded intense rains, at temperatures close to 25°C and relative humidity around 80 %. All organisms that required a capture time > 1 min were excluded from the statistical analyzes.

2.4 Statistical analysis

We used linear multiple regression [MLR] and best subsets regression [BSR] analysis for selecting the variables of MLR by systematically searching through the different combinations of T_a and T_s and selecting the subsets of variables that best contribute to predicting T_b for each species. We used the values of R^2 by BSR as best criterion to establish tigmothermy or heliothermy tendencies: if R^2 was higher between T_b vs T_a it indicates heliothermy, but if R^2 is higher between T_b vs T_s is a tendency to tigmothermy. On the other hand, we use the value of the slopes generates by BSR to establish active thermoregulation, or passive thermoregulation (thermoconformers)

tendencies: if T_b vs $T_a - T_s$ is close to zero, the organisms are active thermoregulators. If the value of the slope between T_b vs $T_a - T_s$ is close to one, the organisms are thermoconformers (criterion of Huey & Slatkin, 1976). We used ANOVA and Bonferroni t-test post-hoc to compare T_a and T_s with the three species. To test the difference in T_b s among species, we realized a covariance analysis [ANCOVA], using T_s as covariable.

3. Results

Means T_b , T_a and T_s for each species are detailed in Table 1. The best equations obtained by BMR that explained the thermal relationships were: $T_b = 8.39 + 0.74 * T_s$ ($R^2 = 0.27$, $p > 0.05$, $n = 11$); $T_b = 4.79 + 0.86 * T_a$ ($R^2 = 0.51$, $p < 0.05$, $n = 17$); and $T_b = 2.14 + 0.96 * T_s$ ($R^2 = 0.71$, $p < 0.05$, $n = 37$) for *D. bifurcus*, *R. marina*, and *S. ruber*, respectively.

Table 1. Mean T_b , T_a , and T_s for *D. bifurcus*, *R. marina*, and *S. ruber* from Juri-Juri Kawsay Amazon Scientific Station, province of Pastaza, northeastern Ecuador. Means are given \pm 1 S.E. In brackets are the minimum and maximum temperatures.

Species	T_b	T_a	T_s
<i>D. bifurca</i>	25.2 \pm 0.5 °C (23.2 - 28.3)	22.8 \pm 0.3 °C (21.4 - 24.3)	22.8 \pm 0.3 °C (21.3 - 24.3)
<i>R. marina</i>	25.8 \pm 0.5 °C (22.6 - 31.2)	24.5 \pm 0.4 °C (21.9 - 24.3)	25.4 \pm 0.5 °C (22.9 - 30.3)
<i>S. ruber</i>	23.2 \pm 0.6 °C (18.1 - 29.9)	21.5 \pm 0.4 °C (17.9 - 27.8)	22.0 \pm 0.5 °C (17.9 - 30.3)

Thermoconformity tendencies are observed in the three species; tigmothermy tendencies are presented by *D. bifurcus* and *S. ruber*, and a heliothermy tendency is presented by *R. marina*. T_s did not present differences between species (ANOVA; $F_{2,65} = 0.84$, $p > 0.05$), while T_a presented significant differences for the three species (ANOVA; $F_{2,65} = 11.39$, $p < 0.05$; Table 2). We observed different T_b s among the species (ANCOVA with T_s as the covariate; $F_{1,44} = 4.16$, $p < 0.05$).

Table 2. Differences in T_a between the three species. All Pairwise Multiple Comparison Procedures (Bonferroni t-test). Overall significance level = 0.05.

Comparison	Diff of Means	t	$p < 0.05$
T_a <i>R. marina</i> vs. T_a <i>S. ruber</i>	3.046	4.765	Yes
T_a <i>R. marina</i> vs. T_a <i>D. bifurcus</i>	1.906	2.420	No
T_a <i>D. bifurcus</i> vs. T_a <i>S. ruber</i>	1.141	1.666	No

4. Discussion

Dendropsophus bifurcus.-- The mean T_b of *D. bifurcus* (25.2 \pm 0.5 °C; 23.2 - 28.3; $n = 11$), was within the range of T_b s observed for other *Dendropsophus* species found at lower elevation, range from 24.8° to 25.8°C (Navas et al., 2013), but higher than those found in the mountain, range from 12.2° to 15.8°C (Navas, 1996). Considering our observations on the T_b s of *D. bifurcus*, we suggest that it is not different from the other congeners that inhabit tropical sites at low altitudes (≤ 90 m): *D. ebraccatus* (24.8 °C); *D. microcephalus* (25.8 °C), and altitude can be a limiting factor to reach T_b s greater than 20 °C: *D. labialis* (15.8 °C and 12.2 °C at 2,900

meters; 14.7 °C and 10 °C, at 3,500 meters; Navas et al., 2013). Considering the values of BMR, we suggest that *D. bifurcus* showed tendencies towards thermoconformity and tigmothermy (Huey & Slatkin, 1976).

Rhinella marina. -- The mean T_b for this species (25.8 ± 0.5 °C; 22.6 - 31.2; $n = 17$), is similar to other populations, range 24.2 - 27 °C, mean 25.2 °C; (Brattstrom, 1963). Under controlled conditions, at a humidity close to 80%, *R. marina* presented a similar T_b , which could indicate the optimal physiological for this species (Malvin & Wood, 1991). We observed that T_b s were higher than others congeners (*R. spinulosa*) distributed at different altitudes in the North, Center, and South of Chile: 19.8 °C, near to 2,469 meters; 20.7 °C, at 2,390 meters; and 20.3 °C, at 1,410 meters, respectively (Alveal Riquelme, 2015); *Rhinella arenarum* (18.3 °C, around 730 meters) in Argentina (Sanabria et al., 2011); and *Rhinella schneideri* (20.8 °C, near to 630 meters) in Brazil (Noronha-de-Souza et al., 2015). However, these T_b s fell within the activity ranges, because below 13.7 °C and above 37.4 °C, their locomotion is limited (Kearney et al., 2008). BMR showed trends towards heliothermy and thermoconformity, this trend is similar in invasive populations inhabiting the tropical east coast of Australia (Seebacher & Alford, 2002).

Scinax ruber.-- The mean T_b in this study (23.2 ± 0.6 °C; 18.1 - 29.9; $n = 37$), was lower that observed for other population: 24.1 °C, at 218 meters of elevation (Romero Barreto, 2013), but higher than *S. fuscovarius* and *S. hiemalis* distributed at higher altitudes, 22.5 °C, at 1,800 meters, and 12.5 °C, 1,200 meters, respectively (Navas & Araujo, 2000). Our results may suggest that altitude is a determining factor in the T_b s presented by different populations of *Scinax* frogs, observing a decline in T_b s with elevation at tropical latitudes (Andrews, 1998; Janzen, 1967). BMR showed trends towards tigmothermy and thermoconformity, a tendency similar to *S. acuminatus* and *S. nasicus* from Argentina (Novo, 2009).

Species comparison.-- T_b s observed in *D. bifurcus*, and *R. marina* were similar, contrary to *S. ruber* which had a significantly lower T_b . The locomotor performance dependent of T_b can explain these differences, since the best performance has been observed at T_b s close to the one presented by *R. marina* (Malvin & Wood, 1991), and other *Scinax* species in similar environments (Navas et al., 2008). In tropical forests, at low elevations, T_b s tend to be stable (Navas et al., 2008), thus the thermoconformity tendency of the three species can obey to variation of few degrees between the coldest and the warmest month in tropical latitudes (Janzen, 1967), shade forest environments (Huey, 1974), and high thermal quality reported for tropical environments (Vickers et al., 2011); while the tigmothermy tendency presented by *D. bifurcus* and *S. ruber* is characteristic of shade-dwelling organisms (Ruibal, 1961), and heliothermy presented by *R. marina* seems a strategy to avoid potential impacts of thermal stressor on physiology, ecology and survival (Narayan & Hero, 2014).

Our results suggest that thermal environment is influencing different thermoregulatory strategies, such as the tigmothermy and heliothermy of frogs and toads distributed in tropical environments at low elevation. Further studies are needed, specifically focused on the effect of both, deforestation at local scale, and climate change at regional scale on these thermoregulatory strategies and performance at different T_b s.

5. Conclusions

The observations on T_b s of *D. bifurcus*, show that it is not similar to the other congeners that inhabiting tropical sites at low altitudes (≤ 90 m), yet it is higher than the one observed for those from high altitudes (over 2,900 m elevation). Thus, the values of BMR, suggest that *D. bifurcus* present tendencies towards thermoconformity, and tigmothermy.

The mean T_b for *R. marina* was 25.8 ± 0.5 °C (22.6 - 31.2; $n = 17$); a similar T_b was exhibited under controlled conditions, at a humidity close to 80%, which could indicate the optimal physiological for this species. Also, its mean T_b is higher than the one recorded within other populations at similar altitudes (600-700 m elevation), but in different geographical areas of South America. Moreover, the mean T_b of this toad is higher than others congeners distributed at altitudes over 1,410 meters. The values of BMR showed trends towards heliothermy, and thermoconformity.

The mean T_b for *S. ruber* in this study was 23.2 ± 0.6 °C (18.1 - 29.9; $n = 37$), being reduced than other population at lower elevations, but higher than other congeners distributed over 1200 meters of altitude. These results may suggest that altitude is a determining factor in the T_b s, observing a decline in temperatures with elevation at tropical latitudes. The values BMR showed trends towards tigmothermy and thermoconformity.

The T_b s observed in *D. bifurcus*, and *R. marina* were similar contrary to *S. ruber* which showed a T_b significantly lower. Thus, the thermoconformity tendency of the three species may obey mainly to variation of

few degrees between the coldest and the warmest month in tropical latitudes; while the tigmothermy tendency presented for *D. bifurcus* and *S. ruber* is more characteristic of shade-dwelling organisms, and finally, heliothermy presented for *R. marina* seems a strategy to avoid potential impacts of thermal stressor on physiology, ecology, and survival.

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Contributor Roles

- Marco A. Altamirano-Benavides: conceptualization, investigation, methodology, funding acquisition, resources, project administration, writing – review & editing.
- Guillermo A. Woolrich-Piña: investigation, formal analysis, methodology, validation, visualization, writing – original draft, writing – review & editing.

Ethical Issues

Research authorization AC-FAU-DPAP/MAE-2017-006 by Ministerio del Ambiente del Ecuador-Pastaza office.

Conflict of Interest

The authors declare that they have no affiliation with any organization with a direct or indirect financial interest that could have appeared to influence the work reported.

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