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Dehydration Hardly Slows Hopping Toads (*Rhinella granulosa*) from Xeric and Mesic Environments

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ABSTRACT

The locomotor capacity of amphibians depends strongly on temperature and hydration. Understanding the potential interactions between these variables remains an important challenge because temperature and water availability covary strongly in natural environments. We explored the effects of temperature and hydration on the hopping speeds of *Rhinella granulosa*, a small toad from the semiarid Caatinga and the Atlantic Rain Forest in Brazil. We asked whether thermal and hydric states interact to determine performance and whether toads from the Caatinga differ from their conspecifics from the Atlantic Forest. Both dehydration and cooling impaired hopping speed, but effects were independent of one another. In comparison to performances of other anurans, the performance of *R. granulosa* was far less sensitive to dehydration. Consequently, dehydrated members of this species may be able to sustain performance through high body temperatures, which agrees with the exceptional heat tolerance of this species. Surprisingly, toads from both the Caatinga and the Atlantic Forest were relatively insensitive to dehydration. This observation suggests that migration or gene flow between toads from the forest and those from a drier region occurred or that toads from a dry region colonized the forest secondarily.

Introduction

Locomotion plays a critical role in the ecology of many vertebrate lineages through its influence on survival (Husak 2006a; Calsbeek 2008; Irschick et al. 2008), foraging (Higham 2007), escape (Walker et al. 2005; Husak 2006b), territoriality (Calsbeek and Cox 2010), and mating (Husak et al. 2006). More than just a product of morphology and physiology, locomotion also depends on the abiotic environment, especially for ectothermic animals (Angilleta et al. 2002). For amphibians, locomotor performances strongly depend on environmental temperature and water availability. Low temperatures and poor hydration reduce exercise capacity by slowing heart rate, cellular metabolism (Whitford 1973; Carey 1979; Hillman 1984; Gatten 1987), and muscular activity (Renaud and Stevens 1981; Hillman 1982; Navas et al. 1999). Consequently, cool or dehydrated individuals move more slowly (Prest and Pough 1989, 2003; Titon et al. 2010) and fatigue more rapidly (Moore and Gatten 1989) when exercising. Thermal and hydric constraints have broad effects on the ecology of terrestrial amphibians, whose body temperatures change with environmental conditions (Navas 1996; Seebacher and Alford 2002) and whose skin has evolved to be permeable (Lillywhite 2006).

Hydrated anurans jump better at higher temperatures within the range of body temperatures typical for vertebrate ectotherms (Navas et al. 2008). However, the influence of environmental factors on locomotion can be complicated by interactive effects. Hydration state can change responses to thermal variation, sometimes leading to similar levels of performance at different combinations of temperature and hydration. For instance, moderately dehydrated cricket frogs (*Acris crepitans*) at low temperatures jumped as well as hydrated individuals at high temperatures (Walvoord 2003). In cane toads (*Rhinella marina*), dehydration decreased hopping endurance more at higher temperatures (Prest and Pough 1989). Understanding the ecological significance of these interactions constitutes an important challenge because organisms experience covariation of multiple factors in nature.

Although such interactive effects possibly reflect constraints in amphibian physiology, they might also involve ecological benefits. Dehydrated anurans may reduce losses on performance by favoring lower body temperatures (Beuchat et al. 1984; Prest and Pough 1989, 2003; Walvoord 2003). However, studies performed to date have focused on species from mesic environments. In contrast to these species, those from extreme thermal environments (both hot and cold) should have limited ecological opportunities for thermoregulation (Sinsch 1989; Navas 1996; Navas et al. 2007; Sanabria et al. 2011). To assess whether interactions between body temperature and hydration

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correlate with different ecological settings, we evaluated the hydric and thermal sensitivities of locomotor performance in *Rhinella granulosa* Spix 1824 (previously *Bufo granulosis*) from both the semiarid Caatinga and the Atlantic Rain Forest in northeastern Brazil. We addressed several questions regarding the sensitivity of locomotor performance to environmental factors. Do thermal and hydric states affect hopping speeds in *R. granulosa*? Do the two populations possess different sensitivities to these factors? Do thermal and hydric states interact to influence locomotion in this species? And, if so, is this interaction similar for toads from the Atlantic Forest and those from the Caatinga?

Material and Methods

Experimental Animals and Environments

Rhinella granulosa has been observed to be predated by snakes (Santos et al. 2010; Ribeiro and Freire 2012) and birds (Mesquita 2009) with no signs of poisoning their predators. Contrasting with larger species in the genus, this species has diminutive paratoid poison macroglands (Narvaes and Rodrigues 2009) and uses short hops to flee when threatened. These observations motivated us to measure hopping speeds as an ecologically relevant index of locomotor performance.

This small bufonid occurs in both the Atlantic Forest and the semiarid Caatinga in northeastern Brazil. The former consists of dense ombrophilous or semideciduous vegetation, which experiences an annual precipitation of 1,200–1,800 mm and a mean annual temperature of 18°–23°C (INMET 1990; Morellato and Haddad 2000). By contrast, the Caatinga is a semiarid environment characterized by xerophytic vegetation, unpredictable rainfall (usually between 300 and 800 mm yr⁻¹), and high mean temperatures (26°–28°C). In the Caatinga, dry years occur occasionally and sometimes sequentially (Reis 1976; INMET 1990). Individuals of *R. granulosa* from a Caatinga population have been reported to be active during the day on soils exceeding 40°C (Navas et al. 2007).

Toads from the Atlantic Forest were collected at Ilhéus, in the state of Bahia, whereas those from the Caatinga were collected at Angicos, in the state of Rio Grande do Norte; both sites are located in northeastern Brazil. Toads were collected in February 2006, which corresponds to the beginning of the rainy season in both localities. Our experiment began within a week of capture to minimize acclimatization to laboratory conditions. We used 17 toads from the Atlantic Forest (mean mass = 6.92 g, range = 3.55–13.01 g) and 21 toads from the Caatinga (mean mass = 5.94 g, range = 3.54–9.83 g) for our experimental treatments. An additional 14 toads from the Caatinga (mean mass = 5.84 g, range = 2.61–10.84 g) were used as a control group (see below). Before the experiment, toads were kept in terraria (80 cm × 30 cm × 35 cm) with rocks and roofing tiles as shelters. A photoperiod of 14L : 10D and daily temperature range of 22°–27°C was maintained. Toads were fed cockroaches and mealworms while in captivity but fasted for 2 d before experiments.

Experimental Design and Locomotor Trials

To measure hopping speeds, we used a stopwatch to record the time that each toad took to hop along a 1-m track. Each toad was assessed at two body temperatures (20° and 30°C) and several hydration states, ranging from fully hydrated to severely dehydrated (see below). Thermal treatments were imposed on separate days with a day of rest in between. To avoid confounding temporal and thermal effects, toads from each population were divided in two sets that experienced the thermal treatments in opposite orders. Between these treatments, toads were kept in terraria with access to water.

The experiment was performed in a walk-in climatic chamber with an air temperature equal to the test temperature. Before starting the experiment, we hydrated toads for 2 h by placing them inside plastic containers with 2 cm of aged tap water. Since cannulation of urinary bladder is a complicated and dangerous procedure in small anurans, we did not estimate standard masses (sensu Ruibal 1962); however, toads were stimulated to urinate before trials through manual pressure on the abdomen. Toads were patted dry with a paper towel, and their hydrated mass was recorded (± 0.01 g). We visually inspected plots of hydration state versus time of experimentation for every individual. Since evaporative water loss was always linear throughout the trials, we considered sudden decreases in body mass as an indication of urination. Toads that urinated during a trial were removed from the analyses.

To stimulate hopping, we gently tapped each toad's posterior and repeated this stimulation as needed to encourage the toad to reach the end of the track. We performed 6–7 hopping trials for each individual, with the first three trials occurring at intervals of 30 min and the following trials occurring at intervals of 60 min. Between trials, toads were kept individually in nylon net bags on a dry surface. Since these bags permitted evaporation, toads lost an average of 3.7% of their body mass (range = 1%–7%) between each run. Experiments were performed until toads reached 75%–80% of their initial body mass, after which recovery proved difficult and individuals occasionally died. Some toads reached this state of hydration after six trials, while others took seven trials to do so. For the control group, we kept toads inside plastic containers with 2 cm of tap water between trials. All measurements were taken between 1400 and 1900 hours.

Data Analysis

We used linear mixed models to estimate the effects of hydration, temperature, group (or population), and snout-vent length on the hopping speed of *R. granulosa* (Zuur et al. 2009). Hydration (percentage of initial body mass) was a covariate; temperature (20° or 30°C) and group (Caatinga, Atlantic Forest, or control) were fixed factors. Individual was a random factor. We explored the potential effect of fatigue during the experiment by including time of experimentation as a covariate. Initially, we modeled all main effects and interactions. Then, we removed nonsignificant terms from the highest order to the

lowest order until the most parsimonious model was obtained (Crawley 2005; Zuur et al. 2009). Model selection was based on the Akaike Information Criterion (AIC; Burnham and Anderson 2002). Mixed modeling was performed using the *nlme* library of the R statistical package (Pinheiro et al. 2011). Before analysis, the normality of data was assessed by plotting distributions of variables and residuals, as well as by measures of skew and kurtosis.

Results

The most likely statistical model indicated that hopping speed varied among individuals (a random effect estimated to correspond to a SD of 0.044 m s^{-1}) but was unrelated to snout-vent length. Table 1 presents the effects of hydration state, time of experimentation, temperature, and group (Caatinga, Atlantic Forest, or control) on the hopping speeds of *Rhinella granulosa*. A significant time effect indicated that hopping speed decreased among consecutive trials independently of hydration state, suggesting that toads fatigued over the course of the experiment. The model excluded an interaction between time and group, indicating that control and experimental groups were affected by fatigue in the same way. After accounting for this temporal effect, changes in hydration still affected hopping speed significantly (table 1). The effect of hydration on hopping speed differed among the three groups (fig. 1), but toads from the Caatinga and the Atlantic Forest did not differ significantly in their locomotor response to dehydration (table 1). An interaction term between group and hydration suggested that toads from the Caatinga and the Atlantic Forest hopped slower as they lost water throughout the experiment ($\approx 0.1 \text{ cm s}^{-1}$ for each 1% of body mass lost), while toads in the control group hopped slower as they gained water throughout the experiment ($\approx 0.1 \text{ cm s}^{-1}$ for each 1% of body mass gained; from table 1).

Thus, dehydration below initial levels impaired performance, but hydration above initial levels also impaired performance. We found no evidence that hydration affected hopping speed differently at 20° and 30°C (i.e., the best model excluded an interaction between temperature and hydration). As expected, temperature positively affected performance (fig. 1); when accounting for body hydration, toads hopped three times faster at 30° than they did at 20°C (from table 1, by comparing the 30°C coefficient to the intercept value).

Discussion

Both cooling and dehydration impaired the hopping performance of *Rhinella granulosa*, as has been observed for other anurans (John-Alder et al. 1989; Moore and Gatten 1989; Navas 1996; Wilson 2001; Titon et al. 2010; Tingley et al. 2012). However, we found no evidence that temperature and hydration interact to determine hopping speed in this species. By contrast, dehydration had a greater impact on the hopping performance of cane toads at 30° than it did at 15°C (Preest and Pough 1989). Similarly, dehydrated cricket frogs at 15° surprisingly jumped as well as fully hydrated individuals at 30°C (Walvoord 2003). Although methodological differences among studies are a possible source of disparity (Preest and Pough 2003), interactions between environmental factors seem to be species specific, possibly due to habitat, behavior, or life history. For instance, the sensitivity of locomotion to dehydration is lower at 15° than at 25° or 35°C for the winter breeder *Rhinella icterica*, while the locomotion of *Rhinella ornata*, a species with broader reproductive season, shows high sensitivity to dehydration throughout this same range of temperatures (Titon et al. 2010).

Since anurans may reach similar speeds at different combinations of temperature and hydration (Walvoord 2003), dehydrated individuals could reduce losses in performance

Table 1: Parameters of the best general linear mixed model fitted to data for locomotor performance of *Rhinella granulosa*

Effect	Coefficient	SE	df	P
Intercept	.0307	.0452	482	.50
Group (control)	.2394	.0940	482	.01
Group (Atlantic Forest)	.0466	.0530	482	.38
Temperature (30°C)	.0958	.0090	97	<.0001
Time (min)	-.0001	<.0001	482	.04
Hydration state (% mass)	.0011	.0005	482	.02
Group (control) \times hydration state	-.0024	.0010	482	.01
Group (Atlantic Forest) \times hydration state	-.0004	.0006	482	.43

Note. Coefficients are expressed in meters per second and denote variation in hopping speeds with reference to the intercept value. The intercept represents the predicted speed of a hypothetical toad from the Caatinga with a hydration state of 0% of body mass and body temperature of 20°C . For covariates, coefficients denote the variation in hopping speed resulting from an increase of one unit of the predictor variable (time or hydration state). For instance, a 1% increase in hydration results in a 0.0011 m s^{-1} increase in the speed of Caatinga toads (represented by the intercept). For fixed factors, coefficients denote the variation of hopping speed as an effect of being assigned to a given category (of group or temperature). For instance, a toad from the control group is $\approx 0.24 \text{ m s}^{-1}$ faster than one from the Caatinga group (represented by the intercept). Group \times hydration state refers to an interaction term between group (in parentheses) and body hydration, denoting a group-specific response to a 1% increase in hydration. Effects are additive (i.e., predicted speeds can be calculated by summing coefficients). The random effect of individual was estimated to be a SD of 0.044 m s^{-1} .

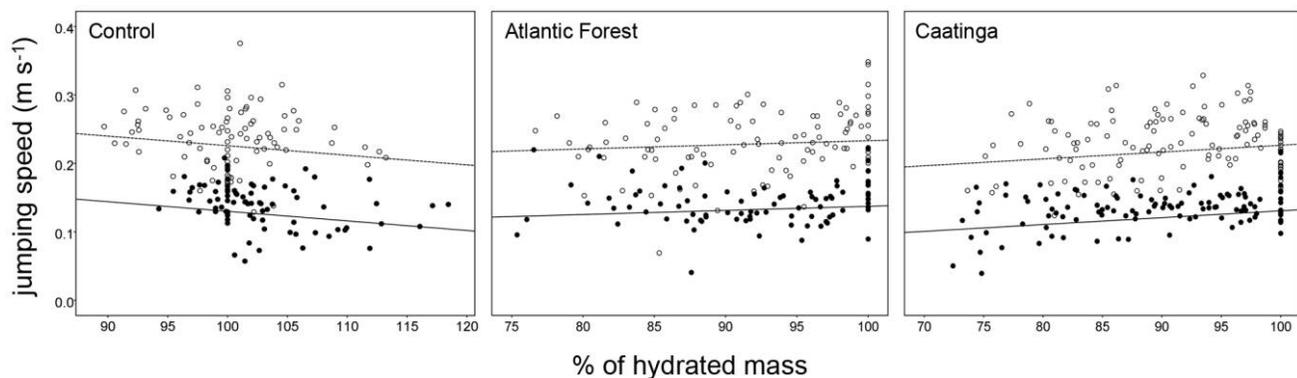


Figure 1. Hopping performance decreased with water loss in toads subjected to dehydration. The plot depicts linear models fitted to data for a control group and two experimental populations, Atlantic Forest and Caatinga, as estimated by general linear mixed modeling. All groups were tested at 20° (solid lines, filled circles) and 30°C (dashed lines, open circles). Data were adjusted for random variation among toads and for time effects related to fatigue, allowing for a direct ascertainment of the relationship between hopping speed (m s^{-1}) and hydration state (expressed as percentage of initial body mass).

through thermoregulation. In fact, several species select lower temperatures when dehydrated (Shoemaker et al. 1989; Tracy et al. 1993; Williams and Wygoda 1993) or in dry conditions (Malvin and Wood 1991), and species that are more prone to dehydration tend to select lower temperatures than less vulnerable ones (Tracy and Christian 2005). However, lower temperatures would probably not benefit *R. granulosa*, as dehydration effects on hopping speed were independent of body temperature. Instead, we expect that *R. granulosa* might maintain higher body temperatures to offset the effect of dehydration. Interestingly, *R. granulosa* exhibits the highest critical thermal maximum reported for toads ($>42.5^{\circ}\text{C}$; Navas et al. 2007). The absence of an interaction between temperature and hydration may help this species to survive in xeric environments, where occasional exposure to very high temperatures may occur. Nevertheless, it is important to note that higher body temperatures in *R. granulosa* could also lead to increased rates of evaporative water loss (Buttemer and Thomas 2003).

We found that hopping speed also decreased among trials independently of water loss, which suggests that toads fatigued. Anaerobic locomotion, such as rapid jumping, depletes energy and generates lactate within muscles, both of which can impair subsequent performance. Anurans require minutes to hours to remove the majority of the lactate accumulated in blood after brief exercise (Gleeson 1996). Therefore, the interval that we applied between trials (30–60 min) might have been insufficient for lactate removal in *R. granulosa*, which could explain the decrease in performance not related to dehydration (table 1). To test for the possibility that fatigue might have obscured the actual relationship between hydration state and performance, we used a control group of toads that were not subjected to dehydration while experiencing fatigue. Fatigue effects were the same for this group and both Caatinga and Atlantic Forest toads, as revealed by the rejection of an interaction term between group and time in our AIC-based procedure of model selection. By factoring out fatigue effects, the model allows for

an ascertainment of the relationship between hydration state and locomotor performance (fig. 1). Furthermore, the low sensitivity of *R. granulosa* locomotion to dehydration (see below) is a robust (and also a conservative) finding with respect to fatigue because fatigue would actually exaggerate the negative effects of dehydration over performance.

In the control group, the decrease in performance with increasing hydration probably stemmed from overweighting. If so, maximal speed cannot be reached at the maximal hydration state. From the perspective of locomotion, hydration above the level that enables maximal performance could merely constitute additional mass to transport (Beuchat et al. 1984). As a consequence, animals may regulate hydration at submaximal levels when foraging, a hypothesis that can be tested through field studies. Interestingly, some individuals of the control group reached hydration levels different from 100% (fig. 1). Body hydration fluctuated despite obligatory contact with water, with toads both gaining and losing small amounts of water between trials. This finding agrees with previous suggestions that complete hydration in anurans is in fact a state of dynamic equilibrium (Jørgensen 1994a, 1994b). These studies also found that terrestrial anurans perform anticipatory cutaneous drinking, taking in water before they in fact become dehydrated.

Dehydration affected hopping speed much less than temperature did. For example, even if a Caatinga toad dehydrates to 75% of its initial mass value (which occasionally resulted in death), speed should decrease by only 2.75 cm s^{-1} (from table 1). At 30°C, the speed of Caatinga toads dehydrated by 20% is only $\approx 10\%$ slower than that of fully hydrated animals from the same group. By contrast, previous studies of other anurans found that both brief (Walvoord 2003) and sustained (Preest and Pough 1989; Titon et al. 2010) jumping were profoundly affected by dehydration. For instance, the same level of dehydration (20%) at the same temperature (30°C) reduced the distance of single jumps by 40% in cricket frogs (Walvoord 2003) and reduced the distance that *Rhinella marina* could hop

in 10 min by 55% (Preest and Pough 1989). The low locomotor sensitivity to dehydration exhibited by *R. granulosa* might contribute to its success in the dry Caatinga. Interestingly, endurance performance of savannah-associated *Rhinella schneideri* had lower sensitivity to dehydration than that of forest-restricted *R. icterica* and *R. ornata*, at both 25° and 35°C (Titon et al. 2010). Still, body temperature and hydration interactively affected endurance performance in these three species, which contrasts with our data on *R. granulosa*.

Contrary to our expectations, we found no differences in thermal and hydric sensitivities between toads from the Caatinga and toads from the Atlantic Forest. Toads from the Atlantic Forest possess traits that presumably confer advantages in hot, dry conditions. Several hypotheses emerge from this observation. First, toads from a xeric region could have colonized the forest, bringing with them traits that confer benefits in dry regions. Second, gene flow might occur between toads from xeric and forested regions, transferring alleles for dehydration tolerance between populations. Finally, dehydration tolerance could be genetically correlated with traits that benefit toads in the forest. Regardless of the cause, we are not the only researchers who failed to detect physiological divergence among populations from contrasting environments. John-Alder et al. (1989) observed no significant difference between the thermal sensitivities of swimming by spring peepers (*Pseudacris crucifer*) from northern and southern populations. Moreover, thermal physiologies of reptilian species can be highly conserved over wide geographic ranges (Hertz et al. 1983; Crowley 1985; Van Damme et al. 1989). These observations suggest that costs or constraints prevent the divergence of locomotor physiology within ectothermic species. Nevertheless, two exceptional cases of physiological divergence within species of anurans have been documented: tropical populations of striped marsh frogs (*Limnodynastes peronii*) jumped better at higher temperatures than temperate populations, and vice versa at lower temperatures (Wilson 2001); and invasive cane toads in the Australian semiarid present higher endurance and longer jump distances than mesic-area conspecifics when dehydrated by 20% of the initial body mass (Tingley et al. 2012).

Dehydration tolerance may be particularly important to *R. granulosa*, given its low resistance to cutaneous water loss. These toads dehydrate at the same rate as a wet surface of comparable area and shape (Prates and Navas 2009). In the Caatinga, where water remains available for short periods only, toads may maintain high body temperatures while suffering little impact of dehydration on performance. On the other hand, favoring higher temperatures could result in higher rates of water loss, imposing a trade-off between performance and hydration levels. Contrasting with *R. granulosa*, other species of anurans presented high sensitivities to dehydration and strong interactions between thermal and hydric sensitivities. Importantly, these species occupy mesic environments. Future studies should focus on the ecological and evolutionary processes that might explain this difference in physiological tolerance between species.

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