RESEARCH ARTICLE

Variation in the Thermal Parameters of *Odontophrynus occidentalis* in the Monte Desert, Argentina: Response to the Environmental Constraints

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ABSTRACT

We studied the variation of thermal parameters of *Odontophrynus occidentalis* between season (wet and dry) in the Monte desert (Argentina). We measured body temperatures, microhabitat temperatures, and operative temperatures; while in the laboratory, we measured the selected body temperatures. Our results show a change in the thermal parameters of *O. occidentalis* that is related to environmental constraints of their thermal niche. Environmental thermal constraints are present in both seasons (dry and wet), showing variations in thermal parameters studied. Apparently imposed environmental restrictions, the toads in nature always show body temperatures below the set point. Acclimatization is an advantage for toads because it allows them to bring more frequent body temperatures to the set point. The selected body temperature has seasonal intraindividual variability. These variations can be due to thermo-sensitivity of toads and life histories of individuals that limits their allocation and acquisition of resources. Possibly the range of variation found in selected body temperature is a consequence of the thermal environmental variation along the year. These variations of thermal parameters are commonly found in deserts and thermal bodies of nocturnal ectotherms. The plasticity of selected body temperature allows *O. occidentales* to have longer periods of activity for foraging and reproduction, while maintaining reasonable high performance at different temperatures. The plasticity in seasonal variation of the thermal parameters has been poorly studied, and is greatly advantageous to desert species during changes in both seasonal and daily temperature, as these environments are known for their high environmental variability. *J. Exp. Zool. 00:1–9, 2012.* © 2012 Wiley Periodicals, Inc.

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The body temperature in several lineages of ectothermic animal plays a major role in physiological and behavioral functions (Angilletta, 2009). Patterns such as seasonal and daily activity, locomotor performance, digestion rate, growth rate, oxygen consumption, and gas exchange routes are affected by body temperature (Lillywhite et al., '73; Huey and Stevenson, '79; Choi et al., 2000; Witters and Sievert, 2001; Marvin, 2003; Viscor et al., 2003; Navas et al., 2008).

Amphibians generally rely on the environment to regulate body temperature (Hutchison and Dupré, '92). Nocturnal amphibians maintain body temperature mostly by conduction and convection and their body temperatures tend to be lower than diurnal amphibians (Pough et al., 2001). The wet skin of amphibians increases the rate of evaporated water loss, which is one of the main causes of heat loss (Spight '67; Johnson '71; Tracy '76; Sinsch '89; Shoemaker et al., '92). Therefore, thermoregulation in amphibians is directly affected by water loss through the skin and individuals are in a constant flux between dehydration and temperature gain (Tracy, '76; Wygoda, '88; Tracy et al., '93, 2010; Zug et al., 2001; Köhler et al., 2011). The ability to resist water loss differs from one habitat to another and life history of different amphibian species (Young et al., 2005, 2006; Kearney et al., 2008). Many amphibians thermoregulate by behavioral thermoregulation (Brattstrom, '63), or moving across different types of microhabitats during the day and night, because quantity and quality of the energy resource varies continuously in time and space (Tracy and Christian, '86). This allows toads to adjust their body temperature for maintaining an optimal range of temperature (Lillywhite, '70; Stebbins and Cohen, '95; Zug et al., 2001; Sanabria et al., 2006). The benefit of maintaining an optimum temperature is restricted by energetic costs that the animal would incur while selecting different thermal environments (Lillywhite et al., '73). There are predation risks and loss of opportunity, since an animal that spends much time thermoregulating spends less time on other activities such as feeding and reproduction (Zug et al., 2001; Angilletta, 2009). The main difference in the efficiency of thermoregulation or thermoconforming behavior relies on the costs and benefits to the species. Combinations of these two extreme strategies are often used and depend on factors such as season, habitat occupation, predation risk, and water balance (Huey and Slatkin, '76; Tracy et al., '93; Herczeg et al., 2008).

The body temperatures of amphibians are influenced by changes in environmental temperature, thus restricting the spatial and temporal distribution of these organisms (Zug et al., 2001). Sanabria et al. (2004) reported variations in body temperature of *Rhinella arenarum* in the natural setting for the months of the year, and these changes are related to average environmental temperatures. In *Bufo woodhousii*, *B. americanus*, and *B. marinus*, selected body temperatures were related to substrate moisture (O'Connor and Tracy '92; Tracy et al., '93; Seebacher and Alford, 2002), indicating that it is also an important factor in a model of thermoregulation in amphibians (Oromí et al., 2009). The body temperatures of various anurans are highly dependent on the environmental temperature (Navas, '97). This dependence has been studied in amphibians of the Monte desert, Argentina, as well as *Odontophrynus occidentalis* (Sanabria et al., 2007), *Pleurodema nebulosum* (Sanabria et al., 2006), *Leptodactylus latrans* (Sanabria et al., 2003a), and *R. arenarum* (Sanabria et al., 2003b, 2004, 2006).

Apparently, the toads have the capacity to acclimatize seasonally, showing changes in the thermal parameters as well as select body temperature and extreme temperatures. In *R. arenarum,* these changes are in relationship with the reproduction (Sanabria and Quiroga, 2011a) or in the presence of thermal environmental constraints, such situation was reported for *R. arenarum* in the Monte desert (Sanabria et al., 2011). We performed a comparative study of the thermoregulation of *O. occidentalis* during the wet and dry seasons in the Monte desert, San Juan, Argentina. Assessing thermoregulatory patterns during these two extreme seasons allows one to better understand the thermoregulatory strategy, as it relates to the regulation of water loss and other physiological and behavioral processes. We measured body temperature of selected species, field body temperature, and behaviorally selected microenvironmental temperatures. We also followed the methodology proposed by Hertz et al. ('93) to measure the accuracy and efficiency of thermoregulation in this species.

METHODS

Study Area

The Quebrada de Las Flores is localized to 55 km east of the San Juan city, in the Caucete Department (31°31′ S, 67°51′ W, elevation: 800 m). There is a small stream (Conductivity: 7710 μScm^{-1}) with daily and seasonal fluctuations in its flow, and the dominant vegetation in the area includes *Deuterocohnia longipetala* (chaguar), *Larrea cuneifolia,* and *L. divaricata* (jarillas), *Prosopis sp*. (Algarrobos), *Tipha dominguensis* (totoras), and *Bacharis salicifolia* (chilca dulce). This region is part of the Monte desert characterized by an arid climate. In wet season, the mean maximal temperature is 30.7°C and mean minimum temperature is 19.6°C with a mean annual rainfall of 89 mm , whereas in the dry season the mean maximal temperature is 20°C and mean minimum temperature is 6°C (Cabrera, '76; Warner, 2004). The samplings were carried out from November 2008 to October 2009. We traversed the study area and collected individuals randomly using the technique of visual encounter (Heyer et al., 2001).

Field Body Temperatures (T_b) and Environmental Temperatures

The body temperature *(T_b)* of all individuals was measured at the time of capture (catheter probes TES TP-K01, Taipei, Taiwan) with a digital thermometer TES 1312 (TES Electrical

Electronic Corp., Taipei, Taiwan, ±0.1°C). Also, we recorded the microenvironment temperature—the substrate temperature (T_s) at the site of capture (TES TP-K03 substrate probe, Taipei, Taiwan), and air temperature (T_a) 1 cm from the soil surface (TES TP-K02 gas probe, Taipei, Taiwan). Both temperatures were taken with independent thermocouples to avoid variations for water evaporation. Also, we measured the snout-vent-length (SVL) of each toad captured.

Determination of Operative Temperatures (T_e)

Using the methodology proposed by Tracy et al. (2007) four plaster models were constructed. The models had a water source to prevent dehydration. We inserted a silicone tube (outer diameter 4 mm, inner diameter 2 mm) connected to a plastic bottle with 1 L of distilled water, which hydrates the models by capillarity. Also, to prevent water exchange between models and substrate, the models were placed on a thin plastic film (0.01 mm). Moreover, in the null model, we inserted a thermistor of the data logger (Hobo, H8, Onset Computer Corporation, USA).

The models were calibrated with two toad males. They were anesthetized with a 2.5 mL injection of Xylocaine 2% into the lymph sac. The calibration was performed under field conditions (Bakken, '92), toads were placed in water-conserving posture and the sensor of the logger was inserted inside the body to record variation of temperature with intervals of 5 min. The duration of the calibration was 100 min.

The models were placed in the field in microhabitat extremes, two models near water body (0.10 m from water)—this microenvironment was dominated by high vegetation (about 3 m) that is dominated by *T. dominguensis* and *B. salicifolia*—and other two models far from water body (50 m from water)—this place is dominated by shrubs of Larrea sp. In desert, this configuration is considered as extreme conditions. During the activity time of the toads, the T_e (sensu Bakken, '92) was recorded at 5-min intervals. Also, we calculated the difference between the T_e and T_b obtained from the toad used for calibration. This difference is smaller at 2°C (Dzialowski, 2005).

Laboratory Experiments

Experiments were performed with a subsample of toads for dry season (April, September—November) and the wet season (December—March) (Austral summer). To determine the temperature selected (T_{sel}), the toads were transferred immediately to the laboratory and placed in open-top terraria (180 cm long, 60 cm wide, and 60 cm high). The thermal linear gradient was generated in the terrarium floor. The floor of terrarium was built with metal (galvanized sheet No. 12). The heat source consisted of four 400-W heating elements controlled with a digital thermostat (AG, model TC-120L, San Juan, Argentina). The cold end was maintained through the circulation of cold water in metal tubes that are in a direct contact with the floor of the terrarium. We used a water pump of 1/2 HP (Starke, 340W, China) to mobilize the cold water from a container with 30 L of water with an ice block (25 kg). The terraria were covered with moistened cotton cloth to avoid dehydration of individuals.

The terrarium was divided into 15-cm-wide sections with a height of 15 cm to avoid interactions between neighboring animals (Light et al., '66). The gradient was linear and varied between extremes from 50 ± 2°C to 8 ± 2°C. To determine T_{sel}, individuals were subjected to this gradient for 9 hr uninterrupted from 2000 hr until 0500 hr. The time frame was chosen as this species is nocturnal. Body temperature readings were recorded every hour using a TES 1312 digital thermometer (TES Electrical Electronic Corp, Taipei, Taiwan, ±0.1°C). Toads were held by the head and inserted into the thermocouple (diameter < 0.2 mm) with about 2 cm of the cloaca in the thermocouple.

All indices were calculated based on the methodology proposed by Hertz et al. ('93). We calculated the T_{sel} and maximum and minimum value of the "set point" by calculating the 50% interquartile temperatures selected for each toad. The *db* index was calculated (accuracy of thermoregulation) as the absolute deviation from the T_b and T_{set} for each individual (individual variation). The index of the average thermal quality of habitat from the organism's perspective (*de*) was calculated as the deviation from the mean (T_e) for each station, with respect to the mean of minimum and maximum T_{set} for each season. The effectiveness of temperature regulation was calculated following this mathematical expression $E =$ (mean *db*/mean *de*) (Hertz et al., '93). The methods of Hertz et al. ('93) provide information to understand thermal relationships with the environment, and especially the quality of the thermal environment. For example, comparing the index *db* and *de* between seasons in study allows us to understand the variations of environmental thermal quality related to organisms. However thermoregulation in amphibians is mainly governed by water loss through the skin.

Statistical Analyses

Normality and variance-homogeneity assumptions were tested using the Kolmogorov–Smirnov and Levene tests. The descriptive statistics are shown with means ±1 SE. We calculated the mean of T_e for all plaster models and used the frequency of occurrence during activity period.

RESULTS

Calibration of Plasters Models

The significant regression coefficient between the models and toads used for the calibration was obtained (T_b toad 1 = −46506 + 11881×T_e model 1 and T_b toad 2 = −18975 + 10896×$T_e$model 1). The mean difference of temperatures between T_b toad 1 and T_e model 1 was 1.2 ± 0.2°C and the difference of temperatures between toad 2 and T_e model 2 was 0.9 ± 0.2°C. According to Dzialowski (2005), the difference between T_b and T_e should not exceed 2°C, therefore our models were

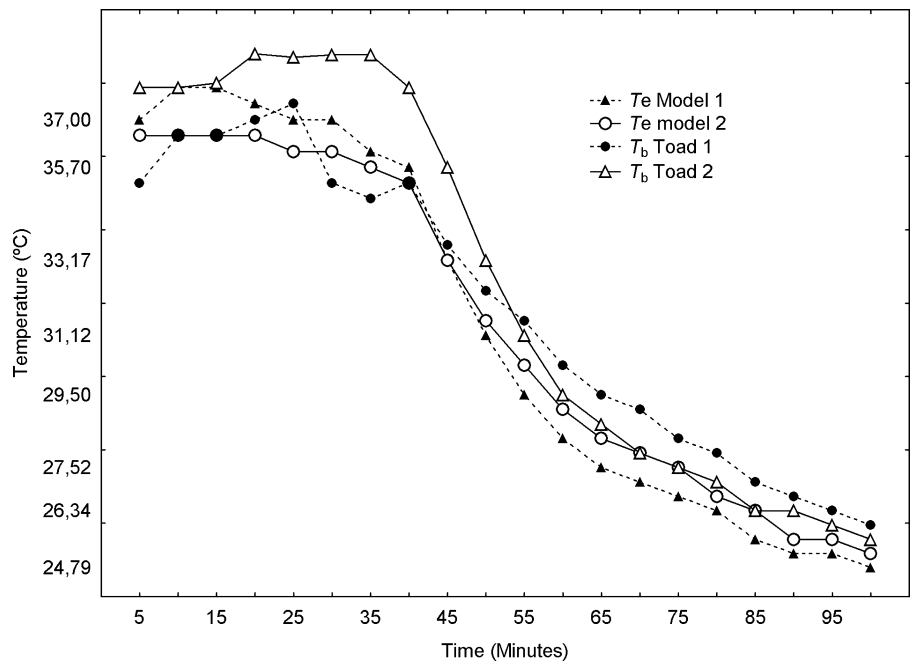

Figure 1. Variation of operative temperature obtained for models (T_e model 1 and T_e model 2) and temperatures of toads used for calibration (T_b toad 1 and T_b toad 2).

good mimics of toads. There were no significant differences in the temperature of the models and toads used for calibration T_b toad 1 and T_e model 1 (Paired t-test, t19 = −0.79, $P > 0.43$) and T_b toad 2 and T_e model 2 (Paired t-test, t19 = −0.59, $P > 0.5$) (Fig. 1).

Microenvironmental Temperatures

Microenvironmental temperatures (T_a and T_s) did not differ significantly during the dry season (paired t-test, $t_{494} = -1.79$, $P > 0.07$). The mean of T_a was 20.2 ± 0.41°C and the mean of T_s was 19.2 ± 0.38°C. However, in the wet season, the data show significant differences (paired t-test, $t_{408} = -12.53$, $P < 0.001$), as the T_a (25.7 ± 0.18°C) is higher than the T_s (22.7 ± 0.15°C).

Body Temperature and Size

The T_b varied significantly among the sampled season (t-test, $t_{163} = 18.54$, $P < 0.01$), being higher during the wet season. The T_b during wet season had an average of 20.9 ± 0.18°C, the T_b in this period is positively correlated with T_s ($r2 = 0.69$, $P < 0.001$, $N = 106$) (Fig. 2A) and T_a ($r2 = 0.35$, $P < 0.001$, $N = 106$) (Fig. 2C). The index for comparing regression coefficients indicates that they differ significantly ($P < 0.001$).

Field body temperature (T_b) during dry season had an average of 15.7 ± 0.23°C and shows relationships significant with the T_s ($r2 = 0.79$, $P < 0.001$, $N = 61$) (Fig. 2) and Ta ($r2 = 0.63$, $P < 0.001$, $N = 61$) in this period (Fig. 2D). The index for comparing regression coefficients indicates that they are not different significantly ($P > 0.49$).

The mean body size (SVL) was 5.79 ± 0.05 cm (minimum = 4, maximum = 7.3). The relationship between the SVL and the T_b was not significant ($r2 = 0.03$, $P > 0.6$). The mean body size between female (6.25 ± 0.07) and male (5.87 ± 0.05) was not significant (t-test, t125 = −1.13, $P > 0.25$).

Operative Temperature (T_e), Selected Temperatures (T_{sel}), and Efficiency in Regulating Temperature

In the wet season, the mean of T_e (range = 16.1–22°C) was higher than the mean of T_e in dry season (range = 10.9–19). The mean limits to Tset varied between dry and wet seasons. The differences for the lower limit (t-test, t27 = −5.8, $P < 0.001$) as well as for the upper limit of Tset (t-test, t27 = −6, $P < 0.001$) in the wet season were significant. Mean lower and upper limits of Tset for the dry season are 19.6 ± 0.71°C and 22.4 ± 0.68°C, respectively, while the average values of Tset for upper and lower limits for the wet season were 24.3 ± 0.46°C and 27.16 ± 0.36°C, respectively. In the wet season, 92.3% of the T_{bs} were found below the lower limit of Tset (Fig. 3). In the dry season, 88.5% of T_{bs} were below the lower limit of the Tset (Fig. 4).

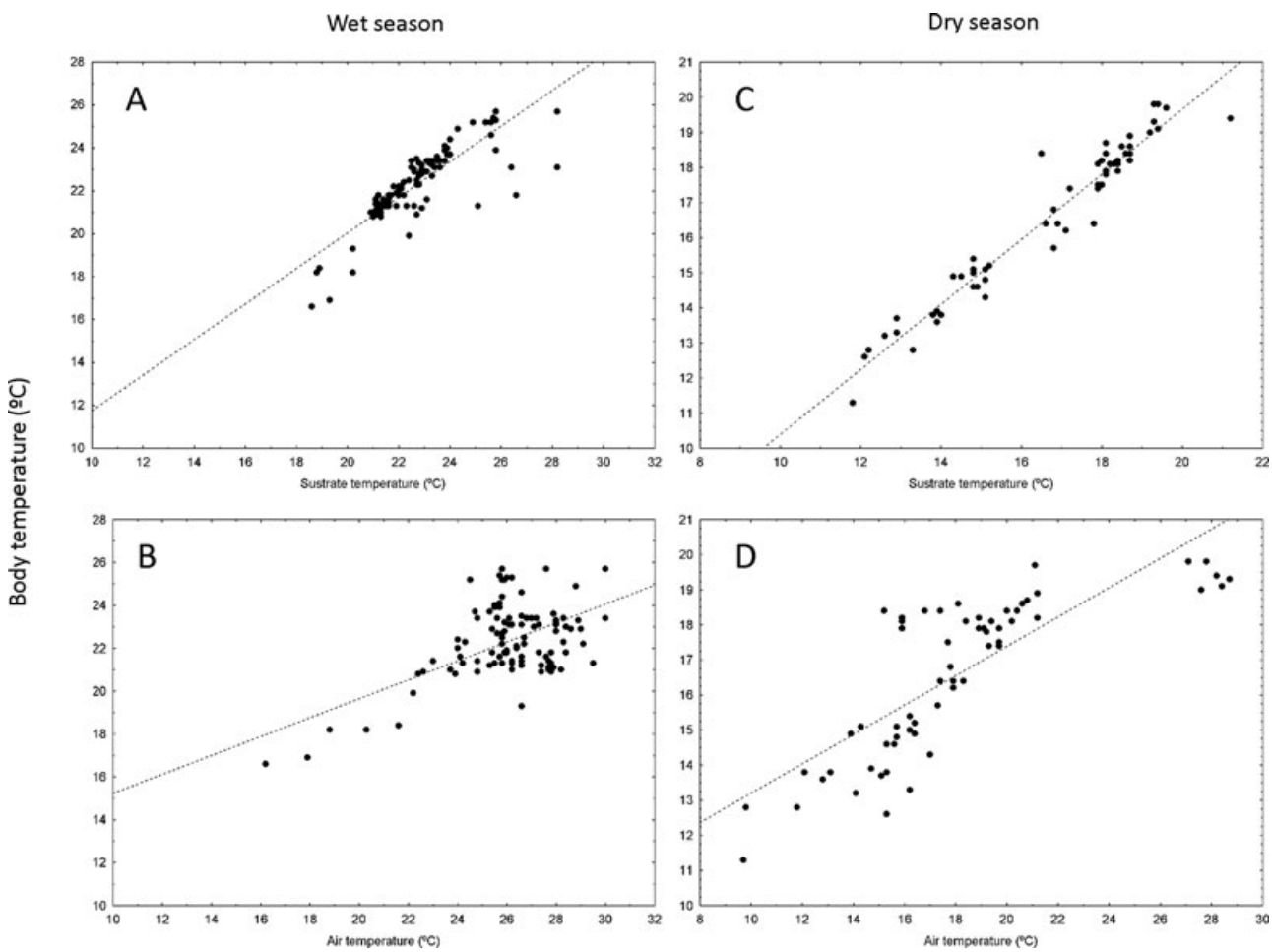

Figure 2. Relationship of body temperature (T_b) of *O. occidentalis* and microenvironmental temperatures. (A) Air temperature. (B) Substrate temperature in the wet season. (C) Relationship between body temperature (T_b) and air temperature. (D) Substrate temperature in the dry season.

The average T_b was significantly lower than the T_{sel} in the wet season (Paired *t*-test, t30 = 6.66, $P < 0.001$), and dry season (Paired *t*-test, t24 = −6.16, $P < 0.001$) (Fig. 5). The T_{sel} varied significantly between the dry seasons (21 ± 0.68°C) and wet (25.7 ± 0.68°C), being highest in the wet season (*t*-test, t27 = 6.36, $P < 0.001$). The T_b of *O. occidentalis* was positively correlated with T_{sel} ($r2 = 0.52$, $P < 0.001$). The *db* index showed no significant differences between dry and wet seasons (*t*-test, t27 = −1.31, $P < 0.19$). The *de* index was higher in the wet than the dry season.

DISCUSSION

Microenvironmental temperatures (Ta and Ts) were different between dry and wet seasons. In the dry season, there were no differences between the substrate temperature and air temperature as compared to wet season where air temperatures are higher than the substrate temperatures. In desert environments, changes in temperature at both macro- and microscale are abrupt in time (Warner, 2004). These variations in ambient temperatures depend mainly on cloud cover, wind speed, vegetation cover, boundary layer, relative humidity, among others. These factors influence the convection, conduction, and radiation of operating temperatures to microscale (Angilletta, 2009).

Average field body temperature for the wet season (20.17°C) was similar to that found for the species in this study area five years ago, in December (Sanabria et al., 2007); this month is considered as wet season in the present study. Body temperature was determined largely by the temperature of the

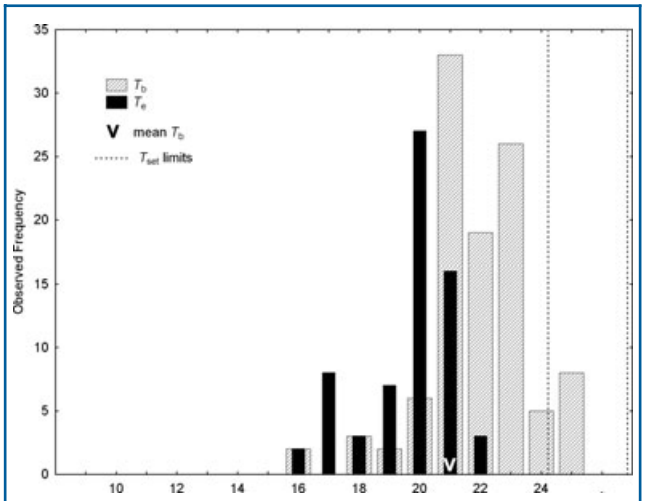

Figure 3. Distribution of body temperature (T_b) (gray bars) and operative temperatures (T_e) at the time of capture (black bars) in the wet season (December–March). The arrow shows the mean T_b and the dashed lines indicate the upper and lower limit of the T_{set}.

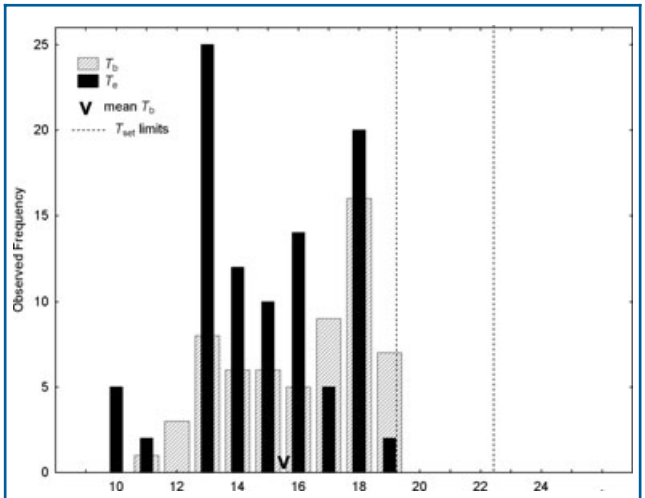

Figure 4. Distribution of body temperature (T_b) (gray bars) and operative temperatures (T_e) at the time of capture (black bars) in the dry season (April, September–November). The arrow indicates the average value of T_b and the dashed lines indicate the upper and lower limit of the T_{set}.

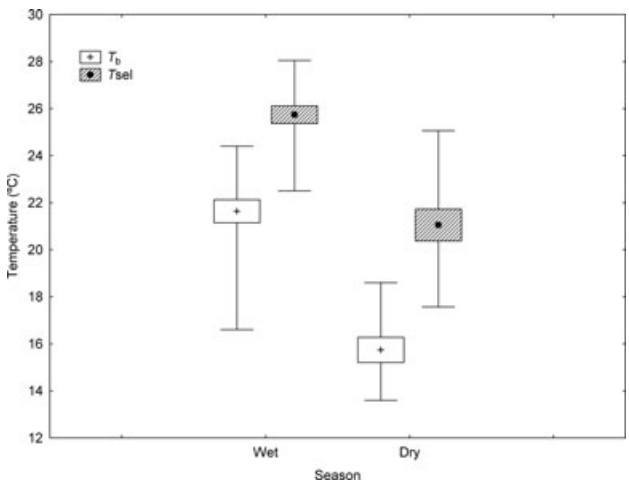

Figure 5. Variation in body temperature of field (T_b) and laboratory-selected temperature (T_{sel}) between dry and wet seasons. Centre point: Mean; Box: SE; Whisker: Min–Max.

microenvironment in both seasons (dry and wet). This likely occurred because during the wet season, air temperature is higher than substrate temperature, and body temperature was coupled to air temperature. Furthermore, in the wet season, the body temperature would likely be determined by heat loss through evaporation (Tracy, '76). The high air temperature in the wet season would result in a high rate of water loss through the skin; therefore, the heat loss of the animals is high. This has been known to be one of the main mechanisms of heat loss in amphibians (Spight, '67; Johnson, '71; Tracy, '76; Sinsch, '89; Shoemaker et al., '92). In *O. occidentalis,* there is no control over water loss through the skin and lack of control over evaporative water loss, which does not allow this species to raise body temperature near to the air temperature.

Field body temperatures of *O. occidentalis* during the wet and dry season are within a small percentage of field body temperatures near the lower set point. Sanabria et al. (2011) observed in *R. arenarum* that field body temperatures were always below the set point. These results strongly suggest that animals always experience thermal environmental constraints during both seasons.

Limitations that individuals experience while thermoregulating, such as those imposed by the thermal environment, lack of operative temperatures close to Tset, predation risk, water balance, among others (Huey and Slatkin, '76; Herczeg et al., 2008), restrict the possibility for individuals to obtain T_b similar to the T_{sel}. Selected body temperature (T_{sel}) is the "target" body temperature to be achieved by an animal in the field (Labra et al., 2008), since near the selected temperature values, physiological processes such as digestion, swimming performance, and locomotion are optimized (Wells, 2007). Also, we should pay attention to the seasonal intraindividual variability in the T_{sel}. These variations can be due to thermo-sensitivity of toads and life histories of individuals that limit their allocation and acquisition of resources (Angilletta, 2009). Possibly the range of variation found in T_{sel} is a consequence of the thermal environmental variation. These variations of thermal parameters

are common in the deserts thermal environment and thermal bodies of nocturnal ectotherms. The plasticity of T_{sel} allows O. occidentales to have longer periods of activity for foraging and reproduction, while maintaining reasonable high performance at different temperatures. Probably *O. occidentalis* has performance curves of typical generalist (Angilletta et al., 2002). An example is the nocturnal lizard (Gekkonids), which has maximum physiological performance at elevated temperatures like a diurnal lizard. However, the decrease in the performance at low temperatures is acceptable and incurs no costs to individuals (Zug et al., 2001).

This is reflected in higher T_{sel} during wet season, which is determined by acclimatization process. This period (wet season) is dominated by higher environmental temperatures (Austral summer). The acclimatization process could be determined by the temperature or the length of photoperiod (Hutchison, '61; Hutchison and Kosh, '64; Hutchison and Ferrance, '70; Hutchison and Maness, '79). As suggested tadpoles of *O. occidentalis* respond to changes in thermal parameters related to the number of hours of light, a mechanism that would facilitate the thermal suitability to long days (Sanabria and Quiroga, 2011b). Seasonal variations of T_{sel} in desert amphibians have been poorly studied. Acclimation is likely related to increase of the biological performance of toads.

The average of the *de* index ($de = 7.82$) in the wet season is less than the dry season ($de = 4.13$), which indicates that the optimum temperatures are less frequent in the environment during wet season compared to dry season. Consequently, this is reflected in the ability of toads to bring the selected temperature near the field body temperature . During the wet season, the toads are able to bring the field body temperatures closest to the selected body temperature in the laboratory ($db = 2.6$) as compared to the dry season ($db = 3.8$). According to the index of Hertz et al. ('93), the toads are moderate thermoregulators ($E = 0.62$) in the wet season, because the optimal environment for thermoregulatory temperatures is rare. That is, the ambient temperatures are patchy in the middle with nonuniform distribution and are highly variable in time (Angilletta, 2009). Conversely, the thermal environment during the dry season with the thermal constraints is apparently more rigorous, as reflected by the E index ($E = 0.05$), suggesting low or no thermoregulation in *O. occidentalis* during this period.

Environmental thermal constraints are present in both seasons (dry and wet), showing variations in thermal parameters studied. Apparently under imposed environmental restrictions, the toads in nature always show body temperatures below the set point. Acclimatization is an advantage for toads because it allows them to bring more variable body temperatures to the set point. The plasticity in seasonal variation of the thermal parameters has been poorly studied, and is greatly advantageous to desert species during changes in both seasonal and daily temperature, as these environments are known for their high environmental variability.

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