Preferred Temperature Correlates with Evaporative Water Loss in Hylid Frogs from Northern Australia

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ABSTRACT

We measured temperature preferences of 12 species of hylid frogs (*Litoria* and *Cyclorana*) from northern Australia in a laboratory thermal gradient. These species represented a range of ecological habitat use (aquatic, terrestrial, arboreal), adult body size (0.5–60 g), and cutaneous resistance to water loss (R_c = 0.6–63.1 s cm^{-1}). We found significant differences among species in selected skin temperature and gradient temperature but not in the variances of these measures (an index of precision of temperature selection). The species' differences correlated significantly with cutaneous resistance to water loss, with more-resistant frogs selecting higher skin and substrate temperatures in the thermal gradient, even after phylogenetic relationships are taken into account. Because cutaneous resistance to water loss also correlates with ecological habit (arboreal > terrestrial > aquatic), we suggest that their higher resistance to water loss allows arboreal and terrestrial species better ability to tolerate high temperatures, where growth or locomotory speed may be higher, without the associated risk of desiccation.

Introduction

Thermoregulation strategies are important for ectothermic species because performance of various functions (e.g., locomotion, digestion, growth) is often tied to body temperature (Huey and Stevenson 1979; Rome et al. 1992). Amphibians face a unique challenge among vertebrate ectotherms because the skin of many amphibians offers little or no resistance to water loss (Adolph 1932; Thorson 1955; Schmid 1965; Spight 1967; Johnson 1971; Tracy 1976; Shoemaker et al. 1992). Indeed, a moist skin is necessary because many amphibians respire through their skin (Feder and Burggren 1985; Boutilier et al. 1992). Because of constant evaporation of water through the skin, amphibians have difficulty reaching body temperatures as high as ambient air temperatures or substrate temperatures (Hadfield 1966; Pearson and Bradford 1976; Sinsch 1989) and often are found at temperatures below ambient. To prevent dehydration, amphibians must either remain close to a water source or have some mechanism to reduce evaporative water loss (EWL; Thorson and Svihla 1943; Thorson 1955). Some amphibians use skin secretions to reduce EWL (Wygoda 1984; Christian et al. 1985; Shoemaker et al. 1989), some also adopt a water-conserving posture with eyes closed to reduce the wet surface area exposed to air, and others simply remain in or near a water source (see review by Shoemaker et al. [1992]).

The methods for reducing water loss have different consequences for thermoregulation. Assumption of a water-conserving posture would not allow precise temperature regulation, although animals could use temperature to select a place to rest. Aquatic amphibians can easily remain hydrated, but opportunities to regulate temperature in water are limited to either selecting a particular water temperature or basking just under the water surface or at the water's edge (e.g., Lillywhite 1970, 1971). Species that can reduce EWL while still remaining mobile have the best opportunities for precise control of temperature (Tracy 1976; Buttemer 1990). With low EWL, such as is found in many reptiles, an animal could move to regulate its temperature precisely without experiencing the cooling and dehydrating effects of evaporation. This may be particularly important in seasonally dry habitats, such as the wet-dry tropics of northern Australia, where frogs may have to survive 6 mo without rain.

The hylids from the wet-dry tropics of northern Australia make an ideal system for studying the relationship between EWL and thermoregulation because relatively closely related frogs (species in the genera *Litoria* and *Cyclorana*) show a wide range of resistances to EWL (Young et al. 2005). Young and colleagues found skin resistances ranging from barely above that of a free water surface in *L. meiriana* (R_c = 0.7 s cm^{-1}) to relatively high resistance in *L. bicolor* (R_c = 63.1 s cm^{-1}). Furthermore, species of *Litoria* and *Cyclorana* occupy a wide range of ecological habits, even though they can often be found in the same area. Some species are largely arboreal (e.g., *L. bicolor*, *L. caerulea*, *L. rothii*, *L. rubella*) or rock dwelling (*L. coplandi*), some are largely ground dwelling (e.g., *L. nasuta*, *L. tornieri*, *L. wotjulumensis*, *C. australis*), and some are either largely aquatic or nearly always found within a short distance

of open water (e.g., *L. dahlii*, *L. meiriana*). This suite of species also represents a wide range of adult body sizes, from ∼1 g (*L. bicolor*, *L. meiriana*) to nearly 100 g (*L. caerulea*), which may also influence thermal relations (Tracy 1976).

Thus, to begin to unravel the complex interrelationship between water loss, body size, and thermoregulation, we measured temperature preferences in a laboratory thermal gradient in 12 species of hylid frogs from northern Australia: *L. bicolor*, *L. caerulea*, *L. coplandi*, *L. dahlii*, *L. meiriana*, *L. nasuta*, *L. rothii*, *L. rubella*, *L. tornieri*, *L. wotjulumensis*, and *C. australis*. We hypothesized that (1) frogs with high EWL (i.e., low resistance to water loss, R_c) would have lower body temperatures (T_b) than frogs with low EWL because of greater evaporative cooling and concomitant difficulty in reaching higher body temperatures, and (2) frogs with low EWL would have lower variance in T_b because evaporative cooling would have a smaller influence on precise thermoregulation.

Material and Methods

Thermal Gradient

Two thermal gradients 1.7 m long were constructed from half of a 100-mm-diameter copper pipe (2-mm thickness). The inner surface of the pipe was painted with a black stove paint. To cool one end, we sealed a PVC chamber to the underside of one end of the gradient and connected it to a pump that circulated ice water from an insulated cooler. The warm end was heated by attaching thermal wires to the underside of the gradient. The wires were connected to a rheostat for control of temperature. This created a gradient range of 8°–50°C over ∼1.5 m of the gradient. The lid of the gradient was nylon fly screen stretched over a wooden frame. The gradient was covered over most of its length (∼12°–45°C) for uniform illumination and was housed in a temperature-controlled room at 26°C.

Frog Capture, Handling, and Measurement

We captured eight to 11 frogs of each species at nighttime at several locations around Darwin and at Robin Falls (∼120 km south of Darwin) in the Northern Territory, Australia. They were held overnight in plastic boxes lined with a moistened paper towel or a moist cotton bag in a temperature-controlled room at 26°C. The next day, they were put into temperature preference trials in the thermal gradient. After the trial, frogs were given free access to food (crickets) and water and released.

Before they were placed into the thermal gradient, the mass of the frogs was measured to the nearest 0.01 g. Skin temperature at the middle of the dorsal surface of the frog was measured to the nearest 0.1°C with a Raytek Raynger IP-K infrared thermometer, which integrates over a field of view of ∼3-mm diameter, an area smaller than the breadth across the dorsal surface of even the smallest species. Frogs were allowed to

acclimate to the gradient for at least 1 h or until they stopped obviously exploring the gradient. Individuals who were still exploring the gradient after 3 h were not used in the analysis. Skin and substrate temperatures were measured every 30 min for 3 h (six measurements). Substrate temperature was measured immediately adjacent to the frog at the same position along the gradient axis. Because water condensed in the cold end of the gradient, we misted water over the entire gradient after each temperature measurement to provide a uniform substrate moisture. After 3 h, the frogs were removed from the gradient and reweighed. Because the entire gradient was misted every 30 min, the frogs were not in water stress during the trials. Most frogs gained mass over the course of the trial, and none lost more than 5% of its initial mass.

We used skin resistance to water loss, R_c, as an index of EWL, with high R_c values indicating low water loss rate. These values were taken from Young et al. (2005).

Statistics

For each animal, we obtained a mean and a variance for the six half-hourly measurements of skin temperature. These were then used in ANOVA with species as the independent variable. Student's post hoc *t*-test was used to determine pairwise differences among species. We calculated correlations between mass, resistance to EWL, R_c, and the temperature variables we measured. We used a multiple regression to determine the relative importance of selected gradient temperature and R_c in explaining variance in mean skin temperature of each individual. We performed this multiple regression both with and without parameter centering, which accounts for interaction terms with continuous regressors by adjusting the sums of squares of the interaction term to the mean value of the main effects. We also used the mean selected temperature for each species in a regression analysis with R_c as the independent variable. All calculations were made with JMP 5.0.1a (SAS Institute) for Macintosh. Because cutaneous resistance to water loss, R_c, had a skewed distribution, we used a log transformation, and because some values were between 0 and 1, we transformed the data as $\log(R_c + 1)$, hereafter referred to as $\log R_c$.

To determine whether there was phylogenetic signal in our comparative data, we calculated the K statistic (Blomberg et al. 2003) for selected temperature and body mass. These calculations were made with PHYSIG.M (Blomberg et al. 2003), and a tree was constructed from molecular data (Young et al. 2005) with branch lengths set using Pagel's arbitrary branch lengths (Garland et al. 1992; Pagel 1992), with appropriate diagnostic checks. The K statistics indicated that there was significant phylogenetic signal in log body mass ($K = 0.788$, $P = 0.038$, $N = 12$) and nearly significant phylogenetic signal in selected temperature ($K = 0.627$, $P = 0.057$, $N = 12$). In addition, Young et al. (2005) found a significant phylogenetic signal in $\log R_c$ with a larger data set that included all 12 species studied

Table 1: Mean skin and gradient temperatures and the means of the variances in skin and gradient temperatures selected by *Litoria* and *Cyclorana* species in a laboratory thermal gradient

Species	N	Mass (g)[a]	T_{skin} (°C)[b]	Var T_{skin} (°C)[b]	T_{grad} (°C)[b]	Var T_{grad} (°C)[b]
L. bicolor	11	.76 (.57–.96)	31.0[A] (.7)	1.25[BC] (.37)	31.6[ABC] (.8)	2.21 (.94)
L. rothii	10	6.13 (4.60–10.71)	29.4[B] (.4)	1.50[AB] (.36)	30.4[C] (.4)	2.36 (.53)
L. caerulea	10	36.87 (13.9–64.2)	29.3[BC] (.3)	.46[C] (.19)	30.7[C] (.6)	.77 (.19)
L. rubella	9	2.81 (2.28–4.14)	30.9[A] (.6)	2.33[A] (.43)	33.0[A] (.8)	3.65 (.68)
L. coplandi	8	3.28 (1.83–4.19)	28.8[BCD] (.5)	1.55[AB] (.30)	32.7[AB] (.7)	4.99 (1.22)
L. wotjulumensis	10	10.15 (6.30–15.70)	28.3[BCDE] (.4)	1.19[BC] (.30)	30.0[CD] (.7)	3.49 (.84)
C. australis	10	39.15 (22.1–64.2)	28.0[CDE] (.3)	.99[BC] (.15)	30.3[C] (.6)	4.02 (.90)
L. nasuta	9	5.97 (5.17–7.48)	27.7[DE] (.3)	.97[BC] (.16)	30.0[CD] (.4)	2.80 (.72)
L. tornieri	8	3.31 (2.42–5.35)	28.6[BCD] (.2)	1.0[BC] (.11)	31.2[ABC] (.4)	4.76 (1.58)
L. dahlii	9	13.85 (7.78–29.81)	26.3[F] (.5)	1.23[BC] (.33)	28.4[D] (.6)	3.55[c] (1.79)
L. inermis	10	1.95 (1.44–2.26)	27.2[EF] (.4)	1.12[BC] (.19)	3.8[BC] (.6)	4.11 (1.19)
L. meriana	10	.96 (.61–1.22)	27.0[EF] (.7)	1.61[AB] (.39)	28.2[D] (.9)	3.35 (.83)

Note. Superscripts represent statistically distinguishable groups for temperatures and variances. Species are arranged in order of decreasing evaporative water loss. See table 2 for results of ANOVA and for definitions.

[a] Range in parentheses.

[b] SE in parentheses.

[c] $N = 7$ for *L. dahlii* for Var T_{grad}.

here. Thus, to correct for phylogenetic relationships among the species studied, we also analyzed the correlation between $\log R_c$ and T_{skin} with phylogenetically independent contrasts (Felsenstein 1985; Garland et al. 1992), using the PDTREE module in PDAP (Garland et al. 1993; Garland and Ives 2000).

Results

Most frogs appeared to explore the gradient for about 1 h and then settled into a narrower thermal area afterward. Most individuals also remained alert throughout the 4–5-h trials. Some individuals adopted a water-conserving posture between measurements, but many sat with head up in an alert posture. Some frogs were disturbed by the approach of the IR thermometer and moved away, but most quickly returned to an area close to their premeasurement location once the measurement was taken. Some individuals moved and returned in this manner multiple times during a 3-h trial.

Mean selected skin temperatures ranged from 26.3°C ($\pm 0.5°$) in *L. dahlii* to 31.0°C ($\pm 0.7°$) in *L. bicolor* (Table 1), and there were highly significant differences among species in selected skin temperature (T_{skin}) and variance in skin temperature (Var T_{skin}; Tables 1, 2). There were also significant differences among species in selected gradient temperature (T_{grad}), ranging from 28.2°C ($\pm 0.9°$) in *L. meiriana* to 33.0°C ($\pm 0.8°$) in *L. rubella*, but no species effect on variance in selected gradient temperature (Var T_{grad}). Both T_{skin} and T_{grad} were positively correlated with $\log R_c$ (T_{skin}: $R = 0.871$, $P < 0.0001$; T_{grad}: $R = 0.577$, $P = 0.049$) and were positively correlated with each other ($R = 0.779$, $P = 0.003$). Regression of T_{skin} versus $\log R_c$ was highly significant ($F_{1,11} = 31.37$, $P = 0.0002$), with

more-resistant species selecting higher temperatures (Fig. 1). There was no significant correlation between $\log R_c$ and either Var T_{skin} ($R = 0.056$, $P = 0.865$) or Var T_{grad} ($R = -0.457$, $P = 0.139$). The correlation between $\log R_c$ and T_{skin} using phylogenetically independent contrasts also produced a significant correlation (contrast for selected temperature = $2.17 \times$ contrast for $\log R_c + 26.8$, df = 10, $r^2 = 0.57$, $P = 0.005$; Fig. 2). There was no indication of a significant correlation with body mass for any variable.

Multiple regression showed significant effects of T_{grad} ($F_{1,110} = 45.2$, $P < 0.0001$), $\log R_c$ ($F_{1,110} = 4.3$, $P = 0.04$) and their interaction ($F_{1,110} = 5.5$, $P = 0.003$). When we reanalyzed the data using parameter centering to account for continuous variables in the interaction term, we found similar results (T_{grad}: $F_{1,110} = 322.7$, $P < 0.0001$; $\log R_c$: $F_{1,110} = 97.8$, $P < 0.0001$; interaction: $F_{1,110} = 9.0$, $P = 0.003$). Analysis of correlation coefficients showed positive correlations between T_{skin} and both $\log R_c$ and T_{grad} (Table 3). Partial correlation coefficients showed

Table 2: ANOVA tables for temperatures of frogs in a thermal gradient

Dependent variable	df	MS	F	P
T_{skin}	11, 102	20.634	9.586	**<.0001**
Var T_{skin}	11, 102	1.957	2.326	**.014**
T_{grad}	11, 102	18.955	4.645	**<.0001**
Var T_{grad}	11, 100	12.89	1.469	.155

Note. For these analyses, species was the independent variable. T_{skin} = selected skin temperature, Var T_{skin} = variance in selected skin temperature, T_{grad} = selected gradient temperature, and Var T_{grad} = variance in selected gradient temperature. Boldface = significant at $P \leq 0.05$.
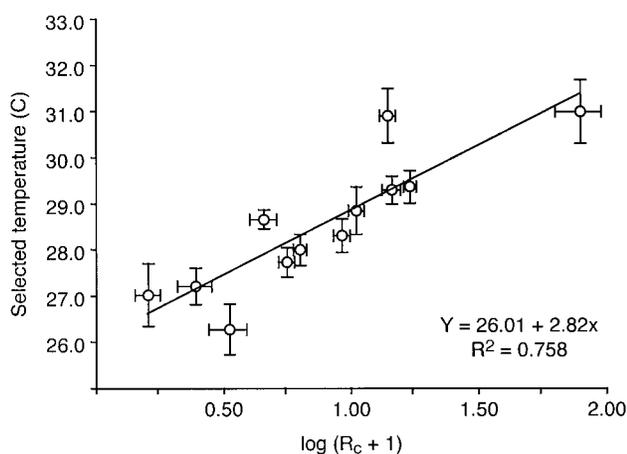
Figure 1. Mean selected temperature in the thermal gradient for each species versus log resistance to evaporative water loss. Resistances were transformed as $\log(R_c + 1)$ to avoid negative numbers. Error bars are $\pm$ SE on both axes.

a negative correlation between $\log R_c$ and T_{grad} and positive correlations between T_{skin} and both $\log R_c$ and T_{grad} (Table 3).

Two individual *L. dahlii* had extremely high values for Var T_{grad} (more than two times all other data points) because one of the six repeated measures of temperature for each was quite different from the remaining five. These two individuals were therefore removed from this analysis. T_{skin} at the times of these two measurements was not much different from T_{skin} at other times, suggesting that the frog had moved to that spot on the gradient from another temperature just before the measurement and subsequently moved back. When these individuals were included in the analysis, mean square = 60.39, $F_{11,102} = 2.239$, $P = 0.018$, and *L. dahlii* were significantly different from all other species in post hoc comparisons.

Discussion

We have shown that these 12 species of hylid frogs differ in temperatures selected in a thermal gradient (Table 1). Furthermore, these differences show a strong relationship with cutaneous resistance to water loss, as we hypothesized, with more-resistant frogs selecting higher temperatures in the gradient. However, although there were significant differences among species in the variance of selected temperatures, there was no relationship between this variance and cutaneous resistance to water loss. This suggests that EWL rates may not be a significant predictor of capacity, or "inclination," for precise body temperature regulation in anuran amphibians, at least under laboratory conditions. Under natural conditions, where factors affecting evaporation may be more variable or extreme (e.g., wind speed, relative humidity), EWL may play a more significant role. However, Buttemer and Thomas (2003) have

suggested that under natural conditions, differences in microhabitats occupied by species may balance differences in cutaneous resistance to water loss, causing total EWL to be similar between species with different resistances. If true, this would suggest that there may be little correlation between resistance and precision of thermoregulatory precision because species with different resistances would face similar challenges to thermoregulation by evaporative cooling.

Frogs with high cutaneous resistance to water loss tend to be those naturally found farther from water (Shoemaker et al. 1992; Amey and Grigg 1995; Young et al. 2005), and they selected high temperatures in the thermal gradient in this study. For example, truly arboreal frogs, such as *L. caerulea* or *L. rothii*, have relatively high cutaneous resistance to water loss (14.3 and 16.2 s cm^{-1}, respectively), and they selected relatively high temperatures in the gradient (Table 1), while aquatic frogs (or those always found within one or two hops of water), such as *L. dahlii* or *L. meiriana*, have relatively low resistance (2.3 and 0.6 s cm^{-1}, respectively), and they selected lower temperatures in the gradient. It is impossible to tell whether evolution of increasing resistance to water loss allowed frogs to move farther from water or whether increasing terrestriality selected for increased resistance; however, one can speculate that increasing resistance allowed more terrestrial/arboreal frogs to take advantage of thermal opportunities without the risks of desiccation faced by low-resistance frogs.

There is a large body of literature on the effect of temperature on various functions of amphibians, including metabolic rates, muscle power, locomotory rate, digestion, oxygen uptake, calling rate, development rate (pre- and postmetamorphic), and growth (Rome et al. 1992). In general, most of these rates increase with temperature to a point beyond which they decrease sharply (e.g., Huey 1991; Rome et al. 1992). For example, several species of North American hylids showed this pattern for jumping distance when they were hopped at temperatures from 0° to 35°C (John-Alder et al. 1988). There is also a large body of literature on the effects of desiccation on various functions, including foraging ability, metabolism, and locomotory speed (Shoemaker et al. 1992). For example, Moore and Gatten (1989) found that dehydration to 80% of hydrated body mass caused a significant reduction in endurance in four species (genus *Rana* and *Bufo*). Further, studies on the combined effects of temperature and dehydration generally show synergistic effects of these two stressors, with hydration state having a larger effect on performance at higher temperatures (e.g., Rome et al. 1992; Shoemaker et al. 1992). Thus, it becomes clear that an ability to tolerate high temperatures without risk of desiccation could be very selectively advantageous for individuals of terrestrial and arboreal species of anurans.

The moist skin of most frogs adds a dimension to thermoregulation not seen in other terrestrial ectotherms (Spotila 1972; Tracy 1975, 1976; Spotila et al. 1992). Because of their need to maintain a moist skin for exchange of respiratory gases,

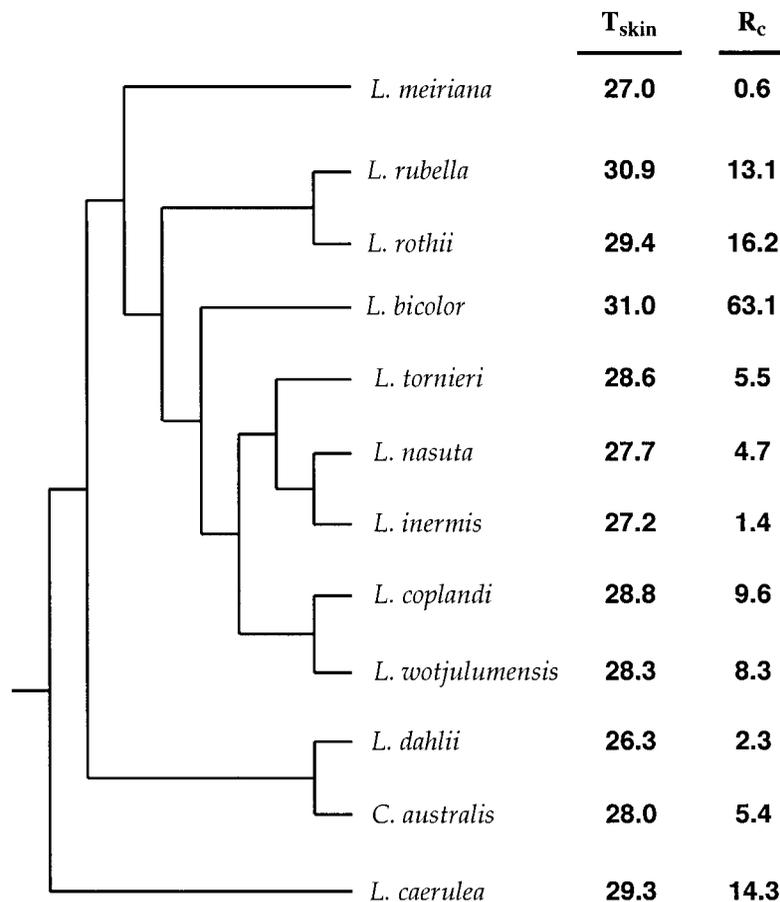|	T_{skin}	R_c
L. meiriana	27.0	0.6
L. rubella	30.9	13.1
L. rothii	29.4	16.2
L. bicolor	31.0	63.1
L. tornieri	28.6	5.5
L. nasuta	27.7	4.7
L. inermis	27.2	1.4
L. coplandi	28.8	9.6
L. wotjulumensis	28.3	8.3
L. dahlii	26.3	2.3
C. australis	28.0	5.4
L. caerulea	29.3	14.3

Figure 2. Phylogenetic relationships among species of hylid frogs from this study. This tree has been trimmed from the one proposed in Young et al. (2005), and branch lengths have been transformed to Pagel's arbitrary branch lengths (Garland et al. 1992; Pagel 1992) with appropriate diagnostic checks. Data at the tips are cutaneous resistance (R_c) from Young et al. (2005) and mean selected skin temperature (T_{skin}) from this study. Phylogenetically independent contrasts show a significant correlation between R_c and T_{skin}.

most frogs have little resistance to water loss (Spotila and Berman 1976; Withers et al. 1984; Wygoda 1984; but see McClanahan et al. 1978; Wygoda 1984; McClanahan and Shoemaker 1987; Wygoda and Williams 1991). This potentially leaves them susceptible to desiccation if they experience high body temperatures. Many species adopt a water-conserving posture to reduce risk of desiccation; however, this behavior limits thermoregulatory opportunities to selecting thermally benign sites and would make precise thermoregulation difficult. On the other hand, in some reptiles, nocturnal retreat sites have been shown to be important for overall daily temperature regulation (Christian et al. 1984). Daytime retreat sites may play a similar thermoregulation role for frogs even when they adopt a water-conserving posture.

EWL may also result in buffering frogs from high body temperatures (Spotila et al. 1992). Evaporative cooling may reduce skin and body temperatures below those of the air or substrate, even when frogs are exposed to direct sunlight (Lillywhite 1975;

Lillywhite and Licht 1975; Tracy 1975, 1976; Carey 1978; O'Connor 1989). Some species may exploit this cooling mechanism by increasing water loss at high temperatures to avoid critically high temperatures. Frogs in the genus *Phyllomedusa* increased EWL at body temperatures above 38°C (Shoemaker et al. 1987), apparently by means of glandular secretions, leading the authors to conclude that the mechanism was analogous to sweating. Some frogs in the genus *Litoria* have also been reported to be buffered from high temperatures by evaporative cooling (Buttemer and Thomas 2003). However, it is unclear whether this is the result of an active secretion onto the skin or simply because of increased evaporation rates (and thus evaporative cooling) due to high temperatures.

Lower skin temperatures in species with higher EWL could be either the result of selecting lower temperatures in the gradient or the result of greater heat loss due to evaporative cooling. Frog skin temperatures would be predicted to be lower than the temperature of the substrate because of evaporation,

Table 3: Correlation coefficients (above diagonal) and partial correlation coefficients (below diagonal) between log skin resistance ($\log R_c + 1$), selected gradient temperature (T_{grad}), and selected skin temperature (T_{skin}) of frogs in a thermal gradient

	$\log(R_c + 1)$	T_{grad}	T_{skin}
$\log(R_c + 1)$	…	.338	.628
T_{grad}	−.442	…	.838
T_{skin}	.670	.854	…

and the deficit should be greater with increasing evaporation rates (lower resistance). Our data support these predictions (Tables 1, 3); T_{skin} was always lower than T_{grad}, and the slope of the regression between these two variables was 0.79. Furthermore, the partial correlation coefficients support the idea that frogs with lower T_{skin} are cooler because of a combination of selecting lower gradient temperatures and losing more heat to evaporation (Table 3). The positive correlation between T_{skin} and $\log R_c$ indicates that, for a given gradient temperature, frogs with higher resistance to water loss have a higher skin temperature, presumably because of reduced evaporative cooling. Similarly, the negative partial correlation between $\log R_c$ and T_{grad} indicates that for a given T_{skin}, frogs with lower R_c select a higher gradient temperature, presumably to compensate for evaporative cooling. Thus, these correlations, in combination with the significant correlation between selected gradient temperature and skin temperature and the significant relationship between cutaneous resistance and water loss, suggest that frogs with higher EWL were in fact selecting cooler temperatures rather than simply losing more heat to evaporation, although evaporative cooling probably magnified this effect.

Despite the presence of significant phylogenetic signal in both cutaneous resistance to water loss and selected temperature, analysis using phylogenetically independent contrasts still shows a positive correlation between the two. This suggests that the correlation between resistance to water loss and selected temperatures is not simply because of historical constraints (i.e., an ancestor had high R_c and high preferred temperature, so the descendents do, too), but, rather, that ecological (or other) factors have driven parallel evolution between these traits within different *Litoria/Cyclorana* clades. This can be seen clearly in Figure 2, where high body temperatures are dispersed across the tree topology.

Thermoregulatory opportunities are generally more limited for nocturnal animals than for diurnal animals (Huey et al. 1989; Kearney and Predavec 2000). However, nocturnal lizards do thermoregulate (Huey et al. 1989; Kearney and Predavec 2000; Kearney 2001, 2002). Furthermore, both diurnal and nocturnal ectotherms may use temperature as one of the cues for selecting retreat sites for their inactive periods. Retreat site selection may therefore influence daily energy budgets and other

physiological functions, such as digestion rate and EWL (Christian et al. 1985; Bulova 2002). High resistance to water loss may allow some frog species to select diurnal retreat sites with high temperatures without desiccating, potentially allowing them to digest or grow more quickly.

In summary, we have shown that these 12 species of hylid frogs from the Top End of Australia select significantly different temperatures in a laboratory thermal gradient and that these differences correlate with cutaneous resistance to water loss even after effects of phylogeny are removed. We suggest that higher resistance allows some frog species, particularly arboreal species, to select warmer temperatures, at which physiological processes such as growth or digestion may operate at a higher rate, without the risk of rapid desiccation.

Acknowledgments

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