

# Not just small, wet, and cold: effects of body size and skin resistance on thermoregulation and arboreality of frogs

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**Abstract.** We used simulations from a biophysical model that integrates interlinked exchanges of energy and water between frogs and their environments to address questions about the limits to thermoregulation and about adaptations for arboreality. Body size and cutaneous resistance ( $R_c$ ) both significantly affected body temperature ( $T_b$ ) and the time to desiccate to 70% of standard mass (an ecologically relevant metric of desiccation). Cutaneous resistances  $< 25$  s/cm allow basking frogs to elevate their  $T_b$  several degrees above ambient, but  $R_c$  above 25 had little additional effect on  $T_b$ . Small frogs ( $< 10$  g) are able to elevate their  $T_b$  above ambient while basking, even with small  $R_c$ . Large frogs must have greater skin resistances to be able to elevate body temperatures above ambient, yet large frogs take longer to desiccate to 70% of their standard mass. Frogs can avoid rapid desiccation with high  $R_c$ , a large body size, or some combination of these traits. Our literature survey indicates that frogs with a combination of  $R_c$  and body size that would result in long times to desiccate to 70% of standard mass tend to be arboreal, suggesting that those species may be selectively favored in a niche that often requires frogs to be away from water sources for extended periods of time.

**Key words:** *amphibian; anuran; biophysical model; body temperature; cutaneous resistance; energy balance; microclimate use; water budget; water loss rate.*

## INTRODUCTION

Many anurans have a skin through which water evaporates as easily as from a pure-water film, and the consequence of that high evaporation rate to their behavioral ability to regulate body temperature has been seen as limiting (Tracy 1975, 1976). For these species, microhabitat selection and behavioral posturing can be used to reduce water loss, but these activities are not necessarily conducive to thermoregulation. Some species of anuran amphibians, however, have skin resistance ( $R_c$ ) to water loss (e.g., Shoemaker et al. 1992, Withers 1998, Young et al. 2005), and are better able to exploit the heterogeneity of the environment to thermoregulate through behavioral selection of different nanoclimates (McClanahan and Shoemaker 1987, Shoemaker et al. 1989, Tracy and Christian 2005) or physiological abilities to adjust their skin resistance (Brattstrom 1970, Shoemaker et al. 1987, 1989, Buttemer and Thomas 2003, Tracy et al. 2008). There is an increasing literature documenting a wide range of skin resistances to water loss among anurans (Shoemaker et al. 1992, Snyder and Hammerson 1993, Amey and Grigg 1995, Withers 1998, Young et al. 2005, 2006, Tracy et al. 2008). This literature indicates that the majority of anurans that have elevated skin resistances are arboreal

frogs in the families Hylidae, Rhacophoridae, and Hyperoliidae, and there is some indication that some clades within these families have higher resistances to water loss than do others (Young et al. 2005, Tracy et al. 2008). Because high skin resistance is associated with arboreality, we wondered if that meant that high skin resistance is the necessary adaptation to emancipate frogs from a source of water and allow frogs to adopt an arboreal habit.

Classic early studies by Thorson and Svihla (1943), Thorson (1955), and Seymour and Lee (1974) found no relationship between rate of water loss by amphibians and the degree of terrestriality, but more recent studies (Wygoda 1984, Buttemer and Thomas 2003, Young et al. 2005) have found a correspondence between ecological habit (arboreal, terrestrial, aquatic) and cutaneous resistance to water loss ( $R_c$ ), indicating that species with higher  $R_c$  are more likely to be arboreal or terrestrial than species with low  $R_c$ . Body size also may influence the effective rate of water loss by affecting surface area-to-volume ratios (e.g., Seymour and Lee 1974) as well as affecting physical interactions with the environment.

Insofar as avoiding desiccation can be achieved several ways, there is some value in employing a metric that reflects the efficacy of the combined traits that influence desiccation rate, and that metric should integrate all of the behavioral, physical, and physiological properties of the animals influencing desiccation. Thus, we use the time it takes a frog to desiccate to 70% of its standard body mass (the mass of a fully hydrated

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frog, with an empty bladder) as an index of the ecological tolerance to dry conditions. This index integrates much of the hydroregulatory strategy composed of the behavioral and physiological traits ( $R_c$ , body size, posture, and microclimate selection) in relation to an ecological milieu into a single variable, reflecting the ecological value of the strategy (Young 2006).

Here, we present a new biophysical model of energy and water balance in frogs. We used this model to ask how different combinations of physical and physiological properties of frogs and their environment affect body temperatures and rates of desiccation in different environments. Such simulations of frogs differing in size and cutaneous resistance to water loss provide a means to determine which combinations of frog and environmental properties are conducive to spending extended periods away from a source of water, and thus make it possible for species to adopt an arboreal habit.

#### BIOPHYSICAL MODELS

Modeling water loss for an amphibian requires recognizing that the processes for the exchange of energy and mass are inextricably linked because each process is part of the other. Specifically, evaporative water loss from amphibians also causes a loss of energy because heat is lost as latent heat, and warmer animals will lose water faster than will cooler animals because the vapor densities of their skin will be greater. Thus, it is not possible to calculate one process without calculating both processes simultaneously. Equations comprising models of heat and water exchanges for amphibians have been described previously (Tracy 1976, 1982), and we have coded those equations into a general, comprehensive, and user friendly model of the water and energy budgets of frogs, created in Microsoft Excel (*unpublished software*). Here, we describe our implementation of the equations described by Tracy (1976, 1982), as well as assumptions used in the project reported here. The model is composed of properties of the animals, properties of the environment, and the equations linking those properties into processes resulting in calculated body temperatures, rates of water loss (g/s and percentage of body mass/h), and time for the animal to desiccate to 70% of its standard (fully hydrated) body mass.

##### *Properties of the animals*

The primary properties of animals required of the model are: (1) body mass, (2) cutaneous resistance to water loss, (3) the shape and posture, and (4) absorptivity to solar radiation. The thermal conductivity of animal tissue is assumed to be  $0.0048846 W \times cm^{-2} \times K^{-1}$  (Chato 1966). Many other important variables of the animals can be derived from these primary variables.

The total surface area of a frog is calculated as  $A_{tot} = 9.9 \times (\text{body mass})^{0.56}$  (McClanahan and Baldwin 1969), and, in a sitting posture, the area of the venter in contact

with the substrate is calculated as  $A_{vent} = 1.15 \times (\text{body mass}/1000)^{0.559}$ , where body mass is in kilograms (Tracy 1976). The area exposed to air for exchange of heat and mass for a frog in a sitting posture is the difference between the total surface area and the area of the venter. Buttemer (1990) has verified the efficacy of these equations for calculating areas of Australian hylid frogs. The area exposed to air for a frog in the water-conserving posture is taken to be two-thirds of the total area. Thus, the surface area of the venter in that posture is taken to be one-third of the total area (Withers et al. 1984). The silhouette area of frogs, which is the area receiving solar radiation, is calculated from  $A_{tot} \times ((0.0000138171z^4) - (0.000193335z^3) + (0.00475761z^2) - (0.167912z) + 45.8228)/100$ , where  $z$  is the angle of the animal's frontal plane relative to the solar beam (Tracy 1976). When the solar beam is normal to the animal's longitudinal axis (i.e., when the sun is directly overhead while the frog is sitting on level ground),  $z = 0^\circ$ . When the solar beam is parallel to the animal's longitudinal axis,  $z = 90^\circ$ . Conduction of energy between the frog's venter (with a small surface area) and the dorsal surface (with a relatively larger surface area) requires calculating conduction heat transfer using a shape factor to account for these differences in surface areas. We used a shape factor of 2.4 (Tracy 1976), and we calculated an area within the core of the frog at which core body temperature would be defined as  $(A_{tot} + A_{vent}) \times 1.3$ .

Transfer of heat and mass by convection from frogs is a complicated process. Importantly, small frogs both have an insulating boundary layer of still air around the body of the animal, and those small animals also can be within the boundary layer of still air above their substratum. On the other hand, large frogs may not be influenced measurably by the substratum boundary layer. Thus, we calculate boundary-layer resistances for frogs differently for large and small frogs. Specifically, we calculate boundary-layer resistances (both for heat and mass transfer) for large frogs using the equations from Tracy (1976), and we calculated boundary layers of small frogs from a regression of reported boundary layers as a function of body mass for several hylid frogs differing in body mass (Young et al. 2005).

##### *Properties of the environment*

Our model of the mass and energy budgets of anurans allows calculation of the processes of heat and water exchange in virtually any combination of physical environmental circumstances. The equations for calculating the following environmental processes and properties are all from Tracy (1982). The required input variables are: air temperature, relative humidity, wind speed, surface temperature of the substratum, latitude, elevation, day of year, hour of the day, time of solar noon, haze and dust index (Gates 1962), and average albedo of the habitat to solar radiation. From these variables, one can calculate (Tracy 1982) the following

variables needed to complete the energy and water budgets of frogs in any set of environmental variables when there are no clouds in the sky: density of the air, vapor density of the air, diffusivity of water vapor in air, kinematic viscosity of the air, conductivity of the air, zenith angle of the sun, optical air mass of the atmosphere, precipitable water in the atmosphere, declination of the sun, radiation from the sun, radiation from skylight, radiation from the ground surface, thermal radiation from the sky, and thermal radiation from the ground.

#### *Validation of the model*

We have previously shown (Tracy et al. 2007a) that wet plaster models give an accurate measurement of the temperature and rate of water loss of real frogs in various environments, so they can be used to measure the operative environmental temperature ( $T_e$ ) experienced by frogs. Therefore, we used plaster models of frogs of different size and shape to test the accuracy of the outputs from our computational model. We measured the temperature and rates of water loss of eight plaster models, representing three species (*Litoria caerulea*, *Cyclorana australis*, *Rhinella* [formerly *Bufo*] *marinus*) with body sizes ranging over 3.6–97 g. Each model was measured in three different localities in the Northern Territory of Australia, in the towns of Elliott (17°33'11.8" S, 133°32'32.8" E) and Darwin (12°22'13.0" S, 130°52'04.4" E), and near lake Woods (17°36'52.7" S, 133°28'00.2" E), and measurements were made at different times of the afternoon. The plaster models were placed in an open spot, with no vegetation cover, allowing an unobstructed view of the sky, and weather conditions were clear and sunny. At each location, we measured all of the input variables for the computational model (air temperature ( $T_a$ ), ground temperature ( $T_g$ ), wind speed, relative humidity, time of day, latitude/longitude, elevation), as well as the temperature of the plaster models. At one location, we measured the internal ("core") temperature of the models (with thermocouples) and the surface temperature (with an IR thermometer). We found that these two temperatures were not significantly different (paired  $t$ : 1.29,  $df = 10$ ,  $P = 0.23$ ), so we subsequently measured only surface temperature. Water loss by the plaster models was measured as the change in mass over 15 min.

The computational model estimates instantaneous properties, and biophysical processes, of the animal (viz.,  $T_b$  and rate of water loss) whereas the physical models integrate complex biophysical processes that incorporate the important property of thermal inertia, interacting with natural variation in wind speed, air temperature, and relative humidity, and causing rates of water loss to be very complex (Spotila et al. 1973, Tracy 1982, Turner and Tracy 1983, Stevenson 1985, Christian et al. 2006). Therefore, the computational model generally will calculate values that are closer to what would be estimated from averages of many  $T_e$  models all

responding slightly differently with naturally turbulent air and because any differences in mass will result in differences in thermal inertia. Thus, our validation experiments compared calculated, instantaneous body temperatures, and water-loss rates with the averages of many  $T_e$  models that simultaneously interacted with the naturally heterogeneous environment over a period of time. Additionally, we measured water loss rates over a period of 15 min, which should integrate the heterogeneity of the environment, and the complex biophysical processes including the effects of thermal inertia, on both  $T_e$  and rates of water loss.

We took data from 6–8 plaster models from each site, and we regressed the  $T_e$  and water loss rates against body mass. We then calculated the differences between these regressions, and the calculated  $T_e$  and water loss rates from the computational model. We summed these deviations to calculate the ability of the computational model to estimate the average deviation between model calculations for  $T_e$  and water loss rates as measured with averages for plaster models. The average deviation for  $T_e$  was 0.7°C with a standard deviation of 5.17°C, and the mean deviation in water loss rate was –1.6 g/h with a standard deviation of 3.5 g/h. Importantly, the calculated  $T_e$  and water loss rates precisely matched the average integrated properties and processes of the physical models. Equally importantly, the variation around these means is huge, and reveals the tremendous effect of environmental heterogeneity interacting with objects that have different thermal inertias. Regardless, the computational model quite precisely estimates the average biophysical interactions between plaster models (and by inference, actual animals) and complex and dynamic physical environments.

## RESULTS AND DISCUSSION

### *Effects of body size and $R_c$ on $T_b$ and water loss*

The model was used to simulate water loss and body temperature of frogs in the water-conserving posture in two environmental conditions: wet nighttime conditions for a 10 June day in Darwin, Australia, at a latitude of 12.4° S and an elevation of 10 m above sea level (air temperature, 15°C; substratum temperature, 15°C; relative humidity, 80%; wind speed, 1 m/s), and dry daytime conditions at the same location (air temperature, 30°C; substratum temperature, 45°C; relative humidity, 30%; wind speed, 1 m/s). These represent conditions that we have measured commonly in the Darwin area in June (C. R. Tracy, unpublished data). Although the daytime conditions may at first seem extreme, and certainly diurnally active frogs are less common than nocturnal species, they represent reasonable daytime conditions for tropical species, and a high percentage of anuran species have tropical distributions (e.g., IUCN 2008). Furthermore, the angle of incident solar radiation, and thus its intensity, at 12.4° S in June (austral winter) would be equivalent to that experienced at ~38° N (roughly the latitude of San Francisco,

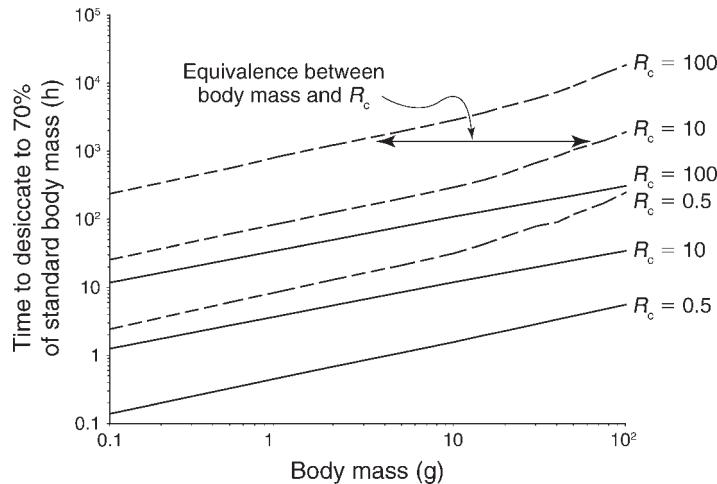


FIG. 1. Relationship between body mass and time to desiccate to 70% of standard mass for hypothetical frogs with cutaneous resistances ( $R_c$ ) of 0.5, 10, and 100 s/cm, at night and during the day (note log scales). Simulations were run for frogs in the water-conserving posture in two hypothetical environments that might be experienced by frogs near Darwin, Australia (12.4° S latitude), in June: one very desiccating (daytime, solid lines; 30% relative humidity, 30°C air temperature, 45°C ground temperature, 1 m/s wind speed) and one relatively neutral with respect to water loss (nighttime, broken lines; 80% relative humidity, 15°C air temperature, 15°C ground temperature, 1 m/s wind speed).

California or Lisbon, Portugal), and would be considerably less intense than the conditions near the tropic of Cancer at that time of year (e.g., Miami or Hong Kong). We have observed at least four species to experience similar conditions around Darwin, Australia in June (C. R. Tracy, *personal observations*).

The simulations calculated the rates of water loss in units of time to desiccate to 70% of the standard body mass and body temperatures ( $T_b$ ) for simulated frogs differing in body mass and skin resistance as a means to assess the sensitivity of the water-loss process to the factors influencing water loss. Importantly, the difference between water loss in daytime environments and nighttime environments is very large (Fig. 1). Indeed, rates of water loss during the night range from 10 to >50 times slower than rates for the daytime, depending on body size and skin resistance. Thus, a 10-g frog with minimal skin resistance to water loss ( $r = 0.5$ ) will desiccate to 70% of its standard mass in ~90 min during the simulated daytime conditions, but it would take >30 h in nighttime conditions before desiccating to 70% of standard mass. This means that the frog could move about through an entire night without threat of severe desiccation, a result that is congruent with the tendency for frogs to be nocturnal.

The simulations also showed that at a given  $R_c$ , smaller animals had a higher body temperature,  $T_b$  (Fig. 2; Appendix A), particularly those with body sizes < 10 g. For example, a 1-g frog basking under simulated, daytime conditions might equilibrate at a body temperature of around 38°C, where a larger frog, with the same  $R_c$ , might be >3°C cooler. Small anurans apparently can reach these high body temperatures, even if they have very high cutaneous evaporation rates, because they

experience the relatively warm microclimatic conditions in the boundary layer of the substrate. That pattern of body temperatures occurred across a range of  $R_c$  and suggests that small, diurnal anurans may be able to thermoregulate to elevate body temperatures above ambient, which could be particularly beneficial to diurnal metamorphs that must grow quickly to escape predation. Increases in  $R_c$  also resulted in higher  $T_b$ , for a given body size. This effect was strongest for skin resistances below 25 s/cm (Fig. 2; Appendix A); increases in  $R_c$  up to 25 s/cm result in substantial increases in  $T_b$ , but further increases in  $R_c$  above 25 s/cm resulted in only slightly higher  $T_b$ . Medium-sized frogs with  $R_c$  over 25 s/cm might reach temperatures >8°C higher than the same-sized individuals with  $R_c < 1$  (a value considered “typical” for most amphibians (e.g., Bentley 1966, Wygoda 1984, Shoemaker et al. 1992). Interestingly, skin resistances higher than 25 s/cm have little effect on body temperature (Fig. 2; Appendix A), suggesting that the extremely high resistances seen in some species serve primarily to lengthen the time a frog can go without access to water rather than increasing their thermoregulatory abilities.

Under nighttime conditions, the effects of body size and  $R_c$  showed trends similar to those during the day, but the limited evaporation in cool, humid, nighttime conditions, and the lack of solar influx, mean that these effects are dramatically reduced (Fig. 2; Appendix A). Thus, the temperature differences at night across the entire range of variation in both body mass and  $R_c$  were less than 1°C.

The relative value of body size and skin resistance in retarding desiccation can be seen in Figs. 1 and 3. For example, the simulations show that a 1-g frog with a

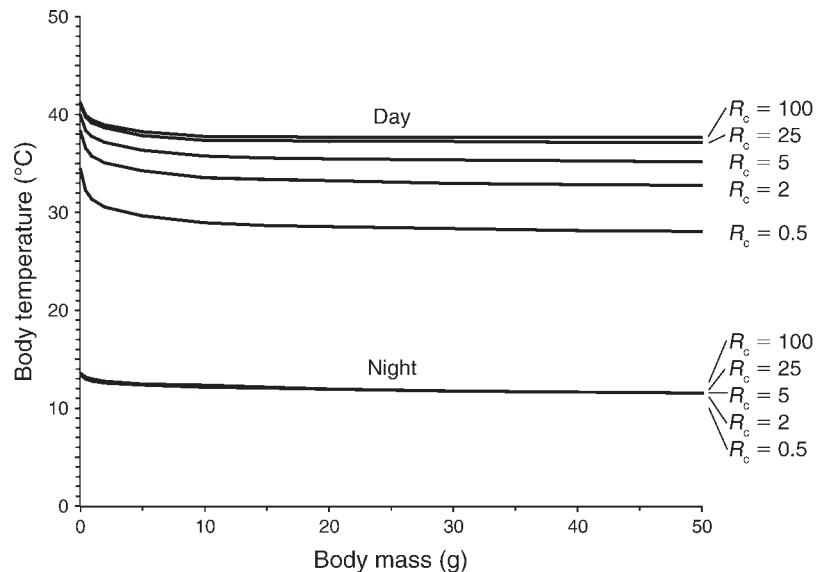


FIG. 2. Effects of body mass and resistance to water loss ( $R_c$ ) on body temperature ( $T_b$ ) for hypothetical frogs in the water-conserving posture, under two environments that might be experienced by frogs near Darwin, Australia (12.4° S latitude), in June: one very desiccating (daytime; 30% relative humidity, 30°C air temperature, 45°C ground temperature, and 1 m/s wind speed) and one relatively neutral with respect to water loss (nighttime; 80% relative humidity, 15°C air temperature, 15°C ground temperature, and 1 m/s wind speed). During the day, body mass has a substantial effect on  $T_b$  for masses <10 g; above this size, mass has little effect on  $T_b$ . Similarly,  $R_c$  has a substantial effect at resistances <25 s/cm, but a minimal effect on  $T_b$  above  $R_c = 25$ . At night, there is little effect of either body size or  $R_c$ .

skin resistance of 55 s/cm can be equivalent to a 50-g frog with a skin resistance of 7 s/cm (a similar case is illustrated in Fig. 3 by the comparison between *L. bicolor* and *L. caerulea*). Thus, frogs can be similarly emancipated from the threats of desiccation either by being large or by having a skin resistant to water loss. Collectively, the various separate traits that can serve to resist desiccation (high skin resistance, large body size, nocturnality, microenvironment selection) can have a substantial effect on time to desiccation. Thus, a 1-g frog sitting upright with an  $R_c$  of 0.5 may only be able to last 30 min in daytime conditions before desiccating to 70% of standard mass, but a 100-g frog in water-conserving posture and with an  $R_c$  of 100 can persist >17 000 hours in nighttime conditions before reaching the same level of desiccation (Fig. 1). That means the large frog with a high skin resistance literally could survive nearly two years without dangerously desiccating, if it could find continuous conditions like those in our nighttime simulations.

#### Implications of body size and $R_c$ for arboreality

We surveyed the literature for data on body size and skin resistance for a wide variety of frogs. Simulations of the desiccation time using known properties of frogs, obtained from the literature, showed that arboreal frogs tended to have longer desiccation times to 70% of standard mass than do frogs that are terrestrial or aquatic (Fig. 3; Appendix B). Indeed, the only non-arboreal frogs that appear in the upper right quadrant of Fig. 3, where desiccation times are longest, are terrestrial

species that are in cocoons formed during periods of dormancy. Some arboreal species do fall in the lower left quadrant, where species dehydrate quickly; however these are mainly species that remain near water, or live in extremely wet conditions (e.g., rain forests; Young et al. 2006). Species with long times to desiccate to 70% of standard body mass have been found in several families (Appendix B), and are distributed globally. However, there is a dearth of species with longer desiccation times in North America and Europe. It is unclear, at this stage, whether that is because such species do not exist on those continents, or whether there has simply been no research on frogs with highly resistant skin there; however, the latter seems unlikely, given the large body of physiological research on anurans in North America and Europe. It is also possible that the lack of frogs with highly resistant skin reflects the lower diversity of arboreal species in those areas, compared to Australia, Africa, and South America.

As mentioned previously, some terrestrial species do achieve very long times to 70% desiccation by entering dormancy and forming cocoons (Appendix B) that reduce water loss during times when water is scarce (Lee and Mercer 1967, McClanahan et al. 1976, Loveridge and Withers 1981, van Beurden 1984, Withers 1995, 1998, Withers and Richards 1995, Christian and Parry 1997, Tracy et al. 2007b). Interestingly, some cocoon-forming, terrestrial species (*Cyclorana australis* and *C. novaehollandiae*) have moderate resistance to water loss even without cocoons (Withers 1998, Young et al. 2005),

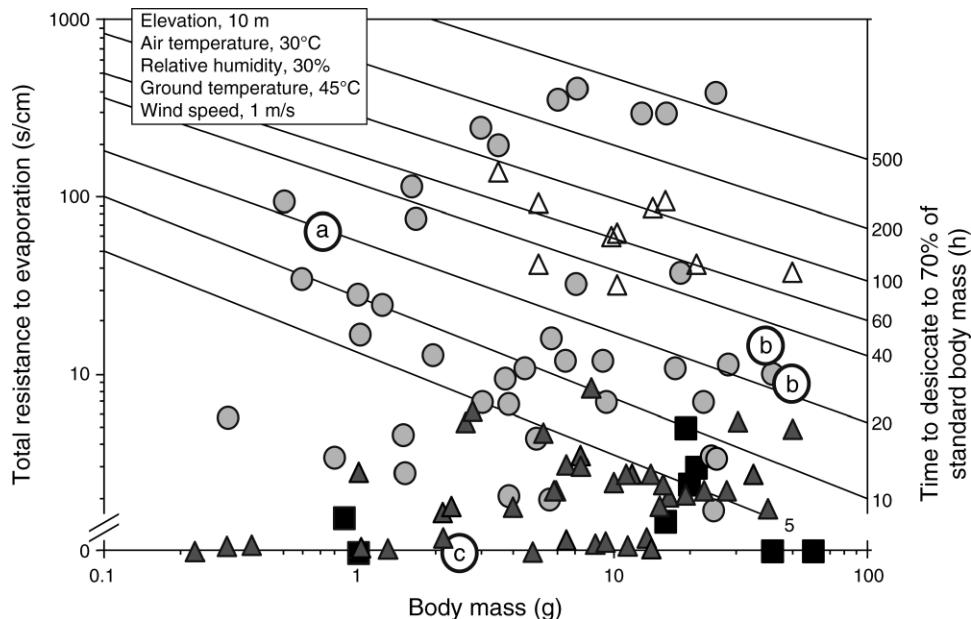


FIG. 3. Relationships between body mass, total resistance to evaporation, and the time it takes a frog to desiccate to 70% of its fully hydrated mass (diagonal axis), calculated for 104 reports of data on body mass and resistance to water loss for 85 species of frogs (note log scales). Times to 70% of standard body mass were calculated for a frog in the water-conserving posture, during the day, under the environmental conditions given in the box. Species that fall in the upper right quadrant of the graph are those able to avoid dangerous levels of desiccation for the longest time, and tend to be arboreal, or terrestrial species that have formed a cocoon during a dormancy period. Circles represent arboreal species, triangles represent terrestrial species, and squares represent aquatic species. Open triangles represent values for terrestrial species while they are in cocoons, for species that form cocoons during periods of dormancy. Three species, described in the text (*Results and discussion: implications of body size...*), have been highlighted to illustrate different strategies for being arboreal: (a) *Litoria bicolor*, a species with small body size and high cutaneous resistance to water loss, (b) *Litoria caerulea*, a species with large body size and moderate resistance to water loss, and (c) *Platymantis vittensis*, a species with small body size and low resistance to water loss but that lives in a very wet habitat. The two points for *L. caerulea* represent values from two different studies of that species.

resulting in them being among the most resistant of the terrestrial species to dehydration (Fig. 3).

Our review of the literature and our model simulations together suggest that arboreality for frogs can be accomplished three ways: (1) frogs can adopt an arboreal habit where water is always available (e.g., in rain forests); (2) they can have skin with a high resistance to evaporative water loss; and/or (3) they can have a reduced surface area (in relation to body volume) from which water is evaporated, which can be accomplished by having a larger body size and/or by adopting a water-conserving posture. These three strategies are illustrated in Fig. 3, with three species: (a) *Litoria bicolor*, which is small but has very high  $R_c$  (Young et al. 2005) and therefore a relatively long time to dangerous levels of desiccation; (b) *Litoria caerulea*, with moderate  $R_c$  and large size (Young et al. 2005), which result in a similar time to 70% of standard mass as *L. bicolor*; and (c) *Platymantis vittensis*, which has small size and no skin resistance but occurs in the rain forests of Fiji, where water is always available (Young et al. 2006).

Obviously, species not found in perpetually wet habitats can achieve the greatest degree of arboreality by having both a high skin resistance and having a large

body size. Terrestrial frogs tend not to have high skin resistance, which suggests a cost to maintain a high skin resistance, possibly stemming from the metabolic costs of synthesizing the secretions that increase cutaneous resistance. Interestingly, terrestrial frogs sometimes modify their skin resistance, during the season in which they hibernate or estivate, by developing a relatively impermeable cocoon. The skin resistances of frogs with cocoons can be very high (Appendix B). While hibernating (or estivating), these frogs would have reduced metabolic rates (Seymour 1973, Loveridge and Withers 1981, Withers and Thompson 2000, McArthur 2006), offsetting the metabolic costs associated with developing a cocoon and associated secretions (Christian and Parry 1997).

Our simulations illustrate that, in a given microclimate, large anurans would take much longer to dry to dangerous levels of hydration than do small anurans (Figs. 1 and 3). However, the absolute water loss rates for large anurans, and thus the amount of water needed to rehydrate, would be higher than that needed by small animals. This suggests a possible trade-off between being large to withstand long periods without a source of water, and being small to be able to rehydrate with a small amount of water. Thus, some environments may

select for arboreal frogs of different sizes. For example, small frogs may be favored in areas that periodically experience nights with heavy dew. In contrast, large frogs may be favored in areas that experience extended periods with little rainfall (e.g., savannas).

#### CONCLUSIONS

We have presented a new biophysical model for energy and water balance of frogs that allowed us to explore the consequences of two variables, body size and skin resistance to water loss ( $R_c$ ), on the body temperature and length of time it would take a frog to desiccate to dangerous hydration levels. Our simulations showed that resistances below 25 s/cm have a significant effect on  $T_b$ , but those above 25 s/cm have little additional effect. Small frogs (<10 g) are able to achieve  $T_b$  higher than ambient, even with relatively low  $R_c$ , which may allow them opportunities to thermoregulate. Large frogs, however, require significant resistance to elevate their temperatures as high as small frogs.

Our simulations also showed that frogs can avoid rapid desiccation by having high  $R_c$ , having a large body size, or some combination of all of these. A survey of real frogs showed that species with a combination of  $R_c$  and body size that allow them long times to desiccate to dangerous hydration levels tend to be arboreal (or dormant and encased in a cocoon), suggesting a link between arboreality and ability to avoid rapid desiccation.

Here, we have demonstrated this model, and its utility for answering questions about physical and physiological interactions between frogs and their environment, by using a limited set of environmental conditions. However, the model should be useful for a variety of questions about frog energy and water balances in a variety of habitats, and for questions about the consequences of skin resistance. The model should also be a useful tool for exploring potential impacts of climate changes on amphibians, including local changes to habitats (e.g., natural or human-caused disturbances, deforestation, changes to local hydrology, urbanization) as well as regional or global changes (e.g., changes in seasonal temperatures or rainfall regimes).

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#### APPENDIX A

Relationship between body mass, resistance to water loss, and body temperature for hypothetical frogs in the water-conserving posture under two environments, one very desiccating and one relatively neutral with respect to water loss, that might be experienced by frogs near Darwin, Australia (*Ecological Archives* E091-102-A1).

#### APPENDIX B

Body mass, cutaneous resistance to water loss, and time required to desiccate to 70% of standard body mass for frogs under daytime and nighttime conditions, as measured in Darwin, Australia, in June (*Ecological Archives* E091-102-A2).