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Tracy, Christopher R.; Laurence, Nathalie; Christian, Keith

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Condensation onto the Skin as a Means for Water Gain by Tree Frogs in Tropical Australia

Christopher R. Tracy,¹,* Nathalie Laurence,¹ and Keith A. Christian¹

1. Research Institute for the Environment and Life Sciences, Charles Darwin University, Darwin, Northern Territory 0909, Australia

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Abstract: Green tree frogs, Litoria caerulea, in the wet-dry tropics of northern Australia remain active during the dry season with apparently no available water and temperatures that approach their lower critical temperature. We hypothesized that this surprising activity might be because frogs that are cooled during nighttime activity gain water from condensation by returning to a warm, humid tree hollow. We measured the mass gained when a cool frog moved into either a natural or an artificial hollow. In both hollows, water condensed on cool L. caerulea, resulting in water gains of up to 0.93% of body mass. We estimated that the water gained was more than the water that would be lost to evaporation during activity. The use of condensation as a means for water gain may be a significant source of water uptake for species like L. caerulea that occur in areas where free water is unavailable over extended periods.

Introduction

Water used by most terrestrial animals either comes from drinking free water, is preformed in food, or comes from oxidation. Most amphibians instead absorb water through the skin (for reviews, see Jørgensen 1997; Hillman et al. 2009), and some arthropods are able to take up water vapor directly from the air (Hadley 1994; Chown and Nicholson 2004). Lasiewski and Bartholomew (1969) posed an additional pathway for gaining water. They hypothesized that poikilotherms in arid areas with wide temperature fluctuations (e.g., deserts) might be able to gain water from condensation onto their skin. They suggested that this could happen when a cool poikilotherm moves from a cool microenvironment to a warm-humid one, such as a nocturnal desert animal entering a burrow on a clear, cool night. Their experiments, performed under artificial conditions, demonstrated that some desert lizards, spiders, and frogs could gain water by this mechanism, but they left open the question of whether this actually occurs in nature.

Water balance poses a particular challenge for amphibians because many maintain a moist skin with copious mucus secretions (Lillywhite 1971), and the skin of most species offers little resistance to water exchange (Wygodz 1984). Thus, evaporative water loss from the skin is a significant part of the water budget for amphibians in general, and this creates a particular problem for species that occur in arid or seasonally arid areas. Many anuran amphibians in seasonally dry regions avoid desiccation by digging into muddy cracks or becoming dormant in burrows or moist tree hollows (Shoemaker et al. 1992; Wells 2007; Hillman et al. 2009). However, some species remain active despite the difficulties of maintaining water balance in arid conditions. The threat of desiccation for amphibians is strong enough that they will engage in rehydration behaviors, even if it increases other costs, like risk of predation due to activity (Wells 2007).

The wet-dry tropics of northern Australia are characterized by having substantial amounts of rain during the wet season and little or no rain during the dry season. In the northern part of the Northern Territory, the median rainfall for June–August is 0.0 mm, and the cumulative median rainfall for May–September is 11.6 mm.¹ Thus, animals in this region experience a prolonged dry season.

Despite the seasonally arid conditions, some northern Australian frogs remain active, or are periodically active, during the dry season. Many of those species are found close to free water sources (e.g., permanent streams or billabongs). However, the green tree frog, Litoria caerulea, is periodically active during the dry season without apparent access to any water source (McArthur 2006). Interestingly, this species is active not just on relatively warm, humid nights but also on relatively cool nights. McArthur

* Corresponding author; e-mail: chris.tracy@cdu.edu.au.

(2006) observed frogs to be active at body temperatures as low as 12.5°C. Temperatures in this range are quite close to the critical thermal minimum (CT\text{min}) for this species, which is approximately 11°C (see the appendix in the online edition of the American Naturalist for the thermal performance curve, including critical temperatures, for L. caerulea). At 12.5°C, L. caerulea may only perform at less than 20% of peak performance levels. With their performance so impaired, it is unlikely that the activity of these frogs is primarily for foraging.

We therefore hypothesized that L. caerulea might use condensation onto the body as a way to gain water during the dry season and that this might explain their activity on cool nights during the dry season. We tested this hypothesis by putting cool frogs into tree hollows, one of which was natural and one of which was artificial, to determine the net gain of water that they could achieve.

**Methods**

**Condensation in a Natural Tree Hollow**

Experiments were conducted in a large Eucalyptus miniata tree that was approximately 1 m in diameter. We had observed at least eight individual Litoria caerulea use this tree hollow (simultaneously) as a daytime refuge during the dry season of 2006. The tree trunk was apparently hollow up to the entrance, which was 4 m above ground and approximately 15 cm in diameter. We monitored the temperature of the tree hollow using iButtons (model DS1921G; Maxim Integrated Products), placed at 4, 3, and 2 m below the hollow entrance (0, 1, and 2 m above ground, respectively) from July 25 through August 9, 2006. Relative humidity showed a sharp gradient at increasing depths below the hollow entrance but was consistent at more than 2 m below the hollow entrance. Thus, we measured humidity at the bottom of the hollow (iButton model DS1923).

We tested for mass gain from condensation by first cooling the frogs with an ice water bath to 10.8°–16.2°C or by allowing them to cool to ambient, operative temperatures in air (18.0°–19.2°C). The skin temperature (measured with a Raytek Raynger IP-K infrared sensor attached to a Fluke 51K/J thermometer) and the body mass of the frogs were measured, and then the frogs were placed in a mesh box (100 mm × 55 mm × 40 mm) made of plastic gutter guard. To account for any condensation onto the cage, an identical empty cage was weighed separately and attached to the bottom of the cage containing the frog. These cages were then lowered 2 m into the tree hollow. A preliminary trial with frogs (\(n = 3\)) that had been implanted with temperature-sensitive radio transmitters allowed us to monitor the change in body temperature. We determined that temperatures had changed by 75% of the difference between initial and equilibrium temperature in 15 min, so we used this as the test duration. After 15 min, we pulled the frogs (\(n = 16\)) out of the hollow and immediately measured body mass and skin temperature of the frog within the cage and the mass of the empty cage. Mass gain was assumed to be caused by condensation.

**Condensation in an Artificial Tree Hollow**

We constructed an artificial tree hollow out of a PVC pipe (800 mm long and 150 mm diameter) that was housed in an incubator comprised of a Fisher and Paykel cabinet with a Shimaden SR47 temperature control attached. The hollow was positioned vertically and sealed at the base. There was a removable lid with a small hole to allow air flow out of the hollow and to allow the insertion of a relative humidity probe into the hollow. The lid also had a hook attached that allowed items to be suspended within the hollow.

Humidity inside the artificial hollow was raised by pumping air through water and then into the pipe. Room air was pumped through a 6-m coil of tubing (8 mm inner diameter) that was housed inside the temperature cabinet to ensure that the pumped air was the same temperature as the cabinet. The air was humidified by passing it through airstones submerged in two 500-mL side-arm flasks that were filled with water and linked in series. The humid air then flowed into the bottom of the artificial hollow. Because airflow was from bottom to top, accessing the hollow through the lid at the top minimized disturbance of the equilibrium hollow conditions.

Trials were conducted with air temperatures in the hollow ranging from 15° to 30°C and relative humidities ranging from 74% to 95% (table 1), and the incubator was allowed to equilibrate for at least 60 min before any measurements were recorded. Frogs were cooled to the test temperatures (7°–11°C) over ice water as described above or were allowed to equilibrate in air in an incubator to test temperatures of 15°–20°C.

The L. caerulea specimen (\(n = 3–7\) per temperature range) was then placed into a mesh cage (as described above), and the combined mass of the frog and cage was measured using a UWE JW-500 balance. As with the field experiment, an identical empty cage was weighed separately and then attached to the bottom of the cage containing the frog, and both were then suspended in the hollow, with the cage containing the frog at a depth of approximately 15 cm from the top of the hollow. The air temperature and relative humidity inside the hollow was measured at this depth using a Vaisala HM141 humidity and temperature indicator.

The frog and the cages were left in the hollow for 20
min. At the end of this period, the air temperature and relative humidity were again measured. The cages were removed from the hollow, the skin temperature of the frog taken, and the mass of the empty cage and that of the cage containing the frog were measured.

**Evaporative Water Loss**

We estimated the amount of water lost by frogs exiting a warm burrow and cooling to equilibrium temperatures on a cool, dry season night using the biophysical model of temperature and water loss of Tracy et al. (2010). We used the time series of temperature change measured by placing a cooled frog into a tree hollow (described above) to define both the amount of time it would take for an average-sized *L. caerulea* (42 g) with a cutaneous resistance to water loss of 12 s cm⁻¹ (Christian and Parry 1997; Young et al. 2005; Tracy et al. 2008), sitting in a typical resting posture, to come to equilibrium on a cool night and also the shape of the temperature change curve, assuming that the time constant for heating and cooling in frogs is equal (Tracy et al. 1992). We then calculated water loss rate for every minute until the frog was in equilibrium with the outside conditions and summed the total water lost over the 30 min it took for the frog to come to equilibrium. We assumed air and ground temperatures of 18°C, wind speed of 0.5 m s⁻¹, and relative humidity of 75%, 85%, or 90%, which were similar to the conditions experienced during the field experiments using the tree hollow. Solar absorbance of the animal was assumed to be 0.76 (C. R. Tracy, unpublished data), and the reflectivity of the ground was assumed to be 0.15. Model simulations were run for a site at 10 m elevation at 12.4°S latitude at 2200 hours on Julian day 180 (June 28), and they were run separately with cloudy and clear skies.

**Water Absorption**

We did a simple test of whether condensed water was absorbed through the skin by putting drops (approximately 50 µg) of water onto the dorsal skin of four *L. caerulea*. We used water colored with red food coloring to help trace the water, and we measured the mass change of the frog every 5 min for 30 min. After 30 min, we blotted all water remaining on the skin with a paper towel and reweighed the frogs, assuming that any body mass change would be caused by absorbed water.

**Results**

**Condensation in a Natural Tree Hollow**

Conditions in the hollow Eucalyptus tree were consistently warm and humid, with temperatures ranging between 22.0°C and 27.7°C (mean temperature [ ± SD] was 24.6 ± 1.5°C at the top of the hollow and 25.4 ± 1.3°C at the bottom), with minimum temperatures (22°C–24.5°C at the top and 23.0°C–25.5°C at the bottom) typically occurring from 1000 to 1200 hours and maximum temperatures (25.0°C–27.5°C at the top and 24.5°C–27.5°C at the bottom) typically occurring from 1900 to 2300 hours, several hours after sunrise and sunset, which were at approximately 0700 and 1840 hours, respectively, at that time of year. Maximum and minimum temperatures usually showed a plateau for 3–5 h. Relative humidity at the bot-

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**Table 1:** Experimental conditions and mass gained by cooled frogs placed into a warm and humid natural tree hollow in a *Eucalyptus miniata* for 15 min or an artificial tree hollow for 20 min

<table>
<thead>
<tr>
<th>Hollow, test condition (sample size)</th>
<th>Temperature (°C)</th>
<th>Hollow relative humidity (%)</th>
<th>Water gain (g)</th>
<th>Mass gain (% body mass)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Eucalyptus</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ice cooled (16)</td>
<td>12.3 ± 1.5</td>
<td>25.7 ± .5</td>
<td>13.3 ± 1.4</td>
<td>88.9 ± 1.9</td>
</tr>
<tr>
<td>Air cooled (2)</td>
<td>18.6 ± .8</td>
<td>26.2 ± .1</td>
<td>7.6 ± .7</td>
<td>88.8 ± .6</td>
</tr>
<tr>
<td><strong>Artificial</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Air cooled (8)</td>
<td>14.2 ± .3</td>
<td>18.8 ± .2</td>
<td>4.6 ± .3</td>
<td>95.1 ± .4</td>
</tr>
<tr>
<td>Air cooled (7)</td>
<td>19.3 ± 2.0</td>
<td>29.7 ± .1</td>
<td>10.7 ± 1.9</td>
<td>87.8 ± 2.5</td>
</tr>
<tr>
<td>Air cooled (7)</td>
<td>14.5 ± .4</td>
<td>25.9 ± .1</td>
<td>11.4 ± .4</td>
<td>91.6 ± .4</td>
</tr>
<tr>
<td>Air cooled (3)</td>
<td>14.7 ± .2</td>
<td>29.8 ± .2</td>
<td>15.8 ± .3</td>
<td>88.3 ± 2.2</td>
</tr>
<tr>
<td>Air cooled (3)*</td>
<td>14.7 ± .2</td>
<td>29.8 ± .2</td>
<td>15.5 ± .3</td>
<td>88.3 ± 2.2</td>
</tr>
<tr>
<td>Air cooled (7)</td>
<td>14.0 ± .8</td>
<td>29.3 ± .5</td>
<td>15.4 ± .9</td>
<td>89.5 ± 3.7</td>
</tr>
<tr>
<td>Ice cooled (5)</td>
<td>7.18 ± 1.1</td>
<td>17.88 ± .7</td>
<td>10.7 ± .9</td>
<td>78.2 ± 6.7</td>
</tr>
<tr>
<td>Ice cooled (5)</td>
<td>11.12 ± 1.7</td>
<td>23.30 ± .1</td>
<td>12.2 ± 1.8</td>
<td>74.0 ± 6.4</td>
</tr>
<tr>
<td>Ice cooled (5)</td>
<td>11.20 ± 1.7</td>
<td>28.78 ± .3</td>
<td>17.6 ± 1.9</td>
<td>81.6 ± 3.9</td>
</tr>
</tbody>
</table>

Note: Values are mean ± SD.

* Frogs were left in the artificial hollow for 40 min, rather than 20 min, as in the other trials.
Condensation in an Artificial Tree Hollow

Frogs in the artificial hollow also consistently gained mass and frequently showed water droplets on their dorsal skin. The amount of water mass gained was related to the temperature difference between frog and hollow (fig. 2), with more mass gained when the temperature differential between the frog and the air in the hollow was larger.

Evaporative Water Loss

Simulations of water loss under the environmental conditions during the field experiment estimated water loss of an average-sized (42 g) *Litoria caerulea* to be −0.003 to 0.07 g, which is less than the frogs could gain after returning to the hollow (see table 1; fig. 2). At high humidity (85%–95%), with a clear sky, radiant heat exchange with a cold sky meant that the equilibrium body temperature of frogs was calculated to be below the dew point, so dew could form on frogs even before they returned to hollows in these conditions.

Water Absorption

Water drops on the dorsal skin of frogs tended to disperse across the skin during the first 15 min, and by 30 min, very little water was visible. After any remaining surface water was blotted (30 min after the drop was placed), the frogs showed a gain of 29 ± 1 μg, or approximately 60% of the drop.

Discussion

Water uptake from condensation onto the body apparently helps explain the activity of *Litoria caerulea* during the dry season at temperatures approaching the CTmin of the species. Our experiments confirmed the results that Lasiewski and Bartholomew (1969) obtained from an artificial burrow by showing that cool frogs entering the atmosphere of a warm, humid tree hollow can consistently gain mass from water condensing on them, under both experimental and natural conditions. This may be an important source of water during a time of year with no rainfall or surface water for months at a time.

For condensation onto the bodies of frogs to be an effective means of maintaining water balance, the amount of water gained would have to at least balance the amount lost while the frog was active. Our calculations suggest that the water gained by cool frogs entering warm, humid hol-
lows exceeds that lost to evaporation during the time it takes to cool to equilibrium. Thus, frogs could achieve a net gain of water simply by leaving their tree hollow refuges on cool nights, even without access to free water and even in ambient temperatures that are too cold for them to forage successfully. Additionally, under some conditions of high humidity and a clear night sky, radiant heat loss to the sky would allow frog body temperature to drop below the dew point outside of a hollow, which would provide additional water gain even before the frog returned to a tree hollow.

The question arises whether water condensed onto frog skin is physiologically useful. Rain-harvesting or dew-harvesting of water from the body occurs in a number of lizards (Bentley and Blumer 1962; Gans and Blumer 1982; Sherbrooke 2002), snakes (Louw 1972; Robinson and Hughes 1978; Andrade and Abe 2000; Cardwell 2006; Glaudas 2009), turtles (Auffenberg 1963), and insects (Louw 1972; Hamilton and Seely 1976; Hamilton et al. 2003; Henschel and Seely 2008). In these cases, water is usually channeled to the mouth through a complex mix of water channels on the skin or carapace and behaviors that combine to move water toward the mouth, where the animal can drink it. However, frogs do not normally drink (Jørgensen 1997) but instead absorb water through the skin. Typically, the ventral skin of frogs is more permeable than the dorsal skin, but even the dorsal skin is relatively permeable to water (McClanahan and Baldwin 1969; Bentley and Main 1972), so it would be reasonable to assume that some condensed water would be absorbed through the skin. Additionally, our simple water drop experiment showed that water placed on the dorsal skin and subsequently blotted off after 30 min still resulted in a mass gain by the frog. Furthermore, the water drops dispersed across the dorsal skin. Similar patterns of water dispersal have been demonstrated in toads of the genus Anaxyrus (formerly Bufo), which have epidermal sculpturing that can channel water from the ventral surface upward along the sides of the animal and onto the dorsal skin (Lillywhite and Licht 1974). Those authors argued that water channeled to the dorsal skin might serve to prevent the desiccation of integumentary surfaces or at least to provide an external supplement to the internal water supplied to the skin surface to prevent its desiccation. Thus, even if water gained by L. caerulea from condensation onto the skin is not actually absorbed, it may serve a physiologically useful purpose by reducing the expenditure of stored internal water.

In addition to creating access to an unusual water source, becoming cool could result in a net metabolic savings for frogs that exit their warm refuge. Anuran amphibians generally have Q10 values of 1.5–4.0 (reviewed in Hillman et al. 2009), and L. caerulea has a Q10 of approximately 3 during the dry season (McArthur 2006). Thus, an active frog at 12°–15°C would have a metabolic rate approximately 30% of what it would be in a tree hollow at 25°C. Such a metabolic savings could be significant during a prolonged dry season where resources or access to resources may be limited. On warmer nights, performance would not be as impaired, so foraging would be possible, although this might result in a net loss of water.

Large trees, such as the one we used to perform our experiments, have a large thermal capacity, which means that hollows within them would remain warm overnight. Indeed, the tree hollow that we used for experiments continued to warm for a few hours after dark, presumably reflecting the slow rate of heat transfer through wood to the hollow inside. This means that the hollow itself remained quite warm and humid overnight, which is an ideal condition for forming condensation onto frogs cooled by activity outside the hollow. We observed at least eight different individual L. caerulea entering or leaving that particular hollow over several nights, which suggests that these frogs congregate at this hollow. Indeed, we have observed groups of L. caerulea in other large trees during the dry season (C. R. Tracy, unpublished data). Presumably, hollows in smaller trees, which are used frequently during the wet season (Reynolds 2005) but less often in the dry season (C. R. Tracy, unpublished data), would change temperature more quickly at night, reducing the temperature differential between frog and the air in the hollow and consequently reducing the potential for water gain.

For amphibians in arid conditions, any source of water gain would be advantageous. The mechanism that we have demonstrated here may provide a key source of water during the dry season in northern Australia, when there is little access to free water and often no rainfall for 3–4 months. This mechanism may also make species that rely on this means of water gain vulnerable to climate change. Current best-estimate predictions of temperatures in 2070 for northern Australia indicate an increase during the dry season of 1.5°–2.5°C on average.1 Warmer overnight temperatures might make it difficult for frogs to cool to temperatures below the dew point found in tree hollows.

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**Literature Cited**


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