



Using pairs of physiological models to estimate temporal variation in amphibian body temperature



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ARTICLE INFO

Article history:

Received 15 March 2014

Received in revised form

15 July 2014

Accepted 18 July 2014

Available online 30 July 2014

Keywords:

Body temperature

Evaporative water loss

Frog

Physical model

ABSTRACT

Physical models are often used to estimate ectotherm body temperatures, but designing accurate models for amphibians is difficult because they can vary in cutaneous resistance to evaporative water loss. To account for this variability, a recently published technique requires a pair of agar models that mimic amphibians with 0% and 100% resistance to evaporative water loss; the temperatures of these models define the lower and upper boundaries of possible amphibian body temperatures for the location in which they are placed. The goal of our study was to develop a method for using these pairs of models to estimate parameters describing the distributions of body temperatures of frogs under field conditions. We radiotracked green-eyed treefrogs (*Litoria serrata*) and collected semi-continuous thermal data using both temperature-sensitive radiotransmitters with an automated datalogging receiver, and pairs of agar models placed in frog locations, and we collected discrete thermal data using a non-contact infrared thermometer when frogs were located. We first examined the accuracy of temperature-sensitive transmitters in estimating frog body temperatures by comparing transmitter data with direct temperature measurements taken simultaneously for the same individuals. We then compared parameters (mean, minimum, maximum, standard deviation) characterizing the distributions of temperatures of individual frogs estimated from data collected using each of the three methods. We found strong relationships between thermal parameters estimated from data collected using automated radiotelemetry and both types of thermal models. These relationships were stronger for data collected using automated radiotelemetry and impermeable thermal models, suggesting that in the field, *L. serrata* has a relatively high resistance to evaporative water loss. Our results demonstrate that placing pairs of thermal models in frog locations can provide accurate estimates of the distributions of temperatures experienced by individual frogs, and that comparing temperatures from model pairs to direct measurements collected simultaneously on frogs can be used to broadly characterize the skin resistance of a species, and to select which model type is most appropriate for estimating temperature distributions for that species.

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1. Introduction

Studying the thermal biology of amphibians is fundamental to understanding their physiology, ecology, behavior, distribution, and evolution (Feder and Burggren, 1992; Wells 2007), and it is becoming increasingly important for understanding, predicting, and managing the effects of disease and climate change on amphibians (Deutsch et al., 2008; Rohr and Raffel, 2010; Rowley and Alford, 2013). Several methods have been developed to measure amphibian body temperatures in the field directly, but most are used for point sampling and do not record temperature semi-continuously (i.e., at regular intervals through time). The most commonly used method is direct measurement with a fluid-

filled thermometer or a thermocouple probe; these can be used to measure skin, oral, or cloacal temperatures (Brattstrom, 1963; Lillywhite, 1970; Wygoda, 1984; Navas, 1996). These methods require handling individuals, which can elevate their body temperature through heat transfer from the researcher's hands (Navas and Araujo, 2000; Lillywhite, 2010). In addition, the stress associated with handling may alter individuals' behavior, which could bias data during longer-term studies that require repeated sampling. Non-invasive methods of measuring amphibian body temperatures that do not require handling include using non-contact infrared thermometers (Rowley and Alford, 2007a) or temperature-sensitive radiotransmitters (Lillywhite, 2010). In such transmitters, a change in temperature results in a corresponding increase or decrease in transmitter pulse rate; this rate can be recorded and later converted to temperature using calibration curves.

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The goal of many studies on the thermal biology of amphibians is to understand how body temperatures are distributed in relation to environmental temperatures and how they change through time (Wells, 2007; Lillywhite, 2010). This aim is best achieved by measuring body temperatures semi-continuously over time, rather than by sampling individual temperatures at discrete points in time (Taylor et al., 2004). Temperature-sensitive radio-transmitters can be implanted or attached externally to amphibians and used with an automated datalogging receiver to record body temperatures at regular intervals (Lillywhite, 1970, 2010; Roznik, 2013). However, such automated telemetry systems are expensive, complex, and typically can only record data from animals within a relatively small area. In addition, because transmitters are too heavy and bulky to be carried by very small amphibians, this method is not feasible for many individuals and species. Another approach to semi-continuous monitoring of body temperatures is the use of physical models. These can be placed in locations used by amphibians and used to estimate body temperatures that would be experienced in those locations by the modeled species over time. Various objects have been used to mimic the thermal properties of amphibians, including dead amphibians (Seebacher and Alford, 2002), casts made of agar (Navas and Araujo, 2000; Rowley and Alford, 2010) and plaster (Tracy et al., 2007), sponges (Hasegawa et al., 2005), and copper casts or tubes covered with wet cotton or cloth (Bradford, 1984; Bartelt and Peterson, 2005).

Designing accurate thermal models for amphibians is difficult because they vary in cutaneous resistance to evaporative water loss. Although many amphibians have little resistance to water loss, some species have much higher levels of resistance, especially arboreal frogs (Wygoda, 1984; Young et al., 2005). In some species, resistance to evaporative water loss can vary substantially among individuals and across time within individuals because they can adjust their skin resistance to water loss, depending on their physiological state and behavior (Wygoda, 1989; Tracy et al., 2008). For these species, no models with fixed rates of evaporation can fully reflect the range of body temperatures available. To account for this variability, Rowley and Alford (2010) designed a system in which pairs of agar models are used together; one model mimics an amphibian with 0% resistance to evaporative water loss, and the other model has 100% resistance. Together, the temperatures of the models define the lower and upper boundaries of possible amphibian body temperatures for the location in which they are placed. Rowley and Alford (2010) tested these models in the field with frogs of one species and found that actual body temperatures fell within the thermal ranges defined by model pairs.

The goal of our study was to develop a method for using the pairs of models designed by Rowley and Alford (2010) to provide accurate estimates of the distributions of body temperatures experienced by frogs under field conditions. These distributions are needed for many ecological studies (Feder and Burggren, 1992; Wells, 2007). We collected thermal data on green-eyed treefrogs *Litoria serrata* using several approaches during a radiotelemetry study. Semi-continuous data were recorded using both types of models and temperature-sensitive radiotransmitters with an automated datalogging receiver, and discrete measurements were taken using a non-contact infrared thermometer. We first determined the accuracy of transmitter temperatures by comparing them to body temperatures measured simultaneously using a non-contact infrared thermometer when frogs were located. We then compared the parameters of distributions of temperatures (mean, minimum, maximum, standard deviation) created using each of these three methods. We also examined how data from model pairs can be used to broadly characterize the relative resistance to evaporative water loss of a species under field conditions by

comparing body temperature measurements to model temperatures, and how this information can be used to select which model type is most appropriate for examining temperature distributions for that species. To determine the utility of data collected using pairs of thermal models in a broader range of species, we examined data on two additional frog species (*Litorianannotis* and *Litoria rheocola*) collected using only model pairs and a non-contact infrared thermometer.

2. Materials and methods

2.1. Radiotracking

We radiotracked a total of 61 male *L. serrata* at two low-elevation (< 400 m ASL) and two high-elevation (> 600 m ASL) rainforest streams in northeastern Queensland, Australia. We chose this combination of sites to provide the widest possible range of environmental temperatures. Tracking took place over a 2-week period at each site during the winter (cool/dry season) in 2011. Our sites were at Kirrama Creek #1 in Girramay National Park (18.203° S, 145.886° E; 100 m ASL; 4–18 July), Stoney Creek in Djiru National Park (17.920° S, 146.069° E; 20 m ASL; 12–25 August), Birthday Creek in Paluma Range National Park (18.980° S, 146.168° E; 800 m ASL; 19 July–1 August), and Windin Creek in Wooroonoan National Park (17.365° S, 145.717° E; 750 m ASL; 26 August–8 September).

Frogs were fitted with temperature-sensitive radiotransmitters (model A2414, 0.30 g, Advanced Telemetry Systems, Isanti, Minnesota, USA; factory-calibrated for 15–30 °C). Each transmitter was attached to a frog externally by a belt made of silicone tubing; a length of cotton thread was passed through the tubing and tied to secure the tubing around the frog's inguinal region (Gouret et al., 2011). The combined mass of the transmitter and belt never exceeded 8% of the frog's body mass, which is below the recommended maximum 10% transmitter-to-body-mass ratio for amphibians (Richards et al., 1994). We tracked all frogs using a Sika receiver (Biotrack Ltd, Wareham, Dorset, UK) with a handheld three-element Yagi antenna. Frogs were located once during each day (10:00–17:00) and once each night (20:00–03:00) throughout the tracking period. At the end of the tracking period, we removed the tracking devices from all recaptured frogs. We excluded all data collected during the 24-hr period following attachment of tracking devices due to potential short-term behavioral effects of handling, which are unlikely to persist after the first night of transmitter attachment (Langkilde and Alford, 2002; Rowley and Alford, 2007b).

2.2. Temperature estimates from *Litoria serrata*

We used three different methods to collect data on *L. serrata* body temperatures: a non-contact infrared thermometer (Rowley and Alford, 2007a), temperature-sensitive radiotransmitters with an automated datalogging receiver, and thermal models (Rowley and Alford, 2010). We measured the body temperature of each frog whenever possible during tracking using a non-contact infrared thermometer (OS425-LS, Omega Engineering Ltd., Irlam, Manchester, UK; factory-calibrated and accurate to ± 1.0 °C), which accurately estimates the core body temperatures (cloacal temperatures) of frogs (Rowley and Alford, 2007a). This device had a distance to spot ratio of 50:1, and the area measured was delineated by a circle of laser points. We set the emissivity to 0.95 (Rowley and Alford, 2007a). To take a temperature reading, we held the device approximately 5 cm away from the frog and aimed it at the lower dorsal region, sufficiently above the transmitter to avoid including it in the area measured.

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