Individual Variation in Thermal Performance of a Temperate, Montane Amphibian (*Rana cascadae*)

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Abstract.—Temperate, montane amphibians are experiencing rapid environmental change. Better mechanistic understanding of the response of montane amphibians to accelerating changes in air and water temperatures can provide a basis for robust predictions of the vulnerability of species to future climate change. Thermal performance curves allow for quantitative predictions of responses to temperatures beyond which locomotor physiology is compromised. We designed a field-based thermal performance assay to evaluate the frequency that adult Cascades Frogs (*Rana cascadae*) are exposed to harmful environmental temperatures. We fit a suite of generalized additive models in an information theoretic framework to estimate thermal performance curves and found *Rana cascadae* optimal performance temperatures (T_{opt}) vary as a function of mass. The T_{opt} for the median mass of individuals in our study (17.9 g) was 20.7° C and critical thermal maximum (CT_{max}) was 34.0° C. We calculated the number of days during the growing season (1 July to 30 September) that the temperature exceeded the upper bound of the 80% maximal performance breadth (T_{br80}), a conservative performance metric beyond which activity drops substantially, and CT_{max} for the median, 25th, and 75th percentile masses in our study using contemporary weather data from 1990 to 2015. *Rana cascadae* did not experience temperatures exceeding CT_{max}, but Tbr80 was exceeded 3-13 d per summer, depending on frog size. Our results emphasize that larger individuals may be more susceptible to extreme warm temperatures. Thermal performance studies not accounting for individual variation should be interpreted cautiously.

Key Words.—Cascades Frog; *in situ*; mass; Mount Rainier National Park; thermal optima; thermal physiology

Introduction

Amphibians are one of the most at risk groups of vertebrates, with at least one third of species threatened with extinction due to habitat loss, disease, and over-exploitation (International Union for Conservation of Nature [IUCN] 2019). Ectotherms are expected to be particularly sensitive to increases in average and maximum air and water temperatures predicted by global climate models (Huey et al. 2009; Blaustein et al. 2010; Duarte et al. 2012). In particular, the thermal sensitivity of temperate, montane amphibians is understudied, yet many of these amphibians are experiencing fast warming (Intergovernmental Panel on Climate Change 2007). These amphibians may exhibit unique responses to climate change relative to other ectotherms given their exposure to challenging environmental conditions generated from protracted winters and short summer growing seasons (Ryan et al. 2014; Mitchell and Bergmann 2015). Montane amphibians may be adapted to cold thermal regimes and, therefore, may have physiological constraints that limit tolerance to warming temperatures (Bernardo and Spotila 2006). Anthropogenic climate warming in montane ecosystems is expected to cause lower winter snowfall, resulting in earlier melt out and longer growing seasons (Corn 2005;

Hamlet et al. 2005). Longer growing seasons have been predicted to allow more time for individuals to breed and acquire resources (McCaffery and Maxell 2010), but may also increase exposure to critical temperatures, impact body condition, and put populations at elevated risk of extinction (Corn 2005; Reading 2007). Additionally, climate change can differentially shift phenologies for amphibians and their prey, causing insufficient resources if timing mismatches (Alford 1989). Environmental temperatures (air, water) influence body temperature and thus metabolism in ectotherms (Bennett 1990; Huey et al. 2009; Duarte et al. 2012), such that warmer environments combined with longer growing seasons could constrain foraging opportunities to cooler hours below critical temperatures and decrease overall survivorship (Reading 2007; Sinervo et al. 2010).

Thermal performance curves measure how performance (e.g., jumping distance, burst swimming speed) changes as a function of body temperature. These curves provide a quantitative framework for evaluating the risk posed by changing thermal environments. The thermal optimum (T_{opt}) represents the temperature coinciding with maximal performance. Because individuals are likely to continue to be active at temperatures beyond T_{opt}, the 80% thermal performance breadth (T_{br80}) represents the temperature range where

individuals exhibit ≥ 80% of their maximal performance, providing a conservative optimal performance range beyond which individuals begin to lose the ability to be active (Huey and Stevenson 1979). Temperatures exceeding T_{br80} result in steep decreases in performance until individuals are non-responsive, coinciding with the critical thermal maximum (CT_{max}; Huey and Stevenson 1979; Bulté and Blouin-Demers 2006). Decreased locomotor performance at temperatures beyond T_{br80} have been shown to negatively affect foraging ability (Greenwald 1974) and increase predation risk (Christian and Tracy 1981).

Research has largely focused on interspecific or inter-population comparisons of thermal limits, but seldom test for individual differences in thermal responses within populations (Artacho et al. 2013; Careau et al. 2014). Studies typically assume individual differences in thermal response within populations are minimal (Knowles and Weigl 1990; Wilson and Franklin 1999); however, individual variation in thermal performance occurs (Preest and Pough 1989; Artacho et al. 2013; Careau et al. 2014; Bartheld et al. 2017), as individual differences in mass, body length, or sex can influence maximum jumping or swimming capacity (Emerson 1978; Bennett 1990; Careau et al. 2014). These traits can affect the shape of thermal performance curves, especially if their influence also changes with temperature. For example, the thermal sensitivity of maximal sprint speed was found to significantly change between individuals for Common Lizards (*Zootoca vivipara*; Artacho et al. 2013). Mechanistic species distribution models used to predict suitable climatic habitats are often based on thermal attributes of a species extracted from thermal performance curves (e.g., Deutsch et al. 2008; Sunday et al. 2012). If the individuals used to develop thermal performance curves represent only a subset of responses within a population or species, predictions of suitable habitat could be over- or under-estimated. Thus, incorporating individual variation into performance studies could provide better insight into the sensitivity of a population to current and future climates.

Although many temperate amphibians do not currently experience temperatures above CT_{max} for sustained periods of time (John-Alder et al. 1988; Navas 1996; Wilson 2001; Navas et al. 2008; Huey et al. 2009), Gerick et al. (2014) estimated that, for larvae of three temperate amphibians, temperatures will exceed the species T_{opt} in 45–82% of current ranges of species by the 2080s. Studies have shown that both temperate and montane ectotherms exhibit wide thermal performance breadths and experience temperatures well below their CT_{max} compared to low elevation or tropical ectotherms which regularly experience temperatures approaching their CT_{max} (John-Alder et al. 1988; Navas 1996; Wilson 2001; Navas et al. 2008; Huey et al. 2009).

Environmental temperatures that exceed T_{opt} may have ecological impacts on the species by increasing the time spent in cooler microrefugia (Pough et al. 1983) and limiting the ability of individuals to forage or evade predators (Greenwald 1974; Huey and Stevenson 1979; Christian and Tracy 1981; Bennett 1990; Jayne and Bennett 1990).

Here we tested for individual variation in thermal performance of adult male Cascades Frogs (*Rana cascadae*), a temperate, montane amphibian, using a field-based performance assay (maximum jump distance). Maximum jump distance trials are a burst locomotor response relying primarily on temperature-dependent anaerobic metabolism (Bennett 1980). We used the resulting quantitative predictions of locomotor performance to estimate T_{opt}, T_{br80}, and CT_{max}, for *R. cascadae* and estimate exposure to harmful environmental temperatures over the previous 26 y (1990–2015).

Materials and Methods

Study site and species sampling.—*Rana cascadae* range from northern Washington to northern California, USA, from 665 m to 2,450 m of elevation, and have a Red List conservation status of Near Threatened (IUCN 2019). To evaluate thermal performance, we hand-caught 30 adult male *R. cascadae* from 47 to 57 mm snout-vent length (SVL) and mass from 12.7 to 20.7 g in the northeastern region of Mount Rainier National Park, Washington, USA (46°55'05"N, 121°35'43"W) in August 2015. We collected frogs at the same wetland, within approximately 30 min to minimize differences in previous environmental temperatures experienced. We recorded SVL, shank length (from ankle to knee), and mass of each individual upon capture.

Temperature acclimation and jumping assays.— We randomly assigned six male frogs to each of five temperature treatment groups, 10, 15, 20, 25 or 30° C (± 2° C) by first placing frogs in individual 14 × 14 × 8.5 cm containers filled with about 2 cm of water from a nearby pond. We then floated individual containers in a large bin filled with about 3 cm of water, maintained at 20° C to ensure all frogs began the experiment at the same temperature (Fig. 1A). After a 2-h acclimation period at 20° C, we slowly raised or lowered the temperature of individual containers (maximum rate ± 0.77° C/min), depending on the temperature treatment group, using ice or water warmed using a camp stove. When the cloacal temperature measured using a MicroTherma 2T hand-held thermometer with a rectal probe attachment (Braintree Scientific Inc., Braintree, Massachusetts, USA) of the first randomly selected frog reached the treatment temperature, we placed individuals on a 2.44 × 1.83 m polystyrene jumping
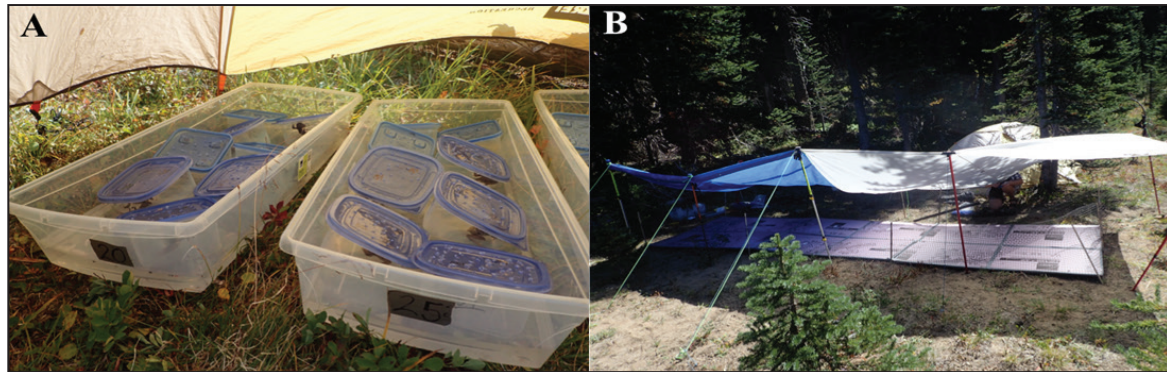
FIGURE 1. Experimental design for *in situ* thermal performance experiment of Cascades Frogs (*Rana cascadae*). (A) Male Cascades Frogs in their individual containers floated in a large treatment bin where water was cooled or warmed to maintain treatment temperature. (B) Jumping platform where frogs were prompted to jump after reaching their treatment temperature. (Photographed by Andrew Boxwell).

platform enclosed in a mesh net and shaded with tarps (Fig. 1B). We prompted frogs to jump by lightly tapping their urostyle and recorded the length of their first three jumps (Renaud and Stevens 1983; Knowles and Weigl 1990; Wilson 2001). We recorded the time, air temperature, and cloacal temperature of frogs before each trial to use as covariates in our models. Frogs were exposed to treatment temperatures from 13 to 110 min, depending on the random order in which they were tested. After jumping, we reacclimatized frogs to ambient temperatures before we released them.

We also tested a subset of frogs in a preliminary experiment at 35° C. Three frogs were non-responsive at this temperature after 20 min and we immediately removed them from the temperature treatment and slowly reacclimatized them to ambient temperature. Despite this, two frogs died, therefore we concluded that 35° C exceeded the CT_{max} for this species and removed the treatment group from the full experiment. We included the data points for two males from the 35° C treatment group in our analysis as the upper boundary

at which individuals are non-responsive (i.e., jump distance was 0 cm) for the thermal limit of the species (Bulté and Blouin-Demers 2006).

Data analysis.—We used the maximum jump distance (out of three jumps) for each individual. Because not all individuals exhibited jumping behavior, we removed two frogs from each treatment group with the shortest maximum jumping distances. Furthermore, we chose to exclude two individuals that we captured with very low body condition (the residual of the length/mass relationship), as they were statistical outliers, resulting in a total sample size of 20 frogs. We constructed nine Generalized Additive Models (GAMs) using the mgcv package (Wood 2011) in the statistical program R (Version 3.4.3: R Core Team 2017) to evaluate individual variation in thermal performance for *R. cascadae* (Table 1). Generalized Additive Models are a non-parametric regression technique that allow for a flexible model that is not bound by specific curves available in a parametric class (Zuur et al. 2009). We

TABLE 1. Akaike Information Criterion corrected for small sample sizes (AICc) table for Generalized Additive Model (GAM) candidates in which we modeled maximum jumping distance (Max Jump) for male Cascades Frogs (*Rana cascadae*) from Washington, USA. Intercept included in all models, not shown (n = 20).

| GAM Model	Number of Parameters (K)	AICc	Delta AICc (Δ_i)	Akaike Weight (w_i)	Deviance
Max Jump~Frog Temperature×Mass	6	153.75	0.00	0.703	1286.88
Max Jump~Frog Temperature+Air Temperature	4	156.27	2.52	0.199	2145.78
Max Jump~Frog Temperature+Time in Treatment	4	158.88	5.13	0.054	3383.93
Max Jump~Frog Temperature×SVL	6	160.61	6.86	0.023	2185.00
Max Jump~Frog Temperature+Mass	4	162.05	8.30	0.011	2398.62
Max Jump~Frog Temperature+SVL	4	163.43	9.68	0.006	2610.47
Max Jump~Frog Temperature×Shank	6	165.58	11.83	0.002	3187.96
Max Jump~Frog Temperature	3	165.58	11.83	0.002	3187.96
Max Jump~Frog Temperature+Shank	4	167.26	13.51	0.001	3141.98
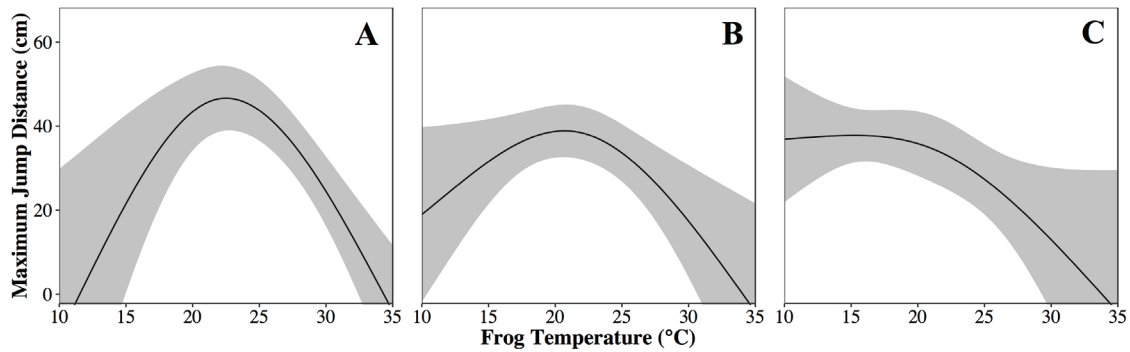
Figure 2. Thermal performance curve and 95% confidence interval (shaded area) for male Cascades Frogs (*Rana cascadae*) from Washington, USA (n = 20) of the 25th percentile mass in our study (A), median mass of our study (B), and 75th percentile mass of our study (C) based on the top Generalized Additive Model.

used cloacal frog temperature (measured immediately before jumping trials), frog mass, air temperature, shank length, and SVL as covariates in the models to predict maximum jumping distance, using a cubic spline smoother with three knots (k = 3; Zuur et al. 2007). Due to our small sample size (n = 20), we limited each model to include an intercept, internal frog temperature, and up to one additional covariate to avoid an overfitted model. We used an Akaike Information Criterion (AIC) corrected for small sample sizes (AICc) model selection framework to compare the relative support for each model (Burnham and Anderson 2002). We used the top ranked model to predict T_{opt}, the upper limit of their T_{br80}, and CT_{max} for the median, 25_{th}, and 75_{th} percentile masses in our study.

We obtained daily maximum air temperatures at our field site from 1990 to 2015 using PRISM climate data (4 km² resolution, Northwest Alliance for Computational & Science Engineering 2016). Generally, adults stay close to water and are known to bask (Lannoo 2005) and therefore frogs may experience microclimates different from PRISM climate data; however, during periods of time when air temperatures exceed the thermal limits of an individual, individuals are restricted to cooler microclimates. To determine if *R. cascadae* experienced environmental temperatures beyond CT_{max}, T_{opt}, or T_{br80} (and thus may be restricted to microclimates) we tabulated the number of summer days during the three hottest months of the year (1 July to 30 September) that

exceeded our estimates of CT_{max}, T_{opt}, and the upper limit of T_{br80} for the median, 25th and 75th percentile masses in our study based our top ranked candidate GAM.

Results

The best model from our candidate set of GAMs included a frog temperature by mass interaction term and carried 70% of the weight (Table 1, Fig. 2). All other models had a ΔAICc > 2, and thus we used only the top model to estimate CT_{max}, T_{opt}, and T_{br80} (Burnham and Anderson 2002). Using the top model, we identified CT_{max}, T_{opt}, and the upper limit of T_{br80} for the, 25th percentile, median, and 75th percentile masses in our study (Table 2, Fig. 3). Heavier individuals exhibit a wider T_{br80} with a lower T_{opt} and CT_{max} (Fig. 2, Table 2). For an individual with a mass of 17.9 g (the median in our study) the top model predicts a T_{opt} = 20.7° C, upper limit of T_{br80} = 26.2° C, and CT_{max} = 34.0° C (Fig. 2B). In comparison, we estimate that frogs of the 25th percentile mass (16.25 g) have a T_{opt} = 22.5° C, upper limit of T_{br80} = 27.3° C, and CT_{max} = 34.3° C. (Fig. 2A). *Rana cascadae* of the 75th percentile mass (18.93 g) had a T_{opt} = 15.2° C, upper limit of T_{br80} = 24.0° C, and CT_{max} = 33.8° C (Fig. 2C).

We calculated the number of summer days where maximum air temperature exceeded CT_{max}, T_{br80}, and T_{opt} for the median, 25th, and 75th percentile masses from 1990–2015 (26 y). We found that maximum air

Table 2. The critical thermal maxima (CT_{max}), optimal temperature (T_{opt}), and lower, upper, and range at 80% of maximum jumping distance (T_{br80}) for the 25th, 50th, and 75th percentile masses for male Cascades Frogs (*Rana cascadae*) from Washington, USA, in our study. Numbers in parentheses indicate the mass of the frog in grams. T_{br80} (lower) is missing for the 75th percentile frogs as the value is below the scope of our study (< 10° C).

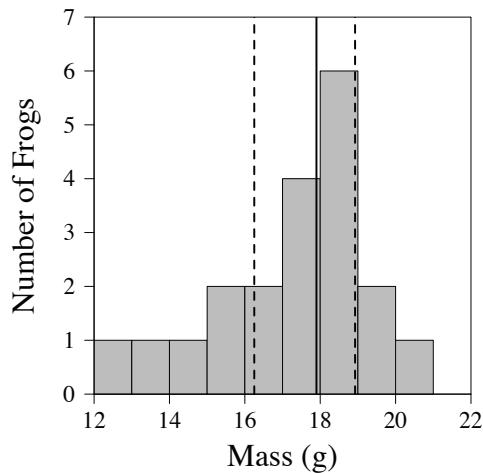| Percentile Mass	CT_{max} (°C)	T_{opt} (°C)	T_{br80} (lower) (°C)	T_{br80} (upper) (°C)	T_{br80} (range) (°C)
25th (16.25g)	34.3	22.5	18	27.3	9.3
50th (17.9g)	34.0	20.7	14.6	26.2	11.6
75th (18.92g)	33.8	15.2	-	24	-

FIGURE 3. Histogram of masses of male Cascades Frogs (*Rana cascadae*) in our study collected from a wetland in Mount Rainier National Park, Washington, USA. Dashed lines represent the 25th and 75th percentiles and solid line indicates the median (50th percentile) mass of individuals in our study (n = 20).

FIGURE 4. Mean number of days during summer (± one standard deviation) exceeding optimal temperature (T_{opt}; black) and 80% thermal performance breadth (T_{br80}; gray) from 1990–2015 for three masses of male Cascades Frogs (*Rana cascadae*) from Washington, USA (n = 20), in our study representing the 25th percentile (16.25 g), 50th (median, 17.90 g), and 75th percentile (18.93 g).

temperatures never exceeded CT_{max}, regardless of mass. For the median, 25th, and 75th percentile masses in our study, the mean number of days in a given summer exceeding T_{br80} were five, three, and 13, respectively, out of 91 summer days, and for T_{opt} the mean number of days was 30, 20, and 60 for the median, 25th, and 75th percentile masses (Fig. 4).

DISCUSSION

We found that the best-supported thermal performance model for adult male *R. cascadae* included an interaction between animal temperature and mass, such that thermal breadth (T_{br80}) was wider, and peak locomotor performance (T_{opt}) occurred at lower temperatures for animals of higher mass. Thermal performance for most species is modelled using individuals from a narrow subset of sizes within a population to minimize variation (e.g., Whitehead et al. 1989; Knowles and Weigl 1990; Samajova and Gvozdik 2010), yet our findings suggest that such studies may risk missing the range of thermal physiology exhibited by the population or species as a whole. Studies have shown that locomotor performance in ectotherms is influenced by mass (Emerson 1978; Huey et al. 1990) and temperature (Knowles and Weigl 1990; Navas 1996; Wilson and Franklin 1999) separately, but rarely have they been evaluated together. Careau et al. (2014) identified individual variation in endurance as a function of temperature for Tropical Clawed Frogs *(Xenopus tropicalis)* and found mass positively affected performance. Based on our estimates, we found heavier animals have a lower T_{opt} but a wider T_{br80}, suggesting
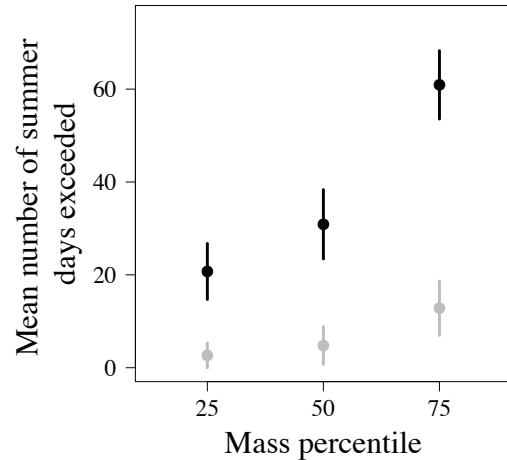
that they may be less sensitive to lower and more variable temperatures than lighter individuals, but are at increased risk of being exposed to temperatures beyond their thermal optima. Although we cannot make mechanistic conclusions from our study, one hypothesis that warrants further investigation is whether the smaller surface area to volume ratio of larger individuals leads to lower rates of heat exchange with the surrounding environment (i.e., larger individuals lose or gain heat at lower rates than smaller individuals). Larger individuals would then be insulated from lethal high temperatures, resulting in both lower T_{opt} and a wider T_{br80}.

Frogs weighing about 19 g, experienced over four times the number of summer days from 1990 to 2015 with peak temperatures exceeding T_{br80} (13 of 91 d), relative to frogs weighing about 16 g (three of 91 d); however, frogs did not experience temperatures exceeding their CT_{max} over this time period. If temperatures continue to rise as predicted, 0.1° C to 0.6° C per decade in the Pacific Northwest (Mote and Salathé 2010), the frequency of days exceeding T_{br80} will increase. During these periods when conditions will compromise locomotor performance, individuals are likely to seek microenvironments with temperatures below T_{br80} (Pough et al. 1983). Employing such thermoregulatory behaviors reduces time available for foraging and other activities, and these constraints have been associated with decreased survivorship (Huey and Stevenson 1979; Christian and Tracy 1981; Bennett 1990; Jayne and Bennett 1990). In addition to exposing individuals to physiologically limiting temperatures, warmer summer temperatures also put individuals at

a greater risk of desiccation (Preest and Pough 1989; Mitchell and Bergmann 2015) potentially compounding vulnerability to a warming climate. Although we found larger individuals to be more susceptible to warmer temperatures, they have a wider 80% performance breadth and thus may have an increased buffer against water loss (Tracy et al. 2010). Increasing environmental temperature may also cause populations to shift their ranges northward or to higher elevations to track their climatic niches (Blaustein et al. 2010).

We evaluated the use of conducting thermal performance assays in the field and suggest that such methods may broaden the range of species that can be studied to include those not appropriate for laboratory experiments. We included air temperature and time of day in our candidate model set and found that they did not rank highly in our model selection process, suggesting that these parameters, typically controlled for in a laboratory setting, may have little influence on jumping distance *in situ*. There are many factors, however, controlled for in laboratory settings (i.e., fasting level, acclimation times) for which we were unable to control and that may influence jumping distance and estimates of thermal optima. Several studies have demonstrated that thermal performance can differ when individuals are acclimated for different lengths of time (Peck et al. 2014; Vinagre et al. 2016) and between constant and varying temperatures (Bartheld et al. 2017). Long term acclimation can generate deleterious effects from long-term exposure to extreme temperatures or beneficial effects when individuals are thermally acclimated to stable temperatures that might not occur in more variable natural conditions (Niehaus et al. 2012).

By conducting our study in the field, individuals experienced natural environmental variability, which may have resulted in more relevant estimates of thermal performance (Niehaus et al. 2012). Despite this benefit, field studies such as ours are often limited by small sample sizes and the inability to perform a repeated measures design. Repeated measures of individual performance at each temperature treatment (*sensu* Careau et al. 2014) would provide further insight into individual variation in thermal performance. Increasing the number of frogs, and including both sexes, would likely also improve our understanding of thermal performance (Artacho et al. 2013). Additionally, we measured cloacal temperature once an individual was removed from its treatment bin, immediately prior to jumping trials. It is possible frog body temperature may have shifted from treatment temperature towards ambient air temperature during jumping trials, where frogs in warmer temperature treatments cooled towards ambient air and frogs in cooler treatments warmed to ambient air. This could lead to an underestimation of T_{opt}, and a narrow estimation of T_{br80}, and ultimately underestimate the number of days environmental temperature is beyond T_{opt} or T_{br80}; however, we found that it took a minimum of 13 min for a frog to reach its treatment temperature from the acclimation temperature (20° C), suggesting that frogs likely did not experience large temperature changes during jumping trials, which were much shorter than 13 min.

Disentangling the physiological response of an organism to temperature from other environmental factors is a critical component to improve predictions of responses of species to rapidly changing environments. Our results suggest that *R. cascadae* thermal performance measures fall within the range observed for other temperate and high elevation amphibians; they similarly include a wide T_{br80}, low T_{opt}, and occupy an environment where individuals do not regularly encounter temperatures approaching CT_{max} (Brattstrom 1968; John-Alder et al. 1988; Navas 1996). We found individuals within our study did not respond to temperature in a uniform manner, and that mass alters the thermal performance relationship, with heavier individuals having a wider thermal breadth and lower thermal optima relative to lighter individuals. Experiments that only sample a limited range of sizes or masses may estimate thermal performance measures that do not accurately represent the population as a whole. This outcome is relevant for mechanistic models that aim to predict suitable habitats under current and future climates.

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