



## Inter-population variation in thermal sensitivity of the tropical toad *Duttaphrynus melanostictus*, across a small spatial scale in Sri Lanka

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### ABSTRACT

Inter-population disparities in a species have been shown to occur as an adaptation to different thermal regimes in the environment. We investigated the thermal sensitivities of the tropical toad *Duttaphrynus melanostictus* (Asia Common Toad) from two populations at different altitudes: Nuwara-Eliya – 1870 m, and Polonnaruwa – 25 m, above mean sea level. The two locations were separated by what may be considered a short direct distance – 110 km. Thermal sensitivity trials were conducted at six temperatures between 12 and 39 °C. Assessments were made using the performance indicators jump distance, jump force, contact time on the test plate following stimulus to jump, and righting time after being overturned. Optimum performance is taken to be the greatest jump distance and jump force, the least contact time on the test plate, and the least righting time. The populations at the two altitudes had markedly different thermal sensitivities – toads in the cool area (Nuwara-Eliya) performed at an optimal level under low temperatures, whereas the toads in the warm area (Polonnaruwa) performed optimally under high temperatures. The finding that the thermal optima (i.e., the temperatures at which the optimal performance for the four performance indicators was recorded) of the toads in Polonnaruwa were below the mean maximum ambient temperature at this location suggests that these toads would be more susceptible to global warming than those in Nuwara-Eliya whose thermal optima were above the mean maximum ambient temperature in that location. This was consistent with the narrower thermal safety margin (i.e., difference between the mean optimum temperature and mean ambient temperature) of toads in Polonnaruwa, compared to those in Nuwara-Eliya. Importantly, these findings demonstrate that, although thermal sensitivity is considered a conservative trait, differentiation does occur even over a small spatial scale presumably because it offers an adaptive advantage to the population concerned.

### 1. Introduction

Body temperature is a crucial factor affecting the physiological performance and behavior of animals. In the case of ectotherms, changes in daily and seasonal ambient temperature affect their body temperature; consequently, changes in the external temperature can influence the performance of these organisms (Preest and Pough, 1989). For example, locomotor performance in anurans, such as jump distance, can be affected, and this may determine the individual's ability to catch prey, escape from predators, and disperse to new habitats (Arnold, 1983; Irschick and Garland, 2001). Animals are generally able to perform such locomotor functions effectively only within a specific temperature range, referred to as their thermal sensitivity range, and this limitation constrains their ability to survive and reproduce under

ambient temperatures outside the range (Cossins and Bowler, 1987).

Thermal sensitivity is reported to be a conservative evolutionary trait that does not readily undergo differentiation (Hertz et al., 1983; Crowley, 1985; Van Damme et al., 1991; John-Alder et al., 1988; Bronikowski et al., 2001). A previous study has shown disparities in thermal sensitivity between populations of the anuran *Limnodynastes peronii* over a wide geographic range “extending from the cool-temperate south to the tropical north of Australia” (Wilson, 2001). We have not come across similar investigations on anurans in the Asian region. Our study is on the anuran *Duttaphrynus melanostictus*, referred to as the Asian Common Toad, which is distributed throughout Sri Lanka. We investigated the thermal sensitivity of toads in two locations at widely different altitudes but separated by a short distance geographically. One population is in Nuwara Eliya (1870 m above mean sea level)

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which has a cool climate and is located in the montane zone within the Central Highlands, and the other is in Polonnaruwa (25 m above mean sea level) with a warm climate, in the lowlands. We hypothesize that the difference in the climate between the two locations, despite being separated by a relatively small geographic distance (110 km), would have led to adaptive changes in the thermal sensitivity within this species. We assessed performance of the individuals at different test temperatures using performance metrics for jumping and for righting after being overturned.

Besides investigating the thermal sensitivities of two populations of a species occupying two locations with distinctly different temperature regimes, our study assumes importance at the present time owing to the current prevalence of global warming (Kingsolver et al., 2013). For a selected species, information as to how the ambient temperature relates to its thermal sensitivity would serve to predict the impact of global warming on its survival (Deutsch et al., 2008; Sunday et al., 2014).

## 2. Materials and methods

### 2.1. Capture of toads and preparation for the trials

*D. melanostictus* is predominantly terrestrial but uses an aquatic medium during its short breeding period (Manamendra-Arachchi and Pethiyagoda, 2006). Toads were collected from scattered home gardens and open areas in Nuwara Eliya (6.92°N, 80.77°E) in the montane zone within the Central Highlands (Wijesinghe et al., 1993) and in Polonnaruwa (7.92°N, 81.04°E) in the north-central lowland plains (Fig. 1). In the two locations the ambient temperature regimes are markedly different, with Polonnaruwa being warmer than Nuwara-Eliya with respect to both maximum and minimum monthly temperatures (Table 1). Taking into consideration the temperature regimes in the two locations, we decided on six test temperatures: 12, 20, 24, 28, 36 and 39 °C for the thermal sensitivity trials.

*D. melanostictus* is nocturnal and is active year round (Manamendra-Arachchi and Pethiyagoda, 2006). The trials were conducted in May and June 2017 at the two locations where temporary study stations with the required facilities were set up. Searches were carried out between 1900 and 2100 h for capturing adult male toads. Only males were taken in order to avoid possible sexual differences in performance, following Zug (1978). They were differentiated from females by the presence of a red patch on the skin at the throat (Manamendra-Arachchi and Pethiyagoda, 2006). A total of six individuals were captured at each location during the period of study. The body mass, snout-vent length, and hind limb length of the experimental toads were measured. The three morphometric metrics did not differ significantly between the two populations (Table 2). However, the effects of these parameters on the performance metrics were tested.

In the field station (at the capture locations) the toads were housed under a 12:12 LD photoperiod using a glass terrarium (0.5 m × 0.6 m × 0.5 m) which was kept in a room exposed to the outside temperature. The terrarium was gradually tilted and aged tap water added so that half the base was under water and the water depth was 2 cm at the lower end, and it was set in that position for housing the toads. The trials at each location commenced with the capture of two toads and housing them in the terrarium; one was used for carrying out the tests commencing the following night, while the other was tagged on a leg loosely with a coloured thread and kept in the terrarium to await testing later. The tag was removed when the toad was taken for testing. Tagging was done to distinguish it from the toad that would be undergoing testing which would be placed in the terrarium after the tests are carried out nightly over a period of three days. After the trials are carried out on a toad it was released at the site of capture. As the trial progressed, toads were captured and housed while ensuring that at no time would there be more than two toads present in the terrarium at any time. The sites of capture were noted to enable release at the site of capture and to ensure that fresh captures are well spaced out. The toads were fed on the night of

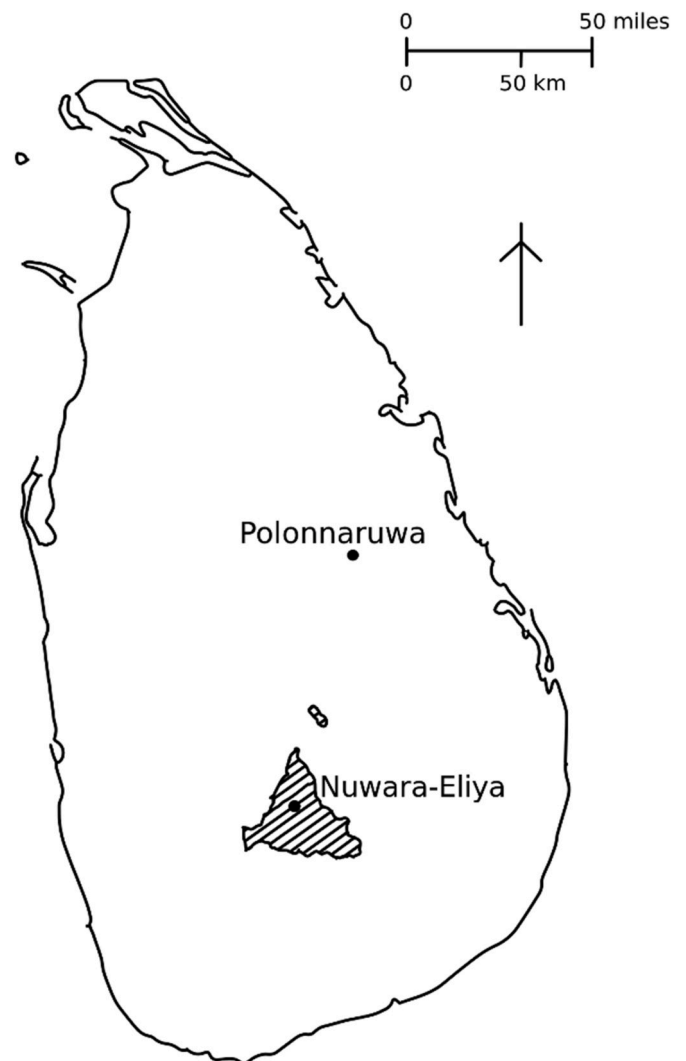


Fig. 1. Map of Sri Lanka showing the two locations from which the test toads (*D. melanostictus*) were collected. The montane zone is also shown (hatched).

Table 1

Monthly temperatures in Nuwara-Eliya and Polonnaruwa during the period 2007 to 2017.

Parameter	Nuwara-Eliya (°C)	Polonnaruwa (°C)
Maximum monthly temperature	17.6–24.0	28.0–37.0
Mean maximum monthly temperature	20.3	33.4
Minimum monthly temperature	7.8–14.3	20.4–27.2
Mean minimum monthly temperature	12.2	23.8

Source: Meteorological Department, Sri Lanka

Table 2

Mean (±standard deviation) of body mass and the snout-vent and hind limb lengths of the experimental animals (n = 6 per location).

Location	Polonnaruwa	Nuwara-Eliya	One-way Anova
Mass (g)	19.85 ± 0.90	16.60 ± 5.72	F = 1.93, P > 0.05
Snout-vent (mm)	58.60 ± 2.30	53.71 ± 8.07	F = 2.05, P > 0.05
Hind limb (mm)	20.80 ± 0.71	17.99 ± 3.22	F = 4.36, P > 0.05

capture, and thereafter nightly until their release, with termites collected from home gardens and open areas, which they readily consumed. The toads were observed to ensure that they fed on the provided termites.

As *D. melanostictus* is nocturnal, the trials were conducted between 1830 and 0100 h, following Cortes et al. (2016) and Manis and Claussen (1986). One individual was tested at a time, and the testing was on not more than three temperatures in one night in order to minimize fatigue. The toad was tested on all the temperatures over a three-day period: 12 and 20 °C on day one, 24, 28 and 36 °C on day two, and 39 °C on day three. On day three the toad was tested once again at 28 °C to ascertain whether the result obtained was at least 90% of the result at that temperature recorded on the previous day (Wilson, 2001), and in all cases the performance was within the acceptable level. The experimental toad was returned to the terrarium after the trials on each day.

## 2.2. Exposing the toads to the test temperatures

The toad to be tested was placed in a beaker (500 ml) containing aged tap water (2 cm depth), where the animal was only partially immersed. The initial test temperature (12 °C) was attained by gradually decreasing the temperature of the water in the beaker where the toad was kept, using ice cubes – a similar procedure being followed when the temperature had to be lowered prior to any test. The temperature was lowered in a stepwise manner, 4 °C or less at a time, with an interval of half hour after each step. Once the required water temperature was reached the toad was again kept at this temperature for at least 1/2 h and the surface temperature of the neck region of the toad was measured using an infra-red thermometer (GM700 1.5" LCD Non-contact Infrared Thermometer, Elecall, Zhejiang, China), and we ensured that this temperature deviated no more than ~0.5 °C from the desired test temperature. At this point, the thermal sensitivity trials were carried out. The procedure described above follows previous studies (Miller and Zoghy, 1986; Wilson, 2001; Mitchell and Bergmann, 2015). After a set of tests at one temperature was completed, the temperature of the water was raised for the next set of tests using a water bath (electrothermal water bath MH8517). The raising of temperature was also done in a stepwise manner as before.

## 2.3. Recording performance

A force plate was custom made following Katz and Gosline (1993); it was constructed by placing lead zirconate titanate ceramic in between two metal plates. This force plate was used for the trials at both locations. It was placed on a large wooden table covered by a sheet of white paper. Once the toad was made ready for testing it was removed from the test water medium and placed on the centre of the force plate. To initiate the test, the urostyle was gently touched with a pair of forceps to stimulate the jump (Wilson, 2001). Three performance indicators were recorded: Contact Time (CT), being the time between touching the urostyle and the toad's feet leaving the force plate, Jump Distance (JD), and Jump Force (JF). CT was recorded to the nearest 0.01 s using a mobile device (Samsung Galaxy J2 Prime). Once the toad landed on the table, the position of the rear centre point of the toad was marked on the paper and the distance from this point to the centre of the force plate was measured using a measuring tape. The difference in the output voltage before and after the jump, being directly proportional to the micro-displacement of the force plate and to the force, was taken as the arbitrary unit to indicate JF in order to compare performance of the toads exposed to the different test temperatures. The jump distance was recorded on two additional jumps and the mean distance was taken. The recording of CT, JF and JD was completed within 2 min (Nowakowski et al., 2017). After this test the toad was placed back in the beaker at the same temperature for ½ hour and then removed for recording Righting Time (RT) after being overturned. The toad was placed on a wooden surface upside down and the time taken for it to turn right-way-up was recorded as the RT (Cortes et al., 2016; Nowakowski et al., 2017), using the mobile device as for CT. Thereafter the toad was returned to the beaker. The temperature of the water bath was then adjusted to the next test temperature following the procedure described earlier and the toad

was kept at this temperature for ½ hr, following which its neck temperature was recorded as before, and the trials were conducted at this test temperature. The protocol was approved by the local ethics committee (Institute of Biology Sri Lanka, ERC IOBSL158 08 17).

## 2.4. Descriptive traits of the thermal performance curves (TPC)

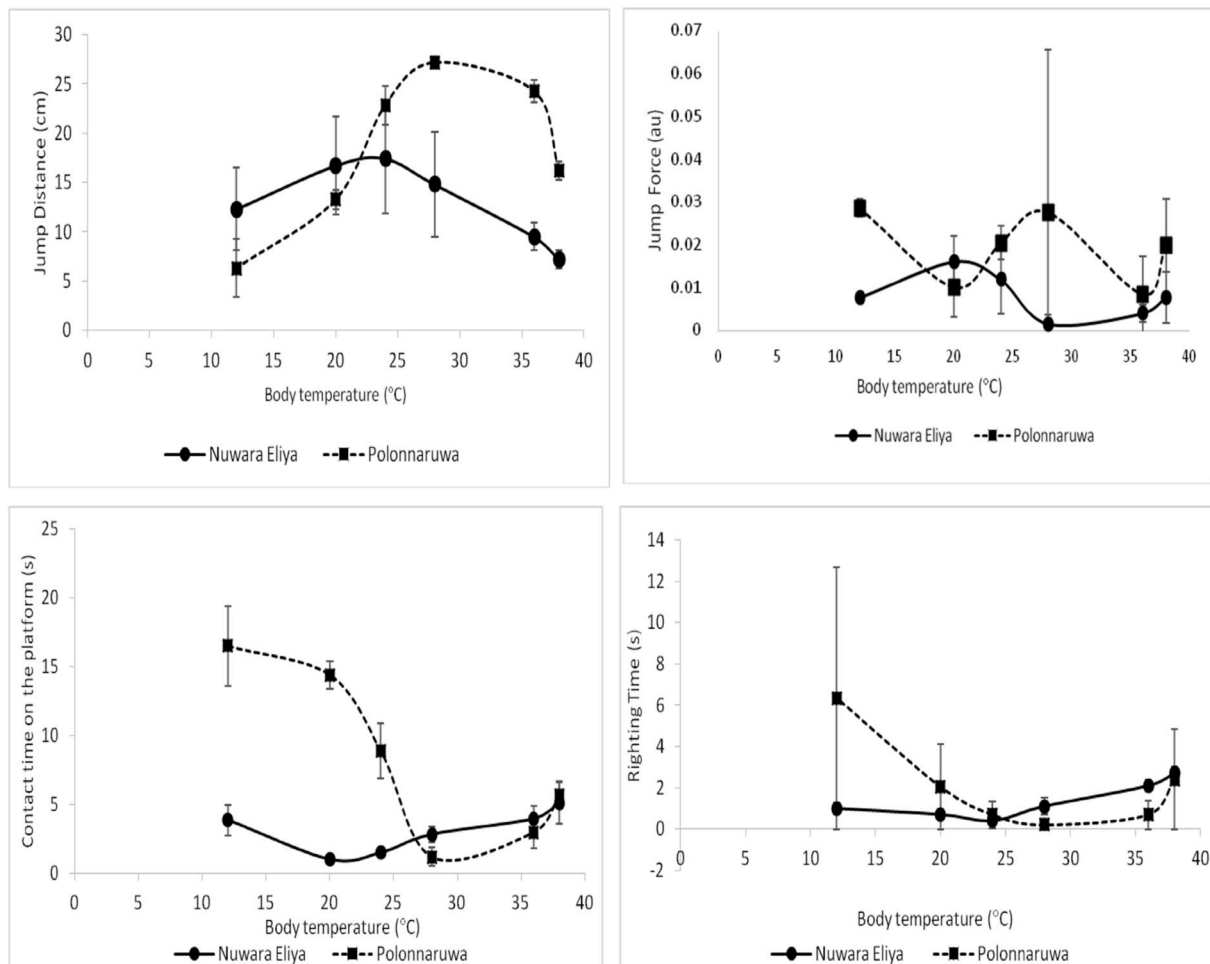
Individual thermal sensitivity curves were constructed for each toad by fitting a third order polynomial to the data set on each performance indicator. Using these thermal sensitivity curves ( $n = 24$ ; 6 toads  $\times$  4 performance indicators, per location), three descriptive traits were determined following Huey and Stevenson (1979). These were: optimum performance (PO) – the best performance level (longest JD, highest JF, shortest CT, shortest RT); thermal optimum (TO) – the temperature at which the best performance is shown; and niche breadth (NB) – the temperature difference between minimum and maximum temperatures at which 80% of PO is indicated in the thermal sensitivity curve. Where two peaks were observed, the higher peak was used to derive TO and for deriving values of 80% PO in calculating NB. Where 80% of the PO was reached in both curves (corresponding to the two peaks) the extreme temperature points were used to calculate NB.

Additionally, the Thermal Safety Margin (TSM) of the toads in each location was calculated. Deutsch et al. (2008) has defined TSM as the difference between an organism's thermal optimum (TO) and the prevailing climate temperature (TH). In the present study for each location we used the mean of the TOs for each performance indicator (JD, JF, CT and RT) as the TO and the averages of the monthly mean maximum and monthly mean minimum temperatures (Table 1) as TH.

## 3. Results

The thermal sensitivity curves, which depict the mean values obtained for the four performance indicators (JD, JF, CT, RT) of the six toads tested in each location (Fig. 2), show that there are marked differences in performance between the toads in Nuwara Eliya and those in Polonnaruwa. The mean values for the descriptive traits (TO, PO and NB) derived from the curves for each toad (Table 3) show that the TO in the Nuwara Eliya population were significantly lower than those in the Polonnaruwa population in the case of the three performance indicators JD, CT and RT. For instance, the greatest mean JD of toads collected in Nuwara Eliya was at 22.7 °C while toads in Polonnaruwa jumped the maximum at 30.0 °C. Similarly, the TO for RT for the toads in Nuwara-Eliya was 22.7 °C while it was 31.30 °C for those in Polonnaruwa. The TO of the toads for all four performance indicators in Nuwara-Eliya (21–26.1 °C, Table 3) were above the mean maximum temperature (20.3 °C, Table 1) at this site, whereas the TO of those in Polonnaruwa (28.21–31.3 °C) were below the mean maximum temperature in the site (33.4 °C). With regard to NB, a significant difference between the two locations was evident only for JF. Considering PO levels, a significant difference was recorded for JD and JF where the toads in Polonnaruwa jumped further and with greater force than those in Nuwara-Eliya.

The effect of each morphometric parameter on each performance indicator was examined through a series of regression analyses, using data on all 12 toads (6 each from the two locations), where the morphometric parameter was used as the independent variable and the performance as the dependent variable. These analyses revealed that the morphometric metrics did not contribute significantly to the disparity in optimal performance between the toads: JD (mass –  $F_{(1,10)} = 2.28$ ,  $P = 0.16$ ,  $R^2_{adj} = 10.45\%$ ; snout-vent length –  $F_{(1,10)} = 0.18$ ,  $P = 0.68$ ,  $R^2_{adj} = 0.0\%$ ; hind limb length –  $F_{(1,10)} = 1.29$ ,  $P = 0.28$ ,  $R^2_{adj} = 2.54\%$ ), JF (mass –  $F_{(1,10)} = 0.80$ ,  $P = 0.39$ ,  $R^2_{adj} = 0.0\%$ ; snout-vent length –  $F_{(1,10)} = 0.82$ ,  $P = 0.38$ ,  $R^2_{adj} = 0.0\%$ ; hind limb length –  $F_{(1,10)} = 0.06$ ,  $P = 0.81$ ,  $R^2_{adj} = 0.0\%$ ), RT (mass –  $F_{(1,10)} = 1.51$ ,  $P = 0.24$ ,  $R^2_{adj} = 0.0\%$ ; snout-vent length –  $F_{(1,10)} = 0.49$ ,  $P = 0.50$ ,  $R^2_{adj} = 0.0\%$ ; hind limb length –  $F = 0.98$ ,  $P = 0.34$ ,  $R^2_{adj} = 0.0\%$ ), CT (mass –  $F = 0.59$ ,  $P = 0.46$ ,  $R^2_{adj} = 0.0\%$ ; snout-vent length –  $F_{(1,10)} = 1.56$ ,  $P = 23$ ,  $R^2_{adj} = 4.0\%$ ;



**Fig. 2.** Thermal sensitivity curves for the mean ( $\pm$ standard deviation) values of the four performance indicators (jump distance, jump force, contact time and righting time) from thermal trials with toads (*D. melanostictus*) collected from Nuwara-Eliya (1870 m above mean sea level) and Polonnaruwa (25 m above mean sea level). Each value represents the mean from six toads. The curves represent 3rd order polynomial fit. Jump force was measured in arbitrary units (au).

hind limb length –  $F_{(1,10)} = 1.13$ ,  $P = 0.31$ ,  $R^2_{adj} = 1.16\%$ .

The TSM of the two populations, which is the difference between the mean TO of the two populations (23.13 °C for Nuwara-Eliya and 29.88 °C for Polonnaruwa, derived from Table 3) and the averages of the mean minimum and mean maximum monthly ambient temperatures of each of the two locations (16.25 °C for Nuwara-Eliya and 28.6 °C for Polonnaruwa, derived from Table 1) showed that the toads in Nuwara-Eliya had a much wider safety margin (6.88°C) than those in Polonnaruwa (1.28° C).

## 4. Discussion

### 4.1. Inter-population disparities in thermal sensitivity

Animals, in general, adapt to temperatures in their local environment (Ficetola and Bernardi, 2005). In a previous study on the anuran species *Lymnodynastes fryperonii* variations in thermal sensitivity were seen to occur between populations that were widely separated, between the temperate south and the tropical north of Australia with distinctly different climatic conditions. The present study is the first to report on disparities in thermal sensitivity in an Asian anuran species. We found that there is a disparity in thermal sensitivity between two populations of the Asian Common Toad (*D. melanostictus*) which occur at two altitudes with an elevation difference of >1800 m and markedly different ambient temperatures – the population inhabiting Nuwara-Eliya (the cool region) performing optimally at lower temperatures, while the

toads in Polonnaruwa performing optimally under warm conditions. The fact that the two locations are separated by a short direct geographic distance (110 km), compared to the study on *Lymnodynastes fryperonii* referred to above, is interesting since thermal sensitivity is reported to be a conservative evolutionary trait (Hertz et al., 1983; Crowley, 1985; Van Damme et al., 1991; John-Alder et al., 1988; Bronikowski et al., 2001), and differences would not be expected to occur over a small spatial scale since gene flow may take place freely if there were no constraints. It is important to note here that Sri Lanka's Central Highlands, which includes the montane zone (where Nuwara-Eliya is located), is considered as a distinct ecological region, separated from the lowlands (where Polonnaruwa is located), because of the presence of many endemic species of plants and animals restricted to this region, and has thus been declared a World Heritage (<https://whc.unesco.org/en/list/&order=country#alphaS>). In the case of *D. melanostictus*, although the toad is widespread in Sri Lanka, the highland population may be isolated from the lowland owing to the sharp differences in both elevation and climatic regime acting as a barrier to dispersal and hence impeding gene flow. The thermal sensitivity of the toads in Nuwara-Eliya differing from that in Polonnaruwa toads is hence most likely an evolutionary adaptation to the prevailing temperature regime in the montane zone.

With respect to PO, the toads in Polonnaruwa were found to jump further and with greater force than the toads in Nuwara-Eliya, supporting a concept put forward by Huey and Kingsolver (1989) that “warmer is better”. It has been documented that climatic niche widths

**Table 3**

The mean ( $\pm$ standard deviation) of the descriptive traits: Performance Optimum (PO), Thermal Optimum (TO), Niche breadth (NB) of the four performance indicators (jump distance, jump force, contact time and righting time) generated through thermal sensitivity trials on *D. melanostictus* at the two sites with distinctly different climatic regimes. The values were generated using the individual curves (representing the 3rd order polynomial fit) of the six toads tested per location. Jump force was measured in arbitrary units (au).

Performance Indicators	Performance indicator	Nuwara-Eliya	Polonnaruwa	One-way ANOVA
<b>Jump Distance</b>	PO(cm)	20.00 $\pm$ 5.20	34.79 $\pm$ 8.00	$F_{(1,10)} = 10.39$ $P < 0.01$
	TO( $^{\circ}$ C)	22.70 $\pm$ 1.10	30.00 $\pm$ 2.57	$F_{(1,10)} = 34.77$ $P < 0.001$
	NB( $^{\circ}$ C)	13.5 $\pm$ 2.60	14.28 $\pm$ 1.40	$F_{(1,10)} = 0.34$ $P > 0.05$
<b>Jump Force</b>	PO(au)	0.02 $\pm$ 0.01	0.03 $\pm$ 0.01	$F_{(1,10)} = 9.76$ $P < 0.05$
	TO( $^{\circ}$ C)	26.1 $\pm$ 3.30	28.21 $\pm$ 0.97	$F_{(1,10)} = 1.77$ $P > 0.05$
	NB( $^{\circ}$ C)	9.60 $\pm$ 0.92	14.90 $\pm$ 1.14	$F_{(1,10)} = 66.35$ $P < 0.001^*$
<b>Contact Time</b>	PO(s)	0.99 $\pm$ 0.06	2.11 $\pm$ 1.21	$F_{(1,10)} = 4.24$ $P > 0.05$
	TO( $^{\circ}$ C)	21.0 $\pm$ 0.71	30.00 $\pm$ 1.11	$F_{(1,10)} = 184.59$ $P < 0.001$
	NB( $^{\circ}$ C)	8.60 $\pm$ 1.17	8.40 $\pm$ 1.15	$F_{(1,10)} = 0.07$ $P > 0.05$
<b>Righting Time</b>	PO(s)	0.23 $\pm$ 0.08	0.16 $\pm$ 0.02	$F_{(1,10)} = 3.67$ $P > 0.05$
	TO( $^{\circ}$ C)	22.70 $\pm$ 0.71	31.30 $\pm$ 1.12	$F_{(1,10)} = 182.96$ $P < 0.001$
	NB( $^{\circ}$ C)	11.9 $\pm$ 1.96	10.16 $\pm$ 12.97	$F_{(1,10)} = 1.23$ $P > 0.05$

for temperature are influenced by the magnitude of change in ambient temperature which an animal would regularly experience in its natural environment (Janzen, 1967; Crowley, 1985; Addo-Bediako et al., 2000; Wilson, 2001). In the present study, which was carried out in two locations with a distinct difference in the ambient temperatures, a difference between the two populations in NB was only evident for JF. The absence of a marked difference in the range of annual temperature regimes (minimum to maximum monthly temperatures; Table 1) between the two zones may have led to the lack of a significant difference in NB in the other three tested performance indicators.

#### 4.2. What implications do these findings have with respect to potential climate change?

The extent to which species are affected by global warming depends in part upon the physiological sensitivity of the organisms (Deutsch et al., 2008). Since performance is linked to temperature, ectotherms in particular would be impacted by an increase in environmental temperature. Hence studies on thermal sensitivity assume significance at the present time due to possible effects of climate change.

It has been reported that ectotherms living in high altitudes would have better thermal tolerance to global warming than those in low altitudes since the ambient temperatures at high altitudes would generally be below the physiological optima of the resident populations, and any increase in the ambient temperature may result in increased fitness (Somero, 2010). In contrast, for those in warmer climates, whose physiological optima are generally below the ambient temperature, a rise in ambient temperature would be expected to result in reduced performance and fitness, leading to detrimental consequences. The results of the present study suggest that the two populations of *D. melanostictus* would be affected in a similar way. The TO of the toads in the two populations when compared with the maximum temperatures in the two locations indicate that only the toads in Polonnaruwa, where the mean maximum ambient temperature is now higher than their thermal optima, would be expected to be adversely affected by a rise in environmental temperature as a result of global warming. The disparities in

the TSM obtained in the present study (i.e., narrower for the toads in Polonnaruwa compared to those in Nuwara-Eliya) are consistent with the view that moderate increases in temperature could trigger a decrease in the performance of the toads in the Polonnaruwa region. It is important to note that 65% of Sri Lanka's land area (the dry zone) shares the temperature regime of Polonnaruwa while the montane zone within the Central Highlands where Nuwara Eliya is located covers 2.5% of the island's land area (derived from the bioclimatic zone map in Wijesinghe et al., 1993).

Many amphibians have already undergone extinctions or population declines attributed to climate change (Poppy et al., 2000; Parmesan and Yohe, 2003; Pounds et al., 2006; Sinervo et al., 2010) and others are experiencing temperatures approaching the edge of their thermal tolerance range (Huey et al., 2009). Thus, populations/species whose optimal performance is at lower temperatures than that which they are now exposed to, could face climate-related adverse impacts and possibly have diminished chances of finding suitable alternative habitats to colonize (Walther et al., 2002). Further studies are necessary to evaluate the potential consequences of climate change for restricted range anurans, particularly those occupying ecosystems that show a greater vulnerability to climate change.

## 5. Conclusions

This study has demonstrated inter-population disparities in the tropical anuran *Duttaphrynus melanostictus* (Asian common toad) between the toads inhabiting two altitudes in locations separated by a direct distance of 110 km. The two populations had different thermal sensitivity ranges – tested across a temperature range taking into account the temperature regimes of both locations. The thermal optima for the toads in the two populations for three performance indicators were related to their environmental temperatures. Those in the warmer location performed better at a higher temperature, while those in the cooler location performed better at a lower temperature. These findings suggest the possibility of thermal sensitivity differentiation occurring across small spatial scales, so enabling populations to better adapt to

their local temperature regimes.

### CRedit authorship contribution statement

**D.P.H. Algiriyage:** Data curation, Formal analysis. **H. Jayaweera:** Data curation, Formal analysis, Software, Resources. **M.R. Wijesinghe:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Supervision, Resources, Writing - review & editing.

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