Non-climatic thermal adaptation: implications for species' responses to climate warming

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There is considerable interest in understanding how ectothermic animals may physiologically and behaviourally buffer the effects of climate warming. Much less consideration is being given to how organisms might adapt to non-climatic heat sources in ways that could confound predictions for responses of species and communities to climate warming. Although adaptation to non-climatic heat sources (solar and geothermal) seems likely in some marine species, climate warming predictions for marine ectotherms are largely based on adaptation to climatically relevant heat sources (air or surface sea water temperature). Here, we show that non-climatic solar heating underlies thermal resistance adaptation in a rocky–eulittoral-fringe snail. Comparisons of the maximum temperatures of the air, the snail's body and the rock substratum with solar irradiance and physiological performance show that the highest body temperature is primarily controlled by solar heating and re-radiation, and that the snail's upper lethal temperature exceeds the highest climatically relevant regional air temperature by approximately 22°C. Non-climatic thermal adaptation probably features widely among marine and terrestrial ectotherms and because it could enable species to tolerate climatic rises in air temperature, it deserves more consideration in general and for inclusion into climate warming models.

Keywords: climate change; global warming; thermal adaptation

1. INTRODUCTION

Understanding how behavioural and physiological capacities of terrestrial ectothermic animals might buffer the effects of climate warming is receiving increasing interest (Helmuth et al. 2005; Glanville & Seebacher 2006; Kearney et al. 2009). For example, behavioural thermoregulation in terrestrial lizards is expected to minimize the effects of climate warming, so that they only become critical through the alteration of available shade (Kearney et al. 2009). However,

comparatively little is known about physiological adaptation to non-climatic heat sources, which could also be important in alleviating climate warming effects. Most predictions on how climate warming will affect the distributions of marine ectotherms are based on physiological resistance adaptations to heat deriving from climatic sources (air or surface sea water; Stillman 2003; Harley et al. 2006; Pörtner & Knust 2007; Harley & Paine 2009); yet, these sources need not be the primary drivers of maximum body temperature. While geothermal heating alone must influence thermal adaptation in hydrothermal vent organisms, the interaction of non-climatic (solar) and climatic factors (air temperature) determines the thermal niche of, and heat flow through, rocky-shore organisms (Denny & Harley 2006). By separating these factors, we show that thermal adaptation in a rocky-shore snail is principally driven by solar heating, and hence propose that non-climatic adaptation be incorporated into models predicting climate warming effects.

2. MATERIAL AND METHODS

We investigated non-climatic thermal adaptation in the tropical, eulittoral-fringe snail, *Echinolittorina malaccana* (Reid 2007), by determining the role of solar radiation in controlling maximum body temperature ($T_{b(max)}$) and the relationship between $T_{b(max)}$ and the thermal limits of physiological performance. We studied a population of *E. malaccana* snails found between 2 and 5 m above chart datum (mean high water level approx. 2.5 m CD) on artificial seawalls at Pantai Tungku in Brunei Darussalam (4°32′ N; 114°43′ E). When immersed in air, this snail species withdraws its foot, cements its shell to the rock surface and closes its operculum, a behaviour that prevents heat conduction (by excluding tissue contact with the rock substratum) and limits evaporative cooling (snails lose water at around 0.01% body mass h^{-1} over 32 days at 30°C, D. J. Marshall 2009, unpublished data; McMahon (1990)). Such behaviour can be maintained for weeks during continuous aerial emersion when tidal conditions are calm.

Field operative body temperature (T_b), rock surface temperature (T_r), habitat air temperature (T_{ah}; 7 mm above the rock surface), and solar irradiance were recorded at 1 min intervals for 21 days (August/September 2009). T_b was measured within silicone-filled shells (7 mm length) glued to horizontal rocks, with maximum exposure to direct sunlight. T_b was determined for two rock types with different thermal properties: a light sandstone rock ('light') and a darker, ferruginous sandstone rock ('dark'). Only the light rock, which resembled the habitat substratum, was used for all other temperature measurements. Live snail body temperature ($T_{b(live)}$) closely correlated with the model's body temperature on the light rock ($r = 0.9086$, $p < 0.001$, $n = 60$; for $T_{b(light)}$ between 35°C and 43.5°C determined in direct sunlight). Simultaneous recordings of local ambient air temperature (T_{am}; 600 mm above the rock surface), $T_{b(light)}$ and solar irradiance were also taken every 10 min over 7 days, after the 21 day recording period. Temperature was measured using fine, K-type thermocouples (shielded from the wind and sun), and logged using Fluke 54 Series II recording thermometers. Global solar irradiance was recorded using a CM11 Kipp and Zonen pyranometer and logged using an ADInstruments PowerLab 4/SP and CHART v. 5. Data analyses were based on recordings for 12.30 to 14.30 each day, or for local ambient air temperature, between 10.00 and 14.30.

Climatically relevant, regional ambient air temperature (T_{am-reg}, independent of the re-radiative heating on the rocky shoreline) was determined from within a Stevenson screen at the Brunei International Airport (6200 m from the study site, 5200 m inland and approx. 10 m in altitude; courtesy of the Meteorological Service, Ministry of Communications). Monthly maxima for T_{am-reg} showed no seasonal variation (mean ± s.d: 34.29 ± 1.08°C, $n = 33$ for 2006, 2008 and 2009 until September).

Heart function was used to assess physiological adaptation to temperature (see Somero 2002). Active snails (shell length, 7–9 mm) were returned to the laboratory, where they were rinsed in filtered sea water, dried with blown air and fitted with infrared sensors (Vishay Semiconductors, CNY70). Signals, sampled at 40 Hz, were amplified and filtered using a custom-built preamplifier, and digitally logged (PowerLab/4SP, Chart v. 5). Heart rate (HR),
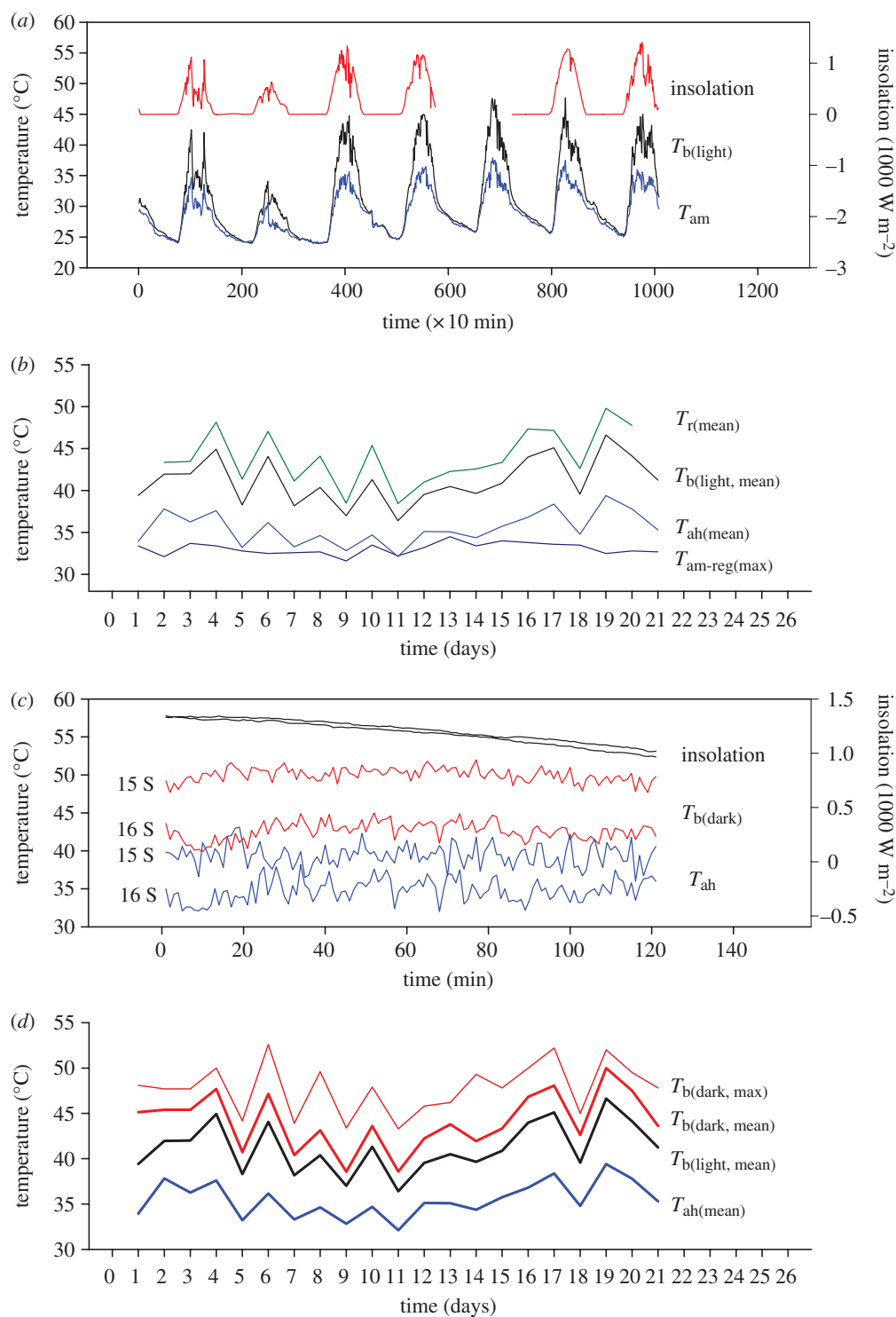
Figure 1. (*a*) Continuous recordings (every 10 min) of body temperature on light rocks ($T_{b(light)}$), local ambient air temperature (T_{am}) and solar irradiance taken over 7 days. (*b*) Mean temperatures between 12.30 and 14.30 for 21 days of the rock substratum (T_r), the snail's body ($T_{b(light)}$), the habitat air (T_{ah}), and daily maximum regional ambient air temperature (T_{am-reg}). (*c*) The effect of factors other than solar irradiance on temperature (probably wind) is shown here by the difference in body temperature on dark rocks ($T_{b(dark)}$) and habitat air temperature (T_{ah}) on two days (15 and 16 September 2009, between 12.30 and 14.30) under similar solar irradiance conditions. (*d*) Daily mean or maximum temperatures showing $T_{b(dark, max)} > T_{b(dark, mean)} > T_{b(light, mean)} > T_{ah (mean)}$.

determined from triangular Bartlett smoothed traces, was logged every 1 min for snails ($n = 7$) held in bags in a Grant GP200 programmable water bath and experiencing constant heating ($0.25{}^\circ\mathrm{C}\ \mathrm{min}^{-1}$), between $30{}^\circ\mathrm{C}$ and $60{}^\circ\mathrm{C}$. The Arrhenius breakpoint temperature (ABT) for heart function was determined from piecewise regressions (STATISTICA v. 6.1, StatSoft) from the plot of the natural log of HR against the inverse Kelvin temperature, between

$45{}^\circ\mathrm{C}$ and $57{}^\circ\mathrm{C}$. Lethal temperature was based on the endpoint of heart function (EPT), when the heart stopped beating; this closely matches the LT_{50} of this species (D. J. Marshall 2009, unpublished data). Although heart function often recovered when the temperature was lowered after EPT was reached, no snails re-emerged from their shells within 24-h at $30{}^\circ\mathrm{C}$, a timeframe typically used to test lethal effects (Somero 2002).

Table 1. Daily mean and maximum temperatures (°C) and daily solar irradiance (W m^{-2}; data recorded every 1 min each day between 12.30 and 14.30).

	mean	s.d.	abs max	min	n
daily means					
$T_{b(light)}$	41.19	2.77	46.62	36.40	21
$T_{b(dark)}$	44.08	3.11	49.99	38.56	21
T_{ah}	35.49	1.94	39.39	32.11	21
T_r	43.94	3.25	49.82	38.44	19
T_{am}	32.90	2.92	35.57	27.85	7[a]
solar irradiance	1084.93	135.25	1263.28	867.64	14
daily maximum					
$T_{b(light)}$	44.93	2.65	49.6	41.3	21
$T_{b(dark)}$	47.80	2.83	52.6	43.3	21
T_{ah}	40.01	2.08	43.8	37	21
T_r	45.96	3.04	50.9	41.4	19
T_{am}	35.48	2.66	37.9	30.6	7[a]
T_{am-reg}	33.07	0.7	34.5	31.6	21
solar irradiance	1457.89	129.59	1662.18	1168.78	14

[a]Data recorded every 10 min between 10.00 and 14.30.

3. RESULTS

Heat generated through solar irradiance and re-radiation (emitted by the rock surface) determines the highest daily maximum body temperatures ($T_{b(max)}$) of *E. malacanna* (figure 1a). The snail's body and the rock substratum gained heat at a greater rate than the air, leading to different maximum temperatures among these variables ($T_r > T_b > T_{ah} > T_{am}$; figure 1a,b; table 1). The regional daily maximum air temperature (T_{am-reg}) was uncorrelated with and distinctly lower than the air temperatures on the rocky shore ($T_{ah} > T_{am} > T_{am-reg}$; figure 1b; tables 1 and 2). Solar irradiance had the greatest effect on $T_{b(max)}$ around noon, when atmospheric attenuation was reduced (decreased haze and cloud cover), and when there was no wind (D. J. Marshall 2009, personal observation; figure 1a,c). Local and regional ambient air temperatures (T_{am} and T_{am-reg}), however, were similar to T_b when solar irradiance was absent (at night), when atmospheric attenuation was high, and on windy days when convective heat loss was rapid (figure 1a,b). Under these conditions, daily $T_{b(max)}$ was relatively low (less than 10°C below the highest T_bs) and thus was unimportant to their adaptive thermal limit. The effect of solar irradiance was enhanced by the substratum's thermal properties (emissivity); snails on dark rocks were hotter than those on light rocks, reflecting relatively lowered convective heat loss as a consequence of elevated habitat air temperature on dark rocks ($T_{b(dark-mean)} > T_{b(light-mean)}$; table 1 and figure 1d). Absolute maxima fell between 34.5°C and 52.6°C for T_{am-reg} and $T_{b(dark)}$, respectively (table 1). Daily maxima for T_{ah}, $T_{b(dark)}$, $T_{b(light)}$ and T_r were correlated with each other ($r^2 \geq 0.84$, $p < 0.001$, $n = 21$; table 2) and with their mean values during the hottest period of the day ($r^2 \geq 0.78$, $p < 0.001$, $n = 21$; table 2).

The mean critical thermal limit of physiological performance of the snails (ABT for heart function)

was 53.9°C, and the mean lethal temperature (EPT) was 56.5°C (figure 2).

4. DISCUSSION

Thermal adaptation in the eulittoral-fringe *E. malacanna* appears to be driven by heat deriving from solar irradiance, which raises body temperatures directly and through re-radiative heating of the rock substratum. Highest body temperatures were recorded when the effect of solar heating was greatest. While the lethal temperature and adaptive thermal limit for heart function (ABT) of this snail exceed the maximum body temperature recorded ($T_{b(light)}$) by more than 4.3°C, they exceed the maximum climatically relevant ambient air temperature (T_{am-reg}) by more than 19.4°C, even without accounting for behavioural thermoregulation through seeking shade, holding the shell off the rock substratum or orienting to minimize exposure to the sun (Garrity 1984). Although *E. malacanna* originated before the Eocene Optimum when air temperatures were approximately 6°C higher than at present (Williams *et al.* 2003), and despite interannual and interdecadal temperature oscillations, climatically relevant air temperature alone cannot explain the evolution of thermal tolerance of this snail.

Predictions for climate warming generally make no distinction between the effects of solar heating and heat deriving from the ambient air (Helmuth *et al.* 2006), even though solar heating may principally determine the maximum body temperature and maximum solar irradiance it is unaffected by the climate. Studies have typically considered the combined effect of these two influences, but separating them has important implications on predictions for organisms adapted to solar heating, such as *Echinolittorina*. In these snails, the prediction of a poleward shift in range (Helmuth *et al.* 2006) is questionable because habitat temperature (driven by solar radiation and substratum emissivity) is independent of latitude across their geographical range (equatorial habitats are not necessarily the hottest; Page *et al.* 2001). Moreover, predictions at the community level will be confounded by differences in adaptation to climatic and non-climatic heat sources among rocky-shore organisms. For example, in contrast to *Echinolittorina*, rocky-shore porcelain crabs are adapted to air temperature in the shade under rocks, which is relatively independent of solar heating (Stillman 2003).

Although some consideration has been given to how terrestrial ectotherms may buffer climate warming effects through behavioural thermoregulation (Kearney *et al.* 2009), our findings suggest that adaptation to non-climatic heat sources could be important to both benthic marine and terrestrial ectotherms (particularly small epilithic insects and other invertebrates) with limited thermoregulatory ability and body temperatures dictated by solar heating (see Edgerly *et al.* 2005; Angilletta *et al.* 2006). These findings prompt critical consideration of non-climatic adaptation in ectotherms and the incorporation of this concept into general predictive models of climate warming (see Helmuth *et al.* 2005; Kearney *et al.* 2009).
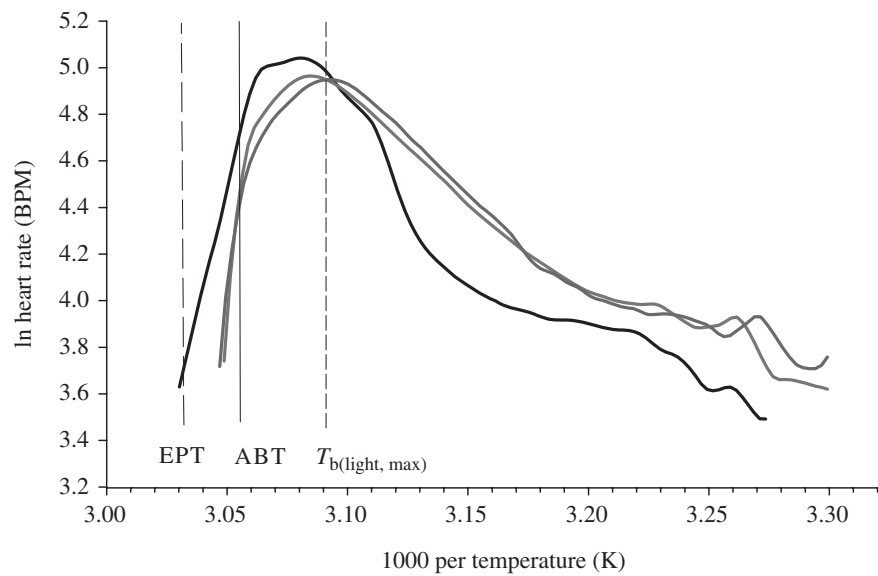
Figure 2. Arrhenius plots for heart rate against temperature (fitted with Loess curves) for three representative snails. Endpoint temperature (EPT), Arrhenius breakpoint temperature (ABT, means $\pm$ 1 s.e., $n = 7$) and absolute maximum body temperature on light rock ($T_{b(light,\ max)}$) are indicated. EPT = $56.5 \pm 0.18°C$; ABT = $53.9 \pm 0.07°C$; T_b (light, max) = $49.6°C$.

Table 2. Linear regressions ($y = B_0 + B_1 x$) parameters for maximum temperature against mean temperature and other relationships (data recorded every 1 min between 12.30 and 14.30). ns = non-significant relationship.

daily maximum temperature (y) against daily mean temperature (x)	r^2	r	B_0	B_1	p	n	
$T_{b(light)}$	0.84	0.92	8.43	0.88	<0.001	21	
$T_{b(dark)}$	0.84	0.92	10.72	0.84	<0.001	21	
T_{ah}	0.78	0.89	6.08	0.95	<0.001	21	
T_r	0.89	0.95	6.69	0.89	<0.001	19	
T_{am}	0.94	0.97	6.63	0.87	<0.001	7[a]	
maximum temperature relationships							
$T_{b(dark)}$ (y) against $T_{b(light)}$ (x)	0.86	0.93	3.59	0.98	<0.001	21	
T_{ah} (y) against $T_{b(light)}$ (x)	0.84	0.92	7.66	0.72	<0.001	21	
T_r (y) against $T_{b(light)}$ (x)	0.93	0.96	−3.89	1.10	<0.001	21	
T_{am} (y) against T_{am-reg} (x)	0.03	0.53	−0.76	1.11	0.219	7[a]	n.s.
T_{am} (y) against $T_{b(light)}$ (x)	0.99	0.99	8.38	0.63	<0.001	7[a]	
T_{ah} (y) against T_{am-reg} (x)	0.01	0.06	34.09	0.18	0.791	21	n.s.

[a]Data recorded every 10 min between 10.00 and 14.30. n.s., Non significant relationship.

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