Journal of Thermal Biology 47 (2015) 99–108

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Gross mismatch between thermal tolerances and environmental temperatures in a tropical freshwater snail: Climate warming and evolutionary implications

Gianluca Polgar [a], Tsung Fei Khang [b], Teddy Chua [a], David J. Marshall [a,*]

[a] *Environmental and Life Sciences Programme, Faculty of Science, Universiti Brunei Darussalam, Brunei Darussalam*
[b] *Institute of Mathematical Sciences, Faculty of Science, University of Malaya, 50603 Kuala Lumpur, Malaysia*

ARTICLE INFO

Article history:
Received 10 July 2014
Received in revised form
21 November 2014
Accepted 22 November 2014
Available online 25 November 2014

Keywords:
Animal ectotherms
Buccinidae
Clea nigricans
Cold tolerance
Heat tolerance
Thermal safety margins

ABSTRACT

The relationship between acute thermal tolerance and habitat temperature in ectotherm animals informs about their thermal adaptation and is used to assess thermal safety margins and sensitivity to climate warming. We studied this relationship in an equatorial freshwater snail (*Clea nigricans*), belonging to a predominantly marine gastropod lineage (Neogastropoda, Buccinidae). We found that tolerance of heating and cooling exceeded average daily maximum and minimum temperatures, by roughly 20 °C in each case. Because habitat temperature is generally assumed to be the main selective factor acting on the fundamental thermal niche, the discordance between thermal tolerance and environmental temperature implies trait conservation following 'in situ' environmental change, or following novel colonisation of a thermally less-variable habitat. Whereas heat tolerance could relate to an historical association with the thermally variable and extreme marine intertidal fringe zone, cold tolerance could associate with either an ancestral life at higher latitudes, or represent adaptation to cooler, higher-altitudinal, tropical lotic systems. The broad upper thermal safety margin (difference between heat tolerance and maximum environmental temperature) observed in this snail is grossly incompatible with the very narrow safety margins typically found in most terrestrial tropical ectotherms (insects and lizards), and hence with the emerging prediction that tropical ectotherms, are especially vulnerable to environmental warming. A more comprehensive understanding of climatic vulnerability of animal ectotherms thus requires greater consideration of taxonomic diversity, ecological transition and evolutionary history.

1. Introduction

There is considerable interest in developing frameworks for predicting how species and communities are likely to respond to climate change. One approach to determining the vulnerability of ectotherm animals to environmental warming involves assessing the upper thermal safety margin (*TSM*), that is, the difference between the upper thermal performance limit (heat tolerance) and the environmental temperature (Dillon et al., 2010; Deutsch et al., 2008; Huey et al., 2012; Tewksbury et al., 2008). Generally, longer exposure to temperatures above the thermal optimum for locomotor performance leads to fitness consequences in populations and species, as maintenance costs are raised, whereas organism mortality is inevitable when environmental temperatures exceed performance limits (upper lethal temperatures, *ULT*) (Dillon et al., 2010; Huey et al., 2012; Tewksbury et al., 2008). Most empirical studies suggest that marine and terrestrial ectotherms living in tropical regions (and Antarctic marine organisms; Peck et al., 2014) are under greater threat of climate warming than temperate species, because their *TSM*s are relatively narrow, despite the prediction of a poleward increase in the rate of environment warming (Compton et al., 2007; Dillon et al., 2010; Huey et al., 2012; Nguyen et al., 2011; Tewksbury et al., 2008). Additionally, the capacities of tropical ectotherms to adapt and acclimate *ULTs* in the face of environmental temperature variation are considered relatively limited (Araújo et al., 2013; Hoffmann et al., 2013; Stillman, 2003). Whereas the upper limit to heat tolerance in ectotherms is constrained by biophysical limits of membrane and protein functioning, having been established early in metazoan lineages, the lower thermal limit is set by thermodynamic effects on reaction rates, and is thus rapidly modified through evolutionary adaptation (Angilletta, 2009; Araújo et al., 2013).

Although the above framework for considering climate warming vulnerability is intuitively compelling and useful, it is not

* Corresponding author.
E-mail addresses: gianluca.polgar@gmail.com, gianluca.polgar@ubd.edu.bn (G. Polgar), tfkhang@um.edu.my (T.F. Khang), teddy.chua@ubd.edu.bn (T. Chua), davidmarshall11@gmail.com (D.J. Marshall).

http://dx.doi.org/10.1016/j.jtherbio.2014.11.009
0306-4565/

without limitation. Questions have been raised regarding assessing *TSMs* using climatically-relevant ambient air temperatures, as opposed to the heterogeneous temperatures of the habitat to which species adapt (Bonebrake and Deutsch, 2012; Helmuth et al., 2006; Scheffers et al., 2014). Further, debate concerns which specific environmental temperature parameters (e.g., daily maximum temperatures or daily mean temperatures) are more likely to impact thermal safety margins along latitudinal gradients (Bozinovic et al., 2011; Clusella-Trullas et al., 2011; Kingsolver et al., 2013). Additionally, *TSMs* do not account for chronic sublethal (growth and reproductive) effects, which potentially impact fitness and population viability. Within the context of thermal adaptation, climatic vulnerability and *TSMs* for non-marine ectotherms, the potential problem of taxonomic bias towards insects and lizards has received little consideration (Angilletta, 2009; Deutsch et al., 2008; Dillon et al., 2010; Huey et al., 2012; Sunday et al., 2011; Tewksbury et al., 2008). We know relatively little about how well existing models for tropical animals generalise across taxonomic groups and ecological domains (terrestrial, freshwater, marine). There are also gaps in our understanding of thermal adaptation and climatic resilience in animal lineages that traverse discrete ecological thermal boundaries and are represented in both warmer and relatively cooler tropical habitats (DJM, pers. obs.).

Here, we present a case study for a tropical freshwater snail (Mollusca: Gastropoda), representing a vastly underexplored taxonomic and ecological system. Gastropods are unlikely to conform to the strongly locomotor-performance-centred perspective for thermal adaptation theory appropriate to insects and lizards (Angilletta, 2009), given their preponderance for a sedentary existence and for behavioural avoidance (isolation) of environmental change (Marshall et al., 2013a; Marshall and McQuaid, 1991). Belonging to the second most diverse animal phylum, with an evolutionary history dating back to the Upper Cambrian, gastropods are predominantly marine (Lindberg et al., 2004; Ponder and Lindberg, 2008), but have uniquely colonised all of the major ecological domains (marine, freshwater and terrestrial; Webb, 2012). They therefore present more complex evolutionary histories than those of the ectotherms usually investigated in climate vulnerability studies. Our study species was *Clea nigricans* A. Adams, 1855, a snail inhabiting fast-flowing freshwater streams in Borneo, and the only freshwater genus of the large marine neogastropod family, Buccinidae (sensu Bouchet and Rocroi, 2005; Strong et al., 2008). We determined the upper and lower acute thermal tolerances of this species, and related these to habitat temperatures. The observed difference between the fundamental and realised niches was used to discuss hypotheses for the adaptation or conservation of thermal tolerance in this snail. This was also used to assess its vulnerability or resilience to environmental warming in terms of *TSMs*, relative to that of other tropical land dwelling ectotherms.

2. Materials and methods

2.1. *Clea nigricans*

Species of the genus *Clea* are distributed from western India (Benson, 1860), eastward to southern China (Liu et al., 1980), but most species are found in Southeast Asia (Brandt, 1974). *Clea* snails live in streams of hilly or mountainous areas, with some representation in reservoirs and other lentic habitats (Kittivorachate and Yangyeun, 2004). Very few studies have been undertaken on *C. nigricans*, and these essentially deal with its taxonomy and distribution, only providing anecdotal accounts for its habitat. *C. nigricans* (Adams and Adams, 1855; 1858: 623, pl. 137; Adams, 1861; Smith, 1895) is however known to occur in riverine habitats in the Malay Peninsula (Adams, 1861), Borneo (Adams and Adams, 1855; Smith, 1895) and on Sirhassen (=Serasan) island (Smith, 1895), South Natuna Islands, off the west coast of Borneo.

2.2. Field sampling

Fifteen snails were collected by hand from two small torrents flowing into the Temburong river, about 1 km apart, in sites presenting essentially identical habitat conditions (Fig. 1A). Sungai Mata Ikan (site A, 04°32′51.00″N, 115°09′26.00″E) and Sungai Esu (site B, 04°32′17.00″N, 115°09′36.00″E) are located inside the Ulu rainforest national park and near the Kuala Belalong Field Studies Centre (KBFSC, Universiti Brunei Darussalam), at topographical altitudes of 200–250 m above mean sea level. These study sites are at the foot of steep hills, reaching 1000 m at distances <1 km, and temperatures were relatively cool (see Sections 2.3 and 3.1). These tropical torrents are characterised by clear waters, small waterfalls, and rocky to coarse sandy bottoms. Their banks are

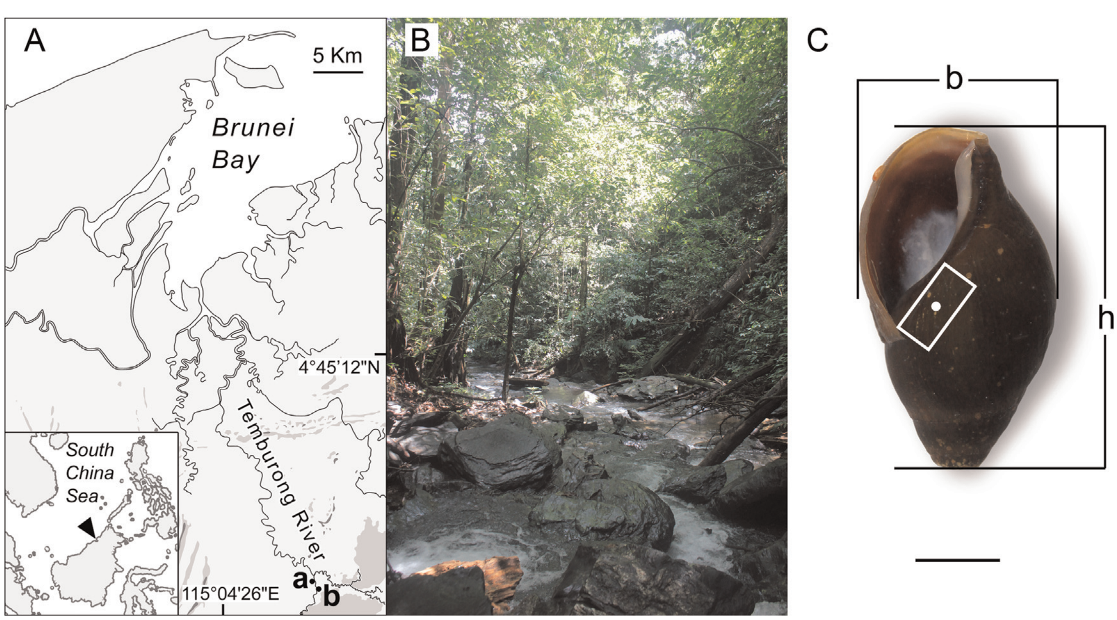

Fig. 1. Study sites (A), habitat (B) and experimental specimen (C) of *Clea nigricans*; (A) a=Sungai Mata Ikan; b=Sungai Esu; map redrawn from a satellite image (Google Earth Plus, v. 7.1, 2013); inset: *black arrow*=Brunei Bay. (C) *b*=shell breadth, *h*=shell height; scale bar=5 mm; white rectangle and spot=position where optoelectronic reflective sensor was fitted, during heart-beat recordings; operculum not visible in this image.