



Plasticity of thermoregulatory behaviour in response to the thermal environment by widespread and alpine reptile species



Amanda J. Caldwell^a, Geoffrey M. While^{a, b}, Erik Wapstra^{a, *}

^a School of Biological Sciences, University of Tasmania, Hobart, Tasmania, Australia

^b Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, U.K.

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Phenotypic plasticity plays a central role in determining how organisms respond to environmental change over short timescales. Despite this, we know little about how phenotypic plasticity varies between populations or species. We tested the extent of plasticity in basking behaviour in low- and high-altitude populations of two widespread lowland and two highland species of a cool-climate lizard genus: *Niveoscincus*. We found evidence of divergence in basking behaviour between populations and species, with highland species and high-altitude populations of all species basking more than the widespread lowland species and low-altitude populations. Furthermore, we found differences in the extent of behavioural plasticity between species. Widespread lowland species altered their basking behaviour depending on basking opportunity whereas the highland species maintained high levels of basking independent of basking opportunity. These differences in basking behaviour were concordant with the differences in body temperature across all populations, species and treatments. Combined, this suggests that divergence in thermoregulatory behaviour and thermophysiology between populations and species may have been facilitated by adaptive behavioural plasticity within populations. We discuss this and the implications of our findings for the ability of these animals to cope with ongoing climate change.

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Human-mediated impacts on the environment are placing increasing pressure on species worldwide (Pecl et al., 2017). As a direct result of these anthropogenic effects, a large proportion of the Earth's biodiversity is threatened with extinction (e.g. Edwards & Richardson, 2004; Parmesan, 1996; Pereira et al., 2010; Thomas et al., 2004). Species can respond to changing environments in three ways: by adapting in situ (Parmesan, 2006), by keeping pace with the preferred environment in physical space (e.g. dispersal; Pecl et al., 2017) or via plastic responses (Davis, Shaw, & Etterson, 2005; Jump, Peñuelas, & Hurtt, 2005). As climate change is progressing at a rate predicted to outpace evolutionary change in many species (Skelly et al., 2007) and habitat fragmentation and species interactions prevent many species from tracking their preferred environment in space (Chevin, Lande, & Mace, 2010), plasticity will be vital if species are to persist under changing environments (Davis et al., 2005; Hoffmann & Sgrò, 2011; Jump et al., 2005).

Populations and species differ in the magnitude of behavioural plasticity (Coppens, de Boer, & Koolhaas, 2010; Dingemanse & Wolf, 2013). The extent to which organisms possess an intrinsic capacity for plastic responses will depend, to some extent, on their historical exposure to different selection regimes (Komers, 1997; Snell-Rood, 2013). However, our understanding of how environmental conditions shape plasticity in behaviour remains incomplete. On the one hand, extreme environments can result in the canalization of behaviour (see Uller et al., 2011) resulting in reduced behavioural plasticity, while relatively benign environments may promote selection for behavioural plasticity (Snell-Rood, 2013). Conversely, fluctuating or changeable conditions might select for greater plasticity. Importantly, the extent of behavioural consistency/plasticity will affect the potential for behaviour to mediate responses to altered environmental conditions and ultimately its impacts on key physiological processes. This may have significant implications for the extent to which populations and species can persist under ongoing environmental change (Dingemanse & Wolf, 2013). Therefore, we need to understand the extent to which behavioural plasticity varies across populations as a result of historical selection

* Correspondence: E. Wapstra, School of Biological Sciences, University of Tasmania, Hobart, Tasmania 7050, Australia.

E-mail address: Erik.Wapstra@utas.edu.au (E. Wapstra).

pressures and the consequences of this for fundamental physiological processes.

Squamate reptiles provide a particularly interesting test case in this context. A growing number of studies predict dire consequences for reptile biodiversity under climate change (Araújo, Thuiller, & Pearson, 2006; Bickford, Howard, Ng, & Sheridan, 2010; Böhm et al., 2013; Sinervo et al., 2010; Thomas et al., 2004; Whitfield et al., 2007) as reptiles rely on a narrow, species-specific range of body temperatures for activity and the proper functioning of fundamental biological processes (Sunday et al., 2014). However, reptiles possess a variety of mechanisms which may allow them to persist under changing environmental conditions. In particular, behavioural thermoregulation can buffer the impact of changes in the thermal environment, allowing the maintenance of target temperatures under novel thermal environments via the modification of activity time and the exploitation of sun/shade (Kearney, Shine, & Porter, 2009). Despite this, our understanding of the extent to which plasticity in thermoregulatory behaviour varies between or within populations and the extent to which this plasticity has the potential to mediate the effects of environmental change is still relatively limited.

Here, we examined differences in the thermoregulatory behaviour of two widespread lowland (*Niveoscincus ocellatus* and *Niveoscincus metallicus*) and two highland (*Niveoscincus greeni* and *Niveoscincus microlepidotus*) Tasmanian snow skink species. Widespread lowland *Niveoscincus* occur over a wide geographical and altitudinal range (0 to ca. 1150 m above sea level), while highland *Niveoscincus* are limited to disjunct mountain top localities (> ~1100 m above sea level). As a result of their different distributional ranges, populations of the widespread lowland and highland species have experienced historically divergent local thermal environments both within and between species. Specifically, environmental conditions at high-altitude sites are much cooler and temporally variable than those at low-altitude sites, resulting in shorter activity seasons and greater climate-mediated constraints on basking opportunity. This may have resulted in stronger selection to optimize basking behaviour and tightly regulate selected body temperatures in high-altitude populations compared to low-altitude populations (Cadby, Jones, & Wapstra, 2014; Uller et al., 2011). To test whether the thermoregulatory strategies of high-altitude populations and highland species are more responsive or less responsive to environmental change than those of low-altitude populations and widespread lowland species, respectively, we exposed individuals to high or low basking opportunity and examined basking behaviour and body temperature responses. We predicted that high-altitude populations and highland species would spend more time basking, show reduced plasticity in basking time in response to basking opportunity and maintain higher body temperatures (irrespective of basking opportunity) than low-altitude populations and widespread lowland species, respectively.

METHODS

Study Species, Collection and Husbandry of Animals

Adult male lizards of two widespread lowland species, *N. ocellatus* and *N. metallicus*, and two highland species, *N. greeni* and *N. microlepidotus*, were collected from six sites within Tasmania (Table 1) over a 1-month period in November and December 2010. Sites differed considerably in their temperature and rainfall profiles (Appendix Fig. A1). We caught adult males for this experiment to avoid the potential confounding effects of the female reproductive cycle on thermal traits (Atkins, Swain, Wapstra, & Jones, 2007; Schwarzkopf & Shine, 1991). We targeted populations at the

altitudinal extremes of each species distribution, resulting in a lowland and a highland population for each species (hereafter referred to as 'low' and 'high', respectively; see Table 1). For highland species, these populations differed by only a small distance, owing to the smaller geographical distributions overall (they are restricted to disjunct mountain tops). Therefore, to confirm that these populations differed in their climatic regimes we distributed nine thermal loggers (model number DS1921G, Thermochron, Baulkham Hills, NSW, Australia) for a 2-week period in late summer/early autumn across the capture locations for the two populations for each of the highland species and collected data on average temperature (°C). These data showed that conditions for the high-altitude populations of both highland species were significantly cooler than for the low-altitude populations (*N. greeni*, low population = 9.81 ± 0.17 °C, high population = 8.71 ± 0.26 °C; one-way ANOVA: $F_{1,16} = 12.27$, $P < 0.01$; *N. microlepidotus*, low population = 10.16 ± 0.03 °C, high population = 9.41 ± 0.12 °C; one-way ANOVA: $F_{1,15} = 21.00$, $P < 0.01$). See Appendix Figs A2 and A3 for daily and hourly temperature profiles for the two sites. Such fine-scale differences in thermal conditions have been shown to have impacts on fundamental biological processes in this species (e.g. Cunningham, While, & Wapstra, 2017; Wapstra et al., 2009). There are no strong phylogenetic affiliations between species in either of the species groups (lowland and highland), with phylogenetic analyses separating *Niveoscincus* into three sister clades: *N. metallicus* and *N. microlepidotus* in separate clades and *N. ocellatus* and *N. greeni* grouped together (Melville & Swain, 2000). Therefore, any consistency in results gained from this study across species groups (see below) are unlikely to be driven by a shared evolutionary history.

Upon capture, the field active temperature of each lizard was measured using an infrared thermometer (805 Infrared Thermometer, resolution 0.1 °C, Testo, Lenzkirch, Germany; Appendix Table A1). Temperature readings were taken at a close range (ca. 10 mm) using a consistent lateral orientation to ensure readings produced measurements of surface temperature that were closely related to core temperature (Hare, Whitworth, & Cree, 2007; Jones & Avery, 1989). Lizards were transported to the University of Tasmania's Terrestrial Ecology Laboratories at the School of Biological Sciences. On arrival at the laboratory, lizards were weighed (± 0.01 g), and measured for snout–vent length (Appendix Table A1), vent – tail length and tail regrowth (± 0.5 mm). We excluded lizards that had experienced recent tail autotomy. None of the lizards included in the study was shedding upon capture or shed during the experiment.

Lizards were then transferred into individual housing (30 × 20 cm and 10 cm high) and maintained under standard laboratory conditions. Each terrarium had a mesh cover, absorbent bedding (paper pellets), a retreat for cover (wood block), a water dish and a tile beneath a basking lamp. The lamp was suspended 120 mm above the terrarium to generate a temperature gradient of ca. 15 °C (under the retreat away from the lamp) to ca. 40 °C (under the basking lamp; Wapstra, 2000). During the acclimation period, basking opportunity was provided between 0900 and 1600 hours. Bright UV lights at an intensity of 20 000 lx operated overhead between 0700 and 1900 hours. Lizards were fed twice weekly, 48 h prior to each set of behavioural observations, 24 h prior to each set of body temperature readings. This ensured lizards were in a postabsorptive state when behavioural observations were made and body temperatures were measured, as digestion has an unpredictable effect on thermal traits (Regal, 1966; Van Damme, Bauwens, & Verheyen, 1991). Lizards were fed *Tenebrio* larvae and fruit (pureed pear and banana or pureed apple, Heinz Australia, Victoria, Australia) supplemented with calcium (Repti-Cal, Aristopet, Queensland, Australia; alternating with premium calcium with

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