Journal of Thermal Biology 52 (2015) 208–216

Contents lists available at ScienceDirect

Journal of Thermal Biology

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

Energy expenditure of the spotted snow skink, *Niveoscincus ocellatus*, at two climatic extremes of its distribution range

Luh P.E.K. Yuni, Susan M. Jones, Erik Wapstra*

School of Biological Sciences, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia

ARTICLE INFO

Article history:
Received 29 November 2014
Received in revised form
11 June 2015
Accepted 9 July 2015
Available online 17 July 2015

Keywords:
Energy expenditure
Doubly labelled water
Lizards
Activity time
Metabolism

ABSTRACT

The study of energy expenditure between populations of a wide ranging ectothermic species may provide an insight into how organisms respond to variation in environmental conditions. In this study, the energy expenditure of male spotted snow skinks, *Niveoscincus ocellatus,* living at the two extremes of the species' distribution range (warm lowland versus cold alpine site) was measured using the doubly labelled water method. Males at the cold alpine site expended more energy per gram per hour compared to their counterparts living at the warm lowland site. Lizards living at high altitude were active at lower temperatures compared with those at the low altitude site, which resulted in a longer activity time for the highland population. However, the differences in energy expenditure cannot be explained only by these differences in activity time. We further suggest that at the cold alpine site, lizards compensated for the low temperatures by elevating their metabolism which subsequently increased their energy expenditure. An elevated metabolic rate combined with modified thermoregulatory behaviour is likely an important mechanism allowing *N. ocellatus* to cope with the cold environments at high altitude sites.

1. Introduction

Studying energy expenditure and energy allocation by an animal in nature helps us to understand how organisms have adapted to the environmental conditions. Such studies can also provide insights into how species respond to temperature differences between different latitudes or altitudes (Porter, 1989; Angilletta, 2001a). This is especially important for ectotherms in which life processes, including metabolism (DeVries et al., 2013), are strongly affected by the thermal environment (de Queiroz and Ashton, 2004; Fernandez et al., 2011).

An animal's metabolism, often measured as standard or resting (in ectotherms) or basal (in endotherms) metabolic rate, reflects the cost of maintenance of an animal's energy expenditure (Hulbert and Else, 2000). Energy expenditure of an animal comprises of several components including those associated with maintenance, growth, activity, and reproduction (Nagy et al., 1984; Pontzer et al., 2010). Among these, maintenance comprises the largest proportion of an animal's energy expenditure (Angilletta, 2001b; Clarke, 2003). Accordingly, basal metabolic rate is generally related to energy expenditure in endotherms (e.g., Pontzer et al., 2010; Dalton et al., 2014), and standard or resting metabolic rate in ectotherms (e.g., Beaupre and Duvall, 1998; Angilletta and Sears, 2000) because standard or resting metabolism relates to the energy required for maintenance (Pörtner et al., 2000; Homyack et al., 2010). Energy expenditure (and metabolic rate) of ectotherms is typically related to activity patterns (e.g., Sears, 2005; Smith et al., 2008). This is because higher level of activity is typically associated with higher body temperatures: thus, within species, energy expenditure varies with season or geographic variation in altitudes or latitudes (Karasov and Anderson, 1984; Patterson and Davies, 1989; Grant and Dunham, 1990; Clarke, 1991, 2003; Hare et al., 2010; Powers and Anderson, 2010; Schaefer and Walters, 2010). The relationship between energy expenditure and activity patterns is likely to be especially pronounced in ectotherms compared to endotherms because of the stronger relationship between activity patterns and higher body temperatures in ectotherms. In general, ectotherms living in warmer environments have higher resting metabolic rates because the speed of chemical reactions, including aerobic respiration, increases exponentially with temperature (Clarke and Fraser, 2004; Martinez del Rio and Karasov, 2010). For example, eastern fence lizards, *Sceloporus undulatus*, living in a warmer environment (lower latitude) had higher resting metabolic rates than those living in colder environment (higher latitude) (Angilletta, 2001b). Similarly, energy expenditure was higher in a population of the same species that experienced a longer activity time at their preferred temperature than in a population with a shorter activity time (Angilletta, 2001a). In addition, the population with the higher energy expenditure also had a significantly higher

---

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

http://dx.doi.org/10.1016/j.jtherbio.2015.07.003
0306-4565/

metabolisable energy intake than those with the lower energy expenditure (Angilletta, 2001a).

However, it may not be as straightforward as previously thought. Ectotherms primarily respond to the the variation in their thermal environment by behaviourally regulating their body temperatures (Seebacher et al., 2004; Kearney et al., 2009; Zamora-Camacho et al., 2013; Sunday et al., 2014), although it may be limited by several factors, e.g., thermal quality of the environment (Scheers and Van Damme, 2002; Besson and Cree, 2010), predation risk (Gutierrez et al., 2010), and time allocation for activities other than thermoregulatory behaviour (Huey and Slatkin, 1976; Sinervo et al., 2010). When thermoregulatory opportunities are limited due to a trade-off between multiple costs and benefits (Huey and Stevenson, 1979; Seebacher, 2009), ectotherms may shift their physiological and biochemical rates in order to allow an optimum physiological or physical performance (Seebacher, 2005; Beldade et al., 2011). Individuals from cooler environments such as high altitudes or latitudes may have adaptations that extend their daily activity (e.g., Van Damme et al., 1989; Addo-Bediako et al., 2000; McConnachie et al., 2009; Bonino et al., 2011), therefore affecting energy expenditure. For example, to be active at low temperatures, ectotherms can shift the body temperatures downward to allow basic physiological processes, such as performance (e.g., sprint speed or endurance) are optimised at low body temperatures (Clarke, 1993; Angilletta, 2009; Lourdais et al., 2013). A downward shift in lower limit of performance curve and thermal optima in locomotor performance have been documented in many ectotherms species (reviewed in Angilletta (2009)). Basic physiological processes at low body temperatures can be achieved by elevating standard or resting metabolic rates at specific temperatures in populations living in cold environments compared to those from warm environments (e.g., Hare et al., 2010; Schaefer and Walters, 2010). This is known as metabolic cold adaptation or MCA (Clarke, 1991, 2003; Hare et al., 2010; White et al., 2012). Metabolic cold adaptation (MCA) reflects compensation to cold temperatures (Clarke, 1991). It has been demonstrated within populations of eurythermal species living in the cold environment especially where the environment is highly variable, but not in stenothermal species due to stable temperatures (Pörtner, 2006). MCA occurs via adjustments of mitochondrial density and capacity according to the environmental temperature regime (Pörtner et al., 2000, 2008). For example, an elevation of mitochondrial density causes a rise in energy expenditure due to the cost of mitochondrial maintenance (Pörtner et al., 2000; White et al., 2012). Elevated standard or resting metabolic rates have been associated with a downward shift of critical temperatures in cold adapted populations of a species (Sommer and Pörtner, 2002; Pörtner, 2006). Metabolic cold adaptation has been observed in many species, including in reptiles species. One example of evidence of MCA was found in 'cold populations' of several species (*Hoplodactylus maculatus*, *H. chrysosireticus*, and *H. stephensi)* of nocturnal geckos from New Zealand where they had a higher standard and resting metabolic rate than diurnal 'warm' populations (Hare et al., 2010). Similarly, a northern (cold) population of cottonmouth snakes (*Agkistrodon piscivorus leucostoma*), had a higher standard metabolic rate at low temperatures than a southern (warm) population (Zaidan, 2003).

Niveoscincus ocellatus are small viviparous lizards (adult body mass 3–12 g) living over a wide geographic and climatic range in Tasmania with concomitant effects on life history traits (Wapstra and Swain, 2001; Wapstra et al., 2001; Atkins et al., 2007; Cadby et al., 2010, 2014; Pen et al., 2010; Uller et al., 2011). Individuals are considerably larger in body size at maturity (and larger overall) at the colder extremes (65 mm versus 55 mm) of the species' range (Wapstra et al., 2001) where the active season is reduced to approximately October to April, compared to their counterparts that are active approximately from September to May at the warmer extreme of the species' range (Wapstra et al., 1999). Individuals reach maturity at three years old at the warm lowland sites compared to four to five years old at the cold alpine sites (Wapstra et al., 2001; Pen et al., 2010). Key reproductive events such as mating and parturition occur approximately one month later at cold highland sites compared with lowland warmer sites (Wapstra et al., 1999; Pen et al., 2010; Uller et al., 2011). The effect of climate on life history traits, especially on embryonic development and the associated effects on the offspring traits such as on offspring birth date, size and sex, has created divergent selection pressures on basking behaviour in this species (Wapstra et al., 1999, 2004, 2009, 2010; Pen et al., 2010; Cadby et al., 2014). Divergence in basking behaviour has been demonstrated in a laboratory study where females from high altitude populations thermoregulated more actively (i.e. bask more) than low altitude lizards especially under reduced thermal opportunities (Uller et al., 2011; Cadby et al., 2014) presumably because of past selection to maximise the use of the limited opportunities that occur in the colder environments. *N. ocellatus* at the high altitude site are probably active at lower temperatures than those at the lower altitudes: at the high altitude site, opportunistic basking has been under selection in order to ensure the offspring's optimal development and potentially offspring fitness (Atkins et al., 2007; Uller et al., 2011; Cadby et al., 2014). It is clear that the thermal environment can create selection on basking and presumably other thermoregulatory behaviour, such behaviour that can certainly translate to males if the trait is under selection in females only because it is also likely that her offspring inherit the traits (Cadby et al., 2014). Although *N. ocellatus* has been extensively studied, the physiological flexibility that underpins the observed geographic variation in life history traits has not yet been studied.

In this study, we investigated the energy expenditure of *N. ocellatus,* under natural living conditions at the two climatic extremes of its distribution range: a warm lowland site versus a cold alpine site. Both cold alpine and warm lowland sites are located near the upper and lower limit of this species distribution ranges (Jones et al., 1997; Cadby et al., 2010). Accordingly, this species presents ideal opportunity to understand how a wide ranging ectothermic species has adapted to the environmental conditions they live in. The climate at the cold alpine site is colder than at the warm lowland site (Fig. 1; see Pen et al., 2010). *N. ocellatus* are typical temperate shuttling heliotherms that actively bask in the morning (when weather permits) and then use shade and sun intermittently to maintain temperatures at or near their optimum body temperature. During these periods of activity *N. ocellatus* is an active forager (Wapstra and Swain, 1996). On warmer days (especially in the warmer months), activity is distinctly bimodal with active basking only in the mornings and later afternoon. Typically, studies have found that ectotherms living in cold environments, such as at high altitudes or latitudes, have more restricted activity times than those living at lower altitudes or latitudes, which is due to more limited thermal opportunity. However, we suggested that it is not as straightforward as this because lizards at the cold alpine site might have physiological adaptations that allow them to cope with cold environments. This resulted in a higher energy expenditure in this population than that at the warm lowland site.

Energy expenditure was estimated using the doubly labelled water (DLW) method which allowed us to calculate the cost of living in the wild (Hulbert and Else, 2000). Only male lizards were used in this study because during the spring and summer months female snow skinks are at various stages of pregnancy (Jones et al., 1997; Wapstra et al., 1999) which affects both basking behaviour and energy expenditure in lizards (e.g., Beuchat and Vleck, 1990; Schwarzkopf and Shine, 1991; DeMarco, 1993; Robert and