



Differences in metabolic rate and evaporative water loss associated with sexual dimorphism in thynnine wasps



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ARTICLE INFO

Article history:

Received 12 August 2014

Received in revised form 28 April 2015

Accepted 29 April 2015

Available online 30 April 2015

Keywords:

Pollinator

Wasp

Metabolic rate

Evaporative water loss

Sexual dimorphism

Temperature

ABSTRACT

Species with sexual dimorphism provide powerful study systems for understanding adaptation to different lifestyles as it removes the potentially confounding effects of phylogeny. Thynnine wasps have a stark sexual dimorphism where males fly patrols in search of the flightless, predominantly fossorial females with which to mate. Using flow-through respirometry, we tested the prediction that the highly active males of the thynnine wasp *Zaspilothynnus nigripes* would have high metabolic rates (VCO_2) relative to females. Further, the females, which spend more time underground, were predicted to exhibit lower evaporative water loss (EWL) than males. Metabolic rate of both sexes increased exponentially between 12 and 28 °C. As predicted, males had higher mass-corrected VCO_2 at identical temperatures than females. Alternatively, there were no differences in the EWL at identical temperatures between sexes, suggesting that experiencing the same environmental conditions during mating may favour similar EWL. Interestingly, *Z. nigripes* were estimated to undergo a decrease in metabolism at approximately 30 °C. It is proposed that *Z. nigripes* persist despite sensitivity to high temperatures using a combination of behavioural strategies and emergence during a period of relatively benign climate that ameliorates the impacts of high temperatures.

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1. Introduction

Interspecific variation in the standard metabolic rates (SMR) of insects is correlated with broad differences in ecology (Schmidt-Nielsen, 1983; Withers, 1992). In particular, after accounting for the pervasive effects of mass, taxa with lifestyles that have high energy demands are expected to have higher basal energy requirements at any given temperature to fuel these lifestyles (Reinhold, 1999). Since maximal metabolic rate (MMR) reflects a proportional increase above resting levels (Clarke and Fraser, 2004), higher MMR may impart a detectable signal of increased SMR by the increase in maintenance requirements of highly metabolically-active tissues (Addo-Bediako et al., 2002; Daan et al., 1990; Reinhold, 1999). The profile of the metabolic response curve across a range of temperatures may also be associated with differences in ecology. The decline in metabolic rate above some critical threshold, which is associated with thermal inhibition of metabolism by enzyme inactivation or denaturation (Withers,

1992 #105), may be indicative of the thermal tolerance of the species and is expected to occur at higher temperatures in species from hot climates (Tomlinson and Phillips, 2012; Angilletta, 2006).

Differences in lifestyle activity may not exhibit a relationship with the evaporative water loss (EWL) of a species, though increasing endogenous metabolic water production may lead to increased water use efficiency (WUE; (Hinds and MacMillen, 1986; Klok and Chown, 1998; MacMillen and Hinds, 1983; Zachariassen et al., 1987)). However, other aspects of a species' biology do inform predictions concerning EWL. For example, there is a tendency for lower EWL in species that inhabit arid rather than mesic environments (Addo-Bediako et al., 2001; Klok and Chown, 1998; Mason et al., 2013; Zachariassen, 1996; Zachariassen et al., 1987). In an even more extreme contrast, fossorial taxa typically exhibit higher water losses than related epigeal taxa (Ahearn and Howarth, 1982; Hadley et al., 1981; Humphreys and Collis, 1990), as there is reduced selection pressure on water conservation capabilities due to the reduced ambient temperature (T_a) fluctuations and higher relative humidity underground (Gray, 1968; Hadley, 1970; Mason et al., 2013; Nevo, 1999). On average, more active taxa in drier environments are expected to have low EWL and high WUE compared to less active taxa in high humidity environments.

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Theoretically, in a species where males and females have different lifestyles, there may also be differences in physiological traits between the sexes. Associated with these different lifestyles is often a level of sexual dimorphism, the morphological differences between males and females of a species beyond the reproductive structures (Kardong, 2012). Species with sexual dimorphism, and contrasting lifestyles between the sexes, provide powerful study systems for understanding adaptations, as it removes the potentially confounding effects of phylogeny. Studies of differences in resting metabolic rates between sexes in invertebrates have typically recorded higher resting metabolic rates (RMRs) in males than females (Rogowitz and Chappell, 2000; Shillington, 2005; Shillington and Peterson, 2002; Tanaka and Ito, 1982; Watson and Lighton, 1994), although some research reports no differences in sexually dimorphic species (Humphreys, 1977; Penteado and Hebling-Beraldo, 1991). Higher metabolic rates in males have usually been ascribed to higher energy lifestyles of males actively searching for, or defending access to mates (Rogowitz and Chappell, 2000; Shillington, 2005; Shillington and Peterson, 2002; Watson and Lighton, 1994). For example, studies of flight energetics in the Hymenoptera have suggested that this trend is likely to arise through higher energy requirements of the tissues associated with flight (Suarez, 2000; Suarez et al., 2005) and structural dimorphism in the mass of flight muscles between males and females (Darveau et al., 2014; Radloff et al., 2003; Skandalis and Darveau, 2012). Alternatively, differences in EWL between the sexes has received little attention, despite its importance in understanding adaptations to the physical environment (Chown and Nicholson, 2004; Withers, 1992). However, in most cases minimal variation would be expected as both sexes typically inhabit environments with similar water vapour potentials, and similar evaporative gradients.

The Thynnidae (Hymenoptera) is a diverse family of strongly sexually dimorphic solitary wasps (Fig. 1), with over 1600 species in Australia (Brown, 2009) and a lesser diversity in South America (Austin et al., 2004). Males fly rapidly, patrolling for the flightless females, which typically crawl to a prominent perch and release a pheromone plume to attract mates (Alcock and Gwynne, 1987; Bohman et al., 2014; Schiestl et al., 2003). Pairs copulate in flight, with males carrying the female to food sources (Alcock and Gwynne, 1987), typically nectar or the sugary secretion of scale insects or lerps (Brown and Phillips, 2014). When not *in copula* females remain underground, while during the day males continue to feed or search for mates (Ridsdill Smith, 1970). As the flight of the males should require much higher energy expenditure than the terrestrial locomotion of females, this pronounced difference in locomotion between the sexes is more extreme than other species where energetic differences between the RMR of males and

females have been demonstrated (Rogowitz and Chappell, 2000; Shillington, 2005; Shillington and Peterson, 2002; Watson and Lighton, 1994).

Here we present the first study comparing the metabolic physiology and thermal tolerance of volitant and fossorial sexes of the same species. We compared SMR (VCO_2) and EWL between sexes of *Zaspilothynnus nigripes* (Hymenoptera:Tiphiidae:Thynninae, Guérin-Méneville, 1842) at a range of temperatures. Specifically, we aimed to test whether males have higher standard metabolic rates than females, resulting from maintenance costs of highly metabolically active tissues such as flight muscles. Males were also expected to have lower EWL than females as a result of adaptation to environments with low atmospheric relative humidity, compared to the subterranean environments which females typically encounter. Further, males should have higher WUE than females as a result of both their volitant locomotion and aerial lifestyle. By investigating metabolic rates near the high end of the thermal tolerance of *Z. nigripes*, we also tested if females show greater sensitivity to high temperatures.

2. Method

2.1. Study species

Zaspilothynnus nigripes is distributed throughout the higher rainfall parts of south-western Australian from Eneabba to Esperance (Phillips et al., 2014), favouring areas with sandy soil. Males generally only fly at temperatures above 18 °C (Peakall, 1990). The flying season extends between August and November, though at any one site they typically fly for approximately two months at the beginning of spring (Phillips, unpublished data).

Thirty-seven pairs of *Z. nigripes* were collected *in copula* (eight naïve pairs per experimental temperature, with the exception of five pairs at the highest temperature treatment) by sweep netting pairs feeding on *Pericalymma ellipticum* (Myrtaceae) from a single site (Ambergate Reserve, Busselton, Western Australia; 33.7 °S, 115.3 °E) and transported from the field in vials held at 4 °C in a portable refrigerator. Respirometry trials began early in the day. Wasps were assumed to be post-absorptive because they did not feed overnight, and were given no opportunity to feed prior to introduction to the respirometer.

2.2. Respirometry trials

The standard metabolic rate (SMR) of both sexes was measured using flow-through respirometry after protocols described by (Withers, 2001) and consistent with (Tomlinson and Phillips, 2012). Due to the limitations of small body size, only CO_2 production (VCO_2) was considered a reliable and sensitive enough measure of SMR. Body temperature (T_b) in the metabolic chamber is assumed to be nearly equal to T_a of exposure. Ambient temperatures for testing were nominally 12, 25, 28, 30 and 32 °C. A pilot study (Tomlinson and Phillips, unpublished) found that *Z. nigripes* lost co-ordination in the chamber in some individuals at 30 °C and suffered frequent mortality following acute exposure at $T_a = 32$ °C. We used these observations to define our upper experimental temperature. The rationale for selecting this range of temperatures was to provide a low T_a reference point for minimal metabolism below the T_a that elicits activity in the field (approximately 18 °C), but to focus attention at the upper limits, to more closely refine the T_a where metabolism is compromised. The 25 °C temperature was chosen to facilitate direct comparison with the data presented by Chown et al. (2007), where this was the most commonly measured experimental temperature in studies of insect metabolism.



Fig. 1. (A) *Zaspilothynnus nigripes* ♂ (left) and ♀ (right) showing extreme sexual dimorphism where males are volitant, while females are flightless, and are carried by the male to a food source during copulation (B). Photographs by (A) S. Tomlinson and (B) K. Smith.

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