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Does metabolic rate and evaporative water loss reflect differences in migratory strategy in sexually dimorphic hoverflies?

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ABSTRACT

A typical explanation for ecologically stable strategies that apply to only a proportion of a population, is bet hedging, where increased reproductive success offsets reduced reproductive rate. One such is partial migration, where only a proportion of a population moves seasonally to avoid inclement climatic conditions. Bet hedging may overlook unseen costs to maintain broad physiological resilience, implied by encountering a breadth of environmental conditions. We investigated the physiological correlates of partial migration by measuring standard metabolic rates, and rates of evaporative water loss, and then estimating upper and lower thermal tolerance in males and females of two hoverfly species, Episyrphus balteatus and Eristalis tenax. In central Europe, females of these species may either migrate or overwinter, whereas males may migrate south to the Mediterranean, but have not been found overwintering. Both species were sexually dimorphic; female Ep. balteatus were lighter than males, but female Er. tenax were heavier than males. While allometrically- corrected metabolic rate in both species increased with temperature, the most parsimonious models included no sex-specific differences in metabolic rate for either species. Evaporative water loss of both species also increased with temperature, but was higher for females of both species than males. Assuming that resting metabolism is congruent with the activity requirements of migration, highly consistent thermal tolerance and metabolic rate suggests that any given fly could migrate, although water loss patterns suggest that females may be less well-adapted to Mediterranean climates. We infer that partial migration probably results from the imperatives of their reproductive strategies.

1. Introduction

The basic premise of macrophysiology is that animals can only persist where they can tolerate the local climatic conditions and capture enough resources to maintain themselves, grow and reproduce (Chown et al., 2004; Chown and Gaston, 2008). Outside the stable climatic conditions of the tropics, however, few ecosystems are perennially suitable for many taxa, and seasonality imparts predictable, cyclical challenges. These challenges may be especially relevant to the ecological energetics of ectotherms due to their tight linkages between environmental conditions (particularly temperature), physiological efficiency and subsequent energetic demand and supply (Buckley et al., 2012).

Climates at the latitudinal extremes tend to be relatively invariable, either with consistent benign conditions to which physiological responses of ectotherms can become tightly adapted, such as the tropics (Logan et al., 2013), or nearly perennially hostile, such as the arctic and Antarctic (Klok and Chown, 1997). Temperate climates, however, show predictable patterns of seasonal variability (Chown and Terblanche, 2006), where periods of warmth and high ecosystem productivity are interspersed with comparable or longer periods of suboptimal climate. In climates like these, many taxa have evolved life history patterns (such as emergence phenology (Waldbauer, 1978; Brooks, 1988; Danforth, 1999; Hodgson et al., 2011)) or behavioural responses (such as migration (Dingle, 2014; Chapman et al., 2011)), which are thought to buffer species against these challenges. There is evidence that seasonal responses of insects coincide broadly with their energetics and thermal tolerance thresholds (Schmidt-Nielsen, 1983; Withers, 1992; Chown and Nicholson, 2004), and a substantial literature on the energetic drivers of migration, coupled with ecosystem productivity and reproductive patterns in vertebrates (e.g., Klaasen (1996), Bowlin et al. (2005), Cochran and Wikelski (2005), Marra et al. (2005), and Zera and Brisson (2012)). However, the ecological energetics of migration has been much less explored with invertebrates (Urquhart and Urquhart, 1978; Nielsen, 2009; Chapman et al., 2011).

Partial migration, where part of the population overwinters in the summer habitat while part of the population migrates, is a widespread phenomenon in migratory species (Chapman et al., 2011). The mechanisms supporting partial migration typically include ecological factors (Ketterson and Nolan, 1976; Gauthreaux, 1982; Chapman et al., 2011; Skov et al., 2011), and the explanations of the pattern typically revolves

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around 'bet hedging', where the reduced reproductive rate resulting from one strategy is offset against the likelihood of increased reproductive success (Danforth, 1999; Hopper, 1999). Analogous to the systems described by Cohen (1966), we would assume that females would only overwinter to increase their reproductive success if pregnant and should otherwise migrate to increase their chances of survival to the next breeding season (assuming the individual as a maximising agent, critically reviewed in this context by Grafen (1999). Ideally, these strategies may alternate according to some cycle that offsets the costs of overwintering. Thus, females should remain resilient to a breadth of physiological conditions, and different energy and water budgets, or should incorporate the costs of up-regulating these tolerances into the 'bet hedging' strategy. Alternatively, males should remain more physiologically specialised, with a lesser investment in reproduction and no need to offset reproductive rate against success, and predictable annual migration. However, there have been relatively few studies investigating physiological variation in migratory tendency (but see Bevan et al. (1994), Bevan et al. (1995), Bowlin et al. (2005), Cochran and Wikelski (2005), Gillis et al. (2008) and Nilsson et al. (2011)). With regard to insect physiology, the previous literature has focused on the oogenesis-flight syndrome, the trade-off between migratory ability and development of the reproductive organs (Johnson, 1969; Gatehouse and Zhang, 1995; Dingle, 2014; Zera and Harshman, 2001; Attisano et al., 2013) For example, resident female milkweed bugs (*Oncopeltus fasciatus*) typically have higher levels of oosorption compared to migrants (Attisano et al., 2013). By extension, where a partial migration strategy differs between sexes, then the physiological drivers of migration may differ between the sexes (Gatehouse and Zhang, 1995). However, the direction of the differences that might be expected will be dependent upon the trait in question, and the specific selection pressures applied by different migration strategies. We chose to investigate aspects of the energy and water budget and also how these traits may respond to temperature since these ecological aspects differ markedly between seasons and migration destinations. While the aspects of thermal tolerance may be predictable, where non-migrants might be hardier to lower temperatures, aspects of metabolic rate and EWL are difficult to predict, where high flight requirements may imply higher resting metabolism due to higher maintenance requirements (Marden, 2000; Darveau et al., 2002) and endurance, or may imply greater efficiency to reduce costs of transport and reduce metabolic rate (Lehmann, 2001; Niven and Scharlemann, 2005). Patterns of EWL are more complicated still, where high rates of loss might also be offset by high rates of metabolic water production (Woods and Smith, 2010) and a liquid diet.

Hoverflies (Diptera: Syrphidae) are a diverse family, comprising approximately 6000 species worldwide (Marshall, 2012). In temperate climates, hoverfly species overwinter as larvae, pupae or adults (Schneider, 1948; Dušek and Láska, 1974; Sarthou et al., 2005). Alternatively, in Europe, some hoverfly species are partially migratory, where part of the population overwinters, while the rest migrate south to milder climates for the winter, often in large numbers (e.g., Aubert et al. (1976), Aubert and Goeldlin de Tiefenau (1981), Gatter and Schmid (1990) and Nielsen (2009)). Migrating swarms include both males and fertilised females with undeveloped reproductive systems (Rotheray and Gilbert, 2011). In species that overwinter as adults, overwintering individuals are almost exclusively fertilised females in facultative reproductive diapause (Rotheray and Gilbert, 2011). Adult hoverflies have been shown to have poor cold-hardiness (Hart and Bale, 1997; Hart et al., 1997) but are thought to be able to overwinter by exploiting refugia such as buildings or vegetation (Hondelmann and Poehling, 2007; Rotheray and Gilbert, 2011; Speight, 2012). Nonetheless, overwintering syrphids have been observed to be active at ambient temperatures as low as 7 °C–8 °C (Gilbert, 1985; Hondelmann and Poehling, 2007). Intraspecific differences in ecology and lifestyle between sexes have frequently been shown to have physiological correlates in metabolic rates (Tanaka and Ito, 1982; Watson and Lighton, 1994; Rogowitz and Chappell, 2000; Shillington and Peterson, 2002; Shillington, 2005; Tomlinson and Phillips, 2015), and although these have yet to be associated with migratory strategies, many of the ecological correlates of high metabolic rate, including aerial lifestyle are relevant to migration (Lighton and Fielden, 1995; Reinhold, 1999; Chown et al., 2007; Irlich et al., 2009).

In this study, we compared the thermal tolerance and resting metabolic physiology between the sexes of two common migratory hoverfly species in Europe, *Episyrphus balteatus* (de Geer, Diptera: Syrphidae: Syrphinae) and *Eristalis tenax* (L., Diptera: Syrphidae: Eristalinae). Both are widespread taxa, with a worldwide distribution (Speight, 2012). In Europe, *Ep. balteatus* and *Er. tenax* are partially migratory, where some individuals (both males and females) migrate south in large numbers in the autumn (e.g., Aubert et al. (1976), Aubert and Goeldlin de Tiefenau (1981) and Gatter and Schmid (1990)), while some females overwinter as adults in the summer quarters (Sarthou et al., 2005; Hondelmann and Poehling, 2007). Consequently, we hypothesised that females will have lower minimum thermal tolerance thresholds than males, as females may either overwinter or migrate south to warmer climes, whereas males tend not to overwinter (e.g., Dušek and Láska (1974), Hart and Bale (1997) and Hondelmann and Poehling (2007)). Given that both sexes experience similar summer conditions, the upper thermal tolerance thresholds are expected to be similar for both sexes.

Evidence has been accumulating that metabolic rate and evaporative water loss (EWL) are related responses (Zachariassen et al., 1987; Klok and Chown, 1997; Woods and Smith, 2010; Groenewald et al., 2013), and the calculation of water use efficiency (WUE) has provided some insights into thermal physiology of insects (Tomlinson and Phillips, 2015). Patterns of EWL have not previously been shown to differ between sexes (Willmer, 1988; Terblanche et al., 2006; Parkash et al., 2008; Tomlinson and Phillips, 2015), and patterns of WUE are most often related to patterns of metabolic rate (Willmer, 1988; Zachariassen, 1996), suggesting that WUE may follow similar patterns of thermal tolerance to metabolic rate.

2. Methods

2.1. Animal collection

Forty *Ep. balteatus* and 30 *Er. tenax* were collected in an even partition of sexes by sweep netting from ruderal meadows around the city of Bern, Switzerland (46°56′49.4"N, 7°26′35.9"E) during the boreal summer (late July–early August). Prior to respirometry trials, the flies were kept in laboratory rearing cages at room temperature and photoperiod with pollen pack, crystalline sucrose, and water available *ad libitum*. No flies were maintained in this way for more than 3 days prior to measurement. Respirometry trials were begun early in the day, and the flies were assumed to be post-absorptive because they were deprived of food overnight and were given no opportunity to feed prior to introduction to the respirometer.

2.2. Respirometry trials

Carbon dioxide production (VCO_2) was measured as a proxy of standard metabolic rate (SMR) of both sexes using flow-through respirometry after Withers (2001), Tomlinson and Phillips (2012) and Tomlinson and Phillips (2015). We are confident in reporting SMR of these flies since they were post-absorptive and the respirometry outputs suggested that their behaviour in a darkened incubator was at rest (see Supplementary Material). Body temperature (T_b) in the metabolic chamber is assumed to be nearly equal to T_a of exposure.

Experimental temperature (T_a) was maintained to within ±0.05 °C in a Sanyo MIR-253 (SANYO Electric Biomedical Co., Ltd., Osaka, Japan) incubator at nominal temperatures of 5 °C, 15 °C, 25 °C, 35 °C and 40 °C. These temperatures were selected to provide a broad range