

Inter-individual variation in shivering behaviour in the migratory painted lady *Vanessa cardui*

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Abstract. 1. Thermoregulation abilities are likely to play a fundamental role in ectotherms' response to current environmental changes, including through their implication in interspecies and interindividual variations in life-history strategies (e.g. dispersal syndromes). However, differences in thermoregulatory behaviours, and especially interindividual differences, are largely neglected in the literature, and there is still no global understanding of their importance in determining population and evolutionary processes, even in extensively studied taxa such as butterflies.

2. Interindividual variation in shivering in the painted lady, a migratory butterfly, was investigated. This behaviour has been very poorly studied, despite being widespread in insects in general, including butterflies. Using a warming experiment in the laboratory on 94 different individuals caught in the wild during the same migratory event, interindividual variation in shivering behaviour was investigated, and the effects of wing morphology and boldness (a behavioural axis known to be associated with mobility in butterflies) on shivering decision and efficiency were tested.

3. The study shows that individuals strongly differ in their shivering behaviour. Wing morphology affected both individuals' decision on whether or not to use shivering and heating rate while shivering. In contrast, no effect was found of individuals' age and boldness on shivering decision and efficiency. The findings also reveal that shivering strongly increased heating rate and allowed higher flight temperatures to be reached, while bolder individuals also took off at higher temperatures.

4. Overall, the results of the present study underline how variation in a neglected thermoregulatory behaviour could affect general life-history strategies in butterflies, and stress the need to consider this behaviour when investigating butterfly life-history syndromes.

Key words. Basking, boldness, butterfly, insect, Lepidoptera, personality, thermoregulation.

Introduction

In response to climate change, organisms are known to change their latitudinal distributions, elevation ranges, and phenology. Understanding what makes some species capable of adapting to such changes while others are not is crucial for conservation. Northward shifts due to climate change are apparent in various organisms, from endotherms to ectotherms (Perry *et al.*, 2005;

Hickling *et al.*, 2006; Parmesan, 2006; Hitch & Leberg, 2007; IPCC, 2007). Butterflies, probably because they are relatively easy to observe and identify, have yielded among the most complete long-term datasets to investigate range shifts. From a pioneering work focused on European butterflies by Parmesan *et al.* (1999), they were indeed extensively used as a model group to investigate range shifts in Europe (Hill *et al.*, 1999; Warren *et al.*, 2001; Konvicka *et al.*, 2003; Thomas *et al.*, 2004; Wilson *et al.*, 2005), North America (Crozier, 2003, 2004), and Asia (Kwon *et al.*, 2014). Similarly, butterflies yielded information of major importance with regard to changes in phenology in response to climate change (Roy & Sparks, 2000; Forister & Shapiro, 2003;

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Stefanescu *et al.*, 2003). Because butterflies are particularly well known, they allowed researchers to investigate how species traits can explain variation in responses to climate change (Hill *et al.*, 1999; Warren *et al.*, 2001; Pöyry *et al.*, 2009; Diamond *et al.*, 2011; Mattila *et al.*, 2011), revealing that habitat generalist and more mobile species are better able to move northwards, whereas species with a narrower diet and more advanced overwintering stage experience greater phenological advancement.

As ectotherms, butterfly phenology, mobility, and habitat use strongly rely on their sensitivity to external climatic conditions (Van Dyck & Matthysen, 1998; Kharouba *et al.*, 2014), and on mechanisms allowing them to regulate body temperature according to external conditions. Such thermoregulation abilities are thus likely to determine how species will respond to climate change (Buckley *et al.*, 2012). For example, wing coloration plays a fundamental role in insects' thermoregulation abilities (Kalmus, 1941; Kingsolver, 1995; Clusella-Trullas *et al.*, 2007); light-coloured butterflies and dragonflies were recently shown to be at an advantage in a warm climate, and differently coloured butterflies were shown to react differently to changes in climate (Zeuss *et al.*, 2014). Variation in thermoregulation strategies was also shown to be part of both interspecific (Stevens *et al.*, 2014) and intraspecific (Ducatez *et al.*, 2013, 2014) mobility syndromes, also suggesting that a better understanding of variation in thermoregulation might provide fundamental information for our study of butterflies' responses to environmental changes in general. However, thermoregulation in insects, and in butterflies in particular, is complex, implying a large range of mechanisms and traits (including physiological, morphological, and behavioural traits), and stressing the need for more studies.

A particularly well-known thermoregulation behaviour in butterflies is basking, whereby individuals select a particular habitat and use specific wing orientation and postures according to solar radiation and wind direction (Rutowski *et al.*, 1994). Different basking postures and wing colorations were shown to lead to different thermoregulation mechanisms, including conductance of absorbed heat to the thorax (Kingsolver, 1987), reflectance of solar radiation on to body tissues (Kingsolver, 1985), and the shielding of body tissues from solar radiation (Rawlins, 1980). Another potentially widespread, though very poorly studied and often neglected, thermoregulation behaviour is shivering, whereby butterflies produce heat by contracting their flight muscles primarily against each other, raising thoracic temperature by as much as $10^{\circ}\text{C min}^{-1}$. Although shivering does not free butterflies from the constraints of external temperature, it allows them to reach temperatures far above the ambient temperature, and makes it possible to fly under suboptimal conditions (Kammer, 1970; Loli & Bicudo, 2005). The phenomenon has mostly been observed in large species [e.g. red admiral *Vanessa atalanta* (Krogh & Zeuthen, 1941); monarch butterfly *Danaus plexippus* (Kammer, 1970; Masters *et al.*, 1988); black swallowtail *Papilio polyxenes* (Rawlins, 1980); Camberwell beauty *Nymphalis antiopa* (Douglas, 1986); painted lady *Vanessa cardui* and peacock *Inachis io* (Maier & Shreeve, 1996); owl butterflies *Caligo* and *Opsiphanes* (Srygley, 1994)], but how shivering behaviour varies between individuals, and how it is integrated into general ecological and

life-history strategies remain unknown. The only study we are aware of that actually investigated the ecological functions of shivering considered tropical owl butterflies (Srygley, 1994) and showed that, in these species, individuals mostly shivered before crepuscular flights involved in reproductive encounters.

Because shivering implies the contraction of flight muscles, it is likely to be energetically more costly than basking, suggesting that this thermoregulation strategy will mostly be used as an alternative, for example, under suboptimal conditions or when needing to take off quickly (e.g. in response to a predator). Although this idea requires more investigation, it suggests that shivering decision and efficiency might be associated with behavioural traits, especially traits characterizing butterfly response to predators. We might thus expect boldness, defined as an individual's reaction to any risky situation (Réale *et al.*, 2007), to affect butterflies' decision to use shivering. Indeed, the recent behavioural ecology literature shows that between individuals, variations in behavioural traits are often consistent across time (personality traits; see Réale *et al.* 2007), and are included in general syndromes associating behavioural, physiological, morphological, and life-history traits (see Réale *et al.* 2010). But whether and how shivering, and thermoregulation behaviour in general, are associated with other behavioural traits remain to be investigated.

Here, we studied shivering behaviour in a widespread migratory butterfly, the painted lady *V. cardui*. We aimed to investigate interindividual variation in shivering behaviour, and to test how wing morphology and boldness affect shivering decision and efficiency. The painted lady occurs in most areas of North America, Europe, Western Asia, and North Africa (Shields, 1992). This species has been extensively studied, mostly for its migratory behaviour and phenology (Abbott, 1951; Pollard *et al.*, 1998; Stefanescu *et al.*, 2007, 2011, 2012; Nesbit *et al.*, 2009), although its thermoregulation behaviour remains under-investigated. Each year, the painted lady colonizes the European continent from its African overwintering range (Pollard *et al.*, 1998; Stefanescu *et al.*, 2011). In 2009, an exceptional migration event occurred, where numbers of *V. cardui* migrating across Europe were extremely high (Stefanescu *et al.*, 2013). We took advantage of this event to characterize interindividual variation in shivering behaviour, catching wild butterflies involved in the same migration event. Using a warming experiment in the laboratory, we tested whether the decision to shiver was affected by individuals' age, sex, wing morphology, or boldness. Using an infrared thermometer to assess heating rate and take-off temperature, we also directly measured the effect of shivering on heating rate, tested whether individuals differed in their shivering efficiency (heating rate while shivering), and whether wing morphology, sex, age, and boldness could explain these eventual differences.

Methods

Butterflies sampling and captivity conditions

A total of 94 butterflies were collected nectaring on flowers of the same *Buddleja davidii* tree located in an urban park in Brunoy (Essonne, France; latitude $48^{\circ}41'40.50''\text{N}$, longitude $2^{\circ}29'47.71''\text{E}$). Captures occurred daily from 28 June 2009 to 14

July 2009, between 10.00 and 15.00 hours, weather permitting. Butterflies were then kept in cages of $20 \times 20 \times 20$ cm with artificial flowers containing a solution of 10% sugar in water. We first measured butterfly behaviour in the tunnel test (boldness), and then in the warming experiment, and finally took pictures of each individual before marking the butterflies with individual numbers and releasing them on the capture day. We aimed to test whether the butterflies we used were still on the move, or whether they settled in the capture area. During daily mark-recapture sessions over the same period (28 June 2009 to 14 July 2009), we marked a total of 265 butterflies (including the 94 used in this study), but recaptured none, suggesting that, indeed, all individuals were migrating through the area. Note that by releasing the butterflies, we were not able to weigh their thorax and abdomen.

Tunnel test

The tunnel test was previously described in Ducatez *et al.* (2012, 2014). This test was specifically designed to measure individual bold/shy tendency. In a dark room held at a constant temperature of 24 ± 1 °C, butterflies were individually released at the entrance of a 3-m-long opaque pipe of 80 cm diameter with a light source at its end. Each individual was released in the air, at a height of 40 cm, to avoid any take-off effort, so that test scores mainly depended on a behavioural choice rather than a physiological capacity. The novelty of this experimental situation, in addition to the small diameter and the darkness of the tunnel, was particularly challenging to the butterflies. We consequently expected butterflies with a bold temperament to fly into the tunnel, whereas butterflies with a shy temperament would stay at the entrance. We observed strong differences among individuals: some flew into the tunnel (flyers), while others did not (non-flyers). This test was repeated five times (the five trials were successive and carried out within less than 1 h) for each individual, to test for behavioural repeatability (fraction of behavioural variation that is due to differences among individuals; Bell *et al.*, 2009). For each trial, we recorded whether the butterfly flew into the tunnel. To verify whether those butterflies that did not fly during the five trials were physiologically able to fly at the temperature of the tunnel, we released them in the same room after switching the room light on. Our observations confirmed that indeed all were physiologically able to fly, strongly suggesting that the observed differences were related to differences in boldness. As a measure of boldness, we used the number of trials during which an individual flew into the tunnel (from 0 to 5).

Heating rate measurement

To assess individuals' heating rate and heating behaviour, we performed a warming experiment in the laboratory. Each butterfly was first cooled in a refrigerator (4 °C) for 10 min, and then warmed up at 24 ± 1 °C under a 300 W Ultra vitalux (Osram, Munich, Germany) solar lamp placed at a distance of 72 cm, while its thorax surface temperature was measured continuously with a TESTO845 (Forbach, France) infrared thermometer (emissivity $\epsilon = 0.95$, one data point s^{-1} up to 180 s).

The temperature recording was stopped once the butterfly flew off, and the last recorded value was thus considered as the individual take-off temperature. While measuring thorax surface temperature, we also recorded the butterflies' behaviour. Specifically, the observer (S.D.) noted whether the butterfly was shivering, using dorsal basking, or kept its wings closed, and recorded the moment each individual changed its behaviour. It allowed us to fit, for each individual, the heating curve with changes in thermoregulation behaviour, and to separately analyse bouts corresponding to different behaviours. We estimated heating rate for each different bout and each individual. The heating rate was expressed as the slope of the thorax surface temperature versus time (log-transformed) curve (Van Dyck & Matthysen, 1998; Ducatez *et al.*, 2013); in our data, the corresponding linear regression very well described the increase in thorax surface temperature with time ($r^2 = 0.952$). Butterflies that warmed up fast were characterized by high heating rate values. Note that, as individuals' temperature at the beginning of the different bouts varied, it was included in models with heating rate as response variable.

Morphology

Wing morphology was measured from photographs taken on the capture day after the warming experiment. Butterflies were anaesthetized with nitrogen monoxide, fixed between two transparent plastic pieces, and photographed with a digital camera equipped with a 105 mm lens using a decimeter scale to allow measurement comparisons across individuals. Each forewing was extracted from the picture using the GIMP software (GNU Image Manipulation Program), and its surface and length were measured with the IMAGEJ software. We adopted two widely used variables that describe wing morphology in butterflies differently, the wing length measured from the base to the apex and the wing shape measured as the wing aspect ratio ($4 \times$ forewing length²/forewing area). Individuals with rounder wings have lower aspect ratios, while those with angular wings have higher aspect ratios. Note that, as expected from the very high correlation between wing length and wing surface (Pearson correlation = 0.981; $P < 0.001$), considering wing surface instead of wing length in our analyses did not change the results. We also tested for an effect of age using an age index classically used in the literature (Baguette & Neve, 1994), based on the wear of the wings and varying from 1 (fresh) to 4 (extensive wing wear). For each individual, we averaged wing length, aspect ratio and age index over the two wings.

We finally determined the butterflies' sex, considering the length and shape of the last abdominal segment. Females indeed have a larger and pointier terminal segment, whereas it is narrower and rounder in males. To validate this sexing method, we also measured the abdomen length (in mm), and found that females had significantly longer abdomens ($P = 0.014$; $t = -2.517$; males: $n = 47$, mean = 9.814 ± 0.139 mm; females: $n = 51$, mean = 10.318 ± 0.142 mm).

Analyses

We first tested for repeatability of our boldness measurement. We estimated repeatability using the R package rptR, considering

a multiplicative overdispersion model with a logit link, as advised by Nakagawa and Schielzeth (2010) for binary data. Because some individuals used shivering and others did not, we then tested which factors predicted whether an individual was using shivering or not. We built generalised linear models with shivering (binary variable, with 1 for individuals that used shivering and 0 for those that did not) as the response variable, fitted with a binomial distribution and a logit link function. As explanatory variables, we included individuals' age, wing length, wing aspect ratio, boldness score, and sex. Interactions between sex and all other covariables were also included to test for sexual differences in the effects of the covariables. We then aimed to estimate the effect of shivering on heating rate during the warming experiment. To that end, we used linear mixed models with heating rate as response variable, heating behaviour (shivering or not) as explanatory variable, and individual as random effect (as some individuals had several heating rates corresponding to several heating bouts). Temperature at the beginning of each bout was included as a fixed effect. Note that we initially considered three levels for the heating behaviour variable, including shivering, dorsal basking, and closed wings. However, because dorsal basking did not affect heating rate in our experimental conditions, we gathered dorsal basking and 'closed wings' behaviours into one category, and focused on the effects of shivering behaviour. In parallel, we tested how shivering affected individuals' heating duration (time between exiting the fridge and take-off) and take-off temperature, by considering the effect of shivering on these variables in linear models. Age, wing length, wing aspect ratio, boldness score, sex, and all interactions between sex and the other covariables were also included in these models. Finally, we aimed to compare shivering efficiency between individuals that used shivering, focusing on heating rates while shivering. We built linear mixed models with heating rate during shivering bouts as response variable, individuals' age, wing length, aspect ratio, boldness score, sex and all interactions between sex and all other covariables as explanatory variables, and individual's identity as random factor. Analyses were conducted using R 3.0.1 and the nlme package, and normality of residuals and homogeneity of variance were validated through visual inspection of graphical model evaluation plots.

Results

Tunnel behaviour

The behavioural response of butterflies in the tunnel was significantly repeatable ($r = 0.573$; 95% CI: 0.367–0.624; $P < 0.001$).

Who are the shivers?

In all, 77 out of 94 individuals used shivering during the warming experiment. Aspect ratio was the sole significant predictor of whether or not a butterfly shivered during the warming experiment. Individuals with rounder wings (and thus lower aspect ratios) were significantly more likely to use shivering (estimate = -1.525 ± 0.606 ; $z = -2.517$; $P = 0.012$; all other $P > 0.417$).

Effects of shivering on heating rate, time to take-off, and take-off temperature

Heating rate was affected by both initial bout temperature and heating behaviour. Indeed, heating rates were higher for bouts starting at low initial temperatures (estimate = -0.004 ± 0.001 ; $t = -6.096$; $P < 0.001$), and higher when individuals were shivering than when they were not (estimate = 0.073 ± 0.005 ; $t = 14.982$; $P < 0.001$; see Fig. 1a). The time to take-off (time between exiting the fridge and taking flight) was determined by wing aspect ratio and heating behaviour, as individuals with rounder wings (estimate = -47.623 ± 23.790 ; $t = -2.001$; $P = 0.048$) as well as shivering individuals (estimate = -128.601 ± 26.057 ; $t = 26.057$; $P < 0.001$; Fig. 1b) took flight sooner. Similarly, shivering significantly increased the take-off temperature (estimate = 5.387 ± 0.740 ; $t = 7.275$; $P < 0.001$; take-off temperature in individuals using shivering = 29.526 ± 0.345 °C; and take-off temperature in individuals that did not use shivering = 23.835 ± 0.210 ; Fig. 1c). In addition, bold butterflies (individuals that flew more often in the tunnel) took off at higher temperatures (estimate = 1.080 ± 0.475 ; $t = 2.276$; $P = 0.025$), the effect of boldness being additive to the effect of shivering, and males took-off at a lower temperature than females (estimate = -1.495 ± 0.570 ; $t = -2.624$; $P = 0.010$; take-off temperature in males = 27.862 ± 0.497 °C; in females = 29.080 ± 0.506 °C). Other tested variables did not affect heating rate, time to take-off or take-off temperature ($P > 0.457$).

Variation in shivering efficiency

Focusing on shivering bouts, we then tested for predictors of shivering efficiency. We found that shivering heating rate was significantly predicted by aspect ratio, individuals with narrower wings (and thus higher aspect ratios) having higher heating rates (estimate = 0.024 ± 0.009 ; $t = 2.638$; $P = 0.010$; Fig. 2). Heating rates also decreased when initial bout temperatures were higher (estimate = -0.003 ± 0.001 ; $t = -4.285$; $P = 0.003$). None of the other variables was significant ($P < 0.226$).

Discussion

These results show that shivering behaviour is particularly variable between individuals of the same species. The fact that this variation occurred between butterflies caught on the same tree while taking part in the same long-distance migration suggests the existence of different thermoregulatory strategies between individuals following similar migratory pathways. Indeed, we show that both the decision to shiver and the efficiency of shivering differ between individuals. As we were not able to detect any age effect on these differences, they seem unlikely to rely on ontogenetic changes in thermoregulation behaviours. Similarly, sex did not explain this variation. Note that our results could still be explained by differences in individuals' origin, developmental temperature, or genetic adaptation to conditions in the native environment leading to variation in shivering. In addition, as we were not able to weigh individuals, we cannot exclude

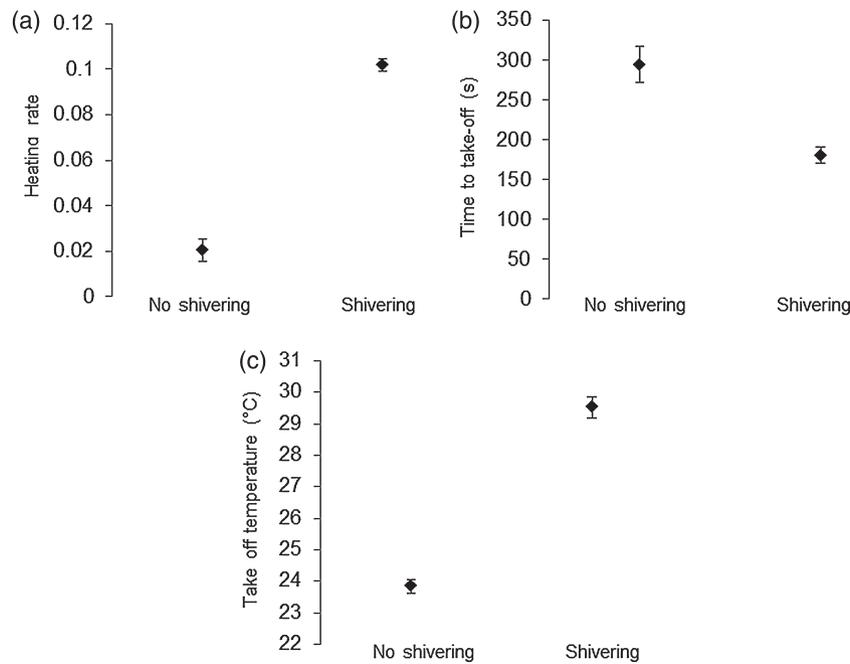


Fig. 1. Effects of shivering on heating rate (a), time to take-off (b) and take-off temperature (c) in a laboratory warming experiment on painted lady butterflies *Vanessa cardui*. Heating rate is expressed as the slope of the thorax surface temperature versus time (log-transformed) curve (see text for details).

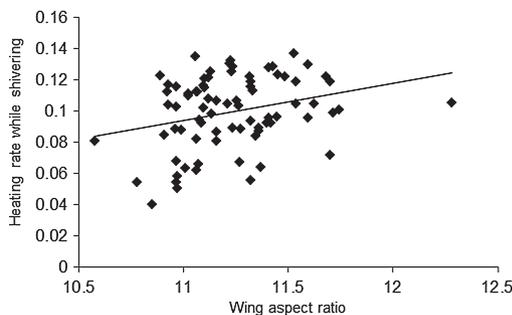


Fig. 2. Effects of wing aspect ratio on shivering efficiency (estimated by heating rate while shivering) in painted lady butterflies *Vanessa cardui*. Heating rate is expressed as the slope of the thorax surface temperature versus time (log-transformed) curve (see text for details).

the possibility that this variation was somehow related to variation in body condition and amount of reserves available. More experiments, especially in captivity, are needed to discard or validate these hypotheses.

We confirm that shivering allowed butterflies to reach thorax surface temperatures far above ambient temperature (5.5 °C higher, on average), to warm up faster and to take off earlier and at higher temperatures. Using shivering thus allows butterflies to limit their dependency on external conditions, and may be particularly useful in some situations where a quick take-off is required, such as in response to predators or to a potential sexual partner (e.g. Srygley, 1994). How different situations may or may not elicit a shivering behaviour deserves more attention.

Wing morphology, through wing aspect ratio, predicted whether or not butterflies decided to shiver, and how fast

shivering individuals warmed up. Individuals with rounder wings were more likely to shiver, whereas among individuals using shivering, shivering was more efficient in individuals with narrower wings. Unfortunately, these results do not allow us to determine the causality of the relationship between wing morphology and shivering. Because shivering implies the contraction of flight muscles, we expected variation in wing morphology to indirectly affect shivering behaviour and efficiency through associations with flight muscles, which are indeed likely to covary with wing morphology. Alternatively, as wing morphology is likely to affect performance at basking, another thermoregulatory behaviour, we could expect trade-offs between investments in basking versus shivering efficiency. The maintenance of interindividual variation in shivering behaviour might then be explained by the existence of different thermoregulation strategies, some butterflies optimizing basking efficiency, and others optimizing shivering. If shivering is costly (and there is evidence to suggest that it is; see Srygley, 1994), individuals developing a particular wing shape that increases their basking efficiency might indeed limit their investment in shivering. On the other hand, adaptation to local environmental conditions might lead to positive associations between different thermoregulatory abilities. Here again, our results call for direct investigation into whether or not the development of these thermoregulation abilities is costly, whether different thermoregulatory strategies and behaviours are traded off or positively associated, and how wing morphology is implied in these different behaviours.

We estimated boldness using a test previously used in other butterfly species (Ducatez *et al.*, 2012, 2014), and show here that individuals' response to this test is repeatable in the painted lady,

suggesting that it measures persistent differences between individuals. The fact that our repeatability estimates were obtained from behaviours measured within an hour, however, requires caution with regard to the interpretation of this result, and more investigations, in which the same behavioural tests are repeated after larger time gaps, are needed to confirm the consistency of this behaviour. Individuals' scores in this boldness test were shown to be related to flight endurance and exploration tendency in five other butterfly species (Ducatez *et al.*, 2012, 2014), revealing the existence of a mobility syndrome common to several species. In our analyses, we did not detect any association between boldness and either the decision to shiver or shivering efficiency, although we might have expected shy individuals to be more likely to use shivering as a way to take off quickly when exposed to danger (here, the observer recording thorax surface temperature). This absence of effect may suggest that a syndrome similar to the one found in other species does not occur in migratory *V. cardui*, or that shivering is not strongly associated with such a syndrome. However, the repeatability of behaviour in the tunnel test, the finding that shy individuals (i.e. those that rarely fly during the tunnel test) also took off at lower temperatures during the warming experiment, and the effect of wing morphology on shivering suggest that associations among behavioural, physiological, and morphological traits likely to affect activity and mobility also exist in painted ladies, and can even be detected when considering individuals taking part in the same migration event. The finding that shy individuals take off at lower temperatures during the warming experiment suggests that taking off at low thorax temperature is costly, so that only shy individuals are likely to take that decision, whereas bold individuals take the risk of waiting to reach a higher temperature. These results therefore suggest a strong association between behavioural and thermoregulation strategies, and call for further investigation into how variation in shivering behaviour, and in thermoregulation behaviour in general, can affect individual variation in life-history strategies. The fact that thermoregulation is associated with behavioural choices (e.g. the choice to shiver or not), physiological abilities, and morphology (e.g. wing aspect ratio) suggests that these different trait types, all expected to affect movement abilities as well, should co-evolve, and that variation in these traits is likely to involve the existence of life-history syndromes.

These preliminary results provide a description of interindividual variation in a poorly understood thermoregulation behaviour, shivering. Providing evidence that variation in this behaviour is likely to be integrated into wider life-history syndromes concerning a variety of traits, our results also call for further investigation into the general importance of variation in thermoregulation abilities as constraints or adaptations in determining life-history strategies. *Vanessa cardui* is known to migrate at high altitudes (up to 1200 m above ground level; Stefanescu *et al.*, 2013), and is thus likely to experience relatively low temperatures during migration. A better understanding of thermoregulatory behaviours in this species may also help to determine how long-distance migratory butterflies deal with thermal conditions encountered at these altitudes.

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S.D. and M.B. designed the project, S.D. collected and analysed the data, and S.D. and M.B. wrote the paper.

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