Variation of thorax flight temperature among twenty Australian butterflies (Lepidoptera: Papilionidae, Nymphalidae, Pieridae, Hesperiidae, Lycaenidae)

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Key words. Lepidoptera, Papilionidae, Nymphalidae, Pieridae, Hesperiidae, Lycaenidae, thorax flight temperature, wing loading, infra red thermometer, warming-up rate, physical constraint, allometry

Abstract. Thermal requirements for flight in butterflies is determined by a combination of external factors, behaviour and physical constraints. Thorax temperature of 152 butterflies was monitored with an infra-red thermometer in controlled laboratory conditions. The temperature at take-off varied from 13.4°C, for a female Heteronympha merope to 46.3°C, for a female Junonia villida. Heteronympha merope, an understorey species, had the lowest recorded take-off temperature, with females flying at a much lower thorax temperatures than males. Among the tested butterfly species, warming-up rate was positively correlated with take-off temperature and negatively with body mass. Wing loading is a major variable in determining the thorax flight temperature. Butterflies with the highest wing-loadings experienced the highest thorax temperatures at take-off. A notable exception to this rule is Trapezites symmomus, the only Hesperiidae of our data set, which had thorax flight temperatures of 31.5°C and 34.5°C, well within the range of the observed butterflies, despite a wing load ca. five times higher. The high thorax temperature recorded in J. villida is probably linked to its high flight speed. The results highlight the importance of physical constraints such as body size on the thermal requirements for flight across a range of butterfly species.

INTRODUCTION

Butterflies, being facultative endotherms (Bartholomew, 1981), rely on both external factors and internally produced heat for the maintenance of their body temperature. The thorax temperature depends on ambient temperature, irradiant heat gained by basking behaviour and heat generated by muscle movements, while heat loss occurs through body irradiance and air convection around the body (Wickman, 2009). Thermoregulation in insects is therefore dependent ultimately on behaviour, either directly through shivering or basking, or indirectly by moving to or away from sunlit patches (Kingsolver, 1985a). Butterflies of the genera Papilio, Colias and Pieris, need a thorax temperature between 28 and 42°C for flight, while rigorous flight is restricted to thorax temperatures between 33 and 38°C (Kingsolver, 1985b; Srygley & Chai, 1990). The lowest recorded flight thorax temperatures are found in large species, such as Parnassius phoebus, which may fly with a thorax temperature of 17 to 20°C (Guppy, 1986).

The wing loading, defined as \( p_w = m/S \), where \( m \) is the total individual mass and \( S \) the total wing surface is a major variable determining the energy required for insect flight (Heinrich, 1986). Compared with other insects, butterflies have much lower wing loading values, suggesting that wing size and shape in butterflies evolved not only for flight functions, but also for other functions such as thermoregulation, sexual behaviour, mimicry and camouflage (Dudley, 1991). Wing loading generally increases with body mass in butterflies (Heinrich, 1986; Dudley, 1990), but skipper butterflies (Hesperiidae) are heavier than other butterflies of the same wing surface (see below). Species with a high wing loading require faster wing beats, and hence a higher thorax flight temperature (Bartholomew & Casey, 1978). Thorax flight temperature in moths (Noctuidae and Geometridae) has been reported as correlated with wing loading (Bartholomew & Heinrich, 1973) or with mass (Casey & Joos, 1983). In butterflies, the data are sparse. As wing loading and mass are usually correlated, it is difficult to disentangle these two effects (Dudley, 1990; Heinrich, 1986).

The aims of this study were to document variation of thorax temperature among the studied species, and to test the effect of wing loading and mass on thorax flight temperature. Interspecific variation in thorax temperature needed
for flight can have a significant impact on species fitness. For example, the ability to fly at lower temperatures may lead to more time available for dispersal and searching for mates and food (Kingsolver, 1983). Conversely, the more thorax temperature increases above ambient air temperature, the greater the risk of overheating, potentially leading to reduced survival and fitness. For example, in *Colias* butterflies, a thorax temperature of above 40°C causes individuals to cease flying to avoid overheating (Kingsolver & Watt, 1983). With the predicted increase in global temperatures and frequency of extreme temperatures, it is increasingly important to understand physical constraints on thermal tolerances which ultimately impact species fitness and dispersal ability.

Within a locality, the temperatures experienced by individual butterflies will largely depend on both their habitat preferences and timing of flight activity. Generally, species inhabiting forests will experience more stable conditions than species found in open habitats. A previous study, carried out in Mediterranean France (Nève, 2010), suggested that forest habitat species show lower thorax flight temperatures compared to open habitat species because of the lower temperature of the forest floor relative to open habitats. A secondary aim of the present study was to test this hypothesis with the available Australian species.

**MATERIAL AND METHODS**

A total of 152 butterflies were captured with hand nets (Upton & Mantle, 2010) in the field, 85 near Adelaide (mainly Bedford Park 35°01’S, 138°34’E and Wotton Scrub, 34°59’S, 138°47’E, South Australia) and 67 at Cedar Creek, 27°49’S, 153°11’E (Queensland) (Table 1); only *Pieris rapae* was collected at both locations. The tested specimens belonged to twenty species, mostly from open habitat, or linked with the canopy (e.g. *Graphium sarpedon*). Only four species were specialist understorey species (pers. observ., Braby, 2000): *Trapezites symmomus*, *Melanitis leda*, *Heteronympha merope* and *Nacaduba kurava*.

![Fig. 1. Example of individual warming up process, here a male *Pieris rapae*. The solid line indicates the 4th degree function fitted to the raw data. Its derivative at y = 26°C gives the warming up rate at this temperature, here 0.13°C/s, indicated by the slope at this point.](image)

Upon capture, specimens were put into glassine envelopes and cooled to ca. 11°C in a portable fridge. The same day, in an air conditioned room at 22 to 25°C lit with fluorescent lamps, each specimen was taken out of the fridge and placed on a piece of cotton under a 150 W neodymium daylight lamp, giving an irradiance of ca. 280 W/m² at the butterfly level. The thorax temperature of each specimen was measured with a testo®895 IR thermometer with the emissivity set at ε = 0.95, and the recorded temperature was automatically input into a computer database, one datum per second. The behaviour of individuals was reported as they were warming up, especially the basking behaviour, and the position of the wings. The take-off temperature was taken as the last temperature recorded before the butterfly took off. A 4-th degree curve was fitted to the raw data, and its slope was used to estimate the

**Table 1. Numbers of individuals tested per species and sex, with measured total wing surfaces and weights.**

<table>
<thead>
<tr>
<th>Family</th>
<th>Subfamily</th>
<th>Species</th>
<th>State of Capture</th>
<th>Females</th>
<th>Males</th>
<th>Total</th>
<th>Mean total Wing surfaces (mm²) Females</th>
<th>Males</th>
<th>Mean weights (mg) Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hesperiidae</td>
<td>Trapezitinae</td>
<td><em>Trapezites symmomus</em> (Hübner, 1823)</td>
<td>Queensland</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>1086</td>
<td>340</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Papilionidae</td>
<td>Graphininae</td>
<td><em>Graphium sarpedon</em> (Linnaeus, 1758)</td>
<td>Queensland</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>2200</td>
<td>200</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Athyma</td>
<td>Papilio</td>
<td><em>Papilio aequus</em> (Donovan, 1805)</td>
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<td>2</td>
<td>2</td>
<td>4259</td>
<td>399</td>
<td></td>
<td></td>
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<tr>
<td>Pieridae</td>
<td>Colladinnae</td>
<td><em>Catopsilia poromona</em> (Fabricius, 1775)</td>
<td>Queensland</td>
<td>5</td>
<td>4</td>
<td>9</td>
<td>2202 1847</td>
<td>276</td>
<td>208</td>
<td></td>
</tr>
<tr>
<td>Pieridae</td>
<td>Colladinnae</td>
<td><em>Catopsilia pyrante</em> (Linnaeus, 1758)</td>
<td>Queensland</td>
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<td>1</td>
<td>1</td>
<td>1400</td>
<td>116</td>
<td></td>
<td></td>
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<tr>
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<td>Colladinnae</td>
<td><em>Eurema brigitta</em> (Stoll, 1780)</td>
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<td>3</td>
<td>4</td>
<td>513 342</td>
<td>31</td>
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<tr>
<td>Pieridae</td>
<td>Colladinnae</td>
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<td>3</td>
<td>6</td>
<td>488 591</td>
<td>43</td>
<td>26</td>
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</tr>
<tr>
<td>Pieridae</td>
<td>Pierinae</td>
<td><em>Pieris rapae</em> (Linnaeus, 1758)</td>
<td>Qld, Sth Austr.</td>
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<td>20</td>
<td>21</td>
<td>1050 959</td>
<td>70</td>
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<tr>
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<td>Pierinae</td>
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<td>South Australia</td>
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<td>2</td>
<td>2</td>
<td>1373</td>
<td>130</td>
<td></td>
<td></td>
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<td>Satyrinae</td>
<td><em>Melanitis leda</em> (Linnaeus, 1758)</td>
<td>Queensland</td>
<td>8</td>
<td>8</td>
<td>16</td>
<td>1972 1878</td>
<td>1164</td>
<td>113</td>
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<td>Satyrinae</td>
<td><em>Hypocosta adianta</em> (Hübner, 1831)</td>
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<td>0</td>
<td>1</td>
<td>529</td>
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<td>Satyrinae</td>
<td><em>Hypocosta metrius</em> (Butler, 1875)</td>
<td>Queensland</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>355 461</td>
<td>22</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>Nymphalidae</td>
<td>Satyrinae</td>
<td><em>Geitaneura klugii</em> (Guérin-Méneville, 1830)</td>
<td>South Australia</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>633</td>
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<td>Satyrinae</td>
<td><em>Heteronympha merope</em> (Fabricius, 1775)</td>
<td>South Australia</td>
<td>18</td>
<td>32</td>
<td>50</td>
<td>1935 1402</td>
<td>173</td>
<td>111</td>
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<tr>
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<td>Satyrinae</td>
<td><em>Hypolimnas bolina</em> (Linnaeus, 1758)</td>
<td>Queensland</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>2701 2181</td>
<td>255</td>
<td>208</td>
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</tr>
<tr>
<td>Nymphalidae</td>
<td>Satyrinae</td>
<td><em>Junonia villida</em> (Fabricius, 1798)</td>
<td>South Australia</td>
<td>11</td>
<td>3</td>
<td>14</td>
<td>908 777</td>
<td>103.6</td>
<td>83</td>
<td></td>
</tr>
<tr>
<td>Nymphalidae</td>
<td>Satyrinae</td>
<td><em>Vanessa kershawi</em> (McCoy, 1868)</td>
<td>South Australia</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1086</td>
<td>127</td>
<td></td>
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<td>Nymphalidae</td>
<td>Biblidinae</td>
<td><em>Pseudohippocrepis</em> (Linnaeus, 1758)</td>
<td>Queensland</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1464</td>
<td>154</td>
<td></td>
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<td>Nymphalidae</td>
<td>Danainae</td>
<td><em>Euploea core</em> (Cramer, 1780)</td>
<td>Queensland</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>2351 2158</td>
<td>268</td>
<td>237</td>
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<tr>
<td>Nymphalidae</td>
<td>Danainae</td>
<td><em>Euploea tulliolus</em> (Fabricius, 1793)</td>
<td>Queensland</td>
<td>0</td>
<td>7</td>
<td>7</td>
<td>2076 173</td>
<td>173</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lycanidae</td>
<td>Polyommatini</td>
<td><em>Nacaduba kurava</em> (Moore, 1858)</td>
<td>Queensland</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>361</td>
<td>25</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
rate of warming, in °C/s (Fig. 1). The warming up rate at 26°C was used as an index of warming-up speed. This estimate was not possible on 21 specimens for which too few temperature points could be recorded during the warming-up process, hence the lower numbers of available warming-up rate estimates compared with available take-off temperatures.

As a control, three *Heteronympha* specimens were tested with a testo® thermocouple sensor set inside their thorax, at the same time as the outside thorax temperature was monitored. The temperature inside the thorax had a mean of 1.3°C warmer than the one measured on the surface, with a low variance of this difference (variance = 0.31).

After the warming-up experiment, each individual was weighed. Twenty-eight of the specimens were released after the experiment, while the rest were retained for references and measurements. These specimens were set with the trailing edge of the hind wing perpendicular to the thorax (Upton & Mantle, 2010). All 125 set specimens were photographed in a standard way with a 60 mm Macro Canon Lens, together with a scale, and the total wing surface was estimated for each specimen using ImageJ (Rasband, 2012). The area of overlap between the forewing surfaces are given in the supplementary Table S1.

The observed take-off temperatures varied widely among species, ranging from 13.4 to 46.3°C, with an among-species median value of 32.4°C (Fig. 2). The minimum temperature (13.4°C) was recorded for a *Heteronympha merope* specimen, and the highest (46.3°C) for a *Junonia villida* specimen. Warming-up rate at 26°C also varied widely among the twenty tested species, with the lowest values found in *Melanitis leda* (0.02°C/s) and *Hypolimnas bolina* (0.02°C/s) specimens. The highest value were found for *Junonia villida* (0.54°C/s) (Fig. 3).

The two Nymphalidae forest understorey species, *Melanitis leda* and *Heteronympha merope*, showed very similar take-off temperatures (*Melanitis leda*: mean = 30.2°C, *Heteronympha merope*: mean = 30.3, t\(_{22}\) = 0.04, P = 0.97; Fig. 4). In *Heteronympha merope*, females display a wider range of possible take-off temperatures, with a lower mean, than the males (females: from 13.4°C to 39.2°C, mean = 25.2°C +/- sd 7.9°C, n = 18; males: from 16.6°C to 39.9°C, mean = 33.2°C +/- sd = 3.9°C, n = 32). The difference in take-off temperatures between males and females of *H. merope* is highly significant (t\(_{22}\) = –4.00, P < 0.001).

**RESULTS**

The observed take-off temperatures varied widely among species, with available take-off temperatures. All data points are shown in filled circles for species with less than five data points.

**Fig. 2.** Thorax take-off temperatures of twenty Australian butterfly species. The vertical lines indicate the median values, and the boxes the range from first to third quartile; dotted lines indicate extreme values if they fall within 1.5 times the interquartile difference, otherwise open circles indicates outliers. All data points are shown in filled circles for species with less than five data points.

**Fig. 3.** Warming up speeds at 26°C for all tested Australian butterfly species. Symbols as in Fig. 2.
However, in *Melanitis leda*, there is no significant difference in take-off temperatures between the sexes (\( t_{14} = 0.49, P = 0.63 \)).

The species with the highest recorded thorax temperature was *Junonia villida*, with temperatures ranging from 36.8°C to 46.3°C, implying an excess temperature (thorax temperature minus ambient temperature) of up to ca. 20°C. The three species with the highest recorded take-off thorax temperatures were *Junonia villida* (median = 39.7°C), *Bellenois java* (median = 37.5°C) and *Pieris rapae* (median = 34.7°C). The latter species is the only non-native species in our data set, having been introduced from Europe (Lokkers & Jones, 1999), allowing comparison with data from its natal range. Australian specimens of *Pieris rapae* flew with a temperature on average one degree warmer (median = 34.7°C, \( n = 20 \)) than the ones from France (median = 33.7°C, \( n = 126 \); \( W = 821, P < 0.05 \), Fig. 5). Australian specimens also warm up more quickly (median = 0.16°C/s, \( n = 19 \)) than French specimens (median = 0.12°C/s, \( n = 126 \), \( P < 0.001 \)).

The among species variation of warming-up rate did correlate significantly with take-off temperature (\( r_{18} = 4.89, P < 0.001 \), Fig. 6). When the species were looked at individually for the same relationship, among the ones for which at least ten individuals had been tested, only *Melanitis leda* showed such a positive relationship (\( r_{12} = 2.66, P = 0.02 \), Fig. 7).

With a value of 0.524 mg/mm², *Trapezites symmomus* had a much larger wing loading than all other species, which had values ranging from 0.035 mg/mm² (for *Hypocysta metirius* males) to 0.127 mg/mm² (for *Catopsilia pomona* females). *Trapezites symmomus* is also the only species in the data set to have a linear relationship between thorax temperature and time during the warming-up process, suggesting a different warming-up process than in other Lepidoptera lineages. *Trapezites symmomus* was then discarded from the data set for the analysis of the effect of wing load on take-off temperature. Among species variation showed that temperature at take-off was positively correlated with wing-loading (\( t_{17} = 2.28, P = 0.036 \), Fig. 8).

Wing loading \( p_w \) and body mass \( w \) were correlated by the allometric function \( p_w = 0.030 w^{0.225} \) (\( t = 3.86 \) and \( t = 4.31, P = 0.001 \) and \( P < 0.001 \); Fig. 9).

**DISCUSSION**

Very few temperature data on the studied species has been published before. Notable exceptions are *Papilio aegeus*, *Melanitis leda* and *Pieris rapae*. Heinrich (1986) gave thorax temperatures of 35°C for *Papilio aegeus* flying in the shade and 42.8°C when flying in the sunshine. Our data on this species shows lower values (30.4 and 35.4°C).

Studies by Kemp (2002) gave inside thoracic temperatures of *Melanitis leda* males ranging from 28.2 to 38.9°C. Our data on the same species are lower, ranging from 23.7 to 34.8°C. Even allowing for the difference between inside and outside (about 1.3°C), our estimates in both cases remain lower, probably as a result of our laboratory conditions testing the thorax temperature from which flight is possible, rather than the thorax temperature at which individuals usually fly or, in the latter case, perform their courtship.

*Pieris rapae* was the only species tested from European and Australian populations, and as such provides an interesting comparison between its native and introduced range. The 1°C higher thorax take-off temperature, and the quicker warming-up in Australia may be due its adaptation to the higher temperatures experienced in Australia compared with the native range. Such physiological plasticity...
in thermal requirements for flight may impact not only on the invasive ability of a species but also on its ability to adapt to climate change (Matilla, 2015).

As in European butterflies (Nève, 2010), understory specialists require a lower thorax temperature for flight activities when compared to open habitat species. *Melanitis leda* and *Heteronympha merope* are two butterflies active in the forest understorey; as such they experience cooler temperatures than species found in more open habitats (Wickman, 2009), and they have fewer opportunities to bask to gain higher temperatures. In *Heteronympha merope*, females may fly at a much lower thorax temperature than males. This sex difference is unusual, as females need a higher thorax temperature for flight than males in *Colias philodice* (Kingsolver, 1983) and in *Thymelicus lineola* (Pivnick & McNeil, 1986), whereas no difference were found in *Hedodes virgaureae* (Douwes, 1976). Unlike these species, *H. merope* shows mainly disjunct population peaks for males and females, with males most abundant in spring and females in autumn (pers. observ., Braby, 2000). The difference in flight thorax temperatures between males and females of *H. merope* may reflect the different climatic conditions experienced by each, and hence an adaptation to minimize excess temperature, thus reducing metabolic costs. Alternatively, differences between sexes may also reflect difference in wing shape and flight behaviour, as in the case of *Pararge aegeria* (Berwaerts et al., 2006).

*Melanitis leda*, unlike *H. merope*, flies mainly at dusk and dawn (Braby, 1995; Kemp, 2002, 2003), and may be present throughout the year in many localities (Braby, 2000). Their habit of flying during the coolest parts of the day may be linked to their low temperature requirements for flight activities.

The case of *Junonia villida*, with the highest recorded thorax temperatures, half of which close to or above 40°C, raises interesting questions. Previous studies (Kingsolver & Watt, 1983; Matilla, 2015) suggest that *J. villida* may be
at risk of heat shock at such high temperatures. This species, however, has a flight pattern with quick reactions and fast flights (Braby, 2000; pers. observ.), suggesting a high amount of muscular activity and thus may have adapted to cope with higher than normal flight temperatures. Junonia villida may then be an extreme case of high wingbeat frequency related to a high temperature (Pivnick & McNeil, 1986). This species seems thus to have evolved a fast escape strategy against insectivorous bird predators, which also requires high thorax flight temperature, as palatable species often do (Chai & Srygley, 1990).

It should be noted that Trapezites symmomus, which has a wing loading ca. five times higher than all other tested butterflies only showed take off temperatures of 31.5°C and 34.5°C, well within the range of the observed butterflies (Fig. 3). It has been shown that the genotypes of the individuals was a major determinant of the ambient temperature at which individual fly (Colias butterflies; Watt et al., 1983, Monarch Danaus plexippus: Hughes & Zalucki, 1993). Whether Junonia villida holds special variants of the loci adapted to high temperature remains an open question.

In our data set, wing loading \( p_w \) showed an allometric relationship with body mass \( w \) \( (p_w = 0.030 w^{0.225}) \). As the exponent is <1, this is a negative allometric relationship (Huxley & Teissier, 1936; Gould, 1966) between wing loading and body mass. Dudley (1990) also obtained a negative allometry (which he erroneously called “positive allometry”), but with a much higher exponent (0.474); only a small part of the difference between our result and Dudley’s are due to the use of the direct function for the estimate: an estimate using the classical log-log relationship gives an exponent factor of 0.238 with our data. It should be noted here that for comparative purposes, the exponent does not depend on the units being used, only the multiplying factor does; this was the cause of some debate between Huxley and Teissier (Gayon, 2000). Despite the fact that wing loading and body mass are correlated variables, our analysis clearly shows a correlation between thorax temperature at take-off and wing loading, but not with body mass. Heinrich (1986) could not differentiate these two effects, due to insufficient data. Our data shows that wing loading is more relevant than body mass in respect to thorax flight temperature.

In many insect species, the rate of warming-up is related to muscular activity and body mass, whereas heat loss depends on their external body surface, smaller individuals and species taking longer to warm up than large ones (May, 1976), although in within species comparison, the reverse has occasionally been found (Thymelicus lineola: Pivnick & McNeil, 1986; Hypolimnas bolina: Kemp & Krockenberger, 2004). In our experimental setting, when looking at multiple species comparison, large butterflies warm up more quickly than small ones. The lack of significance for tests in individual species may be due to the small sample sizes or lower variance of intra-specific variation compared with inter-specific variation.

In the present data set, there is also a trend for the butterflies to warm up faster if they have to reach a higher temperature for flight activity. In this way, the time spent to reach the needed temperature does not increase in proportion with the required flight temperature. However, the energy required to reach a high temperature must be accounted for. While solar energy pays a role in increasing body temperature in butterflies (Wasserthal, 1975), muscular activity is also needed to reach this temperature, especially, as in the case of Junonia villida, it is well above the ambient air temperature.

Species showing a low wing loading generally fly with lower wing beat frequencies than the ones with higher wing loadings (Casey & Joos, 1983), and low wing beat
frequencies require a lower thorax temperature for flight activity. It is thus no surprise that the species with the lowest take-off temperature, Eurema brigitta, Nacaduba kurava and Hypocysta adiantae were also among the ones with the lowest wing loading and total weight. On the other hand, wing loading per se is not sufficient to infer the thorax temperature necessary for flight, as microhabitat and behaviour also have an influence.

The increase of thorax temperature of Tratepezites symmenus in a linear fashion is similar to the sphinx moth Manduca sexta (Heinrich & Bartholomew, 1971), while other butterflies generally show a curve with decreasing rates until the take-off temperature is reached in a plateau fashion (Nève, 2010). This may be related to the shape of these two species, which have a lower surface to volume ratio than butterflies of the families others than Hesperiidae; they have thus a lower heat loss rate (Heinrich, 2003).

The increase in temperature is therefore mainly the result of the muscular activity, heat loss being negligible in comparison.

CONCLUSIONS

Temperature needs of butterflies are an important component of their ecological requirements (Wickman, 2009), both at the adult and larval stages (Serratore et al., 2013). The thorax temperature needed for flight activity is the result of multiple effects. Individual weight and total wing surface are physical factors influencing wing beat frequency, but individual differences in behaviour also plays a role. The optimal flight thorax temperature is adaptively determined through selection of enzymes variants active at specific temperatures. Species living in cooler environments, such as the forest understorey, may be adapted to fly at lower temperature as they would mainly rely on their muscular activity for thorax heating. The temperature needed for flight activity is thus the result of trade-off between environmental variables and internal physical and biochemical processes. The results highlight the importance of understanding this dynamic in the face of environmental change. While butterflies can behaviourally adapt to changes in temperature, factors such as body size and wing loading may impose physiological limits to future climate adaptation.

ACKNOWLEDGEMENTS. We wish to thank A. Thiéry, E. Meglécz and D. Mackay for help during the field work and for numerous discussions. R. Kitching introduced the two authors to each other, and he and B. Kitching allowed the field and laboratory work in Queensland to take place. Field work in South Australia was carried out with permit number A26006-1. No such permit was necessary in Queensland, as research there was not undertaken on protected grounds.

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Received August 31, 2016; revised and accepted November 14, 2016
Published online December 19, 2016

Supplementary file:
S1 (http://www.eje.cz/2016/077/S1.pdf). Data set with details for every specimen tested: Identifier, species, sex, wing surface, weight, date and location of capture, body temperature at takeoff, warming-up rate at 26°C and, if applicable, South Australian Museum voucher number. NA indicates missing data.