Variation of flight thorax temperature among Mediterranean butterflies

Gabriel Nève

Summary: Thorax temperatures necessary for flight behaviour was measured in 347 butterflies belonging to 40 species captured at two sites in Mediterranean France. There is a wide variation among species; the recorded minimum was 20.9°C in some *Pieris rapae* specimens, and the maximal was 39.9°C in an *Iphiclides podalirius* specimen. Median values ranged from 30.2°C for *Polyommatus icarus* and 31.5 for *Gonepteryx cleopatra* to 37.2°C for *Melitaea didyma* and 37.3°C for *Iphiclides podalirius*. Foraging habitat may be a key variable explaining this variation. The variation in flight temperature may be a variable linked with the range size of the relevant species, as the widespread *Pieris rapae* displays a higher flight thorax temperature variance than the Mediterranean species *E. crameri*. How robust these hypotheses are remains to be tested on a range of species and locations.

Key words: thorax, flight temperature, Lepidoptera, Lycaenidae, Papilionidae, Nymphalidae.

Introduction

Butterflies, as all living organisms, may be active between physiological limits to their body temperature (Somero *et al.* 1996). Their body temperature is the result of the interaction of ambient temperature, incoming solar radiation, heat radiation, and the inner production of heat by the body, mainly by thorax muscles (Kingsolver 1985a). In order to allow vigorous flight activity, the thorax temperature needs to be within the range of 33 to 38°C, while stressed individuals may fly at thorax temperatures from 28°C to 42°C (Kingsolver 1985a).

In a general context of global warming, the physiological adaptation to temperature range is a major factor in the understanding the adaptative range of species. The likely future range of species has been forecasted using climatic envelope models, based on their current distribution and climatic conditions (Settele *et al*. 2009). It is thus explicitly hypothesized that butterflies would not change their ecological requirements within the framework of the likely climatic change.

Thorax temperature has been shown to vary according to location and microhabitat (Wickman 2009). It seems that the thorax temperature necessary for flight activity varies mainly among genera rather than among congeneric species, as shown by lower temperatures in *Colias* than in *Pieris*, both within the Pieridae family (Dennis 1993). Studies of thermal biology of butterflies have focussed on the way their behaviour and wing pattern affect their thermoregulation (see reviews in Kingsolver 1985a and b). However, the thermal aspect of any given species' ecology, which is one component of its ecological requirements, is rarely documented. The aim of the present paper is to give some raw information on the recorded thorax temperature of a spectrum of species from the Mediterranean climatic zone of south France. I wish in particular to address the following two questions: (1) do butterflies flying in a given locality vary in their thorax temperature ? (2) How much does this temperature vary among individuals of a given species?

Material and methods

All butterflies were captured in the field in the south of France, either in Aubagne (43°18'N 5°33'E, 200 m altitude) or in Allauch (43°22'N 5°34'E, 330 m altitude). The specimens were then stored in glassine envelopes stored in a 11°C fridge and brought back to the laboratory. The same day or the next day, each butterfly was then placed under a 150 W neodymium daylight lamp in a 25°C environment. The thorax temperature was monitored continuously with a TESTO845® infrared thermometer, with the emissivity set as ε=0.95, inputting 1 data point per second. Individual behaviour was recorded during the warming up of each individual, especially the occurrence of basking with wings kept parallel or wide open. The

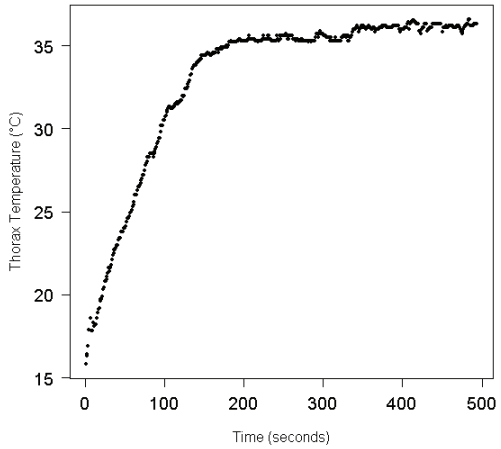

Fig. 1. Thorax temperature increase recorded on *Melitaea cinxia* specimen P523, on 5 May 2008. The recording started when the specimen was placed under the 150 W neodymium daylight lamp, and stopped when the individual took off, here after 494 seconds.

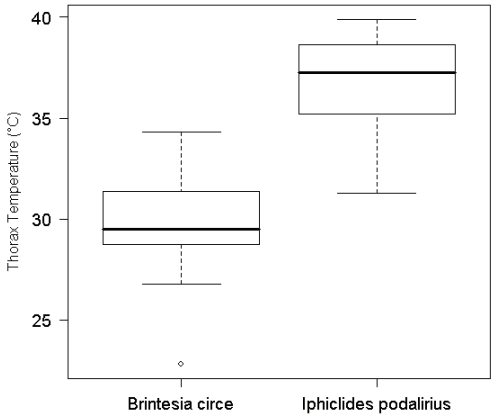

Fig. 2. Flight thorax temperature of *Brintesia circe* (n=12) and *Iphiclides podalirius* (n=8), the difference is highly significant.

temperature recording was stopped once the butterfly flew off. The last recorded temperature was then taken as the flight temperature of the tested individual. Individuals which were reluctant to fly after ca. two minutes at the plateau temperature were prodded to fly by a gentle tapping on the surface they were standing on. Data from individuals which did not take off were discarded. All individuals were then weighted, and later killed and prepared for morphology studies.

All together 347 individuals belonging to 40 species were tested between 28 June 2006 and 15 October 2008. Between 1 and 126 individual butterflies were tested for each species.

All statistical analyses and graphs were prepared using R (R Development Core Team 2004).

Results

When released under the 150 W lamp in the laboratory, most individuals showed a quickly increasing thorax temperature until a plateau is reached. The individuals then took off, and the recording was stopped (Fig.1).

All together, the recorded flight temperature ranged between 20.9°C (for a *Pieris rapae* specimen) and 39.9°C (for an *Iphiclides podalirius* specimen). The range of observed flight thorax temperatures varies among the surveyed species (Table 1). This temperature does not correlate with the mass of the individuals (Spearman rank correlation, rho=0.061, P=0.24). Even among the heaviest species, the flight thorax temperature may vary a lot, as between *Iphiclides podalirius* (median temperature: 37.3°C) and *Brintesia circe* (29.5 °C) (Wilcoxon test : W=3.5, p<0.001; Fig. 2).

More noticeably, the variance of the recorded temperature also varies. Between *Pieris rapae* and *Euchloe crameri*, the recorded median thorax flight temperature (33.7°C for both) does not vary (P=0.92), while the variance is much higher in *P. rapae* than in *E. crameri* ($F_{125,21}$=2.535, P=0.016, Fig. 3).

Dicussion

Butterflies within given climatic zone vary in their thorax flight temperature.

Preferred chosen habitat for foraging may be a ma-

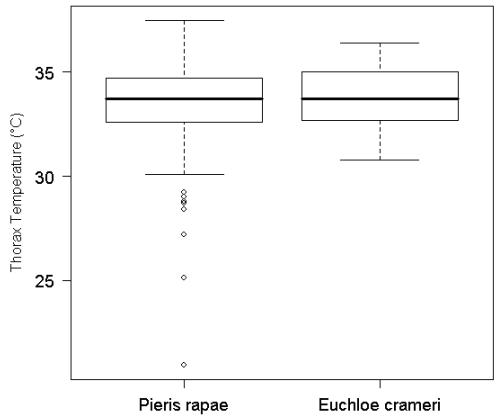

Fig. 3. Flight thorax temperature of *Pieris rapae* and *Euchloe crameri*, the difference in variance is highly significant.

Table 1. Recorded lowest, median and highest thorax temperatures of butterflies captured in south France. For up to three data available, all are mentioned; otherwise the minimum, median and maximum values are given.

Species	Recorded temperature			Number of tested individuals
	Min.	Median	Max.	
Hesperiidae				
Chalcarodius alceae (Esper, 1780)		33.6 ºC		1
Thymelicus sylvestris (Poda, 1761)		32.4 ºC		1
Ochlodes sylvanus (Esper, 1777)		28.5 ºC		1
Papilionidae				
Iphiclides podalirius (Linné, 1758)	31.3 ºC	37.3 ºC	39.9 ºC	8
Pieridae				
Pieris brassicae (Linné, 1758)	29.8 ºC	33.9 ºC	36.6 ºC	17
Pieris rapae (Linné, 1758)	20.9 ºC	33.7 ºC	37.5 ºC	126
Pieris napi (Linné, 1758)	31.7 ºC	33.7 ºC	35.5 ºC	10
Pontia daplidice (Linné, 1758)		36.5 ºC		1
Anthocharis cardamines (Linné, 1758)	28.9 ºC	34.1 ºC	37.1 ºC	8
Euchloe crameri Butler, 1869	30.8 ºC	33.7 ºC	36.3 ºC	26
Colias crocea (Fourcroy, 1785)	29.8 ºC	35.0 ºC	37.1 ºC	14
Gonepteryx cleopatra (Linné, 1767)	29.5 ºC	31.5 ºC	33.9 ºC	9
Lycaenidae				
Satyrium spini (Denis & Schiffermüller, 1775)		37.2 ºC		1
Lycaena phlaeas (Linné, 1761)	28.8 ºC		35.1 ºC	2
Lampides boeticus (Linné, 1767)	34.1 ºC		35.6 ºC	2
Glaucopsyche melanops (Boisduval, 1828)	34.4 ºC		38.3 ºC	2
Agrodiaetus dolus Hübner, 1823		33.5 ºC		
Polyommatus icarus (Rottembourg, 1775)	27.4 ºC	30.2 ºC	32.5 ºC	4
Lysandra coridon (Poda, 1761)	31.5 ºC		31.9 ºC	2
Aricia agestis (Denis & Schiffermüller, 1775)	30.4 ºC	31.7 ºC	34.9 ºC	6
Nymphalidae				
Limenitis reducta (Stautinger, 1901)		37.5 ºC		1
Vanessa cardui (Linné, 1758)	34.9 ºC		37.7 ºC	2
Melitaea cinxia (Linné, 1758)	25.7 ºC	36.3 ºC	39.0 ºC	13
Melitaea phoebe (Denis & Schiffermüller, 1775)	35.2 ºC		36.1 ºC	2
Melitaea didyma (Esper, 1778)	32.8 ºC	37.2 ºC	39.3 ºC	19
Mellicta parthenoides (Keferstein, 1851)	31.5 ºC	34.8 ºC	39.3 ºC	3
Argynnis paphia (Linné, 1758)	29.8 ºC	33.7 ºC	34.0 ºC	3
Argynnis niobe (Linné, 1758)		38.5 ºC		1
Brenthis daphne (Denis & Schiffermüller, 1775)	35.6 ºC		37.9 ºC	2
Lasiommata megera (Linné, 1758)	25.8 ºC	35.3 ºC	36.8 ºC	17
Coenonympha dorus (Esper, 1782)	31.9 ºC		35.8 ºC	2
Pyronia tithonus (Linné, 1771)	25.9 ºC		35.7 ºC	2
Pyronia cecilia (Vallantin, 1894)	30.2 ºC	33.0 ºC	35.3 ºC	4
Pyronia bathseba (Fabricius, 1793)	33.6 ºC		34.4 ºC	2
Maniola jurtina (Linné, 1758)	32.1 ºC	34.7 ºC	37.6 ºC	8
Melanargia galathea (Linné, 1758)	25.9 ºC	35.1 ºC	39.7 ºC	27
Melanargia occitanica (Esper, 1789)	34.0 ºC	34.7 ºC	39.9 ºC	3
Brintesia circe (Fabricius, 1775)	22.8 ºC	29.5 ºC	34.3 ºC	12
Hipparchia statilinus (Hufnagel, 1766)	29.2 ºC	29.9 ºC	32.4 ºC	4
Hipparchia fagi (Scopoli, 1763)		29.8 ºC		1

jor factor, as the forest species *B. circe* displays a chosen thoracic temperature lower than the open habitat species *I. podalirius*.

The air temperature at which the different species may fly varies: *Papilio polyxenes* Fabricius, 1775 flies at air temperatures from 19°C to 30°C (Rawlins 1980), while the montane *Colias nastes* (Boisduval 1832) flies at air temperatures of 6°C to 20°C (Roland 1982). These two species have similar ranges of body temperatures with thorax temperatures of ca. 35°C necessary for vigorous flight. The difference was attributed to differences in thermoregulatory mechanisms (Kingsolver 1985a). The data presented here suggest that on top of these physiological and physical differences, the requested temperature varies among butterfly species.

Thorax flight temperature seems thus to be a variable to be taken into account in the thermal ecology of butterflies.

Two Pierid species, *Pieris rapae* and *Euchloe crameri*, have similar flight thorax temperatures, but highly different variances. The variation in thorax flight temperature among *P. rapae* specimens was observed as being far larger than among *E. crameri* ones. This suggests that the range of latitudes, and hence of thermal conditions, may vary with the degree of variation of flight thorax temperatures. Of course such a hypothesis would need to be tested further across the range of the relevant species, and with other species pairs of different range sizes.

Conclusions

The data collected at two sites in Mediterranean France show that the minimal thorax temperature necessary for flight varies widely among butterfly species, from 20.9°C in some *P. rapae* to 35.6°C in *Brenthis daphne*. Foraging habitat may be a key variable explaining this variation, and a widespread species such as *Pieris rapae* displays a higher flight thorax temperature variance than the Mediterranean species *Euchloe crameri*. How robust these hypotheses are remains to be tested on a range of species and locations.

Acknowledgements

This study could not have taken place without the help of numerous students and colleagues. I wish in particular to thank Alain Thiéry, Emese Meglécz and Yvan Perez for their valuable help. The then students Grégory Charre, Judith Mazur, Elsa Gourlaouen, Anthony Luciano and Hélène Prouillet-Leplat helped both in the field and in the laboratory.

References

Dennis R.L.H. (1993) Butterflies and climate change. Manchester University Press, Manchester.

Kingsolver J.G. (1985a) Butterfly thermoregulation, organismic mechanisms and population consequences. *Journal of Research on the Lepidoptera* 24: 1-20.

Kingsolver J.G. (1985b) Butterfly engineering. *Scientific American* 253(2): 106-113.

R Development Core Team (2004) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from http://www.R-project.org.

Rawlins J.E. (1980) Thermoregulation by the black swallowtail butterfly *Papilio polyxenes* (Lepidoptera, Papilionidae). *Ecology* 61: 345-357.

Roland J. (1982) Melanism and diel activity of alpine *Colias* (Lepidoptera: Pieridae). *Oecologia* 53: 214-221.

Settele J., Kudrna O., Harpke A., Kühn I., van Swaay C., Verovnik R., Warren M., Wiemers M., Hanspach J., Hickler T., Kühn E., van Halder I., Veling K., Vliegenthart A., Wynhoff I. & Schweiger O. (2008) Climatic Risk Atlas of European Butterflies. Pensoft, Sofia & Moscow.

Somero G.N., Dahlhoff E., Lin J.J. (1996) Stenotherms and eurytherms: mechanisms establishing thermal optima and tolerance ranges, pp: 53-78. In: Johnston I.A., Bennett A.F. (eds.). Animals and temperature : Phenotypic and Evolutionary Adaptation, Cambridge University Press, Cambridge.

Wickman P.O. (2009) Thermoregulation and habitat use in butterflies, pp: 55-61. In: Settele J., Shreeve T., Konvička M. & Van Dyck H. (eds.): Ecology of Butterflies in Europe, Cambridge University Press, Cambridge.

Gabriel Nève
Aix-Marseille Université, UMR CNRS
IRD 6116 – IMEP,
Case 36, 3 place Victor Hugo, 13331
Marseille Cedex 3, France.
gabriel.neve@univ-provence.fr

Received: 25.05.2009
Accepted: 21.04.2010
Printed: 20.12.2010