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Thorax temperature of butterflies (Papilionoidea) in natural habitats of Austria

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Abstract: Thorax temperature of butterflies (Papilionoidea) in natural habitats of Austria. Body temperature of butterflies mainly depends on abiotic factors and is relevant for metabolic processes, flight behaviour, and the distribution in various altitudes. We developed a technique for contactless measurement of body temperature of butterflies in the field using a modified infrared thermometer. We caught 522 butterflies from 31 species in lowland and alpine habitats of Austria during flight, and their thorax temperature was immediately measured. The thoracic temperatures ranged from 14.5 °C in alpine Satyrinae species to 39.9 °C in a lowland species. Body temperatures (mean 28.9 ± 6.1 °C) showed highly significant, positive correlation ($r = 0.89$, $p < 0.001$) with air temperatures (mean 21.9 ± 7.6 °C). Small alpine species had lowest, but highly variable thorax temperatures while butterflies of lowland areas had higher and lower variable temperature. The mean thoracic temperature was 7.0 ± 3.5 °C higher than air temperature with a maximal difference of 20.2 °C in an alpine species. In hot lowland areas some butterflies had a body temperature of up to 3 °C below air temperature. *Pieris rapae* were active in all habitats showing body temperature tolerance from 34.2 °C in lowland to only 20.8 °C in the alpine area. These data allow conclusions on upper and lower temperature limits for flight. The applied new non-invasive method turned out to be a simple and reliable technique to measure body temperature of butterflies in the field that opens new opportunities for understanding species-specific natural histories.

Keywords: body temperature, flight activity, infrared thermometer, Lepidoptera, insects

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Introduction

The body temperature of insects such as butterflies is strongly dependent on the air temperature (e.g., May 1997, Kingsolver 1985a, Heinrich 1995, Kleckova et al. 2014). In insects and other ectothermic organisms, most metabolic processes are controlled by the body temperature which is crucially influenced by the ambient temperature. The mechanisms and physiological processes of heat exchange between insects and their environment are reviewed in Lahondère (2023). Like in many other insects, such as dragonflies (May 1976, 1995), scarabid beetles (Verdú 2012) or cicadas (Sanborn 2000), various butterflies can regulate their body temperature by different mechanisms: They may gain heat by basking behavior at warm, sunny spots in their habitats and by muscle activity, while heat loss mainly occurs through body irradiance, fluid cooling, and air convection around the body (Wickman 2009, Lahondère 2023). Behavioral and physiological thermoregulation (e.g., shivering) and microhabitat choice enable butterflies to achieve the physiological conditions required, for example, to start flight (Mattila 2015, Nève & Hall 2016). In addition, heat avoiding behavior, specializations of circulatory system and/or special wing scale nanostructure can remove excess heat (Kingsolver 1985a, Shanks et al. 2015, Bladon et al. 2020, Tsai et al. 2020, Zischka et al. 2024). All thermoregulatory strategies allow adjustment of specific body temperature in various habitats that is needed for activity, such as flight (Kleckova & Klecka 2016, Bladon et al. 2020). The most important behavioral adaptation is basking, in which the temperature in the wing muscles is increased by "sunbathing". This involves positioning the wings, which serve as absorbing radiating surfaces, at specific angles to the sun that leads to an increase in body temperature (Kingsolver 1985a, b, Kleckova & Klecka 2016, Akand et al. 2018). Butterflies with a lower body mass warm up faster than butterflies with a larger body mass, but they also lose temperature faster through convection currents in flight (Heinrich 1986, Nève & Hall 2016).

Studies on wing melanization in butterflies, such as those by Watt (1969), Kingsolver (1985b), and Gautam & Kunte (2020) have examined how darker wings can lead to higher body temperatures during basking. Watt (1969) found significant thermoregulatory effects of wing melanisation in *Colias* butterflies, correlating darker colours with higher temperatures in certain wing veins. Conversely, in *Pieris* butterflies, Kingsolver (1985b) found the opposite effect. Shanks et al. (2015) presents a possible influencing factor: The white structural protein pterin, which is present in white or yellow wing scales of the butterflies, contributes to radiation absorption. Recent research by Gautam & Kunte (2020) underscores the impact of wing melanization on thermoregulation but notes that environmental factors like altitude and season may play significant roles.

Tsai et al. (2020) confirmed that butterfly body temperatures are extremely heterogeneous and variable but found that thorax temperatures remained relatively homogeneous, based on thermal imaging measurements during experiments. The relatively stable thoracic temperature could be a possible condition for maintaining the ability to fly, even when other regions of the body reach minimum or maximum temperature values. Other body parts such as the head or abdomen are considered to be of less importance for thermoregulation and hardly differ from the ambient air temperature (Kingsolver 1985a, Schmitz & Wasserthal 1993). Measurement of thoracic flight temperature has been assessed under semi-natural condition or in lab using infra-red thermometers as a contactless method in butterflies as a proxy for internal body temperature (Mattila 2015, Nève & Hall 2016).

In addition, there are various attempts to measure butterfly body temperature in the field and to study relationships to environmental factors by measuring thorax temperatures. Some used invasive measuring devices like micro-needles, others used contact thermometers (Kleckova et al. 2014, Kleckova & Klecka 2016, Bladon et al. 2020, Ashe-Jepson et al. 2023). Contactless measuring devices have been rarely used in insects under natural conditions. To date, contactless infrared thermometers were often used for detection of fever in humans (Bleckwenn 2020), but likewise appear to be suitable for fast and simple temperature assessments of insects.

The focus of the present study is the measurement of thorax temperatures of various butterfly species caught during flight in the field. The aim of the study is to gain field data about the body temperature of different Austrian butterflies under natural condition in various habitats, and to establish a new, non-invasive and contactless method for temperature measurements in insects.

Material and methods

Study areas

Butterflies were caught and their thorax temperature was measured on five days in July and August 2020 between 9:15 am and 5:15 pm in the field. The study was carried out at three areas with different altitudes in Austria, each with three sampling sites (Tab. 1). All areas were known to be rich in butterflies from field courses and previous studies (Hickel et al. 2016, Savchenko et al. 2018, Puhm 2020, Steiner 2020). Each site had

Tab. 1: Areas in Austria where thorax temperature was measured in butterflies. Suitable weather conditions (Van Swaay et al. 2012, Hickel et al. 2016) were present with one indicated exception; cloudiness estimated according to Hickel et al. 2016; 0: cloudless, 1: less than 20% cloud cover, 2: between 20% and 50% cloud cover, 3: about 50% cloud cover or complete thin cover, 4: more than 50% cloud cover, 5: cloudy.

Study area with 3 sites each	Coordinates	Altitude asl	Plant community	Date	Estimated cloudiness
Zemmgrund 1 Zillertal, Tyrol	N 47° 1' 19.10208" O 11° 48' 50.1084"	2005 m	Alpine grassland/turf over metamorphic silicate rocks	19.07.2020	2 – 5*
Zemmgrund 2 Zillertal, Tyrol	N 47° 1' 16.89636" O 11° 48' 48.61044"	1998 m	Alpine grassland/turf over metamorphic silicate rocks	20.07.2020	0
Zemmgrund 3 Zillertal, Tyrol	N 47° 1' 19.66764" O 11° 48' 26.4564"	1880 m	Alpine grassland/turf over metamorphic silicate rocks	20.07.2020	0 – 1
Herrenholz 1 Bisamberg, Vienna	N 48° 18' 53.97804" O 16° 24' 17.379"	225 m	Clearing with Pannonian gravel meadows	27.07.2020	0
Herrenholz 2 Bisamberg, Vienna	N 48° 18' 56.12544" O 16° 24' 18.52452"	232 m	Clearing with Pannonian gravel meadow	27.07.2020	1
Herrenholz 3 Bisamberg, Vienna	N 48° 18' 58.3092" O 16° 24' 19.12932"	240 m	Clearing with Pannonian gravel meadow	27.07.2020	0
Verschiebebahnhof 1 Breitenlee, Vienna	N 48° 15' 37.3284" O 16° 29' 37.608"	156 m	Ruderal area on former railroad station site	05.07.2020	0
Verschiebebahnhof 2 Breitenlee, Vienna	N 48° 15' 40.9788" O 16° 29' 33.3024"	156 m	Ruderal area on former railroad station site	02.08.2020	0–3
Verschiebebahnhof 3 Breitenlee, Vienna	N 48° 15' 37.4904" O16° 29' 37.77"	156 m	Ruderal area on former railroad station site	02.08.2020	4

* Air temperature dropped below 10 °C and data sampling was interrupted by rain in the afternoon.

a size of 1000-4000 m². They were characterized by sun exposure, low shading by the surrounding vegetation and a rich supply of flowers. Another benefit of these sampling sites was that they provided both rather cold (alpine sites) and hot temperatures (lowland sites), which gave insights into butterflies' thorax temperature at the potential limits of their flight activity. The coordinates of the study sites and the altitude above sea level were recorded on a smartphone using the Google Maps app. All coordinates of the study sites, their altitude, the sampling time, the predominant plant communities, and the degree of cloud cover on the sampling days are given in Tab. 1.

Temperature measuring device

Temperature values were measured using a Testo 845 infrared near-field thermometer (Testo Industrial Services GmbH, Vienna, Austria), which allowed point measurements of the surface temperature from a minimal distance of 10 cm and a minimal diameter of one millimeter. The accuracy of measurements were ±0.75 °C at +20.0 °C to +99.9 °C, and ± 1.5 °C at -20 °C to +19.9 °C (Testo Industrial Services GmbH, Vienna, Austria).

Prior to the field measurements, the Testo 845 was tested under laboratory conditions at the Department of Evolutionary Biology, University of Vienna. (1) To determine the accuracy of the measurements, temperatures of dead butterflies were measured and compared using other measuring devices, such as an analog alcohol thermometer, a digital thermometer equipped with a Testo 440 sensor, and the Testo 845 infrared near-field measuring device. The thorax temperature of the butterflies was measured under three conditions (room temperature, heated by incandescent lamps, cooled in a refrigerator). Several dead individuals of *Heliconius melpomene* (Linnaeus, 1758) (Nymphalidae) from the rearing facility at the University of Vienna were measured for calibration. The thorax temperature was measured dorsally on the thorax next to the wings. At room temperature, 15 measurements with the Testo 845 resulted in a mean thorax temperature value of 25.30 °C ± 0.3 °C SD. In the same test setting, the Testo 440 sensor measured a mean thorax temperature of 25.27 °C ± 0.31 °C SD. (2) The temperature of the dead *H. melpomene* specimens when heated or cooled were measured. Three individuals were placed under a light bulb and illuminated from above or put in the refrigerator. Every five minutes, all three butterflies were measured at approximately the same measuring distance. The experiments showed that the specimens became continuously warmer and cooler, respectively, in a reproducible manner. (3) To practice measuring living butterflies with the Testo 845 infrared near-field device, several lab-reared individuals of *Antherina suraca* (Boisduval, 1833) (Saturniidae) and *Vanessa cardui* (Linnaeus, 1758) (Nymphalidae) were used under laboratory conditions. The reliability and repeatability of the measurements using Testo 845 were tested by S.G and H.K.

We modified the Testo 845 infrared near-field thermometer to allow exact measurement in a small area of the thorax of a living butterfly in a fixed, standardized distance from the side. For this purpose, a spacer consisting of a thick, flexible wire that protruded from the near-field thermometer, was attached to the top of the thermometer. A drilled clothespin was attached to the wire, fitted with cardboard plates on the inside to provide flat surfaces between which the butterfly wings were fixed without damaging them (Fig. 1).

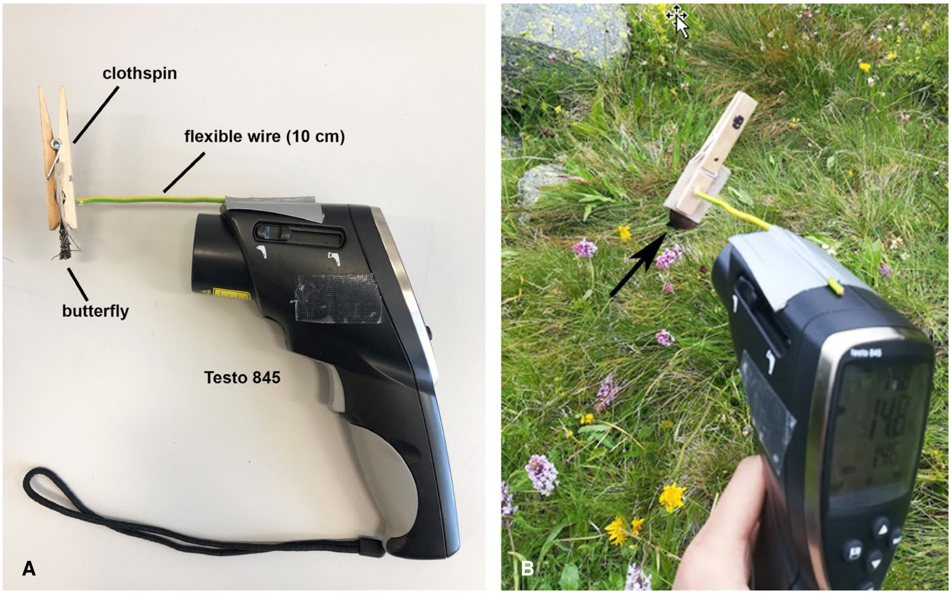

Fig. 1: A. Near-field infrared thermometer Testo 845 equipped with a 10 cm long wire as spacer to exactly adjust a butterfly, which is fixed in a clothespin. B. Modified Testo 845 during field work; external thorax temperature is measured on the butterfly fixed in front (arrow).

By adjusting the flexible wire, the fixed insects were positioned so that the laser measuring point (1 mm in diameter at approximately 10 cm distance) was aimed precisely at the lateral side of the butterfly's thorax. The temperature was recorded and displayed digitally of the near-field thermometer in degree Celsius with two decimal places. This simple modification allowed constant distance during measurements and enabled precise positioning of the butterfly's thorax. In addition, an analog alcohol thermometer with accuracy of 0.5 °C was used to measure the air temperature at hip height at the study sites.

Measurement procedure

The investigations were carried out according to the same procedure at all sites. Three persons were involved in all measurements; each person carried out a specific activity. The division of activities ensured that the measurement procedure was carried out quickly and that any measurement errors and deviations due to personal differences in procedure were kept to a minimum. The measurement protocol consisted of (1) catching the butterflies, (2) temperature measurement and (3) wing size measurement. The abiotic factors were recorded by the measuring persons. A digital clock was used to record the daytime.

Only flying butterflies were caught using a butterfly net. Some small species of Lycaenidae were excluded since our preliminary field tests indicated that small butterflies quickly detached from the measuring apparatus, and it was therefore not possible to guarantee reliable temperature measurements.

For the measurement, the captured butterflies were immediately removed from the net and fixed at the wing tips between the cardboard plates of the clothespin. The wire of the apparatus was then bent so that the infrared point aimed precisely at the lateral side of the thorax. Approximately 30 seconds elapsed between capture and measurement of the thorax temperature. Subsequently, the length of the forewing was measured from wing joint to distal end using an analog caliper (Helios Digi-Met 1220; 0.01 mm measuring accuracy) as an indicator of butterfly size (Krenn & Penz 1998). The measurements were taken to one decimal place in the millimeter range. To avoid pseudo replication, a point with a felt-tip marker was placed on the underside of the left hind wing and recaptured individuals were excluded from a second measurement. If necessary, the species was identified afterwards using an identification key (Stettmer et al. 2011). Finally, each butterfly was released.

Abiotic factors

The abiotic factors (i.e., temperature, cloud cover, rain, wind) were recorded every 15 to 30 minutes during sampling. Data was collected on five sunny days between 9:15 am and 5:10 pm. On one day it started to rain in the afternoon after temperature dropped below 10 °C and the sky was completely overcast. The degree of cloud cover was estimated on a 6-level scale (0: cloudless, 1: less than 20% cloud cover, 2: between 20% and 50% cloud cover, 3: about 50% cloud cover, 4: more than 50% cloud cover, 5: cloudy) (Hickel et al. 2016).

The data were analyzed using the Microsoft Office Excel (2010) spreadsheet program. All measured data such as air temperature, thorax temperature and forewing length as a measure of butterfly size were analyzed. Linear regressions were performed for the underlying variables (air temperature, thorax temperature, wing length). For the thorax temperature of the different species and the size of the butterflies, skewness and kurtosis were calculated to test whether the data are normally distributed. The Microsoft Excel formulas “SKEW” (skewness) and “KURT” (kurtosis) were used and the approximate standard errors (S.E.), i.e., S.E. Schiefe=$\sqrt{(n/6)}$ and S.E. Kurtosis=$\sqrt{(n/24)}$) were calculated manually (Urban & Mayerl 2018). For both parameters, the ratio between the skewness or kurtosis value and the corresponding standard error was smaller than the reference range ±1.96 and therefore a normal distribution was assumed (Urban & Mayerl 2018).

Pearson correlations were established for all tests comparing normally distributed variables (Untersteiner 2007). Pearson’s correlation coefficient r was specified for all correlations and a significance test was carried out on the basis of the two-sided t-distribution. The significance σ is symbolized next to r in the scatter plots. The symbolization of the significance level is indicated with ns (not significant) for $p > 0.05$, with * (significant) for $p \leq 0.05$, ** (very significant) for $p \leq 0.01$ and with *** (highly significant) for $p \leq 0.001$. A regression line was inserted into the scatter plots to show possible linear dependencies (Untersteiner 2007).

Results

Collected butterflies

A total of 522 butterfly individuals were caught and measured at the nine study sites in three areas of Austria (Tab. 1). The butterflies belonged to 31 species from Papilionidae, Pieridae, Lycaenidae, and Nymphalidae. The number of individuals caught per species varied greatly ranging from 1 to 82 individuals per species (Tab. 2). Tab. 2 presents an overview of the results of all butterfly individuals on a species level and includes mean values and standard deviations for the measured thorax temperature and wing length, as well as minimal and maximal values of the thorax temperature.

Tab. 2: Number of all butterflies measured (n = 522), listed by family and species (in alphabetical order). The study areas include the alpine sites in Zemmgrund (Zillertal Alps) (A), Herrenholz site (H) in Vienna, and Verschiebebahnhof (V); mean values of Thorax temperature ($\overline{T}$) are given in °C; mean values $\overline{L}$ of length of forewing are given in mm. If more than one individual per species were caught, the minimal and maximal values (Min – Max) of thorax temperature are indicated.

Taxon	n	Area	$\overline{T}$ ± *SD*	$\overline{L}$ ± *SD*	Min – Max *T* °C
Papilionidae					
Iphiclides podalirius (Linnaeus, 1758)	4	V, H	35.8 ± 0.96	41.8 ± 1.71	34.8 – 37.1
Parnassius sacerdo Stichel, 1906 = *P. phoebus*	17	A	27.5 ± 3.64	34.1 ± 1.74	17.3 – 33.2
Pieridae					
Colias alfacariensis (Ribbe, 1905)	3	V	34.8 ± 2.68	24.3 ± 1.52	32.6 – 37.8
Colias hyale (Linnaeus, 1758)	1	V	36.9	29.0	
Colias phicomone (Esper, 1780)	18	A	25.6 ± 2.81	24.0 ± 2.10	21.1 – 29.9
Gonepteryx rhamni (Linnaeus, 1758)	1	H	31.0	29.0	
Lepidea sp. (Billberg, 1820)	9	V	32.2 ± 0.86	21.3 ± 1.12	31 – 33.6
Pieris napi (Linnaeus, 1758)	14	V, H	31.4 ± 2.3	25.7 ± 2.08	27.1 – 35.5
Pieris rapae (Linnaeus, 1758)	48	A, V, H	30.1 ± 2.99	25.5 ± 2.29	20.8 – 34.8
Pontia edusa (Fabricius, 1777)	2	V, H	33.3 ± 0.92	26 ± 5.66	32.7 – 34.0
Lycaenidae					
*Maculinea arion (*Linnaeus*, 1758)*	1	A	22.6	19.0	
Lysandra coridon (Poda, 1761)	36	V	35.3 ± 1.26	18.7 ± 1.63	31.5 – 38.0
*Cyaniris semiargus (*Rottemburg*, 1775)*	1	A	16.8	16.0	
Nymphalidae					
Argynnis paphia (Linnaeus, 1758)	39	V, H	33.5 ± 1.68	33.7 ± 1.95	29.5 – 37.7
Boloria euphrosyne (Linnaeus, 1758)	4	A	23.2 ± 4.08	21.5 ± 1.68	19.1 – 28.3
Boloria pales ([Denis & Schiffermüller], 1775)	12	A	23.8 ± 3.65	20.0 ± 2.94	18.7 – 31.2
Boloria selene ([Denis & Schiffermüller], 1775)	19	A	21.9 ± 2.62	19.5 ± 1.30	16.6 – 27.0
Brintesia circe (Fabricius, 1775)	1	V	37.9	36.0	
Coenonympha gardetta (Prunner, 1798)	56	A	22.5 ± 3.89	15.5 ± 1.68	14.7 – 32.7
Coenonympha pamphilus (Linnaeus, 1758)	1	H	36.6	24.0	
Erebia epiphron (Knoch, 1783)	2	A	20.0 ± 3.32	16.5 ± 0.71	17.6 – 22.3
Erebia eriphyle (Freyer, 1836)	25	A	20.8 ± 3.12	16.6 ± 1.29	14.5 – 26.3
Erebia euryale (Esper, 1805)	5	A	26.6 ± 1.27	20.8 ± 3.42	24.8 – 28.3

Taxon	n	Area	$\bar{T}$ ± *SD*	$\bar{L}$ ± *SD*	Min – Max *T* °C
Erebia manto ([Denis & Schiffermüller], 1775)	10	A	26.3 ± 2.47	20.5 ± 2.15	22.3 – 30.4
Erebia medusa ([Denis & Schiffermüller], 1775)	3	A	22.9 ± 1.95	20.7 ± 2.08	21 – 24.9
Erebia pharte (Hübner, 1804)	64	A	22.7 ± 3.59	18.1 ± 1.79	15.1 – 31.7
Issoria lathonia (Linnaeus, 1758)	2	V, H	33.6 ± 4.38	23.0	30.5 – 36.7
Lasiommata megera (Linnaeus, 1767)	1	H	30.2	22.0	
Maniola jurtina (Linnaeus, 1758)	82	V, H	34.2 ± 2.08	24.9 ± 2.11	29.8 – 38.9
Melanargia galathea (Linnaeus, 1758)	23	V	34.5 ± 2.03	29.2 ± 1.78	30.7 – 39.2
Minois dryas (Scopoli, 1763)	18	V, H	36.9 ± 1.52	28.1 ± 2.69	34.1 – 39.9
Total	**522**	**A, V, H**	**28.9 ± 6.13**	**23.1 ± 6.08**	**14.5 – 39.9**

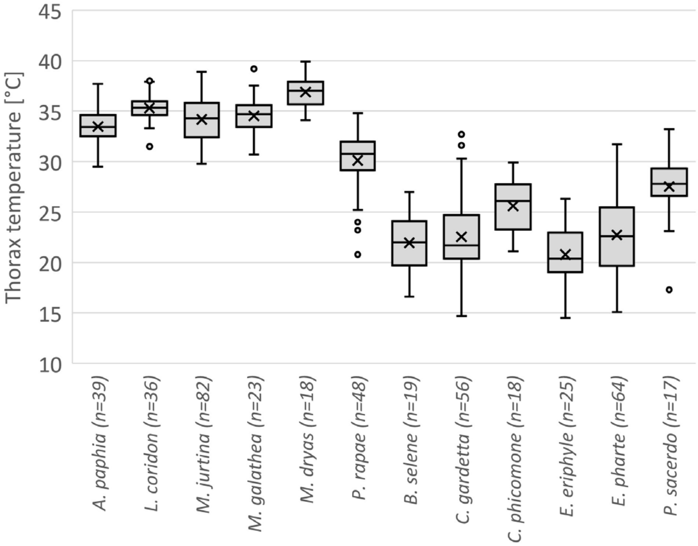

Fig. 2: Thorax temperature [°C] of butterfly species sampled with n ≥ 15. The five species on the left side of the chart, i.e., *A. paphia, L. coridon, M. jurtina, M. galathea,* and *M. dryas* were restricted to the lowland study areas, while *P. rapea* occurred in all areas. The species on the right side, i.e., *B. selene, C. gardetta*, *C. phicomone*, *E. eriphyle*, *E. pharte,* and *P. sacerdos* were found in the alpine capture sites.

Thorax temperature

The measured thorax temperatures of active butterflies ranged from 14.5 °C to 39.9 °C. In the butterfly species with three or more measured individuals (21 species), the mean thorax temperature was between 20.8 °C ± 3.12 °C for the alpine *Erebia eriphyle* and 36.9 °C ± 1.52 °C for *Minois dryas* caught at the lowland sites. Fig. 2 shows boxplots of the measured temperatures for those 12 species, where more than 15 individuals were caught.

As Fig. 2 illustrates, individuals of alpine *Coenonympha gardetta* butterflies exhibited the greatest temperature range from 14.7 °C to 32.7 °C, whereas the smallest range (31.5 °C-38.0 °C) was found in the lowland lycaenid species *Lysandra coridon*. In general, butterfly

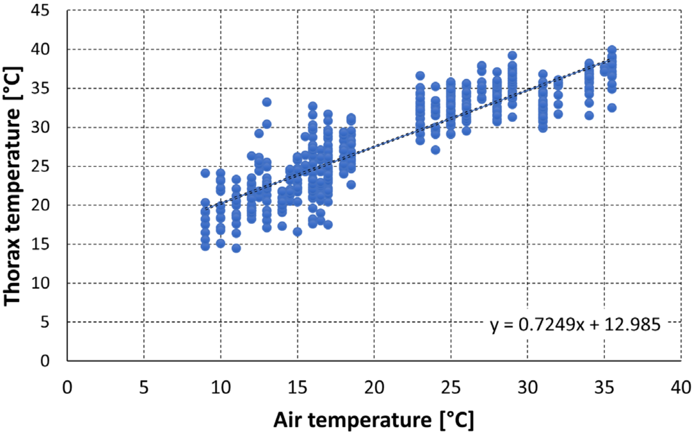

Fig. 3: Active butterflies from 31 European species show highly significant correlation of thorax temperature and air temperature in various natural habitats (n = 522). The correlation between forewing length and the thorax temperature was highly significant (r = 0.89, p < 0.001).

individuals from lowland areas had a higher thorax temperature (i.e., minimal value 27.1 °C in one specimen of *Pieris napi* to maximal temperature of 39.9 °C in one *M. dryas*) than species in the alpine area where temperature values ranged from 14.5 °C in *Erebia eriphyle* to 33.2 °C in *Parnassuis sacerdos*. These differences were also related to the different air temperatures at these sites (see below).

Pieris rapae was the only species that occurred at all sites and showed a mean thorax temperature of 30.1 °C ± 2.99 °C and an overall span from 20.8 °C to 34.8 °C in the individuals of the various habitats (Fig. 2). The largest variation of temperature within a species was found in small, alpine butterflies such as *C. gardetta* and *Erebia pharte*. Within these species, the lowest measured thorax temperature was less than half of the highest measured thorax temperature.

Correlation of thorax temperature with air temperature

All measured thorax temperatures (n = 522) and air temperature values were strongly correlated (r = 0.89, p ≤ 0.001) (Fig. 3). The highest air temperature at which a flying butterfly could be collected was 35.5 °C at the lowland Verschiebebahnhof site. The lowest air temperature at which butterflies could be caught was 9.0 °C at the alpine Zemmgrund site. The different climate in lowland and alpine sites provided insights into how thorax temperature and air temperature differ, particularly at ambient temperatures at the lower and upper boundaries of flight activity.

In order to analyse species-specific differences, the correlation of thorax temperatures and air temperature was calculated for those eleven species with n ≥ 30. Significant correlations between the air temperature and the thorax temperature were found for all six species. In all six species, the body and air temperatures correlated moderately (0.5 < r < 0.75) to strongly (0.75 > r). The strength of the correlation varied between the species: *Argynnis paphia* (r = 0.56***), *C. gardetta* (r = 0.62***), *E. pharte* (r = 0,67***), *Maniola jurtina* (r = 0.61***), *P. rapae* (r = 0.77***), *L. coridon* (r = 0.51**).

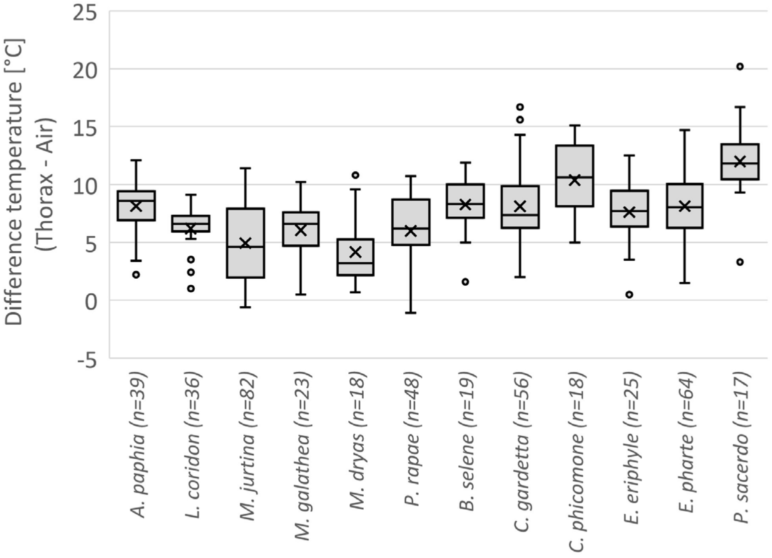

Fig. 4: Difference between thorax temperature and air temperature [°C] for all species sampled with n ≥ 15 individuals. Body temperature is higher than air temperature except in a few individuals in lowland areas. The five species (*A. paphia, L. coridon, M. jurtina, M. galathea, M. dryas*) were restricted to the lowland; *P. rapae* occurred in all study sites while six species *(B. selene, C. gardetta, C. phicomone, E. eriphyle, E. pharte,* and *P. sacerdos)* were found in the alpine sites.

Differences between air temperature and thorax temperature

The mean value of the thorax temperature of all butterflies (n = 522) was 6.96 °C ± 3.45 °C higher than the air temperature in the habitats. The biggest difference between thorax temperature and air temperature was observed in one individual of the alpine species *P. sacerdos* having a thorax temperature of 32.2 °C, which was 20.2 °C above the air temperature of only 12 °C. In total, only 10 individuals out of 522 butterflies showed lower body temperatures than the air temperatures at the capture sites (Herrenholz and Verschiebebahnhof). These individuals belonged to *Leptidea* sp., *P. napi*, *P. rapae* and *M. jurtina*, with nine individuals out of ten belonging to the Pieridea family. One *Leptidea* butterfly even had a thorax temperature of 3 °C below ambient temperature of 35.5 °C.

To analyse the species-specific relationship between the measured thorax temperatures and the respective air temperatures, the differences between these two values were calculated for each of the species with n ≥ 15. Fig. 4 illustrates the differences between thorax temperature and air temperature for these species, and it highlights that the thorax temperature is higher than the air temperature for most of the butterflies measured. Fig. 4 also underscores that the ranges vary between the species, with some species (e.g., *P. sacerdo*) having rather large differences to the air temperature. *Lysandra coridon* had the smallest variation of temperature difference, which is potentially connected to the high air temperatures on the collection day.

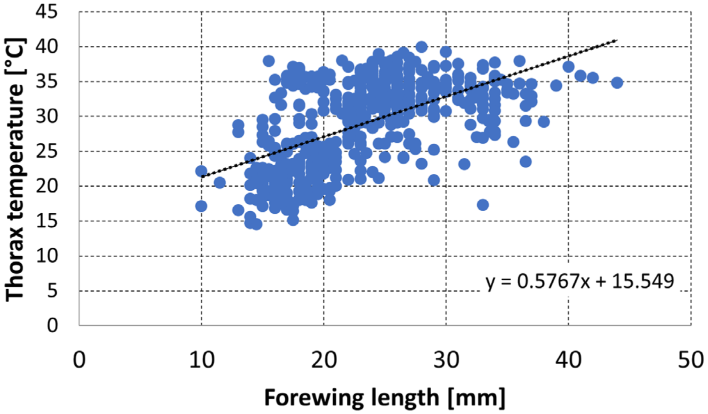

Fig. 5: Thorax temperature of butterflies (n = 522) correlated highly significantly with wing length (r = 0.57, p < 0.001). Smaller butterflies (wing length < 20 mm) show higher variation in thorax temperature than larger species (> 20 mm wing length).

Correlation of body size with thorax temperate and air temperature

The thorax temperature correlated highly significantly (r = 0.57, p < 0.001) with the length of the forewing (n = 522), which was taken as a measure of body size (Fig. 5). The thorax temperature was higher in larger butterflies; small butterflies (< 20 mm) showed the highest variation in thorax temperature while large butterflies (> 30 mm) showed the lowest variation. It is concluded that the greatest influence of ambient temperature on body temperature occurred in small, alpine species, such as the alpine Satyrinae *C. gardetta*, *E. eriphyle*, and *E. pharte*.

Thorax temperature of *Pieris rapae* in various habitats

Pieris rapae (n = 48) was the only species that occurred at all three study areas at different altitudes. To compare the thorax temperature with the air temperature and body size, the data of this species were analysed separately (Tab. 3). In total, *P. rapae* had a mean body temperature of 30.1 °C ± 2.99° C ranging from 20.8 °C to 34.8 °C in the various individuals of the studied habitats (Tab. 2, Fig. 2). The lowest thorax temperatures were measured at the alpine sites with a mean of 24.9 °C ± 1.9 °C, whereas the highest temperatures were recorded at the Verschiebebahnhof sites with a mean of 31.8 °C ± 1.4 °C. Again, the thorax temperatures corresponded with the ambient temperatures of the respective habitats, although air temperature showed less variation than the individual thorax temperatures. The lowest air temperature at which a *P. rapae* individual could be caught was 12 °C. This butterfly displayed a thorax temperature of 20.8 °C; while at the highest air temperature of 34 °C, one representative of *P. rapae* had a thorax temperature reaching 34.2 °C. Three individuals of *P. rapae* had a lower thorax temperature than the 30 °C air temperature (Tab. 3).

The differences between the *P. rapae* thorax temperatures and the air temperature were greatest at the alpine sites where the mean body temperature was 8.1 °C ± 1.1 °C warmer than the ambient temperature. In contrast, *P. rapae* butterflies were only 0.8 °C ± 1.6 °C

Tab. 3: Thorax temperatures and fore wing lengths of *Pieris rapae* in the three study areas (V, H, Z) compared to air temperature and wing length in respective habitat. Thorax temperature was higher than air temperature in all, but three individuals collected at air temperature >30 °C (indicated in bold letters); Diff. to air = difference between thorax and air temperature. The last two rows show the mean values ± standard deviations for each site.

Study area											
Verschiebebahnhof (V) 156 m asl				**Herrenholz (H)** 225–240 m asl				**Zemmgrund (Z)** 1880–2050 m asl.			
Thorax [°C]	Air [°C]	Diff. to air [°C]	Wing [mm]	Thorax [°C]	Air [°C]	Diff.to air [°C]	Wing [mm]	Thorax [°C]	Air [°C]	Diff. to air [°C]	Wing [mm]
29.9	31.0	**-1.1**	29.0	29.1	25.0	4.1	23.5	23.2	16.0	7.2	28.0
30.1	31.0	**-0.9**	29.0	29.1	24.0	5.1	24.5	20.8	12.0	8.8	29.0
30.8	31.0	**-0.2**	28.0	29.1	23.0	6.1	26.0	24.0	18.0	6.0	26.5
31.3	31.0	0.3	28.0	29.2	25.0	4.2	22.0	25.2	18.0	7.2	29.0
32.5	31.0	1.5	28.0	29.2	23.0	6.2	26.5	25.3	16.0	9.3	27.5
32.8	31.0	1.8	26.0	30.0	24.0	6.0	23.4	26.1	17.0	9.1	24.5
32.9	31.0	1.9	25.0	30.2	25.0	5.2	22.0	26.1	18.0	8.1	27.0
32.1	28.0	4.1	24.0	30.3	23.0	7.3	25.0	26.1	18.0	8.1	27.5
34.2	34.0	0.2	26.0	30.3	23.0	7.3	26.0	27.0	18.0	9.0	26.0
				30.4	25.0	5.4	22.0				
				30.4	23.0	7.4	27.0				
				30.5	25.0	5.5	23.0				
				30.7	26.0	4.7	23.0				
				31.0	26.0	5.0	25.0				
				31.1	25.0	6.1	24.0				
				31.2	25.0	6.2	24.0				
				31.3	26.0	5.3	23.0				
				31.5	25.0	6.5	22.0				
				31.7	26.0	5.7	25.0				
				31.7	23.0	8.7	26.0				
				31.7	23.0	8.7	26.0				
				31.8	23.0	8.8	22.0				
				31.8	23.0	8.8	24.0				
				32.0	25.0	7.0	25.5				
				32.1	23.0	9.1	26.5				
				32.2	23.0	9.2	24.0				
				32.6	26.0	6.6	25.0				
				33.7	23.0	10.7	32.5				
				34.7	25.0	9.7	24.0				
				34.8	25.0	9.8	25.0				
31.8 ± 1.4	31.0 ± 1.5	0.8 ± 1.6	27.0 ± 1.8	31.2 ± 1.5	24.3 ± 1.2	6.9 ± 1.8	24.6 ± 2.1	24.9 ± 1.9	16.8 ± 2.0	8.1 ± 1.1	27.2 ± 1.4

warmer than the air temperature at the hottest sites. The difference between *P. rapae* butterflies and the air temperature in the Herrenholz area was 6.9 °C ± 1.8 °C lying between the values of the other two sampling areas. Wing sizes had similar variation in all study areas, with slightly smaller wing sizes at the Herrenholz site. The smallest *P. rapae* butterflies (22 mm wing length) were found at the Herrenholz site, while the largest *P. rapae* butterflies (29 mm wing length) were measured at both the alpine Zemmgrund and the lowland Verschiebebahnhof (Tab. 3).

Discussion

Butterfly body temperature at various study areas

This study analysed thoracic temperature of active butterflies in different habitats and altitudes of Austria in relationship to air temperature and body size. Due to the contactless measuring procedure we can conclude on temperature limits for flight activity in the natural habitats. Active butterflies exhibited thorax temperatures from 14.5 °C to 39.9 °C, suggesting that the lower and upper limits of flight ability are close to these values. Thorax temperatures correlated significantly with the air temperatures in all habitats; and larger species (i.e., butterflies with greater wing length) had higher temperatures than smaller butterflies.

In most individuals the thorax temperature was well above the air temperature, as has been shown in similar studies (Mattila 2015, Kleckova & Klecka 2016, Bladon et al. 2020). Only ten butterflies out of 522 totally measured individuals showed thorax temperature below air temperature at the time of capture. They flew in lowland habitats at temperatures over 30 °C and belonged to three pierid species and one Satyrinae suggesting heat avoiding behaviour and/or the ability of active cooling under such hot conditions, like has been assumed in tropical butterflies (Tsai et al. 2020). Most of our field data are in the range of previously measured body temperatures in European and tropical butterflies, regardless which thermometers have been used (Kleckova et al. 2014, Kleckova & Klecka 2016, Bladon et al. 2020, Aspe-Jepson et al. 2023). Likewise, our results fit well into published data of thorax temperatures measured under semi-natural conditions (Mattila 2015). Furthermore, thorax temperatures of Australian butterflies measured during take-off varied in similar range from 13.4 °C to 46.3 °C in different species (Nève & Hall 2016). The reported range of the thoracic temperatures for flight in other insect groups is similar (e.g., in bumble bees), but slightly higher in tropical taxa (Church 1960, Bartholomew & Heinrich 1978, May 1979, Lahondère 2023).

In field studies highest measured body temperatures exceed 40 °C in tropical species (Ashe-Jepsen et al. 2023). This is close to the highest temperature of 39.9 °C that we observed in a rather large, dark-brown, lowland satyrine species (*M. dryas*) in the present study. The lowest previously recorded flight temperature was found in *Parnassius sacerdos* (= *P. phoebus*), which can fly with thorax temperature of 17 °C to 21 °C (Guppy 1986). However, some of the *Erebia* butterflies and *C. gardetta* caught in flight remarkably had even lower body temperature. These butterfly species are distributed only in alpine areas and their particularly low temperature indicates possible physiological adaptations to low habitat temperatures in mountain regions. Thermal requirements and temperature dependent behaviour have been compared in *Erebia* butterflies in lowland and alpine species (Klecka et al. 2014, Kleckova & Klecka 2016). In all individuals, the body temperature was above 20 °C, measured using a hypodermic micro needle after capture. However, like in our study, the body temperature of active butterflies was 5 °C-10 °C above air temperature (Kleckova & Klecka 2016).

In general, alpine butterflies were smaller, had lower thoracic temperatures and were active under cooler environmental conditions compared to butterflies in other locations. Since their thoracic temperature had the highest range and fluctuation, we conclude that small alpine species were more influenced by ambient temperature. This suggests that they cool down rapidly during flight in cold air and must warm up by basking in short intervals under unfavourable weather conditions as they were present in one sampling day in the alps. The eurytopic *P. rapae* is distributed throughout all habitats in Austria (Stettmer et al. 2011) and occurred in all study sites. They were active regardless of altitude and ambient temperature during sampling. This demonstrated their thermoregulatory ability to warm up approximately 10 °C over ambient air temperature in cool habitats as well as to cool down even below air temperature in hot environments.

Gautam & Kunte (2020) discussed possible effects of dark colouration on thermoregulation. In our study however, dark coloured Satyrinae occurred in all areas and exhibited a high range of thorax temperature as well as various differences between body and air temperature. Brown colored Satyrinae showed lowest as well as highest thorax temperature and were active under all environmental conditions, even just before rain and temperatures under 10 °C. Our field observations indicated that they are able to heat up by basking at the warm ground, if necessary, but cool down quickly during flight in cold air similarly to other similar-sized butterflies. There is no indication that colour and body size is related to distribution or altitude in Austrian butterflies.

Evaluation of the method

The method developed in this work has the advantage that the butterflies are not touched at the thorax, and that the measurement is contactless, non-invasive, reliable, and fast. It has the potential to be used in the future to measure body temperature of insects in the field and possibly to relate it to various behavior, like courtship, nectar-feeding and overwintering. Body surface temperature was found to be close to internal body temperature in Lepidoptera (Casey 1976, Knapp & Casey 1986). Comparisons between external and internal body temperatures indicated only small differences (Nève & Hall 2016, Bladon et al. 2020). It can be concluded that the external thorax temperature that we measured using an infrared contactless thermometer gives a good proxy for internal body temperature, which is important for all physiological processes such as muscle activity for flight behavior (Nève & Hall 2016, Bladon et al. 2020). Therefore, our method presumably provides reasonable estimates for internal body temperature. However, a detailed comparison of internal and external body temperatures was not performed with the Testo 845.

To date, animal temperature data has often been collected using invasive measurement methods (Kingsolver 1985a, Heinrich 1986, Schmitz & Wasserthal 1993, Kleckova et al. 2014, Silva et al. 2020, Tsai et al. 2020). In these studies, thermal sensors were introduced into the living organisms. In measurements of *Erebia* butterflies, for example, hypothermic microneedles were inserted into the body of the animals to determine the temperature (Kleckova & Klecka, 2016). These invasive methods, however, have limitations in their applicability in the field and in assessing large sample size.

Contactless measuring devices are a potential way forward for fieldwork applications. However, contactless measuring devices have been mainly used in the lab previously

(Mattila 2015, Nève & Hall 2016). In our study, we modified the infrared near-field thermometer (Testo 845) for measuring the body temperature of living insects in the field. So far, this contactless measuring device was mainly used for monitoring temperature of food materials, moving parts of machines or in industry (https://www.aura-nord.com/testo-845-Infrarot-Temperatur-Messgeraet). Preliminary studies demonstrated that this instrument can, with little effort, be used in insects (Osuyi 2010, Paces & Soliman 2016). However, these preliminary studies clearly showed that a precise adjustment of the measuring cone to the object for measuring is crucially required. To be able to measure a small object, such as a butterfly's thorax, an infrared thermometer that can measure at less than 1 mm^2 measuring area is required. According to these requirements we modified the Testo 845 in a way that the measured butterflies always had the exact position and same distance in front of the thermometer. Each butterfly was fixed at the wings between a clothespin and was flexibly attached in front of the Testo 845. In this way, it was not necessary to handle butterflies between the fingers during the measuring process, and only a short transfer touching the wings is required, without touching the thorax. This avoided possible interference factors like the measuring cone not exactly aligned, radiation of human body heat, and various diameters of the measurement area due to different measuring distances. This simple, quick and inexpensive modification can easily be applied to the commercially available infrared near-field thermometer using just a few items that are available in DIY stores. Furthermore, the battery-powered Testo 845 is light and can therefore be used well for field work, even in alpine regions, to measure at a standardized distance with pinpoint accuracy.

The division of activities between three people during field work ensured quick measurements of thorax temperature and forewing length in living butterflies. The time between catching and measuring the butterflies was around 30 seconds, keeping their possible cooling as short as possible. As a result, the measurement results represent good approximate values for the actual body temperature of flying butterflies as it is suggested by recent similar studies of butterflies that used different methods (Kleckova & Klecka 2016, Nève & Hall 2016, Bladon et al. 2020, Ashe-Jepson et al. 2023). By using our new temperature measuring method, insect body temperature can easily be assessed in the field and these data could expand our knowledge for the understanding of behavioral activities in different species, their possible climatic boundaries in habitats, and their species-specific natural histories. It might even have future implications regarding the impact of climate change and distribution of various insects as it was already shown in some butterfly species (MacLean et al. 2016).

Zusammenfassung

Die Körpertemperatur von Tagfaltern hängt von abiotischen Faktoren ab und ist für Stoffwechselprozesse, Flugverhalten und die Verbreitung der Arten in verschiedenen Höhenlagen wesentlich. Wir stellen eine neue nicht-invasive, berührungslose Methode zur Messung der Körpertemperatur von Schmetterlingen im Freiland vor, die ein modifiziertes Infrarot-Nahfeld-Thermometer nutzt. Es wurden 522 Schmetterlinge aus 31 Arten im Tiefland und in alpinen Lebensräumen Österreichs im Flug gefangen und unmittelbar danach wurde ihre Thoraxtemperatur gemessen. Die Thoraxtemperaturen reichten von 14,5 °C bei alpinen Satyrinae bis zu 39,9 °C bei einer Tieflandart. Die Körpertemperaturen (Mittelwert 28,9 °C ± 6,1 °C) zeigten eine hochsignifikante, positive Korrelation zu den Lufttemperaturen (Mittelwert 21,9 °C ± 7,6 °C). Kleine alpine Arten wiesen die niedrigsten, aber stark schwankende, Thoraxtemperaturen auf, während die Schmetterlinge der Tieflandgebiete höhere und weniger variable Temperaturen hatten. Die mittlere Thoraxtemperatur war um 7,04 °C ± 7,6 °C höher als die Lufttemperatur und die Differenz erreichte bei einer alpinen Art einen Höchstwert von 20,2 °C. Einige Tagfalter in heißen Tieflandlebensräumen hatten eine Körpertemperatur, die 3 °C unter der Lufttemperatur lag. *Pieris rapae* war in allen Lebensräumen aktiv und zeigte eine Anpassungsfähigkeit der Körpertemperatur von 34,2 °C im Tiefland bis zu nur 20,8 °C im alpinen Bereich. Diese Daten lassen Rückschlüsse auf obere und untere Temperaturgrenzen für die Flugfähigkeit zu. Die angewandte neue Methode erwies sich als einfache und zuverlässige Technik zur Messung der Körpertemperatur von Schmetterlingen im Freiland, was neue Möglichkeiten für das Verständnis artspezifischer Lebensraumansprüche eröffnet.

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