1 **Capacity for heat absorption by the wings of the**

2 **butterfly *Tirumala limniace* (Cramer)**

3 Huaijian Liao [1, 2, 3], Ting Du[1, 2], Yuqi Zhang[4], Lei Shi[1, 2], Xiyu Huai[1], Chengli

4 Zhou[1, 2], Jiang Deng[1]

5 [1] Research Institute of Resources Insects, Chinese Academy of Forestry, Kunming, 650224, China
6 [2] Key Laboratory of Cultivating and Utilization of Resources Insects of State Forestry
7 Administration, Kunming, 650224, China
8 [3] Institute of Leisure Agriculture, Jiangsu Academy of Agricultural Sciences, Nanjing, 210014，
9 Jiangsu, China
10 [4] College of Life Science, Southwest Forestry University, Kunming, 650224, China

11 Corresponding Authors: Huaijian Liao, Lei Shi
12 Email address: huaixiyu_08@126.com, leishi@139.com

13 **ABSTRACT**

14 Butterflies can directly absorb heat from the sun via their wings to facilitate autonomous

15 flight. However, how is the heat absorbed by the butterfly from sunlight stored and

16 transmitted in the wing? The answer to this scientific question remains unclear. The

17 butterfly *Tirumala limniace* (Cramer) is a typical heat absorption insect, and its wing

18 surface color is only composed of light and dark color. Thus, in this study, we measured a

19 number of wing traits relevant for heat absorption including the thoracic temperature at

20 different light intensities and wing opening angles, the thoracic temperature of butterflies

21 with only one right fore wing or one right hind wing, the spectral reflectance of the wing

22 surfaces, the thoracic temperature of butterflies with the scales removed or not in light or

23 dark areas, and the real-time changes in heat absorption by the wing surfaces with

24 temperature. High intensity light (600–60000 lx) allowed the butterflies to absorb more

25 heat and 60−90° was the optimal angle for heat absorption. The heat absorption capacity

26 was stronger in the fore wings than the hind wings. Dark areas on the wing surfaces were

27 heat absorption areas. The dark areas in the lower region of the fore wing surface and the

28 inside region of the hind wing surface were heat storage areas. Heat was transferred from

29 the heat storage areas to the wing base through the veins near the heat storage areas of the

30 fore and hind wings.

INTRODUCTION

Sunlight is the most important source of energy and it supports the survival and reproduction of most creatures on Earth. Butterflies can directly utilize the heat from the sun to facilitate their autonomous flight. Previous studies have shown that butterflies must directly absorb the heat from sunlight to increase their thoracic temperature above that of their surroundings in order to allow autonomous flight to occur (*Kemp & Krockenberger, 2004; Barton et al., 2014; Bonebrake et al., 2014; Kleckova et al., 2014; Mattila 2015; Liao et al., 2017*). Autonomous flight is required for the reproductive activities of butterflies, including dispersal, courtship behavior, mating behavior, and oviposition behavior (*Shreeve, 1992; Bennett et al., 2012*). Therefore, heat absorption is an indispensable prerequisite for the reproductive success of butterflies (*Gibbs et al., 2010; Westerman et al., 2014; Gibbs et al., 2018*).

Butterflies primarily absorb heat via their wings (*Shanks et al., 2015; Han et al., 2016; Niu et al., 2016*). When adult butterflies require heat for autonomous flight, they adjust their body posture and either fully expand their wings or angle them to allow the optimal absorption of sunlight, where the heat absorbed is then transferred to the thoracic muscles to enable flight (*Heinrich, 1990; Huey et al., 2003*). Some studies indicate that the angle of the incoming sunlight and the wing opening angle can both significantly influence the rate and amount of heat absorption in butterflies (*Plattner, 2004; Shanks et al., 2015; Niu et al., 2016*). Indeed, heat absorption is important, but it has to be modulated via behavior to avoid overheating (*Kingsolver, 1985*).

Based on a study of a new mechanism of behavioral thermoregulation, Kingsolver (1985) suggested that *Pieris* butterflies use their wings as solar reflectors to reflect solar radiation onto the body and to increase their body temperature. Some studies also indicate that butterflies rely on "photonic crystal" structures in their wings to absorb heat (*Li et al., 2004; Han et al., 2013; Luohong, 2014; Han et al., 2015a*). Therefore, the transfer of heat in a butterfly not only depends on reflection from the wing surface, but it also is due to the internal tissue in the wing. Thus, what is the specific tissue involved with heat transfer in the wing? The answer to this question remains unclear. Previous studies of solar heat absorption by butterfly wings have focused on the forewings (*Devries, 2015; Wu et al., 2015*) whereas none have considered the hind wings. As a consequence, it is

62   not clear whether the fore wings or hind wings have a greater capacity for heat
63   absorption.

64   Light intensity also significantly affects heat absorption by butterflies. In the butterfly
65   *Heteronympha merope*, as the intensity of solar radiation increases, the thoracic
66   temperature excess increases significantly regardless of wings being fully extended or
67   closed (*Barton et al., 2014*). Kingsolver (1983) found that short-term meteorological
68   variations, such as intermittent cloudy periods, can rapidly reduce the body temperature
69   excess and flight activity to zero in *Colias* butterflies. The light intensity also
70   significantly influences the ability of the butterfly *Tirumala limniace* to absorb heat,
71   where it was shown that the equilibrium thoracic temperature of adults was higher when
72   exposed to 2240 lx compared with other light intensities and the time required to reach it
73   was shorter. In addition, the thoracic temperature excess and rate of thoracic temperature
74   increase were higher and achieved more quickly (*Liao et al., 2017*), the sunlight intensity
75   is about 2240 lx from 07:00am to 08:00am in summer in Yuanjiang county, Yunnan
76   province, China.

77   Previous studies have shown that color significantly affects the absorption of heat in
78   butterflies (*Schmitz, 1994; Van Dyck et al., 1997; Brashears et al., 2016; Stuart-Fox et al.,*
79   *2017*). Some studies indicate that more heat is absorbed when the wings of butterflies are
80   darker, (*Kingsolver, 1987; Schmitz, 1994; Berwaerts et al., 2001; Trullas et al., 2007*).
81   Some butterflies exhibit wing surface melanism to increase their ability to absorb heat
82   (*Guppy, 1986; Trullas et al., 2007*), but wing melanization is not directly functional to
83   increasing heat absorption, as melanin is involved in numerous functions (Stuart-Fox et
84   al., 2017). Compared with the distal wing area, melanism on the wing surface near the
85   body is more conducive to heat absorption by butterflies (*Kingsolver, 1987; Brashears et*
86   *al., 2016*). However, few studies have considered the specific wing surface areas that are
87   used for heat absorption.

88   In this study, we aimed to understand the effects of the light intensity and wing opening
89   angle on heat absorption, as well as clarifying the differences in the heat absorption
90   capacity of the fore and hind wings, the distribution of heat absorption and non-heat
91   absorption areas on the wing surfaces, and whether the wing has the ability to store heat
92   temporarily and the location of the heat storage areas on the wing surfaces in order to
93   identify the wing tissue that serves as the heat transfer channel. Elucidating the heat

94   absorption capacity of butterflies may provide a deeper understanding of the utilization of

95   solar heat by insects.

96   *Tirumala limniace* (Cramer) is a typical butterfly that directly utilizes solar heat. In

97   field, we have investigated that adults are highly flight active when on the sunny day, but

98   on cloudy and rainy days, the butterflies do not fly even when the air temperature is high.

99   The wings of the male and female butterflies have the same morphology and the wing

100   surface only comprises black (black background) and light blue (light blue bands) areas

101   (*Chen et al., 2008*). According to the color depth, the wing surface can be divided into

102   dark and light areas, while the wings of other butterflies in Yuanjiang County have more

103   colors composition. Thus, the color composition of the wing surface is suitable for

104   studying the heat absorption capacity of butterflies. At 243–2240 lx, high light intensity

105   enabled adult butterflies to quickly absorb more heat than at low light intensities to

106   elevate their thoracic temperature to above that of the environmental temperature and to

107   take off earlier than at low light intensities (*Liao et al.*, *2017*). However, the light

108   intensity range considered in a previous study by Liao *et al.* (2017) was too narrow to

109   determine the appropriate light intensity for heat absorption by the adult *T. limniace*

110   butterfly. In China, *T. limniace* is mainly distributed in the dry hot valleys of south

111   Yunnan Province, Guangxi Province, and Guangdong Province (*Chen et al., 2008*).

112   Yuanjiang County, Yunnan Province, China, which was the site of the artificial breeding

113   ground, is also in the actual habitat range for this butterfly. In this study, according to the

114   natural light intensity in Yuanjiang County, a light intensity range of 600–60000 lx was

115   selected to study the heat absorption capacity of *T. limniace* butterflies in order to

116   investigate the mechanism responsible for solar heat utilization by insects.

117   Thus, in the present study, we measured the absorption of heat by the butterfly *T.*

118   *limniace* at different light intensities and wing opening angles in order to determine the

119   most appropriate light intensity and wing opening angle for heat absorption. The thoracic

120   temperature was measured in a butterfly with only one right fore wing or one right hind

121   wing to elucidate the difference in the heat absorption capacity of the fore and hind wings.

122   The spectral reflectance was measured for the wings to identify the distribution of the

123   heat absorption and non-heat absorption areas on the fore and hind wings. In order to

124   demonstrate that dark areas are responsible for heat absorption on butterfly wings, we

125   investigated heat absorption in butterflies with the scales removed or present in light or

126 dark areas. To identify the wing surface areas involved with heat storage and transfer
127 after heat absorption by butterfly wings, we monitored the real-time temperature changes
128 on the wing surface during heat absorption in adult *T. limniace*. We also monitored the
129 real-time temperature changes in the heat storage areas and non-heat storage areas, as
130 well as the wing veins involved with heat transfer, to further determine the heat storage
131 areas and the transfer channel on the wing surface. Based on the results, we obtained a
132 clear understanding of the heat absorption capacity of the wings in the butterfly *T.*
133 *limniace* to facilitate further research into the mechanism responsible for the utilization of
134 solar heat by insects.

MATERIALS AND METHODS

Insects

137 *T. limniace* pupae were purchased from the Ornamental Insect Technology Development,
138 Kunming Zhonglin Co. Ltd, Kunming, China. The pupae were placed on a cylindrical net
139 (height: 65 cm, diameter: 50 cm) on top of a towel so they could readily spread their
140 wings after emergence. Subsequently, the pupae were transferred to a room at 25 ± 1°C
141 with a relative humidity of 75% ± 5% under a 14:10 light:dark photoperiod. After the
142 adults emerged, the females and males were reared separately in two different cages to
143 prevent mating. Five-day-old unmated adults were used in this study. All the butterflies
144 used in the experiment were living.

145 In China, *T. limniace* is mainly distributed in the dry hot valleys of south Yunnan
146 Province, Guangxi Province, and Guangdong Province. Yuanjiang County, Yunnan
147 Province, China, which was the artificial breeding ground, is also in their normal range
148 habitat. This butterfly is important for ecological and environmental quality monitoring in
149 south China. The optimal temperature range for survival and flight is 25–36°C. During
150 the first and second day after emergence, adult *T. limniace* gradually unfurl their wings
151 and exhibit low flight activity. Their flight activity increases significantly from 3 days and
152 the peak flight activity occurs from 4 days to 7 days during the summer and autumn when
153 the thermal absorption activity is also very high. Thus, unmated adults aged 5 days were
154 used in this study.

Effects of light intensity and wing opening angle on the heat absorption

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capacity

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157   We investigated the effects of the light intensity and wing opening angle on the heat
158   absorption capacity of adult *T. limniace* butterflies. Yuanjiang County, Yunnan Province,
159   China, is a suitable habitat for the butterfly *T. limniace*, and its population is mainly
160   observed from July to October every year. Thus, the natural light intensity on September
161   11, 2017 in Yuanjiang County, Yunan Province, China, was selected as the reference
162   standard for the light intensity in this study because the skies were clear and cloudless on
163   this day. Based on the natural light intensity levels between 07:00 to 20:00 h on
164   September 11, 2017 (Figure 1), six light intensity levels were selected for this study, i.e.,
165   600, 5000, 15,000, 25,000, 40,000, and 45,000 lx. The left and right wings form a
166   specific angle when they are open where this angle ranges from 0° to 180°. Based on this
167   angle range, 10 wing opening angles were tested in this study, i.e., 15°, 30°, 45°, 60°, 75°,
168   80°, 90°, 120°, 150°, and 180°. An orthogonal design was used in this experiment to
169   study the effects of the light intensity and wing opening angle on heat absorption by the
170   butterfly wings.

171   According to the specific angle required, a plane with the selected angle was cut with a
172   knife along the middle line of a white plastic foam board (side length: 10 cm, thickness: 6
173   cm) and the adult *T. limniace* wings were fixed on this plane. Thus, a new unmated
174   5-day-old adult butterfly was fixed on the plane at a specific wing opening angle using
175   double-sided adhesive tape. The plane with the affixed adult butterfly was placed in a
176   dark room (length: 100 cm, width: 80 cm, height: 80 cm). The walls of the dark room
177   were made of black-out cloth and the front wall of the dark room comprised a curtain
178   made of awning cloth to facilitate the placement of butterflies. A 75 W halogen lamp
179   (OSRAM-64841FLSP, Osram China Lighting Ltd, Shanghai, China) was hung 60 cm
180   above the bottom of the dark room. The light intensity of the lamp was adjusted with a
181   potentiometer (CHILFU, Shanghai Wenfu Electric Co. Ltd, Shanghai, China).

182   Before turning the lamp on, the butterfly fixed on the plane was maintained in the dark
183   room for 15 min in order to stabilize its body temperature to avoid the influence of body
184   temperature on heat absorption by the butterfly. After switching the lamp on, the thoracic

185   temperature was recorded every 10 s until the temperature was maintained at a set

186   temperature for 90 s, thereby indicating that the thoracic temperature of the butterfly had

187   reached equilibrium under the specific light intensity. The thoracic temperature was

188   measured using a thermocouple thermometer (Thermometer GM1312, Shenzhen

189   Jumaoyuan Science and Technology Co. Ltd, Shenzhen, China). A thermistor was

190   inserted through the mesoscutellum and placed in or near the dorsal longitudinal muscles

191   to record the thoracic temperature. During each run of the experiment, we recorded the

192   equilibrated thoracic temperature, rate of thoracic temperature increase (Total change in

193   temperature over time), ΔT as the difference in temperature between the thorax and the

194   ambient temperature, and the time when the thoracic temperature reached equilibrium.

195   Three female and three male adult butterflies were tested for each orthogonal treatment

196   with the different light intensities and wing opening angles. In total, 180 female and 180

197   male butterflies were tested in this experiment.

Difference in the heat absorption capacity of the fore and hind wings

199   To determine the difference in the heat absorption capacity of the fore and hind wings, we

200   measure the thoracic temperature in a butterfly with only one right fore wing or only one

201   right hind wing under six light intensities, i.e., 600, 5000, 15,000, 25,000, 40,000 and

202   45,000 lx. The two hind wings and left fore wing were cut from a new unmated 5-day-old

203   adult butterfly using surgical scissors so only the right fore wing remained (fore wing

204   treatment). The two fore wings and left hind wing were cut from another new unmated

205   5-day-old adult butterfly using surgical scissors so only the right hind wing remained

206   (hind wing treatment). The butterfly was then fixed on a horizontal plane (side length: 10

207   cm, thickness: 6 cm) without any angle, before it was placed and maintained in the dark

208   room for 15 min so its body temperature could stabilize before turning the lamp on. After

209   switching the lamp on, during each run of the experiment, we recorded the equilibrated

210   thoracic temperature, the rate (°C/min) of thoracic temperature increase, ΔT, and the time

211   required to reach equilibrium. In this experiment, we tested six female and six male

212   butterflies with only one right fore wing at each light intensity, and six female and six

213   male butterflies with only one right hind wing at each light intensity. In total, we tested

214   36 female and 36 male butterflies in the fore wing treatment, and 36 female and 36 male

215   butterflies in the hind wing treatment. We also measured the wing expanse for both the

216   fore and hind wings of the adult butterflies using 37 female and 34 male adult butterflies.

Reflectance of light and dark areas

218   To determine the distribution of the heat absorption and non-heat absorption areas on the
219   fore and hind wings, we measured the spectral reflectance from the wings of adult
220   butterflies. A higher spectral reflectance indicates weaker light absorption and heat
221   absorption, whereas lower spectral reflectance denotes stronger light absorption and heat
222   absorption. The wing of the *T. limniace* butterfly appears the same in both sexes, but they
223   differ because there is a scaly bag with a protruding ear in the middle of the Cu_2 chamber
224   in the male butterfly. The wing surface is black with many transparent azure markings
225   (Figure 2). Therefore, the wing surface can be divided into light areas and dark areas
226   according to the color shade on the wing surface.

227   The right fore and right hind wings were cut from a female butterfly and a male
228   butterfly. During the cutting process, the integrity of the wings was maintained as far as
229   possible and we prevented scale removal from the wings. The wings were then placed in
230   the dark room. The light intensity in the dark room was set to 5000 lx. The spectral
231   reflectance of the wings was measured using a spectrograph (SOC710 HS-Portable,
232   Surface Optics Corporation, San Diego, USA). As shown in Figure 2, the dorsal surfaces
233   of the fore and hind wings were divided into three parts comprising the border, middle,
234   and inside parts. The spectral reflectance was then calculated for the dark and light areas
235   in these three parts. The average spectral reflectance of all the light areas in each part was
236   taken as the spectral reflectance of the light areas in this part, and the average spectral
237   reflectance of all the dark areas in each part was taken as the spectral reflectance of the
238   dark areas in this part. In addition, the excised fore and hind wings were placed under a
239   VHX-1000 super-high magnification lens zoom 3D microscope (VHX-1000, Keyence
240   (China) Co. Ltd, Shanghai, China) to obtain images. The areas of the light areas, dark
241   areas, and the entire wing surface were measured with an X/Y measurement system under
242   the microscope. The ratios of the light areas and dark areas on the wing surfaces were
243   also determined.

Heat absorption capacities of dark and light areas on the wings

245 In order to demonstrate that the dark area was responsible for heat absorption via the
246 butterfly wings, we investigated heat absorption in butterflies treated with four different
247 scale removal treatments comprising the removal of scales from dark areas (DSR
248 treatment), the removal of scales from light areas (LSR treatment), the removal of all
249 scales from the wings (ASR treatment), and leaving the scales intact on the wings (IN
250 treatment). Scales are the main tissues for heat absorption of butterfly wings. And the
251 structure color of the wing surface is determined by the scale structure and arrangement.
252 Thus, the presence or absence of scales can be used to determine the heat absorption
253 ability of a certain area of wing surface. The scales were gently removed from the wing
254 surfaces with a fine brush in each treatment. The treated butterflies were then placed in
255 the dark room. The light intensity was 5000 lx. After switching the lamp on, during the
256 course of each experiment, we recorded the equilibrated thoracic temperature, rate of
257 thoracic temperature increase, ΔT, and the time required to reach equilibrium. Three
258 female and three male butterflies were tested for each treatment. All of the butterflies
259 used in this experiment were new and unmated 5-day-old adult *T. limniace*.

Heat storage and transfer in the wing

261 We monitored the real-time temperature changes on the wing surface in order to
262 determine the wing surface areas involved with heat storage and transfer during heat
263 absorption by the butterfly wings. The color and markings on the wing surfaces are the
264 same in male and female butterflies, so we only measured the real-time temperature
265 changes on the wing surfaces of male butterflies during heat absorption. A new unmated
266 5-day-old male butterfly was fixed to a square white plastic foam board (10 × 10 cm)
267 using insect dissection needles. The wings were fully extended to facilitate real-time
268 temperature monitoring on the wing surface. The butterfly was then placed in the dark
269 room and the light intensity was set to 5,000 lx. The heat absorption rate under 5,000 lx
270 was slower than that at light intensity levels of 15,000–25,000 lx, but it was too slow at
271 600 lx, so we selected 5,000 lx because it yielded a suitable heat absorption rate for
272 real-time wing temperature monitoring. The real-time temperature changes on the wing
273 surface were recorded using a thermal infrared imager (Flir A600s, FLIR Systems, Inc.,
274 Wilson, OR, USA) until the thoracic temperature reached equilibrium.

275 To determine if dark areas served at heat storage areas, we selected 6 points in the dark

276   area and 6 points in the light area and compared their real-time temperature differences.

277   In addition, we selected evenly distributed pointes from border of wing surface to the

278   wing base to identify heat transfer channels. The distributions of all points on the fore and

279   hind wings are shown in Figure 3A. The distributions of the points on the wing vein on

280   the wing surfaces are shown in Figure 3B. Five to seven points were selected for each

281   heat transfer channel. The initial heat absorption rate of the areas as heat absorption is

282   faster than that of the areas as heat storage. When the heat is transferred from the area as

283   heat absorption to the heat storage area, the heat absorption rate of the storage area

284   increases rapidly and exceeds that of the areas as heat absorption. Finally, the equilibrium

285   temperature of the heat storage area is higher than that of the non-heat storage area.

Statistical analysis

287   The interaction effects of the light intensity and wing opening angle on heat absorption

288   were analyzed using two-way ANOVA. We analyzed ΔT, the thoracic equilibrium

289   temperature, rate of thoracic temperature increase, and the time required to reach

290   equilibrium under different light intensities and wing opening angles simultaneously

291   using one-way ANOVA. Duncan's multiple-range test was used to compare multiple

292   means when significant differences were detected. Differences in ΔT, the thoracic

293   equilibrium temperature, rate of thoracic temperature increase, the time required to reach

294   equilibrium, and the wing expanse between the fore and hind wings were validated using

295   the Student's *t*-test. The differences of spectral reflectance among different areas in male

296   and female wings were analyzed by Kruskal-Wallis test. The differences in the areas of

297   the light and dark wing surface areas were analyzed using chi-square test. Differences in

298   ΔT, the thoracic equilibrium temperature, rate of thoracic temperature increase, and the

299   time required to reach equilibrium in the SDR, SLR, SAL, and IN treatments were

300   analyzed using one-way ANOVA. Duncan's multiple-range test was used to compare

301   multiple means when significant differences were detected. The trends of real-time

302   temperatures of the monitoring points in the dark areas, light areas, and wing veins were

303   analyzed using time-series ExpDec2 of exponential models ($y = A1*exp(-x/t1) +$

304     $A2*exp(-x/t2) + y0$). A1 and A2 is the pre-factor, and they can indicate an increasing

305   trend of the y value; t1 and t2 are the relaxation time; y0 is the offset, it can reflect the

306   final equilibrium temperature.

RESULTS

Interaction effects of light intensity and wing opening angle on heat absorption by adult butterflies

The wing opening angle and light intensity significantly affected the heat absorption capacity of adult *T. limniace* butterflies (Table 1). The equilibrium thoracic temperature, time required to reach equilibrium temperature, ΔT, and the rate of thoracic temperature increase were affected significantly by the wing opening angle and light intensity in both male and female butterflies (Table 1). The interaction effect of the light intensity and wing opening angle on the rate of thoracic temperature increase was significant in both male and female butterflies, but the interaction effects on the equilibrium thoracic temperature, time required to reach equilibrium, and ΔT were not significant (Table 1).

Effects of light intensity on the heat absorption capacity

The light intensity significantly affected the heat absorption capacity in adult *T. limniace* (Tables 2–5). In both the female and male butterflies, within the range of 600–60,000 lx, the equilibrium thoracic temperature became significantly higher as the light intensity increased under the same wing opening angle (Table 2). The time required to reach the equilibrium temperature became shorter as the light intensity increased (Table 3). ΔT became significantly higher as the light intensity increased (Table 4). The rate of thoracic temperature increase also became faster as the light intensity increased (Table 5).

However, we also found that when the light intensity was above 40,000 lx, the equilibrium temperature could rapidly exceed 70°C, which was much higher than the butterflies could tolerate, and thus exposure to a light intensity above 40,000 lx caused the death of the butterflies half an hour after the experiment finished. In summary, a higher light intensity could allow butterflies to absorb more heat (Tables 2–5).

Effects of wing opening angles on the heat absorption capacity

The wing opening angle also significantly influenced the heat absorption capacity of adult *T. limniace* (Tables 2–5). Compared with wing opening angles 15–45° and

334   120–180°, when male and female butterflies were at wing opening angles 60–90°, the

335   equilibrium temperatures were higher (Table 2), the times required to reach the

336   equilibrium temperature were much shorter (Table 3), the values of ΔT were much higher

337   (Table 4), and he rates of thoracic temperature increase were faster (Table 5). However,

338   the influence of wing opening angle was only seen at some light intensities, particularly

339   the higher light intensities. Thus, the optimal wing opening angles for heat absorption

340   ranged from 60° to 90°.

Heat absorption capacities of the fore wing and hind wing

342   The heat absorption capacities of both the fore wing and hind wing were significantly

343   affected by the light intensity where the capacity of the fore wings was higher than that of

344   the hind wings (Table 6). The Student's *t*-test was used to analyze the differences in the

345   heat absorption capacities of the fore wing and hind wing in both female and male

346   butterflies (Table 6). The results showed that the heat absorption capacity of the fore wing

347   was much higher than that of the hind wing in both female and male butterflies (details

348   see Table 6). The equilibrium temperatures and values of ΔT were positively higher for

349   the fore wings than the hind wings under 600–40,000 lx (Table 6), while the times

350   required to reach equilibrium temperature under 600–60,000 lx were significantly shorter

351   in the fore wings than the hind wings, and the rates of thoracic temperature increase were

352   also significantly faster in the fore wings than the hind wings (Table 6). In addition, we

353   found that in both male and female butterflies, the expanse of the fore wing was

354   significantly longer than that of the hind wing (male: $t_{66} = 24.717$, $P < 0.0001$; female: t_{72}

355    $= 29.124$, $P < 0.0001$; Figure 4). In summary, within the range of 600–60,000 lx, the fore

356   and hind wings could both absorb much more heat at a faster rate as the light intensity

357   increased (Table 6). The heat absorption capacity of the fore wing was much higher than

358   that of the hind wing (Table 6), and the expanse of the fore wing was also much larger

359   than that of the hind wing (Figure 4).

Identification of heat absorption and non-heat absorption areas

361   The spectral reflectance of the wings indicated that the dark areas of the wings were used

362   for heat absorption, whereas the light areas did not absorb heat (Figure 5). The spectral

reflectance values of the light areas on both the fore and hind wings were all much higher than those of the dark areas (Male fore wing: $Z=585.340$, $P<0.0001$; Male hind wing: $Z=589.787$, $P<0.0001$; Female fore wing: $Z=583.716$, $P<0.0001$; Female hind wing: $Z=574.677$, $P<0.0001$; Figure 5). The dark areas were significantly larger on both the fore and hind wings than the light areas (male fore wing: $X^2 = 20.841$, $P < 0.0001$; male hind wing: $X^2 = 10.562$, $P = 0.0012$; female fore wing: $X^2 = 16.237$, $P < 0.0001$; female hind wing: $X^2 = 7.242$, $P = 0.0071$). However, the light areas still accounted for about 20% of the fore wing area and about 29% of the hind wing area. In summary, the dark areas could be used to absorb heat, whereas the light areas may prevent the butterfly from absorbing too much heat.

Heat absorption capacities of dark and light areas on the wings

Scale removal treatment significantly impacted equilibrium thoracic temperature (Figure 6). Based on the multirange tests, that the effect was due to removal of the dark scales and all scales, while there was no difference in the response variables between intact butterflies and those with light scales removed. When the scales were removed from the light areas of the wings, the equilibrium thoracic temperature, ΔT, the time required to reach equilibrium temperature, and the rate of thoracic temperature increase were not significantly different from those in the butterflies without scale removal. However, their equilibrium thoracic temperatures (male: $F_{3,8} = 28.269$, $P < 0.0001$; female: $F_{3,8} = 21.132$, $P < 0.0001$) and the values of ΔTs (male: $F_{3,8} = 15.686$, $P < 0.0001$; female: $F_{3,8} = 29.17$, $P < 0.0001$) were significantly higher, and the time required to reach the equilibrium temperature (male: $F_{3,8} = 5.96$, $P = 0.0019$; female: $F_{3,8} = 29.170$, $P < 0.0001$) and the rates of thoracic temperature increase (male: $F_{3,8} = 34.839$, $P < 0.0001$; female: $F_{3,8} = 31.613$, $P < 0.0001$) were significantly shorter and faster, respectively, than those of butterflies with all scales removed from the wings or with scales removed from the dark areas (Figure 6). These results indicate that the dark areas of the wings are the areas where the butterflies absorb heat, whereas the light areas cannot absorb heat.

Heat storage and transfer in the wings

Real-time temperatures on the wing surface during heat absorption

392   The wing temperature increased significantly in *T. limniace* as the lighting time increased,

393   and the temperatures of the wing base and thorax also increased (Figure 7). After the light

394   was switched on, heat absorption by the wings began immediately. The thoracic

395   temperature reached equilibrium after lighting for 480 s. The temperatures of the light

396   areas on both the fore and hind wings were always lower than those of the dark areas

397   during heat absorption in adult *T. limniace*.

398   As the lighting period continued, heat clearly started to accumulate in some areas of

399   the wing surface and the temperature was significantly higher than that of other areas

400   (Figure 7). The temperatures of the dark areas in the middle of wing cell 1A-Cu$_2$ on the

401   hind wing were higher than those of the other wing areas after lighting for 240 s. The

402   temperatures of the dark area in the mid-posterior region near the wing base were

403   markedly higher in wing cells A-CU$_3$ and Cu$_2$-Cu$_3$ on the fore wing, and wing cells

404   1A-Cu$_2$, Cu$_1$-Cu$_2$, M$_3$-Cu$_1$, and R$_2$-M$_1$ on the hind wings compared with other wing areas

405   during lighting from 300–540 s. These results indicate that the dark areas in the

406   mid-posterior region near the wing base in wings cells A-CU$_3$ and Cu$_2$-Cu$_3$ on the fore

407   wings, and wing cells 1A-Cu$_2$, Cu$_1$-Cu$_2$, M$_3$-Cu$_1$, and R$_2$-M$_1$ on the hind wings were the

408   temporary heat storage areas on the wing surfaces (Figure 3 & Figure 7).

409   According to the real-time temperature changes on the wing surface, it appeared that

410   heat was transferred from the heat storage areas to the wing base and thorax through

411   veins Cu$_2$, Cu$_3$, Cu, and A on the fore wings, and veins 1A, Cu$_2$, Cu$_1$, Cu, M$_1$, M$_3$, M, R$_2$,

412   and R on the hind wings during lighting for 0–540 s.

413   **Real-time temperatures in the heat storage and non-storage areas on the wing**

414   **surface during heat absorption**

415   The temperature at each point on the fore and hind wing surfaces increased as the lighting

416   period increased as the analysis of time-series ExpDec2 of exponential models (Figure 8

417   & Table 7). On the fore wing, the base of the wing (Sp7) heated at a conspicuously slow

418   rate initially (A1=-7.40247), then heated at a higher rate than other points at later times

419   (A2=-18.4286). The points in the dark area heated at a similar rate initially (Sp8:

420   A1=-11.7911; Sp9: A1=-11.158; Sp10: A1=-10.0475; Sp11: A1=-11.7152; Sp12:

421   A1=-11.173), then the points Sp8−Sp11 heated at a higher rate than the point Sp12

422   without heat storage (Sp8: A2=-10.7115; Sp9: A2=-11.5553; Sp10: A2=-11.7129; Sp11:

A2=-10.5312; Sp12: A2=-9.14257). The points in the light area always heated at a similar rate with the points in the dark area, but the temperatures were always lower than the points for heat storage (the values of y0s of the points Sp1−Sp6 was significantly lower than the points Sp8−Sp11: t_8=2.864, P=0.021). In summary, Sp8–Sp11 could temporarily store heat and then transfer it to Sp7, and the heat storage was greater closer to Sp7. Sp12 could absorb heat from the light source but it could not store the heat.

In the hind wing, the base of the wing (H-Sp7) heated at a conspicuously slow rate initially (A1=-6.07772), then heated at a higher rate than other points at later times (A2=-19.64). The points in the dark area heated at a similar rate initially (H-Sp8: A1=-10.7477; H-Sp9: A1=-13.0178; H-Sp10: A1=-10.9644; H-Sp11: A1=-12.9741; H-Sp12: A1=-13.2487), then the points for heat storage heated at a higher rate than the point Sp12 without heat storage (H-Sp8: A2=-13.9014; H-Sp9: A2=-10.1396; H-Sp10: A2=-11.233; H-Sp11: A2=-9.03949; H-Sp12: A2=-7.43888). We also found that the values of y0s of H-Sp1, H-Sp2 and H-Sp3 were similar with the y0s of the points H-Sp8−H-Sp11 (t_5=20.683, P=0.525); The possible reason is that these points were too close to the base of the wing and were affected by the heat of the base of the wing, but their y0 values were still lower than the point H-Sp8 in the dark area close to them. The temperatures of other three points in the light area were always lower than the points H-Sp8−H-Sp11 (y0: t_5=2.986, P=0.031). In summary, H-Sp8−H-Sp11 could temporarily store heat and then transfer the heat to H-Sp7, and the heat storage was greater closer to H-Sp7. H-Sp12 could absorb heat from the light source, but it could not store the heat (Figure 8C–D).

Real-time temperatures in the heat transfer channel in the wing veins during heat absorption

Both in the fore and hind wings, the temperatures of all the veins increased as the lighting time increased as the analysis of time-series ExpDec2 of exponential models (Figure 9 & 10). The heat rate of the points in all veins failed to show a certain rule according to the distance from the base of the wing (Figure 9 & 10). But, in all vein channels, the closer points get to the base of the wing, the higher the final equilibrium temperature was (Figure 9 & 10), and the value of y0 was higher (table 8). These indicated that with the heat transfer in the vein, the closer the points were to the wing base, the higher the

454   temperatures; conversely, the farther the points were from the wing base, the lower the

455   temperatures (Figure 9 & 10). In thus, heat may mainly transfer along the veins from the

456   points at the edge of the wing surface to the points at the base of the wing. The potential

457   transfer channels were showed in Figure 3 and Figure 9.

DISCUSSION

Effects of the light intensity on heat absorption

460   We found that the light intensity significantly affected the heat absorption capacity of the

461   butterfly *T. limniace*. Within the light intensity range from 600 lx to 60000 lx, as the light

462   intensity increased, the thoracic equilibrium temperature and ΔT increased significantly,

463   the time to reach the equilibrium temperature was significantly shorter, and the rate of

464   thoracic temperature increase was significantly faster. Our previous studies also showed

465   that compared with other light intensities (243, 860, and 1280 lx), the equilibrium

466   thoracic temperature of adults exposed to 2240 lx was higher and the time required to

467   reach it was shorter. In addition, the value of ΔT was higher and the rate of thoracic

468   temperature increase was achieved more quickly (*Liao et al., 2017*). These results suggest

469   that in an appropriate range, a high light intensity can allow adult *T. limniace* butterflies

470   to rapidly absorb more heat to elevate their thoracic temperature compared with low light

471   intensities. Similar results were obtained for the butterfly *Heteronympha merope* where

472   its body temperature excess also increased as the level of solar radiation increased

473   (*Barton et al., 2014*).

474   The heat absorbed by butterflies is used mainly for autonomous flight and it is directly

475   involved with reproductive behavior (*Shreeve, 1992; Kemp and Krockenberger, 2004;*

476   *Bennett et al., 2012; Bonebrake et al., 2014; Kleckova et al., 2014; Mattila 2015; Shanks*

477   *et al., 2015; Han et al., 2016; Niu et al., 2016*). In *Bicyclus anynana*, active males

478   increase their own likelihood of copulation and active females increase their likelihood of

479   being courted (*Westerman et al., 2014*). The flight activity of *T. limniace* butterflies is

480   higher under a high light intensity compared with those exposed to a low light intensity

481   (*Liao et al., 2017*). The high thorax temperature recorded in *Junonia villida* is probably

482   linked to its high flight speed (*Nève and Hall, 2016*). We found that a higher light

483   intensity increased the heat absorbed by *T. limniace* adults from light sources. Thus,

484   within an appropriate light intensity range, a higher light intensity can allow *T. limniace*
485   adults to absorb more heat to facilitate autonomous flight and increase the flight activity,
486   thereby enhancing the likelihood of reproduction.

487   We also found that when the light intensity was above 40,000 lx, the equilibrium
488   temperature could rapidly exceed 70°C, which was much higher than the butterflies could
489   tolerate, and thus exposure to a light intensity above 40,000 lx caused the death of the
490   butterflies half an hour after the experiment finished. In the summer and autumn season
491   of Yuanjiang county, Yunan province, China, the peak of flight activity of butterfly *T.*
492   *limniace* mainly appeared at 09:00-12:00 and 15:00-17:00 (*Chen et al., 2008*). During
493   these time periods, the sunlight intensity is lower than 40,000 lx, which allows the
494   butterfly to absorb the right amount of heat for autonomous flight. More than 40,000 lx
495   light intensity could make the butterflies to absorb more heat than the body can tolerate,
496   burning the body and causing death. Some studies indicated that butterflies can adjust
497   their basking posture to reduce heat absorption (*Rawlins, 1980; Tsuji et al., 1986*), e.g.
498   closing the wings and turning the body opposite the sunlight. In *T. limniace*, in the field
499   we observed that when the sunlight was above 40,000 lx, the butterflies would fly into the
500   woods and perch on branches to avoid the sunlight.

501   **Effects of the wing opening angle on heat absorption**

502   The wing opening angle also significantly influenced the heat absorption capacity of *T.*
503   *limniace* adults. Some previous studies have shown that butterflies with fully open wings
504   have the highest heat absorption capacity (*Tsuji et al. 1986; Berwaerts et al., 2001; De*
505   *Keyser et al., 2015*). When the butterfly *Polyommatus icarus* fully opens its wings, the
506   warming rates are maximized and its body temperature is also highest (*De Keyser et al.,*
507   *2015*). *Pararge aegeria* butterflies with fully opened wings are able to absorb more heat
508   and cool faster compared with those with half-opened wings (*Berwaerts et al., 2001*).
509   Other studies suggest that the heat absorption capacity of butterflies is highest in the
510   optimal range for the wing opening angle (*Kingsolver and Moffat, 1982; Barton et al.,*
511   *2014*). For example, in *Pieris*, normal and black base manipulation of butterflies can
512   achieve maximum temperature excesses at wing angles of 30−40°, whereas the optimal
513   wing angles for the highest temperature excess in black distal treatment butterflies are
514   60−90° (*Kingsolver, 1987*). Thus, regardless of whether the wings are normal or

515 melanized, heat absorption by butterflies requires the optimal wing opening angle. We
516 found that the optimal wing opening angle range for heat absorption by *T. limniace* was
517 60−90°. In this range, the equilibrium temperatures were significantly higher, the times
518 required to reach the equilibrium temperature were much shorter, the values of ΔT were
519 higher, and the rates of thoracic temperature increase were significantly faster. Thus, an
520 appropriate wing opening angle can enhance the heat absorption capacity of butterflies. In
521 wild, when butterflies need heat to automous fly, adults *T. limniace* doesn't fully open
522 their wings, however, they would make the wings maintained a certain angle. Thus, wing
523 opening angles 60−90° were suitable for heat absorption of butterfly *T. limniace*.

Differences in heat absorption between the fore and hind wings

525 Our results showed that the heat absorption capacity of the fore wings was significantly
526 higher than that of the hind wings. The equilibrium temperatures and values of ΔTs were
527 significantly higher for the fore wings than the hind wings in males exposed to light at
528 600–40,000 lx and females exposed to light at 600 lx, 15000 lx and 40,000 lx. The times
529 required to reach equilibrium temperature and the rates of thoracic temperature increase
530 were significantly shorter and faster, respectively, in the fore wings than those in the hind
531 wing for both males and females exposed to light at 600–60,000 lx. These results suggest
532 that the fore wing is the major tissue used for heat absorption in butterflies. Thus, the
533 wing size significantly limits the heat absorption capacity of butterflies (*Kammer and*
534 *Bracchi, 1973; Berwaerts et al., 2001, 2002*). Some studies suggest that butterflies with
535 larger wings can absorb more heat than those with smaller wings (*Heinrich, 1986;*
536 *Kingsolver, 1987; Schmitz, 1994*). Thus, a study of 20 Australian butterflies showed that
537 those with the highest wing loadings had the highest thorax temperature at take-off (*Nève*
538 *and Hall, 2016*). In our study, the wing expanse of the fore wing was significantly larger
539 than that of the hind wing in both male and female butterflies. Therefore, the fore wings
540 allow *T. limniace* butterflies to absorb more heat than the hind wings under the same
541 lighting conditions. However, in *Pararge aegeria*, butterflies with larger wings heated up
542 more slowly compared with those with small wings (*Berwaerts et al., 2001*).

Identification of heat absorption and non-heat absorption areas

544 The spectral reflectance from light areas on both the fore and hind wings was much

545 higher than that from dark areas in *T. limniace* adults. Thus, the absorbance and thermal

546 absorptivity of the dark areas was significantly greater than that of the light areas. Color

547 can affect an animal's temperature because dark surfaces absorb more solar energy than

548 light surfaces and the energy is converted into heat (*Stuart-Fox et al., 2017*). Previous

549 studies indicate that wing color can limit the heat absorption capacity, where darker

550 coloration can absorb more heat from sunlight or other light sources than lighter

551 coloration (*Watt, 1968; Kingsolver, 1987, 1988; Berwaerts et al., 2001*). For example,

552 darker *Pararge aegeria* butterflies have a much higher warming rate (*Van Dyck et al.,*

553 *1997*). We found that when the scales were removed from the light areas on the wings,

554 the equilibrium thoracic temperature and value of ΔTs were significantly higher, and the

555 time required to reach the equilibrium temperature and the rate of thoracic temperature

556 increase were significantly shorter and faster, respectively, than those in butterflies with

557 all the scales removed from the wings or with scales removed from the dark areas. Thus,

558 the dark areas of the wings absorb heat in the butterfly *T. limniace* rather than the light

559 areas.

560 Some studies suggest that melanization of the wing surfaces can promote the

561 absorption of heat from sunlight in butterflies (*Kingsolver and Wiernasz, 1991; Stoehr*

562 *and Wojan, 2016*). The butterfly *Parnassius phoebus* lives at high altitudes and high

563 latitudes, and it uses melanization to obtain heat from solar radiation, where the color of

564 its wings becomes darker as the altitude and latitude increase (*Guppy, 1986*).

565 Melanization inside the wing surfaces can improve the heat absorption capacity of

566 butterflies whereas melanization at the distal wing surfaces cannot affect heat absorption

567 (*Kammer and Bracchi, 1973; Kingsolver, 1987; Brashears et al., 2016*). Wasserthal (1975)

568 showed that the most of the heat transferred from the wing to the body originates from

569 the 15% of the wing surface nearest to the body in the butterflies *Papilio machaon*,

570 *Apatura ilia*, and *Papilio troilux*. Thus, the dark areas of the wing surface near the body

571 are the main heat absorption areas in butterflies. Our results are similar to those obtained

572 in previous studies. In *T. limniace*, we found that the temperatures were markedly higher

573 in the dark areas in the mid-posterior region near the wing base in wing cells $A-CU_3$ and

574 Cu_2-Cu_3 in the fore wings, as well as in wing cells $1A-Cu_2$, Cu_1-Cu_2, M_3-Cu_1, and R_2-M_1

575 in the hind wings compared with other wing areas during lighting for 300–540 s.

576 The color of a butterfly wing mainly comprises iridescence and structural colors

577 (*Nijhout, 1991; Michielsen et al., 2010; Han et al., 2016; Siddique et al., 2017*). The part

578 of the wing with a structural color is used to absorb heat from the sun (*Bosi et al., 2008*).

579 In *Pararge aegeria*, normal butterflies reach a higher equilibrium thoracic temperature

580 than descaled butterflies, probably because the wings without scales absorb less radiation

581 (*Berwaerts et al., 2001*). In the present study, we found that removing the scales from the

582 dark areas of the wings significantly reduced the heat absorption capacity of butterflies,

583 whereas removing the scales from the light areas did not affect normal heat absorption.

584 Therefore, the dark areas on the dorsal wing surfaces in *T. limniace* may mainly comprise

585 structural colors.

586 High reflectance can reduce the absorption of heat from sunlight (*Stuart-Fox et al.,*

587 *2017*). Thus, light colors are not conducive to heat absorption by butterflies. We found

588 that removing the scales from the light areas on the wing surfaces did not affect the

589 absorption of heat by butterflies. In *Anartia fatima*, it was previously shown that

590 blackening the white bands on the wing surface did not affect its equilibrium temperature,

591 but adding white bands decreased the rate of heating (*Brashears et al., 2016*). Thus, the

592 light areas on the wing surfaces may prevent butterflies from absorbing heat excessively

593 quickly and increasing the body temperature to an intolerable level. We also found that

594 light areas accounted for about 20% of the fore wing area and about 29% of the hind

595 wing area. However, some studies indicate that light areas have high spectral reflectance

596 and they could be used as information for intraspecies identification or for detecting the

597 opposite sex in butterflies (*Emmel, 1972; Taylor, 1973; Seymoure and Aiello, 2015*). The

598 role of the light areas on butterfly wings in heat absorption will be addressed in our future

599 research.

600 **Heat storage and transfer in the wing**

601 In the butterfly *T. limniace*, the temperatures of the dark areas were markedly higher in

602 the mid-posterior region near the wing base in wing cells A-Cu_3 and Cu_2-Cu_3 on the fore

603 wings, as well as in wing cells $1A$-Cu_2, Cu_1-Cu_2, M_3-Cu_1, and R_2-M_1 on the hind wings

604 compared with the other wing areas during lighting for 300–540 s. Hence, the heat

605 absorbed by the wings of the butterfly *T. limniace* needs to be temporarily stored in heat

606 storage areas on the wing surface, before it is transferred to the wing base and thorax to

607 elevate the thoracic temperature above the ambient level to trigger autonomous flight.

608   Thus, the dark areas in the mid-posterior region near the wing base in wing cells A-Cu_3

609   and Cu_2-Cu_3 in the fore wings, and in wing cells 1A-Cu_2, Cu_1-Cu_2, M_3-Cu_1, and R_2-M_1 in

610   the hind wings were temporary heat storage areas on the wing surface. The heat was

611   transferred from the heat storage areas to the wing base and thorax through the veins near

612   the storage areas. During the heat transfer process, the temperatures of the wing base and

613   thorax were the same as the heat storage areas and much higher than those of other areas

614   of the wing surfaces on both the fore and hind wings, and the thoracic temperature

615   reached equilibrium after lighting for 480 s. Thus, the channels for heat transfer were the

616   veins near the storage areas.

617   Kingsolver (1985) suggested that the wings act as solar reflectors in *Pieris* butterflies

618   to reflect solar radiation onto the body in order to increase its temperature. However,

619   some studies have shown that the absorption of heat by butterfly wings depends mainly

620   on the internal structure of the scale itself, where the structure called a "photonic crystal"

621   can convert the absorbed light into heat for autonomous flight (*Li et al., 2004; Han et al.,*

622   *2013; Luohong, 2014; Han et al., 2015a, b*). In the butterfly *Trogonoptera brookiana*, the

623   scales have longitudinal ridges that run through the scales and the surfaces of the scales

624   comprises a set of raised longitudinal quasiparallel lamellae (ridges), where the spaces

625   between adjacent ridges are filled with a netlike reticulum comprising pores (*Han et al.,*

626   *2015a*). This "photonic crystal" structure in the scales may help the wings to absorb heat.

627   Therefore, the heat absorbed is not reflected to the wing base and thorax through the wing

628   surface, but instead it is transmitted via the internal tissue in the wing. Our results showed

629   that the heat was transferred from the heat storage areas to the wing base and thorax

630   through veins Cu_2, Cu_3, Cu, and A in the fore wings, and veins 1A, Cu_2, Cu_1, Cu, M_1, M_3,

631   M, R_2, and R in the hind wings during lighting for 0–540 s. This suggests that the heat

632   absorbed by the wings is transferred from the heat storage areas on the wing surface to

633   the wing base and thorax through wing veins.

634

CONCLUSIONS

636   In this study, we showed that in the optimal light intensity range, a higher light intensity

637   could help butterflies to absorb more heat, and the optimal wing opening angles for heat

638   absorption ranged from 60° to 90°. The heat absorption capacity of the fore wing was

639   much greater than that of the hind wing. The dark areas on the wing surfaces were the

640   areas where heat was absorbed by the butterfly wing. The dark areas in the mid-posterior

641   region near the wing base in wing cells A-CU_3 and Cu_2-Cu_3 in the fore wing, and in wing

642   cells 1A-Cu_2, Cu_1-Cu_2, M_3-Cu_1, and R_2-M_1 in the hind wings were temporary heat

643   storage areas on the wing surface. The heat was transferred from heat storage areas to the

644   wing base and thorax through veins Cu_2, Cu_3, Cu, and A in the fore wings, and veins 1A,

645   Cu_2, Cu_1, Cu, M_1, M_3, M, R_2, and R in the hind wings during lighting for 0–540s. In the

646   future, we will investigate the heat storage mechanism in butterfly wings, as well the heat

647   transfer mechanism in the wing veins and the role of light areas on the wings in heat

648   absorption.

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814   **Table 1** Effects of the light intensity and wing opening angle on heat absorption by adult *Tirumala*

815   *limniace* butterflies.

Sex	Source		d.f.	Type Ⅲ SS	Mean Square	F	P
Male	Equilibrium thoracic temperature	Wing opening angle	9	2154.7588	239.4176	6.1	<0.0001
		Light intensity	5	44467.6879	8893.5375	226.55	<0.0001
		Wing opening angle*Light intensity	45	443.29354	9.85097	0.25	1
	Time required to reach equilibrium temperature	Wing opening angle	9	161.94397	17.993775	6.91	<0.0001
		Light intensity	5	1165.495037	233.099007	89.46	<0.0001
		Wing opening angle*Light intensity	45	87.682895	1.948509	0.75	0.8659
	ΔT	Wing opening angle	9	2009.57726	223.28636	6.16	<0.0001
		Light intensity	5	40432.775	8086.555	223.02	<0.0001
		Wing opening angle*Light intensity	45	503.31054	11.18468	0.31	1
	Rate of thoracic temperature increase	Wing opening angle	9	2912.84731	323.6497	19.99	<0.0001
		Light intensity	5	11774.35845	2354.67169	145.42	<0.0001
		Wing opening angle*Light intensity	45	3145.22568	69.8939	4.32	<0.0001
Female	Equilibrium thoracic temperature	Wing opening angle	9	1651.61128	183.51236	2.59	0.0093
		Light intensity	5	40823.08502	8164.617	15.02	<0.0001
		Wing opening angle*Light intensity	45	730.02801	16.22284	0.23	1
	Time to reach equilibrium temperature	Wing opening angle	9	394.8589642	43.8732182	25.28	<0.0001
		Light intensity	5	975.0365768	195.0073154	112.36	<0.0001
		Wing opening angle*Light intensity	45	88.2546565	1.9612146	1.13	0.2964
	ΔT	Wing opening angle	9	1441.50025	160.16669	4.28	<0.0001
		Light intensity	5	41421.11186	8284.22237	221.13	<0.0001
		Wing opening angle*Light intensity	45	815.41275	18.12028	0.48	0.9967
	Rate of thoracic temperature increase	Wing opening angle	9	1873.31856	208.14651	11.76	<0.0001
		Light intensity	5	10673.83577	2134.76715	120.64	<0.0001
		Wing opening angle*Light intensity	45	1574.69478	34.99322	1.98	0.0018

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825 **Table 2** Effects of the light intensity and wing opening angle on the equilibrium thoracic temperature in
826 adult *Tirumala limniace* butterflies.

Sex	Wing opening angle	600 lx	5000 lx	15000 lx	25000 lx	40000 lx	60000 lx
Male	15°	30.60±2.47d,A	47.47±4.78c,A	61.85±2.64b,A	64.06±2.33ab,BCDE	72.26±3.87ab,A	78.19±8.12a,A
	30°	32.62±2.01d,A	48.05±3.00c,A	61.75±2.44b,A	63.43±1.81b,CDE	69.34±2.23b,A	80.98±6.65a,A
	45°	34.22±2.72d,A	52.803±4.29c,A	63.45±2.99bc,A	67.96±2.55bc,ABC	77.26±4.81ab,A	87.41±9.68a,A
	60°	36.25±1.73d,A	54.39±5.48c,A	63.57±2.12bc,A	70.69±2.07ab,AB	80.81±6.56a,A	81.81±5.69a,A
	75°	36.28±1.53d,A	53.34±3.85c,A	67.06±2.05b,A	71.79±1.44b,A	77.52±4.41ab,A	86.84±5.13a,A
	80°	35.51±1.73e,A	48.82±3.57d,A	63.98±2.44c,A	67.63±1.51bc,ABC	76.42±4.39ab,A	81.78±6.66a,A
	90°	35.30±0.91e,A	49.27±4.10d,A	63.11±3.13c,A	67.27±3.19bc,ABCD	75.28±2.94ab,A	83.51±3.45a,A
	120°	32.87±1.87d,A	43.78±1.73c,A	61.23±2.08b,A	62.36±1.34b,CDE	72.93±1.17a,A	77.19±1.48a,A
	150°	30.31±2.60d,A	43.00±2.11c,A	59.17±1.15b,A	60.67±2.68b,DE	68.85±0.98a,A	73.48±3.16a,A
	180°	30.43±2.13d,A	41.35±4.96c,A	59.55±1.66b,A	59.47±1.10b,E	64.21±1.69b,A	74.19±4.27a,A
Female	15°	33.52±5.12d,A	45.10±5.42cd,A	57.63±7.47bc,A	64.89±1.50b,AB	83.30±5.27a,A	86.27±3.67a,A
	30°	32.07±4.44d,A	46.89±5.00cd,A	59.37±6.11bc,A	58.90±0.52bc,B	71.30±0.63ab,BC	77.09±7.57a,A
	45°	35.93±5.03d,A	50.09±5.39cd,A	62.10±5.85bc,A	64.56±0.49bc,AB	76.66±1.29ab,AB	84.23±8.49a,A
	60°	34.67±3.96d,A	48.99±6.29cd,A	60.34±6.50bc,A	66.43±0.69abc,A	74.06±2.34ab,AB	82.65±11.00a,A
	75°	35.58±3.65d,A	49.26±5.81c,A	60.35±6.09bc,A	65.64±1.50ab,A	73.80±1.58ab,AB	78.40±5.21a,A
	80°	34.63±3.72d,A	47.24±3.47cd,A	59.25±8.07bc,A	65.10±2.46ab,AB	72.25±2.24ab,BC	79.32±6.60a,A
	90°	35.73±3.51d,A	46.15±6.78cd,A	55.56±6.46bc,A	63.21±2.30ab,AB	69.86±3.54ab,BC	74.39±4.54a,A
	120°	31.95±4.10e,A	43.89±5.97de,A	54.64±4.56cd,A	62.38±1.96bc,AB	69.66±3.65ab,BC	75.95±3.63a,A
	150°	31.01±3.62d,A	43.53±6.31cd,A	52.33±7.15bc,A	58.90±3.08ab,B	62.78±2.66ab,BC	71.76±0.62a,A
	180°	30.80±3.33d,A	42.39±5.36cd,A	51.79±5.90bc,A	58.93±2.11ab,B	67.12±3.97a,C	71.81±4.26a,A

827 Different lowercase and capital letters indicate significant differences at $P < 0.05$ in the results
828 obtained at different light intensities and wing opening angles, respectively.

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843 **Table 3** Effects of the light intensity and wing opening angle on the time required to reach equilibrium

844 temperature in adult *Tirumala limniace* butterflies.

Sex	Wing opening angle	600 lx	5000 lx	15000 lx	25000 lx	40000 lx	60000 lx
Male	15°	11.97±1.36a,A	9.68±1.17ab,A	7.94±0.81b,A	4.44±0.27c,A	4.32±0.46c,A	3.89±0.35c,AB
	30°	10.60±1.72a,A	8.64±1.84ab,A	6.26±0.43bc,AB	4.12±0.42c,A	4.36±0.31c,A	4.67±0.77c,A
	45°	7.92±1.31a,A	6.35±0.50ab,A	4.73±0.20bc,BC	3.84±0.10c,AB	3.84±0.65c,A	3.48±0.71c,ABC
	60°	9.81±1.25a,A	6.22±1.11b,A	3.52±0.53c,C	3.18±0.08c,BC	3.18±0.69c,AB	2.68±0.95c,ABCD
	75°	8.98±2.04a,A	6.11±1.45ab,A	3.25±0.51bc,C	2.47±0.04c,C	2.08±0.54c,BC	1.60±0.40c,CD
	80°	10.89±1.49a,A	6.33±1.77b,A	3.70±0.29bc,C	2.81±0.18c,C	2.93±0.52c,ABC	2.56±0.69c,BCD
	90°	6.51±0.05a,A	5.85±0.58a,A	4.04±0.41b,BC	2.84±0.27c,C	1.38±0.10d,C	1.29±0.14d,D
	120°	11.62±1.54a,A	6.24±1.89b,A	4.67±1.00b,BC	2.64±0.48b,C	2.69±0.54b,ABC	2.64±0.73b,ABCD
	150°	9.23±0.56a,A	7.17±1.43a,A	3.77±0.71b,C	2.49±0.11b,C	2.83±0.40b,ABC	2.95±0.65b,ABCD
	180°	11.04±1.53a,A	5.83±1.65b,A	5.33±1.48b,BC	3.05±0.25b,BC	2.13±0.53b,BC	3.16±0.40b,ABCD
Female	15°	13.64±1.40a,A	10.25±0.94b,A	9.51±1.26b,A	4.72±0.52c,A	6.22±0.81c,A	5.03±0.37c,A
	30°	12.74±2.15a,A	10.71±1.52a,A	8.69±1.29ab,A	4.12±0.40c,AB	4.69±0.65bc,B	4.66±0.79bc,AB
	45°	8.01±0.41a,B	6.27±0.71b,B	4.84±0.21bc,B	3.21±0.24cd,BC	3.46±0.50cd,BC	2.79±0.94d,BC
	60°	8.18±1.14a,B	4.77±0.37b,B	4.23±0.93b,B	3.02±0.61b,BC	2.65±0.47b,C	3.18±1.15b,ABC
	75°	6.48±0.11a,B	4.73±0.30b,B	3.14±0.56c,B	2.16±0.21cd,C	2.34±0.09cd,C	1.46±0.28d,C
	80°	9.13±0.40a,B	6.91±0.57ab,B	4.93±1.68bc,B	2.92±0.32c,BC	2.76±0.52c,C	2.64±0.71c,C
	90°	8.31±1.10a,B	4.85±0.66b,B	3.47±0.66bc,B	2.83±0.20bc,BC	1.98±0.50c,C	1.43±0.11c,C
	120°	9.26±0.42a,B	5.37±0.48b,B	3.84±0.51c,B	3.21±0.21c,BC	3.55±0.17c,BC	2.57±0.49,C
	150°	9.32±0.46a,B	6.47±0.32b,B	3.47±0.35c,B	3.15±0.34cd,BC	2.96±0.33cd,C	2.33±0.14d,C
	180°	9.12±1.22a,B	6.67±1.31a,B	3.76±0.75b,B	3.55±0.67b,AB	3.33±0.43b,BC	2.36±0.35b,C

845 Different lowercase and capital letters indicate significant differences at $P < 0.05$ in the results

846 obtained at different light intensities and wing opening angles, respectively.

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856 **Table 4** Effects of the light intensity and wing opening angle on the thoracic temperature excess (ΔT) in

857 adult *Tirumala limniace* butterflies.

Sex	Wing opening angle	600 lx	5000 lx	15000 lx	25000 lx	40000 lx	60000 lx
Male	15°	9.01±2.01b,B	21.41±4.01a,A	37.71±1.57a,BC	41.07±2.45a,BCD	48.96±3.53a,ABC	50.80±8.71a,A
	30°	10.89±0.95d,AB	22.78±2.84c,A	37.17±0.89b,BC	40.81±2.72b,BCD	45.79±1.62ab,BC	54.47±7.13a,A
	45°	12.72±2.23d,AB	27.52±3.91cd,A	39.25±1.60bc,AB	45.68±2.00ab,ABC	54.01±3.95ab,AB	60.34±9.89a,A
	60°	14.56±1.06d,A	28.97±5.05c,A	39.37±0.66bc,AB	47.58±1.70ab,AB	57.72±5.74a,A	55.18±6.36a,A
	75°	15.15±1.40e,A	27.84±3.42d,A	42.39±0.89c,A	49.25±1.10bc,A	54.77±3.86ab,AB	61.35±5.88a,A
	80°	14.33±1.09c,A	23.47±3.78c,A	40.12±1.01b,AB	45.40±1.36ab,ABCD	53.87±4.12a,AB	56.87±7.37a,A
	90°	14.07±0.14e,A	25.01±3.60d,A	38.89±1.73c,ABC	45.12±3.13bc,ABCD	52.65±2.55ab,AB	58.93±3.89a,A
	120°	11.65±1.70d,AB	18.68±2.47c,A	37.27±1.26b,BC	39.27±1.85b,CD	49.94±0.41a,ABC	52.34±1.58a,A
	150°	8.96±1.52d,B	18.52±1.62c,A	35.26±0.62b,C	38.98±2.36b,CD	45.20±1.22a,BC	48.16±3.48a,A
	180°	10.34±1.95c,AB	15.36±4.23c,A	36.91±0.49b,BC	38.22±2.28b,D	41.65±2.45ab,C	48.49±4.22a,A
Female	15°	10.24±3.12c,A	21.09±3.81c,A	33.06±5.95b,A	43.37±0.72b,A	60.16±4.40a,A	62.58±3.01a,A
	30°	9.03±2.63d,A	23.27±3.72c,A	34.91±4.65b,A	36.35±1.35b,A	48.04±1.25b,BC	53.51±5.89a,A
	45°	12.80±3.10e,A	25.18±3.54d,A	37.53±4.31c,A	42.57±0.93bc,A	53.81±0.51ab,AB	59.59±6.94a,A
	60°	11.70±1.87d,A	25.03±4.51cd,A	35.51±4.96bc,A	44.49±0.82ab,A	51.30±1.48a,BC	58.97±8.52a,A
	75°	12.75±2.00e,A	25.38±4.17d,A	35.78±4.52c,A	43.78±0.82bc,A	51.18±0.81ab,BC	55.04±3.50a,A
	80°	11.16±1.34e,A	23.37±1.52d,A	34.66±6.53c,A	43.84±1.72bc,A	49.71±1.48ab,BC	56.05±4.39a,A
	90°	12.66±2.06d,A	22.96±4.84cd,A	31.16±4.79bc,A	38.83±4.68ab,A	47.80±2.59a,BCD	50.24±2.28a,A
	120°	8.83±1.69e,A	19.94±4.02d,A	28.71±3.80c,A	41.82±1.33b,A	47.11±2.69ab,BCD	52.35±2.16a,A
	150°	9.21±1.90c,A	20.21±4.04b,A	27.40±5.23b,A	38.11±2.12a,A	40.48±2.06a,D	47.85±1.97a,A
	180°	7.62±1.42d,A	18.72±3.19c,A	28.16±4.02b,A	39.17±1.76a,A	45.71±3.01a,CD	47.28±2.82a,A

858 Different lowercase and capital letters indicate significant differences at $P < 0.05$ in the results

859 obtained at different light intensities and wing opening angles, respectively.

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870 **Table 5** Effects of the light intensity and wing opening angle on the rate (°C/min) of thoracic temperature

871 increase in adult *Tirumala limniace* butterflies.

Sex	Wing opening angle	600 lx	5000 lx	15000 lx	25000 lx	40000 lx	60000 lx
Male	15°	0.78±0.19d,E	2.36±0.67d,A	4.86±0.59c,D	9.26±0.46b,D	11.42±0.42a,CD	12.87±1.09a,B
	30°	1.07±0.16e,CDE	2.94±0.79d,A	6.01±0.52c,CD	10.00±0.49b,D	10.55±0.39ab,D	11.82±0.54a,B
	45°	1.63±0.24d,ABC	4.46±0.92d,A	8.32±0.50c,BCD	11.88±0.33b,CD	14.58±1.66b,CD	17.72±1.14a,B
	60°	1.55±0.26d,BCD	4.96±1.30cd,A	11.65±1.58bc,AB	14.98±0.50b,BC	19.31±2.67ab,CD	23.93±4.76a,B
	75°	1.80±0.31d,AB	5.49±2.09d,A	13.71±2.12cd,A	19.98±0.61bc,A	29.28±5.61b,B	41.47±6.65a,A
	80°	1.36±0.20e,BCDE	4.50±1.78de,A	10.99±0.99cd,AB	16.37±1.45bc,AB	19.12±2.17ab,CD	24.63±4.40a,B
	90°	2.16±0.03e,A	4.49±1.12de,A	9.82±1.05cd,ABC	16.16±1.88c,AB	38.36±2.75b,A	46.26±3.92a,A
	120°	1.00±0.05d,DE	4.07±1.81cd,A	8.92±2.21bcd,BCD	15.88±2.78abc,BC	20.19±4.18ab,BCD	23.83±7.42a,B
	150°	0.96±0.12c,DE	2.92±0.87c,A	9.97±1.69b,ABC	15.68±1.13ab,BC	16.65±2.37a,CD	17.98±3.74a,B
	180°	0.94±0.17e,DE	3.00±1.23de,A	7.90±1.77cd,BCD	12.61±0.71bc,BCD	21.47±4.12a,BC	15.59±1.00ab,B
Female	15°	0.77±0.26c,B	2.14±0.55c,B	3.44±0.18c,C	9.40±1.02b,BC	10.00±1.53ab,C	12.60±1.25a,C
	30°	0.72±0.16d,B	2.33±0.60cd,B	4.03±0.06c,C	8.93±0.58b,C	10.63±1.38ab,BC	11.75±0.81a,C
	45°	1.57±0.30d,AB	4.27±1.13cd,AB	7.80±1.00bcd,B	13.45±1.24bc,BC	16.17±2.19b,BC	25.35±6.32a,BC
	60°	1.52±0.37c,AB	5.18±0.57c,A	8.82±1.17bc,AB	16.26±3.79ab,AB	20.79±4.24a,ABC	21.32±3.89a,C
	75°	1.97±0.31d,A	5.50±1.24cd,A	11.64±0.82c,A	20.61±1.99b,A	21.92±1.01b,AB	39.78±5.38a,A
	80°	1.23±0.18c,AB	3.47±0.53c,AB	7.77±1.35bc,B	15.36±1.65ab,ABC	19.67±4.50a,ABC	24.23±5.83a,BC
	90°	1.64±0.45e,AB	4.69±0.59d,AB	9.38±1.39c,AB	14.00±2.36b,BC	27.93±8.03a,A	35.74±3.70a,AB
	120°	0.97±0.23c,B	3.68±0.57c,AB	7.50±0.62bc,B	13.22±1.34b,BC	13.40±1.42b,BC	22.46±5.58a,BC
	150°	0.98±0.19d,B	3.13±0.65d,AB	7.92±1.22c,B	12.46±1.69b,BC	13.89±0.92b,BC	20.64±0.93a,C
	180°	0.86±0.21d,B	3.30±1.32cd,AB	7.92±1.48bc,B	12.14±2.95bc,BC	14.15±1.72b,BC	20.87±2.81a,C

872 Different lowercase and capital letters indicate significant differences at $P < 0.05$ in the results

873 obtained at different light intensities and wing opening angles, respectively.

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889   **Table 6** Heat absorption capacities of the fore wing and hind wing in adult *Tirumala limniace.*

Light intensity		Equilibrium thoracic temperature (°C)		Time (min) required to reach equilibrium temperature		ΔT (°C)		Rate (°C/min) of thoracic temperature increase	
		Fore wing	Hind wing	Fore wing	Hind wing	Fore wing	Hind wing	Fore wing	Hind wing
Male	600 lx	30.99±0.65*	27.52±0.88	8.79±0.39*	11.23±0.83	11.56±0.55 ns	10.37±0.75	1.32±0.06*	0.95±0.11
	5000 lx	47.55±0.67**	40.82±1.17	5.73±0.22*	8.43±0.94	27.12±0.54**	21.53±1.20	4.78±0.25*	2.69±0.27
	15000 lx	60.63±0.73**	50.57±2.06	4.65±0.18*	7.93±0.52	38.96±0.87**	29.70±2.31	8.45±0.42*	3.83±0.40
	25000 lx	67.32±0.52**	62.38±1.07	4.17±0.25*	6.28±0.46	44.49±0.34*	40.80±1.31	10.85±0.59**	6.74±0.69
	40000 lx	68.18±1.02**	60.44±0.55	3.51±0.10*	5.96±0.41	45.23±0.81**	38.44±1.12	12.98±0.55**	6.59±0.45
	60000 lx	76.96±2.88 ns	70.55±0.72	3.65±0.09*	6.12±0.52	51.98±2.77 ns	45.97±0.59	14.25±0.68**	7.78±0.63
Female	600 lx	31.38±0.46**	26.90±0.90	9.39±0.21*	11.44±0.78	13.28±0.81**	5.90±0.90	1.41±0.08*	0.54±0.10
	5000 lx	47.72±1.31 ns	42.96±2.51	8.02±0.18*	12.23±1.34	27.49±1.01 ns	21.96±2.51	3.43±0.13*	1.80±0.13
	15000 lx	61.47±0.53**	57.82±0.67	4.98±0.13*	8.64±0.22	40.16±0.75**	34.82±0.67	8.09±0.27*	4.05±0.17
	25000 lx	65.92±0.62 ns	64.12±0.60	4.03±0.17*	8.06±0.75	43.06±0.75 ns	41.12±0.60	10.80±0.52**	5.26±0.35
	40000 lx	72.87±0.46**	67.18±1.1	3.73±0.21*	6.58±0.48	50.43±0.56**	44.18±1.1	13.72±0.71	6.86±0.43
	60000 lx	75.57±1.05 ns	72.84±1.44	3.74±0.17*	6.22±0.33	50.26±1.19 ns	49.84±1.44	13.54±0.56**	8.12±0.47

890   **, *, and ns indicate the significance levels of differences in the results (equilibrium thoracic temperature, time
891   required to reach equilibrium temperature, ΔT, and rate of thoracic temperature increase) according to the Student's
892   *t*-test between the fore and hind wings at $P < 0.01$, $P < 0.05$, and $P > 0.05$, respectively.

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897 **Table 7** The results of time-series ExpDec2 of exponential models analysis for trends of real-time
898 temperatures of the monitoring points in the heat storage areas and non-heat storages in butterflies
899 *Tirumala limniace*.

ExpDec2 Model: $y = A1*exp(-x/t1) + A2*exp(-x/t2) + y0$

Wing type	Area	Point	y0	A1	t1	A2	t2	*r*	F	*P*
Fore wing	Light area	Sp1	49.10929	-12.4412	27.33323	-9.97643	204.0954	0.99816	1.74E+08	<0.0001
		Sp2	49.57089	-11.0479	179.7561	-11.9106	24.73968	0.99842	1.96E+08	<0.0001
		Sp3	47.28997	-10.1232	24.05404	-10.6675	137.0862	0.99856	2.35E+08	<0.0001
		Sp4	48.98872	-10.933	140.0638	-11.428	23.81826	0.99847	2.13E+08	<0.0001
		Sp5	47.99227	-10.6245	129.5564	-10.7854	25.69463	0.99846	2.14E+08	<0.0001
		Sp6	48.50339	-11.4961	26.27294	-10.2551	137.9374	0.99842	2.09E+08	<0.0001
	Wing base	Sp7	52.29589	-7.40247	12.81485	-18.4286	217.0853	0.99897	2.03E+08	<0.0001
	The dark area for heat storage	Sp8	50.75721	-11.7911	228.043	-10.7115	24.1697	0.99702	1.09E+08	<0.0001
		Sp9	49.82083	-11.158	143.3776	-11.5553	21.9387	0.99868	2.56E+08	<0.0001
		Sp10	49.65997	-10.0475	166.3924	-11.7129	24.33015	0.9976	1.50E+08	<0.0001
		Sp11	49.53145	-11.7152	24.88213	-10.5312	138.5937	0.99852	2.28E+08	<0.0001
	Border in dark area	Sp12	47.91015	-11.173	24.91333	-9.14257	145.2361	0.99726	1.43E+08	<0.0001
Hind wing	Light area	H-Sp1	49.17633	-10.4439	25.37711	-11.6125	215.0843	0.99741	1.18E+08	<0.0001
		H-Sp2	50.26874	-14.1702	238.9041	-8.59803	22.34626	0.99829	1.59E+08	<0.0001
		H-Sp3	49.76717	-7.90298	21.82562	-15.0295	244.5349	0.99901	2.50E+08	<0.0001
		H-Sp4	48.85711	-11.3694	25.41496	-10.9769	161.4886	0.99852	2.08E+08	<0.0001
		H-Sp5	48.40098	-10.3218	159.2493	-11.6644	29.78131	0.99848	1.97E+08	<0.0001
		H-Sp6	48.54843	-12.3569	31.24274	-9.28688	151.8395	0.9983	1.89E+08	<0.0001
	Wing base	H-Sp7	52.09365	-6.07772	11.27207	-19.64	235.8899	0.99925	2.53E+08	<0.0001
	The dark area for heat storage	H-Sp8	51.53298	-10.8477	218.4568	-13.9014	28.09526	0.99883	2.47E+08	<0.0001
		H-Sp9	50.90148	-13.0178	30.27843	-10.1396	194.0823	0.99808	1.60E+08	<0.0001
		H-Sp10	49.46966	-10.9644	24.55755	-11.233	145.7819	0.99839	2.01E+08	<0.0001
		H-Sp11	49.06514	-12.9741	31.49138	-9.03949	155.2494	0.9979	1.53E+08	<0.0001
	Border in dark area	H-Sp12	48.04232	-13.2487	34.84247	-7.43888	185.9954	0.99798	1.74E+08	<0.0001

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904 **Table 8** The results of time-series ExpDec2 of exponential model analysis for trends of real-time
905 temperatures of the monitoring points in the heat transfer channels of butterflies *Tirumala limniace*.

906 **ExpDec2 Model:** y = A1*exp(-x/t1) + A2*exp(-x/t2) + y0

Wing type	Heat transfer channel	Point	y0	A1	t1	A2	t2	r	F	P
Fore wing	Vein A channel	A-1	51.65031	-7.84003	12.75891	-17.2268	207.2903	0.99856	1.60E+08	<0.0001
		A-2	50.5731	-11.4145	195.1354	-11.8801	24.10951	0.99828	1.81E+08	<0.0001
		A-3	49.41572	-11.5431	23.41794	-10.7117	148.3088	0.99858	2.39E+08	<0.0001
		A-4	49.06832	-10.6785	24.03947	-11.0778	133.0077	0.9985	2.25E+08	<0.0001
		A-5	47.6016	-10.7138	26.48365	-9.33575	144.2478	0.9974	1.45E+08	<0.0001
	Vein Cu-Cu$_3$ channel	Cu-1	52.26994	-18.9101	211.9113	-6.97851	12.25504	0.99928	2.77E+08	<0.0001
		Cu-2	49.67318	-11.2014	21.28217	-10.1931	197.2287	0.99303	5.58E+07	<0.0001
		Cu-3	49.61431	-8.88343	204.3245	-11.9366	23.56786	0.99061	4.53E+07	<0.0001
		Cu$_3$-4	49.38674	-11.2699	22.10509	-10.4084	150.2459	0.99763	1.55E+08	<0.0001
		Cu$_3$-5	49.59448	-11.1955	22.80552	-10.8877	135.7532	0.99861	2.52E+08	<0.0001
		Cu$_3$-6	49.06385	-11.857	25.909	-9.68216	144.6714	0.99801	1.80E+08	<0.0001
	Vein Cu-Cu$_2$ channel	Cu-1	52.26994	-18.9101	211.9113	-6.97851	12.25504	0.99928	2.77E+08	<0.0001
		Cu-2	49.67318	-11.2014	21.28217	-10.1931	197.2287	0.99303	5.58E+07	<0.0001
		Cu-3	49.61431	-8.88343	204.3245	-11.9366	23.56786	0.99061	4.53E+07	<0.0001
		Cu-4	48.88576	-11.0924	23.04441	-9.71285	160.9608	0.9957	9.08E+07	<0.0001
		Cu$_2$-5	48.67759	-9.81106	147.3665	-11.1861	26.23936	0.9984	2.25E+08	<0.0001
		Cu$_2$-6	47.66185	-9.15046	138.1042	-11.0852	25.98615	0.99752	1.55E+08	<0.0001
Hind wing	Vein A channel	1A-1	52.1982	-24.3625	250.3032	-2.16858	17.72072	0.99953	2.62E+08	<0.0001
		1A-2	50.81314	-14.4636	236.0123	-8.44482	17.70421	0.99773	1.26E+08	<0.0001
		1A-3	50.97916	-12.6379	26.86096	-11.4056	233.0519	0.99857	2.06E+08	<0.0001
		1A-4	49.37377	-10.3706	212.6243	-12.156	29.12618	0.99859	2.17E+08	<0.0001
		1A-5	47.77004	-12.3352	38.22446	-7.54459	313.1892	0.9978	1.71E+08	<0.0001
	Vein Cu-Cu$_2$ channel	Cu-1	52.06394	-4.74979	11.58034	-21.4292	239.0546	0.99951	3.26E+08	<0.0001
		Cu-2	50.40223	-9.85654	22.84531	-12.667	238.1548	0.99708	1.05E+08	<0.0001
		Cu-3	50.69774	-12.9494	23.92048	-10.4392	219.3316	0.99674	1.04E+08	<0.0001
		Cu$_2$-4	50.08737	-13.0645	30.0606	-9.55433	198.0817	0.99787	1.51E+08	<0.0001
		Cu$_2$-5	47.87697	-12.3765	33.8684	-7.79342	191.6719	0.99745	1.42E+08	<0.0001
	Vein Cu-Cu$_1$ channel	Cu-1	52.06394	-4.74979	11.58034	-21.4292	239.0546	0.99951	3.26E+08	<0.0001
		Cu-2	50.40223	-9.85654	22.84531	-12.667	238.1548	0.99708	1.05E+08	<0.0001
		Cu-3	50.45283	-12.7617	23.48126	-10.4624	201.8555	0.99669	1.02E+08	<0.0001
		Cu-4	50.10416	-12.5917	28.82723	-9.83279	178.2873	0.99704	1.10E+08	<0.0001
		Cu$_1$-5	49.79113	-13.0948	31.51791	-9.12978	159.7369	0.99766	1.39E+08	<0.0001
		Cu$_1$-6	48.74334	-13.6109	37.68257	-7.2046	208.5855	0.9979	1.65E+08	<0.0001

Vein Cu-M-M_3 channel	Cu-1	49.43767	-11.7424	28.44878	-10.0544	141.542	0.99771	1.46E+08	<0.0001
	Cu-2	48.1947	-11.6759	29.62228	-8.88782	150.9702	0.99744	1.41E+08	<0.0001
	Cu-3	52.06394	-4.74979	11.58034	-21.4292	239.0546	0.99951	3.26E+08	<0.0001
	Cu-4	50.40223	-9.85654	22.84531	-12.667	238.1548	0.99708	1.05E+08	<0.0001
	M-5	50.45283	-12.7617	23.48126	-10.4624	201.8555	0.99669	1.02E+08	<0.0001
	M_3-6	49.65581	-12.0016	27.14308	-10.1177	170.5792	0.9977	1.44E+08	<0.0001
	M_3-7	49.23426	-10.7417	184.3841	-11.596	26.7489	0.99845	2.00E+08	<0.0001
Vein R-M-M_1 channel	R-1	52.24029	-20.6188	232.3034	-5.47058	11.76307	0.99934	2.63E+08	<0.0001
	R-2	50.9655	-8.43454	13.48904	-15.4319	215.4063	0.99783	1.24E+08	<0.0001
	R-3	49.8506	-10.9777	207.8621	-10.8279	24.80101	0.99655	9.79E+07	<0.0001
	M-4	49.69803	-10.7669	184.4267	-11.2514	23.31607	0.99702	1.16E+08	<0.0001
	M_1-5	49.16783	-11.2546	26.17524	-10.719	143.3344	0.99783	1.50E+08	<0.0001
	M_1-6	48.86012	-10.2357	135.2823	-10.939	26.87515	0.99784	1.61E+08	<0.0001
	M1-7	48.2474	-11.5281	29.4377	-8.72021	176.2904	0.99685	1.19E+08	<0.0001
Vein R-R_2 channel	R-1	52.24029	-20.6188	232.3034	-5.47058	11.76307	0.99934	2.63E+08	<0.0001
	R-2	50.9655	-8.43454	13.48904	-15.4319	215.4063	0.99783	1.24E+08	<0.0001
	R-3	49.8506	-10.9777	207.8621	-10.8279	24.80101	0.99655	9.79E+07	<0.0001
	R_2-4	49.27588	-11.1911	23.79768	-10.8977	151.1524	0.99836	2.04E+08	<0.0001
	R_2-5	48.42841	-10.3834	27.89841	-10.5232	146.3984	0.99825	1.89E+08	<0.0001

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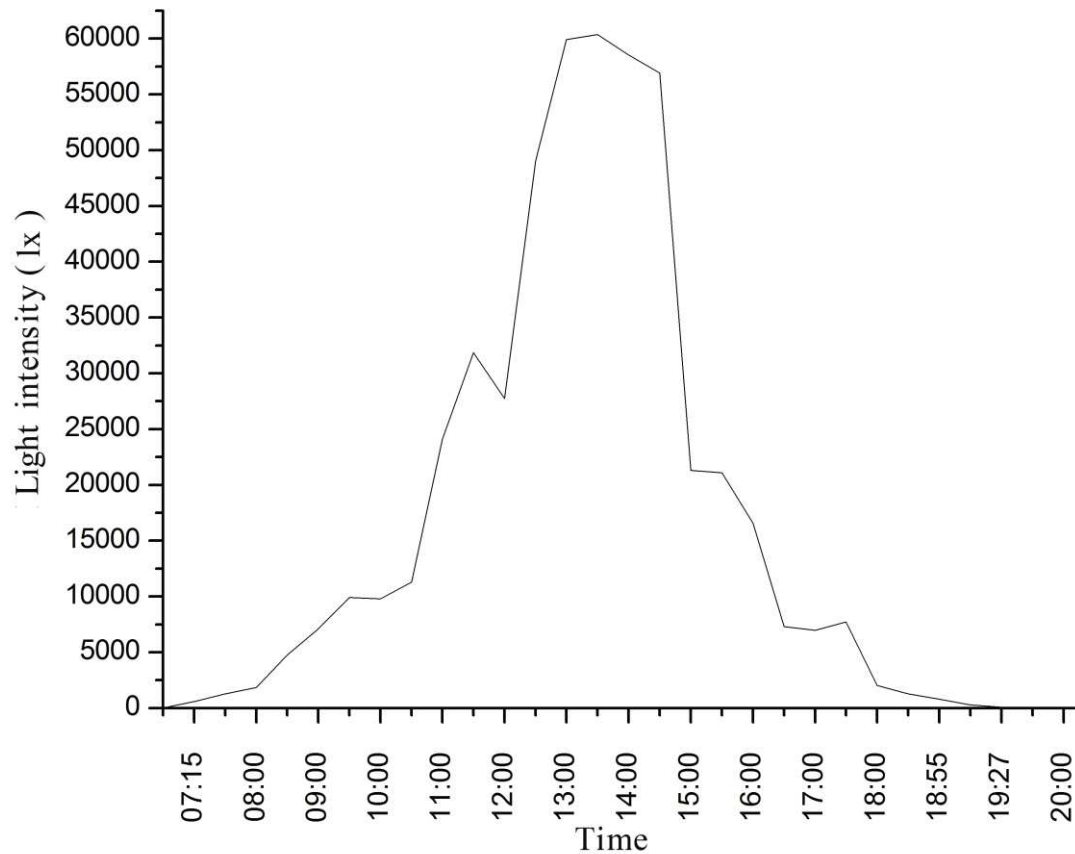
909 **Figure 1** Natural light intensity on September 11, 2017 in Yuanjiang County, Yunnan Province, China.
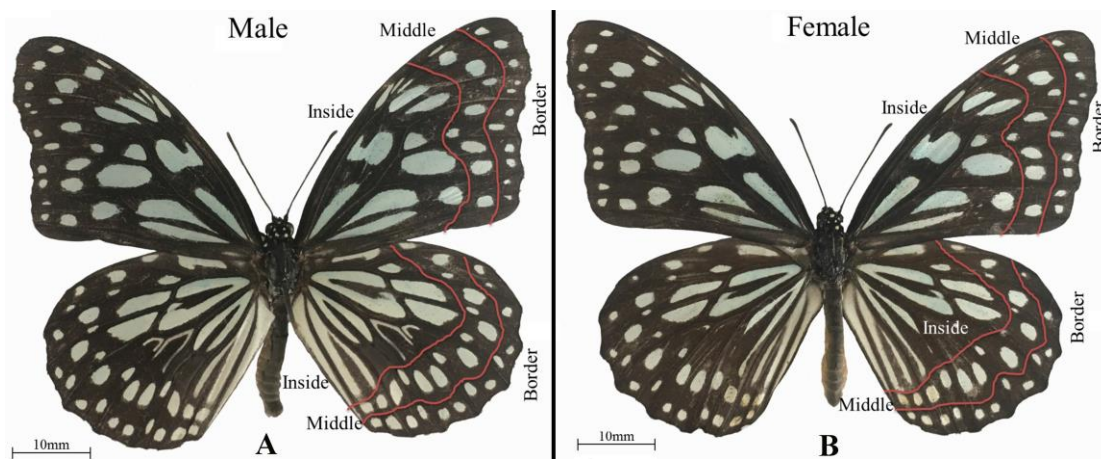

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911 **Figure 2** The wing surface was divided into border, middle, and inside parts to obtain spectral
912 reflectance measurements from the wings of adult *Tirumala limniace* butterflies. A: Male, B: female.
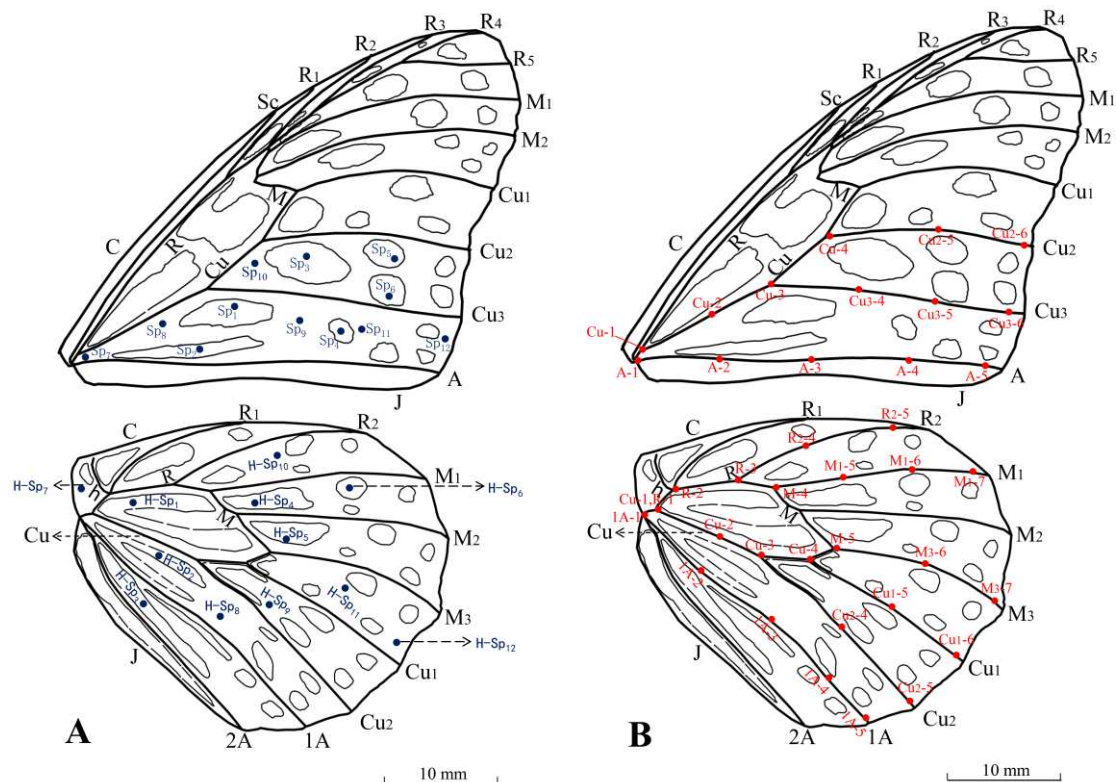
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Figure 3 Distribution of the potential heat storage areas (A) and potential heat transfer channels (B) on the wing surface in adult *Tirumala limniace* butterflies. In A, the light gray area represents the heat storage area and the blue points are points used for real-time temperature monitoring in the heat storage areas (fore wing: Sp8–Sp11, hind wing: H-Sp8–H-Sp11), light areas (fore wing: Sp1–Sp6, hind wing: H-Sp1–H-Sp6), wing base (fore wing: Sp7, hind wing: H-Sp7) and non-storage areas (fore wing: Sp12, hind wing: H-Sp12). In B, the red points are the points used for real-time temperature monitoring during heat transfer in the wing veins. The heat transfer channels are the vein Cu-Cu_2 channel, vein Cu-Cu_3 channel, and vein A channel in the fore wing, and the vein R-R_2 channel, vein R-M-M_1 channel, vein Cu-M-M_3 channel, vein Cu-Cu_1 channel, vein Cu-Cu_2 channel, and vein 1A channel in the hind wing.

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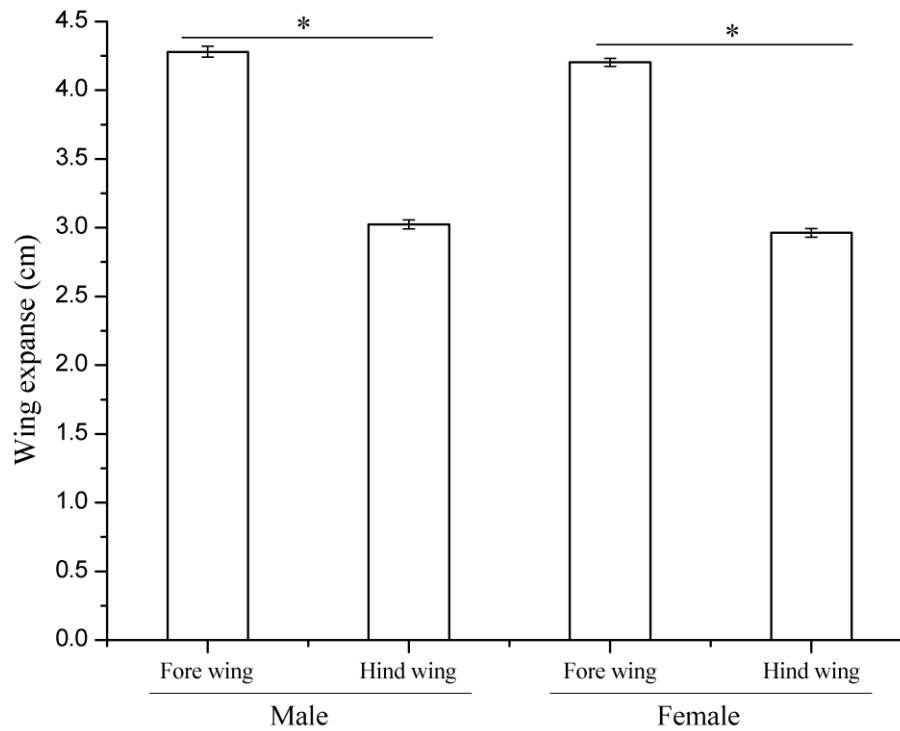
Figure 4 Expanse of the fore and hind wings in adult *Tirumala limniace* butterflies. * indicates a
significant difference at $P < 0.05$ in the wing expanse between the fore and hind wings.

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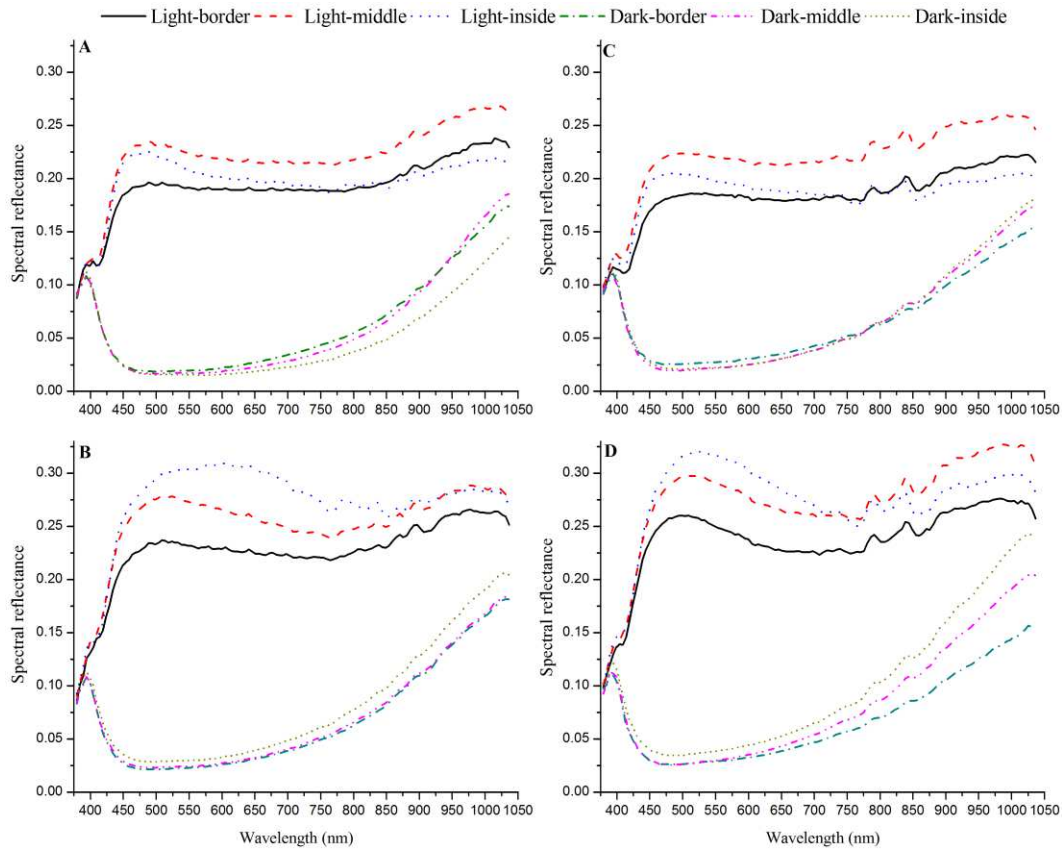
Figure 5 Spectral reflectance of the male fore wing (A), male hind wing (B), female fore wing (C) and female hind wing (D) in adult *Tirumala limniace* butterflies.
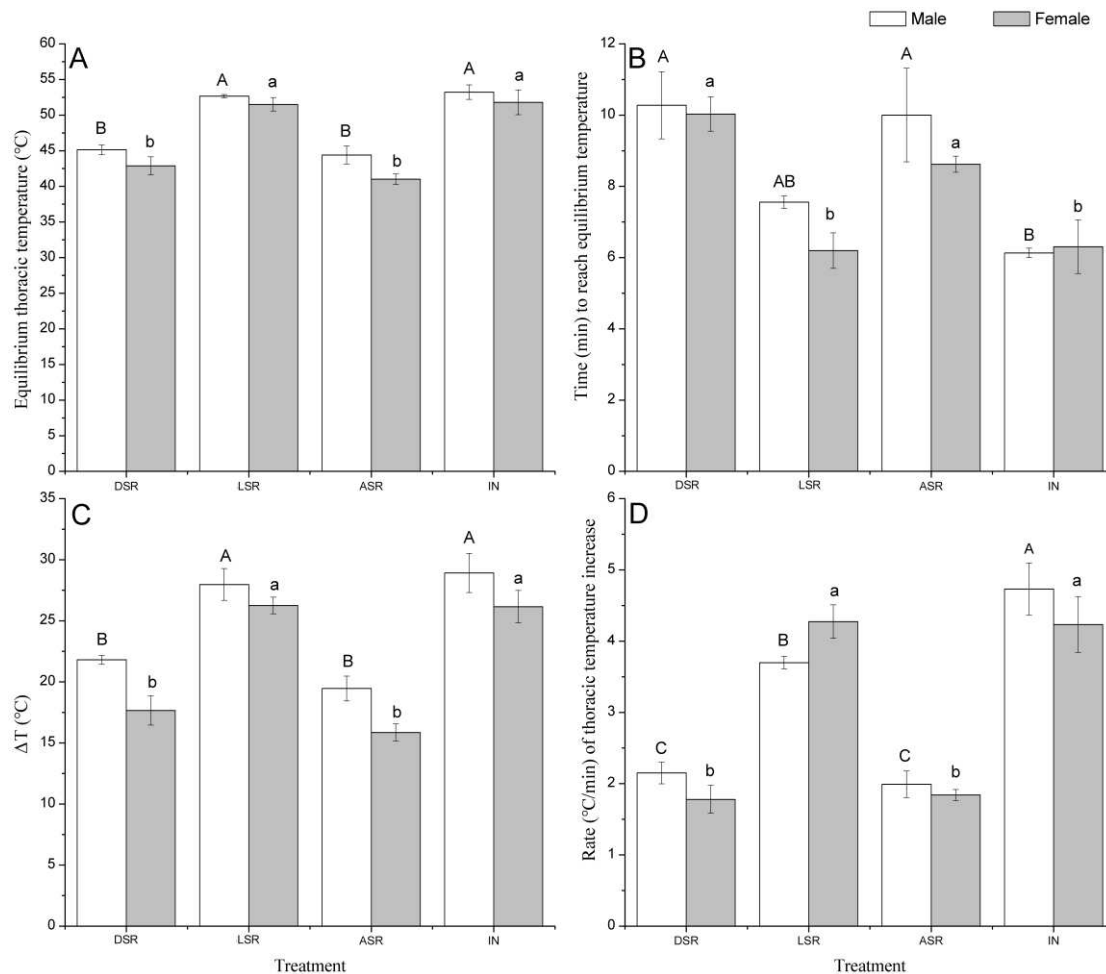
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Figure 6 Equilibrium thoracic temperature (A), time required to reach the equilibrium temperature (B), thoracic temperature excess (ΔT) (C) and rate of thoracic temperature increase (D) in adult *Tirumala limniace* under four scale removal treatments. DSR treatment: scales removed from dark areas; LSR treatment: scales removed from light areas; ASR treatment: all scales removed from the wing surface; and IN treatment: scales on the wings were left intact. Different lowercase and capital letters indicate significant differences at $P < 0.05$ in the results obtained for males and females among the four scale removal treatments.
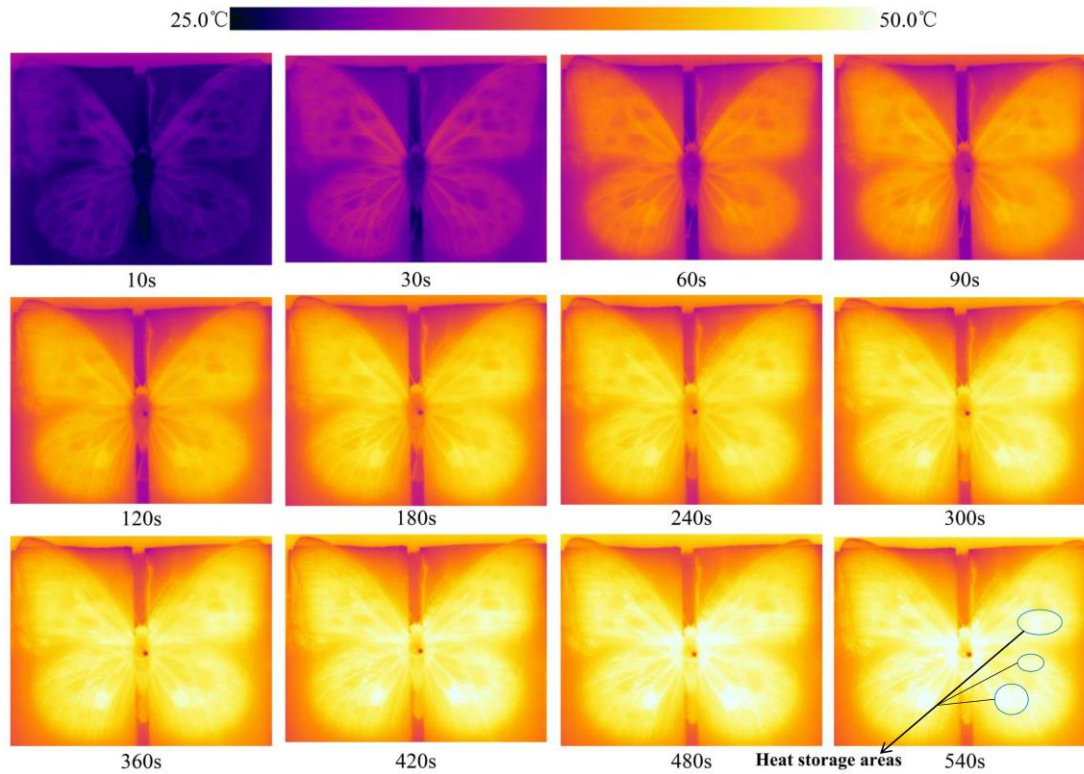
Figure 7 Real-time temperature on the wing surface during heat absorption by adult *Tirumala limniace* butterflies. The numbers below each subgraph indicate the monitoring time in seconds.
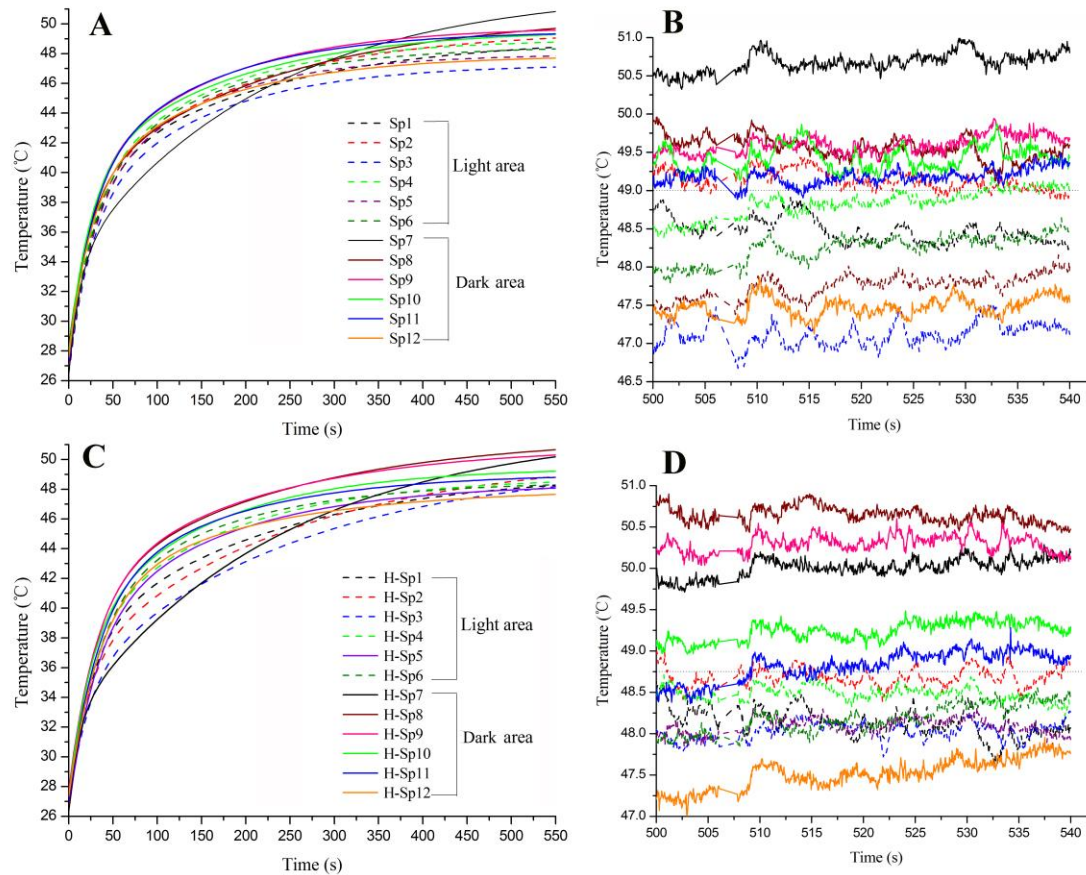
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Figure 8 Real-time temperature at the monitoring points in the heat storage areas and non-heat storage areas during heat absorption by the wing surfaces in adult *Tirumala limniace* butterflies. A: Fore wing; B: real-time temperatures at monitoring points on the fore wing during lighting for 500–540 s; C: hind wing; D: real-time temperatures at monitoring points on the hind wing during lighting for 500–540s.
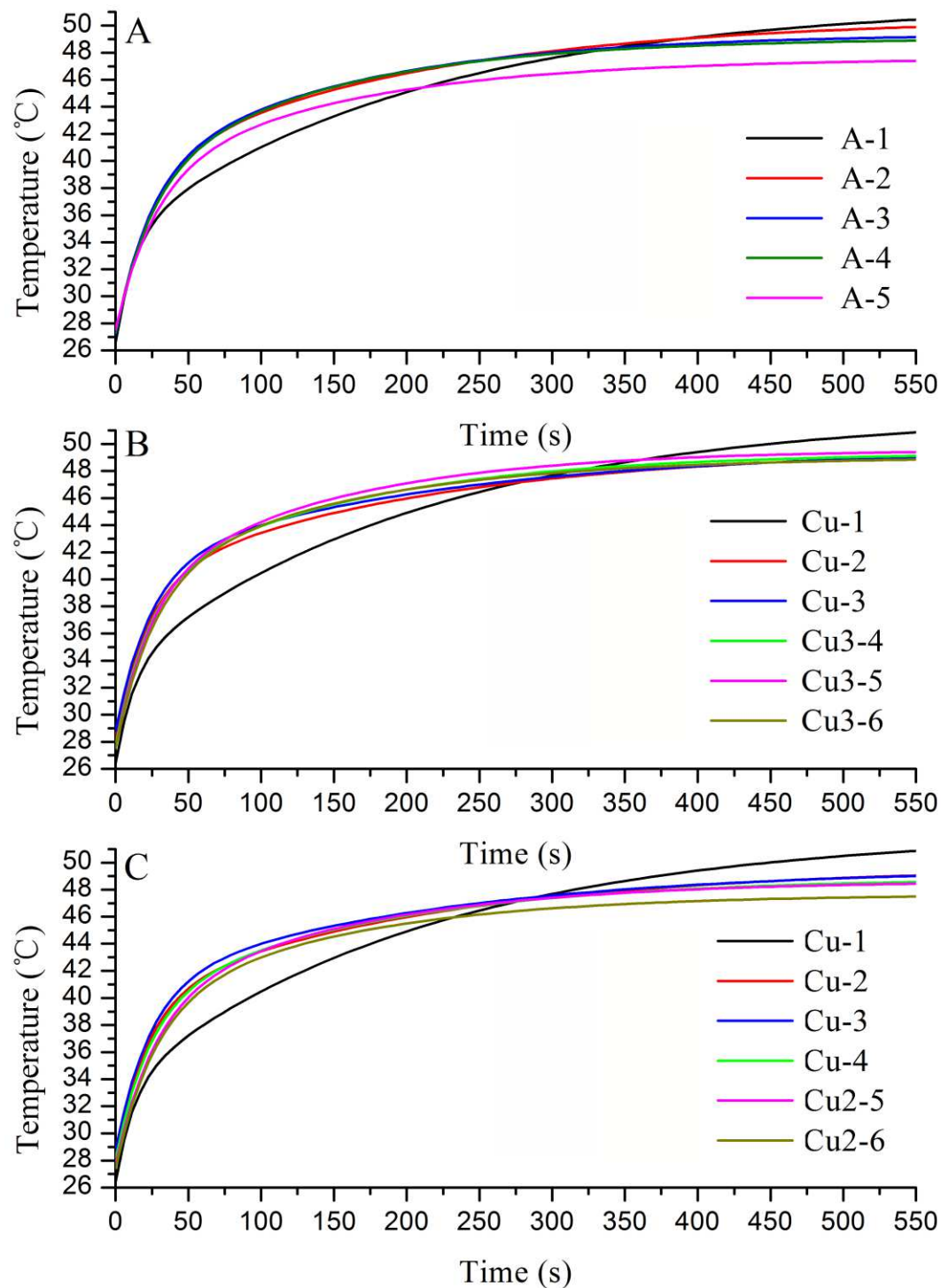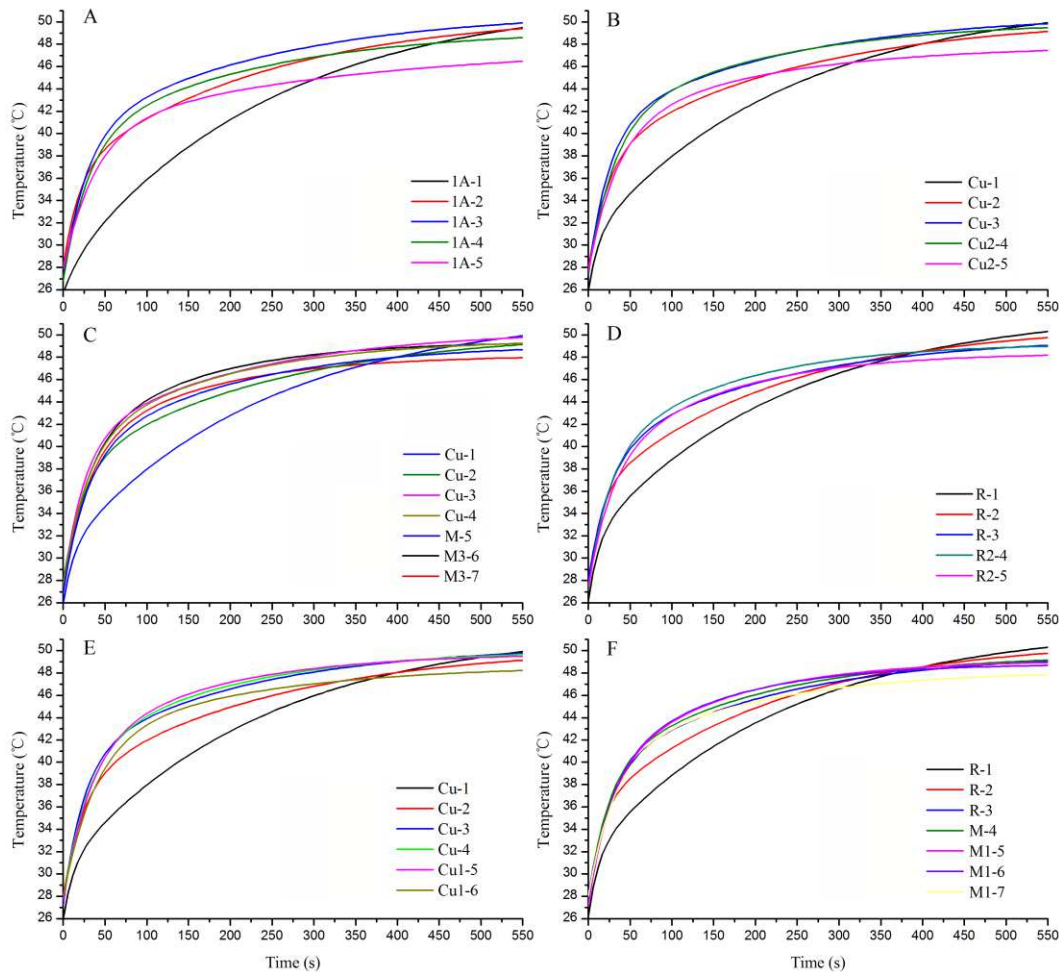
Figure 10 Real-time temperatures at monitoring points on the heat transfer channels on the hind wing during heat absorption by adult *Tirumala limniace* butterflies. A: vein 1A channel; B: vein Cu-Cu$_2$ channel; C: vein Cu-M-M$_3$ channel; D: vein R-R$_2$ channel; E: vein Cu-Cu$_1$ channel; F: vein R-M-M$_1$ channel.