Capacity for heat absorption by the wings of the butterfly *Tirumala limniace* (Cramer)

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Butterflies can directly absorb heat from the sun via their wings to facilitate autonomous flight. However, how is the heat absorbed by the butterfly from sunlight stored and transmitted in the wing? The answer to this scientific question remains unclear. The butterfly *Tirumala limniace* (Cramer) is a typical heat absorption insect, and its wing surface color is only composed of light and dark color. Thus, in this study, we measured a number of wing traits relevant for heat absorption including the thoracic temperature at different light intensities and wing opening angles, the thoracic temperature of butterflies with only one right fore wing or one right hind wing; In addition, the spectral reflectance of the wing surfaces, the thoracic temperature of butterflies with the scales removed or present in light or dark areas, and the real-time changes in heat absorption by the wing surfaces with temperature were also measured. We found that high intensity light (600–60000 lx) allowed the butterflies to absorb more heat and 60−90° was the optimal angle for heat absorption. The heat absorption capacity was stronger in the fore wings than the hind wings. Dark areas on the wing surfaces were heat absorption areas. The dark areas in the lower region of the fore wing surface and the inside region of the hind wing surface were heat storage areas. Heat was transferred from the heat storage areas to the wing base through the veins near the heat storage areas of the fore and hind wings.

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ABSTRACT

Butterflies can directly absorb heat from the sun via their wings to facilitate autonomous flight. However, how is the heat absorbed by the butterfly from sunlight stored and transmitted in the wing? The answer to this scientific question remains unclear. The butterfly *Tirumala limniace* (Cramer) is a typical heat absorption insect, and its wing surface color is only composed of light and dark color. Thus, in this study, we measured a number of wing traits relevant for heat absorption including the thoracic temperature at different light intensities and wing opening angles, the thoracic temperature of butterflies with only one right fore wing or one right hind wing; In addition, the spectral reflectance of the wing surfaces, the thoracic temperature of butterflies with the scales removed or present in light or dark areas, and the real-time changes in heat absorption by the wing surfaces with temperature were also measured. We found that high intensity light (600–60000 lx) allowed the butterflies to absorb more heat and 60−90° was the optimal angle for heat absorption. The heat absorption capacity was stronger in the fore wings than the hind wings. Dark areas on the wing surfaces were heat absorption areas. The dark areas in the lower region of the fore wing surface and the inside region of the hind wing surface were heat storage areas. Heat was transferred from the heat storage areas to the wing base through the veins near the heat storage areas of the fore and hind wings.

INTRODUCTION

29 Sunlight is the most important source of energy and it supports the survival and reproduction of

30 most creatures on Earth. Butterflies can directly utilize the heat from the sun to facilitate their

31 autonomous flight. Previous studies have shown that butterflies must directly absorb the heat from

32 sunlight to increase their thoracic temperature above that of their surroundings in order to allow

33 autonomous flight to occur (*Kemp & Krockenberger, 2004; Barton et al., 2014; Bonebrake et al.,*

34 *2014; Kleckova et al., 2014; Mattila 2015; Liao et al., 2017*). Autonomous flight is required for

35 the reproductive activities of butterflies, including dispersal, courtship, mating, and oviposition

36 behaviors (*Shreeve, 1992; Bennett et al., 2012*). Therefore, heat absorption is an indispensable

37 prerequisite for the reproductive success of butterflies (*Gibbs et al., 2010; Westerman et al., 2014;*

38 *Gibbs et al., 2018*).

39   Butterflies primarily absorb heat via their wings (*Shanks et al., 2015; Han et al., 2016; Niu et*

40 *al., 2016*). When adult butterflies require heat for autonomous flight, they adjust their body posture

41 and either fully expand their wings or angle them to allow the optimal absorption of sunlight,

42 where the heat absorbed is then transferred to the thoracic muscles to enable flight (*Heinrich, 1990;*

43 *Huey et al., 2003*). Some studies indicate that the angle of the incoming sunlight and the wing

44 opening angle can both significantly influence the rate and amount of heat absorption in butterflies

45 (*Plattner, 2004; Shanks et al., 2015; Niu et al., 2016*). Indeed, heat absorption is important, but it

46 has to be modulated via behavior to avoid overheating (*Kingsolver, 1985*).

47   Based on a study of a new mechanism of behavioral thermoregulation, Kingsolver (1985)

48 suggested that *Pieris* butterflies use their predominantly white wings as solar reflectors to reflect

49 solar radiation onto the body and to increase their body temperature. Some studies also indicate

50 that butterflies rely on "photonic crystal" structures in their wings to absorb heat (*Li et al., 2004;*

51 *Han et al., 2013; Luohong, 2014; Han et al., 2015a*). Therefore, the transfer of heat in a butterfly

52 not only depends on reflection and absorption from the wing surface, but it also is due to the

53 internal tissue in the wing. Thus, what is the specific tissue involved with heat transfer in the wing?

54 The answer to this question remains unclear. Previous studies of solar heat absorption by butterfly

55 wings have focused on the forewings (*Devries, 2015; Wu et al., 2015*) whereas none have

56 considered the hind wings. As a consequence, it is not clear whether the fore wings or hind wings

57 have a greater capacity for heat absorption.

58   Light intensity also significantly affects heat absorption by butterflies. In the butterfly

59 *Heteronympha merope*, as the intensity of solar radiation increases, the thoracic temperature

60 excess increases significantly regardless of wings being fully extended or closed (*Barton et al.,*

61 *2014*). Kingsolver (1983) found that short-term meteorological variations, such as intermittent

62 cloudy periods, can rapidly reduce the body temperature excess and flight activity to zero in *Colias*

63 butterflies. The light intensity also significantly influences the ability of the butterfly *Tirumala*

64 *limniace* to absorb heat, where it was shown that the equilibrium thoracic temperature of adults

65 was higher when exposed to 2240 lx compared with other light intensities and the time required to

66 reach it was shorter. In addition, the thoracic temperature excess and rate of thoracic temperature

67 increase were higher and achieved more quickly (*Liao et al., 2017*), the sunlight intensity is about

68 2240 lx from 07:00am to 08:00am in summer in Yuanjiang county, Yunnan province, China.

69   Previous studies have shown that color significantly affects the absorption of heat in butterflies

70 (*Schmitz, 1994; Van Dyck et al., 1997; Brashears et al., 2016; Stuart-Fox et al., 2017*). Some

71 studies indicate that more heat is absorbed when the wings of butterflies are darker, (*Kingsolver,*

72 *1987; Schmitz, 1994; Berwaerts et al., 2001; Clusella Trullas et al., 2007*). Some butterflies

73 exhibit wing surface melanism to increase their ability to absorb heat (*Guppy, 1986; Clusella*

74 *Trullas et al., 2007*), but wing melanization is not directly functional to increasing heat absorption,

75 as melanin is involved in numerous functions (Stuart-Fox et al., 2017). Compared with the distal

76 wing area, melanism on the wing surface near the body is more conducive to heat absorption by

77 butterflies (*Kingsolver, 1987; Brashears et al., 2016*). However, few studies have considered the

78 specific wing surface areas that are used for heat absorption.

79   In this study, we aimed to understand the effects of the light intensity and wing opening angle

80 on heat absorption, as well as clarifying the differences in the heat absorption capacity of the fore

81 and hind wings, the distribution of heat absorption and non-heat absorption areas on the wing

82 surfaces, and whether the wing has the ability to store heat temporarily and the location of the heat

83 storage areas on the wing surfaces in order to identify the wing tissue that serves as the heat transfer

84 channel. Elucidating the heat absorption capacity of butterflies may provide a deeper

85 understanding of the utilization of solar heat by insects.

86   *Tirumala limniace* (Cramer) is a typical butterfly that directly utilizes solar heat. In the field, we

87 have investigated that adults show high flight activity on the sunny days, but on cloudy and rainy

88 days, the butterflies do not fly even when the air temperature is high. The wings of the male and

89 female butterflies have the same morphology and the wing surface only comprises black (black

90 background) and light blue (light blue bands) areas (*Chen et al., 2008*). Hence, according to the

91 color depth, the wing surface can be divided into dark and light areas, while the wings of other

92 butterflies in Yuanjiang County have more colors composition. Thus, the color composition of the

93   wing surface is suitable for studying the heat absorption capacity of butterflies. At 243–2240 lx,

94   high light intensity enabled adult butterflies to quickly absorb more heat than at low light

95   intensities to elevate their thoracic temperature to above that of the environmental temperature and

96   to take off earlier than at low light intensities (*Liao et al.*, *2017*). However, the light intensity range

97   considered in a previous study by Liao *et al.* (2017) was too narrow to determine the appropriate

98   light intensity for heat absorption by the adult *T. limniace* butterfly. In China, *T. limniace* is mainly

99   distributed in the dry hot valleys of south Yunnan Province, Guangxi Province, and Guangdong

100 Province (*Chen et al., 2008*). Yuanjiang County, Yunnan Province, China, which was the site of

101 the artificial breeding ground, is also in the actual habitat range for this butterfly. In this study,

102 according to the natural light intensity in Yuanjiang County, a light intensity range of 600–60000

103 lx was selected to study the heat absorption capacity of *T. limniace* butterflies in order to

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

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

106 different light intensities and wing opening angles in order to determine the most appropriate light

107 intensity and wing opening angle for heat absorption. The thoracic temperature was measured in a

108 butterfly with only one right fore wing or one right hind wing to elucidate the difference in the

109 heat absorption capacity of the fore and hind wings. The spectral reflectance was measured for the

110 wings to identify the distribution of the heat absorption and non-heat absorption areas on the fore

111 and hind wings. In order to demonstrate that dark areas are responsible for heat absorption on

112 butterfly wings, we investigated heat absorption in butterflies with the scales removed or present

113 in light or dark areas, respectively. To identify the wing surface areas involved with heat storage

114 and transfer after heat absorption by butterfly wings, we monitored the real-time temperature

115 changes on the wing surface during heat absorption in adult *T. limniace*. Once identified the heat

116 storage areas and non-storage areas, we also monitored real-time temperature changes in these

117 areas, as well as the wing veins involved with heat transfer, to further determine the heat storage

118 areas and the transfer channel on the wing surface. Based on the results, we obtained a clear

119 understanding of the heat absorption capacity of the wings in the butterfly *T. limniace* to facilitate

120 further research into the mechanism responsible for the utilization of solar heat by insects.

MATERIALS AND METHODS

Insects

123   *T. limniace* pupae were purchased from the Ornamental Insect Technology Development,

124   Kunming Zhonglin Co. Ltd, Kunming, China. The pupae were placed on a cylindrical net (height:

125   65 cm, diameter: 50 cm) on top of a towel so they could readily spread their wings after emergence.

126   Subsequently, the pupae were transferred to a room at $25 \pm 1°C$ with a relative humidity of $75\% \pm$

127   5% under a 14:10 light:dark photoperiod. After the adults emerged, the females and males were

128   reared separately in two different cages to prevent mating. Five-day-old unmated adults (306

129   female and 308 male adults) were used in this study. All the butterflies used in the experiment

130   were living.

131   In China, *T. limniace* is mainly distributed in the dry hot valleys of south Yunnan Province,

132   Guangxi Province, and Guangdong Province. Yuanjiang County, Yunnan Province, China, which

133   was the artificial breeding ground, is also in their normal range habitat. This butterfly is important

134   for ecological and environmental quality monitoring in south China. The optimal temperature

135   range for survival and flight is 25–36°C. During the first and second day after emergence, adult *T.*

136   *limniace* gradually unfurl their wings and exhibit low flight activity. Their flight activity increases

137   significantly from 3 days of age and the peak flight activity occurs from 4 to 7 days of age during

138   the summer and autumn when the thermal absorption activity is also very high. Thus, unmated

139   adults aged 5 days were used in this study.

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

141   We investigated the effects of the light intensity and wing opening angle on the heat absorption

142   capacity of adult *T. limniace* butterflies. Yuanjiang County, Yunnan Province, China, is a suitable

143   habitat for the butterfly *T. limniace*, and its population is mainly observed from July to October

144   every year. Thus, the natural light intensity on September 11, 2017 in Yuanjiang County, Yunan

145   Province, China, was selected as the reference standard for the light intensity in this study because

146   the skies were clear and cloudless on this day. Based on the natural light intensity levels between

147   07:00 to 20:00 h on September 11, 2017 (Figure 1), six light intensity levels were selected for this

148   study, i.e., 600, 5000, 15,000, 25,000, 40,000, and 45,000 lx. The left and right wings form a

149   specific angle when they are open which angle ranges from 0° to 180°. Based on this angle range,

150   10 wing opening angles were tested in this study, i.e., 15°, 30°, 45°, 60°, 75°, 80°, 90°, 120°, 150°,

151   and 180°. An orthogonal design was used in this experiment to study the effects of the light

152   intensity and wing opening angle on heat absorption by the butterfly wings.

153   According to the specific angle required, a plane with the selected angle was cut with a knife
154   along the middle line of a white plastic foam board (side length: 10 cm, thickness: 6 cm) and the
155   adult *T. limniace* wings were fixed on this plane. Thus, a new unmated 5-day-old adult butterfly
156   was fixed on the plane at a specific wing opening angle using double-sided adhesive tape. The
157   plane with the affixed adult butterfly was placed in a dark room (length: 100 cm, width: 80 cm,
158   height: 80 cm). The walls of the dark room were made of black-out cloth and the front wall of the
159   dark room comprised a curtain made of awning cloth to facilitate the placement of butterflies. A
160   75 W halogen lamp (OSRAM-64841FLSP, Osram China Lighting Ltd, Shanghai, China) was hung
161   60 cm above the bottom of the dark room. The light intensity of the lamp was adjusted with a
162   potentiometer (CHILFU, Shanghai Wenfu Electric Co. Ltd, Shanghai, China).

163   Before turning the lamp on, the butterfly fixed on the plane was maintained in the dark room for
164   15 min in order to stabilize its body temperature to avoid the influence of body temperature on
165   heat absorption by the butterfly. After switching the lamp on, the thoracic temperature was
166   recorded every 10 s until the temperature was maintained at a set temperature for 90 s, thereby
167   indicating that the thoracic temperature of the butterfly had reached equilibrium under the specific
168   light intensity. The thoracic temperature was measured using a thermocouple thermometer
169   (Thermometer GM1312, Shenzhen Jumaoyuan Science and Technology Co. Ltd, Shenzhen,
170   China). A thermistor was inserted through the mesoscutellum and placed in or near the dorsal
171   longitudinal muscles to record the thoracic temperature. During each run of the experiment, we
172   recorded the equilibrated thoracic temperature, rate of thoracic temperature increase (Total change
173   in temperature over time), ΔT as the difference in temperature between the thorax and the ambient
174   temperature, and the time when the thoracic temperature reached equilibrium. Three female and
175   three male adult butterflies were tested for each orthogonal treatment with the different light
176   intensities and wing opening angles. In total, 180 female and 180 male butterflies were tested in
177   this experiment.

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

179   To determine the difference in the heat absorption capacity of the fore and hind wings, we measure
180   the thoracic temperature in a butterfly with only one right fore wing or only one right hind wing
181   under six light intensities, i.e., 600, 5000, 15,000, 25,000, 40,000 and 45,000 lx. The two hind
182   wings and left fore wing were cut from a new unmated 5-day-old adult butterfly using surgical

183   scissors so only the right fore wing remained (fore wing treatment). The two fore wings and left
184   hind wing were cut from another new unmated 5-day-old adult butterfly using surgical scissors so
185   only the right hind wing remained (hind wing treatment). The butterfly was then fixed on a
186   horizontal plane (side length: 10 cm, thickness: 6 cm) without any angle, before it was placed and
187   maintained in the dark room for 15 min so its body temperature could stabilize before turning the
188   lamp on. After switching the lamp on, during each run of the experiment, we recorded the
189   equilibrated thoracic temperature, the rate (°C/min) of thoracic temperature increase, ΔT, and the
190   time required to reach equilibrium. In this experiment, we tested six female and six male butterflies
191   with only one right fore wing at each light intensity, and six female and six male butterflies with
192   only one right hind wing at each light intensity. In total, we tested 36 female and 36 male butterflies
193   in the fore wing treatment, and 36 female and 36 male butterflies in the hind wing treatment. We
194   also measured the wing expanse for both the fore and hind wings of the adult butterflies using 37
195   female and 34 male adult butterflies.

196   Reflectance of light and dark areas

197   To determine the distribution of the heat absorption and non-heat absorption areas on the fore and
198   hind wings, we measured the spectral reflectance from the wings of adult butterflies. A higher
199   spectral reflectance indicates weaker light absorption and heat absorption, whereas lower spectral
200   reflectance denotes stronger light absorption and heat absorption. The wing of the *T. limniace*
201   butterfly appears the same in both sexes, but they differ because there is a scaly bag with a
202   protruding ear in the middle of the Cu_2 chamber in the male butterfly. The wing surface is black
203   with many transparent azure markings (Figure 2). Therefore, the wing surface can be divided into
204   light areas and dark areas according to the color shade on the wing surface.
205   The right fore and right hind wings were cut from a female butterfly and a male butterfly. During
206   the cutting process, the integrity of the wings was maintained as far as possible and we prevented
207   scale removal from the wings. The wings were then placed in the dark room. The light intensity in
208   the dark room was set to 5000 lx. The spectral reflectance of the wings was measured using a
209   spectrograph (SOC710 HS-Portable, Surface Optics Corporation, San Diego, USA). As shown in
210   Figure 2, the dorsal surfaces of the fore and hind wings were divided into three parts comprising
211   the border, middle, and inside parts. The spectral reflectance was then calculated for the dark and
212   light areas in these three parts. The average spectral reflectance of all the light areas in each part
213   was taken as the spectral reflectance of the light areas in this part, and the average spectral

214   reflectance of all the dark areas in each part was taken as the spectral reflectance of the dark areas

215   in this part. In addition, the excised fore and hind wings were placed under a VHX-1000 super-

216   high magnification lens zoom 3D microscope (VHX-1000, Keyence (China) Co. Ltd, Shanghai,

217   China) to obtain images. The areas of the light areas, dark areas, and the entire wing surface were

218   measured with an X/Y measurement system under the microscope. The ratios of the light areas

219   and dark areas on the wing surfaces were also determined.

220   **Heat absorption capacities of dark and light areas on the wings**

221   In order to demonstrate that the dark area was responsible for heat absorption via the butterfly

222   wings, we investigated heat absorption in butterflies treated with four different scale removal

223   treatments comprising the removal of scales from dark areas (DSR treatment), the removal of

224   scales from light areas (LSR treatment), the removal of all scales from the wings (ASR treatment),

225   and leaving the scales intact on the wings (IN treatment). Scales are the main tissues for heat

226   absorption of butterfly wings. And the structure color of the wing surface is determined by the

227   scale structure and arrangement. Thus, the presence or absence of scales can be used to determine

228   the heat absorption ability of a certain area of wing surface. The scales were gently removed from

229   the wing surfaces with a fine brush in each treatment. The treated butterflies were then placed in

230   the dark room. The light intensity was 5000 lx. After switching the lamp on, during the course of

231   each experiment, we recorded the equilibrated thoracic temperature, rate of thoracic temperature

232   increase, ΔT, and the time required to reach equilibrium. Three female and three male butterflies

233   were tested for each treatment. All of the butterflies used in this experiment were new and unmated

234   5-day-old adult *T. limniace*.

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

236   We monitored the real-time temperature changes on the wing surface in order to determine the

237   wing surface areas involved with heat storage and transfer during heat absorption by the butterfly

238   wings. The color and markings on the wing surfaces are the same in male and female butterflies,

239   so we only measured the real-time temperature changes on the wing surfaces of male butterflies

240   during heat absorption. In this experiment, five new unmated 5-day-old male butterflies were

241   examined. A new unmated 5-day-old male butterfly was fixed to a square white plastic foam board

242   (10×10 cm) using insect dissection needles. The wings were fully extended to facilitate real-time

243   temperature monitoring on the wing surface. The butterfly was then placed in the dark room and
244   the light intensity was set to 5,000 lx. The heat absorption rate under 5,000 lx was slower than that
245   at light intensity levels of 15,000–25,000 lx, but it was too slow at 600 lx, so we selected 5,000 lx
246   because it yielded a suitable heat absorption rate for real-time wing temperature monitoring. The
247   real-time temperature changes on the wing surface were recorded using a thermal infrared imager
248   (Flir A600s, FLIR Systems, Inc., Wilson, OR, USA) until the thoracic temperature reached
249   equilibrium.

250   To determine if dark areas served at heat storage areas, we selected 6 points in the dark area and
251   6 points in the light area and compared their real-time temperature differences. In addition, we
252   selected evenly distributed points from border of wing surface to the wing base to identify heat
253   transfer channels. The distributions of all points on the fore and hind wings are shown in Figure
254   3A. The distributions of the points on the wing vein on the wing surfaces are shown in Figure 3B.
255   Five to seven points were selected for each heat transfer channel. Here, we define heat absorption
256   areas as those with fast initial heating rates, but not necessarily high equilibrium temperatures. In
257   contrast, heat storage areas are defined as areas with delayed but rapid heating rates and a high
258   equilibrium temperature.

Statistical analysis

260   The interaction effects of the light intensity and wing opening angle on heat absorption were
261   analyzed using two-way ANOVA. We analyzed ΔT, the thoracic equilibrium temperature, rate of
262   thoracic temperature increase, and the time required to reach equilibrium under different light
263   intensities and wing opening angles simultaneously using one-way ANOVA. Duncan's multiple-
264   range test was used to compare multiple means when significant differences were detected.
265   Differences in ΔT, the thoracic equilibrium temperature, rate of thoracic temperature increase, the
266   time required to reach equilibrium, and the wing expanse between the fore and hind wings were
267   validated using the Student's *t*-test. The differences of spectral reflectance among different areas
268   in male and female wings were analyzed by Kruskal-Wallis test. The differences in the areas of
269   the light and dark wing surface areas were analyzed using chi-square test. Differences in ΔT, the
270   thoracic equilibrium temperature, rate of thoracic temperature increase, and the time required to
271   reach equilibrium in the SDR, SLR, SAL, and IN treatments were analyzed using one-way
272   ANOVA. Duncan's multiple-range test was used to compare multiple means when significant
273   differences were detected. The trends of real-time temperatures of the monitoring points in the

274   dark areas, light areas, and wing veins were analyzed using time-series ExpDec2 of exponential

275   models (y = A1*exp(-x/t1) + A2*exp(-x/t2) + y0). A1 and A2 is the pre-factor, and they can

276   indicate an increasing trend of the y value (the temperature of the points); t1 and t2 are the

277   relaxation time; y0 is the offset, it can reflect the final equilibrium temperature.

278   **RESULTS**

279   **Interaction effects of light intensity and wing opening angle on heat absorption**

280   **by adult butterflies**

281   The wing opening angle and light intensity significantly affected the heat absorption capacity of

282   adult *T. limniace* butterflies (Table 1). The equilibrium thoracic temperature, time required to reach

283   equilibrium temperature, ΔT, and the rate of thoracic temperature increase were affected

284   significantly by the wing opening angle and light intensity in both male and female butterflies

285   (Table 1). The interaction effect of the light intensity and wing opening angle on the rate of thoracic

286   temperature increase was significant in both male and female butterflies, but the interaction effects

287   on the equilibrium thoracic temperature, time required to reach equilibrium, and ΔT were not

288   significant (Table 1). The direction of such results is described into detail in the following sections

289   **Effects of light intensity on the heat absorption capacity**

290   The light intensity significantly affected the heat absorption capacity in adult *T. limniace* (Tables

291   2–5). In both the female and male butterflies, within the range of 600–60,000 lx, the equilibrium

292   thoracic temperature became significantly higher as the light intensity increased under the same

293   wing opening angle (Table 2). The time required to reach the equilibrium temperature became

294   shorter as the light intensity increased (Table 3). ΔT became significantly higher as the light

295   intensity increased (Table 4). The rate of thoracic temperature increase also became faster as the

296   light intensity increased (Table 5).

297   However, we also found that when the light intensity was above 40,000 lx, the equilibrium

298   temperature could rapidly exceed 70°C, which was much higher than the butterflies could tolerate,

299   and thus exposure to a light intensity above 40,000 lx caused the death of the butterflies half an

300   hour after the experiment finished. In summary, a higher light intensity could allow butterflies to

301   absorb more heat (Tables 2–5).

302 **Effects of wing opening angles on the heat absorption capacity**

303 The wing opening angle also significantly influenced the heat absorption capacity of adult *T.*
304 *limniace* (Tables 2–5). Compared with wing opening angles 15–45° and 120–180°, when male and
305 female butterflies were at wing opening angles 60–90°, the equilibrium temperatures were higher
306 (Table 2), the times required to reach the equilibrium temperature were much shorter (Table 3),
307 the values of ΔT were much higher (Table 4), and he rates of thoracic temperature increase were
308 faster (Table 5). However, the influence of wing opening angle was only seen at some light
309 intensities, particularly the higher light intensities. Thus, the optimal wing opening angles for heat
310 absorption ranged from 60° to 90°.

311 **Heat absorption capacities of the fore wing and hind wing**

312 The heat absorption capacities of both the fore wing and hind wing were significantly affected by
313 the light intensity where the capacity of the fore wings was higher than that of the hind wings
314 (Table 6). The Student's *t*-test was used to analyze the differences in the heat absorption capacities
315 of the fore wing and hind wing in both female and male butterflies (Table 6). The results showed
316 that the heat absorption capacity of the fore wing was much higher than that of the hind wing in
317 both female and male butterflies (details see Table 6). The equilibrium temperatures and values of
318 ΔT were positively higher for the fore wings than the hind wings under 600–40,000 lx (Table 6),
319 while the times required to reach equilibrium temperature under 600–60,000 lx were significantly
320 shorter in the fore wings than the hind wings, and the rates of thoracic temperature increase were
321 also significantly faster in the fore wings than the hind wings (Table 6). In summary, within the
322 range of 600–60,000 lx, the fore and hind wings could both absorb much more heat at a faster rate
323 as the light intensity increased. The heat absorption capacity of the fore wing was much higher
324 than that of the hind wing (Table 6).

325 **Identification of heat absorption and non-heat absorption areas**

326 The spectral reflectance of the wings indicated that the dark areas of the wings were used for heat
327 absorption, whereas the light areas did not absorb heat (Figure 4). The spectral reflectance values
328 of the light areas on both the fore and hind wings were all much higher than those of the dark areas
329 (Male fore wing: $Z=585.340$, $P<0.0001$; Male hind wing: $Z=589.787$, $P<0.0001$; Female fore

330   wing: $Z=583.716$, $P<0.0001$; Female hind wing: $Z=574.677$, $P<0.0001$; Figure 4). The dark areas

331   were significantly larger on both the fore and hind wings than the light areas (male fore wing: X^2

332    $= 20.841$, $P < 0.0001$; male hind wing: $X^2 = 10.562$, $P = 0.0012$; female fore wing: $X^2 = 16.237$, P

333   < 0.0001; female hind wing: $X^2 = 7.242$, $P = 0.0071$). However, the light areas still accounted for

334   about 20% of the fore wing area and about 29% of the hind wing area. In summary, the dark areas

335   could be used to absorb heat, whereas the light areas may prevent the butterfly from absorbing too

336   much heat.

Heat absorption capacities of dark and light areas on the wings

338   Scale removal treatment significantly impacted equilibrium thoracic temperature (Figure 5). Based

339   on the multirange tests, the effect was due to removal of the dark scales and all scales, while there

340   was no difference in the response variables between intact butterflies and those with light scales

341   removed. When the scales were removed from the light areas of the wings, the equilibrium thoracic

342   temperature, ΔT, the time required to reach equilibrium temperature, and the rate of thoracic

343   temperature increase were not significantly different from those in the butterflies without scale

344   removal. However, their equilibrium thoracic temperatures (male: $F_{3,8} = 28.269$, $P < 0.0001$;

345   female: $F_{3,8} = 21.132$, $P < 0.0001$) and the values of ΔTs (male: $F_{3,8} = 15.686$, $P < 0.0001$; female:

346    $F_{3,8} = 29.17$, $P < 0.0001$) were significantly higher, and the time required to reach the equilibrium

347   temperature (male: $F_{3,8} = 5.96$, $P = 0.0019$; female: $F_{3,8} = 29.170$, $P < 0.0001$) and the rates of

348   thoracic temperature increase (male: $F_{3,8} = 34.839$, $P < 0.0001$; female: $F_{3,8} = 31.613$, $P < 0.0001$)

349   were significantly shorter and faster, respectively, than those of butterflies with all scales removed

350   from the wings or with scales removed from the dark areas (Figure 5). These results indicate the

351   dark areas of the wings are the areas where the butterflies absorb heat, whereas the light areas

352   cannot absorb heat.

Heat storage and transfer in the wings

Real-time temperatures on the wing surface during heat absorption

355   The wing temperature increased in *T. limniace* as the lighting time increased, and the temperatures

356   of the wing base and thorax also increased (Figure 6). After the light was switched on, heat

357   absorption by the wings began immediately. The thoracic temperature reached equilibrium after

358   lighting for 480 s. The temperatures of the light areas on both the fore and hind wings were lower

359 than those of the dark areas during heat absorption in adult *T. limniace* (Figure 7). As the lighting
360 period continued, heat appeared to accumulate in some areas of the wing surface and the
361 temperature was higher than that of other areas (Figure 6 & 7).

362 Real-time temperatures in the heat storage and non-storage areas on the wing surface during
363 heat absorption

364 The temperature at each point on the fore and hind wing surfaces increased as the lighting period
365 increased as the analysis of time-series ExpDec2 of exponential models (Figure 7 & Table 7). On
366 the fore wing, the base of the wing (Sp7) heated at a conspicuously slow rate initially (A1), then
367 heated at a higher rate than other points at later times (A2). This suggests that the base of the wing
368 does not absorb heat but is a heat storage area, as further supported by the high equilibrium
369 temperature parameter (y0). The points in the dark area heated at a high, similar rate initially (A1
370 of Sp8-Sp12), followed by points not in the border (Sp8−Sp11) continuing to heat at a high rate,
371 while the border point (Sp12) showed a decrease in later heating, suggesting it is poor at heat
372 storage (A2 values).The points in the light area always heated at a similar rate with the points in
373 the dark area, but the equilibrium temperatures were lower than the non-border dark areas (y0s of
374 the points Sp1−Sp6 were significantly lower than the points Sp8−Sp11: t_8=2.864, P=0.021), while
375 being similar to those of the border.

376 In the hind wing, the results were qualitatively the same as for the forewing, with the base of
377 the wing heating at a conspicuously slow rate initially, followed by a very high late heating rate
378 and high equilibrium value. The non-border dark areas had high heating rates throughout the trial,
379 while the border dark area showed a slow heating rate late in the trial. In contrast to the forewing,
380 we found the equilibrium parameters for the light areas near the base of the wing (y0 of H-Sp1, H-
381 Sp2 and H-Sp3) were similar to those of the non-border dark areas (H-Sp8−H-Sp11; t_5=20.683,
382 P=0.525). The possible reason is that these points were close to the base of the wing and were
383 affected by the heat of the base of the wing. The temperatures of other three points in the light area
384 were lower than the non-border dark areas (y0: t_5=2.986, P=0.031). In summary, for both wings,
385 the non-border dark areas could temporarily store heat and then transfer it to the base of the wing.
386 The dark area of the border could absorb heat from the light source but it could not store the heat,
387 similar to most light areas on the wing (Figure 7).

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

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

DISCUSSION

Effects of the light intensity on heat absorption

398 We found that the light intensity significantly affected the heat absorption capacity of the butterfly
399 *T. limniace.* Within the light intensity range from 600 lx to 60000 lx, as the light intensity
400 increased, the thoracic equilibrium temperature and ΔT increased significantly, the time to reach
401 the equilibrium temperature was significantly shorter, and the rate of thoracic temperature increase
402 was significantly faster. Our previous studies also showed that compared with other light
403 intensities (243, 860, and 1280 lx), the equilibrium thoracic temperature of adults exposed to 2240
404 lx was higher and the time required to reach it was shorter. In addition, the value of ΔT was higher
405 and the rate of thoracic temperature increase was achieved more quickly (*Liao et al., 2017*). These
406 results suggest that in an appropriate range, a high light intensity can allow adult *T. limniace*
407 butterflies to rapidly absorb more heat to elevate their thoracic temperature compared with low
408 light intensities. Similar results were obtained for the butterfly *Heteronympha merope* where its
409 body temperature excess also increased as the level of solar radiation increased (*Barton et al.,*
410 *2014*).
411   The heat absorbed by butterflies is used mainly for autonomous flight and it is directly involved
412 with reproductive behavior (*Shreeve, 1992; Kemp and Krockenberger, 2004; Bennett et al., 2012;*
413 *Bonebrake et al., 2014; Kleckova et al., 2014; Mattila 2015; Shanks et al., 2015; Han et al., 2016;*
414 *Niu et al., 2016*). In *Bicyclus anynana*, active males increase their own likelihood of copulation
415 and active females increase their likelihood of being courted (*Westerman et al., 2014*). The flight
416 activity of *T. limniace* butterflies is higher under a high light intensity compared with those
417 exposed to a low light intensity (*Liao et al., 2017*). The high thorax temperature recorded in
418 *Junonia villida* is probably linked to its high flight speed (*Nève and Hall, 2016*). We found that a

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

420   within an appropriate light intensity range, a higher light intensity can allow *T. limniace* adults to

421   absorb more heat to facilitate autonomous flight and increase the flight activity, thereby enhancing

422   the likelihood of reproduction.

423   We also found that when the light intensity was above 40,000 lx, the equilibrium temperature

424   could rapidly exceed 70°C, which was much higher than the butterflies could tolerate, and thus

425   exposure to a light intensity above 40,000 lx caused the death of the butterflies half an hour after

426   the experiment finished. In the summer and autumn season of Yuanjiang county, Yunan province,

427   China, the peak of flight activity of butterfly *T. limniace* mainly appeared at 09:00-12:00 and

428   15:00-17:00 (*Chen et al., 2008*). During these time periods, the sunlight intensity is lower than

429   40,000 lx, which allows the butterfly to absorb the right amount of heat for autonomous flight.

430   More than 40,000 lx light intensity could make the butterflies to absorb more heat than the body

431   can tolerate, burning the body and causing death. Some studies indicated that butterflies can adjust

432   their basking posture to reduce heat absorption (*Rawlins, 1980; Tsuji et al., 1986*), e.g. closing the

433   wings and turning the body opposite the sunlight. In *T. limniace*, in the field we observed that

434   when the sunlight was above 40,000 lx, the butterflies would fly into the woods and perch on

435   branches to avoid the sunlight.

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

437   The wing opening angle also significantly influenced the heat absorption capacity of *T. limniace*

438   adults. Some previous studies have shown that butterflies with fully open wings have the highest

439   heat absorption capacity (*Tsuji et al. 1986; Berwaerts et al., 2001; De Keyser et al., 2015*). When

440   the butterfly *Polyommatus icarus* fully opens its wings, the warming rates are maximized and its

441   body temperature is also highest (*De Keyser et al., 2015*). *Pararge aegeria* butterflies with fully

442   opened wings are able to absorb more heat and cool faster compared with those with half-opened

443   wings (*Berwaerts et al., 2001*). Other studies suggest that the heat absorption capacity of butterflies

444   is highest in the optimal range for the wing opening angle (*Kingsolver and Moffat, 1982; Barton*

445   *et al., 2014*). For example, in *Pieris*, normal and black base manipulation of butterflies can achieve

446   maximum temperature excesses at wing angles of 30−40°, whereas the optimal wing angles for

447   the highest temperature excess in black distal treatment butterflies are 60−90° (*Kingsolver, 1987*).

448   Thus, regardless of whether the wings are normal or melanized, heat absorption by butterflies

449   requires a certain optimal wing opening angle that can vary depending on the butterfly species.

450   We found that the optimal wing opening angle range for heat absorption by *T. limniace* was
451   60−90°. In this range, the equilibrium temperatures were significantly higher, the times required
452   to reach the equilibrium temperature were much shorter, the values of ΔT were higher, and the
453   rates of thoracic temperature increase were significantly faster. Thus, an appropriate wing opening
454   angle can enhance the heat absorption capacity of butterflies. In the wild, when butterflies need
455   heat for autonomous fly, adults *T. limniace* doesn't fully open their wings, however, they would
456   make the wings maintained a certain angle. Thus, wing opening angles 60−90° were suitable for
457   heat absorption of butterfly *T. limniace*.

458   **Differences in heat absorption between the fore and hind wings**

459   Our results showed that the heat absorption capacity of the fore wings was significantly higher
460   than that of the hind wings. The equilibrium temperatures and values of ΔTs were significantly
461   higher for the fore wings than the hind wings in males exposed to light at 600–40,000 lx and
462   females exposed to light at 600 lx, 15000 lx and 40,000 lx. The times required to reach equilibrium
463   temperature and the rates of thoracic temperature increase were significantly shorter and faster,
464   respectively, in the fore wings than those in the hind wing for both males and females exposed to
465   light at 600–60,000 lx. These results suggest that the fore wing is the major tissue used for heat
466   absorption in butterflies. Thus, the wing size significantly impacts the heat absorption capacity of
467   butterflies (*Kammer and Bracchi, 1973; Berwaerts et al., 2001, 2002*). Some studies suggest that
468   butterflies with larger wings can absorb more heat than those with smaller wings (*Heinrich, 1986;*
469   *Kingsolver, 1987; Schmitz, 1994*). For example, a study of 20 Australian butterflies showed that
470   those with the highest wing loadings had the highest thorax temperature at take-off (*Nève and Hall,*
471   *2016*). Therefore, the fore wings allow *T. limniace* butterflies to absorb more heat than the hind
472   wings under the same lighting conditions. However, in *Pararge aegeria*, butterflies with larger
473   wings heated up more slowly compared with those with small wings (*Berwaerts et al., 2001*).

474   **Identification of heat absorption and non-heat absorption areas**

475   The spectral reflectance from light areas on both the fore and hind wings was much higher than
476   that from dark areas in *T. limniace* adults. Thus, the absorbance and thermal absorptivity of the
477   dark areas was significantly greater than that of the light areas. Color can affect an animal's
478   temperature because dark surfaces absorb more solar energy than light surfaces and the energy is
479   converted into heat (*Stuart-Fox et al., 2017*). Previous studies indicate that wing color can limit

480   the heat absorption capacity, where darker coloration can absorb more heat from sunlight or other
481   light sources than lighter coloration (*Watt, 1968; Kingsolver, 1987, 1988; Berwaerts et al., 2001*).
482   For example, darker *Pararge aegeria* butterflies have a much higher warming rate (*Van Dyck et*
483   *al., 1997*). We found that when the scales were removed from the light areas on the wings, the
484   equilibrium thoracic temperature and value of ΔTs were significantly higher, and the time required
485   to reach the equilibrium temperature and the rate of thoracic temperature increase were
486   significantly shorter and faster, respectively, than those in butterflies with all the scales removed
487   from the wings or with scales removed from the dark areas. Thus, the dark areas of the wings
488   absorb heat in the butterfly *T. limniace* rather than the light areas.

489   Some studies suggest that melanization of the wing surfaces can promote the absorption of heat
490   from sunlight in butterflies (*Kingsolver and Wiernasz, 1991; Stoehr and Wojan, 2016*). The
491   butterfly *Parnassius phoebus* lives at high altitudes and high latitudes, and it uses melanization to
492   obtain heat from solar radiation, where the color of its wings becomes darker as the altitude and
493   latitude increase (*Guppy, 1986*). Melanization inside the wing surfaces can improve the heat
494   absorption capacity of butterflies whereas melanization at the distal wing surfaces cannot affect
495   heat absorption (*Kammer and Bracchi, 1973; Kingsolver, 1987; Brashears et al., 2016*).
496   Wasserthal (1975) showed that the most of the heat transferred from the wing to the body originates
497   from the 15% of the wing surface nearest to the body in the butterflies *Papilio machaon*, *Apatura*
498   *ilia*, and *Papilio troilux*. Thus, the dark areas of the wing surface near the body are the main heat
499   absorption areas in butterflies. Our results are similar to those obtained in previous studies. In *T.*
500   *limniace*, we found that the temperatures were markedly higher in the dark areas in the mid-
501   posterior region near the wing base in wing cells A-CU$_3$ and Cu$_2$-Cu$_3$ in the fore wings, as well as
502   in wing cells 1A-Cu$_2$, Cu$_1$-Cu$_2$, M$_3$-Cu$_1$, and R$_2$-M$_1$ in the hind wings compared with other wing
503   areas during lighting for 300–540 s.

504   The color of a butterfly wing mainly comprises iridescence and structural colors (*Nijhout, 1991;*
505   *Michielsen et al., 2010; Han et al., 2016; Siddique et al., 2017*). The part of the wing with a
506   structural color is used to absorb heat from the sun (*Bosi et al., 2008*). In *Pararge aegeria*, normal
507   butterflies reach a higher equilibrium thoracic temperature than descaled butterflies, probably
508   because the wings without scales absorb less radiation (*Berwaerts et al., 2001*). In the present
509   study, we found that removing the scales from the dark areas of the wings significantly reduced
510   the heat absorption capacity of butterflies, whereas removing the scales from the light areas did
511   not affect normal heat absorption. Therefore, the dark areas on the dorsal wing surfaces in *T.*

512   *limniace* may mainly comprise structural colors.

513   High reflectance can reduce the absorption of heat from sunlight (*Stuart-Fox et al., 2017*). Thus,

514   light colors are not conducive to heat absorption by butterflies. We found that removing the scales

515   from the light areas on the wing surfaces did not affect the absorption of heat by butterflies. In

516   *Anartia fatima*, it was previously shown that blackening the white bands on the wing surface did

517   not affect its equilibrium temperature, but adding white bands decreased the rate of heating

518   (*Brashears et al., 2016*). Thus, the light areas on the wing surfaces may prevent butterflies from

519   absorbing heat excessively quickly and increasing the body temperature to an intolerable level.

520   We also found that light areas accounted for about 20% of the fore wing area and about 29% of

521   the hind wing area. However, some studies indicate that light areas have high spectral reflectance

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

523   sex in butterflies (*Emmel, 1972; Taylor, 1973; Seymoure and Aiello, 2015*). The role of the light

524   areas on butterfly wings in heat absorption will be addressed in our future research.

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

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

527   posterior region near the wing base in wing cells A-Cu_3 and Cu_2-Cu_3 on the fore wings, as well as

528   in wing cells $1A$-Cu_2, Cu_1-Cu_2, M_3-Cu_1, and R_2-M_1 on the hind wings compared with the other

529   wing areas during lighting for 300–540 s. Hence, the heat absorbed by the wings of the butterfly

530   *T. limniace* needs to be temporarily stored in heat storage areas on the wing surface, before it is

531   transferred to the wing base and thorax to elevate the thoracic temperature above the ambient level

532   to trigger autonomous flight. Thus, the dark areas in the mid-posterior region near the wing base

533   in wing cells A-Cu_3 and Cu_2-Cu_3 in the fore wings, and in wing cells $1A$-Cu_2, Cu_1-Cu_2, M_3-Cu_1,

534   and R_2-M_1 in the hind wings were temporary heat storage areas on the wing surface. The heat was

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

536   storage areas. During the heat transfer process, the temperatures of the wing base and thorax were

537   the same as the heat storage areas and much higher than those of other areas of the wing surfaces

538   on both the fore and hind wings, and the thoracic temperature reached equilibrium after lighting

539   for 480 s. Thus, the channels for heat transfer were the veins near the storage areas.

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

541   solar radiation onto the body in order to increase its temperature. However, some studies have

542   shown that the absorption of heat by butterfly wings depends mainly on the internal structure of

543   the scale itself, where the structure called a "photonic crystal" can convert the absorbed light into
544   heat for autonomous flight (*Li et al., 2004; Han et al., 2013; Luohong, 2014; Han et al., 2015a,*
545   *b*). In the butterfly *Trogonoptera brookiana*, the scales have longitudinal ridges that run through
546   the scales and the surfaces of the scales comprises a set of raised longitudinal quasiparallel lamellae
547   (ridges), where the spaces between adjacent ridges are filled with a netlike reticulum comprising
548   pores (*Han et al., 2015a*). This "photonic crystal" structure in the scales may help the wings to
549   absorb heat. Therefore, the heat absorbed is not reflected to the wing base and thorax through the
550   wing surface, but instead it is transmitted via the internal tissue in the wing. Our results showed
551   that the heat was transferred from the heat storage areas to the wing base and thorax through veins
552   Cu_2, Cu_3, Cu, and A in the fore wings, and veins 1A, Cu_2, Cu_1, Cu, M_1, M_3, M, R_2, and R in the
553   hind wings during lighting for 0–540 s. This suggests that the heat absorbed by the wings is
554   transferred from the heat storage areas on the wing surface to the wing base and thorax through
555   wing veins.

CONCLUSIONS

557   In this study, we showed that in the optimal light intensity range, a higher light intensity could
558   help butterflies to absorb more heat, and the optimal wing opening angles for heat absorption
559   ranged from 60° to 90°. The heat absorption capacity of the fore wing was much greater than that
560   of the hind wing. The dark areas on the wing surfaces were the areas where heat was absorbed by
561   the butterfly wing. The dark areas in the mid-posterior region near the wing base in wing cells A-
562   Cu_3 and Cu_2-Cu_3 in the fore wing, and in wing cells 1A-Cu_2, Cu_1-Cu_2, M_3-Cu_1, and R_2-M_1 in the
563   hind wings were temporary heat storage areas on the wing surface. We speculate that the heat was
564   transferred from heat storage areas to the wing base and thorax through veins Cu_2, Cu_3, Cu, and A
565   in the fore wings, and veins 1A, Cu_2, Cu_1, Cu, M_1, M_3, M, R_2, and R in the hind wings during
566   lighting for 0–540s. In the future, we will investigate the heat storage mechanism in butterfly
567   wings, as well the heat transfer mechanism in the wing veins and the role of light areas on the
568   wings in heat absorption.

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719   **Figure Legends**

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

721   **Figure 2** The wing surface was divided into border, middle, and inside parts to obtain spectral reflectance

722   measurements from the wings of adult *Tirumala limniace* butterflies. A: Male, B: female.

723   **Figure 3** Distribution of the potential heat storage areas (A) and potential heat transfer channels (B) on the wing

724   surface in adult *Tirumala limniace* butterflies. In A, the light gray area represents the heat storage area and the

725   blue points are points used for real-time temperature monitoring in the heat storage areas (fore wing: Sp8–Sp11,

726   hind wing: H-Sp8–H-Sp11), light areas (fore wing: Sp1–Sp6, hind wing: H-Sp1–H-Sp6), wing base (fore wing:

727   Sp7, hind wing: H-Sp7) and non-storage areas (fore wing: Sp12, hind wing: H-Sp12). In B, the red points are

728   the points used for real-time temperature monitoring during heat transfer in the wing veins. The heat transfer

729   channels are the vein $Cu-Cu_2$ channel, vein $Cu-Cu_3$ channel, and vein A channel in the fore wing, and the vein

730     $R-R_2$ channel, vein $R-M-M_1$ channel, vein $Cu-M-M_3$ channel, vein $Cu-Cu_1$ channel, vein $Cu-Cu_2$ channel, and

731   vein 1A channel in the hind wing.

732   **Figure 4** Spectral reflectance of the male fore wing (A), male hind wing (B), female fore wing (C) and female

733   hind wing (D) in adult *Tirumala limniace* butterflies.

734   **Figure 5** Equilibrium thoracic temperature (A), time required to reach the equilibrium temperature (B), thoracic

735   temperature excess (ΔT) (C) and rate of thoracic temperature increase (D) in adult *Tirumala limniace* under four

736   scale removal treatments. DSR treatment: scales removed from dark areas; LSR treatment: scales removed from

737   light areas; ASR treatment: all scales removed from the wing surface; and IN treatment: scales on the wings

738   were left intact. Different lowercase and capital letters indicate significant differences at $P < 0.05$ in the results

739   obtained for males and females among the four scale removal treatments.

740   **Figure 6** Real-time temperature on the wing surface during heat absorption by adult *Tirumala limniace*

741   butterflies. The numbers below each subgraph indicate the monitoring time in seconds.

742   **Figure 7** Real-time temperature at the monitoring points in the heat storage areas and non-heat storage areas

743   during heat absorption by the wing surfaces in adult *Tirumala limniace* butterflies. A: Fore wing; B: real-time

744   temperatures at monitoring points on the fore wing during lighting for 500–540 s; C: hind wing; D: real-time

745   temperatures at monitoring points on the hind wing during lighting for 500–540s.

746   **Figure 8** Real-time temperatures at monitoring points on the heat transfer channels on the fore wing during heat

747   absorption by adult *Tirumala limniace* butterflies. A: Vein A channel; B: vein $Cu-Cu_3$ channel; C: vein $Cu-Cu_2$

748   channel.

749   **Figure 9** Real-time temperatures at monitoring points on the heat transfer channels on the hind wing during heat

750 absorption by adult *Tirumala limniace* butterflies. A: vein 1A channel; B: vein Cu-Cu$_2$ channel; C: vein Cu-M-

751 M$_3$ channel; D: vein R-R$_2$ channel; E: vein Cu-Cu$_1$ channel; F: vein R-M-M$_1$ channel.

Table 1(on next page)

Effects of the light intensity and wing opening angle on heat absorption by adult *Tirumala limniace* butterflies.

1   **Table 1** Effects of the light intensity and wing opening angle on heat absorption by adult *Tirumala limniace*
2   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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Table 2(on next page)

Effects of the light intensity and wing opening angle on the equilibrium thoracic temperature (℃) in adult *Tirumala limniace* butterflies.

Different lowercase and capital letters indicate significant differences at *P* < 0.05 in the

results obtained at different light intensities and wing opening angles, respectively. Data:

mean±se.

1   **Table 2** Effects of the light intensity and wing opening angle on the equilibrium thoracic temperature (℃) in adult

2   *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

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

4   different light intensities and wing opening angles, respectively. Data: mean±se.

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Table 3(on next page)

Effects of the light intensity and wing opening angle on the time (min) required to reach equilibrium temperature in adult *Tirumala limniace* butterflies.

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

results obtained at different light intensities and wing opening angles, respectively. Data:

mean±se.

1 **Table 3** Effects of the light intensity and wing opening angle on the time (min) required to reach equilibrium

2 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

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

4 different light intensities and wing opening angles, respectively. Data: mean±se.

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Table 4(on next page)

Effects of the light intensity and wing opening angle on the thoracic temperature excess (ΔT) (°C) in adult *Tirumala limniace* butterflies.

Different lowercase and capital letters indicate significant differences at $P < 0.05$ in the results obtained at different light intensities and wing opening angles, respectively. Data: mean±se.

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

2   *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±1.25a,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±2.00d,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

3   Different lowercase and capital letters indicate significant differences at *P* < 0.05 in the results obtained at

4   different light intensities and wing opening angles, respectively. Data: mean±se.

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Table 5(on next page)

Effects of the light intensity and wing opening angle on the rate (°C/min) of thoracic temperature increase in adult *Tirumala limniace* butterflies.

Different lowercase and capital letters indicate significant differences at $P < 0.05$ in the results obtained at different light intensities and wing opening angles, respectively. Data: mean±se.

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

2 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±2.95b,BC	14.15±1.72b,BC	20.87±2.81a,C

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

4 different light intensities and wing opening angles, respectively. Data: mean±se.

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Table 6(on next page)

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

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

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±1.11	3.73±0.21**	6.58±0.48	50.43±0.56**	44.18±1.11	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

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

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Table 7(on next page)

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

1 **Table 7** The results of time-series ExpDec2 of exponential models analysis for trends of real-time
2 temperatures of the monitoring points in the heat storage areas and non-heat storages in butterflies *Tirumala*
3 *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
	Non-border dark areas	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
	Non-border dark areas	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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Table 8(on next page)

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

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

3   **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

4

Figure 1

Natural light intensity on September 11, 2017 in Yuanjiang County, Yunnan Province, China
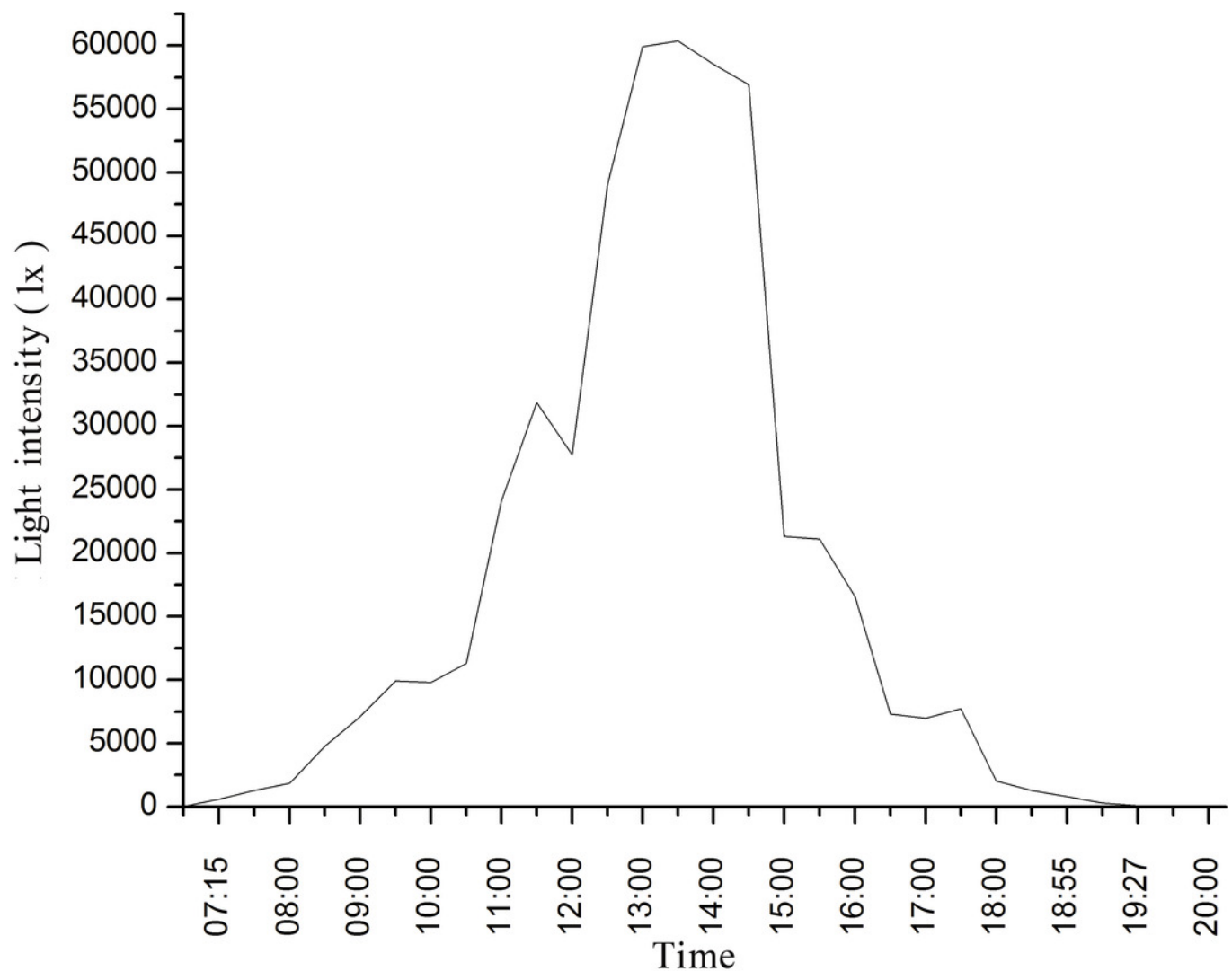
Figure 2

The wing surface was divided into border, middle, and inside parts to obtain spectral reflectance measurements from the wings of adult *Tirumala limniace* butterflies.
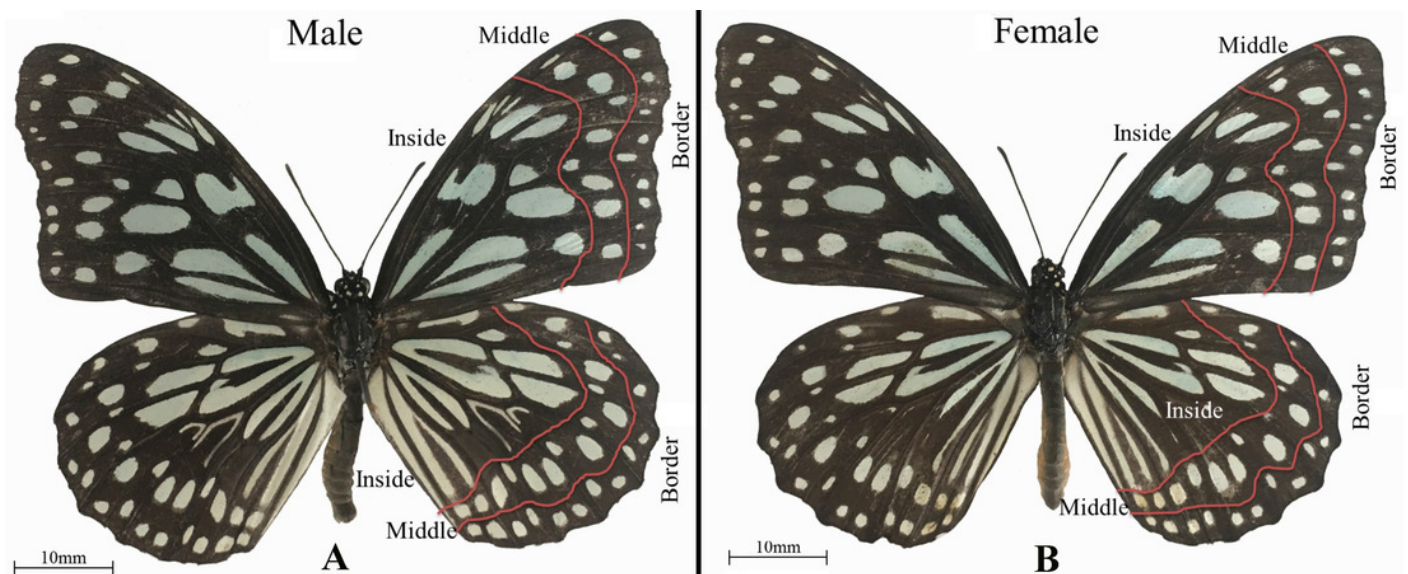
A: Male, B: female

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.
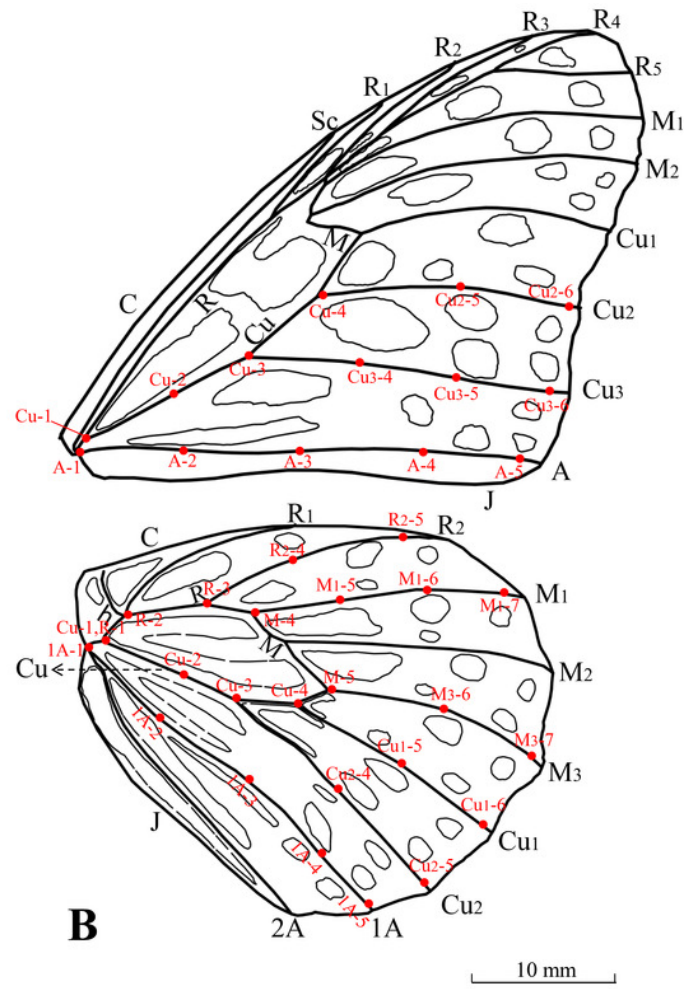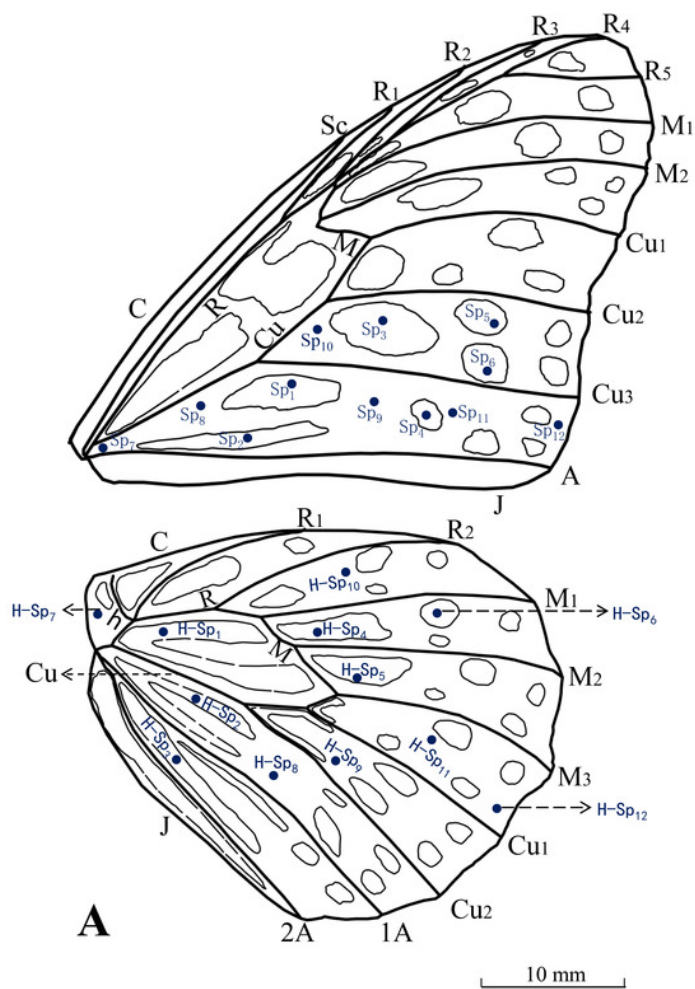
Figure 4

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.
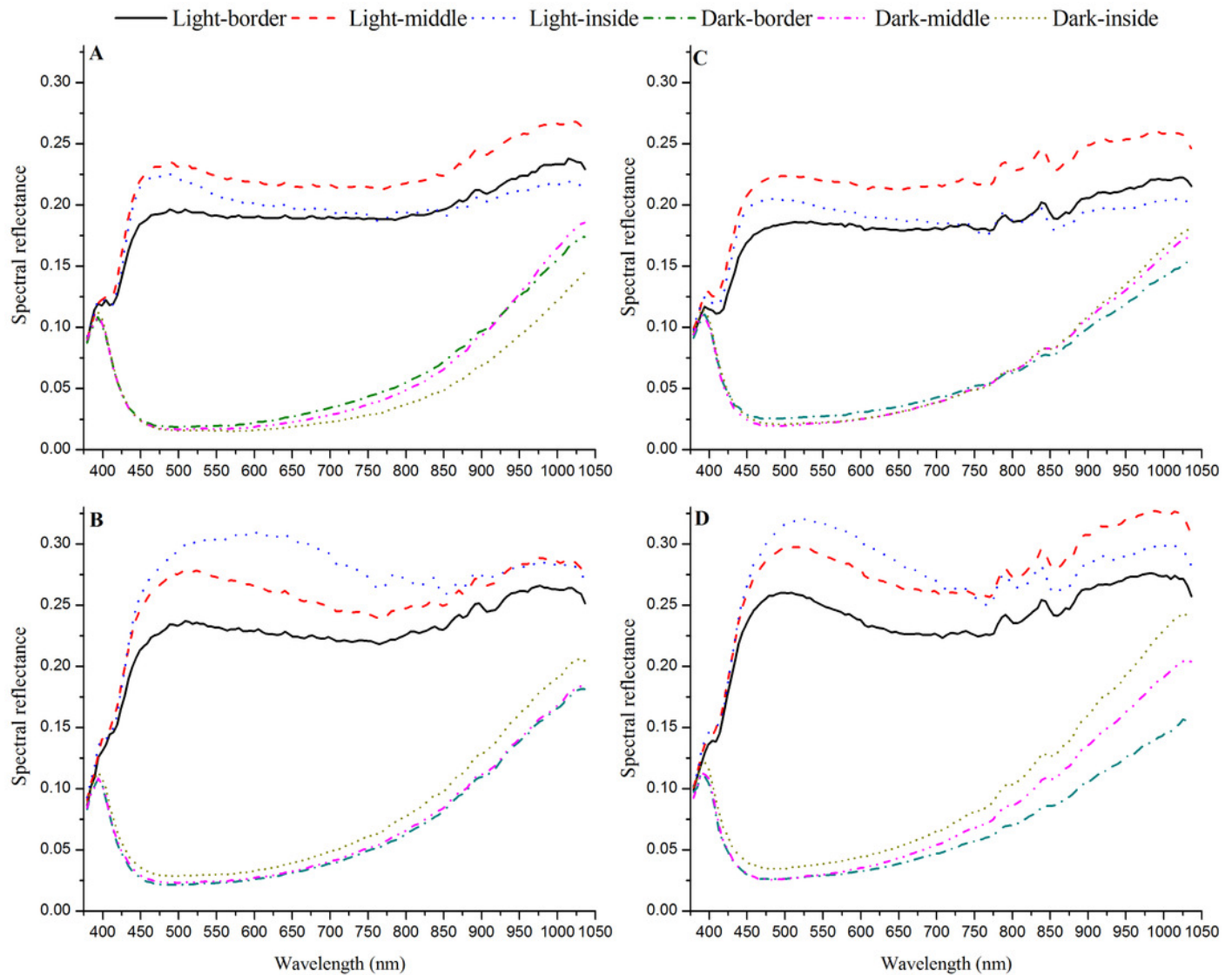
Figure 5

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.
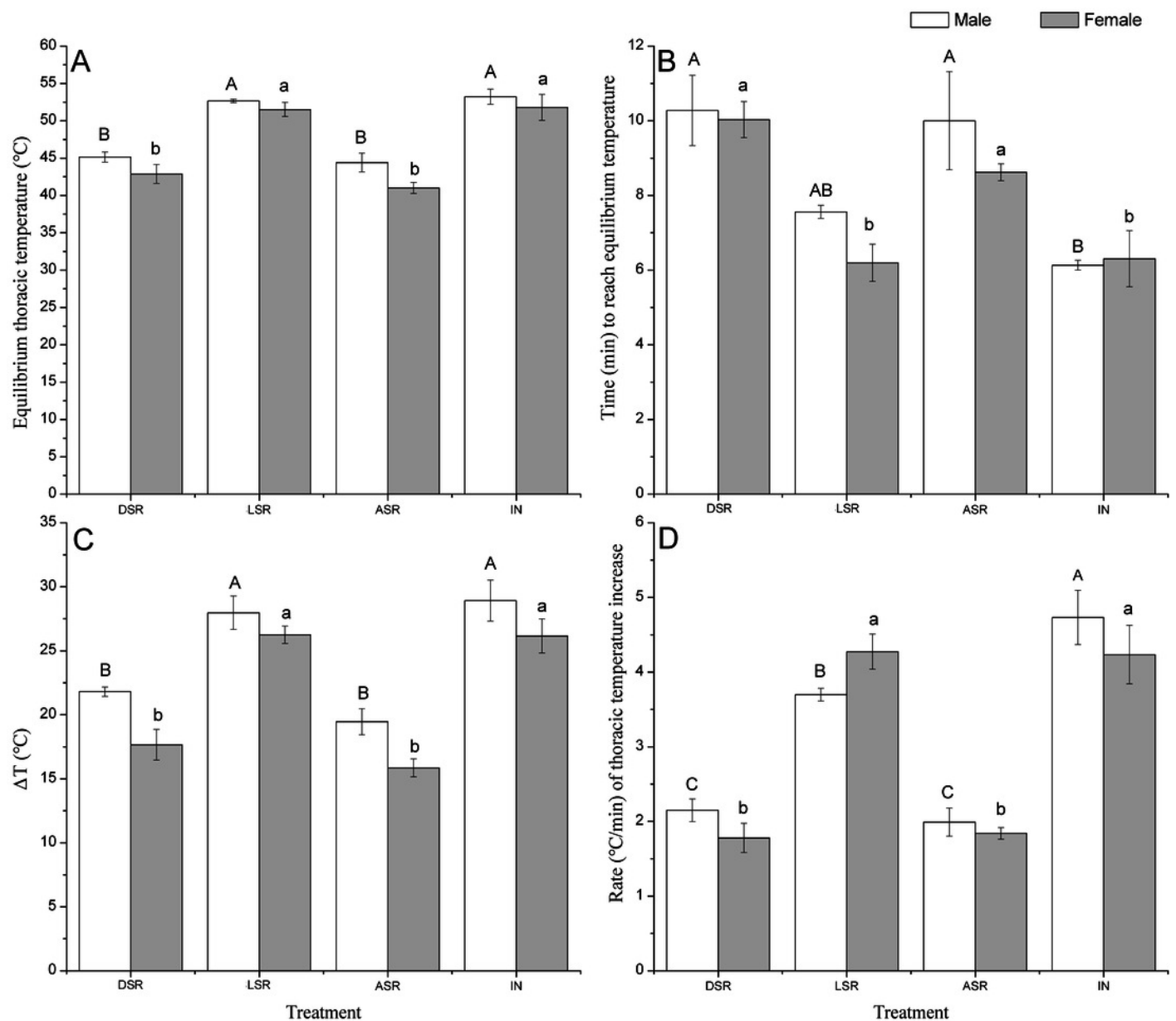
Figure 6

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.
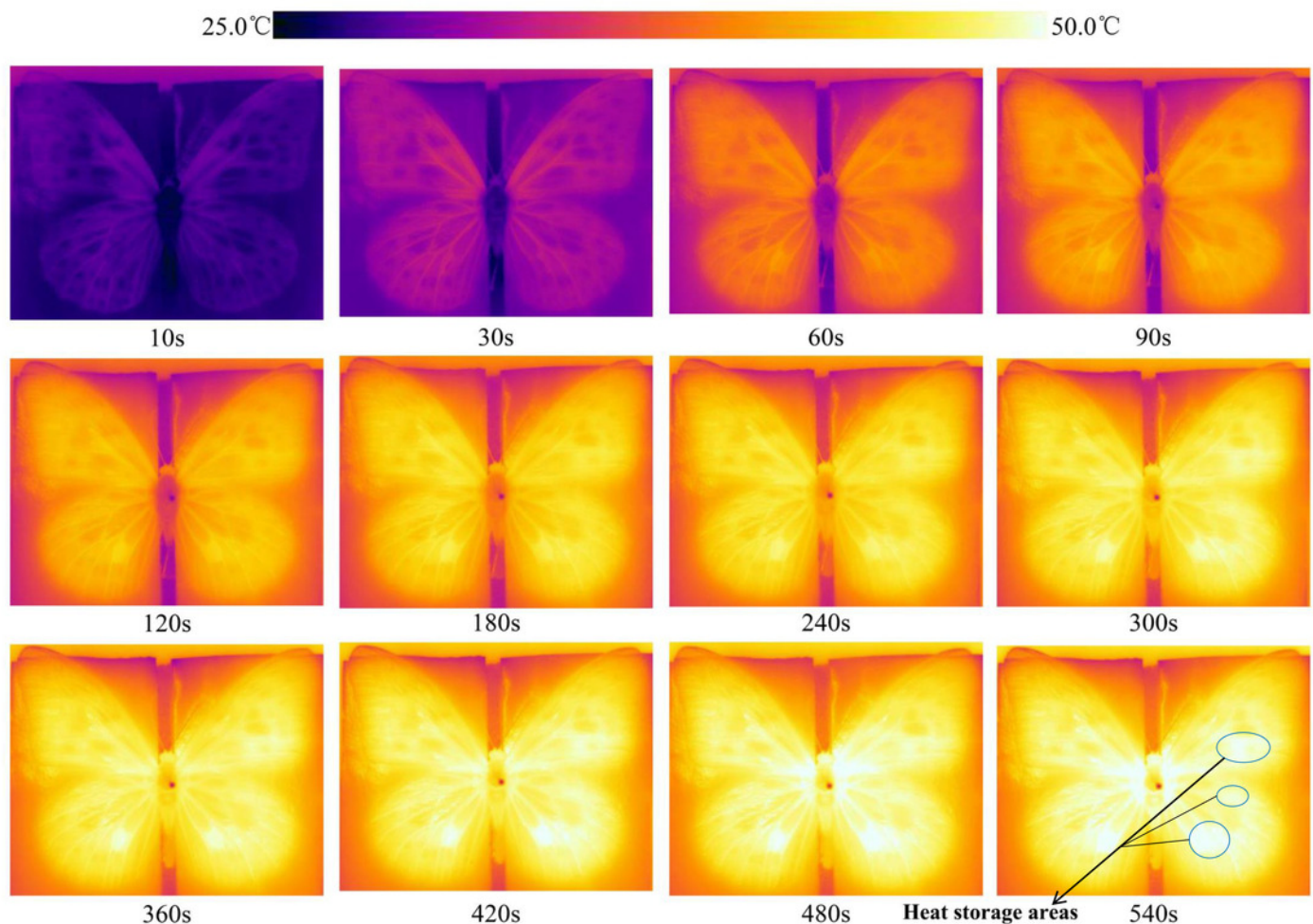
Figure 7

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.
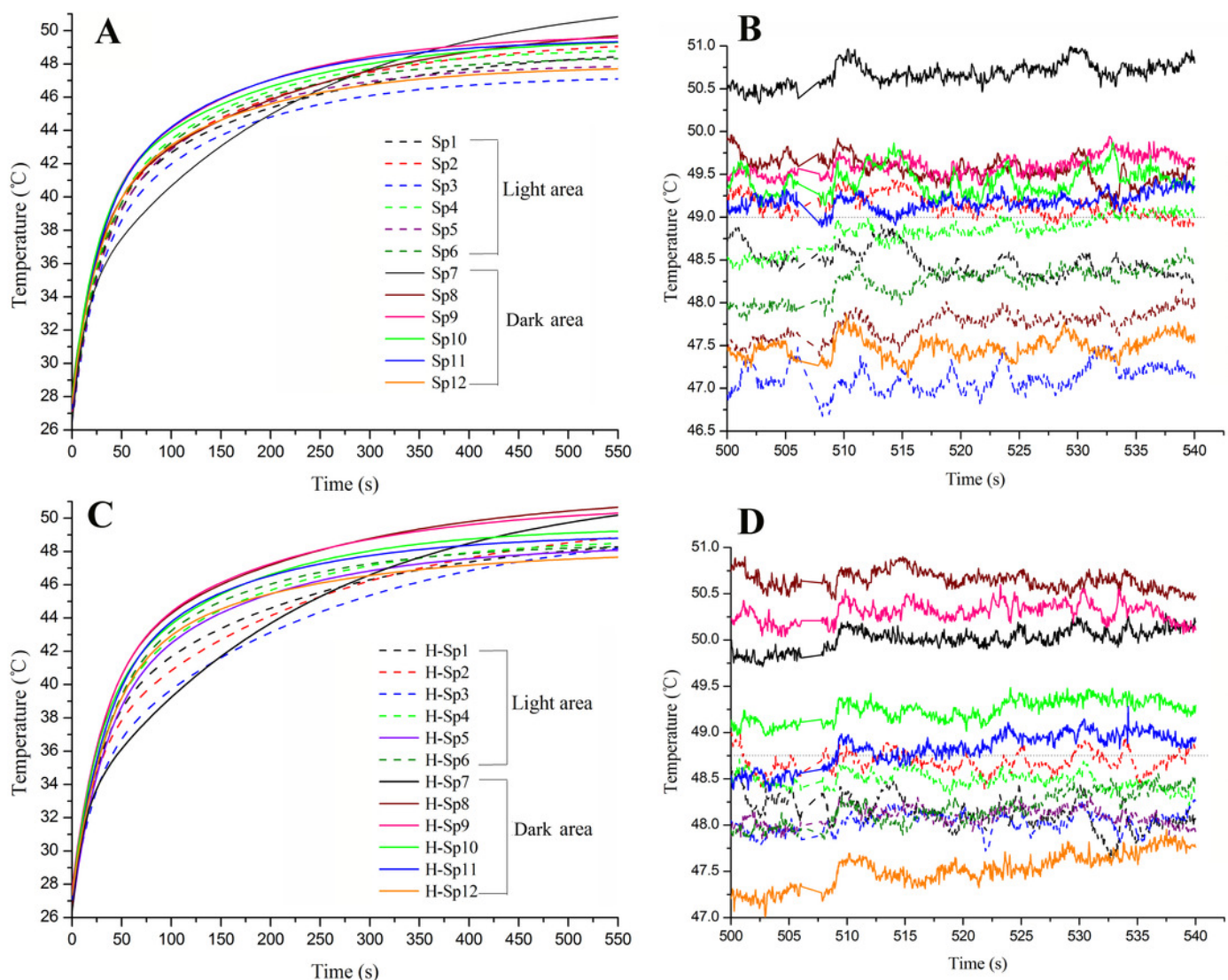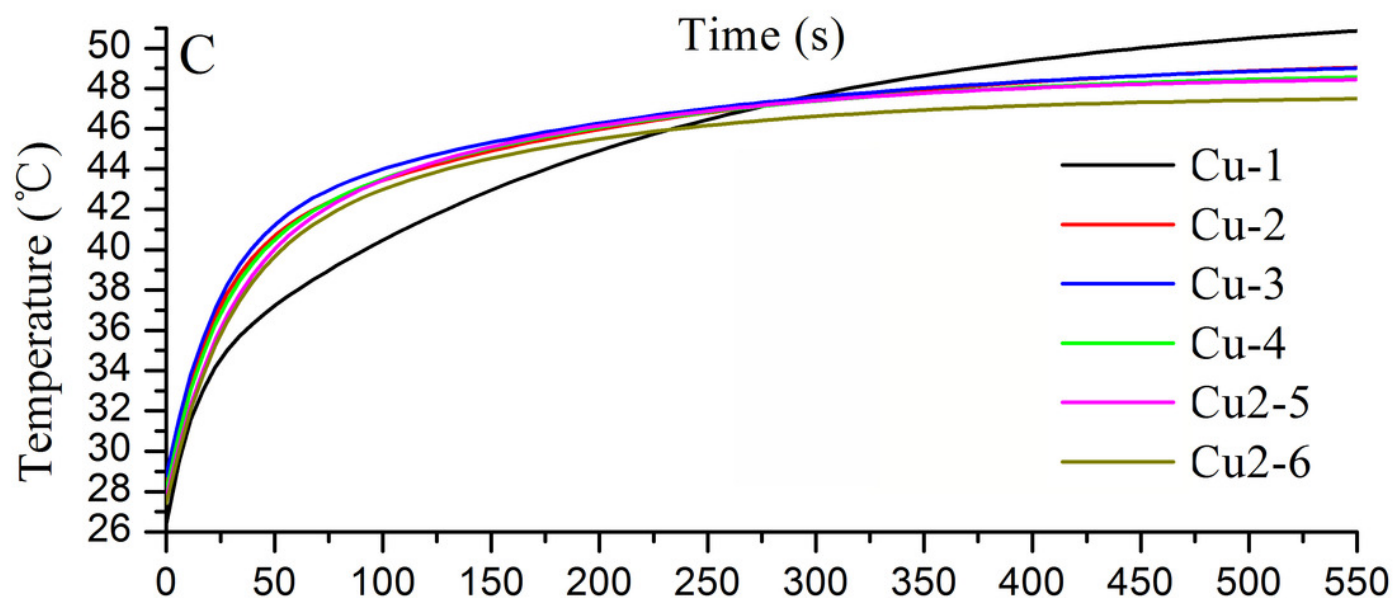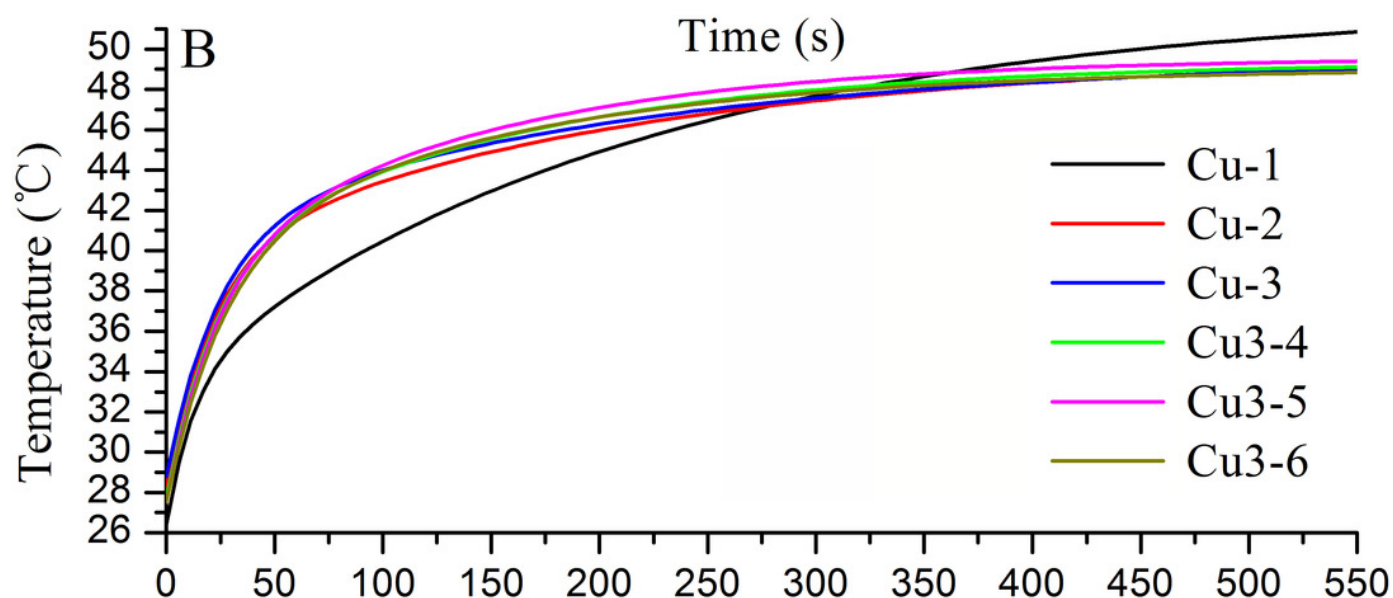
Figure 8

Real-time temperatures at monitoring points on the heat transfer channels on the fore wing during heat absorption by adult *Tirumala limniace* butterflies.

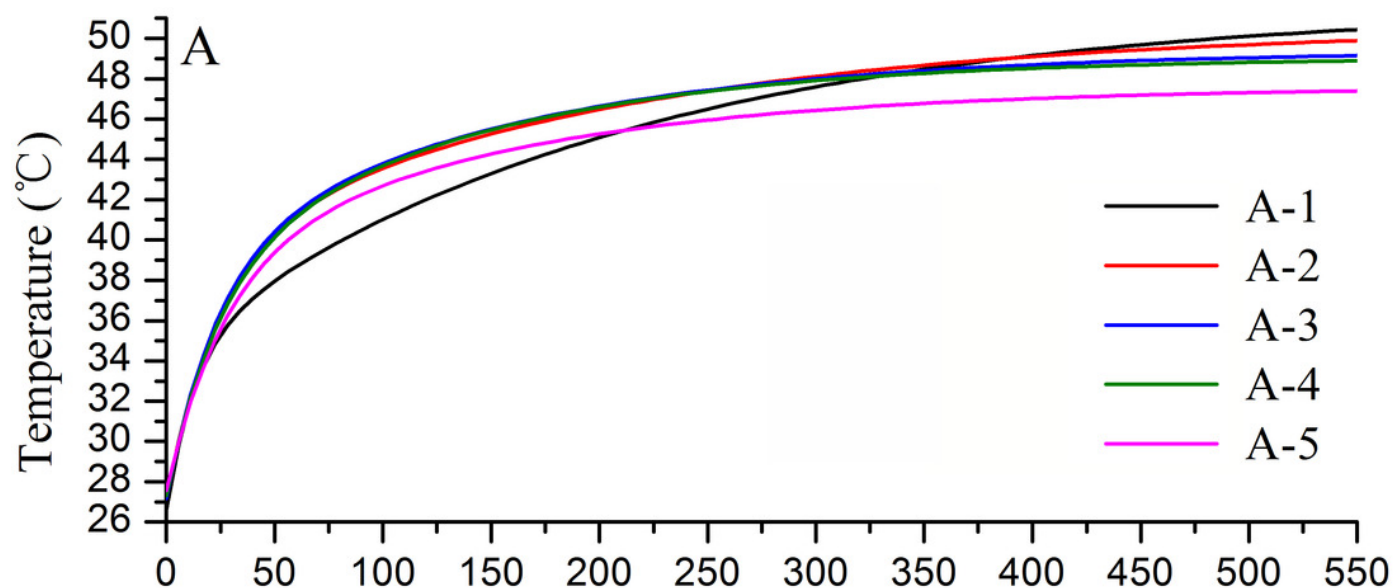A: Vein A channel; B: vein $Cu-Cu_3$ channel; C: vein $Cu-Cu_2$ channel.

Figure 9

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 $Cu\text{-}Cu_2$ channel; C: vein $Cu\text{-}M\text{-}M_3$ channel; D: vein $R\text{-}R_2$ channel; E: vein $Cu\text{-}Cu_1$ channel; F: vein $R\text{-}M\text{-}M_1$ channel.