EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz

Eur. J. Entomol. **122**: 73–78, 2025
doi: 10.14411/eje.2025.008

ORIGINAL ARTICLE

Comparison of flight behaviour and flight morphology between perching *Lycaena phlaeas* and patrolling *Zizeeria maha* (Lepidoptera: Lycaenidae)

Michio IMAFUKU

Department of Zoology, Graduate School of Science, Kyoto University, Sakyo-ku, Kyoto City, 606-8502 Japan;
e-mail: imafuku@dream.jp

Key words. Body/thorax mass ratio, flight directional change, flight velocity, relative flight time, wing aspect ratio, wing loading

Abstract. Perching (territorial) and patrolling are recognised as mate-locating tactics adopted by male butterflies. It is said that males adopting the former fly fast with high acceleration, whereas those adopting the latter fly at continuous and lower speeds. However, no previous studies have demonstrated these flight properties using quantitative data. In the present study, the flight properties of two lycaenid species, the perching *L. phlaeas* and the patrolling *Z. maha*, were investigated based on three-dimensional analysis. Males of *L. phlaeas* had higher flight velocities and higher relative flight time than those of *Z. maha*. Furthermore, the flight morphology that supports flight properties was examined. The perching *L. phlaeas* exhibited higher thorax-to-body mass ratios and greater wing loadings than patrolling *Z. maha*.

INTRODUCTION

Shapes and behaviours of animals are expected to be optimized to enhance their survival and reproductive success in their respective environments (Darwin, 1911). In butterflies, which have relatively large wings compared to their bodies, most aspects of their lives depend on flights powered by wing movements. In feeding, evading predators, mate-location and so on, flight properties adequate to attain the purpose should have been acquired.

With respect to mate-location strategies in butterfly males, two tactics are widely recognised, "waiting" and "seeking" (Magnus, 1963) or "perching" and "patrolling" (Scott, 1973; Silberglied, 1984; Wickman, 1992; Lederhouse, 1995; Rutowski, 1997; Wiklund, 2003; Honda, 2005). Males of the perching species "sit at characteristic sites and dart out at passing objects in search of females," while males of patrolling species "fly almost always constantly in search of females" (Scott, 1973). Perching species are also called territorial species because their males occupy and defend a site from intruding males settling (Baker, 1972; Davies, 1978; Bitzer & Shaw, 1981; Alcock, 1983; Takeuchi & Imafuku, 2005; Biswas et al., 2023). This dichotomy of mating tactics is not always valid for some species; both perching and patrolling behaviours have been observed in a single species (Heinrich, 1986; Benson et al., 1989; Kemp, 2001). For the species with typical mate locating tactics, it is said that males of the perching species have high acceleration ability and speed, whereas males of the patrolling species have increased flight endurance (Wickman, 1992; Wiklund, 2003).

Flight behaviour is related to flight morphology. Higher acceleration at take-off is associated with higher flight muscle-to-total body mass ratio (Marden & Chai, 1991). As the thorax of insects is largely occupied by flight muscles, approximately 90% (Wickman, 1992), larger thorax should allow butterflies to fly with higher velocity, as shown by Dudley (1990) and Dudley & Srygley (1994). Furthermore, because a large thorax positions the centre of body mass closer to the wing base, it should contribute to flight with high manoeuvrability and high speed (Srygley & Dudley, 1993).

In birds, another major animal group that can fly, relationship between flight properties and wing morphology has well been studied; large birds such as albatrosses that fly fast with lower wingbeat frequency in extensive open space over oceans tend to have smaller wings relative to body mass (higher wing loading, wing loading = body mass/wing area) and longer or slender wings (higher aspect ratio, aspect ratio = [wing span]^2/wing area), while small birds such as songbirds that fly slowly and agilely with higher wingbeat frequency in restricted spaces or dense vegetation tend to have larger wings relative to body mass (low wing loading) and shorter or rounder wings (low aspect ratios) (Azuma & Kira, 2000). These patterns are partly observed in butterflies. Betts & Wootton (1988) compared six butterfly species and suggested that high flight velocities were associated with high wing loadings

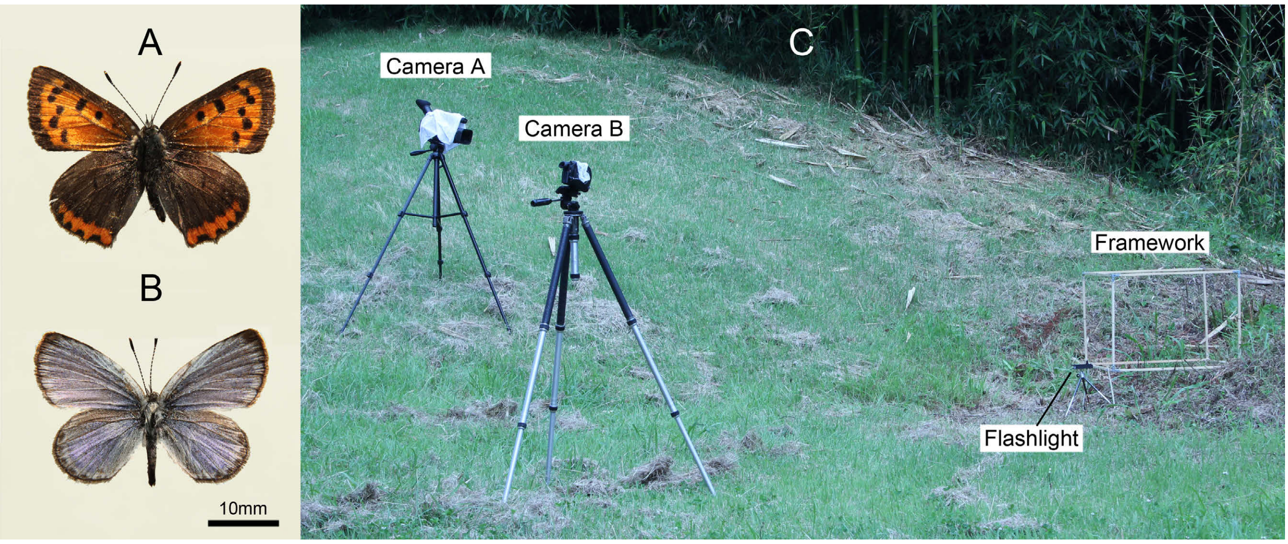

Fig. 1. A – *Lycaena phlaeas*, male; B – *Zizeeria maha*, male; C – Layout of station E. The experimental framework is positioned on the right and monitored using two video cameras placed on the left. An LED flashlight is positioned near the bottom of the front face of the framework.

and aspect ratios (4 × [forewing length]^2/total wing area). Based on the measurement of flight velocities of 62 butterfly species flying freely in nature, Dudley & Srygley (1994) demonstrated that increased flight speeds were positively correlated with higher wing loadings and negatively correlated with higher aspect ratios.

These findings suggest that mate-acquisition tactics are related to flight morphology. Wickman (1992) found that perching species had higher thorax-to-body mass ratios, wing loadings, and aspect ratios than patrolling species. Although some studies have described the relationship between mating tactics and flight behaviour (Wickman, 1992; Wiklund, 2003), none have quantitatively characterised this relationship. This is probably because the exact measurement of butterfly flight behaviour is challenging. In the present study, the flight behaviours of free-flying males of two lycaenid species with different flight tactics were compared, focusing on the following five properties: flight velocity, change in flight direction, acceleration during take-off, relative flight time, and flight morphology. The first three properties were determined based on three-dimensional flight reconstruction. Predictions were that the perching species show shorter relative flight time, faster flight with higher acceleration than the patrolling species, and that they have higher thorax mass ratios and higher wing loadings.

MATERIAL AND METHODS

Studied butterfly species

The perching species *Lycaena phlaeas* (Linnaeus, 1761) from the subfamily Lycaeninae, and the patrolling species *Zizeeria maha* (Kollar, 1844) from the subfamily Polyommantinae were selected (Fig. 1A and B). The mating behaviour of the former species was described by Suzuki (1976), and the mate-searching behaviour of the latter species was investigated by Wago et al. (1976) and Wago (1977, 1978). Both species are commonly found in open grasslands and along the edges of agricultural fields, where their larval food plants, *Rumex acelosa* and *R. japonicus* for *L. phlaeas*, and *Oxalis corniculata* for *Z. maha*, are abundant. Both lycaenid species were observed in the same field.

Flight velocity, acceleration, and directional change

L. phlaeas males are active from 8:30 to 17:00, and establish perching sites in the morning (Suzuki, 1976). Adults of *Z. maha* are active from 8:00 to 19:00, with mating behaviour occurring more frequently in the morning than in the afternoon (Wago et al., 1976). The fieldwork of the present study was conducted from 9:30 to 13:00 in April to June and October 2021. The air temperature near the shadowed ground was measured during flight recording using a data logger Gemini Tinytag (Gemini Data Loggers Ltd., UK).

Sex differentiation was straightforward in *Z. maha*, where males have blue dorsal wings and females have black dorsal wings. In *L. phlaeas*, males have the forewing of linear outer margin, contrast to females with the forewing of round outer margin. When sex identification was difficult, especially in *L. phlaeas*, individuals were captured after recording and examined based on the shape of the abdominal tip.

Flight velocity, acceleration, and change in flight direction were measured using three-dimensional analysis. A three-dimensional analysis of butterflies flying in nature was recently performed by our group (Imafuku et al., 2024). In this section, I describe our basic methodology. Five stations (A–E) were selected in Kyoto and Shiga prefectures, each separated by at least 3 km, which seemed to prevent the same butterflies from moving between the stations. A space where butterflies frequently appeared, but without nectar sources or larval foodplants, was determined at each station, and a rectangular framework (62 × 62 cm, 46 cm high) made of wooden bars (9 mm thick) was placed in this space to obtain 12 reference points (8 corners of the framework and 4 midpoints of its long sides) (Fig. 1C). Two video recorders, A: VX2100 and B: DCR810 (Sony Co., Tokyo, JPN), were firmly fixed to video-record this space. Their shutter speeds were set high: 1/1000 s for Camera A and in "Sports Mode" for Camera B. The distance from each camera to the space was 4–7 m. The lens axes of the cameras were set almost horizontally (−11° from the horizon on average, ranging from −21 to −2°), and crossed nearly at a right angle (85° on average, ranging from 63 to 115°). The framework occupied 33% on average (ranging from 15 to 48%) of the total area of the video view. The video recorders recorded

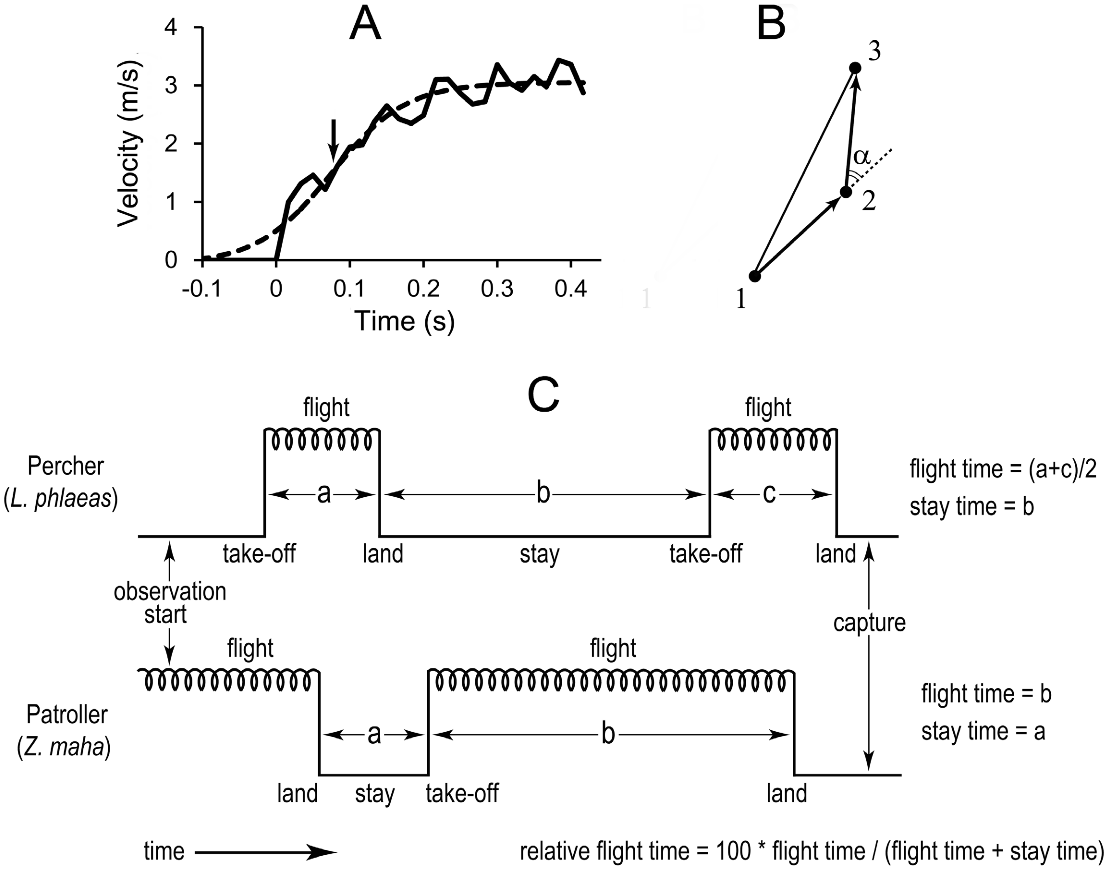

Fig. 2. Illustrations depicting the determining the acceleration during take-off (A), change in flight direction (B), and relative flight time (C). A – the change in flight velocity (solid line) is fitted with a sigmoid curve (dashed line), with acceleration determined at the inflection point of this curve (indicated by an arrow). B – numerals 1, 2, and 3 represent three successive 3D coordinates of butterfly positions. The change in flight direction (directional change; angle α) is the external angle of coordinate 2 in the triangle formed by coordinates 1, 2, and 3. C – typical observation patterns of *L. phlaeas* (top) and *Z. maha* (bottom). Butterfly capture was primarily conducted when individuals were stationary.

for a maximum of 1 h. After shooting the framework, it was removed. A light-emitting diode (LED) flashlight (Fig. 1C) emitting a flash of light for 0.1 s every 3 s was continuously recorded to synchronise the two series of video images.

After field recording, the video images were copied to a home video recorder DMR-BR590 (Panasonic Co., Tokyo, JPN). Images taken using Camera B were first copied to Camera A with a frame-numbering function and then to the home video recorder to add the frame numbers. Part of the series of images necessary for analysis (21–60 frames) was downloaded manually frame-by-frame to a personal computer Windows 7 using software GV-USB2 (IO Data Device, Inc., Ishikawa, JPN), which produced a series of tif-images at a rate of 60 frames/s. The position of the butterfly (thorax, where possible) in the image was digitized using ImageJ ver. 5-3. The 3D coordinates of the butterfly were calculated using a direct linear transformation (DLT) method. First, 11 coefficients (whose values depended on the location of the cameras) in the transformation expressions were determined (calibration) using the 12 reference points mentioned above. Subsequently, the 3D coordinates of the butterfly position in the wild were calculated using two sets of camera images and the determined coefficients. Biewener & Full (1992) briefly explained the expression of the DLT.

A 50 cm-bar held horizontally, vertically, or obliquely, including inside and outside of the framework was video-viewed under the same condition as above to address an error caused in the process of shooting by two video cameras and digitizing butterfly positions into the computer, with an error of 0.5 ± 0.5% (m ± SD, n = 20).

Wind significantly affects the flight velocity of butterflies (Dudley, 2000). Therefore, video images recorded under windy conditions (judged by the movements of the surrounding leaves) were not used for analysis. Flight velocity and acceleration were calculated using a fourth-order central difference (Biewener & Full, 1992). During take-off, flight velocity increased with large fluctuations due to the flapping of large wings; therefore, acceleration was determined at the inflection point of a sigmoid curve fitted to the velocity-time curve (Fig. 2A). The magnitude of the change in flight direction (directional change) was expressed using an angle calculated using three successive coordinates, as shown in Fig. 2B.

Five to six flights were recorded for velocity and directional changes at each station. Take-offs were observed at four stations (1–2 take-offs each) for *L. phlaeas* and at three stations (1–3 take-offs each) for *Z. maha* to determine acceleration. These flight properties were averaged within the stations and compared between perching and patrolling species.

Relative flight time

Observations to determine relative flight time were conducted from 9:30 to 12:30 in April and May 2024. A butterfly was tracked in the field, and the durations of consecutive flights and stays were recorded using a voice recorder to determine the relative flight time (ratio of flight time to the sum of flight time and stay time) (Fig. 2C). Ten individuals of each species (*L. phlaeas*

Table 1. Compariason of flight behaviours between perching *Lycaena phlaeas* and patrolling *Zizeeria maha*.

Station	Temperature [°C]*		Velocity [m/s]		Directional change [°]		Accerelation [m/s²]	
	L. phlaeas	*Z. maha*	*L. phlaeas*	*Z. maha*	*L. phlaeas*	*Z. maha*	*L. phlaeas*	*Z. maha*
A	15.7	24.4	1.39 (6)	0.84 (5)	37 (6)	53 (5)	34.0 (2)	12.2 (3)
B	20.0	20.0	1.44 (5)	0.97 (5)	29 (5)	47 (5)	9.5 (2)	2.8 (1)
C	19.6	19.6	1.70 (5)	0.90 (5)	30 (5)	46 (5)	6.5 (1)	
D	24.2	24.2	1.34 (5)	0.86 (5)	30 (5)	51 (5)	18.0 (1)	
E	15.9	26.6	1.71 (5)	0.77 (5)	23 (5)	45 (5)		4.9 (1)
Av ± SD	19.1 ± 3.5	23.0 ± 3.0	1.52 ± 0.18	0.87 ± 0.07	30 ± 5	48 ± 3	17.0 ± 12.3	6.6 ± 4.9
		P > 0.09		P < 0.001		P < 0.001		P > 0.2

*Average temperature at the time of recording of butterfly flight. Numerals in parentheses () indicate numbers of records, but not of independent individuals.

and *Z. maha*) were tracked. These recordings were made for naturally active single males and evading males bathing in the sun, feeding on flowers, or interacting with other conspecifics. Especially, patroller *Z. maha* males frequently fell into conspecific interaction, and the successful observations were less than 50% in this species.

Flight morphology

The thorax-to-body mass ratios, wing loadings, and aspect ratios were determined for all tracked individuals, as described in the previous section. After tracking the butterflies, they were captured, brought to the laboratory in a dark cool box, and kept at −20°C in a freezer. Within 15 d of freezing, the samples were defrosted and immediately subjected to weight measurements. The total body mass and thoracic (head, wings, and abdomen removed) mass were measured to 0.1 mg using a balance AUW220D (Shimadzu Co., Kyoto, JPN). Images of the fore and hind wings of a butterfly were transferred onto a computer using a scanner GT-7600UF (Seiko Epson Co., Nagano, JPN) and measured using ImageJ to determine the forewing length (wing base to the outer forward tip) and wing areas.

Statistics

All statistical analyses were conducted using R software (ver. 3.1.3). Flight properties, flight morphologies, and air temperatures at the time of recording were compared between species with different mate-locating tactics, using Student's t-test.

RESULTS

The results of the comparison of flight parameters are presented in Tables 1 and 2. Perching *L. phlaeas* males travelled significantly faster than patrolling *Z. maha* males (Table 1, velocity). The flight paths of perching *L. phlaeas* males were more linear, with smaller directional changes, compared to those of patrolling *Z. maha* males (Table 1, directional change). In contrast, no significant difference in acceleration during take-off was observed between the two species (Table 1, acceleration). The relative flight time was significantly lower in the perching species (Table 2). Air temperature at the time of recording did not differ between the two species (Tables 1 and 2).

The results of the comparison of flight morphology are presented in Table 3. Perching *L. phlaeas* males had significantly greater total body mass and thorax mass than patrolling *Z. maha* males. Although both masses were higher in *L. phlaeas*, the thorax-to-body mass ratio was also significantly greater in this species. The total wing area (sum of two forewings and two hindwings) was significantly larger in perching *L. phlaeas* than in patrolling *Z. maha*, and wing loading was significantly higher in the former species. However, no significant difference in aspect ratio was observed between the two species.

DISCUSSION

Flight behaviour

Regarding the behavioural aspects of mate-locating tactics in male butterflies, perching species are said to have ability to exert high flight acceleration and high flight velocity (Wickman, 1992; Wiklund, 2003). In contrast, patrolling species are said to have ability to sustain continuous flight (Scott, 1973). Among these flight properties, the tendency for continuous flight in the patrolling species was confirmed in the present study (Table 2).

Table 2. Relative flight time (%) of perching *Lycaena phlaeas* and patrolling *Zizeeria maha*.

Lycaena phlaeas					*Zizeeria maha*				
Indiv.	Temp. (°C)	Flight time (s)	Stay time (s)	Relative flight time	Indiv.	Temp. (°C)	Flight time (s)	Stay time (s)	Relative flight time
L1	23.5	8	416	2	Z2	22.8	12	6	67
L4	19.3	2	100	2	Z3	22.9	8	12	40
L5	23.3	20	54	27	Z4	19.1	6	20	23
L6	23.3	6	76	7	Z5	18.9	34	14	71
L7	23.1	6	94	6	Z6	19.4	18	10	64
L8	23.3	2	38	5	Z7	20.4	22	10	69
L9	25.7	14	78	15	Z8	20.3	16	28	36
L10	18.1	6	44	12	Z9	20.3	34	30	53
L11	18.6	2	78	3	Z10	24.3	53	14	79
L12	19.9	4	72	5	Z11	24.6	12	9	57
Av ± SD	21.8 ± 2.6	7 ± 6	105 ± 111	8 ± 8	Av ± SD	21.3 ± 2.2	21 ± 15	15 ± 8	56 ± 18
						P > 0.6			P < 0.001

Table 3. Comparison of flight morphology between perching *Lycaena phlaeas* and patrolling *Zizeeria maha*. (n = 10)

	L. phlaeas	*Z. maha*	P
Total body mass (mg)	30.4 ± 4.3	15.3 ± 2.4	< 0.001
Thorax mass (mg)	18.7 ± 3.0	7.4 ± 1.2	< 0.001
Thorax / body mass (%)	61.4 ± 3.1	48.3 ± 2.9	< 0.001
Total wing area (cm^2)	3.52 ± 0.33	2.98 ± 0.34	< 0.002
Wing loading (N/m^2)	0.84 ± 0.07	0.50 ± 0.04	< 0.001
Forewing length (cm)	1.49 ± 0.06	1.38 ± 0.07	< 0.003
Aspect ratio	2.53 ± 0.07	2.58 ± 0.08	> 0.2

Flight velocity has been shown to be associated with body mass (Dudley & Srygley, 1994). In the present study, the perching species *L. phlaeas* exhibited higher flight velocity and greater body mass compared to the patrolling species *Z. maha*. Therefore, the faster flight of *L. phlaeas* may be attributed to its greater body mass. Dudley & Srygley (1994) provided an equation relating body mass to flight velocity [velocity (m/s) = 8.7 × mass (g) $^{0.56}$], which I used to calculate the expected flight velocity of the studied species. The actual flight velocity was 23% higher in *L. phlaeas* and only 3% higher in *Z. maha* compared to the expected flight values. This suggests that flight velocity of these species is influenced not only by body mass but also by their respective mate-locating tactics.

Flight morphology

The relationship between mate-locating tactics and flight morphology in butterflies was first explored by Wickman (1992) who examined 44 species and found that males of perching species exhibited higher thorax-to-body mass ratios, higher wing loadings, and higher aspect ratios compared to patrolling species. The first two properties align well with the results of this study, whereas a higher aspect ratio was not observed in my perching species.

Regarding lycaenid butterflies, Wickman (1992) examined seven perching species and one patrolling species. The aspect-ratio values extracted from Fig. 2B in Wickman (1992) were 3.06 ± 0.09 (m ± SD) (n = 7) for the perching species and 3.18 (n = 1) for the patrolling species. Similarly, in the present study, the perching species did not exhibit a higher aspect ratio. This finding suggests that among small butterflies such as lycaenids, there is no clear correlation between reproductive tactics and wing aspect ratio.

Three-dimensional analysis in natural conditions

This study demonstrated that perching species fly at high flight velocity with limited flight duration and that these flight properties are associated with a high thorax-to-body mass ratio and high wing loading. The differences in male mating tactics – perching or patrolling – should also be related to female behaviour. Higher reproductive success in territorial males has been reported in *Pararge aegeria* (Wickman & Wiklund, 1983) and *Cenonympha pamphilus* (Wickman, 1985). Further investigation into female behaviour in the studied species is needed.

To accurately assess flight performance, precise measurements of flight properties must be obtained. In most studies, butterfly flight properties have been measured under artificial conditions, such as in illuminated rooms, outdoor cages, and wind tunnels (see Dudley, 2000; Almbro & Kullberg, 2008, 2012; Kleckova et al., 2024). Under such conditions, flight parameters can be altered, as evidenced by the reduction in flight velocity observed in controlled environments (Dudley & Srygley, 1994). In the present study, a three-dimensional tracking method was employed to analyse butterflies flying freely in natural conditions, providing accurate estimates of flight velocity, acceleration, and directional changes, with an error of only 0.5% (see Material and Methods). However, the dataset was limited, and only two species were examined. Future studies should incorporate a larger sample of species and consider phylogenetic comparisons. Additionally, applying ~~a~~ three-dimensional analysis to other behavioural phenomena, such as foraging and anti-predator strategies, could provide valuable insights into butterfly behaviour.

ACKNOWLEDGEMENTS. I sincerely thank N. Ogihara of Tokyo University for his valuable advice on three-dimensional analysis.

REFERENCES

Alcock J. 1983: Territoriality by hilltopping males of the great purple hairstreak, *Atlides halesus* (Lepidoptera, Lycaenidae): convergent evolution with a pompilid wasp. — *Behav. Ecol. Sociobiol.* **13**: 57–62.

Almbro M. & Kullberg C. 2008: Impaired escape flight ability in butterflies due to low flight muscle ratio prior to hibernation. — *J. Exp. Biol.* **211**: 24–28.

Almbro M. & Kullberg C. 2012: Weight loading and reproductive status affect the flight performance of *Pieris napi* butterflies. — *J. Insect Behav.* **25**: 441–452.

Azuma A. & Kira Y. 2000: Statistical configuration of bird's flight performance. — *J. Jpn. Soc. Aeronaut. Space Sci.* **28**: 578–581 [in Japanese].

Baker R.R. 1972: Territorial behaviour of the nymphalid butterflies, *Aglais urticae* (L.) and *Inachis io* (L.). — *J. Anim. Ecol.* **41**: 453–469.

Benson W.W., Haddad C.F.B. & Zikán M. 1989: Territorial behavior and dominance in some Heliconiine butterflies (Nymphalidae). — *J. Lepid. Soc.* **43**: 33–49.

Betts C.R. & Wootton R.J. 1988: Wing shape and flight behaviour in butterflies (Lepidoptera: Papilionoidea and Hesperioidea): a preliminary analysis. — *J. Exp. Biol.* **138**: 271–288.

Biewener A.A. & Full R.J. 1992: Force platform and kinematic analysis. In Biewener A.A. (ed.): *Biomechanics – Structures and Systems*. Oxford University Press, Oxford, New York, Tokyo, pp. 45–73.

Biswas C., Bhowal A., Roy E., Dutta W. & Ray P. 2023: Territorial and courtship behaviour of Indian common crow butterfly (*Euploea core*). — *J. Lepid. Soc.* **77**: 169–179.

Bitzer R.J. & Shaw K.C. 1981: Territorial behavior of the red admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae). — *J. Res. Lepid.* **18**: 36–49.

Darwin C. 1911: *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*. Murray, London, 703 pp.

Davies N.B. 1978: Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the resident always wins. — *Anim. Behav.* **26**: 138–147.

Dudley R. 1990: Biometrics of flight in Neotropical butterflies: morphometrics and kinematics. — *J. Exp. Biol.* **150**: 37–53.

Dudley R. 2000: *The Biomechanics of Insect Flight. Form, Function, Evolution*. Princeton University Press, Princeton, NJ, 476 pp.

Dudley R. & Srygley R.B. 1994: Flight physiology of Neotropical butterflies: allometry of airspeeds during natural free flight. — *J. Exp. Biol.* **191**: 125–139.

Heinrich B. 1986: Thermoregulation and flight activity of a satyrine, *Coenonympha inornata* (Lepidoptera: Satyridae). — *Ecology* **67**: 593–597.

Honda K. 2005: Mating behaviour. In Honda K. & Kato Y. (eds): *Biology of Butterflies*. University of Tokyo Press, Tokyo, pp. 302–349 [in Japanese].

Imafuku M., Ogihara N. & Uchida A. 2024: Flight behavior of a territorial Theclini species, *Favonius taxila* (Lycaenidae), mainly based on three-dimensional analysis. — *J. Lepid. Soc.* **78**: 149–158.

Kemp D.J. 2001: Investigating the consistency of mate-locating behavior in the territorial butterfly *Hypolimnas bolina* (Lepidoptera: Nymphalidae). — *J. Insect Behav.* **14**: 129–147.

Kleckova I., Linke D., Rozende F.D.M., Rauscher L., Le Roy C. & Matos-Maravi P. 2024: Flight behaviour diverges more between seasonal forms than between species in *Pieris* butterflies. — *Ecol. Evol.* **14**: e70012, 13 pp.

Lederhouse R.C. 1995: Comparative mating behavior and sexual selection in North American butterflies. In Scriber J.M., Tsubaki Y. & Lederhouse R.C. (eds): *Swallowtail Butterflies: their Ecology and Evolutionary Biology.* Scientific Publications, Gainsville, Tokyo, pp.117–131.

Magnus D.B.E. 1963: Sex limited mimicry II – Visual selection in the mate choice of butterflies. — *Int. Congr. Zool.* **16**: 179–183.

Marden J.H. & Chai P. 1991: Aerial predation and butterfly design: how palatability, mimicry, and the need for evasive flight constrain mass allocation. — *Am. Nat.* **138**: 15–36.

Rutowski R.L. 1997: Sexual dimorphism, mating systems and ecology in butterflies. In Choe J.C. & Crespi B.J. (eds): *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge University Press, Cambridge, pp. 257–272.

Scott J.A. 1973: Mating of butterflies. — *J. Res. Lepid.* **11**: 99–127.

Silberglied R.E. 1984: Visual communication and sexual selection among butterflies. In Vane-Wright R., Ackery P. & DeVries P. (eds): *The Biology of Butterflies*. Academic Press, London, pp. 207–223.

Srygley R.B. & Dudley R. 1993: Correlations of the position of center of body mass with butterfly escape tactics. — *J. Exp. Biol.* **174**: 155–166.

Suzuki Y. 1976: So-called territorial behaviour of the small copper, *Lycaena phlaeas daimio* (Lepidoptera, Lycaenidae). — *Kontyû* **44**: 193–204.

Takeuchi T. & Imafuku M. 2005: Territorial behavior of *Favonius taxila* (Lycaenidae): territory size and persistency. — *J. Res. Lepid.* **38**: 59–66.

Wago H. 1977: Studies on the mating behavior of the pale grass blue, *Zizeeria maha argia* (Lepidoptera, Lycaenidae). II. Recognition of the proper mate by the male. — *Kontyû* **45**: 92–96.

Wago H. 1978: Studies on the mating behavior of the pale grass blue, *Zizeeria maha argia* (Lepidoptera: Lycaenidae). III. Olfactory cues in sexual discrimination by males. — *Appl. Entomol. Zool.* **13**: 283–289.

Wago H., Unno K. & Suzuki Y. 1976: Studies on the mating behavior of the pale grass blue, *Zizeeria maha argia* (Lepidoptera: Lycaenidae). I. Recognition of conspecific individuals by flying males. — *Appl. Entomol. Zool.* **11**: 302–311.

Wickman P.-O. 1985: Territorial defence and mating success in males of the small heath butterfly, *Coenonympha pamphilus* L. (Lepidoptera: Satyridae). — *Anim. Behav.* **33**: 1162–1168.

Wickman P.-O. 1992: Sexual selection and butterfly design – a comparative study. — *Evolution* **46**: 1525–1536.

Wickman P.-O. & Wiklund C. 1983: Territorial defence and seasonal decline in the speckled wood butterfly (*Pararge aegeria*). — *Anim. Behav.* **31**: 1206–1216.

Wiklund C. 2003: Sexual selection and the evolution of butterfly mating systems. In Boggs C.L., Watt W.B. & Ehrlich P.R. (eds): *Butterflies. Ecology and Evolution, Taking Flight*. University of Chicago Press, Chicago, London, pp. 67–90.

Received September 25, 2024; revised and accepted March 15, 2025