

Does flight morphology relate to flight performance? An experimental test with the butterfly *Pararge aegeria*

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Summary

1. The relationship between maximal acceleration capacity and flight morphology was tested experimentally in the butterfly *Pararge aegeria*. Such relations are often assumed but seldom tested.
2. In both sexes acceleration capacity was positively correlated with total body mass, thorax mass, forewing area, forewing length, wing loading, aspect ratio and centre of forewing area (centroid). Relationships with total body mass, forewing area, forewing length and wing loading were stronger in males. This can be explained by different mass allocation: males allocate proportionally more mass to the thorax, females more to the abdomen.
3. Evidence for the combined effect of morphological traits on acceleration capacity was found by multivariate analysis. In males and females, a more distant relative centroid and higher relative thorax mass were related to a higher flight capacity. In addition, aspect ratio was positively related to acceleration capacity in males only.
4. Our results support the assumed mechanism behind the relationship between flight morphology and mate-locating behaviour.

Key-words: Lepidoptera, mate-locating, maximal acceleration capacity, resource allocation

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Introduction

Organisms differing in morphology may have different behavioural repertoires or may vary in the performance (i.e. degree in which individuals fulfil ecologically relevant functions) of particular behaviours. In the case of discrete morphological variation such differences can be obvious. For example, several insects have wingless (or brachypterous) and winged (or macropterous) forms in which only the latter are able to fly (i.e. dispersal polymorphism in crickets and waterstriders; Zera & Denno 1997). For traits with continuous variation the relationships between design (i.e. particular value of a trait or suite of traits) and performance may be more subtle and require careful testing. Quite often evolutionary ecological studies directly interpret variation in design (including morphology) as variation in fitness components assuming, but only seldom testing, differential performance. However, only variation in performance can be the direct result of variation in design, and in turn may cause variation in fitness (Arnold 1983).

Such conceptual short cuts between morphological design and fitness components have often been made

in studies on insects with continuous variation in their flight apparatus (e.g. butterflies and dragonflies). Their morphological traits are commonly studied in a context of adaptations to particular ecological conditions (e.g. Dempster, King & Lakhani 1976; Dempster 1991; Taylor & Merriam 1995; Witkowski & Adamski 1996; Berwaerts *et al.* 1998; Thomas, Hill & Lewis 1998; Hill, Thomas & Blakeley 1999a; Hill, Thomas & Lewis 1999b). In most of these intraspecific studies direct evidence for a relationship between the observed morphological variation and ecologically relevant variation in flight performance (e.g. velocity and acceleration) is lacking. A larger relative thorax mass is, for instance, thought to reflect a higher flight capacity (e.g. Thomas, Hill & Lewis 1998), but whether and to what extent such relationships apply at the intraspecific level have received only little attention.

Studies on neotropical butterflies give instructive information on the interspecific relationship between morphology and flight characteristics (reviewed by Srygley 1994 and Dudley 2000). These butterflies have different tactics to escape from visual predators: palatable species fly fast and erratic, unpalatable species fly slow and regular. Mass allocation to the thorax (i.e. flight muscle ratio – FMR), is positively related to acceleration capacity. The position of centre of body mass (cm_{body}) is directly related to manoeuvrability

(Srygley & Dudley 1993; Srygley & Kingsolver 1998). Since FMR and cm_{body} are highly interrelated, Srygley & Kingsolver (2000) experimentally altered these traits to estimate the independent effect on flight speed and manoeuvrability but surprisingly no consistent relationship was found.

In this paper, we explicitly evaluate in an experimental set-up to what extent variation in flight morphology leads to variation in flight performance in a temperate-zone butterfly. We analyse an ecologically relevant flight performance measure – i.e. acceleration capacity – in relation to flight morphology in both females and males of the Speckled Wood Butterfly (*Pararge aegeria* L.). Included flight-morphological traits are size (i.e. total mass, forewing length, forewing area), flight muscle investment (i.e. relative thorax mass), wing shape (i.e. aspect ratio and the position of centre of forewing area or centroid) and wing loading (total body mass/area forewing). These traits have often been studied in relation to animal flight (see Dudley 2000 and references therein).

In butterflies, sexual morphological differences may have important consequences for flight (Gilchrist 1990). Male butterflies spend most of their active time locating mates. Speckled Wood males may adopt two different mate-locating strategies that involve different flight patterns: perching and patrolling (*sensu* Scott 1974; Shreeve 1984). Perchers exhibit a sit-and-wait strategy and defend a territory by rising to intercept passing females and intruding males and by spiral flights in which contesting males collide with each other. Hence, their flight is associated with high levels of acceleration. Patrollers on the other hand fly from one spot to another in search for females, which requires a more sustained flight at lower speed. Perchers have been shown to have a larger relative thorax size than patrollers (Van Dyck, Matthysen & Dhondt 1997). This pattern was interpreted as having adaptive value for the different mate locating strategies. We tested four predictions:

1. Flight performance is positively related with relative thorax size in males and females. Since females invest proportionally more in abdomen mass, we expect a lower performance for females compared to males with similar body mass (Marden & Chai 1991).
2. Flight performance is positively related with aspect ratio (Betts & Wootton 1988).
3. Butterflies with a wing centroid located more distally have a larger flight capacity: they can move air with a larger relative speed and thus generate higher aerodynamic forces per unit area (Dudley 2000).
4. A positive relationship between wing loading and flight performance – this relationship should be stronger within males than within females: for the same forewing area, males are characterized by a larger flight muscle mass than females (Gilchrist 1990).

Methods

FLIGHT PERFORMANCE MEASUREMENT

Directly developed butterflies were used from a recently established laboratory breeding stock consisting of three generations (P–F1–F2) and a large number of families (41, 46 and 55 resp.). The stock originated from 41 wild caught females. Therefore, large genetic variation was retained. Before experiments, naive animals had *ad libitum* access to honey-water. Next, they were placed for 15 min at a temperature of 5 °C to minimize activity. This allowed removal of thoracic hairs where we glued the bent tip of a needle (standard length: 17 mm, mean mass \pm SD: 14.44 \pm 0.58 mg) to the dorsal surface of the pterothoracic segment (Superglue Super-Matic Loctite). The upward pointing end of the needle fitted into a freely hinging holder (290 mg; Fig. 1).

Tarsal reflex was used to initiate flight (Tsuji, Kingsolver & Watt 1986) by which the animals lifted the needle about the hinge axis (Fig. 1). This was videotaped by means of a Panasonic F15 camera (50 Hz). For each animal, this tarsal stimulation was repeated 10 times, without changing the needle (i.e. identical set-up). Next, the 10 video-sequences were screened in order to retain only those sequences with the widest angle, at least when the position of the needle was constant (within the resolution of the video-frames) over three or more wingbeat cycles. For these cycles no flight power is spent in overall accelerations, which means that the averaged flight force is directly proportional to the gravitational force (i.e. the moment induced by gravity is entirely countered by the moment of the flight force). For all animals tested, at least 6 out of the 10 flight sequences could be retained in this way. Of these sequences, the static lift angle over these three wingbeat cycles was measured from the videorecordings by means of a NAC XY-coordinator. The median of these measurements was calculated per individual. Finally, the largest of this series of static lift angles was selected for each individual for further analysis (i.e. the maximal individual lift angle). Preliminary tests using a Redlake HR 1000 high-speed video showed that the wing stroke plane did not change with respect to the long axis of the body, irrespective of the angle at which the needle was lifted (note that the body axis has a fixed orientation against the needle). Hence, a measure for flight performance – which is called here *Maximal Individual Relative Flight Force* or MIRFF – could be calculated from this maximal individual lift angle. The magnitude of a force perpendicular to the stroke plane countering the gravitational moment was used for this purpose (Fig. 1). Notice that this force probably does not represent the average thrust vector (Dudley 2000), but it provides us with a reliable and repeatable technique to compare individual (relative) performance (see below). In total 62 females and 67 males were tested in this way. Maximal and median lift angle were correlated within individuals ($r^2_{\text{females}} = 0.57$, $n = 62$;

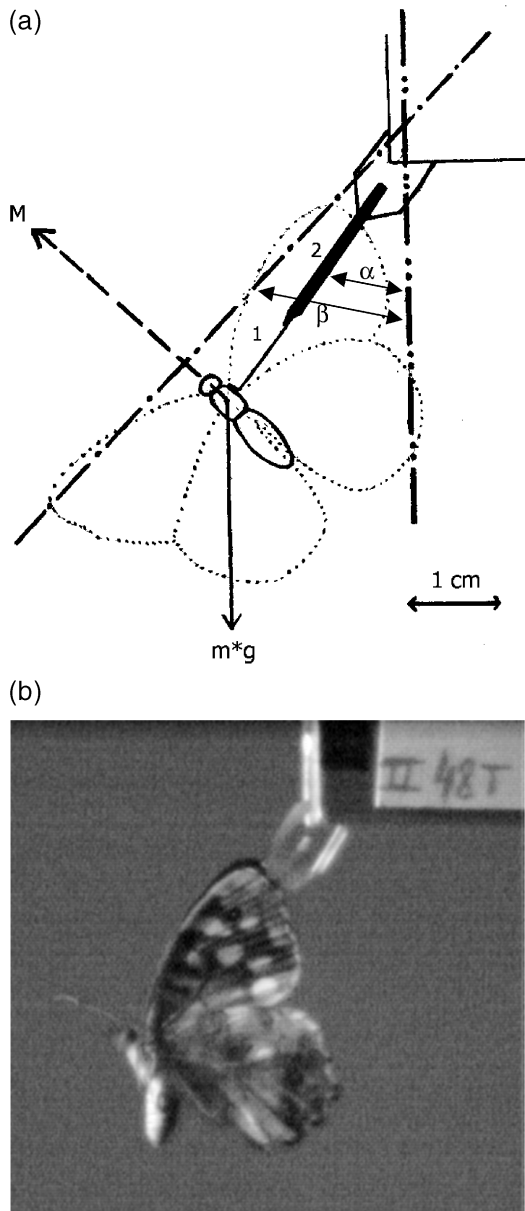


Fig. 1. Experimental set-up for measurement of MIRFF (lateral view). (a) Schematic diagram of butterfly with wings drawn in down- and upstroke (symbols: M = flight force, $m \cdot g$ = gravity, α = needle angle, β = wing stroke plane angle, 1 = needle, 2 = holder). (b) Video frame.

$r^2_{\text{males}} = 0.63$, $n = 67$) and were therefore considered as repeatable. After the experiments individuals were frozen to measure morphological traits later on.

MORPHOLOGICAL MEASUREMENTS

Butterflies were dried to constant mass at 60 °C during 24 h. Abdomen, thorax and head were separated from legs and wings and weighed separately with an electronic microbalance (MT5 Mettler). Repeated measurements showed small percentages of difference between first and second measurements for total dry body mass (1.5%, $n = 26$), needle mass (0.1%, $n = 5$), head mass (1.0%, $n = 5$) and thorax mass (1.7%, $n = 5$).

Forewing measurements were performed with an image analysing system (OPTIMAS 6.51 software – OPTIMAS 1999) from digital photos (Olympus Camedia C-3030 zoom camera) of dorsal forewing surfaces. Repeated measurements indicated small differences between first and second measure ($n = 19$) for forewing area, wing centroid and forewing length (0.9%, 1.3% and 0.6%, respectively). Wing loading was calculated as total dry body mass/forewing area, and aspect ratio as $4 \times \text{forewing length}^2/\text{forewing area}$, using each time untransformed data. Note that for one female values of total dry body mass and wing loading are lacking, which explains different sample sizes within females for different traits (Table 1).

STATISTICS

Prior to analysis all data were \log_{10} -transformed to improve normality. Means are given \pm SE unless mentioned otherwise. First, analyses were performed to test the relationship between MIRFF and separate flight morphology traits (total dry body mass, thorax mass, forewing area, forewing length, wing loading, aspect ratio and wing centroid). Secondly, multivariate linear regression analyses were done to see to what extent variation in MIRFF is explained by a combination of the morphological traits (thorax mass, centroid and aspect ratio) including interaction terms. In these multivariate analyses, traits were adjusted for body mass by using their residuals regressed on total dry body mass (therefore we use relative thorax size and relative centroid), except for aspect ratio since it was not correlated with body mass. Total body mass and wing loading were not included in the model because of statistical dependence (*see* calculation of MIRFF); aspect ratio was used as a combined effect of forewing area and forewing length. Multivariate linear regression analyses were done starting each time from a full model including the morphological traits of interest and all interaction terms. Next, model selection towards a final model was done by stepwise backward elimination of factors with the highest P -values. Factors were not eliminated as long as they were incorporated in higher-order interaction terms. All analyses were performed with SAS 6.12 software.

Results

INTER- AND INTRASEXUAL FLIGHT MORPHOLOGY

Sexual differences in flight morphology are summarized by Table 1. Although there was considerable overlap, females had on average larger body masses than males. This was due to their heavier abdomen since thorax mass did not differ, while heads were even heavier in males. Females had larger, but not longer, forewings than males, and forewing centroid was also located more distally in females.

Table 1. Comparison of flight-morphological traits (mean \pm SE) between the sexes. Means are based on untransformed data, and *t*-test results on log-transformed data

	Females			Males			<i>t</i> -test
	Mean	\pm SE	<i>n</i>	mean	\pm SE	<i>n</i>	
Total dry body mass (mg)	21.38	\pm 0.44	61	15.46	\pm 0.29	68	***
Head mass (mg)	0.56	\pm 0.01	62	0.73	\pm 0.01	68	***
Thorax mass (mg)	5.54	\pm 0.09	62	5.65	\pm 0.10	68	NS
Abdomen mass (mg)	10.57	\pm 0.31	62	4.67	\pm 0.16	68	***
Forewing length (cm)	2.11	\pm 0.01	62	2.09	\pm 0.01	68	NS
Forewing area (cm ²)	1.84	\pm 0.02	62	1.67	\pm 0.02	68	***
Distance to centroid (cm)	1.11	\pm 0.01	62	1.08	\pm 0.01	68	**
Aspect ratio	10.07	\pm 0.04	62	10.48	\pm 0.04	68	***
Wing loading (mg/cm ²)	12.06	\pm 0.20	61	9.19	\pm 0.12	68	***

P* < 0.05; *P* < 0.01; ****P* < 0.001.

Table 2. Summary of ANCOVA tests with MIRFF as dependent variable and sex, morphological trait and their interaction as independent variables (NDF = numerator degrees of freedom, DDF = denominator degrees of freedom)

Effect	NDF	DDF	<i>F</i> (type III)	Significance
Body mass	1	124	148.71	***
Sex	1	125	4.17	*
Body mass \times sex	1	124	6.35	*
Thorax mass	1	125	83.89	***
Sex	1	125	3.01	NS
Thorax mass \times sex	1	125	2.05	NS
Forewing area	1	125	102.34	***
Sex	1	125	5.37	*
Forewing area \times sex	1	125	5.87	*
Forewing length	1	125	120.50	***
Sex	1	125	6.08	*
Forewing length \times sex	1	125	5.39	*
Wing loading	1	124	63.16	***
Sex	1	124	3.92	*
Wing loading \times sex	1	124	5.20	*
Aspect ratio	1	125	4.31	*
Sex	1	125	0.16	NS
Aspect ratio \times sex	1	125	0.13	NS
Centroid	1	125	92.18	***
Sex	1	125	2.50	NS
Centroid \times sex	1	125	1.96	NS

P* < 0.05; *P* < 0.01; ****P* < 0.001.

Concerning relative investments (i.e. proportion of body part mass to total body mass), males invested more in their thorax (36.7% (\pm 0.4) vs 26.2% (\pm 0.3)), whereas females invested more in their abdomen (29.8% (\pm 0.5) vs 48.9% (\pm 0.6)). Males had narrower wings (i.e. higher aspect ratio) than females. Females had a significantly higher wing loading (i.e. a lower wing area per unit body mass) than males (Table 1).

MIRFF IN RELATION TO FLIGHT MORPHOLOGY

MIRFF differed significantly between sexes: females had a higher mean relative flight force than males (*t* = 2.44, *df* = 127, *P* = 0.016). MIRFF was on average $2.19 \pm 0.09 \times 10^{-4}$ N (range: 0.96–4.13 $\times 10^{-4}$ N) in females,

and $1.92 \pm 0.10 \times 10^{-4}$ N (range: 0.61–4.07 $\times 10^{-4}$ N) in males.

Statistics of the following results are summarized in Table 2. The effect of body mass on MIRFF differed between sexes (Fig. 2a): force output increased more strongly with body mass in males. In other words, females need a larger increase in body mass to produce a larger amount of MIRFF compared with males. MIRFF also increased with thorax mass in both sexes (males and females with heavier thorax mass produce more MIRFF) but there was no interaction with sex. Forewing area and forewing length were correlated with MIRFF and again there was a stronger increase in MIRFF in males than in females (Fig. 2b,c). A similar result was found for wing loading (Fig. 2d). As in thorax mass, aspect ratio and centroid were correlated with MIRFF but there were no sex effects.

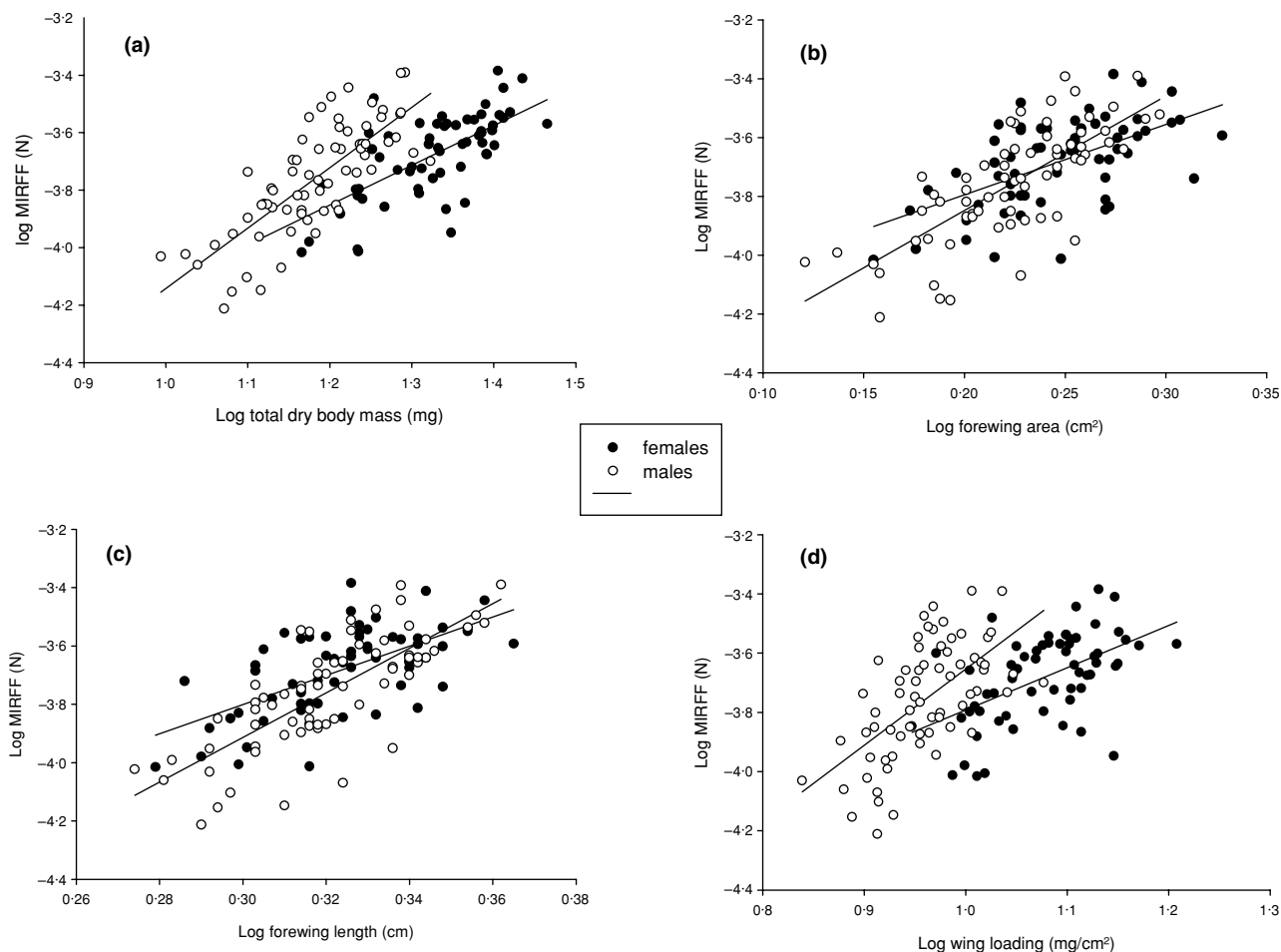


Fig. 2. Regressions of MIRFF in function of: (a) total dry body mass (females: $n = 61$, males: $n = 67$); (b) forewing area (females: $n = 62$, males: $n = 67$); (c) forewing length (females: $n = 62$, males: $n = 67$); and (d) wing loading (females: $n = 61$, males: $n = 67$).

Next, we used multivariate analyses to see to what extent variation in MIRFF is explained by a combination of the morphological traits (see Methods). Variation in MIRFF was analysed in relation to relative thorax size, aspect ratio and relative centroid and their interaction effects for males and females separately. In females, the final regression model contained relative thorax size and centroid as significant factors (thorax size: $F_{1,58} = 7.60$, $P = 0.0078$; centroid: $F_{1,58} = 4.03$, $P = 0.049$ ($n = 62$)). Aspect ratio was removed from the model ($F_{1,57} = 0.81$, $P = 0.4$). In females, a higher MIRFF was associated with a large relative thorax and a more distant centroid. In males, the final model contained all three main morphological traits (thorax size: $F_{1,63} = 19.30$, $P = 0.0001$; aspect ratio: $F_{1,63} = 4.32$, $P = 0.042$; centroid: $F_{1,63} = 8.55$, $P = 0.005$ ($n = 67$)). For both sexes, we obtained the same final model when applying a forward stepwise selection procedure for multivariate linear regression analysis.

Discussion

Our results confirmed the four predictions on the relationships between flight morphology and flight

performance. First, a larger relative thorax mass produced larger MIRFF: the higher the proportion of thorax mass – hence flight muscle mass (Marden 1987; K. Berwaerts, unpublished data) – the higher the acceleration capacity. Such a relationship has often been assumed, but is rarely tested (Van Dyck 2002). Hence, our results are among the first to fill this important gap in the literature. Secondly, our multivariate results showed that beside relative thorax size, aspect ratio also explained a part of the variation in MIRFF in males but not in females: the longer and more slender the forewings, the higher the acceleration capacity. Possible interactions with wing loading can confound the relationship between flight performance and aspect ratio (Betts & Wootton 1988). The position of the centroid also explained a part of the variation in MIRFF in males and females. This follows expectations because for any given wingbeat frequency, wings with a more distant centre of area can move air with a larger relative speed and thus generate higher aerodynamic forces per unit area (Dudley 2000). Finally, females had a higher wing loading than males but MIRFF increased more strongly with wing loading in males. This is what we expected according to the fourth

prediction since females carry more non-flight muscular tissue per unit wing area than males do.

Females are generally heavier than males and allocate more mass to the abdomen. On the other hand, males allocate more to the thorax (Karlsson & Wickman 1990). Females have fewer flight muscles than males per unit of body mass. Without compensation (e.g. by means of higher flight muscle efficiency), we expect a lower flight acceleration capacity. But females had a higher MIRFF than males. However, when including body mass and hence taking into account relative investment, males performed better than females of equal mass. In other words, females have to produce more flight force per unit of flight muscle mass than equally performing males do. As a result of their heavier abdominal loads females may operate at nearer to maximum power output (Berrigan 1991). Owing to the sexual difference in allocation, we expect differences in cm_{body} along the body axis. Owing to the greater abdomen mass and to a small degree lesser head mass, we expect an increased distance between the centre of mass and the wingbases compared with males. Consequently, we expect a detrimental effect on the responsiveness of the body to pitching forces due to larger moments (Srygley & Chai 1990). Since we were not able to measure body motion, we cannot reveal possible effects of differences in position of the centre of mass. However, high-speed video sequences showed that females oscillate their abdomen to a large extent by ventral and dorsal bending. This is a possible mechanism to substantially change body drag and to shift the centre of gravity forwards or backwards and as a consequence to alter flight performance (Brodsky 1994; Gewecke & Niehaus 1981).

Since abdomen mass in females is to a large extent made up of eggs, it can be expected that variation in egg load – and hence variation in relative thorax mass and position of the centre of gravity – affects flight ability (e.g. velocity, acceleration, flight time) (Fischer & Kutsch 2000). This may even apply within individual females as they age and their abdomens lighten as a result of egg-laying. To test for such an effect MIRFF should be measured repeatedly in a series of individual females and analysed in relation to relative egg load. However, predictions are not that straightforward. If females have lighter abdomens, their performance should increase (Gilchrist 1990; Willmott & Ellington 1997). But in *Pararge aegeria* there is evidence that females secondarily allocate resources from flight muscles into egg production as they become older and hence lighter (Karlsson 1994). This would confound predictions; flight performance traits such as acceleration capacity would not change strongly with age. So, further experiments are required to tease apart these confounding factors. Moreover, other confounding processes should possibly be taken into account as well; flight muscle maturation has been suggested to occur in grasshoppers (Fischer & Kutsch

2000) and dragonflies (Marden 1989; Marden 2000), but to our knowledge, there is no evidence for this in butterflies.

Within males, our results support the assumed mechanism behind the relationship between flight morphology and mate-locating related flight types (Van Dyck, Matthysen & Dhondt 1997). We indeed found that larger relative thorax size is associated with higher levels of flight acceleration capacity, which is of particular significance for a territorial perching male. Fighting ability varies among males, as shown by significant interindividual variation in frequency and length of interactions (Wickman & Wiklund 1983), but total size – measured by forewing length – had no effect on the outcome of interactions between males (Shreeve 1987). So, in addition to the role of thermoregulation and heat balance in contesting territorial Speckled Woods (Hardy 1998; Stutt & Willmer 1998), we predict that variation in relative thorax size, relative wing centroid and wing loading contributes significantly to the success of territorial perchers. The evolution of contest behaviour in butterflies is interesting because they lack any obvious morphological traits conventionally associated with animal aggression, hence the means by which individuals are able to inflict costs upon each other during combat are unclear (Kemp & Wiklund 2001). Further experiments are required to examine to what extent relative investments in flight morphology provide some kind of ‘hidden’ weaponry in fighting butterflies.

Our study focused on flight performance in terms of flight force during a relatively short time, mainly representing acceleration capacity. Behavioural differences between Speckled Wood males and females, and between perching and patrolling males can thus be explained in terms of variation in acceleration capacity (cf. Introduction). However, the significance of the studied flight morphology and MIRFF for aspects of flight other than manoeuvrability and acceleration, remains to be tested. This may in particular be relevant for sustained flight as in patrolling males or in the case of dispersal behaviour. Further experiments need to take into account the possibility of trade-offs for flight morphology between different aspects of flight (e.g. speed vs endurance). Moreover, experimental results with tethered butterflies may not translate directly into field circumstances. Morphologies that enhance MIRFF may, for instance, also increase drag and inertial forces, which may be detrimental to free flight. So far, intraspecific studies on insect flight under field conditions (e.g. Srygley & Kingsolver 2000) are even more rare than such work under laboratory and mainly tethered conditions.

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