International Journal of Odonatology, 2015
Vol. 18, No. 1, 55–64, http://dx.doi.org/10.1080/13887890.2015.1013511

High frequency and counterstroking: *Calopteryx splendens* female threatening flight

Dagmar Hilfert-Rüppell*

Institut für Fachdidaktik der Naturwissenschaften, Abteilung Biologie und Biologiedidaktik, Technische Universität Braunschweig, 38106 Braunschweig, Germany

(*Received 19 October 2014; accepted 20 January 2015*)

Thanks to Georg Rüppell for tireless help in the field and for enriching my life with dragonfly research and discussions!

A hitherto unknown flight pattern of female *Calopteryx splendens* is described. On a day with heavy winds, when no damselfly could fly in open space of the river, I observed and filmed four to six females foraging in a small bay sheltered by bank vegetation. Females fought for perches and showed a threatening flight with counterstroking and high frequency wing-beating. In all other female flight modes the fore and hind wings were beaten nearly in parallel with a much lower beat frequency. As the newly observed flight mode resembles the courting flight mode of males of *C. splendens* the female's threatening flight is compared with it. At landings of both sexes the wings were beaten in a counterstroking mode for one to seven beats, as well. The possible development of female's threatening flight from wing beating during landing of *C. splendens* is discussed. The relevance of these findings is to extend the knowledge about the variety of flight modes in *Calopteryx* females.

Keywords: Odonata; dragonfly; damselfly flight; beat frequency; flight speed; phase relationship of wings; beat-angle; aggressive behaviour; female threatening flight

Introduction

Odonata are excellent fliers. Their complex joint and muscle system (Pfau, 1986) allows a lot of variations in frequency, amplitude and direction of wing beating or phase relationship of forewings and hind wings. These variations cause different flight manoeuvres, flight speeds or acceleration. Furthermore the morphological preconditions of the two suborders of Odonata cause different flight performances (Wootton, 1991). Anisoptera are very fast fliers (up to 15 m s^{-1}), while Zygoptera show a high manoeuvrability and accelerations, which are highest in Calopterygidae (Rüppell, 1989, 1999; Rüppell & Hilfert-Rüppell, 2009a). One important reason for that is the very low wing loading in comparison to other Odonata (Grabow & Rüppell, 1995). Another reason is a special feature of their coordination of forewings and hind wings. Both sexes normally beat both wing pairs nearly in parallel, the forewings being about 10% earlier at the end of the upstroke (Rüppell & Hilfert-Rüppell, 2009a). This parallel (= in-phase) beating is aerodynamically very effective (Wang, 2008) because all four wings together accelerate a lot of

*Email: d.hilfert-rueppell@tu-bs.de

air. Another aerodynamic reason for the high accelerations and manoeuvrability of this parallel beating is the clap-and-fling effect (Weis-Fogh, 1973). This effect emerges when the wings at the end of the upstroke clap together and are beaten downwards again (fling). The airstreams generated by this closing and sudden opening produce up to 30% more lift than when wings are not clapped together (Wakeling & Ellington, 1997).

In nearly all their flights *Calopteryx* spp. males show parallel beating of forewings and hind wings to conquer and defend territories (Rüppell, Hilfert-Rüppell, Rehfeldt & Schütte, 2005). But when females approach they switch to a completely different flight mode: a high-frequency counterstroking flight (Anders & Rüppell, 1997; Rüppell, 1985), reaching beat frequencies up to 50 Hz (Hilfert-Rüppell & Rüppell, 2013). *Calopteryx* spp. females always fly very similarly to males by the parallel mode, enabling them to flee successfully when being pursued by males (Rüppell & Hilfert-Rüppell, 2009b). This fleeing together with flight to oviposition sites and foraging flight are the main flight activities of *Calopteryx* females. While foraging they start from a perch and attempt to catch flying insects by high accelerations, when several individuals may fly to the same target (Rüppell, 1999). Obviously there exists a competition for prey. Furthermore females attack each other when returning to the perch. These attacks of females were filmed with 300 fps at 600 fps, and the analysis revealed a flight style that was previously unknown in females. This investigation describes details of this female flight mode and discusses its function and origin.

Material and methods

Filming and behavioural studies were conducted in August 2008 (females expelling other females), in June 2010 (females escaping males), and in August 2011 (males' escalated fights) at the River Oker, north-north-west of Braunschweig (52°26′N, 10°23′E) in northern Germany. The river was *c*.14–18 m wide and up to 1.5 m deep in the main channel. From the middle of June to August several hundred imagines of *Calopteryx splendens* (Harris) were flying in a section of 1 km. At the site on the western bank dense vegetation of *Butomus umbellatus*, *Glyceria maxima*, *Sparganium emersum*, *Phalaris arundinacea* and *Sagittaria sagittifolia* offered wind protection. On 16 August 2008, when the videos of the females expelling each other were filmed, a strong wind (four to six knots Beaufort) blew from south to north just parallel to the river bank. In a small bay of 1–1.5 m diameter four to six females were foraging, returning from capture flight back to the perches on leaves of *Butomus umbellatus*. They attacked and pursued each other. The temperature was between 20 and 22°C. To compare flight modes in 2010 and 2011 the videos with females escaping males and males fighting were made in sunny conditions under an ambient temperature of 23–26°C.

All videos were filmed by a Casio EX F1 Highspeed Camera (Casio Computer Co., Tokyo, Japan) at 300 and 600 fps. Because of the erratic and fast flight of the insects, the camera was moved and orientated with a pre-focused lens parallel to the flying damselflies only correcting the orientation by quick looks on the screen of the camera. Drawings were made by taking the shape of the damselflies from single frames from the slow motion films. Details were added from photos and a dead specimen.

To analyse the videos the freeware programme QuickTime Player Version 7.7.5 (Apple, Inc., Cupertino, CA, USA) was used. To determine the wing beat frequencies the frames of the video were counted, if possible separated into down-stroke, upstroke and wing beat pauses. The mean values of two to three measures were calculated to reduce the possibility of errors. To obtain the wing beat frequency the exposure rate was divided by the numbers of frames per wing beat. The phase relationships of forewings and hind wings were obtained by counting the frames of each beat. The delay of the hind wings to the forewings was measured. To get a measure for the grade of phase shifting the delay was related to the length of the upstroke of the hind wings, resulting in a quotient – the phase relationship index (PRI). A quotient of 0 indicates that no delay was seen; hence, parallel beating was conducted. A quotient of 1 indicates that the length of the delay was as long as the upstroke, so the wings were beaten counterstrokingly. A quotient higher than 1 indicates the delay was longer than an upstroke.

The flight velocities could be measured only when the damselflies flew parallel to the plane of the camera's sensor. To determine the distance and time of the flight to calculate the velocity the whole damselfly body had to pass a prominent structure in the background. The number of frames for this was counted to get the time. To convert the distance measures, the body length of *C. splendens* was taken from Dijkstra and Lewington (2006) (calculated mean 46.5 mm). As each frame had a time length of 1/300 or 1/600 s, the duration of the body passing before a measured point could be determined. The beating angles (amplitude) were constructed, depicting the shifting of the wing tips from frame to frame from frontal and lateral views. When the wings move at the end of each half cycle (up and down) the distortion of the apparent position of the wing tip becomes significant. The error was estimated to be about 10%. To test for a relationship between the wing beat frequency and the PRI, Pearson correlation was applied.

Results

General description of female threat behaviour by counterstroking flight

A common behaviour of perched females was to spread all four wings when approached by a conspecific female (Figure 1). In the special situation of this investigation, on five occasions a female showed counterstroking flights when having been approached or when approaching other females. The duration of these flights were short. In one case a perched female, when a female landed about 7 cm near her on the same leaf, moved her wings counterstrokingly while still sitting for 10 beats during 0.47 s before take-off. She expelled the other female flying by another 16 beats over 0.57 s. In another case a female flew counterstrokingly for 1.7 s. She passed one flying, approached one sitting female, and rammed another sitting female from her perch. During this behaviour she performed 54 counterstroking beats and two parallel beats in between, when ramming. A female exhibited a very short counterstroking flight (0.15 s, six beats) when another female chased her away from her perch. Once a female approached four perched conspecifics. All of them spread their wings. One female then beat only the fore wings backwards and stopped the motion as the incoming female turned.

Phase relationship and beat frequencies

In this counterstroking threatening flight, when one pair of wings began the upstroke the other began the down-stroke and vice versa (Figures 2, 3). But this relationship shifted (Figure 3) when the female had passed the other female, or flew a turn, or switched to normal flight with parallel wing beating. To characterise these shifts the PRI index was calculated (Figure 4).

When the beating frequency was high the PRI was also high. There exists a correlation between these parameters (R $= 0.73$, $p < 0.001$, $n = 448$, Pearson correlation). Wing beat frequencies of the same females were different between counterstroking and parallel beating (Figure 5a). In the counterstroking mode the mean value was 33.7 Hz (SD 5.2), which was more than twice the value for parallel beating (mean value 16.1 Hz, SD 2.8). The beat frequencies of the attacking female were different when she approached the other female closely ($n = 41$) than

Figure 1. A female of *Calopteryx splendens* spreading all wings at an approach of a conspecific female during foraging. Germany, Braunschweig, River Oker, July 2008.

when she passed or pursued at a greater distance ($>$ 10 cm) ($n = 21$; Figure 5b). The phase relationship of forewings and hind wings also shifted (Figure 2, top right).

Flight velocities

The flight velocities of females expelling other females by counterstroking flight were low (between 100 and 150 cm s^{-1}) (Figure 6). Females returning from such conflicts by parallel beating of forewings and hind wings did not have higher flight speed. But the flight speed of both of these flight modes differed significantly from that of females fleeing from males and from males chasing each other in escalated flight.

Beating angles

The beating angles of the wings only could be defined approximately, because of the distortion of the spatial movement of the wings. There were differences in the beating angles at the moment of take-off and full flight. At take-off of one individual 85–88° ($n = 4$, three forewings, one hind wing) were found. In full flight the beat angles were smaller: 60–70° ($n = 7$, five forewings, three hind wings).

Comparison of female counterstroking flight with male courting flight

At the same site at the same time a male was rammed by a female, pursuing another female. He immediately showed courting flight, switching from parallel beating to counterstroking mode.

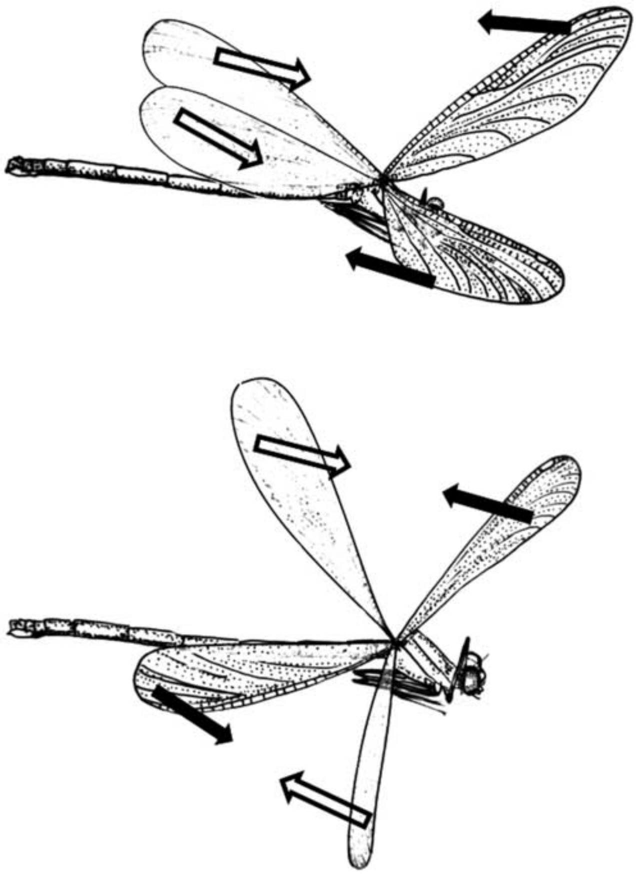

Figure 2. Female of *Calopteryx splendens* flying by parallel (above) and counterstroking wing beats (bottom). Only the two wings of the right side are depicted, each at two different phases of the wing beat. The phases with the same toned arrows and wings move simultaneously in the directions marked (drawn after 300 fps video).

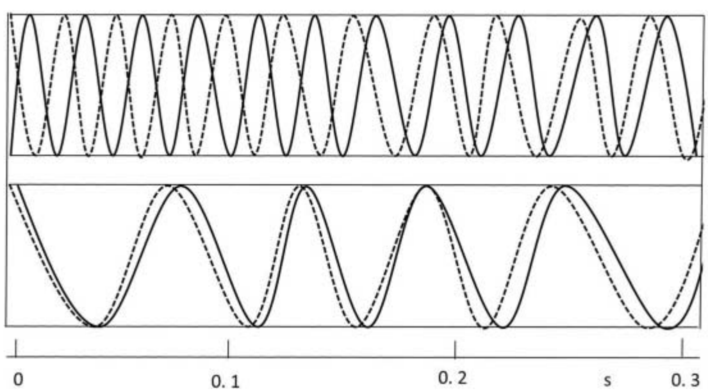

Figure 3. Phase relationships of fore (broken lines) and hind wings (solid lines) of a counterstroking flying female pursuing another female (top, left half). Right half: decreasing beat frequency and shifting phases, forewings leading. Bottom: another female of the same group of four females returning from chasing another female by parallel beats (the forewings leading the motion). Lines up: end of upstrokes, lines down: end of down-stroke. Abscissa: time in seconds (s). Top shows 10 beats in 0.3 s (30 Hz); bottom shows 4.6 (13.8 Hz).

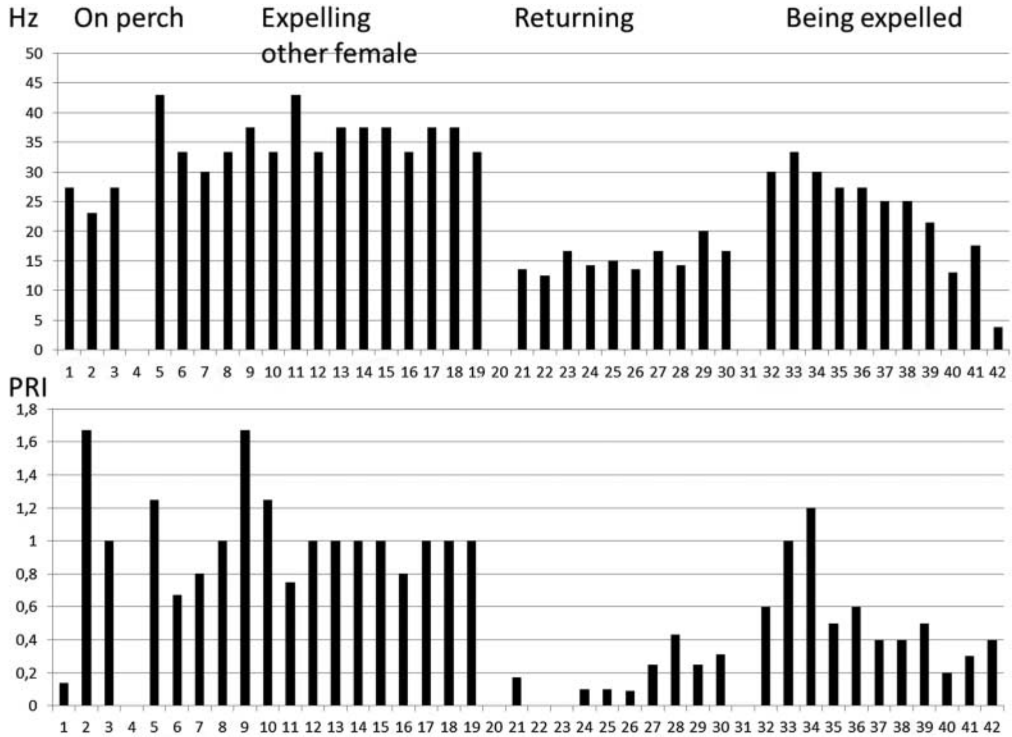

Figure 4. Top: successive beat frequencies (ordinate: Hz) of one female showing different flight manoeuvres, perching (positions 1–3 on horizontal axis), pursuing another female (positions 5–19), coming back for landing (positions 21–30, no. 29 first perch contact) and being expelled by another female (positions 32–42). The last value of 4 Hz results from a beating pause during a sinking phase, just before the damselfly left the frame. Bottom: The relation of PRI (ordinate) to flight mode in the same female and flight situations as above. When PRI = 0 both wing pairs are beating in parallel; a value of 1 means that begins its downstroke before the hind wing by an interval equal to the duration of its upstroke, i.e., both wing pairs are counterstroking, Values above 1 mean that the hind wings are leading the beating.

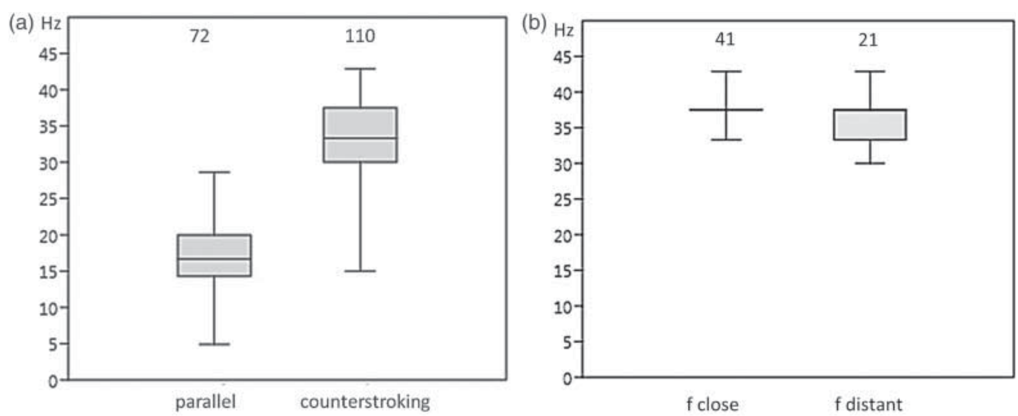

Figure 5. (a) Wing beat frequencies (Hz) of parallel (left) and counterstroking beating (right) females of *Calopteryx splendens* in a small wind-sheltered bay during foraging. Numerals indicate number of wing beats of four flights of four females at this mini site. Bars include 50% of each data set, horizontal lines in the bars show the median, the vertical lines with small terminal crossbars show the range excluding outliers. (b) Wing beat frequencies of a female expelling an opponent closely (f close, $n = 41$, one individual) and more distant (f distant: opponent > 10 cm, $n = 21$).

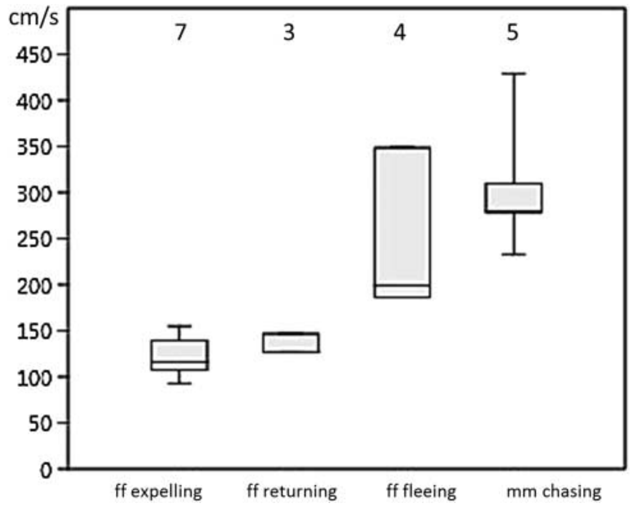

Figure 6. Flight velocities of females (three groups beginning from the left): females expelling other females (= ff expelling), females coming back from that (= ff returning), females fleeing males (= ff fleeing); and of males (right), chasing each other in escalated fights (= mm chasing). Numerals indicate number of individuals measured. Other symbols as in Figure 5.

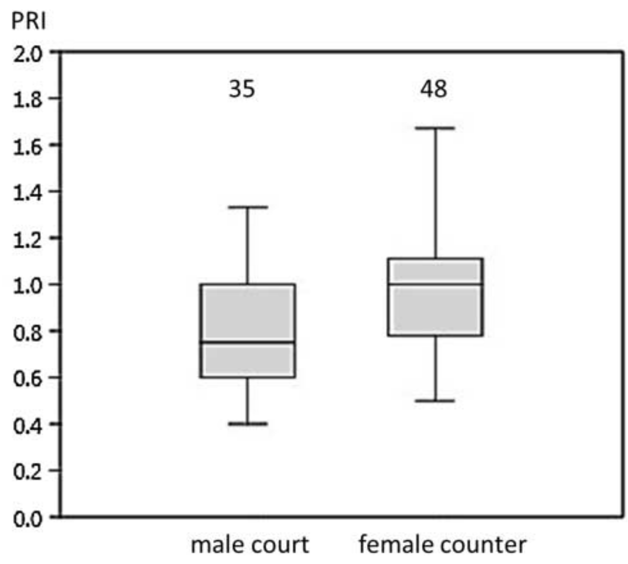

Figure 7. The phase relationship index (PRI) of a courting male (male court, $n = 35$ wing beats) and three females expelling other females (female counter, $n = 48$ wing beats). The value 0 defines parallel stroking, 1 counterstroking. Values < 1 = fore wings are in advance, values > 1 = hind wings are in advance.

The frequency of the male's beating (mean 37.6 Hz, SD = 3.6, $n = 18$, one individual) under the same conditions did not differ from that of the counterstroking threatening females (mean 33.7, SD = 5.2, $n = 104$). The PRI of female flight expelling other females was mean 0.97 (SD 0.22, $n = 48$, five individuals) and of male courting flight 0.83 (SD 0.25, $n = 35$, one individual), thereby nearly counterstroking (Figure 7). The indices differed from each other.

Counterstroking during landing

At landings *Calopteryx* females and males exhibit counterstroking beating. This was shown briefly at each landing, normally with only two to three wing beats, but in difficult conditions (when wind was shaking the perch, a leaf of *Glyceria maxima*), this landing in counterstroking mode lasted seven wing beats. The frequencies of these landings ($n = 7$, seven individuals) in a counterstroking mode did not differ from those of female threatening flights ($n = 104$ wing beats).

Discussion

I observed that *Calopteryx splendens* females show a specific threatening flight. This counterstroking flight mode was filmed only on a single occasion: when five females competed in a narrow space for perches to start from for foraging in heavy winds. As these counterstroking flights led to or followed agonistic behaviour like ramming, these flights probably have a threatening function and could be called female threatening flight. This form of flight was also filmed in a *C. xanthostoma* female (Rüppell & Hilfert-Rüppell, 2014) when a female ready for oviposition was harassed by a male. In that case it was directed towards a male.

The results presented show a similarity between counterstroking female flight and courting flight of *C. splendens* males. The high beat frequencies of both flights did not differ under the same conditions (Figure 4). Furthermore other beat frequencies of male courting flights were also similar in *C. splendens* (Anders & Rüppell, 1997; Rüppell 1989). The decrease in the beat frequency of counterstroking flying females at greater distance or after passing the opponent female resembles the decrease in the beat frequency of the clear forewings of courting *Neurobasis chinensis* males, when the female leaves (Günther, Hilfert-Rüppell, & Rüppell, 2014). The small beat angles found here are also similar to those of courting males of *C. splendens* (Rüppell, 1989). However, female threatening flight when pursuing other females was performed at higher flight velocities than known from courting males. Flight velocities of those males never have been quantified, but the slow flight has been described (Corbet, 2004; Hilfert-Rüppell, 2004). As phase-relationships here were quantified by creating an index for the first time, they cannot be compared with older studies, but since the basic pattern of counterstroking appears essentially identical in both sexes, the PRI should be very similar in the two cases.

As counterstroking flight was shown only in the presence of conspecifics it could have a signalling function (Fincke, 1997). The signal could show the damselflies' power, because counterstroking beating costs more energy than parallel beating. One reason for this is that the wings are not clapped together at the end of the upstrokes, so no clap-and-fling effect is created (Weis-Fogh, 1973); this would decrease the aerodynamic power outcome of the beating significantly (Wakeling & Ellington, 1997). Another reason is that the power production is lower than in parallel (in-phase) flight (Grodnitsky, 1999; Wang, 2008). Furthermore counterstroking flying costs more energy because it is performed at a frequency more than twice that of parallel stroking.

Suggestions on evolution of different flight modes

When landing, females and males of *Calopteryx* spp. also exhibit counterstroke wing beating. This similarity led to speculation about the origin of counterstroking threatening flight of females. Perhaps there existed a small repelling effect of counterstroking while landing. This may have brought small advantages for getting a better perch for those females performing it more intensively. The kinematic needs to repel a competitor for a perch or for other aims are good manoeuvrability and accurate and stable flight. Both features are acquired better by counterstroking beating (Grodnitsky, 1999) than by parallel beating which produces flight swaying and unsteady accelerations (Rüppell, 1989).

Basal insects probably exhibited parallel (in-phase) flapping flight (Grodnitsky, 1999; Wootton & Ellington, 1991). But although aerodynamically less effective (Grodnitsky, 1999; Wootton & Ellington, 1991) there are great advantages to counterstroking: high manoeuvrability and the precise approach to prey, perches or mates. For expelling a competitor as reported, these features are preconditions for success. Threatening behaviour of *C. splendens* females is exhibited at different intensities. The weakest form is wing spreading while perching (Figure 1). The next intensity is beating the spread wings counterstrokingly while still sitting. The highest intensity is shown when a female flies against the competing female, finally to ram her.

The counterstroking mode seems to be an ancient pattern because it is used nearly always in basal groups of Odonata as in Lestidae (Rüppell, 1989) and in Epiophlebidae (Rüppell & Hilfert, 1993). It generates a steady and economic flight by alternating lift and thrust production of forewings and hind wings. From that original counterstroking flight mode, female threatening flight and male courting flight may have evolved. In *C. virgo* threatening males also showed this counterstroking flight mode in interaction with other males (Rüppell & Hilfert-Rüppell, unpublished slow motion films).

When flying suddenly backwards, parallel stroking also occurs in Lestidae, Coenagrionidae and Libellulidae. Together with the development of coloured wings this beat pattern may have evolved into the parallel flight of both male and female calopterygids (Cordoba-Aguilar & Cordero-Rivera, 2005). Courting flight is species-specific in Calopterygidae (Anders & Rüppell, 1997). It should be interesting to find out whether females from other *Calopteryx* species also show the counterstroking threatening flight, or whether they exhibit a different mode more similar to the specific courting flight of their males. In the latter case the presented hypothesis would have to be revised. This slow motion investigation showed once more the variability of *Calopteryx* flight and gives more details about the female's capability, to help form a more complete picture of their behaviour.

Acknowledgements

I would like to thank Frank Suhling, Andreas Martens, André Günther, and Adolfo Cordero-Rivera, and especially Mike May for their comments and for improving the manuscript.

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