Males do not catch up with females in pursuing flight in *Calopteryx splendens* (Odonata: Calopterygidae)

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ABSTRACT

In high densities males of *Calopteryx splendens* showed alternative reproductive behaviour at the river Oker in northern Germany. One of several tactics was to pursue females. Pursuing flight was filmed in summer 2006 in slow motion. Frame by frame analysis showed that males fly in irregular flight patterns: they showed different lengths of wing beat phases in comparison to females which fly more steadily. Females had significantly lower wing beat frequencies than males. The flight patterns of males depended on their position to other pursuing males and to the pursued female. The possible causes of these flight differences are discussed.

INTRODUCTION

Alternative reproductive behaviour has been described in several *Calopteryx* species (Waage 1984; Forsyth & Montgomery 1987; Plaistow & Siva-Jothy 1996; Hilfert & Rüppell 1997; Córdoba-Aguilar & Cordero-Rivera 2005). Unlike in some other animal males which decide for a mating tactic early in their lives (Gross & Charnov 1980) *Calopteryx* males shift from one mating tactic to another depending on their copulation success (Hilfert-Rüppell 2004). In *C. splendens* many alternative mating tactics were described, such as grasping females at the roosting sites, at oviposition even under water, at feeding, attacking tandems even in flight and separating them and, being the most common, pursuing females often in a flock of many males (Hilfert & Rüppell 1997, 2004). When a female passes by perching males at the stream they will follow her (Pl. IVa) for up to 20 m trying to grasp her. In full flight we never saw a capture of a female by a male, only flying tandems and landing females were caught (Pl. IVb, unpubl. obs.).

The flight speed of odonates depends on body parameters such as size of body and wings, shape of the wings, wing loading and kinematic parameters of the wing beats (Rüppell 1989). The body parameters between females and males of European *Calopteryx* species differ: females are a little larger, heavier, and have longer wings – female hind wings are ca 2.5 mm longer at a total length of 32.3 mm – than males (Grabow & Rüppell 1995; Hilfert-Rüppell 2004). The pattern of wing beats may influence flight speed, too. Especially fore- and hind wings interactions influence the

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aerodynamic forces and power (Wang & Russel 2007). The full wing beat cycle in calopterygids consists of down stroke, upstroke, and wing standstill in backward position. Only by means of slow motion filming it is possible to see details, which allow conclusions on the kinematics and on the significance of flight behaviour, which in odonates with coloured wings might be signalling.

Our prediction was that different flight parameters are responsible for males not catching up with females in pursuing flight.

MATERIAL AND METHODS

Filming was conducted in summer 2006 at the Oker River north-northwest of Braunschweig (52°26'N, 10°23'E) in northern Germany. The river was ca 14-18 m wide, up to 0.7-1.5 m deep in the main channel, and supported many males of *Calopteryx splendens* during the investigation period from mid July to mid August. Density of males at river's bank was measured along a transect of 60 m on every filming day between 12:00 and 14:00 h (MSZ). Ambient temperatures ranged between 27-34°C. On the western bank of the river along this transect only a few bushes (*Salix* sp.) grew, but many plants on the bank and in the water: *Glyceria maxima, Sparganium emersum, Phalaris arundanace, Ceratophyllum demersum, Nuphar lutea, Sagittaria sagittifolia*.

Often several males followed a female at the same time from a short distance to up to 20 m and sometimes to the opposite bank of the river . When several males pursued a female (Pl. IVa), the flight was filmed in slow motion with more than 300 frames per second using a 16 mm film camera LOCAM (model 51). Filming frequency needs to be high enough for a sufficient resolution of the movements of the wings. As calopterygids beat their wings between 10 and 50 Hz, at least 300 to 600 frames per second are necessary. By using this camera speeds 10 to 30 single frames of one wing beat circle were available and could be analysed.

Because of the high flight speed and the unpredictable flight path of the damselfly flocks the camera was released without viewing through the viewfinder, by panning the free camera according to the flying damselflies with prefocused lens. The camera was started 1-2 s before the damselflies passed by in order to capture the images. Six hundred and three wing beats were analysed using a single-frame projector (NAC, model DF16B). While filming the camera leaves a light mark on the edge of the film every 1/100 s. With the help of these time markers the wing beat frequency, the upstroke/down stroke ratio, and the length of wing standstills could be measured. The shifting of the damselfly body against prominent optical structures like branches or stems of waterplants in the film was used to analyse flight velocities. This was only possible in five cases where the flight path was perpendicular to the direction of filming.

Statistical analysis was performed with StatView and SPSS using Mann-Whitney-U-test, MANOVA, ANOVA, and post hoc Tukey-Kramer. All pursuing flights happened within two weeks at the same site under similar density conditions of *C. splendens* males. Every pursuing flight of an individual was treated as a replicate, because the likelihood of the same male being filmed several times was very low. The filmed males were not territorial. A total of 20 pursuing flights with different numbers of males was filmed.

RESULTS

Flight behaviour and wing beat frequency

At high densities (Table 1) males pursued a passing by female often in a flock, with increasing numbers at the beginning of the flight and decreasing numbers at the end (n = 3-10). The wings then were moved in parallel, both pairs of wings were beaten together forward and backward. When at the end of the chase the female headed for the vegetation, sometimes the last male showed a fast courting flight, which was counter stroking.

During all pursuing flights the wing beats of the females lasted longer (mean = 0.09 s ± 0.05 s.d.) than those of the males (mean = 0.06 s ± 0.03 s.d.) (Two-way ANOVA: F = 9.22, d.f. = 3, p < 0.001, n = 16 females, 38 males). Accordingly, females showed a lower mean wing beat frequency than males (females: 11.3 wing beats per second, males: 15.15; Fig. 1). The flight behaviour of the leading male (position 1) was different to that of the following males (position 2). There was a tendency for the wing beat duration of the males in position 2 to be shorter and accordingly their wing beat frequency was higher than that of the males in position 1 (Fig. 1).

Table 1. Male numbers of *Calopteryx splendens* at noon in a stretch of 60 m in 2007.

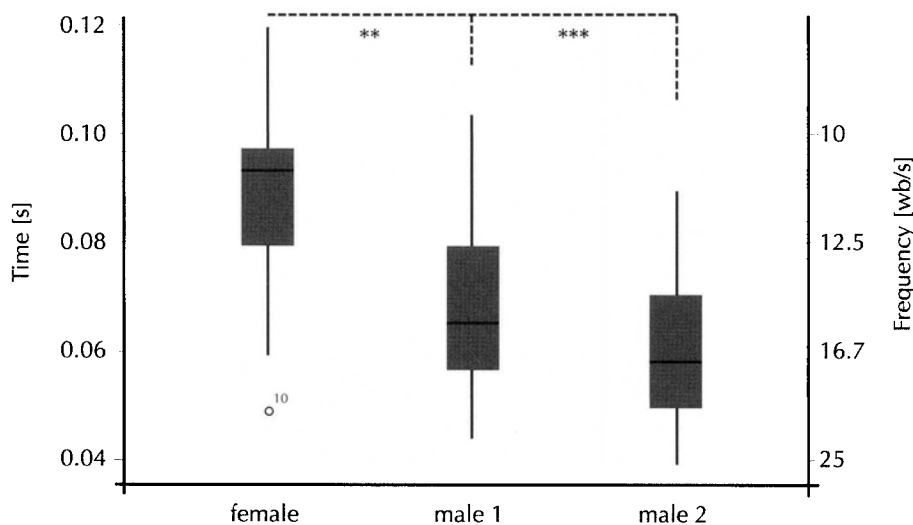| Date	18 vii	19 vii	25 vii	26 vii	11 viii	15 viii	19 viii	12 ix
# males	43	38	47	32	5	3	5	1

Figure 1: Mean wing beat durations and frequencies (wb/s = wing beat per second) (boxplots) of *Calopteryx splendens* females and males during pursuing flights. All pursued females (n = 16) were put together and compared to the pursuing males grouped depending on their position in the pursuing flock (male 1: male in position 1, n = 15; male 2: all males following the leading one = position 2, n = 23) (two-way ANOVA).

Wing standstills in backward position

In females more than 51% of the wing beat duration consisted of wing standstills – the wings then are folded totally in backward position – which were longer than those of the males (Mann-Whitney-U-test: $U = 130.5$, $p < 0.001$, $n = 16$ females, 36 males; Fig. 2). These pauses differed also among the males depending on their position in the flock behind the female. Those males following the female closest showed the longest wing standstills amounting to more than 43% of the whole wing beat, while in males pursuing on position 2 they lasted only about 31% of the wing beat duration. The stroke ratio which describes the relation of upstroke with wing standstills to down stroke was in females $1 : 0.45$ ($n = 141$ strokes of 16 females), in males $1 : 0.7$ ($n = 462$ strokes of 36 males).

In one case a male flew next and laterally to the female and he several times prolonged the wing standstill in backward position (maximum up to 0.16 s), while when the female was flying in front, the mean break lasted only 0.04 s.

Wing beat pattern

Males and females showed different wing beat patterns meaning the relation of upstroke, wing standstill in hind position, down stroke, and wing standstill in front position (MANOVA: Wilks' Lambda = 0.43; $F = 2.63$, NUM d.f. = 16, $p < 0.01$; Fig. 3). Females had a more regular wing beat pattern mainly consisting of down stroke, a long wing standstill in hind position, and a short upstroke. Only when followed at very short distances by two or three pursuers females exhibited 2-3 wing beats one after the other without wing standstills. Males showed a more irregular wing beat pattern (Fig. 4). Males pursuing in a flock performed very short or no wing standstills in backward position and showed other wing displays. In 47 wing beats they hold their wings still after the down stroke in frontal position as well, lasting on average 0.014 s ± 0.003 s.d. The slow motion films showed that the males
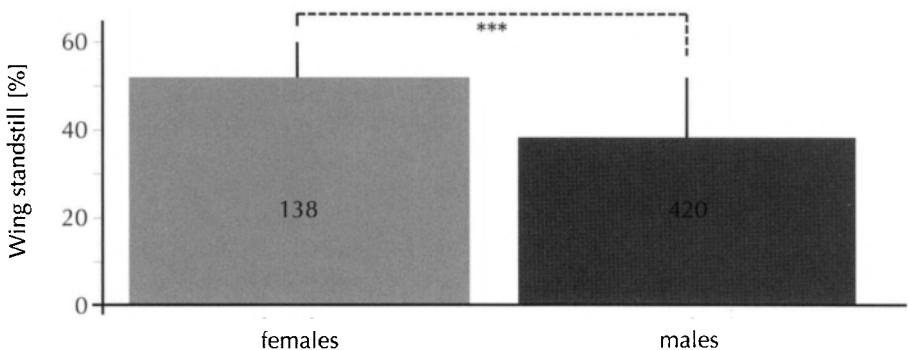

Figure 2: Mean lengths of wing standstills in backward position (in % of the whole wing beat) of *Calopteryx splendens* females ($n = 17$) and males ($n = 36$) during pursuing flights (Mann-Whitney-U-test) — ***: $p < 0.001$. Number of wing beats in the bars.
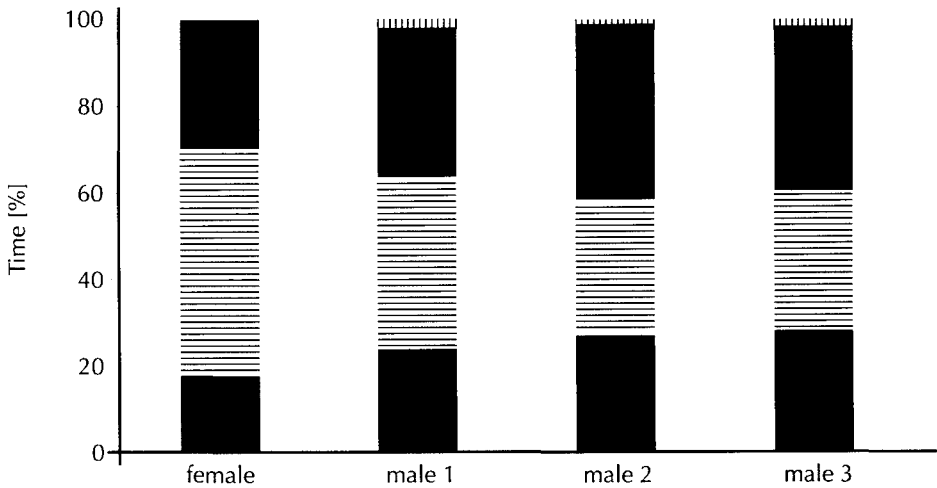
Figure 3: Wing beat patterns of *Calopteryx splendens* females and males during pursuing flights. The flight strokes were divided into upstroke (black), wing standstill in backward position (hatched horizontally), down stroke (grey), and wing standstill in frontal position (checked). The percentages of the whole stroke durations are depicted, female n =17, male 1: n = 17, male 2: n =11, male 3: n = 6).
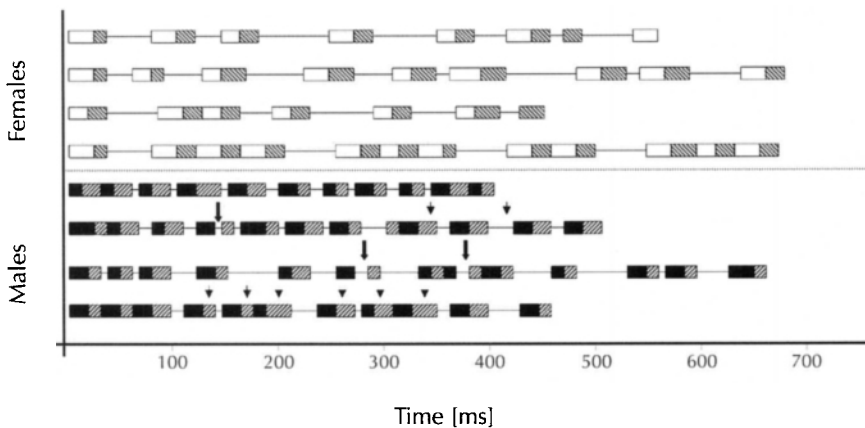

Time [ms]

Figure 4: Examples of flight patterns of four females and four males of *Calopteryx splendens* in different pursuing flights. The white and black rectangles, respectively, show the length of the down strokes, the striped the length of the upstrokes and the lines between show the durations of the wing standstills in backward position. Short arrows (↓) mark a period where all four wings are opened but not beating in lateral position, and the long arrows (↓) show opened but not beating wings in frontal position. The black triangles (▼) mark periods where only the Hind wings are not beating.

in the position 2 (all males behind the female and the first male pursuing her) some-
times stopped wing beating shortly after beginning of the down stroke and glided side
by side to the flying neighbour male with half opened wings. Very rarely they beat
only the fore wings and held the hind wings still.

Flight velocity

In all filmed cases (n = 20) females managed to escape. They flew at higher velocities
than males pursuing in a flock (Fig. 5). These males were only half as fast (1-2 m/s).
Females reached velocities up to 3-4 m/s, similar to males following them alone.

A direct comparison between a fleeing female and her pursuer was possible only
twice. After 0.46 s the female's distance to the leading pursuer increased from 15.1
to 19.75 cm, and after the same time to the second pursuer from 28.6 to 40.1 cm.

Although the flight speed decreased for about 30% during wing standstills in back-
ward position, females showed this stroke pause very often and regularly before the
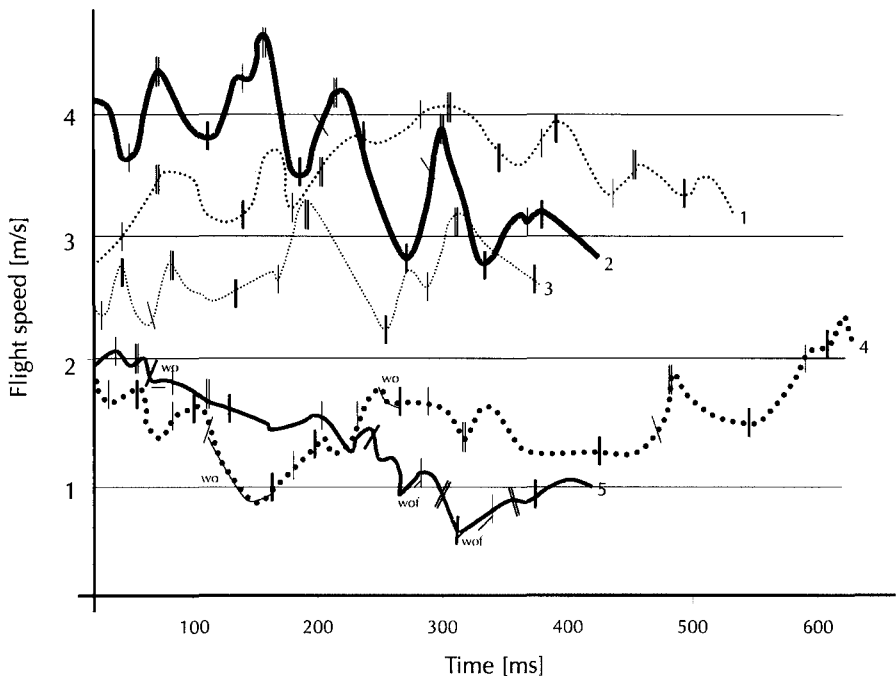upstroke (Fig. 4).

Figure 5: Flight velocities of females (1, 3) and males (2, 4, 5) of *Calopteryx splendens* in dif-
ferent pursuing flights. Male 2 was pursuing alone, while 4 and 5 where in a flock of other pur-
suing males. After the thick bars the down strokes begin, after the thin bars the upstrokes. Wing
standstills in backward position with closed wings begin at the double bars. Some bars are
tilted for better clearness. 'wo' means wings are opened lateral of the body but not beating.
'wof' means the opened wings are hold still in forward position. The durations of these two
cases are marked by thin lines.

DISCUSSION

In pursuing flights females fly differently than males. The mean wing beat frequency of females is the same than Rüppell (1989) found for *Calopteryx splendens* males in fast forward flight. Pursuing males beat their wings much faster especially in the positions behind the first male, indicating that these males try to catch up with the other males. To get high flight speeds a high frequency is shown also in prey catching flight. When flying towards the prey, the wing beat frequency was 1.5 times as high as on the way back to the perch (23 : 16 wing beats/s). The causes for the low frequencies were pauses in wing flapping when gliding with folded wings in backward position (DH-R unpubl.).

Males and females both show wing standstills in backward position in pursuing flights but also in other flights as well (Rüppell 1985, 1989). This is probably to improve the flight: these pauses allow regenerating the locomotory system, similarly as wing flapping pauses in passerine birds (Norberg 1990). Furthermore, it is aerodynamically very useful to begin a new wing beat after this pause from the position with folded wings backwards: only then the clap and fling mechanism is able to work, which enhances the aerodynamic power output considerably (Wakeling & Ellington 1997). These findings are confirmed by the strongly increased speed gain during the following wing stroke in pursuing flights, while during wing standstills the flight speed decreased sharply. The irregular wing beat pattern of males during pursuing does not allow generating positive effects of hind wing and fore wing interactions such as those showed by Wang & Russel (2007), although with other phase relationships of the two wing pairs, for Anisoptera.

Many authors have shown that wing pigmentation and ornaments are the structural base for sexual selection in calopterygids (Córdoba-Aguilar et al. 2007; Contreras-Garduño et al. 2008; Serrano-Meneses et al. 2008). This means that males send signals on which females react by choosing or not choosing them as mates. The presentation of the ornaments by performing a special flight whenever a rival or a female appear must also have a signalling function. In territorial flights males of *C. splendens* vary the flight pattern totally when an intruder approaches: they fly towards the other male, circle around him, undulating in front of him horizontally or vertically or pursuing him. All this is done by fast and complicated manoeuvres in which the wings are presented to the opponent. Sometimes the fore wings or only the wing facing the opponent are hold still while the other wings are beating. Or the wing standstills in backward position are extended, so that a waving flight path results. There are no wing standstills in backward position when meeting frontally the opponent, but they do occur frontally as only then the other male is able to see the wings (Rüppell 1985). All these flight manoeuvres are behavioural consequences of the signals. They are reactions on the flight manoeuvres of the other males. In pursuing flight we saw another behaviour. When gliding side by side at position 2 males sometimes opened their wings and glided with opened wings. They never did this when pursuing a female alone or when flying alone. So this flying with half opened wings must have signalling character and is probably a reaction to the other male's flight performance.

Males probably send signals to the pursued female as well. In one case a female was flying laterally to a pursuing male and his wing standstills in backward position were 2-3 times longer than afterwards when the female was in front. This and short wing standstills in frontal position of pursuing males even in position 1 point out that the female probably must be the target of the signals.

The irregular flight patterns and all these wing standstills in different positions of the males reduce their flight speed. We cannot exclude that the different body parameters and especially the wing lengths of female and male are at least partly responsible for the different flight speeds of the sexes. To be successful in pursuing females in spite of shorter wings, males may try to compensate the effect of their shorter wings by exhibiting a higher wing beat frequency than females.

Males seem to be handicapped by their smaller wings and by signalling during pursuing flights. These are two reasons why they cannot catch up with females.

Perhaps the signalling of the males can influence the female's mating decision: observations showed that in a few cases males following the female the fastest could get to copulate with her, sometimes after an additional courting flight, when the female perched.

As pursuing flights are very costly energetically because males are flying irregularly and at high frequencies and signalling at the same time, they probably provide females with information about male quality. Pursuing flights might be advantageous for males too: at high densities they allow males to copulate more and perhaps they also help improve males status by threatening other males.

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REFERENCES

Contreras-Garduño, J., B.A. Buzatto, M.A. Serrano-Meneses, K. Nájera-Cordero & A. Córdoba-Aguilar, 2008. The size of the red wing spot of the American rubyspot as a heightened condition-dependent ornament. Behavioral Ecology 19: 724-732.

Córdoba-Aguilar, A. & A. Cordero-Rivera, 2005. Evolution and ecology of Calopterygidae (Zygoptera: Odonata): status of knowledge and research perspectives. Neotropical Entomology 34: 861-879.

Córdoba-Aguilar, A., C. Lesher-Trevino & C.N. Anderson, 2007. Sexual selection in *Hetaerina titia* males: a possible key species to understand the evolution of pigmentation in calopterygid damselflies (Odonata: Zygoptera). Behaviour 144: 931-952.

Forsyth, A. & R.D. Montgomery, 1987. Alternative reproductive tactics in the territorial damselfly *Calopteryx maculata*: sneaking by older males. Behavioral Ecology 21: 73-81.

Grabow, K. & G. Rüppell, 1995. Wingloading in relation to size and flight characteristics of European Odonata. Odonatologica 24: 175-186.

Gross, M.R. & E.L. Charnov, 1980. Alternative male life histories in Bluegill Sunfish. Proceedings of the National Academy of Sciences of the United States of America 77: 6937-6940.

Hilfert, D. & G. Rüppell, 1997. Alternative mating tactics in *Calopteryx splendens* (Odonata: Calopterygidae). Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie 11: 411-414.

Hilfert-Rüppell, D., 2004. Optimierung des Fortpflanzungsverhaltens: wichtige Einflussgrößen auf Territorialität und auf Paarungen von europäischen Prachtlibellenmännchen (Odonata: Zygoptera). <http://www.digibib.tu-bs.de/docid=00001567>.

Norberg, U.M., 1990. Vertebrate flight. Mechanics, physiology, morphology, ecology and evolution. Springer, Berlin, Heidelberg, New York, London, Paris, Tokyo & Hong Kong.

Plaistow, S.J. & M.T. Siva-Jothy, 1996. Energetic constraints and male mate-securing tactic in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). Proceedings of the Royal Society of London (B) 263: 1233-1238.

Rüppell, G., 1985. Kinematic and behavioural aspects of flight of the male Banded Agrion *Calopteryx (Agrion) splendens* L. In: Gewecke, L.M. & G. Wendler (eds) "Insect locomotion", Parey, Berlin, pp. 195-204.

Rüppell, G., 1989. Kinematic analysis of symmetrical flight manoeuvres of Odonata. Journal of Experimental Biology 144: 13-42.

Serrano-Meneses, M.A., G. Sánchez-Rojas & A. Córdoba-Aguilar, 2008. Sexual selection as the possible underlying force in calopterygid wing pigmentation: comparative evidence with *Hetaerina* and *Calopteryx* (Zygoptera: Calopterygidae). Odonatologica 37: 221-233.

Waage, J.K., 1984. Female and male interactions during courtship in *Calopteryx maculata* and *C. dimidiata* (Odonata: Calopterygidae). Influence of oviposition behaviour. Animal Behaviour 32: 400-404.

Wakeling, J.M. & C.P. Ellington, 1997. Dragonfly flight III. Lift and power requirements. Journal of Experimental Biology 200: 583-600.

Wang, Z.J. & D. Russell, 2007. Effect of forewing and hindwing interactions on aerodynamic forces and power in hovering dragonfly flight. Physical Review Letters 99 (148101): 4 pp.