

# Double function of flight in *Calopteryx splendens* (Odonata: Calopterygidae) males

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**Abstract.** Different flight manoeuvres of males of *Calopteryx splendens* were analysed by means of slow-motion filming. The wingbeat frequencies of males flying in tandem were higher than those of single flying males. A male exhibited the highest frequencies when carrying a Blue Featherleg tandem over a distance of 20–25 cm. The widest range of variability of values of wingbeat frequencies were recorded in threatening flight, probably due to the simultaneous communicative function of the wings during that behaviour. The upstroke/downstroke ratio of the wings allows to draw conclusions on their aerodynamic effect. It was low in pursuing flight, which is when more thrust is needed, and it was high in flight with an additional load (a Featherleg tandem) when a lot of lift was necessary. Both sexes exhibited wing standstills during forward flight. In males, the variability of the duration of wing standstills was widest, probably due to the communicative function of their blue wings. Because males engage in threatening displays their flight was very irregular and unsteady. In contrast, females were much more regular in their flight, which may explain why they win most pursuit races with males.

**Key words.** Zygoptera, beat frequencies, flight manoeuvres, flight parameters, Odonata flight, sex-dependent differences in flight, slow-motion analysis, upstroke/downstroke ratio, wing standstills

## Research Article

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All relevant data are within the paper.

## Introduction

Odonata are among the insects with the best flying capabilities. They perform flight manoeuvres in all directions with excellent acceleration, including backward or upside-down flight (Rüppell et al., 2020b). Wing movements can be characterised by temporal parameters such as beat frequency, ratio of upstroke/downstroke duration, and phase relationship of the two beating wing pairs influence the production of lift and flight speed (Lehmann, 2017; Rüppell, 1989; Rüppell & Hilfert-Rüppell, 2020a; Usherwood & Lehmann, 2008). These parameters interact with spatial parameters: changing the wingbeat path also changes the flight direction. A more downward flap will increase the forward speed of flight, while a more upward flap will slow forward flight but increase lift. A horizontal flap path with high inclined wings on the downstroke will normally result in backward flight. Adjustments of flap angles and wing deformations such as twisting are further components determining flight capabilities (Rüppell, 1989).

Flight challenges should increase with competition level and also with load such as a mate or large prey. Especially *Calopteryx splendens*, which sometimes occurs at high densities locally, exhibits a high degree of competition between males (Córdoba-Aguilar & Cordero-Rivera, 2005; Pajunen, 1966). Males engage in races to the limit in a quest to obtain mates. Another flight challenge to males is to carry females in tandem or in pairing position. In *C. splendens*, the female usually cooperates, but sometimes she will not, i.e., when a male takes hold of a female busy

ovipositing. A rare example of carrying a heavy load is reported here: a male *C. splendens* carrying a tandem of *Platycnemis pennipes* away from its oviposition spot (Fig. 1).

Unlike other Odonata, Calopterygidae beat their wings mostly in phase. A species-specific phase shift between the fore and hind wings occurs only during courting flight. In *C. splendens*, this phase relationship amounts to 180° (Anders & Rüppell, 1997). Courting flight is rather slow and is used mainly for pair-formation, but in rare cases for threat display between males, too (filmed in *C. virgo*). As most manoeuvres are performed by phase flapping, only this pattern is analysed here.

We report on wingbeat frequencies, wing standstills, and relationships of up- to downstrokes of single and in-tandem flying males as well of a *C. splendens* carrying a tandem of the Blue Featherleg, *P. pennipes*, analysing how flight parameters vary in different manoeuvres.

Because of the clarity of the data obtained by slow-motion filming of the conspicuous blue-winged calopterygids, a close look at their wing movements during different flight manoeuvres in natural habitats should provide new insight into flight performance of damselflies with coloured wings, also in the context of evolutionary aspects.

## Material and methods

The kinematics of flying Odonata can be analysed only by means of slow-motion filming. We used a Panasonic Lumix GH5 and a GH5s (capable of recording at up to 225 fps), as well as a Sony RX 10 III (up to 500 fps) and a Casio EX F1 (up to 600 fps), and selected the data using the editing software Magix Video Deluxe Pro on a PC that was custom-built for video analysis and able to display frame by frame. The camera's recording frequency determined the film's slowing factor. When, for example, filming was done at 250 fps, the slowing factor of the wing behaviour was 10, since the normal speed of a film is 25 fps in PAL format. The camera used was not mounted on a tripod in order to be able to follow the very fast changing points (movements of Odonata) and keep subjects in the frame unobstructed. The basic method of filming was to sit and wait and then react very quickly. Sometimes the camera was started in advance in anticipation of certain manoeuvres. It was not possible to focus the camera on the demoiselles because they flew much faster than it was possible to adjust the focus. Instead, the focus was set in advance in a plane that promised action. Filming then followed the airborne insects quickly in all directions. Weather conditions were always sunny with temperatures between 25 and 30°C. Filming took place from 2016 through 2019 at the river Oker, 20 km north of Brunswick, Germany (52.27° N, 10.52° E). The manoeuvres thus recorded were sometimes very rare events or even unique, so that it was not possible to compare several flights, but only the wingbeats of the different

manoeuvres. Statistics were calculated with SPSS, IBM version 29, and Past, freeware, version 2020. The data obtained were tested for normal distribution and their mean values were compared with a t-test or a Mann-Whitney-U test. The box plots presented in Figure 5 show the distributional characteristics of data, with the middle "box" representing the core 50% of data for the group. The line that divides the box into two parts marks the median (midpoint of the data, given as results  $\pm$  standard deviation). The upper and lower whiskers each represent 25%-scores outside the core 50%.

## Results

### Wingbeat frequencies

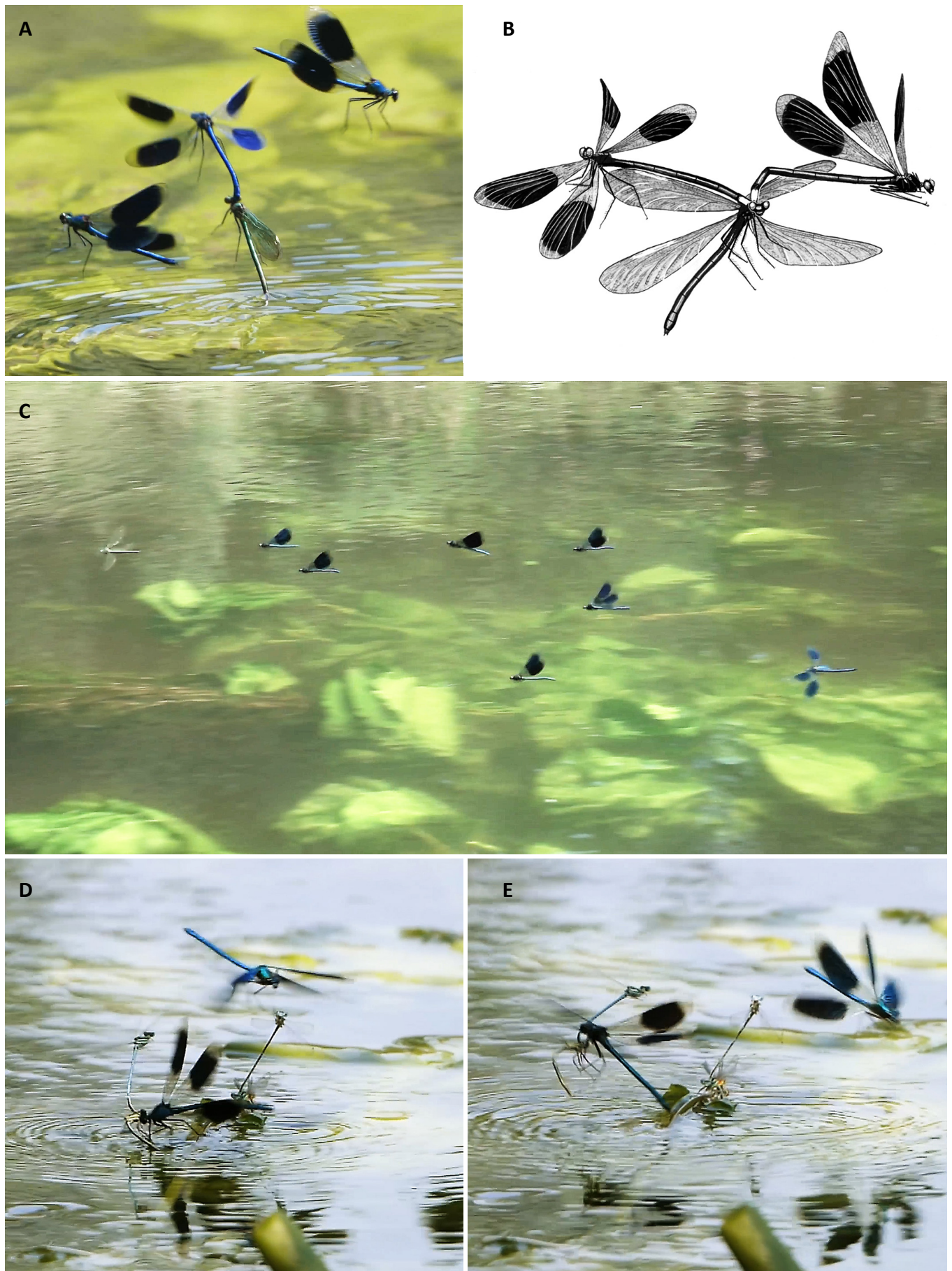
Calopterygid flight was very variable (Fig. 2). The beat frequencies of males flying in tandem (mean  $19.63 \pm 5.26$ ,  $n = 57$ ) was significantly different from that of males flying single (mean  $16.73 \pm 5.75$ ,  $n = 37$ ) (U-test,  $U = 685.5$ ,  $p < 0.001$ ). The forewings and hindwings of a male carrying a Featherleg-tandem did not differ statistically (U-test,  $U = 30.0$ ,  $p > 0.05$ ).

### Tandem males

Wingbeat frequencies changed very suddenly and very often in all manoeuvres. At high densities, when females emerged from underwater after oviposition, males often attacked and took hold of them in an attempt to mate. In most of these cases the females did not cooperate and kept their wings still (Figs 1A, 2A). The load the male then had to carry was  $> 150$  mg (weight of the female + adhering water film). This was in contrast to tandems flying after mating when the female also used her wings (Figs 2B, C). A male flying in tandem over a reed edge against the wind showed wingbeats at a very low frequency (Fig. 2D). In one single case, when two males were coupled to a female, all damselflies involved beat their wings, so that 12 wings were working at the same time in this airborne tridem (Figs 1B, 2E). Another remarkable observation was that the forewings of in-tandem *C. splendens* males had a slightly higher beat frequency than the hindwings, i.e., they effected a faster upstroke.

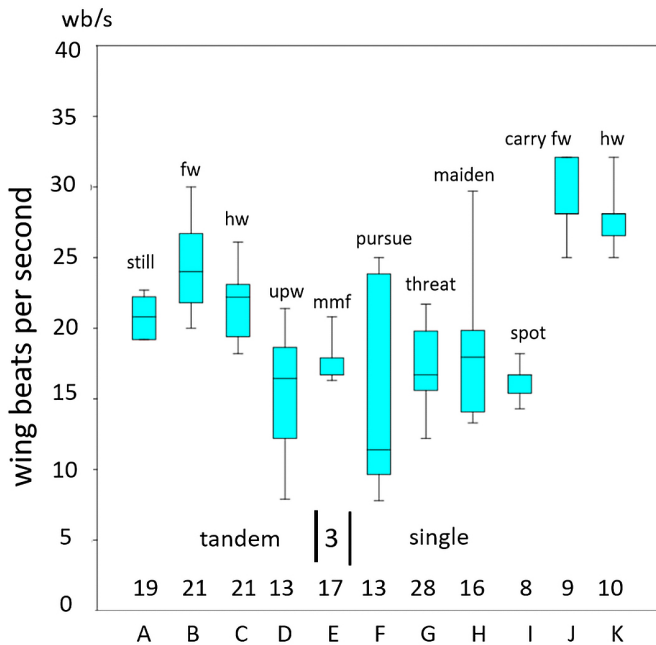
### Single flying males

When present at high densities, males were always very intense in their pursuit of females. Males pursuing a female had the lowest wingbeat frequencies (Figs 1C, 2F). During this fast flight, males often temporarily held their wings still in a backward position. These wing standstills were variable in duration (Fig. 3) and varied the beat frequency widely, so that the variation is widest in this type of flight. Males tried to close in on females by suddenly increasing their flapping speed. In one example, the first three males reduced their distance to the female: from 32.2 to 27.6 cm after two wingbeats, to



**Figure 1.** *Calopteryx splendens* males performing different flight manoeuvres. A – A male pulls an uncooperative female out of the water and into the air; B – two males attached to a female, trying to pull her in different directions; C – a swarm of males chasing a female (left), with often prolonged wing standstills in backward position; D,E – a male carrying a tandem of *Platycnemis pennipes* 20–25 cm away from their oviposition site.

16.1 cm after four wingbeats, to 12.2 cm after six wingbeats, and to 10.7 cm after eight wingbeats. When the distance to her pursuers was decreasing thus, the attacked female would also increase her beat frequency (Fig. 3, female [fe]) and suddenly turn away to escape. Other males near the first three pursuers did not show similar increases in beat frequency.



**Figure 2.** Beat frequencies (wingbeats per second = wb/s, ordinate; box plots) of *Calopteryx splendens* males during different flight manoeuvres. tandem = males flying in tandem, single = males flying single, 3 = two males coupled to one female. A (still) = male flying in tandem, female not beating her wings; B (fw) = forewings and C (hw): hindwings—male flying in tandem—female also beating her wings; D (upw) = tandem male flying upwind with wing-beating female, E (mmf) = one of two males (both coupled to a female and pulling her); F (pursue) = a male pursuing a female; G (threat) = a threatening male flying in close proximity; H (maiden) = a male flying for the first time; I (spot) = a male hovering on the spot; J (carry fw) forewings and K (hw) hindwings = a male carrying a *Platycnemis pennipes* tandem. Numbers = wingbeats

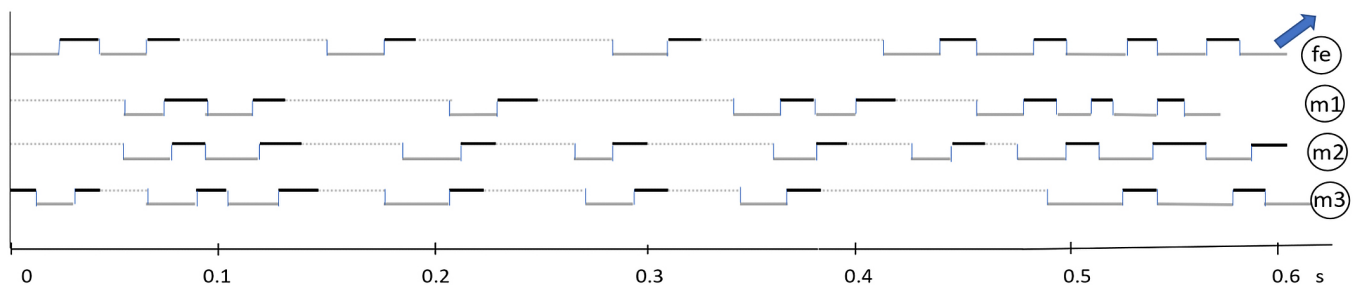
**A male *Calopteryx splendens* carrying a tandem of *Platycnemis pennipes***

When high densities of tandems of *P. pennipes* gathered around water plants to lay eggs, some *C. splendens* males attacked them, ramming the Blue Featherlegs with their legs, often pushing them down to the water. Several attacks were made on the same tandems, with varying success. Some Featherleg tandems would fly away, whereas others would gather and resist for several minutes.

After an attack by two *C. splendens* males on two Featherleg tandems, another male stretched out his fore and middle legs, grabbed a Featherleg tandem and carried it away (Figs 1D, E). This attacking male needed 14 flaps to carry this load over a distance of about 20–25 cm. The beat frequency of this flight was the highest recorded (mean  $26.3 \pm 3.19$ ,  $n = 14$  [wingbeats]) and differed from all other beat frequencies of males performing other manoeuvres (Figs 2J, K, all U-tests,  $p < 0,001$ ,  $n = 162$ ).

**Wing standstills**

Wing standstills were observed in the forward flight of single males, in females, and tandem males. While hovering on the spot, and when the one male above carried away a *P. pennipes* tandem, males of *C. splendens* did not interrupt their flight by such pauses in wingbeat. The longest pauses were noted in pursuing flight, when the damselflies flew the fastest (Fig. 4), with velocities of up to  $3.8 \text{ ms}^{-1}$ . The relationship of standstill to moving wing duration then was slightly above 40%. All other flight types with wing standstills were performed at velocities below  $1 \text{ ms}^{-1}$ . Pursued females inserted similarly long wing standstills in the same pursuits. Another result of our analyses of the wingbeat pattern during pursuits was the differences between the data of the pursued female and those of the pursuing males: the wing movement pattern of the females was steady, i.e., the durations of up- and downstrokes as well as those of the wing standstills were nearly equal, whereas those of the males were highly variable (Fig. 3).



**Figure 3.** Simultaneous wingbeat patterns of a female (fe) being pursued by three males (m1, m2, m3) of *Calopteryx splendens*. The upper dark lines in each row indicate the durations of upstrokes, the dotted lines behind are wing standstills in a backward position of the wings, and the grey lines below specify the durations of downstrokes. The wingbeat pattern of the female is more uniform with relative similar lengths of down- and upstrokes and wing standstills, while those of the males are more variable. The female shortened the duration of her wingbeats (= increasing beat frequency) after the 4<sup>th</sup> beat, when the males approached (after 0.4 s). Then all three males increased their beat frequencies, too. The arrow points out when the female escaped by flying a sudden turn (time in abscissa).

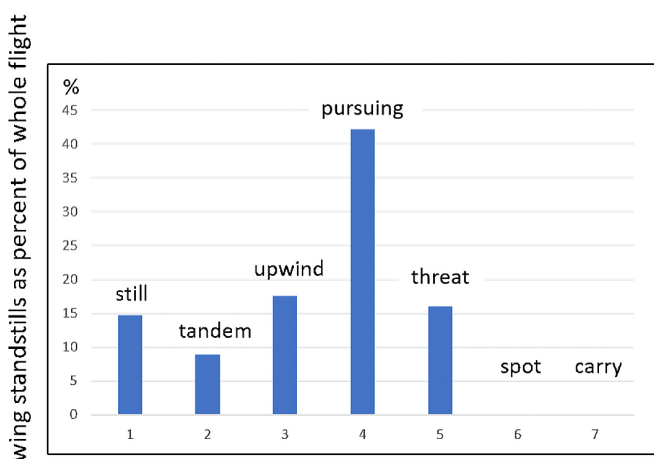
In threatening flight, when a male presented himself sideways, the forewings often were not moved either. In this type of flight manoeuvre, sometimes the forewings alone were held still for more than 3–4 wingbeat cycles of the hindwings. The wings were never held still during turns or flights in narrow spaces.

**Upstroke/downstroke ratio**

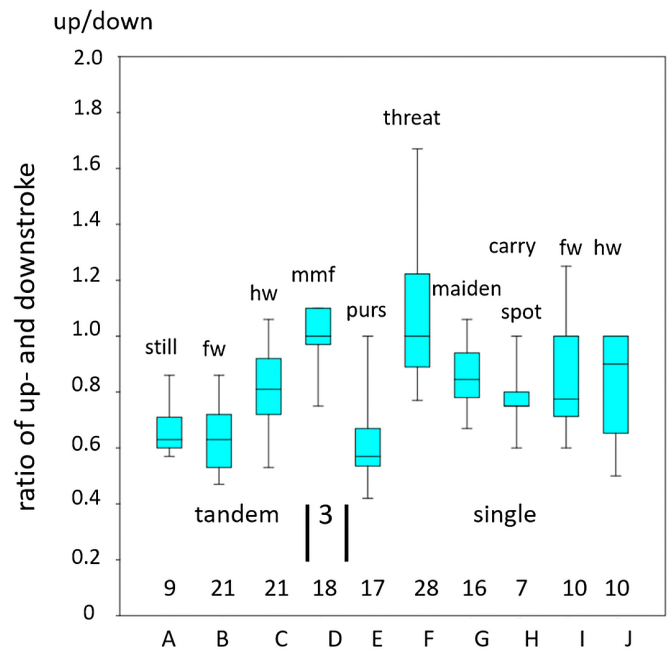
Our analyses of upstroke to downstroke ratio produced some interesting results (Figs 5, 6). In almost all wingbeats, upstrokes were shorter than downstrokes (mean  $0.72 \pm 0.16$ ;  $U = 134.0$ ,  $p < 0.001$ ,  $n = 91$ ) (excluding the instance of the male carrying away the Featherleg tandem and in threatening flight). Only one (tested separately) of the two males coupled to a female had equal durations of upstroke and downstroke (mean  $1 \pm 0.1$ ,  $n = 18$ ). Their ratio was higher than that of males flying in tandem (mean  $0.64 \pm 0.11$ ;  $U = 7$ ,  $p < 0.001$ ).

The upstroke and downstroke ratios were clearly altered in forward threatening flight and in female pursuit by keeping the wings still—it always took up a large amount of space in the straight-ahead passages (Fig. 6). In both flight types the up-/downstroke ratios differed significantly between the values without and with standstills: threatening flights without and with standstills (t-test,  $p < 0.001$ , without: mean  $0.98 \pm 0.03$ ,  $n = 41$  and with: mean  $1.94 \pm 0.32$ ); and pursuing flights without (mean  $0.62 \pm 0.11$ ,  $n = 26$ ) and with standstills (mean  $1.77 \pm 0.83$ ; U-test,  $p < 0.001$ ,  $U = 75$ ).

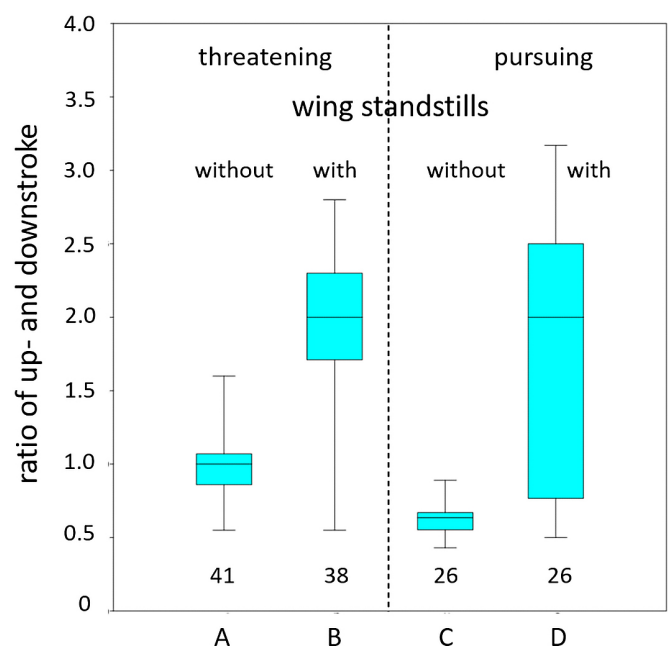
Another result of our analyses of wingbeat patterns during pursuits were the differences between the data recorded for females and those for males: the pattern



**Figure 4.** Wing standstill as a percentage of the total wingbeat duration during forward flight manoeuvres of males of *Calopteryx splendens* in single flights. Standstills did not occur when a male was carrying a *Platycnemis pennipes* tandem away (7 = carry), nor in a nearby male hovering on the spot (6 = spot), but did in all other instances: 1 still = male pulling an uncooperative female out of the water; 2 tandem = a tandem flying forward; 3 upwind = a tandem flying in an upwind zone over reeds; 4 pursuit = a male pursuing a female together with other males, 5 threat = a male displaying threatening flight in a narrow space (same flights as in Fig. 2).



**Figure 5.** Ratio of upstroke to downstroke (excluding wing standstills) in flight manoeuvres of male *Calopteryx splendens*. tandem = males flying in tandem; single = males flying single; 3 = two males coupled to one female. Each box plot represents a flight manoeuvre consisting of different numbers of wingbeats (numbers). A (still) = male flying in tandem—female not beating her wings; B (fw) = forewings and C (hw) = hindwings of a male flying in tandem—female also beating her wings; D (mmf) = one of two males (both coupled to a female and pulling her); E (purs) = a male pursuing a female; F (threat) = a nearby male in threatening flight; G (maiden) = a male flying for the first time; H (spot) = a male hovering on the spot; I (carry) forewings (fw) and J hindwings (hw) = a male carrying a *Platycnemis pennipes* tandem (same flights as in Fig. 2).



**Figure 6.** Ratios of upstroke to downstroke in threatening and pursuing flights without and with wing standstills. Numbers specify wingbeats. In threatening flight, four similar flight types were consolidated, as the behaviour was almost identical. The pursuing flight is another flight than that in Figures 2 and 5.

of the females was steady, i.e., the durations of up- and downstrokes as well as those of the wing standstills were nearly equal, whereas those of the males were highly variable.

## Discussion

In most flight modes, calopterygids beat their wings in parallel (= in phase, Rüppell, 1985). Simultaneous flapping of the two pairs of wings enables Calopterygidae to execute very fast manoeuvres due to the exceptionally high production of force with each beat (Wang & Russell, 2007). Flying means generating lift to overcome gravity and thrust to move in the desired direction. In forward flight, lift is generated mainly during the downstroke, and thrust during the upstroke (Rüppell, 1985, 1989). In forward flight, shortening the upstroke means greater wing speed to generate more thrust—the flight becomes faster. These variations in stroke duration are combined with changes in wing pitch angles, which are important for the production of lift (Thomas et al., 2004). During the phase when most thrust is produced, the wings are inclined more steeply during upstrokes than during downstrokes (Rüppell & Hilfert-Rüppell, 2020a). Another unusual feature of damselfly wings is their large size relative to body weight. Calopterygids have very low wing loading (Grabow & Rüppell, 1995). Their flapping frequencies can be very low (Rüppell, 1985), and as is demonstrated here, individuals are able to vary them widely. Calopterygid flight is furthermore characterized by frequent wing standstills of two, all four, or even only one wing (Rüppell, 1985). All this has communicative functions, too (Hilfert-Rüppell & Rüppell, 2013; Rüppell, 1985), and must have evolved through sexual selection (Córdoba-Aguilar et al., 2007; Svenson & Waller, 2013).

### Wingbeat frequencies

An important wingbeat parameter is frequency. For single males it was lowest in pursuing flight, because of long periods with wing standstills. The wingbeat frequencies of pursuing males were matched to those of the pursued female. When the female's frequency increased due to decreasing distances, the males did the same. This is strong evidence for the influence of beat frequency on flight speed. When carrying a female, more lift is needed because the cooperation of the female cannot be as effective as in a single flying individual. As a consequence, males in tandem have to increase their wingbeat frequency. The load of an uncooperative female is about 150 mg. However, the highest frequencies were observed when a male was carrying a *P. pennipes* tandem. In this transport, the combined weight of the male and female *P. pennipes* was about 85 mg (Grabow & Rüppell, 1985), and the flapping of the Featherleg tandem certainly did not assist this transport. A higher load to be carried resulted, explaining the highest measured beat frequency.

### Forewing-hindwing differences

Another realisation concerns the difference of movements of fore- and hindwings and their interaction at various flight speeds (Sun et al., 2007). In Calopterygidae the hindwings mostly come together at the end of the upstroke, with a delay of 10% to the forewings (Rüppell & Hilfert-Rüppell, 2009a). As a result, the forewings of in-tandem males in forward flight had a higher beat frequency and a lower upstroke/downstroke ratio. The forewings therefore had a higher significance for generating thrust than the hindwings. This indicates that the hindwings are more important for the production of lift. This is due to the more inclined hindwing stroke path in contrast to the more horizontal stroke path of the forewings (Rüppell, 1985).

### Wing standstills

Wing standstill was observed in both males and females during forward flight. The forward speed prevents these damselflies from losing too much height. Wing standstills were longest during fast pursuits. Even during long threatening flights—so called escalated fights (Plaistow & Siva-Jothy, 1996)—the forward movement was accompanied by frequent wing standstills. Wing standstills should therefore be beneficial to endurance, because they should allow flight muscles to rest even if ever so briefly.

Wing standstills may also have another function, however. The males also inserted prolonged wing standstills in threatening flight, probably for signalling rivals. In one type of threatening flight, these standstills are prolonged to the extent that the male will clearly lose height in the process. This form of flight is aptly called wave flight (Rüppell, 1985). Sometimes, as in pendulum flight, only the forewings are held still during passages at right angles to the rival. In one case, a male *C. splendens* effected three beats with three wings while presenting one stationary forewing to his rival.

Wing standstills accounted for a large portion of the beating time in threatening and pursuing flights. As was described above, these wing standstills can serve two functions: to optimise gliding, and to communicate with conspecific males and perhaps females as well. The wide variability of these wing standstills indicate that these damselflies use this kinematic tool to adapt their flight to environmental situations: displaying or optimising flight velocity and path—in which relationships might be changeable.

### Ratio of upstroke to downstroke duration

Measuring the upstroke to downstroke ratio is important for estimating the aerodynamic significance of a stroke phase for a specific manoeuvre. This significance can be blurred by communicative functions of the wings, as in the case of threatening flight.

The durations of the upstroke and downstroke make it possible to calculate the speed of the wings in the two phases. When the ratio of upstroke to downstroke is less than 1, the wings move faster in the upstroke than in the downstroke. Characteristics of a fast acceleration flight forward are short upstrokes in combination with steep angles of attack. In reverse flight, the downstrokes were shorter than the upstrokes (Rüppell & Hilfert-Rüppell, 2020a).

In all cases reported here, the up-/downstroke ratio was lowest in pursuing flight. This means that short upstrokes are required in this flight mode to obtain a maximum of thrust. In tandem flight the male should also try to accelerate to bring the female away from the water and from rivals. In both scenarios, the short upstroke means a high wing speed during the upstroke, which generates a high flight speed (Rüppell et al., 2020). Single males also had a higher up-/downstroke ratio when carrying a female together with another male. Because of the extra weight of the female they needed more lift, which mostly is produced during downstrokes.

Another result of our analyses of the wingbeat pattern during pursuits is the difference between the data of females and those of males. The durations of upstrokes, downstrokes, and wing standstills of females were almost the same, whereas those of males varied considerably.

### **Flight to communicate**

The wings of *Calopteryx* males have different functions. Their main function of course is flight, but because their wings are coloured they can at the same time be used for communication. These two functions, in addition to kinematic requirements, render their flight different from that of species with clear wings (Hilfert-Rüppell & Rüppell, 2013).

This is also the reason why it is difficult to unambiguously assign the variance of temporal flight parameters in dragonfly species with wing ornamentations to either aerodynamic or communicative purposes. Even in species with transparent wings, communicative functions can alter kinematics and not only aerodynamics. As has been shown in courting males of *Chlorocypha cancellata*, wingbeat frequency can vary depending on female behaviour (Günther, 2015), and even females of *C. splendens* can alter their flight into threatening flight in certain scenarios (Hilfert-Rüppell, 2015).

The ratio of upstroke to downstroke was at its highest and most variable during threatening flight, however, because of the simultaneous signalling function of the wings. The flying male then used his wings not just to support himself, but probably also to display his status in order to scare off a rival. This is effected by a slower upstroke. Performance is, therefore, not only determined by aerodynamic needs, but also by signalling. This means that the motivational causes of the male probably influence the beating pattern and cannot be explained aerodynamically.

Long wing standstills also occur when a male is in pursuit of a female. Whether this is due to an optimisation of gliding or signalling must remain unanswered at this stage. It is conceivable, however, that signalling would be an indirect side effect of flight optimisation and thus unintentionally slows down the flight of the male.

### **Conclusions**

In the manoeuvres described in this study, flight parameters changed significantly. Wingbeat frequencies were highest when males had to carry a load, either a female in tandem or, in one instance, a tandem of *P. pennipes*. When pursuing a female, males generate the highest flight speeds by very short upstrokes and probably increase their endurance by inserting long wing standstills.

A male has to overcome several challenges in order to reach a pursued female: (1) It has to follow the female, which is in control of both speed and direction of flight; (2) it has to avoid nearby flying males, which could disturb its own kinematics mechanically or by altering the airflow in the immediate environment; (3) the communicative function of the wings could influence the neuro-motoric system and thus increase its own communicative efforts by threatening other males, which could slow down its flight. In such a pursuit, the flight of the female is consistent, while that of the male is varies considerably. The latter may be the key factor explaining the superiority of females in pursuits. When the wings are held steady, all aerodynamic processes such as vortex formation at the leading edge of the wings and aerodynamic circulation, and possibly the momentum transfer due to recovery of wake energy, can increase lift more effectively at the end of each half-stroke (Bomphrey et al., 2016; Lehmann, 2004; Nabawy & Crowther, 2017; Noda et al., 2023) than in the irregular movements of the pursuing male. For example, Rüppell & Hilfert-Rüppell (2009) showed that females of *C. splendens* are usually able to escape pursuing males if they wish to. This result may be generalised to suggest that the aerodynamic function of the wing movement is more important than their communicative function for females, unlike with the males. This is emphasised by the camouflage colouration of most female dragonflies, in contrast to the conspicuous body and wing colouration of most males, which in some cases may hide them, too.

It can only be hypothesized at this stage that the males developed the gain in communicative importance of their flight at the expense of kinematic variability, which led to aerodynamic limitations. From an evolutionary perspective, the double function of flight in calopterygid males may be considered a trade-off between mechanical flight requirements and signalling in the context of intra- and intersex communication.

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