

Signalling with clear wings during territorial behaviour and courtship of *Chlorocypha cancellata* (Odonata, Chlorocyphidae)

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This article is dedicated to Georg Rüppell, the pioneer of studying dragonfly flight using slow motion footage. More than any other person, he has shaped and refined our knowledge of the kinematics of dragonfly flight and the importance of optical wing signals for communication. I warmly thank Georg for his many suggestions, shared days in the field and last, but not least, for introducing me to the Casio camera.

The reproductive behaviour of the damselfly *Chlorocypha cancellata* (Chlorocyphidae) was filmed at 600 frames per second. Different flight styles including straight, forward flight, threat and courtship display were analysed with respect to changes in wing beat frequency and phase relationships of fore and hind wings. The analysis revealed significant differences in the flight style between non-escalated and escalated threat display as well as changes in the wing beat frequency of a male during courtship dependant on the behaviour of the female. This is the first evidence suggesting that odonate species with clear wings can use specialized flight modes for intraspecific signalling.

Keywords: *Chlorocypha canellata*; reproductive behaviour; courtship display; threat display; wingbeat frequency; signalling

Introduction

In the Chlorocyphidae males of most species are brightly coloured and richly ornamented either on the body or wings or both (Karjalainen & Hämäläinen, 2013). Several studies have shown that there is a close connection between colouration and signalling behaviour (e.g. Günther, 2008; Orr, 1996; Robertson, 1982a, 1982b; Rudolph, 1993; Telford, Barnett, & Polakow, 1996). Comparative studies of the courtship and agonistic displays of coloured-winged chlorocyphids (Günther, 2008; Orr, 1996) revealed a highly specialized display of wing and body ornamentation. All species studied showed several distinct flight patterns in agnostic and courtship behaviour for the presentation of their coloured wings, including pauses in wing beating, presenting all wings front on simultaneously or alternating wing beat with intensified frequency. More generally, Hilfert-Rüppell and Rüppell (2013) found different flight kinematics in coloured-winged Odonata compared with clear-winged species. In particular the wing beat frequencies of coloured-winged species showed a much greater variation than in clear winged species.

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All African Chlorocyphidae have clear wings without specialized ornamentation. Studies in *Platycypha caligata* and *Platycypha fitzsimonsi* (Robertson, 1982a, 1982b; Rudolph, 1992, 1993; Telford et al., 1996) have shown that the body coloration is of importance in signalling. But due to the lack of high-speed cinematography with adequate temporal resolution no previous study has been able to analyse the wing movements of clear-winged chlorocyphids in detail. Only the study of R. Rudolph was based on slow motion footage with a maximum resolution of 250 fps. This footage was of great importance in elucidating details of threat and courtship behaviour but not adequate for a kinematic analysis of wing movements. My own results of behavioural studies in narrow-winged Asiatic *Heliocypha* and *Libellago* species (Günther, 2008 and unpublished results) show that a change of wing beat frequency during counter stroking wing beat mode could have a function in display. The major aim of this study was to investigate the occurrence of changes in wing beat frequencies in the signalling behaviour of a clear-winged African chlorocyphid species.

Material and methods

Study area

Most observations were made at a small rainforest stream within a timber concession area near Moyabi, about 15 km south of Moanda, Gabon (01°42'25.1" S, 13°15'20.5" E). The fast flowing, shallow stream averaged about 5 m in width. The substrate was sandy-gravelly and the stream contained a large amount of semi-submerged timber. The banks were covered by disturbed primary forest. The water was clear in 2013 with light turbidity caused by logging activities in the catchment area. In 2014 turbidity was very high after heavy rainfall. Additional observations were made at Mussingue stream in the Mont de Chaillu, about 35 km north-east of Mouila, Gabon (01°43'43.4" S, 11°18'25.7" E).

Subject of study and methods

Chlorocypha cancellata is a medium-sized chlorocyphid with slender, hyaline wings and entirely black tibiae. Older individuals sometimes have a very light yellowish tinting at the wing base. The thorax of mature males is yellow with thick black stripes, the basal segments of abdomen are yellow to red with thick black apical bars and black dorsal and lateral lines. The terminal four segments are blue (Figure 1).

The species is widely distributed in central Africa from Cameroon in the north-west to Uganda and northern Tanzania in the south-east. The range is thought to be disjunct, probably divided



Figure 1. *Chlorocypha cancellata* male – Mussingue stream, Mont de Chaillu, Gabon, 21 September 2013.

by unsuitable lowland habitats in large parts of the Democratic Republic of Congo (Clausnitzer & Dijkstra, 2010) but the known distribution pattern may also reflect gaps in mapping. A recent record south of Kisangani (Democratic Republic of the Congo, Dijkstra in Odonata Database of Africa (ODA); cf. Kipping, Dijkstra, Clausnitzer, Suhling, & Schütte, 2009) suggests the true range may in fact be continuous.

The flight behaviour was observed and filmed on 17 September 2013 and on 17 September 2014 (Moyabi). Further behavioural observations took place on 20/21 September 2013 at Mussingue stream. I used a Casio EX-F1 camera (Casio Computer Co., Tokyo, Japan) to record at 600 f/s with sufficient resolution for single-frame analysis. For methodological details see Günther, Hilfert-Rüppell, and Rüppell (2013). To analyse the recordings I used QuickTime Player version 7.7.1 (Apple, Inc., Cupertino, CA, USA). To obtain the wing beat frequencies I counted sequential frames, if possible separated into down stroke, up stroke and wing beat pauses. To minimize errors some problematic recordings were analysed at least twice. In order to calculate the wing beat frequency the exposure rate (number of frames per second) was divided by the number of frames per wing beat. Wing stroke angles (i.e. the angle described by the wing in a single beat) were estimated only when the damselflies' flight path and sagittal plane were approximately orthogonal to the direction of recording. While it is acknowledged there are unknown error terms associated with the measured amplitudes it is considered these are sufficiently small to be ignored, given that changes in amplitude are clearly apparent to the human eye on slowed video sequences.

To analyse the wing beat data I used STATGRAPHICS Centurion XVI, Version 16.1.18 (StatPoint Technologies, Inc., Warrenton, VA, USA). After confirming the data were non-normal, the nonparametric Mann–Whitney (Wilcoxon) W-test was used to analyse the data associated with the different displays. The Kruskal-Wallis-Test was used to compare the different categories of behaviour.

Results

General behaviour

Chlorocypha cancellata occurs in Gabon in a wide variety of small and medium sized streams, in mostly forested areas. In small creeks the species seems to be restricted to longer sunny sections and becomes scarce in large streams and small rivers (N. Mézière, pers. comm. and own records). The highest population densities were found in structurally complex, sunlit sections of forest streams with a width between 5 and 10 m.

Mature males established territories 3–5 m in diameter around semi-submerged timber usually in full sunlight. Mostly they perched very low, near the water, on flat stones, emergent twigs or timber. On sunny days males occupied their territories in the forenoon hours. On cloudy days, the first males appeared with the first sunshine, often around noon. After 16:00 h solar time no more territorial behaviour was observed. At times some males remained in their territories even without direct sunshine, but the majority of the males left the stream when the sun disappeared. On days without any sunshine usually no individuals of the species were observed.

Male–male interactions

Territorial males showed characteristic behaviour towards conspecifics. Against rivals, threat behaviour was observed. Territorial neighbours especially engaged in protracted threatening flights. Contests began when one male flew into another's territory. The two males faced each other head to head at a distance of about 8–20 cm. In that flight mode the abdomens were slightly



Figure 2. Posture of two *Chlorocypha cancellata* males during threat display - Moyabi, Gabon, 17 September 2014. Exposure time 1/1600 s.

raised but the four terminal segments with the blue coloration were bent down in a characteristic way, presenting only the orange and red colouration of the abdomen and the yellow markings of the thorax to the rival (Figure 2). Sometimes both males circled slowly around each other. The steady flight was interrupted several times by short periods of increased intensity. These are here termed escalated displays and were a combination of an increase in wing beat frequency and short pauses in wing beating (for details see under *flight kinematics* and Figure 3). To the naked eye the flight during escalated display appeared slightly tremulous in horizontal view. After 1–4 s both males moved the position of the contest slightly with a short pursuing flight. The fights took place within the territories of both males.

Altogether five pairs of fighting neighbouring males were observed in detail. They each used successively 4–5 well-defined positions inside their territories for escalated fights. These ‘contest sites’ remained more or less constant throughout the day. Escalated fights were sometimes ($n = 7$ ascending flights) interrupted by a single ascending flight of both up to about 5 m. In the five cases analysed the contests continued for most of the time that both males were present in the territory, at least during sunny periods in the afternoon. Nevertheless after different bout durations fighting males made short pauses in which the rival returned to his preferred perches. Such pauses were often triggered by the appearance of clouds blocking the sun. During contests between neighbours no winners and losers could be identified. Physical contact was avoided during aggressive interactions. The only exception was the following observation (17 September 2013, 15:09 h solar time): after a contest of more than two hours duration a male suddenly attacked the other, seizing its rival by both right wings, whereupon both males fell into the water.

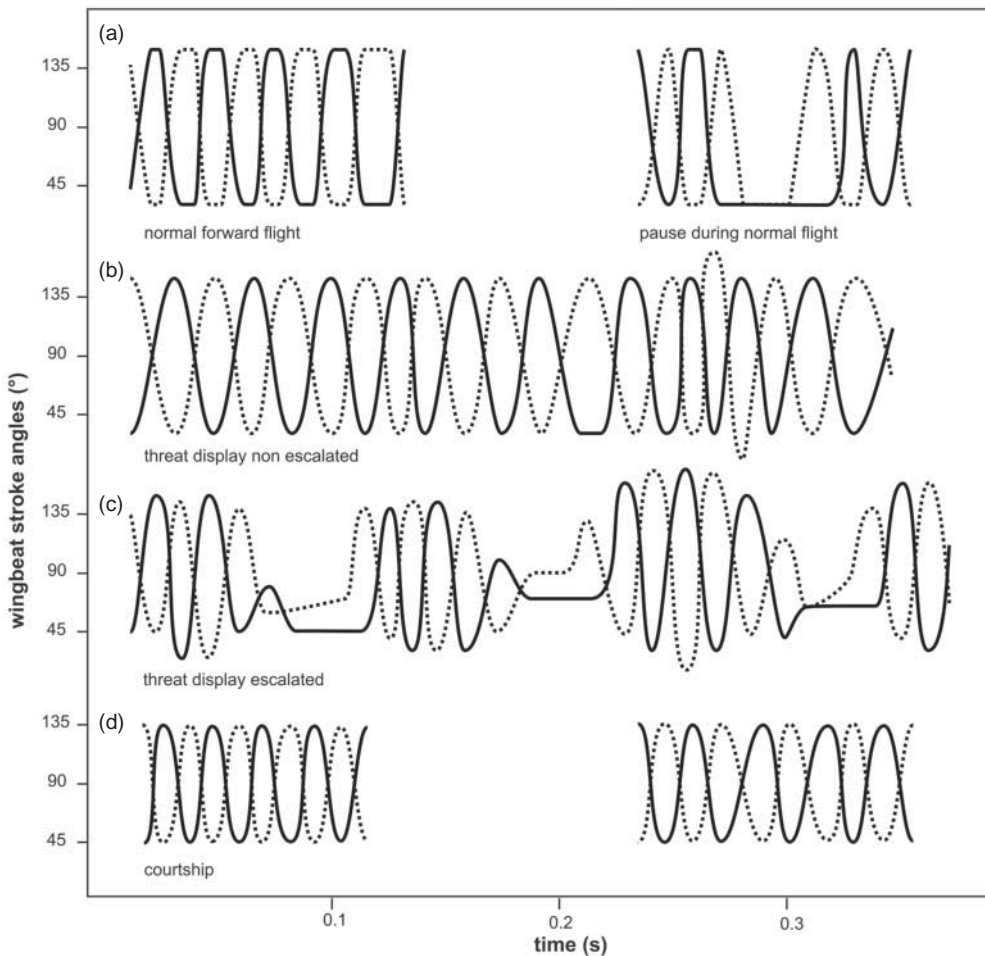


Figure 3. Sequential pattern of wing beat stroke amplitudes of *Chlorocypha cancellata* during different flight styles (from left to right). Fore wings: broken lines, hind wings: unbroken lines. Lines going downwards to right = down-strokes, lines going upwards to right = up-strokes. Horizontal lines indicate the wings were held stationary or nearly so. The greater the amplitude of these lines the wider the stroke angles. Abscissa indicates time in seconds. (a) Normal, straight forward flight: Counter stroking wing beat with short pauses at the end of every stroke (left). In that flight style frequent pauses in beating of both wing pairs occur (right). (b) Non-escalated threat display between two males mainly hovering: counter stroking wing beats. After 0.2 s the wing beating became somewhat irregular. This was most probably caused by an interrupted transition to the escalated type of threat display. (c) Escalated threat display between two males mainly hovering: frequency modulated stroking in an escalated territorial fight. Counter stroking with increased frequency alternating with short breaks at intervals of about 0.1 s. (d): Courtship display: two examples of counter stroking wing beat with higher (left) and lower (right) frequency. See also Figure 5.

After about nine seconds, they disengaged and the attacked male flew up from the water. Shortly afterwards the attacker flew away too. Both males left their territories immediately.

Male–female interactions

Male courtship behaviour was released by females arriving at the stream near the site. When a male discovered a newly arriving female he usually flew immediately in front of her, circling around her, and led the female to a suitable oviposition site. During guiding behaviour the male flew in front of the female with slightly depressed abdomen displaying the blue marking at the apex. In a total of nine cases observed, the female was led seven times to semi-submerged timber

at a sunny place in the centre of the territory. In two cases (different males and territories) the female was led to stranded driftwood along a shady riverbank at the edge of the territory. In both cases the territory owner had not been seen before at this site on the observation day. Females generally followed the display flight of the male, at least initially. Only two females decamped shortly after the beginning of courtship. On reaching the potential oviposition site the females perched and began testing the wood with her ovipositor. The males sometimes ($n = 2$) began courtship display in front of the female but more frequently ($n = 5$) facing the female from the side. During courtship display the male arched up his abdomen, presenting its full dorsal coloration of red and blue. All his legs were folded up close to the thorax. Later he hovered in courtship display behind the female for several seconds. Slowly approaching he then tried to land on her thorax. In four cases the male was successful and mating followed. When they separated the female flew up and perched nearby for a short time. If, after some seconds, the mated female took off, the male again flew ahead of her with depressed abdomen, leading her back to the oviposition site. Sometimes in courtship display the male hovered just beside the female, facing the female, while she searched for a place to oviposit. Oviposition took place in more or less rotten timber. All four females studied curved their abdomen and touched the substrate, followed by apparent oviposition movements well above the water surface, but over several minutes they moved slowly into the water where they remained for more than 1.5 h at a depth of 2–20 cm.

Comparisons of flight kinematics

The movements of fore and hind wings can be characterized by the phase relationships of both wing pairs and their beating frequencies. Another important component of flight is flight velocity. My analysis is based on the study of context dependent wing beat frequency and temporal patterns of wing beating to investigate the importance of wing beating in signalling behaviour. Flight velocity was not considered because the display flights were usually stationary. The sequence of wing beat amplitudes during different flight styles of males of *Chlorocypha cancellata* (normal forward flight, fleeing, courtship, non escalated and escalated threat display) is shown in Figure 3, and the wing-beat frequencies are shown in Figure 4. There were significant differences between the wing-beat frequencies (Kruskal Wallance test: $H = 83.56, p < 0.001$).

Straight, forward flight over a distance

For purposes of comparison normal, straight, forward flight was included in the analysis (Figure 4). The wing beat pattern was counter stroking with short pauses of about 0.005–0.01 s at the end of each upstroke and down-stroke. The mean value of the beat frequency including these short pauses was 35.3 ± 1.1 Hz ($n = 15$, wing beats). During forward flight regularly short beating pauses of both wing pairs occurred (Figure 3, top right). First, the hind wings were paused in a backward position following a down-stroke. Then following the down-stroke of the fore wings the wing beat was paused for about 0.02–0.05 s ($n = 3$), resuming with the upstroke of the fore wings again. If a male was alarmed and chased from his perch, the stroke frequency as he fled had a mean value of 43.1 ± 4.1 Hz ($n = 6$) significantly higher than normal forward flight (Mann–Whitney (Wilcoxon) W-test: $W = 90.0, p < 0.001, \text{d.f.} = 19$).

Threat display

The non-escalated threat display was characterized by a steady counter stroking without pauses and a mean value of the beat frequency of 29.5 ± 3.0 Hz ($n = 20$). In the escalated display the frequency was modulated to counter stroking with increased frequency alternating with short

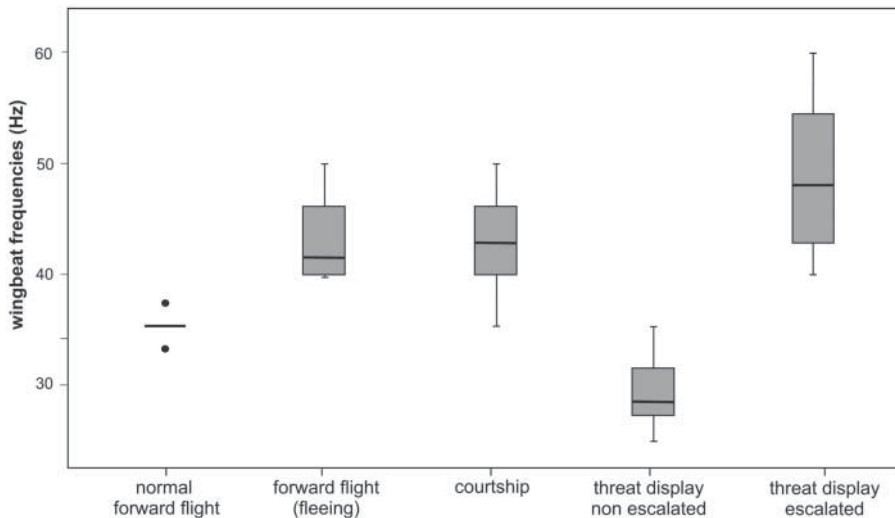


Figure 4. Stroke frequencies of *Chlorocypha cancellata* males for different flight styles. Straight, forward displacement flight ($n = 15$, wing beats), straight, forward flight (fleeing) ($n = 6$), courtship display ($n = 60$, cf. Figure 5), non-escalated threat display ($n = 20$), escalated threat display ($n = 20$). 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, and the small filled circles are outliers.

breaks at intervals of about 0.1 s. After 3–4 wing beats with a mean beat frequency value of 48.3 ± 5.7 Hz ($n = 20$) the wing beat paused for about 0.03 s. In contrast to the straight, forward displacement flight these pauses did not occur at the end of the down stroke. The males held their wings still with a stroke angle of about $50\text{--}60^\circ$ (Figure 3). The wing beat frequencies between non-escalated and escalated display differed significantly (Mann–Whitney (Wilcoxon) W-test: $W = 400.0$, $p < 0.001$).

Courtship display

During courtship display males showed a regular counter-stroking wing beat without any pauses. The mean value of the frequency was 42.9 ± 3.1 Hz ($n = 60$). On 17 September 2013 I filmed the courtship display of a male from the beginning until the female left the site after 6.8 s without mating. The total duration of courtship was 7.01 s. I analysed the stroke frequencies of the male in 6 samples (data set I–IV) during his courtship flight. Every data set includes 10 wing beats. For more details compare Table 1 and Figure 5. The male began courtship with a high frequency wing beat of 45.5 ± 1.4 Hz ($n = 10$). During courtship, the frequency was gradually reduced to 40.5 ± 3.6 Hz ($n = 10$) after 6.5 s. As the female flew off, the male immediately increased his beat frequency to the high value of 46.6 ± 2.1 Hz ($n = 10$). I found significant differences between the wing-beat frequencies (Kruskal Wallance test: $H = 34.28$, $p < 0.001$). The wing beat frequencies between data set I and the data sets II, III, VI, and V, and data set VI and the data sets II, III, IV and V (compare Table 1) differed significantly (Mann–Whitney (Wilcoxon) W-test, $p < 0.001$, d.f. = 18).

Discussion

Visual communication is of outstanding importance in most aspects of the behaviour of Odonata (cf. Corbet, 2004, p. 463). Hilfert-Rüppell and Rüppell (2013) showed the interaction between wing coloration, presentation of wing patterns and flight kinematics. Orr (1996, p. 137) noted

Table 1. Wing beat frequencies during the courtship display of a male *Chlorocypha cancellata*. Every data set includes 10 wing beats. The value for the time represents the mean value of the time after beginning of the courtship for the considered 10 wing beats. Total duration of courtship 7.01 s. Moyabi, Gabon, 17 September 2013.

Number of data set	Time (s)	Number of wing beats	Mean value frequencies	Standard deviation
I	0.01	10	45.5	± 1.4
II	2.65	10	41.7	± 1.5
III	4.26	10	42.0	± 2.0
IV	6.05	10	41.0	± 2.2
V	6.51	10	40.5	± 3.6
VI	6.79	10	46.6	± 2.1
Total		60	42.9	± 3.1

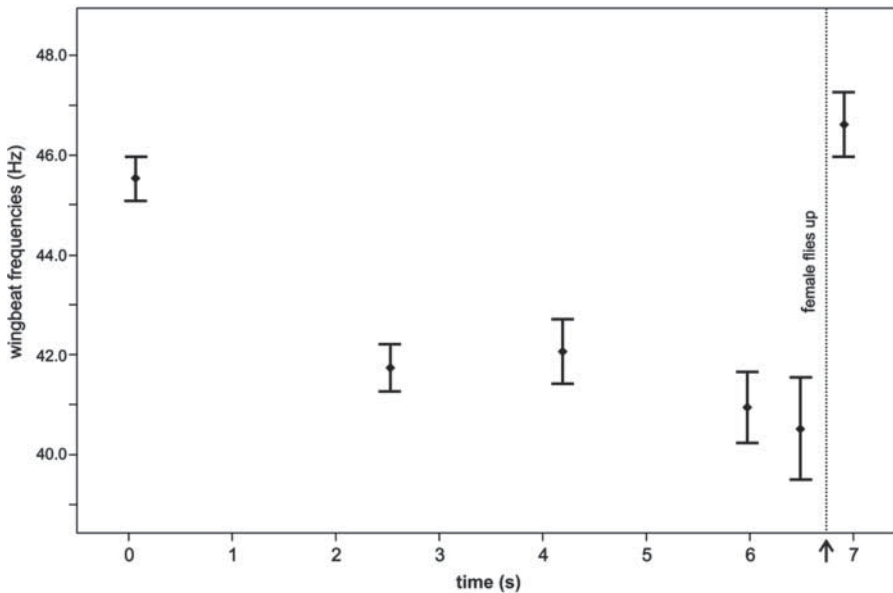


Figure 5. Mean values (points) and standard errors (vertical lines with small terminal crossbars) of stroke frequencies of a *Chlorocypha cancellata* male during courtship flight. Every data set includes 10 wing beats. The position of the graph represents the mean value of the time since the beginning of courtship flight for the 10 wing beats analysed. After 6.7 s the female flew up (arrow and broken line). Moyabi, Gabon, 17 September 2013.

that the display of Chlorocyphidae “include both morphological and behavioural components: i.e. ornaments per se and the actions which reveal them”. The change in the frequency of the wing beat is part of the display flight of many species with coloured wings. These changes range from very high stroke rate, for example during courtship or in escalating territorial fights to pauses in the wing beating and are common in coloured-winged Calopterygidae and Chlorocyphidae (Anders & Rüppell, 1997; Günther, 2006, 2008; Günther et al., 2014; Heymer, 1972; Orr, 1996, 2009; Orr & Hämäläinen, 2007; Pajunen, 1966; Rüppell, 1989; Thompson, 2000) but were also described for Libellulidae, e.g. *Neurothemis fluctuans* by Hilfert-Rüppell & Rüppell (2013).

From a theoretical perspective, there are two explanations for the function of this behaviour. On the one hand the signalling function of wing ornamentation can be increased by changes in the flight style. Examples in Chlorocyphidae are the motionless presentation of the terminally pigmented fore wings (*Libellago*), frontal presentation of the entire, largely iridescent wing surface by simultaneously turning all wings forward (*Aristocypha*, *Heliocypha*, *Rhinocypha*) and the motionless presentation of the hind wings (*Aristocypha*, *Heliocypha*) (Günther, 2008; Orr, 1996, 2009). There is a broad consensus that coloured wings in Calopterygidae have evolved

in response to sexual selection (Córdoba-Aguilar & Cordero Rivera, 2005; Córdoba-Aguilar, Leshner-Trevino, & Anderson, 2007; Serrano-Meneses, Sánchez-Rojas, & Córdoba-Aguilar, 2008; Svensson & Waller, 2013). According to our current knowledge, the same assumption for Chlorocyphidae should be justified. The quality of the visual signal provides information about the fitness of the transmitter *sensu* Siva-Jothy (1999).

On the other hand a flight style with high energy costs can in itself be an expression of the fitness of the individuals. Marden & Waage (1990) have characterized escalated territorial fights as “energetic wars of attrition” while Marden & Rollins (1994) assume that the competing males are able to estimate condition determining the fat reserves of the rival by the change of “flight ability” and “flight performance”. The results of Tsubaki, Samejima, & Siva-Jothy (2010) demonstrate the importance of the beat frequency in communication between males and females during courtship but they found that the courtship wing beat frequency in *Mnais costalis* was positively correlated with the male thorax temperature and not directly with male “quality”. But on the other hand the thorax temperature was influenced by direct solar radiation on the territories and thus at least indirectly from the ability of males, to occupy high-quality territories.

For a species without coloured wings signalling by changes in the wing beat frequency has not previously been recorded. One reason for this is most probably the hitherto inadequate technical equipment needed for studies under field conditions. Even in a well-studied species like *Platycypha caligata* (Martens & Rehfeldt, 1989; Robertson, 1982a, 1982b; Rudolph, 1992, 1993; Telford et al., 1996) the system of signalling was described only in respect to the semiotic function of body coloration. Nevertheless, from an evolutionary perspective, signalling with the wings might be a logical precursor to developing coloured wings with stronger optical signals.

The studies on *Chlorocypha cancellata* provided two clear indications of an augmented signalling function of wing motion: (a) the differences in wing beating between non-escalated and escalated threat display (Figure 3); and (b) the context dependent change in wing beat frequency of the courting male (Figure 5). The behaviour in (a) fits very well with my results in narrow-winged Asiatic *Disparocypha*, *Heliocypha* and *Libellago* species (Günther, 2008 and unpublished results). However, the behaviour of the species with coloured wings is more complex, because there is almost always presentation of the wing ornaments during the flight, which in itself demands adjustments to flight style. The change of frequency during courtship (b) is similar to our results in *Neurobasis chinensis* (Günther et al., 2014, figure 15). A male of the coloured-winged *N. chinensis* changed the beat frequency of the hyaline fore wing during demonstration of the oviposition site in response to the proximity of the female. When the female arrived at the site the male increased his stroke frequency significantly and decreased it as she departed. We reasoned that the male demonstrated his power by maintaining a high stroke frequency for an extended period. In *C. cancellata* courtship probably two aspects play a role: the demonstration of fitness through high frequency wing beating and a non-threatening approach to the female for mating.

It is a reasonable conclusion that the evolution of the extraordinary wing displays of coloured-winged Odonata species was based on a simple display by frequency changes, which already occurs in species with clear wings.

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References

- Anders, U., & Ruppel, G. (1997). Zeitanalyse der Balzflüge europäischer Prachtlibellen-Arten zur Betrachtung ihrer Verwandtschaftsbeziehungen (Odonata: Calopterygidae). *Entomologica Generalis*, 21, 253–264.

- Clausnitzer, V., & Dijkstra, K.-D. B. (2010). *Chlorocypha cancellata*. *The IUCN Red List of Threatened Species*. Version 2014.2. Retrieved August 23, 2014, from www.iucnredlist.org
- Corbet, P. S. (2004). *Dragonflies. Behaviour and ecology of Odonata* (rev. ed.). Colchester: Harley Books.
- Córdoba-Aguilar, A., & Cordero Rivera, A. (2005). Evolution and ecology of Calopterygidae (Zygoptera: Odonata): status of knowledge and research perspectives. *Neotropical Entomology*, *34*, 861–879. Retrieved from <http://dx.doi.org/10.1590/S1519-566X2005000600001>
- Córdoba-Aguilar, A., Leshner-Trevino, A. C., & Anderson, C. N. (2007). Sexual selection in *Heterina titia*: a possible key species to understand the evolution of pigmentation in calopterygid damselflies (Odonata: Zygoptera). *Behaviour*, *144*, 931–952. doi:10.1163/156853907781492672
- Günther, A. (2006). Reproductive behaviour of *Neurobasis kaupi* (Odonata: Calopterygidae). *International Journal of Odonatology*, *9*, 151–164. doi:10.1080/13887890.2006.9748274
- Günther, A. (2008). *Vergleichende Untersuchungen zum Reproduktionsverhalten südostasiatischer Chlorocyphidae und Calopterygidae (Odonata: Zygoptera)* (doctoral thesis). TU Bergakademie Freiberg, Germany. Retrieved from <http://nbn-resolving.de/urn:nbn:de:bsz:105-5111029>
- Günther, A., Hilfert-Rüppell, D., & Rüppell, G. (2014). Reproductive behaviour and the system of signalling in *Neurobasis chinensis* (Odonata, Calopterygidae) – a kinematic analysis. *International Journal of Odonatology*, *17*, 31–52. doi:10.1080/13887890.2014.881305
- Heymer, A. (1972). *Verhaltensstudien an Prachtlibellen. Beiträge zur Ethologie und Evolution der Calopterygidae (SELYS, 1850 (Odonata: Zygoptera))*. Berlin: Parey.
- Hilfert-Rüppell, D., & Rüppell, G. (2013). Do coloured-winged damselflies and dragonflies have flight kinematics different from those with clear-wings? *International Journal of Odonatology*, *16*, 119–134. doi:10.1080/13887890.2013.763332
- Karjalainen, S., & Hämäläinen, M. (2013). *Neidonkorenot – Demoiselle Damselflies*. Helsinki: Caloptera Publishing.
- Kipping, J., Dijkstra, K.-D. B., Clausnitzer, V., Suhling, F., & Schütte, K. (2009). Odonata database of Africa (ODA). *Agrion*, *13*, 20–23.
- Marden, J. H., & Rollins, R. A. (1994). Assessment of energy reserves by damselflies engaged in aerial contests for mating territories. *Animal Behaviour*, *48*, 1023–1030. doi:10.1006/anbe.1994.1335
- Marden, J. H., & Waage, J. K. (1990). Escalated damselfly territorial contests are energetic wars of attrition. *Animal Behaviour*, *39*, 954–959. doi:10.1016/S0003-3472(05)80960-1
- Martens, A., & Rehfeldt, G. (1989). Female aggregation in *Platycypha caligata* (Odonata: Chlorocyphidae): a tactic to evade male interference during oviposition. *Animal Behaviour*, *39*, 369–374. doi:10.1016/S0003-3472(89)80029-6
- Orr, A. G. (1996). Territorial and courtship displays in Bornean Chlorocyphidae (Zygoptera). *Odonatologica*, *25*, 119–141.
- Orr, A. G. (2009). Reproductive behaviour of *Libellago semiopaca* on a Bornean rainforest stream (Odonata: Chlorocyphidae). *International Journal of Odonatology*, *12*, 157–180. doi:10.1080/13887890.2009.9748337
- Orr, A. G., & Hämäläinen, M. (2007). *The metalwing demoiselles of the Eastern Tropics*. Kota Kinabalu: Natural History Publications (Borneo).
- Pajunen, V. I. (1966). Aggressive behavior and territoriality in a population of *Calopteryx virgo* L. (Odonata: Calopterygidae). *Annales zoologici fennici*, *3*, 201–214.
- Robertson, H. M. (1982a). Courtship displays and mating behaviour of three species of Chlorocyphidae (Zygoptera). *Odonatologica*, *11*, 53–58.
- Robertson, H. M. (1982b). Mating behaviour and its relationship to territoriality in *Platycypha caligata* (Selys) (Odonata: Chlorocyphidae). *Behaviour*, *79*, 11–27. doi:10.1163/156853982X00544
- Rudolph, R. (1992). *Platycypha caligata (Platycyphidae) – Fortpflanzungsverhalten. Publikationen zu wissenschaftlichen Filmen, Sektion Biologie*, *21*, 77–86 (Sonderdruck zu Film E 3011 in Encyclopaedia cinematographica Göttingen).
- Rudolph, R. (1993). *Balz- und Territorialverhalten zweier syntoper Libellenarten, Platycypha caligata und Platycypha fitzsimonsi*. [VHS-Video mit Kommentar]. Institut für Wissenschaftlichen Film Göttingen.
- Rüppell, G. (1989). Kinematic analysis of symmetrical flight manoeuvres of Odonata. *Journal of Experimental Biology*, *144*, 13–42.
- Serrano-Meneses, M. A., Sánchez-Rojas, G., & Córdoba-Aguilar, A. (2008). Sexual selection as the possible underlying force in calopterygid wing pigmentation: comparative evidence with *Hetaerina* and *Calopteryx* genera. *Odonatologica*, *37*, 221–233.
- Siva-Jothy, M. T. (1999). Male wing pigmentation may affect reproductive success via female choice in a calopterygid damselfly (Zygoptera). *Behaviour*, *136*, 1365–1377. doi:10.1163/156853999500776
- Svensson, E., & Waller, J. T. (2013). Ecology and sexual selection: evolution of wing pigmentation in calopterygid damselflies in relation to latitude, sexual dimorphism, and speciation. *The American Naturalist*, *82*, E174–95. doi:10.1086/673206
- Telford, S. R., Barnett, M., & Polakow, D. A. (1996). The functional significance of tibial displays in the damselfly *Platycypha caligata* (Selys) (Odonata: Chlorocyphidae). *Journal of Insect Behavior*, *9*, 835–839. doi:10.1007/BF02213559
- Thompson, D. J. (2000). On the biology of the damselfly *Vestalis amabilis*, Liefwinck (Odonata: Calopterygidae) in Borneo. *International Journal of Odonatology*, *3*, 179–190. DOI:10.1080/13887890.2000.9748150
- Tsubaki, Y., Samejima, Y., & Siva-Jothy, M. T. (2010). Damselfly females prefer hot males: higher courtship success in males in sunspots. *Behavioral Ecology and Sociobiology*, *64*, 1547–1554. doi:10.1007/s00265-010-0968-2