

Reproductive behaviour and the system of signalling in *Neurobasis chinensis* (Odonata, Calopterygidae) – a kinematic analysis

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The reproductive behaviour of the damselfly *Neurobasis chinensis* (Calopterygidae) was filmed at 300 and 600 frames per second in Thailand in spring 2009. This was subsequently viewed in slow motion for detailed analysis. Altogether we observed 26 matings at two different sites. Besides visual observations of behaviour of male–female encounters at the reproductive sites, we analysed their flight cinematographically by measuring velocity, wing beat frequency, phase relationships of fore- and hind wings, and described the flight paths of different flight manoeuvres. Wing clapping by the perched insects was analysed in detail. Also filmed were alternative reproductive behaviour and avoidance behaviour when attacked by a hunting spider. By analysing the video footage in slow motion, details of male flight with hind wings held motionless, a typical flight-style for this genus, were revealed. The significance of this behaviour in interactions with conspecifics is discussed.

Keywords: reproductive behaviour; Calopterygidae; *Neurobasis chinensis*; Thailand; flight kinematics; high-speed videography

Introduction

The behaviour of the genus *Neurobasis* has thus far been incompletely studied. An overview of existing knowledge of all *Neurobasis* species by Orr and Hämäläinen (2007) is significant for the gaps it reveals in our knowledge. The species for which reproductive behaviour is best understood is *Neurobasis kaupi* Brauer, 1867 from Sulawesi (Günther, 2006, 2008). Among other species *Neurobasis chinensis* (Linnaeus, 1758) was initially studied by Furtado (1966) in Malaysia and Kumar and Prasad (1977) in India. Moreover, anecdotal descriptions of the behaviour of this and other species have been published by e.g. Fraser (1934), Lieftinck (1934), Orr (2003) and Günther (2008). Orr and Hämäläinen (2007) described *Neurobasis* behaviour mostly based on visual observations and standard 24 fps video footage.

Due to the lack of high-speed cinematography with a sufficient temporal resolution no previous study has been able to analyse the behaviour in detail. Most actions in dragonfly behaviour are very rapid. Many flight movements, especially wing movements, are invisible to the naked eye. With the advent of light, relatively cheap, digital high-speed video cameras it is now possible to

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document rapid behaviour of relatively long duration (Hilfert-Rüppell & Rüppell, 2013; Rüppell & Hilfert-Rüppell, 2009a, 2009b), even in species living in logistically difficult tropical habitats. Thus we are able to demonstrate the possibilities of this new technology on field studies of *Neurobasis chinensis* in Thailand.

The reproductive system of all Calopterygidae thus studied is resource defending promiscuity (Corbet, 2004; Córdoba-Aguilar & Cordero Rivera, 2005; Emlen & Oring, 1977; Hilfert-Rüppell, 2004; Meek & Hermann, 1990). The males fight for territories and employ specialized flight behaviour in their defence (Rüppell, 1985). Furthermore they exhibit species specific courtship flight (Anders & Rüppell, 1997). In both agonistic and courtship flight the wing ornaments are displayed and probably serve together with the flight pattern itself as quality markers which determine the decision of a rival male to leave or to continue threatening flight (Hilfert-Rüppell & Rüppell, 2013) or for a female to accept a male as a mate (Waage, 1984).

In males of the genus *Calopteryx* all four wings are mostly coloured, whereas in *Neurobasis* males only the hind wings have shining metallic green and/or blue ornamentation. In many interactions involving other males or a male and a female the male ceases to beat these coloured hind wings and holds them outstretched and stationary (Fraser, 1934; Günther, 2008; Lieftinck, 1934; Orr, 2003). One major aim of this study was to investigate the influence of reduced hind wing motion on the kinematics of the forewings and on the flight pattern overall, and how this relates to the reproductive behaviour of this species. Our hypothesis was that *Neurobasis* exhibits a flight suitable for an optimal signal presentation in adaptation to different behavioural needs. Therefore the flight of the males is expected to be highly variable as described for other species with coloured wings (Hilfert-Rüppell & Rüppell, 2013).

Material and methods

Study area

Observations were made at two sites in the adjacent forest areas of Khao Sok National Park (Surat Thani province) and Sri Phang Nga (Phangnga province) in southern Thailand:

- (1) Sok River, Khao Sok National Park, 08°54'44.10" N, 98°30'45.10" E

The fast flowing, clear stream averaged about 10 m in width with a substrate dominated by large stones and rocks of which 10–20% were emergent. Vegetation was mostly absent in the stream except for some *Homonoia riparia* scrub on dry gravel bars. The banks were mostly covered by dense secondary forest. The observation site was a 17 m section with aberrant vegetation on the left (northern) bank. The mostly treeless bank was fully exposed to the sun throughout the observation time in contrast to the mostly shaded bank on the opposite side. The observation site was dominated by a tall grass species with floating rhizomes, the only submerged vegetation in the stream section.

- (2) Tamnang Stream just above outlet of the stream from Ton Ton Toei Waterfall, Sri Phang Nga National Park, 08°59'52.6" N, 98°27'39.4"

Below Tamnang waterfall the stream was 4–8 m wide and mostly shaded by overhanging vegetation. At the study site the stream was sunny due to an opening of the canopy caused by the incoming stream from Ton Ton Toei Waterfall. The depth was less than 50 cm with a stony substrate. The bank was mainly vegetated with low shrubs and long grass.

Both observation sites were characterized by a wide range of potential oviposition sites, such sites being generally scarce along both streams.

On most observation days reproductive behaviour ceased due to heavy rainfall about 16:00 h solar time.

Subject of study and methods

The metalwing demoiselle *Neurobasis chinensis* is widely distributed from Pakistan in the north-west to Peninsular Malaysia and Sumatra in the south-east. Over this huge range the species is subject to considerable geographic variation (Orr & Hämäläinen, 2007).

The Thai populations, subject of this study, are considered typical of the species (Hämäläinen & Pinratana, 1999). In a pilot survey the behaviour of *N. chinensis* was observed by AG in March 2008 on four field days at the Sok River site. There the behaviour was monitored from morning, when the males arrived at their territories, until late afternoon, when reproduction activities ceased. Some behavioural elements were documented by photographs with a Canon EOS 40D camera (Canon Inc., Tokyo, Japan).

In 2009 we observed and filmed the behaviour for 4 days at the Sok river site and for 7 days at the Tamnang Stream in March and April. We used three Casio EX-F1 cameras (Casio Computer Co., Tokyo, Japan). These cameras are able to film at 300 and 600 fps with sufficient resolution for kinematic analysis. Equally important, with the EX-F1 it was possible to film at high speed for several minutes without a break. In all cases we sat in the stream motionless at a distance of 1–5 metres from the insects. The cameras were pre-focused to the flight area of the dragonflies and were moved manually to track their flight while maintaining focus.

We measured the body lengths of seven captured specimens with millimetre graduated graph paper and wing areas using Adobe Photoshop version 5.0 LE (Adobe Systems Inc., San Jose, CA, USA). To analyse the films we used QuickTime Player version 7.7.1 (Apple Inc., Cupertino, CA, USA). To obtain the wing beat frequencies we counted sequential frames, if possible separated into downstroke, upstroke and wing beat pauses. To minimize errors some problematic clips 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. Flight velocities were obtained by measuring the shift of an individual's image on an overhead transparency placed on the screen of the computer (Asus Essentio CM 6730-DEMM 19 SILE, ASUSTeK Computer Inc., Taipei, Taiwan). When the camera was moved, structures near the flying insects were drawn on the overhead transparency and were covered by these structures on the video frames when measuring the dragonfly's body displacement. Wing stroke angles (i.e. the angle described by the wing in a single beat) were calculated only when the dragonflies flew orthogonally to the direction of filming.

To analyse the data we used IBM SPSS statistics 20 (IBM, New York, USA). After confirming the data were non-normal, nonparametric Mann–Whitney U-tests and a Wilcoxon test were used to compare means of different displays.

Results

General behaviour

In the early morning we found numerous individuals of both sexes foraging in loose aggregations at parts of the streams without covering vegetation and lacking oviposition sites. In those sections subsequent territorial behaviour was rare. A few males were already foraging in sections where territories were later established. From 08:30 h to 10:30 h solar time most of the mature males established territories at our observation sites. They defended sections of the stream with potential oviposition sites especially those containing floating plant shoots or roots. On a stretch of bank 17 m long at Khao Sok River five males maintained territories, two of them being only peripheral sites. Three other males perched on rocks in the middle of the stream without plants, launching territorial disputes from there, mostly into neighbouring territories. Most of the foraging females started from perches in the bank vegetation in the early morning. They preferred certain perches

and defended these sites even against territorial males. From about 10:00 h solar time females approached near the territories of the males but they were unresponsive to courting males.

Territorial males showed a variety of behaviour: patrol flight, wing clapping, threat display while perching, threat display in flight including long distance pursuing flight, wave shaped pursuing flight, and circling flight. No physical fighting could be observed. On all observation days the activity decreased during the hottest part of the day between 11:00 h and 12:30 h solar time.

Patrol flights

Males regularly performed characteristic patrol flights around the potential oviposition site and as far as the outer boundaries of their territories. In this flight style the males flew through and around their territory near to the water's surface. They only stroked the forewings at full amplitude. The hind wings were spread and moved only at very low stroke angles of about 10–30°. Doing this asymmetrically resulted in slight turns directing the flight path to one side so that the insect yawed and rolled slightly back and forth as the action was performed alternately on one side then the other. In a single action the hind wing leading into the turn/yaw was stroked at angles three to four times as great as the other. In the final strokes it assumed a high angle of attack. This led to banking and turning to the other side, where the process began in reverse, resulting in a yawing flight path for short distances. The beat frequency of all wings was about 20 Hz.

Wing clapping of territorial males with and without females

Territory owners perched on stones and overhanging vegetation mostly 0.1–0.3 m above the water, typically alighting on vegetation higher on the bank after disturbances. They engaged in wing clapping; i.e. brief synchronized flashings of their wings. They opened their hind wings so they formed an angle of 160–190° relative to each other (median 182°, $n = 16$). The hind wing surface was parallel to the ground when firstly opened and from this position they were canted backwards at up to 70° to the ground. The hyaline forewings were opened always with a short delay (0.06–0.17 s, median 0.11 s, $n = 16$), up to an angle of about 40° and then immediately closed without a visible pause. This wing clapping was also exhibited after pairing while the male guarded his ovipositing female. We compared this behaviour between territorial males without a female and guarding males. The durations of wing clapping of guarding males ($n = 19$) were significantly longer than those of single males ($n = 10$) (Mann–Whitney (Wilcoxon) W-test: $W = 85.5$, $p = 0.001$) (Figure 1). The duration of hind wing opening for territorial males without a female was 0.20–0.31 s (average 0.25 s, median 0.26 s, $n = 10$), that of guarding males was 0.28–0.35 s (average 0.32, median 0.33, $n = 9$). The wings were shut much more rapidly than they were opened, range 0.05–0.13 s, average 0.08 s, median 0.07 s and there was no significant difference between single and guarding males.

Guarding males perched in front of the female regularly performed a behaviour somewhat intermediate between wing clapping and courtship display. The males opened their hind wings partially (about 50–70°) or nearly totally (about 150°) for several seconds keeping them motionless (Figure 2). In these cases the tip of the abdomen was commonly turned sharply upward.

Threatening behaviour of perched males

Another form of wing clapping behaviour of perched males was directed against intruding males. The territorial male raised up his abdomen during clapping. Sometimes the approach of an intruding male released this behaviour at a distance of more than 5 m. If the perched male was threatened by the intruder at short range (less than 2 m), he raised his body nearly vertically, turning the tip

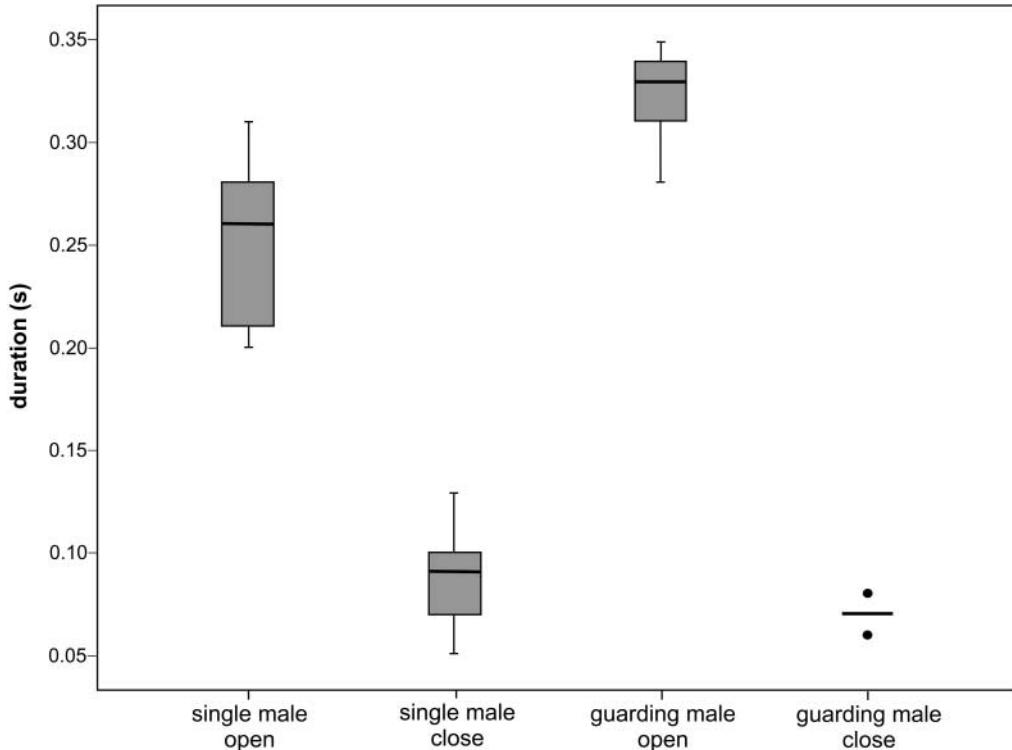


Figure 1. Duration of wing clapping of single territorial *Neurobasis chinensis* males (left, $n = 10$) and of guarding males facing the ovipositing female (right, $n = 9$). For each case the duration of opening and turning of the hind wings and the duration of closing of the hind wings is shown. Bars include 50% of each dataset, 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.

of the abdomen downwards (Figure 3). Always the hind wings were opened between 120° and 180° and aligned so their upper surfaces were facing the rival. Meanwhile they were twisted back and forth (up to 45°) around an axis approximated by the leading edge and were simultaneously waved up and down from the wing base at an amplitude of $ca 5-10^\circ$ (max 20°) with a frequency of 19–25 Hz (average 23 Hz, median 23 Hz, $n = 20$). The sum of these motions could lead to a rotating wing beat with very low amplitude (less than 10 mm). In the case of sustained attacks by an intruder the perched male started to beat the hind wings more intensely while the wings were twisted back and forth. If that threat display was unsuccessful in repelling the intruder, the territorial male finally flew up to engage him in an aerial contest. We never observed a fight with physical contact between the males. We had the impression that the propensity of perched males to ignore intruders was much higher in the afternoon when reproductive behaviour had ended.

Conspecific agonistic behaviour

Pursuing flight. Males contesting territory flew long distances, up to 10 m parallel to the bank, back and forth, sometimes for some minutes, pursuing each other at high velocities (Figure 4). They never clashed together but performed sharp turns to escape the pursuer. The males often held their four wings still, sometimes partly open and then pointing backwards. When these pauses were prolonged and performed regularly the damselflies lost height and a wave like flight path resulted. This flight type followed a regular pattern: after two wing beats a long pause followed



Figure 2. Motionless wing display by a perched *Neurobasis chinensis* male facing a female – Khao Sok National Park, Thailand, 19 March 2008. Photo by AG.

(Figure 5). The first wing beat after each pause was done at a low stroke angles of about $80\text{--}90^\circ$ without clapping the wings together at the end of the upstroke, so the wing surface was more visible to the pursuer. The second half of the down-stroke of the following wing beat employed a high angle of attack. This compensated for the loss of height of some centimetres at each pause in beating. The forewings were clapped together before the hind wings, the shining surfaces of which were thus presented longer to the opponent. This delay between fore- and hind wings was brief at the first down stroke after the pause (about 0.005 s), but prolonged at the end of the second down stroke before the next pause in beating (about 0.03 s).

In other cases the males pursued each other with spread hind wings banking periodically around the axis of flight. By this action a slight rolling movement resulted. The wings were displaced around $30\text{--}40^\circ$ from the horizontal. Forewings and hind wings in this type of pursuing flight were in phase, but the stroke angles were quite different: those of the hind wings were only a fraction of those of the forewings. When clapping together the forewings were held stationary in a backward position and the hind wings were sometimes not spread (Figure 6c). Each hind wing in the lower position was stroked at higher amplitude (about $20\text{--}30^\circ$) than the one in the upper position (about $5\text{--}10^\circ$).

Circling flight. Sometimes pursuing flight with spread hind wings escalated into a circling flight. The males flew around each other in a circle with a diameter of about 15–30 cm. They flew in a banked position with the hind wings about $80\text{--}90^\circ$ to the horizontal, their uppersides presented inwards. Although the wings were standing nearly vertically the head was always maintained in a

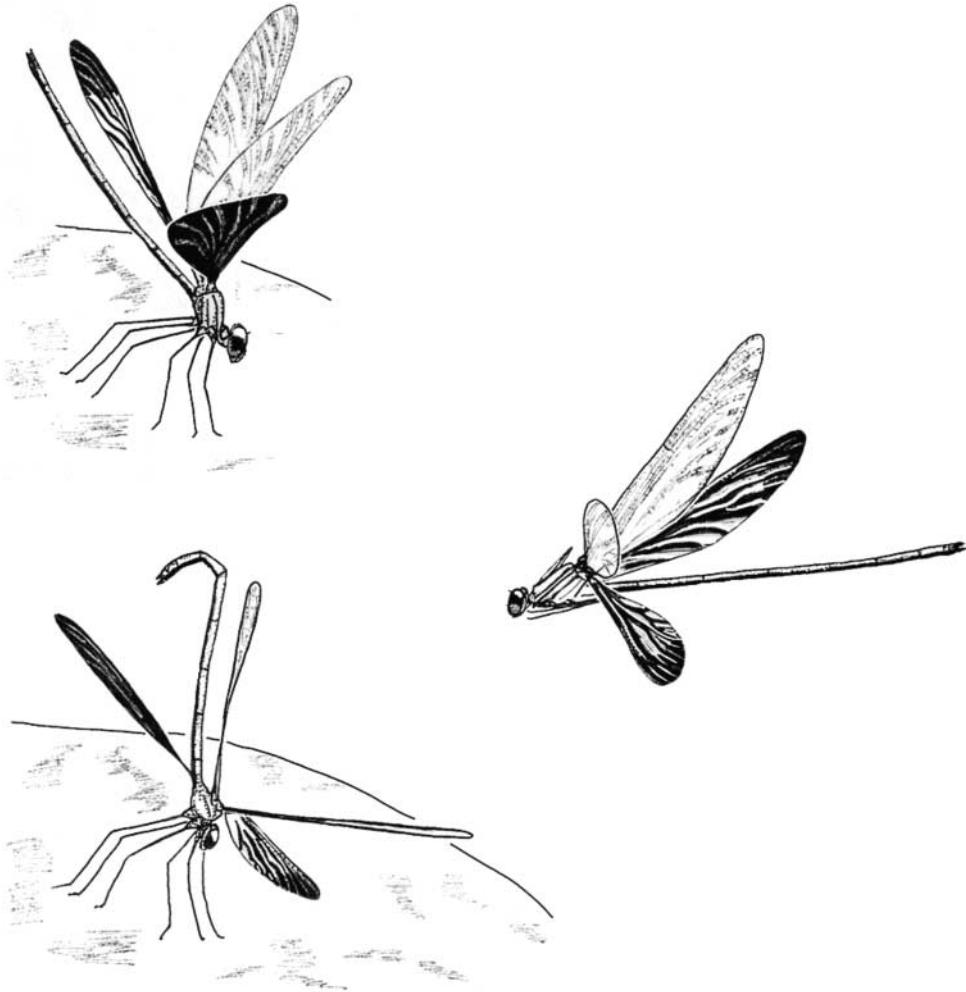


Figure 3. Threatening behaviour of a perched male of *Neurobasis chinensis*. Initial phase as a rival approaches (above) and subsequent threatening posture (two stages of the same event, drawn by GR after slow motion video) – Sri Phang Nga National Park, Thailand, 8 April 2009.

horizontal position, so the transverse axes of head and wings stood nearly at right angles to each other. The damselflies pursued each other by flying mainly with the forewings and flapping the hind wings only at small stroke angles, only little greater than those described for pursuing flight with spread wings. The down strokes now were directed to the outer side of the turn, the upstrokes to the inner side. The turning velocity was a high 3.2 circles a second. In one case the total number of uninterrupted circles was eight circles, then, after a short break the males flew forwards and then another eight circles followed. Another pair circled each other 14 times. Each circle was completed in six ($n = 11$), 7 ($n = 16$) or eight ($n = 10$) wing strokes. As circling progressed the diameter of the circles increased until the cycle ended and forward pursuing commenced. Escalated circling flights were sometimes interrupted by a single ascending flight up to about 8–10 m.

Male–male agonistic behaviour was most intense when the females appeared near the territories.

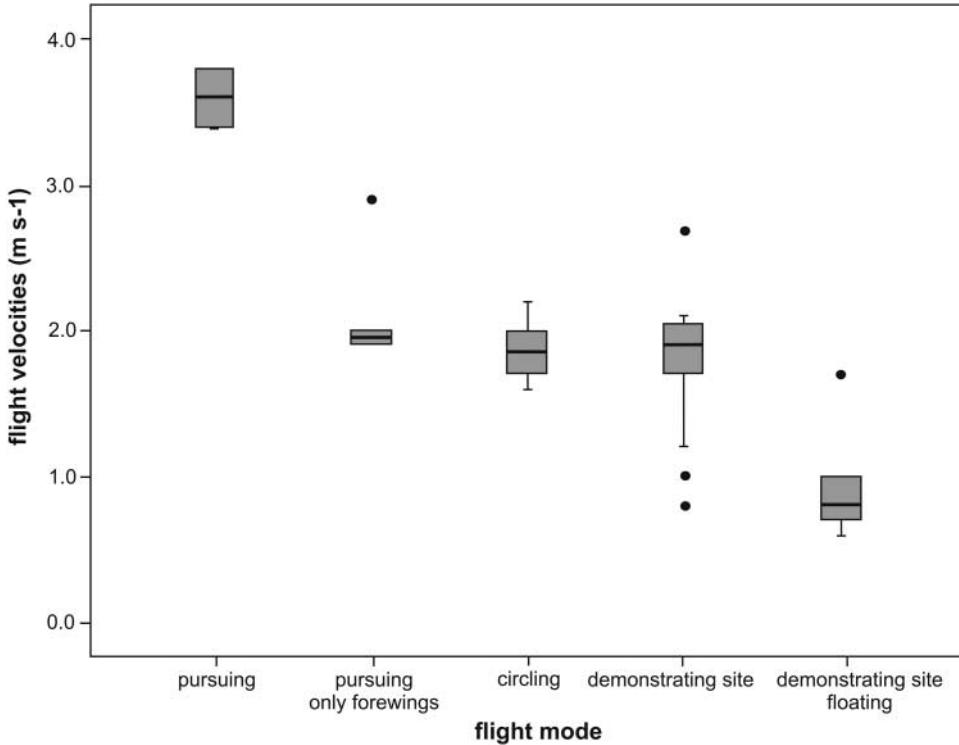


Figure 4. Flight velocities of *Neurobasis chinensis* males in male–male interactions (pursuing another male ($n = 4$), pursuing stroking fore wings only (fw) ($n = 6$), circling around another male, ($n = 14$)) and in male–female interactions (flight demonstrating oviposition site ($n = 16$), beating wings while floating on the water and demonstrating site ($n = 5$)). Graph symbols as in Figure 1. The small filled circles are outliers.

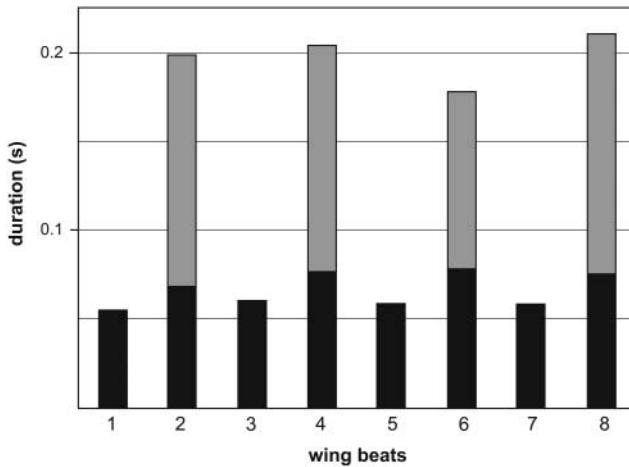


Figure 5. Wave-like pursuing flight of a leading male of *Neurobasis chinensis*: timing of successive wing beats (1–8), showing duration of strokes (black) and of pauses in beating (grey) at each second stroke. The strokes with beating pauses (at the end of each upstroke) are about three times longer than the others. Ordinate: duration of each action in seconds.

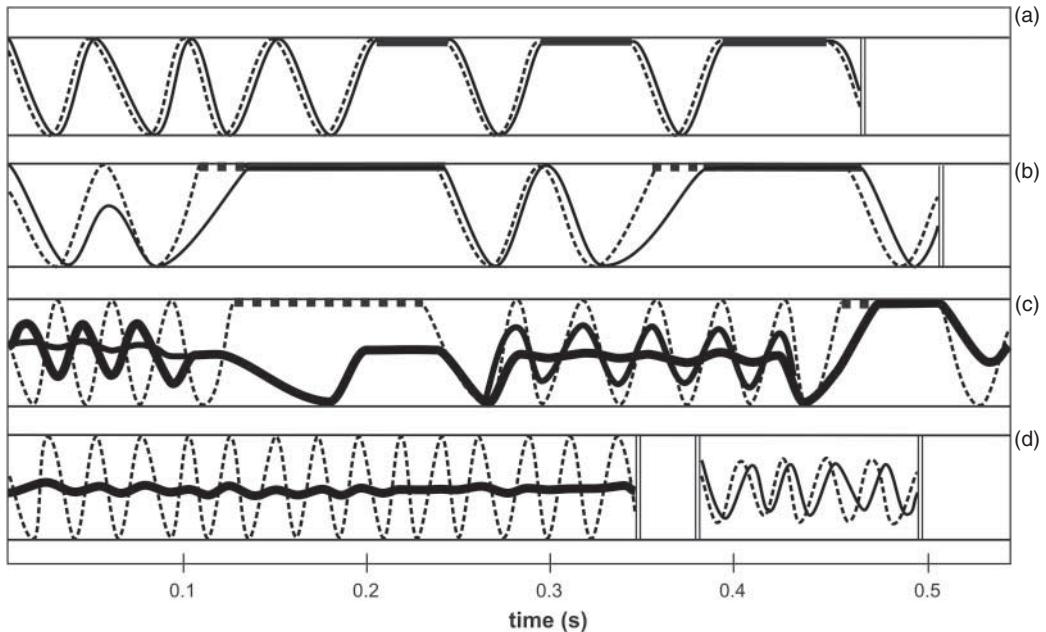


Figure 6. Course of the wings of males of *Neurobasis chinensis* during different flight styles (from left to right). Forewings: broken lines, hind wings: unbroken lines. Lines going downwards = down strokes, lines going upwards = up strokes. Horizontal, thick lines indicate that the wings stood still or were beaten only a little (at the top means at the end of the upstroke, in the middle means at the middle of a stroke). The greater the amplitude of these lines the wider the stroke angles. Abscissa indicates time in seconds. (a) Fast male-male pursuing flight. After three wing beats while turning, the leading male showed pauses in beating with wings held stationary in an upwards position (horizontal black lines) during straight forward flight. (b) Wavelike male-male pursuing flight. The leading male retarded the closing of the hind wings at the end of upstrokes before pausing with all wings in an upwards position. (c) Male-male pursuing flight with hind wings spread. The pursuing male was turning slightly to the right side. The right hind wing (thick solid line) tilted lower was stroked at a greater amplitude than the left (thin solid line). Thereafter the forewings were held still and both hind wings were stroked up to only half of the full wing stroke amplitude (black solid lines). After that the male turned to the left side. Then both forewings were stroked again with maximum amplitude, the left hind wing was stroked through an intermediate angle and the right hind wing was held nearly still. Finally all four wings made a beating pause (all lines up). (d) Left: Male showing the oviposition site flying with spread hind wings which then were held nearly motionless, the forewings beating at maximum amplitude. Right: Courtship flight with high stroke frequencies and small stroke angles (the hind wings were stroked through a slightly smaller angle).

Male-female interactions

Flying females regularly released courtship behaviour in territorial males. This consisted of display flights with outspread hind wings leading the female to the oviposition site and, in cases when the female was perching nearby, of short courting flights in front of her. If a male discovered a newly arrived female he usually flew immediately in front of her, displaying the upper sides of his hind wings. Sometimes he circled around her and demonstrated the oviposition site with wide-spread motionless hind wings. Mostly, when courted, the female followed the male. Initially the female flew besides and behind the male following him to the oviposition site, then they generally flew several circuits of the area, perched on potential oviposition substrate and tested it with the ovipositor. During this behaviour the male followed the female. In all cases of observed matings the females perched nearby after testing the oviposition substrate.

During courtship, which we were only able to film twice, the male approached slowly and steadily while executing a low amplitude high-frequency flight mode. The males stroked their wings through small angles, those of the forewings a little wider than those of the hind wings. The wing beat frequency then was high, up to 50 Hz (Figure 7).

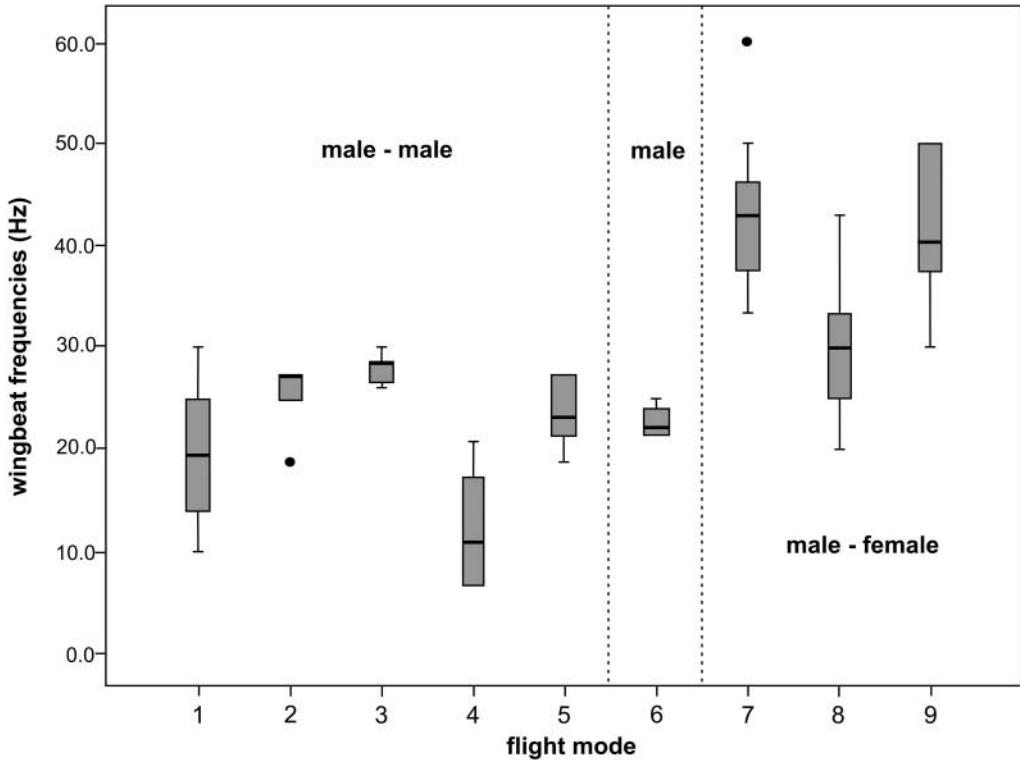


Figure 7. Stroke frequencies of the forewings of *Neurobasis chinensis* males. Flights together with other males: 1, fast pursuing flight ($n = 49$, wing beats); 2, pursuing flight with spread hind wings motionless ($n = 9$); 3, pursuing flight without pauses in stroking ($n = 8$); 4, wavelike flight with periodic pauses in stroking resulting in loss of height ($n = 8$); 5, circling flight ($n = 14$); 6, male flying through territory alone, female not visible ($n = 8$); 7, demonstrating oviposition site, female visible ($n = 74$); 8, demonstrating oviposition site to female at very low velocity or hovering ($n = 28$); 9, courtship flight ($n = 8$). Graphical explanations as in Figure 1 (the small filled circles are outliers).

If the female remained quiescent, the male executed a quick turn above her, lowered himself and grasped her prothorax with his anal appendages thus forming a tandem. He usually carried the female some metres away where the pair formed the copulation wheel. We never saw males grasping females without first landing on their wings.

Our account is based on the observation of 14 matings in 2008 and 12 matings in 2009. Of a total of 26 observed matings only two were before noon. On all observation days it became cloudy about noon, sometimes with short showers. In the early afternoon this was sometimes followed by another sunny period. Then most of the females flew to potential oviposition sites.

Overall copulation duration was 174–304 s (mean 229 s, median 210 s; $n = 15$). The longest copulations involved a change of perching site caused by disturbance from other males or gusts of wind. The pair could fly and change perch without disrupting the wheel but usually they flew in tandem. When they separated, both partners flew up and perched nearby for a short time. If the female took off after this short rest, the male again flew before her with hind wings displayed, leading her rather rapidly back to the oviposition site. The male hovered just above the water surface, while the female searched a place to oviposit (Figure 8a). Sometimes the male perched on floating plants with hind wings displayed and also the tip of his abdomen turned upward in display (Figure 8b).

If the female had located a site and begun ovipositing, the male initially perched nearby with intense wing clapping behaviour. Rivals were always chased. Later the male performed



Figure 8. Presentation of oviposition site after copulation by *Neurobasis chinensis*. (a) The male is floating with spread wings, producing small ripples. (b) A different male settled on the water with outstretched hind wings being inspected by the female. Khao Sok National Park, Thailand, 23 March 2008 (a) and 19 March 2008 (b). Photos by AG.

non-contact guarding flights, periodically hovering above the ovipositing female, displaying his hind wings. In 2008 the postcopulatory behaviour was studied in 14 cases (Figure 9). In eight cases the female was guarded by the male at least initially during oviposition. But harassment by non-territorial males or territorial neighbours led to unguarded oviposition of females outside of the territories at least in two cases.

Oviposition took place into plant shoots or roots either submerged or floating on the water surface. Often the female could oviposit from a perch above the water surface with only part of her abdomen submerged but sometimes they oviposited with thorax and even wings partially submerged. If floating plants bearing ovipositing females were carefully pushed under water by

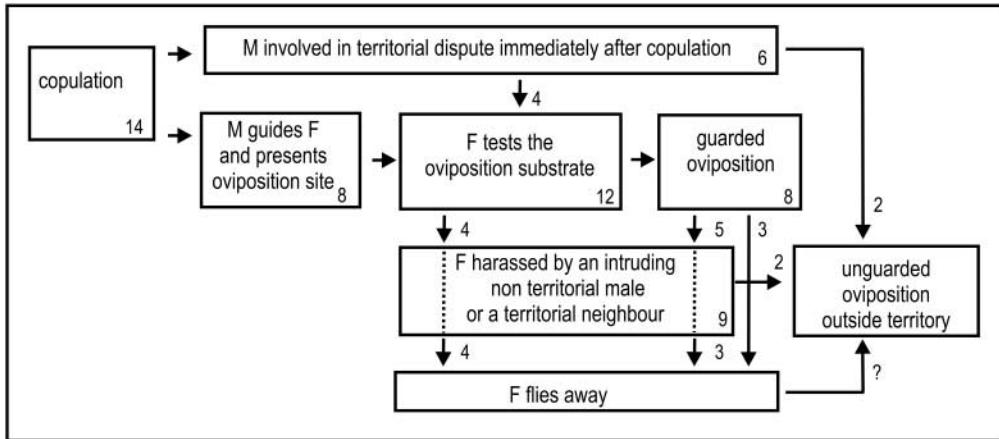


Figure 9. Postcopulatory behaviour of *Neurobasis chinensis*. The numbers represent the number of observed cases ($n = 14$ completely recorded matings in 2008). Khao Sok National Park, Thailand, March 2008.

the observer, the females remained until their wings were totally submerged. At this point they concluded oviposition within less than 10 s ($n = 5$) and flew away.

Spider attack during demonstration of the oviposition site

On one occasion when the male, with hind wings nearly motionless, followed the female near to the oviposition site a spider was lurking. After the male settled for a while about 30 cm from the spider, the damselflies flew in a wide arc and passed its perch (Figure 10). The spider jumped over a distance of 22 cm and 0.016 s before the male was directly in front of it, but it under-compensated, its trajectory intersecting the flight path of the damselfly male 0.1 s after he had passed and 0.36 s after the female, which was leading the pair. The female was 0.16 s earlier at this potential ambush point than the male. After the spider's attack the flight velocities of both increased. The distances covered by single wing strokes increased, too. The males exhibited nearly three times as many wing beats (of the forewings only) in the same time as the females, which means that their stroke frequency was nearly three times as high as that of the female. The lower wing beat frequencies in the lower drawing result from the gliding periods of the female and the male engaging the hind wings, although at low amplitudes, to the stroking of the forewings immediately after the attack.

Alternative reproductive behaviour

Three cases of alternative mating behaviour by males without courtship were observed and filmed. Twice a male headed for a perched female and tried to grasp her, but the female flew away, the event lasting about 1 s on each occasion. Once the action lasted more than 5 s (Figure 11). A male tried to grasp an ovipositing female, but she successfully escaped. In this case the male landed on the wings of the female and crawled downwards and tried to couple (Figure 11, left, above). The female very suddenly and simultaneously beat all four wings downward (3 s after the male made contact, lasting only 0.04 s), striking the male (Figure 11, right, above). She lifted her body and then fell down. The next time when she lifted her body, carrying the male, her right hind wing was bent down sharply at the nodus (right, middle). She then shook the male off by falling and beating her hind wings simultaneously upwards with a velocity (measured at wing tip) of 2.6 m s^{-1} (right, bottom). This mating attempt by the male lasted 4.13 s. Shortly (about 1 s) after

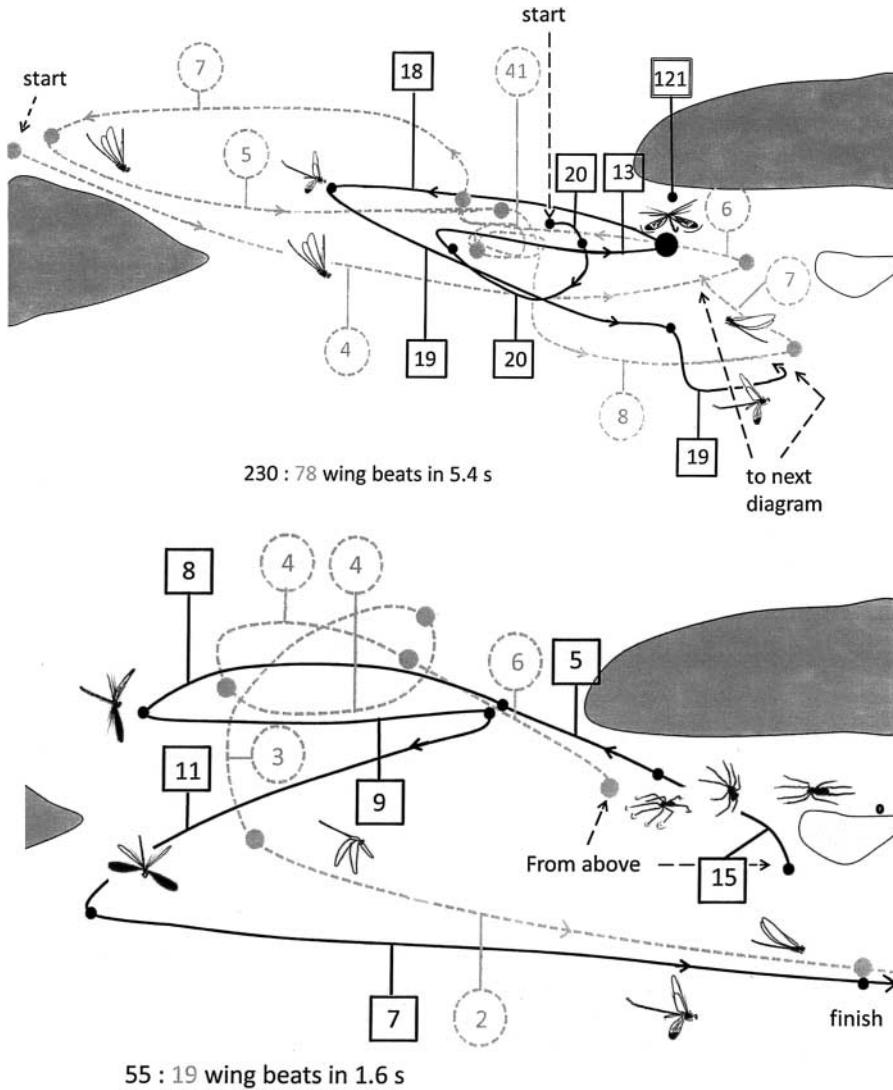


Figure 10. *Neurobasis chinensis* – spider attack while male was demonstrating the oviposition site. The flight paths of the female (grey broken lines with grey circles), and the following male (black lines with black circles) is divided into two continuous parts: The upper diagram shows undisturbed flight (duration 5.4 s with 230 male and 78 female wing beats), the lower one, following in sequence from the upper, their flight paths following a spider attack (duration 1.6 s with 55 male and 19 female wing beats). Numbers indicate the number of wing beats from one circle to the next by female (in broken circles) and male (in solid squares). The female (leading) and the male had passed the trajectory of the spider's jump before it reached them. The schematic drawings of damselflies show the female with clear wings and the male with dark hindwing underside or dark wingtips above. Khao Sok National Park, Thailand, 5 April 2009 (drawn from 600 fps video).

the male departed she took off as well. She then beat those wings which were free of the water nine times until she finally lifted herself into the air.

Comparisons of flight kinematics

The movements of forewings and hind wings can be characterized by the phase relationships of both wing pairs and their beating frequencies. Another important component of flight is overall velocity.



Figure 11. Alternative reproductive behaviour in *Neurobasis chinensis*. A male landed on the wings of a female, while she was ovipositing while perched about a cm deep in the water (above, left). She beat her wings down after 3 s and struck him with her right wings (above, right). Then she raised herself very suddenly (middle, right) twice and fell back to the water. On the second fall she beat her hind wings and shook him off (bottom, right). Sri Phang Nga National Park, Thailand, 8 April 2009 (drawn by GR after slow motion video).

Temporal patterns of wing beating

Pursuing males of *N. chinensis* showed a wide variety of phase relationships of the fore- and hind wings (Figure 6). The most regular form was seen when pursuing each other in fast forward flight over a distance of more than 8–10 metres. In this case the forewings and hind wings were mostly stroked in parallel, the forewings being a little earlier than the hind wings at the end of the upstroke. Wing beat pauses (when wings were briefly stationary) were made in a backward position at the end of upstrokes. In straight flight passages wing beat pauses took place at nearly every stroke. The pursuer made fewer wing pauses than the leading male: pursuer 34 pauses in 52 wing strokes (ratio 1:1.53), leading male 13 in 18 (ratio 1:1.38).

They lasted 54.9% of the pursuer's whole flight time ($n = 52$ strokes) and 85% of that of the leading male ($n = 18$ strokes, $p = 0.09$, U-test) being only a tendency of difference. In the same flight the leading male performed more pauses beating his wings at 15.4 Hz, while the pursuer was measured at 18.2 Hz ($p < 0.01$, U-test). As the distance between the two opponents decreased, and also when turning, the males stroked continuously without pauses, the stroke frequency reaching 25–33 Hz.

Context dependent wing beat frequency in males

The wing-beat frequencies in males during reproductive activity were variable, especially in male–male pursuing flights over long distances (Figure 7, mode 1, 4) and in male–female interactions (mode 7, 8, 9).

In many flight styles the hind wings were held motionless or were stroked only through small angles. However the forewings also differed considerably in their stroking frequencies. Males exhibited highest frequencies when a female was present. In short courtship flights we were able to film mean values of 41.9 Hz and in the much longer flights demonstrating oviposition sites mean values of 43.3 Hz. These values significantly differed from all others, as did the two low values of pursuing flight (1 in Figure 7) and vertical undulating pursuing flight (wavelike flight: 4 in Figure 7).

When a female arrived the male flight style was to spread his hind wings, holding them nearly motionless. The frequency of the forewing stroking changed depending on the flight path of the female. When the female flew in no particular direction at a distance of about 40–20 cm from the male the frequency of the his forewing strokes was between 25 and 27 Hz. When the female approached nearer or was first discovered closer to the male this frequency rose to between 37 and 42 Hz (Figure 10). Following the female in slow flight the male sometimes settled on the water and ceased beating his wings. When in this situation he brought his hind wings well forward and folded his forewings. He usually held this position for some seconds (Figure 8b).

Velocities of male flight

The flight velocities were highest in fast male–male pursuits. They reached $3.6 \text{ m}\cdot\text{s}^{-1}$ and were nearly twice as fast as in any other manoeuvre. The velocities of pursuing in forward flight, of circling and of flight while demonstrating the oviposition site (Figure 4) were all similar. The lowest velocities occurred when demonstrating the site while floating. The distance covered per single wing stroke in pursuing flight was also highest of all flight styles, reaching 15–18 cm. In contrast in circling flight only 5–8 cm were covered by one wing beat and only some millimetres to a few centimetres when demonstrating the oviposition site while floating.

Female flight

The flight of females was more uniform than that of males. The stroke angle was about $100\text{--}110^\circ$ in slow flight and hovering flight, beginning each down stroke with closed wings. When flying forward the wings were stroked regularly with pauses at the end of some upstrokes similar to the males' flight in fast pursuits.

On average the wing-beat frequencies of all investigated flights of females (18.5 ± 3.9 Hz) were only about half those of males (30.3 ± 12.5 Hz) and differed significantly (Mann–Whitney U-test, $p = 0.00$) (Figure 12).

In forward flight during pauses in stroking females covered distances up to 15 cm, depending on the length of the pause. The distance covered per wing beat could reach 8–12 cm when visiting

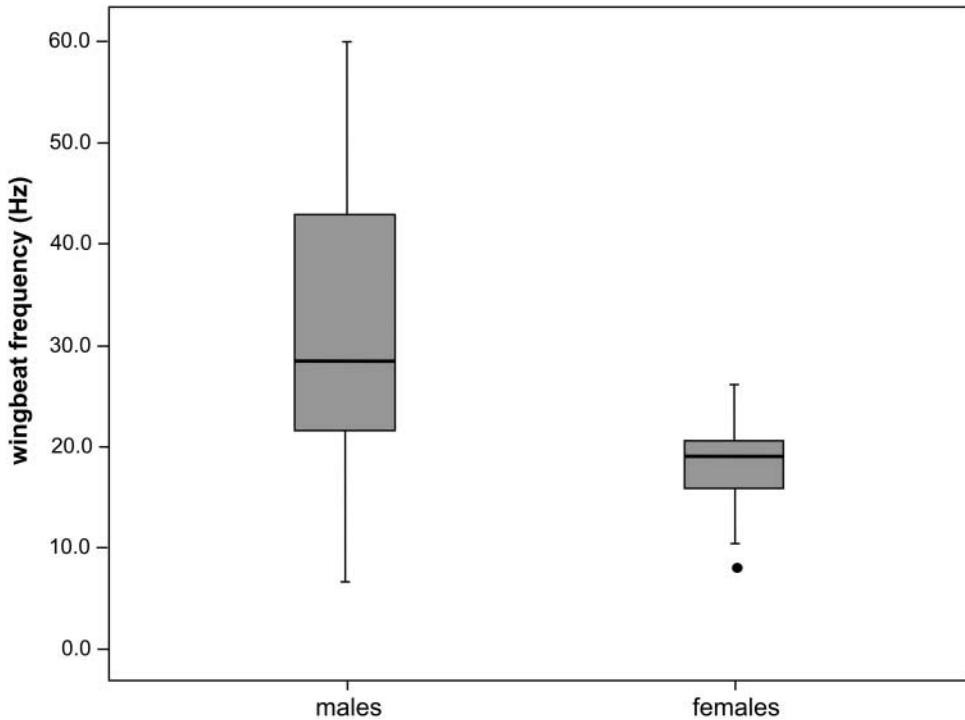


Figure 12. *Neurobasis chinensis* – comparison of the wing beat frequencies of all investigated flights of females (right, $n = 73$) and those of the males (in some cases only the frequency of the forewings, left, $n = 205$). Graph symbols as in Figure 1. The small filled circles are outliers.

a territory. Remarkably, when wing stroking was paused females lost height of only several millimetres to 1 cm.

When flying a curve, on the spot or shortly before landing no pauses were seen. The stroke frequencies then were higher than in forward flight. In backwards flight the wings were stroked less forward than in all other flight types and higher angles of attack were employed.

Discussion

The reproductive behaviour of *Neurobasis chinensis* showed broad similarities with other Calopterygidae (Córdoba-Aguilar & Cordero Rivera, 2005; Karjalainen & Hämäläinen, 2013). Several structures which may be important for communication in the metalwing demoiselles include body coloration and the ventral colour patch near the tip of the abdomen (variously termed “lantern” or “tail light”), but we consider in this paper only wing and flight movements during reproductive behaviour. All these specialized flight patterns of *N. chinensis* and those of other Calopterygidae (Córdoba-Aguilar & Cordero Rivera, 2005; Heymer, 1972; Pajunen, 1966; Rüppell, Hilfert-Rüppell, Rehfeldt, & Schütte, 2005) are normally only displayed in a territorial context and mostly in the presence of a conspecific and therefore must surely have a signalling function.

Kumar and Prasad (1977) stated for *N. chinensis* that “following coitus the male suddenly abandons the female and flies away” adding that “[In] this respect *N. chinensis* shows a different behaviour from the *Calopteryx* species, where the males lead the female to the selected ovipositional site”. Considering the territorial behaviour of the males and the widespread occurrence

of sperm displacement in the Calopterygidae (Córdoba-Aguilar, Uhía-Castro, & Cordero Rivera, 2003; Córdoba-Aguilar & Cordero-Rivera, 2005; Waage, 1979) these observations were difficult to explain. We were able to show that under undisturbed conditions the female was guarded by the male at least initially during oviposition. However harassment by non-territorial males or territorial neighbours could lead to unguarded oviposition outside the territory. The observations of Kumar and Prasad (1977) were based on only four observed matings under high population density. Possibly for these reasons they did not observe typical guarding behaviour.

The basic pattern of flight of *N. chinensis* is similar to that of other Calopterygidae, e.g. *Calopteryx splendens* (Rüppell, 1985, 1989). When covering distances, the males employ synchronous stroking of the two pairs of wings. This was punctuated by frequent short gliding phases with wings held still at the end of the upstroke. The gliding phases could perhaps serve as recovering pauses, similar to those shown in some song birds (Burton, 1990). During turning flight the wings were beaten always. Obviously the aerodynamic requirements of turning in flight do not permit pauses.

This basic flight pattern was always evident in *N. chinensis* females and sometimes in males pursuing each other, especially in straight flight. That aerodynamic needs play an important role in flight style was clear from the differences between pursued male and pursuer. The pursuer showed a higher stroke frequency and fewer pauses in beating. Probably this was because in keeping pace with the leading male he had to follow unexpected turns.

Continuous one-way turns lead to circling flight (“gyro-flight”; Günther, 2006). We also filmed such circling flight in *Calopteryx* species. In *C. splendens* the diameters of the circles were much wider (about 50–90 cm versus 15–30 cm in *N. chinensis*) but the flight velocity was similar (2.5 m s^{-1} in *C. splendens* and 1.8 m s^{-1} in *N. chinensis*). Males of *N. chinensis* could achieve more than three circles per second, twice the number observed in *C. splendens*, probably due to the longer flight path of their larger circle.

In pursuing flights the highest flight velocities were reached, indicating a real chase, probably to reject the competitor from the territory. In contrast the lowest flight velocities were seen when a male courted by guiding the female to an ovipositing site, obviously not to reject but to hold her in the territory, by presenting it, his wing ornaments and his flight performances.

The outstanding characteristic of most members of the genus *Neurobasis* is the broad area of shining metallic blue or green on the upperside of the hind wings (Karjalainen & Hämäläinen, 2013; Lieftinck, 1955; Orr & Hämäläinen, 2007). This upper surface was presented during wing clapping by perching males and in flight by special displays, different from other Calopterygidae. Wing clapping by males was common in territorial and guarding behaviour. It seems to function both as a declaration of territorial ownership, directed against intruding males or as a stronger signal used in the defence of a perch; it also serves as a signal performed in front of the ovipositing female presumably reassuring/reminding her that she is being guarded and perhaps reinforcing their bond. We found significant differences in the duration of opening the hind wings between single males and guarding males in front of their females. The wing clapping behaviour of *N. chinensis* (this study) and *N. kaupii* (Günther, 2006, 2008) was very similar to *Calopteryx splendens* and *Calopteryx virgo* (unpublished observations). But as a consequence of the wing coloration of *Neurobasis* only the hind wings were presented motionless to a rival or a mate, while in *Calopteryx* species all four coloured wings are shown together, sometimes also motionless. The specialized presentation of metallic coloured wing surfaces indicates that this behaviour most probably has a predominantly signalling function as already assumed for other Calopterygidae (Bick & Bick, 1978; Karjalainen & Hämäläinen, 2013; Miller, 1994). It is obvious that brilliantly coloured wings can amplify the signals. Other functions of wing clapping may be thermoregulation (Erickson & Reid, 1989; Miller, 1994; Rüppell, Hilfert-Rüppell, Rehfeldt, & Schütte, 2005) and ventilation to assist respiration (May, pers. comm., 1994, after Corbet, 2004). However in contrast to our own observations in *Calopteryx* species we could find no evidence for

such functions in *Neurobasis*. However these hypothesized functions could only be adequately resolved by laboratory experiments.

Threat display of perched males against intruders was described for *N. chinensis* (Günther, 2008; Orr & Hämäläinen, 2007). The slow motion analysis of this threat behaviour revealed that the hind wings are not shivering and opened and closed but stroked at very low amplitude and simultaneously twisted around the depressed leading edge, the sum of which movements is a rotatory oscillation. This threat display of perched males occurred very extensively at the end of daily reproductive periods. Although this behaviour was intense and dramatic it generally did not last long and it probably was more energy efficient for the resident male than rising to a prolonged threatening flight. The intruder may also have saved energy by flying with normal synchronous stroking of all four wings and not holding the hind wings still.

Flight with nearly stationary hind wings always occurred to some extent when competitors or females appeared in an occupied territory. When circling around each other the rivals continued to stroke the hind wings but through only small angles. This is the case, too, when pursuing each other in forward flight, which sometimes follows a winding flight path. Holding the wings nearly stationary, especially while the insect rolls and yaws slightly, probably conveys a visual signal of high intensity broadcast over the widest possible area. Periods during which only the forewings were held stationary, especially by the leading male, were filmed frequently in *C. splendens* (Rüppell, 1985) and also in *C. xanthostoma* (unpublished). The stationary posture of male hind wings in *N. chinensis* was displayed during slow pursuing flights with rivals. This became more intense in the presence of females when flight velocity dropped so that the hind wings could be displayed as long as possible at in their vicinity. Some signals might come from the undersides of the stationary hind wings as well as from their uppersides. These undersides are nearly black but reflect sparkling golden to the human eye. Although we cannot know how the damselflies interpret these undersides, their presentation in frontal encounters suggests they have some semiotic function, especially at close range (Figure 13). The importance of crypsis at a distance as a mechanism to reduce predation was discussed by Endler and Théry (1996). Based on studies of the courtship behaviour of forest-dwelling birds they found that flashing

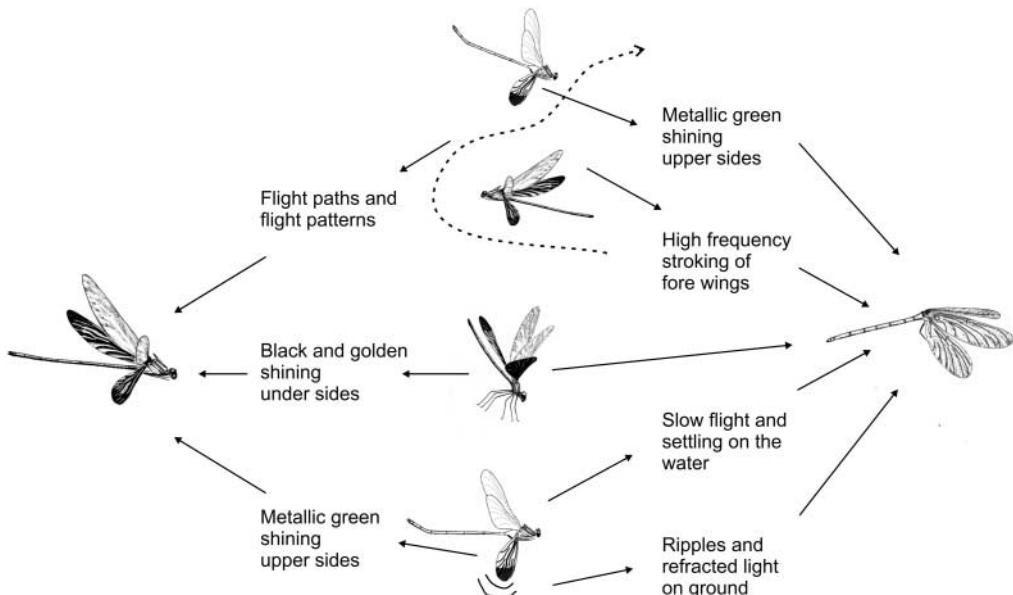


Figure 13. Hypothetical system of male signalling (middle) to other males (left) and to females (right) in *Neurobasis chinensis*. The signals are symbolized by arrows.

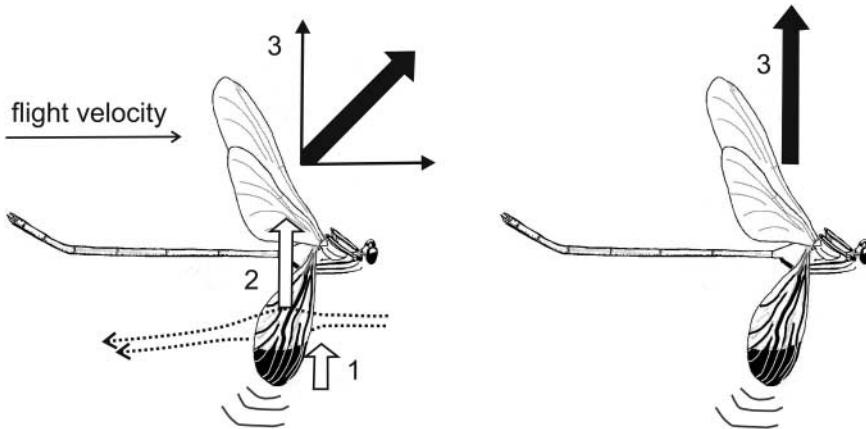


Figure 14. Hypothetical power production by a male *Neurobasis chinensis* demonstrating an oviposition site by flying with hind wings held stationary. When flying on the spot (right) the damselfly must exert more air pressure (thick black arrow) than in forward flight (left, thick black arrow). In forward flight the hind wings serve as air foils and produce additional lift (2). Furthermore in this flight situation the total lift is increased by an air cushion effect (1), caused by the small distance between hind wings and the water surface. In both cases the hind wing tips are touching the water (indicated by three curved lines at the hind wing tip) which might also provide some support. (3) represents lift produced by the beating forewings. Broken lines show the air stream around the hind wings caused by the forward motion. The horizontal thin arrow (in the left sketch) indicates the thrust component of the forewings beating.

(blue) metallic colour produced a very conspicuous visual signal under forest light conditions and most probably is effective in display. But it should be advantageous for a male to be “less conspicuous at other times when predation would be a relatively more important component of fitness” (Endler & Théry, 1996). Following this argument we might postulate that the restriction of the metallic green colour to the upper sides of the wings minimizes conspicuousness when no signal is necessary. However it is uncertain if this effect applies in the case of *Neurobasis*. Because of its strong silhouette a perched territorial *Neurobasis* male is not particularly cryptic, especially when viewed from a low aspect. We can only speculate if the dark under sides of the wings are helpful in avoiding predation, e.g. by birds hunting from perches in the overhanging vegetation, or if they result as part of an optimized cost-benefit developmental system. If the underside had the same laminar complex needed to produce the upper side colour, the wing mass and developmental costs would be greatly increased (A.G. Orr, pers. comm.).

When flying in different manoeuvres at different velocities, the frequency of the forewing stroking changed (Figure 6). Flying slowly the forewings alone must produce lift, because there is no significant air stream from forward flight flowing over the spread hind wings which could produce lift. In contrast when flying at speeds about 2 m s^{-1} through the territory the forward speed induces lift on the hind wings which then function as air foils (Figure 14).

It appears to be difficult to produce adequate lift using only the forewings in slow flight or hovering. In such situations males often touch the water’s surface with their hind wing tips, generating ripples. These, and perhaps the rippled, concentrated reflections from sunlight projected onto the substrate in clear shallow water and lensed by these wavelets, may well serve as additional optical stimuli advertising the presence of a powerful male. Even in this situation flight velocities around 1 m s^{-1} were reached.

Perhaps this forward progression while trailing the hind wing tips in the water serves to keep the body air borne and perhaps may give an additional signal. Other signals of the male to the female were also generated, unexpectedly, from the clear forewings. When a female arrived, males which were almost hovering increased their stroke frequency significantly (up to 43 Hz) and decreased it as she departed (down to 20 Hz) (Figure 15). This was obviously an effect of the approaching

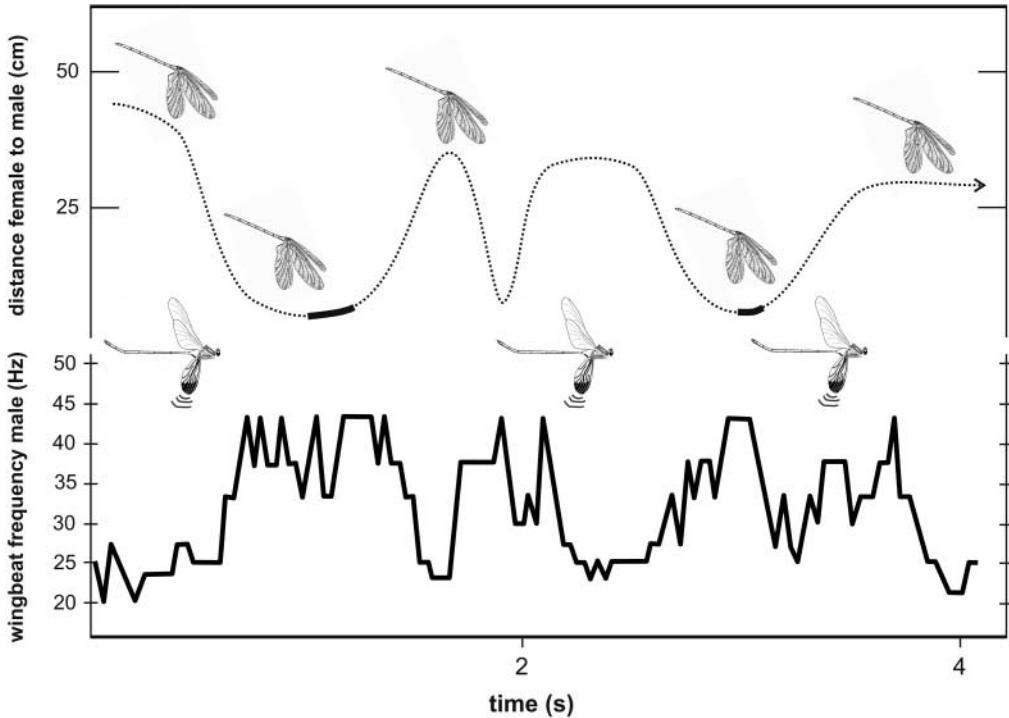


Figure 15. *Neurobasis chinensis* – Forewing stroke frequency of male flight during demonstration of the oviposition site depended on the proximity of the female. Upper diagram: position of the female (with clear wings), proximity of the female to the courting male (cm in the ordinate). When the female approached (broken line going downwards) the male increased the stroke frequency of his forewings, when the female retreated (line going up) the male decreased the frequency. Thick lines in the female path signify first and second female landing attempts on water. Bottom diagram: Changes of stroke frequencies (ordinate: Hz, continuous line drawn from connected values of the stroke frequencies, $n = 126$ wing strokes) of the forewings of the male (with dark hind wing tips) flying with hind wings held motionless; abscissa: time in seconds.

and departing female. The male probably demonstrated his power by maintaining a high stroke frequency for an extended period.

The high frequency wing strokes of about 43 Hz (wb s^{-1}) are similar to the values found in frontal courting flight of *N. chinensis* and other calopterygids, such as *C. splendens* and *C. virgo* (Rüppell, 1985, 1989). These are costly high energy actions. The next step of a signalling male was to float on the water while ceasing to beat all four wings and stretching the hind wings far forward, displaying the metallic uppersides optimally seen from the side and the dark undersides seen from the front.

The cost of all this stationary behaviour might be the risk of being caught by predators, and may also demonstrate to the female the absence of predators at this place. The reaction of the female following a spider attack (Figure 10) was to avoid the dangerous place, finally leaving the site, followed by the male. Departure of the female from the territory following attacks during courtship has been regularly observed in *Calopteryx* species (Hilfert-Rüppell, 2004) and in various Chlorocyphidae (Günther, 2008, and unpublished data).

The reduction of wing movement by the floating male may enable females to evaluate the quality of the hind wing iridescence. It may also be a way of saving energy while displaying to an already interested female, as well as demonstrating lack of predators. This might serve as a surrogate measure of male fitness as suggested by Günther (2008) and demonstrated for other Calopterygidae (Córdoba-Aguilar & Cordero Rivera, 2005; Siva-Jothy, 1999).

Thus the ornamentation, coupled with the quality of flight performances, may indicate to the female the quality of a male viewed as a potential mate.

Maintaining a stationary wing as a method to enhance the intensity of signalling by displaying wing ornaments has been found in other odonate species (Hilfert-Rüppell & Rüppell, 2013; Rüppell, 1985). This display is evidently a trade-off between aerodynamic needs and the benefits of strong sexual selection. For example Tsubaki, Samejima, and Siva-Jothy (2010) showed that in the calopterygid damselfly *Mnais costalis* females prefer males with high quality territories and intensive courtship display. Wing colour comes at a developmental and energetic cost: wings are heavier due to the multilayered cuticular diffraction system (Orr & Hämäläinen, 2007; Vukusic, Wootton, & Sables, 2004). The cost of wing colour was also demonstrated by Hooper, Tsubaki, and Siva-Jothy (1999) even in a pigment based system (*Mnais costalis*). If a costly, plastic secondary sexual trait and its presentation are correlated with the condition of the male, it is expected to provide reliable information about the male's fitness to the female. Thus it is a reasonable conclusion that the evolution of the elaborate ornamentation and complex display repertoire of *N. chinensis* males came about as a result of sexual selection.

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References

- Anders, U., & Rüppell, G. (1997). Zeitanalyse der Balzflüge europäischer Prachtlibellen-Arten zur Betrachtung ihrer Verwandtschaftsbeziehungen (Odonata: Calopterygidae). *Entomologica Generalis*, 21, 253–264.
- Bick, G. H., & Bick, J. C. (1978). The significance of wing clapping in Zygoptera. *Odonatologica*, 7, 5–9.
- Burton, R. (1990). *Birdflight. An illustrated study of birds' aerial mastery*. London: Eddison Sodd Editions.
- Corbet, P. S. (2004). *Dragonflies. Behaviour and ecology of Odonata* (rev. ed.). Great Horkelesley, Colchester, UK: Harley Books, Martins.
- 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., Uhía-Castro, E., & Cordero Rivera, A. (2003). Sperm competition in Odonata (Insecta): The evolution of female multiple mating and rivals' sperm displacement. *Journal of Zoology*, 261, 381–398. doi:10.1017/S0952836903004357
- Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, 197, 215–223. doi:10.1126/science.327542
- Endler, J. A., & Théry, M. (1996). Interacting effects of lek placement, display behaviour, ambient light, and color patterns in three Neotropical forest-dwelling birds. *The American Naturalist*, 148, 421–452. Retrieved from <http://www.jstor.org/stable/2463298>
- Erickson, C. J., & Reid, M. E. (1989). Wingclapping behavior in *Calopteryx maculata* (P. de Beauvois) (Zygoptera: Calopterygidae). *Odonatologica*, 18, 379–383.
- Fraser, F. C. (1934). *The fauna of British India, including Ceylon and Burma. Odonata. Vol. II*. London: Taylor & Francis.
- Furtado, J. I. (1966). *Studies on Malayan Odonata with special reference to larval ecology* (PhD thesis). University of Malaya, Kuala Lumpur.
- 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)* (PhD thesis). TU Bergakademie Freiberg, Germany. <http://nbn-resolving.de/urn:nbn:de:bsz:105-5111029>
- Hämäläinen, M., & Pinratana, A. (1999). *Atlas of the dragonflies of Thailand. Distribution maps by provinces*. Bangkok: Brothers of St. Gabriel.
- Heymer, A. (1972). *Verhaltensstudien an Prachtlibellen. Beiträge zur Ethologie und Evolution der Calopterygidae (SELYS, 1850 (Odonata: Zygoptera))*. Berlin: Parey.
- Hilfert-Rüppell, D. (2004). *Optimierung des Fortpflanzungsverhaltens: wichtige Einflussgrößen auf Territorialität und auf Paarungen von europäischen Prachtlibellenmännchen (Odonata: Zygoptera)* (PhD thesis). Technical University of Braunschweig. <http://www.digibib.tu-bs.de/?docid=00001567>

- 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
- Hooper, E. R., Tsubaki, Y., & Siva-Jothy, M. T. (1999). Expression of costly, plastic secondary trait is correlated with age and condition in a damselfly with two male morphs. *Physiological Entomology*, *24*, 364–369. doi:10.1046/j.1365-3032.1999.00152.x
- Karjalainen, S., & Hämäläinen, M. (2013). *Neidonkorennot – Demoiselle damselflies*. Helsinki, Finland: Caloptera Publishing.
- Kumar, A., & Prasad, M. (1977). Reproductive behaviour in *Neurobasis chinensis chinensis* (Linnaeus) (Zygoptera: Calopterygidae). *Odonatologica*, *6*, 163–171.
- Lieftinck, M. A. (1934). An annotated list of the Odonata of Java, with notes on their distribution, habits and life-history. *Treubia*, *14*, 377–462.
- Lieftinck, M. A. (1955). Notes on Australasian species of *Neurobasis* Selys (Odonata, Agriidae). *Nova Guinea (N.S.)*, *6*, 163–166.
- Meek, S. B., & Herman, T. B. (1990). A comparison of the reproductive behaviours of three *Calopteryx* species (Odonata: Calopterygidae) in Nova Scotia. *Canadian Journal of Zoology*, *68*, 10–16. doi:10.1139/z90-003
- Miller, P. (1994). The functions of wingclapping in the Calopterygidae (Zygoptera). *Odonatologica*, *23*, 13–22.
- Orr, A. G. (2003). A guide to the dragonflies of Borneo: their identification and biology. Kota Kinabalu: Natural History Publications.
- 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.
- Rüppell, G. (1985). Kinematic and behavioural aspects of flight of the male Banded Agrion *Calopteryx (Agrion) splendens* L. In L. Gewecke & G. Wendler (Eds), *Insect locomotion* (pp. 195–204). Berlin: Parey.
- Rüppell, G. (1989). Kinematic analysis of symmetrical flight manoeuvres of Odonata. *Journal of Experimental Biology*, *144*, 13–42. Retrieved from <http://jeb.biologists.org/content/144/1/13.full.pdf>
- Rüppell, G., & Hilfert-Rüppell, D. (2009a). Flugmanöver von *Calopteryx splendens* (Calopterygidae, Odonata) an der Oker nördlich von Braunschweig analysiert mit einer neuen Zeitlupentechnik. *Braunschweiger Naturkundliche Schriften*, *8*, 421–438.
- Rüppell, G., & Hilfert-Rüppell, D. (2009b). Males do not catch up with females in pursuing flights in *Calopteryx splendens* (Odonata: Calopterygidae). *International Journal of Odonatology*, *12*, 195–203. doi:10.1080/13887890.2009.9748339
- Rüppell, G., Hilfert-Rüppell, D., Rehfeldt, G., & Schütte, C. (2005). Die Prachtlibellen Europas. Gattung *Calopteryx*. *Die Neue Brehm-Bücherei 654*, Westarp, Hohenwarsleben.
- Siva-Jothy, M. T. (1999). Male wing pigmentation may affect reproductive success via female choice in a calopterygid damselfly (Zygoptera). *Behaviour*, *136*, 1365–1377. Retrieved from <http://www.jstor.org/stable/4535681>
- 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
- Vukusic, P., Wootton, R. J., & Sambles, J. R. (2004). Remarkable iridescence in the hindwings of the damselfly *Neurobasis chinensis chinensis* (Linnaeus) (Zygoptera: Calopterygidae). *Proceedings of the Royal Society of London Biological Sciences*, *271*, 595–601. doi:10.1098/rspb.2003.2595
- Waage, J. K. (1979). Reproductive character displacement in *Calopteryx*. *Evolution*, *33*, 104–116. Retrieved from <http://www.jstor.org/stable/2407369>
- 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. Retrieved from [http://dx.doi.org/10.1016/S0003-3472\(84\)80276-6](http://dx.doi.org/10.1016/S0003-3472(84)80276-6)