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Biting in dragonfly fights

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Slow motion films of fight behaviour of five different species of Odonata were analysed. In all cases biting played a major role. The biting duration depended on the duration of a stable connection between the two opponents. Sitting odonates showed much longer biting than those that were flying. In fights of *Anax junius* and *Calopteryx splendens* long biting between males led to serious injuries and death. Two males of *Anax imperator* bit each other by very short strikes during looping flights together, better described as hack-biting. This hack-biting was seen in two other fights: a female of *Libellula quadrimaculata* bit a harassing male on the head, immobilizing him, and during a male–male fight in *C. splendens* flying nearly on the spot. Loops, very brief but relatively stable flight positions, were used for biting in three cases. The significance of biting in inter- and intrasexual competition in Odonata is discussed.

Keywords: fight behaviour; inter- and intrasexual competition; dragonfly flight; looping; mandible use; hack-biting

Introduction

Contests among individuals over mating opportunities are common across diverse taxa, yet physical conflict is relatively rare. Due to the potentially fatal consequences of physical fighting, most animals employ mechanisms of conflict resolution involving signalling and ritualistic assessment (Umbers, Tatarnic, Holwell, & Herberstein, 2012). As a consequence, physical fights in insects have been investigated only rarely. Due to the rate of results and to their unimpeded behaviour in laboratories this was done mostly in Orthoptera (Briffa, 2008; Gwynne & Bailey, 1999; Shackleton et al., 2005; Tachon, Murray, Gray, & Cade, 1999; Umbers et al., 2012). On the other hand, adult Odonata do not lend themselves to laboratory studies, because they show their full behavioural spectrum only in nature and mostly in flight.

In Odonata, fights have been described (Corbet, 2004; Marden & Waage, 1990; Pajunen, 1962, 1966; Waage, 1988; Wildermuth, 2008) but not analysed. There are frequent reports of injured specimen of different Odonata species (Corbet, 2004), and the injuries have been taken as an indication of the degree of aggressive behaviour in populations of different latitudes (*Calopteryx splendens*; Hilfert-Rüppell, 2004; Hilfert-Rüppell & Rüppell, 2008).

Since adult Odonata rarely encounter relatives, or at least do not recognize them, both sexes behave selfishly. Consequently, due to the asymmetries of the numbers of male and female gametes there is intense competition among male Odonata for mates (Alcock, 1993). At reproduction

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sites operational sex ratios are usually strongly male-biased, so males fight for limited resources such as territories or females (Emlen & Oring, 1977). Males with coloured wings mostly show threatening flights, but at high densities – as predicted in general by Alcock (1993) – males with clear wings fight with physical contact (Hilfert-Rüppell & Rüppell, 2013). Intersexual fights also may occur: female Odonata try to refuse some males. Although females show special refusal behaviour (Corbet, 2004; Hilfert, 1998), sometimes they fight against harassing males physically (Rüppell & Hilfert-Rüppell, in prep.). Older 16 mm slow-motion films hint that legs and biting may play a role in fights (Rüppell, 1984). In more than 30 field seasons with many observation hours we only had the chance to film around a dozen fights. Only now, by means of digital slow motion filming which allows recording for several minutes (Rüppell & Hilfert-Rüppell, 2009), has it been possible to catch images of biting in flight. In this paper we analyse biting in Odonata for the first time and discuss its role in fights in different situations, with approximate and definite conclusions.

Material and methods

Filming was done near Braunschweig (52°26′ N, 10°23′ E) in Northern Germany in summer 2011 and 2012 at ponds (*Anax imperator*, *Libellula quadrimaculata* and *Coenagrion puella*), and in 1984 (*Orthetrum cancellatum*), and in 1984 and 2011 (*Calopteryx splendens*) at the river Oker. This medium-fast running river is 14–18 m wide. In 1987 we filmed *Anax junius* near Waco in Texas (31°33′ N, 97°9′ W), USA. The older films were reanalyzed with special attention to biting. All fights happened under similar climatic conditions – sunny weather at 25–35°C. Fights were filmed in slow motion at 200–400 frames per second using a 16 mm film camera LOCAM (model 51) (1984, 1987 and 1988) and at 300 and 600 f/s using a digital camera (Casio EX F1) in all other years. Because of the high flight speed and the unpredictable flight path of the insects, the camera was moved parallel to their movement and was triggered without viewing through the viewfinder with a prefocused lens. Drawings were made by taking the positions of the bodies and extremities from single frames from the slow motion films as well as details of structures from photos and dead specimens.

Results

Biting in Zygoptera

At high densities two males of *Coenagrion puella* fought for rare perches by striking with their legs (filmed several times) and by obviously biting, touching the opponent with the mouth parts. This touching could be filmed on only one occasion and lasted 0.05 s.

In fights of *Calopteryx splendens*, which occurred at high densities in which territoriality broke down because of very high intrusion rates among territory holders, biting was frequent. In flight, the opponents grasped each other (Figure 1) and tried to reach the other's body, wings or extremities with their mouth. This was like wrestling while flying nearly on the spot. In this situation, biting lasted 0.27 s. Another instance of short biting was observed in flight, when two males fought for a female. When the female left, one male bit the other on the right forewing (Figure 2), and both crashed onto the water. This biting lasted <0.12 s. Biting was longer in another case when both males rolled, fluttering their wings over the water's surface, performing five turnovers. During this, one male pressed its mouth parts continuously onto the other male, obviously biting or trying to bite for about 1 s (Figure 3, Table 1). Another biting in *C. splendens* occurred when a male landed on the rival, which was already exhausted and injured. The first male bit for 4 s continuously into

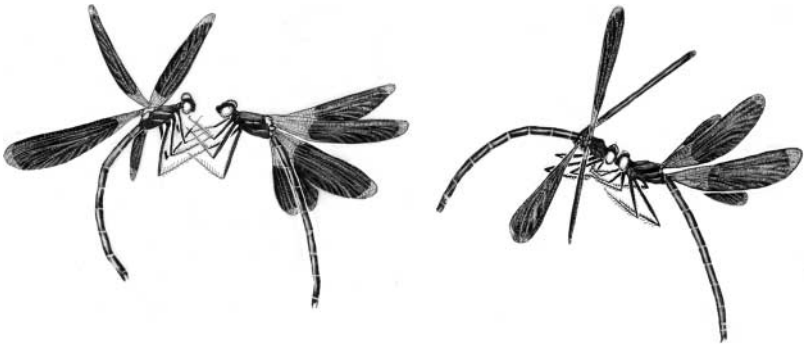

Figure 1. In order to reach the body or extremities of the opponent, males of *Calopteryx splendens* grapple with their legs (left). Only after getting contact with their legs are they able to bite each other (right). Redrawn from high-speed film images.

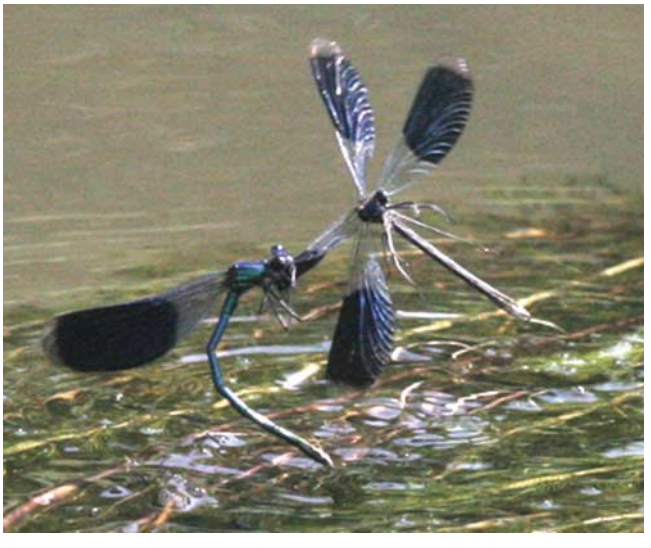

Figure 2. A male of *Calopteryx splendens* biting into the wing of a rival, leading to a crash. Biting in flight is very brief. (Supplementary material is available via the article webpage).

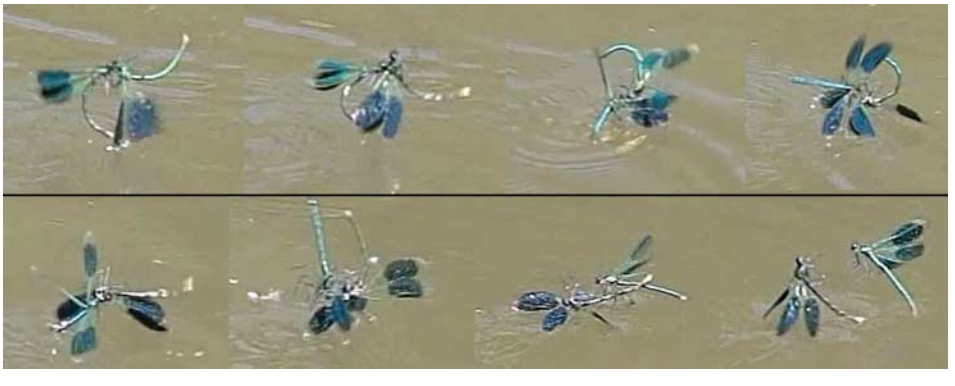

Figure 3. Fight between two males of *C. splendens* with biting during a five-loop manoeuvre (beginning at the top left). From film 300 f/s.

Table 1. Biting behaviour of five Odonata species in different situations.

Species and participants	Location and activity	Event duration (s)	Number of bites or strikes	Duration of one strike (s)	Outcome	Figure
Coenagrion puella; male–male	In air; dashing against each other	0.05	1		Unknown	
Calopteryx splendens; male–male	On water; on submerging female	0.9			Continued fight in air (next row)	
C. splendens; male–male	In air; fluttering nearly on spot	0.27			Separated	Figure 1
C. splendens; male–male	On water; both five loops forward	1.1	1		Unknown	Figure 3
C. splendens; male–male	On water; opponent lying on water	4	1		Death of attacked male	Figure 4
C. splendens; male–male	In air; after a female escaped	<0.12	1		Bitten male left	Figure 2
Anax imperator; male–male	In air; both looping forward		2	0.02	Unknown	Figure 7
A. junius; male–male	On water; biting after being separated	1.17	1		Death of attacking male	Figure 5, 6
Libellula quadri-maculata; female–male	In air; harassed female bit male	0.2	3	0.03	Death of attacking male	Figure 8

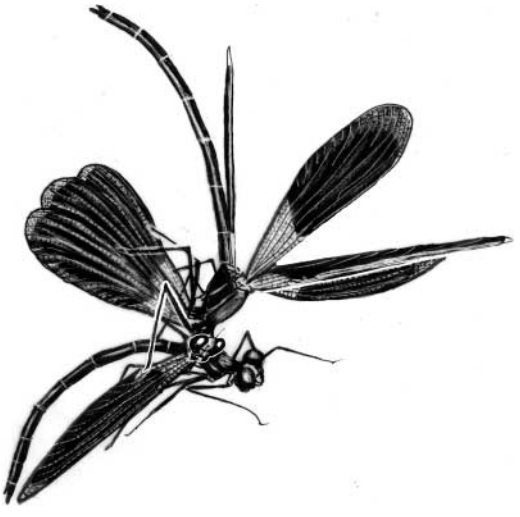

Figure 4. Male *Calopteryx splendens* biting into the right forewing of a rival. Biting in such a stable position can last several seconds. Redrawn from high-speed film images.

the leading edge of the right forewing (Figure 4). This led to immobility of the loser, who then was caught by a frog.

Biting in Anisoptera

Anax

Male–male competition of *Anax junius* was very intense in Texas, due to the hot climate and the scarcity of water bodies. Males tried to grasp females and fought with other males. On one occasion a male seized a female and generated a tandem, another male plunged onto the tandem

and bit into its connection, causing it to split. The original tandem male turned around and bit the new tandem male in the basal area of the right hind wing. This lasted for about 1 s and ended very suddenly before take-off of the attacking male. The new tandem took off, too, but the leading male was unable to beat its injured right hind wing effectively. Immediately the tandem was attacked

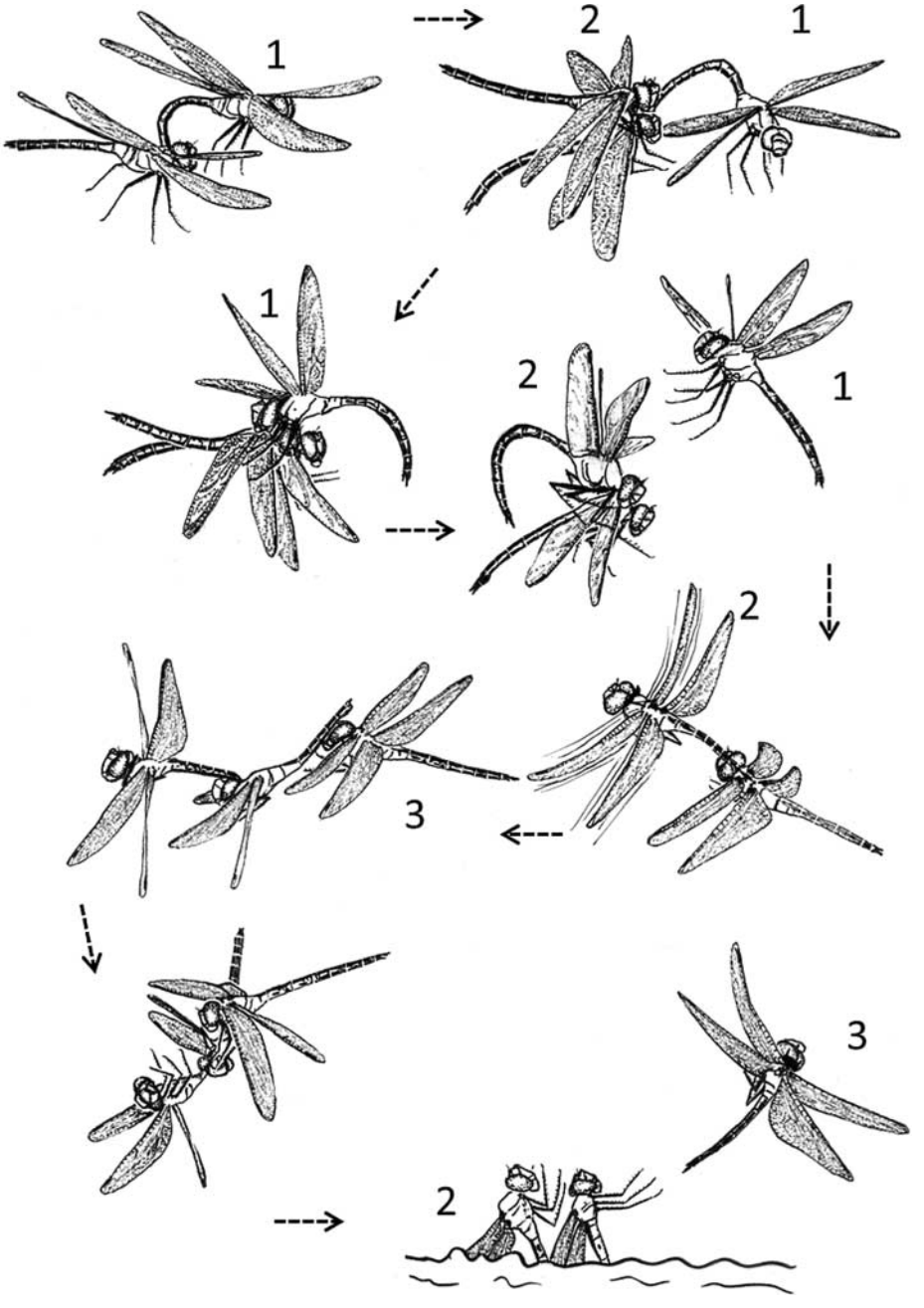

Figure 5. A tandem of *Anax junius* was pursued and seized by another male. The aggressor split the tandem male by biting. The separated male bit back, then departed, while the new tandem male coupled to the female but failed to fight off the attack of a third male. The pair drowned. Behaviour follows the arrows beginning at top. Males are numbered.

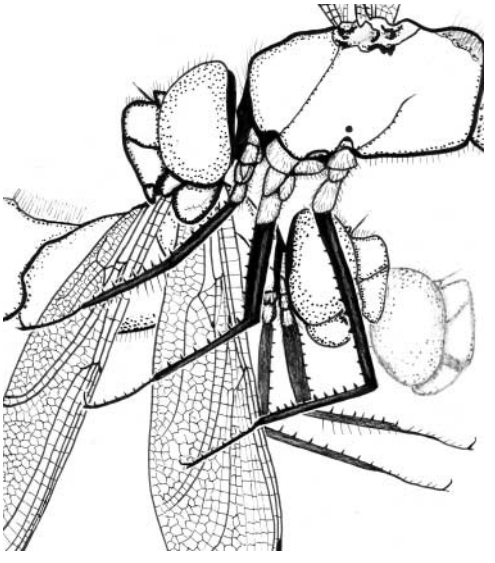

Figure 6. The separated tandem male (*Anax junius*) bit back the attacker, sitting on him. The female's head is shown at reduced contrast. This biting injured the right hind wing in the basal region (wing joint), which impeded normal flapping. Both redrawn from high-speed film images.

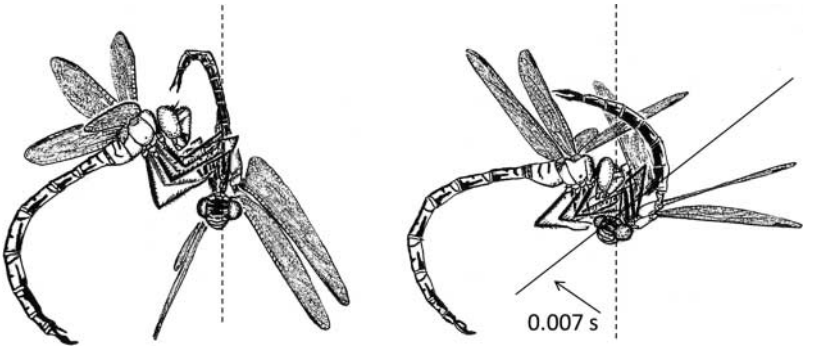

Figure 7. A fight of two males of *Anax imperator*. After grasping, the males hit each other with their mouths. The body axes (depicted only for the lower male as a broken line) were bent (solid line in drawing right) very quickly (within 0.007 s to 48°). Both redrawn from high-speed film images.

by a third male, and they crashed onto the water where they drowned (Figure 5, 6). They were eaten by water beetles (*Dytiscus*).

Fights in mid-air occurred regularly in males of *Anax imperator*. Mostly they pursued each other, but sometimes they clashed together. In such a situation, slow motion film (600 f/s) revealed biting during a forward loop (Figure 7). This biting began with opened mouth and was very short. Two strikes lasting about 0.02 s each were exhibited, which means the male reached a striking frequency of 50 Hz. This strike time consisted of three equal parts: movement of the head towards the opponent = 0.006 s, contact time = 0.006 s and movement backwards to the initial position = 0.007 s. As depicted in Figure 7 the mouth was opened at the beginning of each strike. Whether this was the case during the whole strike is not clear due to the changing perspective of the shifting head.

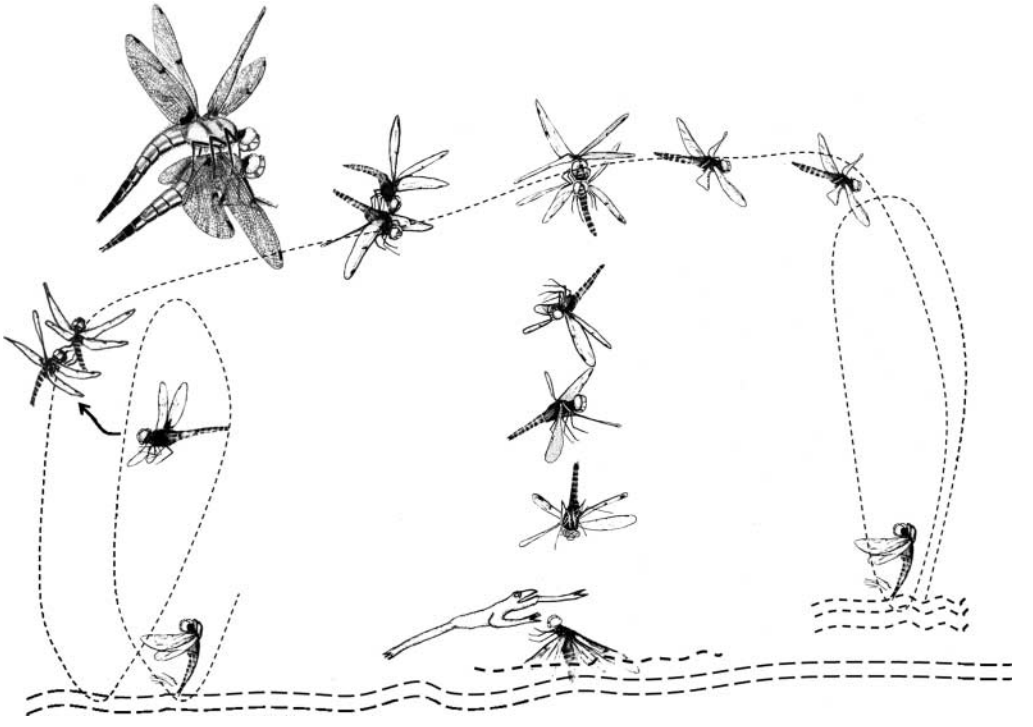

Figure 8. Female *Libellula quadrimaculata* biting a male who was later eaten by a frog (from left). Large drawing shows the moment just before biting. The female continued oviposition nearby (right). Redrawn from high-speed film images.

Libellula quadrimaculata

At high densities, males pursued females for pairings. As a male seized an ovipositing female, the female managed to get above him in flight (Figure 8). In this position she bit him in the head: first for 0.2 s continuously, and then with a series of three very short strikes (see Table 1). The male tried to dislodge her by shaking his body laterally (four times, 0.02 s each). The female released the male 0.75 s after grasping him, and he tumbled onto the water, where he remained motionless. After 25 s a frog swallowed him. The female continued oviposition nearby.

Discussion

Competing male Odonata bite each other in fights. Dead and injured specimens of Odonata can be found, especially in places with a highly male-biased operational sex ratio. In northern Germany the flight periods are short due to the cool and changeable climate; here Hilfert-Rüppell (2004) found more injured specimens (damaged wings or loss of legs) of *C. splendens* (345 injured males out of 1911 = 18.05%) than in the warmer conditions of southern France (111 injured males out of 856 = 13%; chi-square-test: $\chi^2 = 10.26$; $p = 0.001$). It seems fights are mainly responsible for injuries, although other causes such as accidents may play a minor role in damage (personal observations).

In fights Odonata use four different weapons to damage the rival: the legs, which are equipped with many spines; the mouth parts; a ramming device consisting of the prominent frontal parts of the head – frons, clypeus and labrum (especially in Aeshnidae); and clashing wings. In this paper

Figure 9. The toothed mandibles of a male *Aeshna cyanea*, the biting organs (length = *ca*.3 mm).

we report only on biting. The biting weapons of insects are the mandibles (Briffa, 2008; Emlen, 2008; Judge & Bonanno, 2008). Odonata possess very prominent toothed mandibles (Figure 9) with which they are able to cut the hard sclerotized cuticle of prey, hence biting with them should also be very effective in fights. In fights, however, biting movements of the mandibles are hard to recognize, even in slow motion films. We only can describe biting as contact of the mouth parts with the opponent's body, because the interior movements of the mandibles are hidden. But damage, as found for example in a wing of a bitten male after the contact, indicates real biting.

Biting can take place anywhere – in air, on the surface of water, on the ground or in vegetation. In order to bite, a stable position of the body is needed to insert the mandibles into the opponent's surface and to proceed without being dislodged by body movements. Stable positions are hard to maintain because of the opponent's defensive movements, and depend on the contact situation. The longer stable contact lasted, the longer was the duration of the biting. We observed biting durations of 1-4s when the attacker was sitting on the water's surface. In *C. splendens* biting in flight lasted for relatively long periods, however, probably due to the outstanding flight manoeuvrability of this species (Rüppell 1985, 1989). Dashing together is a too short manoeuvre to allow biting, but flying a loop together, which seems to be a controlled flight manoeuvre, requires a longer period and renders biting possible. Odonata often fly loops (unpublished slow motion films). We previously found biting during loops in *Orthetrum cancellatum* (Rüppell, 1984), and in this study in *C. splendens* while turning over five times on the water surface, and in one loop by *A. imperator*. In the latter species biting time was very short. It is highly improbable that the mouth parts can perform real biting in this short time. Due to the short contact time of only 0.006 s in one strike we assume that the mandibles stay motionless relative to the cranium and are used to hack at the opponent. Another argument for that interpretation is that a precise and synchronized closing of the mouth parts seems to be impossible. Within 0.006 s the dragonfly probably cannot predict the exact moment of hitting the opponent's surface, so as to close the mandibles for biting.

The action in such brief encounters should be called hack-biting (Figure 10). The muscles of the mandibles of Odonata have to be relatively large and strong to succeed in rapidly cutting up the chitinous cuticle of prey during eating. Because of the inverse relationship between contraction velocity and maximum force, and the fact that the mechanical arrangement of the mandibles is probably adapted for high force production to crush the prey cuticle, it is unlikely that contraction velocity is high.

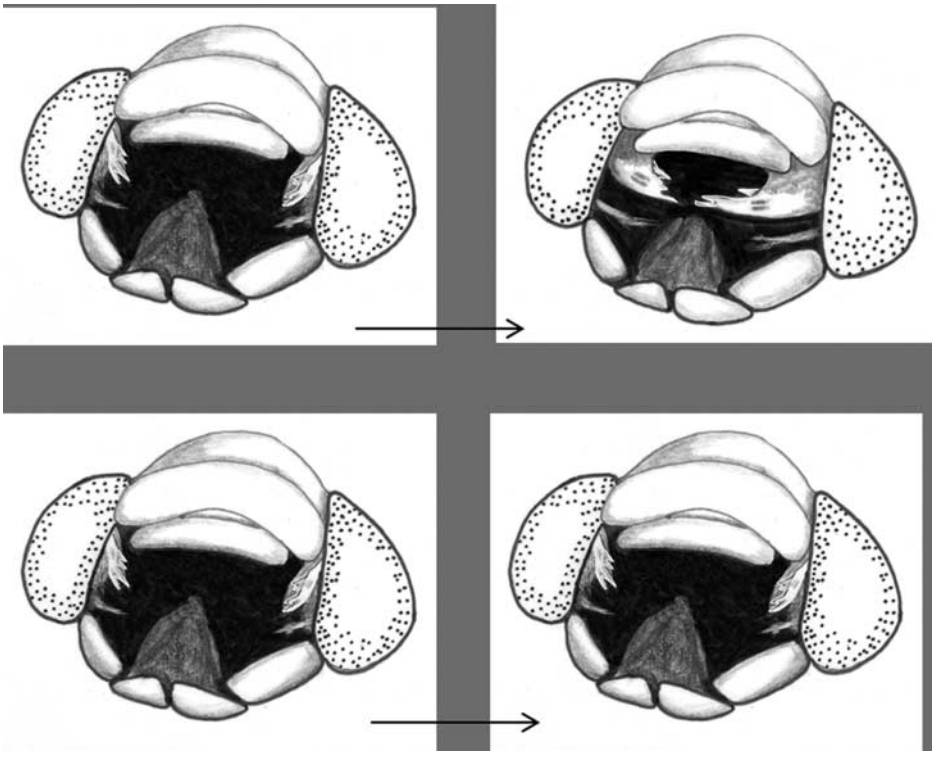

Figure 10. View into the opened mouth of an Anisoptera (*Aeshna cyanea*). Upper row: the mouth parts (mandibles superior, maxillae below) are drawn back (left) at the beginning and, we suggest, close (right) during normal biting. Lower row: the mouth parts probably remain open during hack biting.

We found this hack-biting in a weaker form in *C. splendens*, and distinctly in *L. quadrimaculata*, another species of Anisoptera. The frequency of hack-biting ranged from 33 to 50 Hz (*C. splendens*, *L. quadrimaculata* and *A. imperator)*. These high frequencies were performed for two (*A. imperator*, *C. splendens*) or three strikes (*L. quadrimaculata*) (Table 1).

In view of the brevity of individual encounters in Odonata it is not surprising that mutual assessment may play only a minor role in decisions about whether or not to fight, as described for slower systems (Arnott & Elwood, 2008; Parker, 1974).

Due to the frequency of biting events and the elusiveness of the combatants we do not know the prior condition of the participants, such as residency or their preceding success in fights or pairings. Both conditions are important for the explanation of fight outcomes (Hilfert-Rüppell, 2004; Jennions & Backwell, 1996; Kemp & Wiklund, 2004). We can only state that serious damage resulted from long biting, but not from short events. The mandibles in short bitings in flight impinged on the opponent haphazardly but often first on the legs because of defence reactions. This might explain the loss of legs often seen in dragonflies (unpublished observations; Hilfert-Rüppell, 2004).

Long biting in fights, in two cases, was directed at the wings of the combatant, causing reduced mobility. Long biting led to immobility of males in two cases and to subsequent death by a frog's attack and to drowning after damage to a wing. Thus it can be a very effective behaviour pattern to win a dispute. Despite the paucity of documentation it probably occurs very commonly in fights of Odonata. Bites seem to be an important weapon in intra- and intersexual competition, which are particularly severe in Odonata (Corbet, 2004; Córdoba-Aguilar & Cordero Rivera, 2005; Pajunen, 1962, 1966).

A number of questions are raised by our observations:

(1) There seems to be a relation between fighting with the legs and mouth. Is it true that Odonata with long and fragile legs, e.g. Calopterygidae, tend to bite only, whereas Anisoptera intensively strike with their solid and well-armed legs or ram each other with their prominent frontal parts of their heads? More generally, are fighting techniques reflected in differences in morphology, especially of the legs and head?
(2) Although after being separated from the female the male of *A. junius* had no chance of regaining the female, he bit back at the attacking male. He did this very effectively, so that the bitten hind wing was subsequently nearly useless. Was this purely self-defensive, or was he attempting to resume the tandem with the female?
(3) What did the female *L .quadrimaculata* gain by biting the attacking male to immobility rather than simply flying away?
(4) How frequent and important is biting in intraspecific conflicts in general?

We are convinced that biting occurs every day and everywhere when high densities of dragonflies produce intense competition, reported in general by Knell (2009), and with digital recording techniques it could be filmed more often in slow motion. More studies of biting are needed – not only for answering proximate, mechano-physiological questions but also for clarification of its adaptive value.

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