

## ***Aeshna viridis* is an early bird – matutinal matings in a crepuscular species (Odonata: Aeshnidae)\***

Angelika Borkenstein<sup>1</sup>, Asmus Schröter<sup>2</sup> & Reinhard Jödicke<sup>3</sup>

<sup>1</sup> Lebensborner Weg 5, 26419 Schortens, Germany;  
<angelikaborkenstein@t-online.de>

<sup>2</sup> Rasenweg 10, 37130 Gleichen, Germany; <notulae@osmylus.com>

<sup>3</sup> Am Liebfrauenbusch 3, 26655 Westerstede, Germany;  
<reinhard.joedicke@ewetel.net>

*Received 26<sup>th</sup> November 2015; revised and accepted 7<sup>th</sup> February 2016*

**Abstract.** The hitherto unknown mating activities of *Aeshna viridis* at dawn are described and photographically documented. At first morning light both sexes arrived at the breeding pond flying over dense stands of *Stratiotes aloides*. Their flight style was of two types: the well-known feeding flight and a slow, low, linear and non-aggressive cruising flight. Cruising individuals sometimes formed mating wheels and the couples left the pond. Shortly before sunrise numerous males started to search for receptive females in the tall herbaceous vegetation near the pond. This non-aggressive flight mode was slow and at knee-height, characterised by intrusion into dense thickets; we term it searching flight. It ceased within a period of 45–70 min after sunrise. We assume that the terrestrial vegetation represents the main rendezvous site and that searching flight leads to the majority of matings. One male was recorded grasping a resting female. Wheel formation was completed while perching without further flight, resulting in a distinctive twisted wheel position. Further observations confirmed that such twisted wheels found in the morning are typical. There are also records of occasional matings during the period from noon until late afternoon. The restriction of most mating activities to the period around sunrise rejects the myth of *A. viridis* being a late riser. The mating behaviour of this species with its combination of mainly sunrise-limited searching flight and wheel formation with resting mates seems to be unique in Odonata. In referring to twilight activities – at dawn and dusk – we use the term ‘crepuscular’ in the general sense and eschew the term ‘eocrepuscular’, making a distinction between morning and evening with the terms ‘matutinal’ (at dawn) and ‘vespertine’ (at dusk).

**Further key words.** Dragonfly, Anisoptera, mating behaviour, diel activity pattern, flight patterns, searching flight, cruising flight, twisted wheel position.

---

\* Dedicated to Günther Peters, the expert on aeshnids and our inspiring example, mentor and friend.

## Introduction

*Aeshna viridis* Eversmann, 1836 is a Western Palaearctic species well known for its close association to the Water-soldier *Stratiotes aloides* (MÜNCHBERG 1930; SCHMIDT 1975; PETERS 1987: 70 ff.). It is not only its preference for twilight flight (TÜMPEL 1898-1901), which makes *Aeshna viridis* enigmatic. There is also an astonishing lack of knowledge as to where and when mating takes place (MÜNCHBERG 1956; PETERS 1987: 72; ADOMSSSENT 1996b; SCHRÖTER 2014). The circumstances of its copulation have remained mysterious up to now. Only a few accidental observations of matings have ever been reported (WESENBERG-LUND 1913; JURZITZA 1969; ZIEBELL & BENKEN 1982; ADOMSSSENT 1996a). This gap in our knowledge is in stark contrast with the general significance of this insect as a target species in nature conservation. It is one of several species of the EU Habitats Directive which are particularly well-studied, especially with regard to habitat conservation, restoration and creation, larval development and emergence, adult behaviour and population monitoring (e.g., for northern Germany: ADENA & HANDKE 2001; BÜTTGER & FINCH 2003; MAUERSBERGER et al. 2005; HAACKS & PESCHEL 2007; KASTNER et al. 2011; MAUSCHERNING et al. 2011; BRUNKEN et al. 2012; WITTENBERG et al. 2015; KASTNER et al. 2016, as well as dozens of unpublished surveys, theses, and political strategy statements).

*Aeshna viridis* is reputed to be a late riser, with males starting their patrol flight in late morning and females arriving at the water for oviposition not before noon (MÜNCHBERG 1930; H. Schiemenz in MÜNCHBERG 1956; KÄHLERT 1976; PETERS 1987: 71). Although both sexes meet at the floating *Stratiotes aloides* mats – the exclusive oviposition substrate in Europe and over most of its range – for hours on sunny days, no mating has been recorded. All observers agree in the effectiveness of the female's refusal display, i.e., her downwards curving of the abdomen in flight. This signal makes ovipositing females a taboo for patrolling males (MÜNCHBERG 1930; H. Schiemenz in MÜNCHBERG 1956; JURZITZA 1969). Actually, there have so far been no reports on wheel formation with ovipositing females in *A. viridis*.

To understand the mysterious process of mate location and mating in *A. viridis*, we studied the diel rhythm in this species systematically with special emphasis to its behaviour in the morning twilight. We additionally discussed this problem with colleagues and analysed their results. In this paper

we aim to summarise all available information about the mating tactics in *A. viridis* and present new insight into its hitherto unknown activity in the period around sunrise.

### Material and methods

Our study took place at a woodland pond in northwestern Germany, 1.5 km east of Zetel-Neuenburg, district of Friesland, Lower Saxony (53.3859°N, 07.9827°E; 4 m a.s.l.), which harboured a breeding population of *Aeshna viridis* with an annual output of hundreds up to thousands of emerging adults. The pond had a size of roughly 1 700 m<sup>2</sup> and was completely and densely covered with *Stratiotes aloides* (Fig. 1). Its shoreline was dominated by stands of *Typha latifolia* and *Phragmites australis* and lined by *Alnus glutinosa* and *Salix* sp. The pond adjoined a glade to the south, which had been established for gamekeeping and was annually scythed in July. At its margins, and in adjacent sparse wood with dead *Fraxinus excelsior*, some



**Figure 1.** Breeding pond of *Aeshna viridis* covered with a dense mat of *Stratiotes aloides* near Zetel-Neuenburg, Lower Saxony, northwestern Germany (15-vii-2015), facing north. Photo: RJ

patches of tall herbaceous vegetation remained. To the west, north, and east the pond was surrounded by oak-dominated forest.

We systematically visited the pond and its surroundings in 2014 and 2015 to study flight activities of *A. viridis* at dusk and at dawn (cf. BORKENSTEIN & JÖDICKE 2016). On 04-viii-2015 we noticed flight before sunrise at the pond for the first time. All detailed observations on sexual behaviour of this species refer to the early morning of 14-viii-2015, under overcast and windy conditions with an air temperature of 17°C and incipient rain just at sunrise. On 21- and 23-viii-2015 we confirmed the searching flight of males and documented it photographically under more favourable weather conditions. A final check on 18-ix-2015, at the end of the flying period and low morning temperature (10.5°C), produced no results. Temperature was measured at a height of 0.8 m above the water level or ground, respectively, which corresponded to the height at which the dragonflies mostly flew. Light intensity was measured with a luxmeter against the open sky. Local time was converted to solar time and set into relation to the local sunrise.

### Results

On 14-viii-2015 the first individual of *Aeshna viridis* arrived at the pond 18 min before sunrise at 30 lx. Eight minutes later, at 50 lx, ca 5–10 individuals, females and males, were flying over the *Stratiotes aloides* mats. Some were hunting, with clear flight manoeuvres towards nematocerans ca 0.5–1.5 m above the floating vegetation and sometimes also along the bushes along the shoreline. The others displayed a different flight style at a height of 0.1–0.8 m, which was characterised by a lower velocity and linear paths with incidental shifts in direction and implied a kind of cruising different from foraging. Some individuals would switch from hunting to cruising and vice versa. Altogether, the feeding flight style predominated, and we estimated that at least 10–15 individuals simultaneously flew over the pond at the time of maximum activity a few minutes before sunrise. This was roughly a third of the individuals simultaneously seen in the preceding evening after sunset.

Most individuals did not respond to the approach of another and we only observed one inter-male contest and two wheel formations. The latter occurred 8 min before (58 lx) and 5 min after (115 lx) sunrise, respectively. We

did not observe the initial situation in which the males encountered their mates but the wheel position was adopted immediately after tandem linkage was established and the pairs left the pond and settled in the tall vegetation next to the pond.

Light rain, beginning around sunrise, did not prevent flight activity at the pond. The last female was seen 7 min after sunrise when she left the water body and landed in dense vegetation 20–30 cm above ground near to the water's edge. A few males continued flying at the pond, now predominantly adopting the cruising flight style close to the *S. aloides* mats. Due to the rain, light intensity did not exceed 200 lx in this period. We discontinued our survey of the pond 38 min after sunrise, while two males were still on the wing.

At this point in time we discovered up to ten males flying through the tall herbaceous vegetation in the adjacent area (5–50 m) south of the pond. We repeatedly observed new males arriving from the forest, using a cutting through the forest. At the site they flew slowly *ca* 0.5–1.5 m above ground and penetrated the dense thicket of grass, blackberry, and fern (Figs 2–7) causing a well-audible wing rustling. When two individuals encountered each other they did not react aggressively. The males scanned the grass blades and other leaves thoroughly, hovered, often with hanging hind legs, in front of complex structures and obviously searched for females. This was evident in the male who had grasped the resting female mentioned above. The female's position had not changed in the meantime. We spotted the couple 44 min after sunrise, i.e., 37 min after the female had settled in the grass. The form of the wheel was markedly twisted, with the male's head facing downwards and the female having lost her grip to the rush stem (Fig. 8). The couple appeared to be passive, as the male displayed no pulsating copulation movements. The couple also did not react to the camera's approach and even made no attempt to escape when translocated to an alder twig by hand. Here the male clambered under an alder leaf to avoid the rain drops. In this position in the wheel lost most of its twist, i.e., the female held the male's abdomen by her legs as aeshnids use to do and only the male's abdomen tip remained in an asymmetrical position pointing towards the female's left eye (Fig. 9).

The last searching male was seen 70 min after sunrise. Two subsequent checks in the last half of August confirmed that terrestrial searching flight



**Figures 2–7.** Searching flight of *Aeshna viridis*: males penetrating the thick vegetation to search for roosting females during morning twilight. All these flight manoeuvres were audible to the observer as the wings regularly brushed the vegetation. Spider webs were adroitly avoided (2). Notice hanging hind legs (5, 6) and curved abdomen (7) shown at especially low flight speed. Study site near Zetel-Neuenburg, Lower Saxony, northwestern Germany (21-viii-2015 [2] and 23-viii-2015 [3–7]). Photos: AB (2, 5–7) and RJ (3, 4)

by males started only a few minutes (4 and 6 min, resp.) after the beginning of flight activities at the pond and thus always shortly before sunrise. In this period the number of searching males exceeded that of males flying at the pond before sunrise. The searching flight activity terminated 45 and 46 min after sunrise, respectively, corresponding to a light intensity of more than 2 000 lx. All males left the site for an unknown place. During this time period *A. viridis* was the only odonate species recorded on the wing.



**Figure 8.** *In situ* photograph of *Aeshna viridis* in copula. The male had seized a resting female in the vegetation next to the breeding pond between 7–44 min after sunrise. The twisted wheel construction resulted from the fact that the female did not give up her perching position in the dense plant thicket where the male's manoeuvring room was restricted. In a hanging position the male was able to cling to a grass blade beneath his mate. Study site near Zetel-Neuenburg, Lower Saxony, northwestern Germany (14-viii-2015). Photo: AB

### Discussion

Three aspects of our observations shed new light on the behaviour of *Aeshna viridis*: (1) The species consistently starts its diurnal flight activity at first light in the morning. (2) The activities at dawn include, *inter alia*, sexual behaviour which results in matings. (3) Males fly through surrounding vegetation to search for females ('searching flight') during the morning twilight and grasp females to adopt the wheel position directly at her resting place, without further flight.

TÜMPEL (1898-1901) characterised *A. viridis* as flying exclusively after sunset. This statement was, with respect to daylight activities, soon qualified by WESENBERG-LUND (1913), SCHMIDT (1929: 39), and MÜNCHBERG (1930) but all these authors agreed in the fact that the species is predominately a twilight insect. Were this the case, the species would match CORBET's (1999: 582) definition of a crepuscular flier: »active during evening twilight«.

However, MÜNCHBERG (1930) also mentioned that »...*Ae. viridis* fliegt ... auch schon ... lange vor Sonnenaufgang, was keine andere endemische Aeschnine zu tun pflegt!« [*Aeshna viridis* is on the wing long before sunrise which no other of our aeshnine does!]. He repeatedly observed individuals hunting over a village road on dusty autumn mornings. Subsequently he stated that the species spends the start of the day and the ensuing morning hours roosting in reed, grass, or green cornfields (MÜNCHBERG 1956), evidently contradicting his earlier observations. Just recently early-morning activity has been confirmed: at least three individuals were observed hunting just before sunrise over a cornfield on 06-vii-2006, near Hehm in Dithmarschen, northern Germany (HAACKS et al. 2015; C. Winkler pers. comm.).

We have observed flight at first light in each of the four August mornings when we examined the pond. Based on our results the first individuals of both sexes arrive at the pond at times of low light intensity always before sunrise. Most individuals are active just before sunrise and the pond within half an hour after sunrise. Both sexes are involved but we have noticed a surplus of active males. We assume that twilight flight before sunrise is a regular feature of *A. viridis* at least under suitable weather conditions; unfavourably low morning temperatures are expected to be countered by wing whirring, which seems to be universal among aeshnids (CORBET 1999: 292).

The combination of sunrise and sunset flight activities is – at least in odonatalogical context – so far defined as ‘eocrepuscular’ pattern (CORBET 1999: 583). This term was introduced by HADDOW (1945) to define the bimodal diel periodicity of biting activity in mosquitoes, and was later also used to describe Odonata being active at dawn and dusk (CORBET 1962: 127) as well as to insects in general (CORBET 1965). However, the Latin *crepusculum* generally means twilight, and the Greek prefix *eo-* refers to the dawn goddess Eos, so an eocrepuscular insect should actually be exclusively active at dawn. Due to the potential confusion caused by this little used term, we here use the general term crepuscular in its usual zoological sense (i.e., morning and evening) and eschew the term eocrepuscular. If we need a distinction between activity in the half light in the morning and the evening, we use the well established terms ‘matutinal’ and ‘vespertine’ with regard to the morning and evening, respectively.

Two basic flight styles adopted during morning twilight can be distinguished: feeding flight and cruising flight (a term adopted from WILDERMUTH 2000). The former is not strictly limited to the pond but also includes the bushes along the shoreline and the adjacent glade, while the latter takes place only over *Stratiotes aloides*. Both patterns are also reported from evening twilight flight at this pond (BORKENSTEIN & JÖDICKE 2016). In that paper the behaviour is described and discussed in detail; we term all twilight-flight activities over the pond ‘collective flight’ with respect to the aggregation of individuals at a well-defined site. The number of individuals involved in the morning flight at the pond seems to be generally smaller than in the evening flight.

Wheel formation during early-morning flight, as reported here, demonstrates that receptive females participate in this event and are attractive to males. This is in contrast to the situation at the pond for the rest of the day. We have never seen wheel formation at the pond after early morning. This includes the afternoon when patrolling males encounter ovipositing females but mostly ignore them. Only occasionally we saw attempts of males to approach a female that immediately reacted with an always successful refusal display. In the time after sunset, both sexes meet in the collective flight, but do not show sexual activity. This is broadly confirmed by observations at another breeding site of *A. viridis*, a ditch in the floodplain of the River

Ems (53.1237°N, 07.3565°E; 1 m a.s.l.; AB & RJ unpubl.). WESENBERG-LUND (1913) points out that ovipositing females respond negatively to the approach of patrolling males. According to MÜNCHBERG (1930), males ignore ovipositing females and even do not react to those females flying from one oviposition plant to the next. PETERS (1987: 72) also emphasises that males scarcely respond to females at the oviposition site. We assume that ovipositing females are not in a receptive condition and that males clearly recognise this situa-



**Figure 9.** *Aeshna viridis* couple (same as in Fig. 8) after relocation by hand to an alder twig. It now shows almost the standard wheel position of an aeshnid, only the male's abdomen tip is still twisted and has slipped onto the female's left eye. Study site near Zetel-Neuenburg, Lower Saxony, northwestern Germany (14-viii-2015). Photo: AB

tion. Reports on feeding flight, mainly in the evening, do not refer to any sexual behaviour while hunting (e.g., RANTALAINEN & KANERVO 1928). However, there is one exception, as KRAWUTSCHKE (1999) reports futile attempts by males to locate females during feeding flight after sunset. Given that there is no evidence of successful wheel formation with ovipositing or feeding females so far, we dare to generalise that breeding sites serve as a temporal rendezvous, being exclusively limited to a short period either side of sunrise.

The terrestrial vegetation at the water's edge has proven to be an alternative and presumably the most important spatial rendezvous site of *A. viridis*. Based on our records males arrive every morning around sunrise at all suitable sites characterized by tall herbaceous vegetation, consisting of *Calam-*



**Figure 10.** Another twisted couple of *Aeshna viridis* spotted in early morning. The couple made no attempt to escape. The male is in a typical hanging position with his head facing down. Clay pit near Grindau, Lower Saxony, Germany (08-viii-2012). Photo: Jörg Adelmann

*agrostis epigeios*, *Phragmites australis*, *Juncus effusus*, *Rubus* sp., *Urtica* sp., and others. Here, they exhibit a unique flight style in which they search for females (Figs 2–7), which we call ‘searching flight’ due to the thorough inspection by the males. WILDERMUTH (2000) used the term ‘Inspektionsflug’ (searching flight) to describe the behaviour of *Boyeria irene* searching for females. The matutinal searching flight of *A. viridis* is an impressive and hitherto overlooked spectacle, resembling early-morning reproduction activities of *Sympetrum depressiusculum* males before tandem formation (MILLER et al. 1984; REHFELDT 1993, 1995), designated as ‘dance flight’ by SCHMIDT (1990, 1993). Certain elements are reminiscent of the behaviour of congeneric aeshnids, such as males of *A. juncea* diving deeply into dense vegetation in search for females (WILDERMUTH 1993). Furthermore, conspicuous similarities exist in the behaviour of *A. viridis* and *A. affinis*. During a mass occurrence in Kyrgyzstan dozens of males of the latter species were observed searching for ovipositing females at dried-out temporary ponds and penetrating the dense and low vegetation without showing territoriality or inter-male aggression (AS unpubl., cf. SCHRÖTER 2011). On the other hand, currently no other aeshnid is known to confine its sexual behaviour to a narrow time frame in early morning. To our knowledge, the behaviour of *A. viridis* described here – (1) encounter of sexes at a collective flight before sunrise with aerial formation of mating wheels and (2) early-morning searching flight of males with terrestrial formation of mating wheels – may be unique even within the Odonata. Interestingly, KÄHLERT (1976) mentions a male searching for females in and over reed vegetation in the forenoon. This finding suggests that searching for females in dense vegetation may also occur later in the day. However, Kählert’s observation also raises the question of whether the flight style observed was the same as the searching flight described by us.

Our observations indicate that the terrestrial rendezvous is not used for roosting at night. We speculate that this site is selected by receptive females that had previously participated in the collective morning flight over the pond but did not mate. By chance, we noticed a female that first cruised over *Stratiotes* and then settled deeply in the grass as described by TIMM (1902). This female was later seized by a male and wheel formation was completed without the female having left her perch. This can be clearly reconstructed

by analysis of Figure 8. The female seems to have almost lost her original perch and clings only with one leg to the male's abdomen, while the male clings to a grass blade with his head facing almost downwards. In this situation the rear part of the male's abdomen is twisted, covering the female's left eye. However, this does not hamper the linkage of genitalia. We interpret the twisted position as a consequence of completing a complex manoeuvre in a dense thicket of plants, that is to say, it derives from being unable to form a standard mating wheel exactly in the sagittal plane. It is remarkable that for this kind of wheel formation and the subsequent copulation no aerial phase is needed. We are not aware of any other aeshnid or even odonate species that mates this way (see CORBET 1999: 499 f.).

In summary, there are two different mechanisms to bring receptive females and males together. Both are linked to early morning. This has so far been overlooked, and it explains why mating in *A. viridis* has largely remained unknown and the few reports on this subject are accordingly vague. In obvious contrast to his otherwise precise indications, WESENBERG-LUND (1913) writes that »Paarung wurde oft gesehen aber nur flüchtig« [mating was frequently observed but only fleetingly]. JURZITZA (1969) reports on several wheel formations at a terrestrial feeding site in early afternoon and provides a photograph of a couple hanging in dense vegetation near ground level. This time frame is confirmed by ZIEBELL & BENKEN (1982), who add that copulation is mostly concluded on or near the ground after 55–65 min. ADOMSSSENT (1969a) reports on one wheel formation at noon, when five individuals flew over an *Urtica dioica* stand, and another when a female was flushed and immediately grasped by a male. These published observations on mating initiation during feeding flight at noon and in the afternoon may point to other mating tactics. Published photographs of *A. viridis* wheels (BUCK 1990, 1994; K. Haringsma in BOS & WASSCHER 1997; KÄHLERT 1999) lack particular information. In the caption of a photograph of a twisted mating wheel by C. Brochard in DE BOER et al. (2014: 188) it is mentioned, without further details, that most wheel formations occur in the early morning.

Below we list 17 descriptions of wheel formation observed during full daylight, compiled from correspondence with colleagues and photographers, and arranged sequentially by approximate time of day based on solar time.

### Other documents and reports on couples of *Aeshna viridis*

- (1) Early morning: One couple low in tall herbaceous vegetation, 4–5 m off water's edge, not seen before being flushed, then separated and escaped. 26-vii-2014, peat bog S of Schönberg, Mecklenburg-West Pomerania, Germany (53.8355°N, 10.9330°E); M. Frank.
- (2) Early morning: One twisted couple low in tall, dense rush vegetation, no escape attempt, ♂ not in contact with plants, head facing down. 08-viii-2012, clay pit SW of Grindau, Lower Saxony, Germany (52.6559°N, 09.6050°E), photos (Fig. 10); J. Adelman.
- (3) Mid-morning: One couple with linkage between head and appendices incomplete but normal genital linkage, no escape attempt, site and locality as (2). 07-viii-2012, photo; J. Adelman.
- (4) Mid-morning: One twisted couple, no escape attempt, site, locality, and date as (3), photo; J. Adelman.
- (5) Mid-morning: One twisted couple low in tall herbaceous vegetation next to water. ix-1987, Eggstedter Moor, Schleswig-Holstein, Germany (54.0440°N, 09.2837°E), photo, several comparable findings in 1987–1989; J. Kahlert.
- (6) Mid-morning: One twisted couple at knee height in tall herbaceous vegetation, wheel separated after disturbance and escape by flight. 09-viii-2015, Brack Predölsau in Wendland, Lower Saxony, Germany (53.1239°N, 11.0983°E), photo; E. & W. Kappes.
- (7) Mid-morning: One twisted couple low in rushes along a ditch with *S. aloides*, no escape attempt. 05-ix-1993, Hollerland, Bremen, Germany (53.0710°N, 08.5046°E), photo; J. Arlt.
- (8) Late morning: One couple low in riparian vegetation with rushes. 14-vii-1994, Wolfskuhle, Bremen, Germany (53.0387°N, 08.8092°E), photo; J. Arlt.
- (9) Late morning: One couple low in tall, dense grass along edge of ditch, no escape attempt. 27-viii-2012, ditch near Woudbloem, The Netherlands (53.2165°N, 06.7658°E), photo; F. Peels.
- (10) Late morning: One twisted couple in reed 4–5 m off water's edge, separated during photo series. 30-viii-2014, clay pit SW of Grindau, Lower Saxony, Germany (52.6559°N, 09.6050°E), photos; D. Pape-Lange.

- (11) Noon: One couple in flight and then settling low in a marshy meadow 5–8 m from a melioration ditch with *S. aloides*, escape flight in wheel position after disturbance. 01-viii-2015; Hollerland, Bremen, Germany (53.0710°N, 08.5046°E), photo; J. Arlt.
- (12) Noon: One twisted couple low in dense riparian vegetation along melioration ditch with *Stratiotes*, no escape attempt. 01-viii-2015, Hollerland, Bremen, Germany (53.0710°N, 08.5046°E), photos; J. Arlt.
- (13) Noon: One couple in flight coming from direction of pond and settling after 10 m in tall *F. ulmaria* vegetation, after 10 min wheel opened to tandem. 17-vii-2015, pond in Kiel-Hammer, Schleswig-Holstein, Germany (54.2893°N, 10.0736°E), photos; D. Bettin.
- (14) Afternoon: Wheel formation in flight over water but couple unbalanced and dropping into water. 27-vii-2012, ditch near lake Jokijärvi, Finland (61.2144°N, 24.3755°E), photos of floating couple; F. Peels.
- (15) Afternoon: Patrolling male recognises passive female sitting on *S. aloides*, wheel formation formed in flight and settled in nearby reed at 0.5 m height, escape in wheel position after disturbance. 03-viii-2011, clay pit SW of Grindau, Lower Saxony, Germany (52.6559°N, 09.6050°E), photos of couple in reed; D. Pape-Lange.
- (16) Late afternoon: One couple flying to tall herbaceous vegetation at meadow edge, settling close to ground. 04-viii-2001, Csaronda near Tiszaszalka, Hungary (48.1782°N, 22.2891°E); AS.
- (17) Late afternoon: One couple low in fen vegetation. 19-viii-2000, Prip-yat floodplain E of Hvoensk, Belarus (52.0542°N, 27.9614°E); AS.

Summarizing these reports it is clear that our documentation of a twisted wheel position does not constitute an exceptional case. The majority of all couples spotted between mid-morning and noon refer to twisted wheels. We consider this a clear evidence of regular matings in the morning twilight, when males search for females at the terrestrial rendezvous. The long duration of the twisted wheel position is striking; one couple (12) was still hanging half an hour before solar noon, which corresponds to a duration of seven hours and 20 minutes if the wheel was formed exactly at sunrise. The couple showed no escape attempts when the observer approached it with his cam-

era. This was also emphasized in other reports (2–4, 7, 9) and conforms to our own observation on 14-viii-2015 (Figs 8, 9). As the couple did not react when we clipped all disturbing plant elements for a better photo documentation, or even when we let the male climb on a finger for relocation of the couple to a twig, we had the impression of a lethargic, even catatonic condition. On the other hand, we observed the male's reaction to avoid rain drops and thus it was alert. Reports from mid morning until noon (7, 9, 12) indicate a long duration of the lethargy. We therefore interpret this behaviour as a camouflaging action to avoid predators. Such an explanation is in accordance with suggestions by TIMM (1902) and MÜNCHBERG (1930) that *A. viridis* selects perches on stems and blades that correspond with the species' thoracic coloration. In contrast to single dragonflies, twisted couples will have problems to escape immediately when disturbed or threatened, especially when the male is in an upside-down position. This is why the prolonged inactivity in the wheel may be a behavioural crypsis with an adaptive benefit.

It remains unclear when actual copulation and insemination take place in such long-hanging couples. Untwisted couples found in the morning may also have formed at sunrise, but during the collective flight. Flying wheels are reported from the period between noon and late afternoon. Altogether, the majority of matings will occur in early morning when receptive females participate in the collective flight or settle in the adjacent vegetation. On the other hand, males seem to be opportunistic and will mate whenever they discover a receptive female later in the day. This is also evidenced by three reports of wheels formed at the breeding site, on or over water; one of them when a male picked up a female sitting passively on *Stratiotes* (15), the others in flight (13, 14). However, report 13 lacks information on the situation when the mating was initiated, report 14 implies some reluctance on the part of the female, and report 15 is unusual because the female did not oviposit. All these reservations militate against regular mating initiation at breeding ponds in full daylight. As to vespertine feeding flight and collective twilight flight at the pond, there is so far no indication of participating females being receptive.

In conclusion, *A. viridis* is definitively not a late riser. In contrast, its diel rhythm is more characterised by matutinal activity than in almost all other

Palearctic Odonata species. The main function of its activity at first light seems to be the encounter of receptive females with males at two different rendezvous, where wheels are formed. We estimate that the vast majority of all copulations are initiated in early morning. The functional benefit of matutinal matings however remains a puzzle. The myth that the species sleeps throughout the morning and begins activity around noon has apparently been conceived by late rising observers. The case of *A. viridis* can teach us that our understanding of important details of a dragonfly's biology may remain obscured if research relies on standard temperate region methods in field work only.

This insight into the hitherto unknown mating strategy of *A. viridis* suggests especially that we should take a closer look on the diel activity pattern of several of its congeners. Our results allow us to conclude that, due to a specific diel activity pattern before sunrise, other *Aeshna* species with poorly understood mating behaviour might as well have evaded the eyes of odonatologists so far. We suggest that *A. grandis* especially might be a good candidate for investigation as the species is well-known for its versperine activity (e.g., MÜLLER 1993; BERNARD & KOSTERIN 2010; KARJALAINEN 2010). This Western Palearctic species is common to very common over much of Central and Northern Europe and Western Siberia (PETERS 1987; KARJALAINEN 2010) and, just as *A. viridis*, is characterised by a puzzling discrepancy between general abundance and extraordinary low number of observed instances of copulation. According to preliminary results of genetic analysis recently elucidated by SCHNEIDER et al. (2015), *A. grandis* is very closely related to *A. viridis* and might be its sister species. Thus it would be no coincidence if both species were to share a similar matutinal mating tactic.

Günther Peters remarked in his monograph on European aeshnids (PETERS 1987: 28) »Keine einzige der europäischen Aeshnidenspecies ist so gut bekannt, daß es nicht verlohnte, sich mit einer beliebigen von ihnen noch intensiv zu beschäftigen.« [Not a single one of the European aeshnid species is so well researched that it would not be worth investigating intensively.]. In this sense we hope that our findings are a good start for a better insight into the biology of the fascinating species *Aeshna viridis*.

### Acknowledgements

Hansruedi Wildermuth, Klaus Guido Leipelt, and Albert G. Orr greatly improved the manuscript. Jörg Adelman, Jörg Arlt, Delf Bettin, Christophe Brochard, Michael Frank, Jens Kählert, Eva and Wulf Kappes, Dirk Pape-Lange, and Fons Peels informed about details and/or provided photographs of mating couples. Anne Kruse (née Krawutschke), Julia Lopau, Christian Winkler, and Melanie Wittenberg gave additional information about the behaviour of *Aeshna viridis*. Günther Peters traced the progress of our study with great interest and discussed the results. We are grateful to them all.

### References

- ADENA J. & HANDKE K. 2001. Die Libellenfauna von Grünland-Grabensystemen im Bremer Raum. *Bremer Beiträge für Naturkunde und Naturschutz* 5: 91-104
- ADOMSSSENT M. 1996a. 1. Nachtrag zur laubenburgischen Libellenfauna. *Bombus* 3: 75-77
- ADOMSSSENT M. 1996b. Bitte um Mitteilungen von Beobachtungen zur Kopula von *Aeshna viridis*. *Hagenia* 12: 13-14
- BERNARD R. & KOSTERIN O.E. 2010. Biogeographical and ecological description of the odonata of eastern Vasyugan Plain, west Siberia, Russia. *Odonatologica* 39: 1-28
- BORKENSTEIN A. & JÖDICKE R. 2016. Crepuscular collective flight of *Aeshna viridis* in Central Europe (Odonata: Aeshnidae). *Notulae odonatologicae* 5 (8): accepted
- BOS F. & WASSCHER M. 1997. Veldgids Libellen. KNNV Uitgeverij, Utrecht
- BRUNKEN H., HEIN M. & KLUGKIST H. 2012. Auswirkungen ökologischer Grabenräumung auf Fische und die Grüne Mosaikjungfer (*Aeshna viridis*) in Bremer Natura-2000-Gebieten. *Natur und Landschaft* 87: 370-375
- BUCK K. 1990. Libellen im Kreis Steinburg. *Libellula* 9: 67-70
- BUCK K. 1994. Libellen im Kreis Steinburg – Bestandserfassung der Funde aus den Jahren 1989 bis 1992. *Libellula* 13: 81-171
- BÜTTGER H. & FINCH O.-D. 2003. Libellenzönosen an Krebscherengraben der südlichen Wesermarsch unter besonderer Berücksichtigung der „FFH-Art“ *Aeshna viridis* Eversmann, 1936 [sic] (Insecta: Odonata). *Oldenburger Jahrbuch* 103: 317-331
- CORBET P.S. 1962. A biology of dragonflies. Witherby, London
- CORBET P.S. 1965. Asymmetry in eocrepuscular periodicities of insects. *The Canadian Entomologist* 97: 878-880
- CORBET P.S. 1999. Dragonflies. Behaviour and ecology of Odonata. Harley Books, Colchester
- DE BOER E.P., VAN HIJUM E., BROCHARD C. & VAN SEIJEN R.B. 2014. Libellenrijk Fryslân. Mei ljochtsjende wjukken oer it wetter. Bureau FaunaX, Gorredijk
- HAACKS M. & PESCHEL R. 2007. Die rezente Verbreitung von *Aeshna viridis* und *Leucorhinia pectoralis* in Schleswig-Holstein – Ergebnisse einer vierjährigen Untersuchung (Odonata: Aeshnidae, Libellulidae). *Libellula* 26: 41-57

- HAACKS M., WINKLER C., BRUENS A. & RÖBBELN F. 2015. Grüne Mosaikjungfer – *Aeshna viridis* (Eversmann, 1836). In: Arbeitskreis Libellen in der Faunistisch-Ökologischen Arbeitsgemeinschaft e.V. (Ed.), Die Libellen Schleswig-Holsteins: 242-248. Natur+Text, Rangsdorf
- HADDOW A.J. 1945. The mosquitoes of Bwamba County, Uganda. II. Biting activity with special reference to the influence of microclimate. *Bulletin of entomological Research* 36: 33-73
- JURZITZA G. 1969. Ein Beitrag zur Kenntnis des Verhaltens der *Aeshna viridis* Eversmann (Odonata, Aeshnidae). *Faunistisch-ökologische Mitteilungen* 3: 260-261
- KÄHLERT J. 1976. Beobachtungen an Libellen in Süddithmarschen. Wissenschaftliche Hausarbeit zur Ersten Staatsprüfung für das Lehramt an Realschulen, Flensburg
- KÄHLERT J. 1999. Die Libellen Europas auf CD-ROM. Version 1.2. J. Kählert, Burg
- KARJALAINEN S. 2010. Suomen sudenkorennot. Tammi, Helsinki [In Finnish]
- KASTNER F., MÜNKENWARF M & BUCHWALD R. 2011. Zum Vorkommen der FFH-Libellenart *Aeshna viridis* Eversmann, 1836 (Odonata: Aeshnidae) in Krebscherengraben der Hunte- und Wesermarsch, Niedersachsen. *Drosera* 2010: 103-108
- KASTNER F., BUCHWALD R., KÖRNER F., MARXMEIER U., STEFFENS P., WINKLER C., JÖDICKE K. & MAUSCHERNING I. 2016. Wiederansiedlungen als Maßnahmen des Artenschutzes. Die Grüne Mosaikjungfer (*Aeshna viridis*, Odonata) in Niedersachsen und Schleswig-Holstein – ein Beitrag zum Habitatverbund. *Naturschutz und Landschaftsplanung* 48: 87-96
- KRAWUTSCHKE A. 1999. Zur Ökologie und Biologie ausgewählter Aeshniden-Arten (Odonata: Anisoptera) im Naturpark Westhavelland. Diplomarbeit, Universität Hamburg
- MAUERSBERGER R., BAUHUS S. & SALM P. 2005. Zum Vorkommen der Grünen Mosaikjungfer (*Aeshna viridis* Eversmann) im Nordosten Brandenburgs (Odonata: Aeshnidae). *Naturschutz und Landschaftspflege in Brandenburg* 14: 17-24
- MAUSCHERNING I., JÖDICKE K., NEUMANN H. & WINKLER C. 2011. Artenhilfsprojekt Grüne Mosaikjungfer (*Aeshna viridis*) in Dithmarschen. *Dithmarschen* 1/2011: 21-25
- MILLER A.K., MILLER P.L. & SIVA-JOTHY M.T. 1984. Pre-copulatory guarding and other aspects of reproductive behaviour in *Symptetrum depressiusculum* (Selys) at rice fields in southern France (Anisoptera: Libellulidae). *Odonatologica* 13: 407-414
- MÜLLER O. 1993. Beobachtungen zur abendlichen Dämmerungsaktivität von *Aeshna grandis* (Linnaeus, 1758) und *Aeshna mixta* (Latreille, 1805) (Odonata, Aeshnidae). *Entomologische Nachrichten und Berichte* 37: 39-44
- MÜNCHBERG P. 1930 Zur Biologie der Odonatengenera *Brachytron* Evans und *Aeshna* Fabr. *Zeitschrift für Morphologie und Ökologie der Tiere* 20: 172-232
- MÜNCHBERG P. 1956. Zur Bindung der Libelle *Aeshna viridis* Eversm. an die Pflanze *Stratiotes aloides* L. (Odon.). *Nachrichtenblatt der bayerischen Entomologen* 5: 113-118
- PETERS G. 1987. Die Edellibellen Europas. Aeshnidae. Die Neue Brehm-Bücherei 585. Ziemsen, Wittenberg
- RANTALAINEN E. & KANERVO E. 1928. *Aeshna viridix* esiintymisestä ja elintavoista Suomessa [Occurrence and ecology of *Aeshna viridis* in Finland]. *Luonnon ystävää* 32: 161-170 [in Finnish]

- REHFELDT G. 1993. Heterospecific tandem formation in *Sympetrum depressiusculum* (Selys) (Odonata: Libellulidae). *Odonatologica* 22: 77-82
- REHFELDT G. 1995. Natürliche Feinde, Parasiten und Fortpflanzung von Libellen. Odonatological Monographs 1. Aqua & Terra, Braunschweig
- SCHMIDT B. 1990. Faunistisch-ökologische Untersuchungen zur Libellenfauna (Odonata) der Streuwiesen im NSG Wollmatinger Ried bei Konstanz. Auswirkungen und Bedeutung der Streuwiesenmahd und Überschwemmungen auf die Libellenbesiedlung. *Naturschutzforum* 3/4: 39-80
- SCHMIDT B. 1993. Ökologische Untersuchungen zur Libellenfauna der Petite Camargue Alsacienne 1993; speziell der Sumpf-Heidelibelle (*Sympetrum depressiusculum*) unter Berücksichtigung der Vegetation und der Hydrodynamik. Berichte Forschungsstation RANA Petite Camargue Alsacienne (St. Louis-Neuweg) 1993: 1-6
- SCHMIDT E. 1929. 7. Ordnung: Libellen, Odonata. (Schillebolde, Teufelsnadeln, Augenstecher, Wasserjungfern.). In: Brohmer P., Ehrmann P. & Ulmer G. (Eds), Die Tierwelt Mitteleuropas 4: 1-66. Quelle & Meyer, Leipzig
- SCHMIDT E.G. 1975. *Aeshna viridis* Eversmann in Schleswig-Holstein, Bundesrepublik Deutschland (Anisoptera: Aeshnidae). *Odonatologica* 4: 81-88
- SCHNEIDER T., SCHNEIDER E., SCHNEIDER J., VIERSTRAETE A. & DUMONT H.J. 2015. *Aeshna vercanica* sp. nov. from Iran with a new insight into the *Aeshna cyanea*-group (Odonata: Aeshnidae). *Odonatologica* 44: 81-106
- SCHRÖTER A. 2011. A mass migration of *Aeshna affinis* in southern Kyrgyzstan: attempt to provide a spatial and temporal reconstruction (Odonata: Aeshnidae). *Libellula* 30: 203-232
- SCHRÖTER A. 2014. Abendliches Schwarmverhalten von *Aeshna viridis* – auch in Mitteleuropa? *Libellennachrichten* 22: 13-14
- TIMM W. 1902. Dämmerungsfieger unter den einheimischen Libellen. Biologische Beobachtungen. *Insekten-Börse* 19: 180, 188-189
- TÜMPEL R. 1898-1901. Die Geradflügler Mitteleuropas. M. Wilckens, Eisenach [Chapter on *Aeshna viridis* delivered in 1899]
- WESENBERG-LUND C. 1913. Odonaten-Studien. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 6: 115-228, 373-422
- WILDERMUTH H. 1993. Habitat selection and oviposition site recognition by the dragonfly *Aeshna juncea* (L.): an experimental approach in natural habitats (Anisoptera: Aeshnidae). *Odonatologica* 22: 27-44
- WILDERMUTH H. 2000. Alternative Taktiken bei der Weibchensuche von *Boyeria irene* (Odonata: Aeshnidae). *Libellula* 19: 143-155
- WITTENBERG M., KASTNER F. & BUCHWALD R. 2015. Die Larvenentwicklung von *Aeshna viridis* im NSG Westliches Hollerland, Bremen (Odonata: Aeshnidae). *Libellula* 34: 3-16
- ZIEBELL S. & BENKEN T. 1982. Zur Libellenfauna in West-Niedersachsen (Odonata). *Drosera* '82: 135-150