



## Occurrence of *Aeshna viridis* in marsh ditches in relation to habitat conditions (Odonata: Aeshnidae)

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Habitat loss and fragmentation induce a decline and endangerment of freshwater organisms such as *Aeshna viridis*, an endangered dragonfly species characterised by a specific insect–plant association to the macrophyte *Stratiotes aloides*. In order to implement conservation measures, a good level of knowledge about the occurrence, habitat requirements and quality, as well as patch size of the species is important. We analysed the influence of several habitat parameters on the presence/absence and abundance of *A. viridis* exuviae using habitat models (generalised linear mixed-effect models). The ditches populated by *A. viridis* were classified as moderately polluted and meso- to eutrophic with a high cover of emerged *S. aloides* stands. The main factor contributing to the presence of *A. viridis* was the coverage of emerged *S. aloides* combined with the ditch width. The 90% probability of the presence of *A. viridis* was achieved at a cover of 14% (8.4 m<sup>2</sup>) and/or 77% (46.2 m<sup>2</sup>) of emerged *S. aloides*. The number of *A. viridis* exuviae was positively affected by the cover of emerged *S. aloides* and negatively affected by the sediment thickness, water maintenance and water temperature in March and August. The habitat parameters – water temperature and sediment thickness – are associated with *S. aloides* in the beginning of siltation of ditch succession. If ditch cleaning takes place during larvae development, eggs and larvae are removed by these procedures. In an optimal situation, the *S. aloides* populations occur in a mosaic of different states of siltation, which is managed by adapted water maintenance.

**Keywords:** dragonfly; conservation; habitat quality; patch size; *Stratiotes aloides*; habitat model

### Introduction

The intensification of land use and the degradation of near-natural landscapes by human activities have induced, and still induce, a homogenisation and eutrophication of habitats, habitat loss and landscape fragmentation, as well as their own isolation (Sala et al., 2000; Stoate et al., 2009; Watt et al., 2007). This results in population decline of plant and animal species up to local or regional extinction processes and biodiversity losses (Dolny, Harabis, Barta, Lhota, & Drozd, 2012; Dudgeon et al., 2006; Ekroos, Heliola, & Kuussaari, 2010; Lehtinen, Galatowitsch, & Tester, 1999).

Aquatic ecosystems are particularly affected by anthropogenic impacts (Dudgeon et al., 2006; Richter, Braun, Mendelson, & Master, 1997; Sand-Jensen, Riis, Vestergaard, & Larsen, 2000; Ward, 1998). The degradation of waterbodies has induced a decline and endangerment of freshwater organisms such as dragonflies (Odonata) (Clausnitzer et al., 2009; Kalkman et al., 2010).

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Dragonflies populate rivers, lakes, ponds, ditches, bogs and other (semi-)aquatic habitats as semi-aquatic insects with aquatic larvae and terrestrial adults (Boudot & Kalkman, 2015; Corbet, 1999).

The predominant number of European Odonata are not particularly dependent upon strict habitat requirements (Boudot & Kalkman, 2015; Suhling et al., 2015). However, there are species such as *Aeshna viridis* Eversmann, 1836 with special insect–plant associations, which are strictly linked to specific habitat features and are particularly sensitive to habitat loss and degradation (Corbet, 1999; Harabis & Dolny, 2012; Kalkman et al., 2008). *Aeshna viridis* has a strong association with the macrophyte *Stratiotes aloides* as oviposition substrate and as larval habitat (Münchberg, 1930; Rantala, Ilmonen, Koskimaki, Suhonen, & Tynkynen, 2004; Suutari, Rantala, Salmela, & Suhonen, 2004; Wesenberg-Lund, 1913), which are found in either standing or slowly flowing mesotrophic to moderately eutrophic waters (Boudot & Kalkman, 2015; Wildermuth & Martens, 2014). The dragonfly species can be classified as a habitat specialist and characteristic species of *S. aloides* waterbodies (Boudot & Kalkman, 2015; Suutari et al., 2009). *Aeshna viridis* has been categorised as “near threatened” in the Red List of Europe (Kalkman et al., 2010) and is listed in the Convention on the Conservation of European Wildlife and Natural Habitats (Annex II), as well as the Fauna-Flora-Habitats Directive (Annex IV). The distribution area ranges from the Netherlands, Northern Germany, Southern Scandinavia and Eastern Europe to Western Siberia (Boudot & Kalkman, 2015).

*Stratiotes aloides* is a mostly half-immersed, free-floating water macrophyte with a rosette, which hibernates at the bottom of the waters and rises to the surface in spring. The plant is mainly found in standing meso- to eutrophic waters such as ponds, ditches and lakes, but its natural habitats are waters of regularly inundated flood plains (Casper & Krausch, 2008; Cook & Urmig-König, 1983). However, various changes in water chemistry, particularly eutrophication, have caused a population decrease in *S. aloides* (Roelofs, 1991; Smolders, Lamers, den Hartog, & Roelofs, 2003). The significance of *S. aloides* as oviposition substrate of *A. viridis* has been known for a long time (Fudakowski, 1932; Münchberg, 1930; Wesenberg-Lund, 1913) but there are only a few quantitative studies about the relevance of surface coverage of *S. aloides* for the occurrence of *A. viridis* (Fliedner, 1996; Glitz, Hohmann, & Piper, 1989; Mauersberger, Bauhus, & Salm, 2005; Suhonen, Suutari, Kaunisto, & Krams, 2013) and there are even fewer details about other habitat parameters which influence the presence or absence and abundance of *A. viridis* (De Jong, 1999; Mauersberger et al., 2005). Suhonen et al. (2013) demonstrate that the number of *A. viridis* in lakes is affected by the patch area of *S. aloides*. However, in Central Europe *A. viridis* occurs predominantly in the ditches of wet grasslands (Adena & Handke, 2001; De Jong, 1999; Gerard, 2006; Kastner, Mündenwarf, & Buchwald, 2011; Klugkist, Haacks, & Kruse, 2015). Furthermore, stands of *S. aloides* in ditches are affected by periodic water maintenance (Nagler & Müller, 2012) and, due to the in-line shape of ditches (Handke, 1999), the edge effect is more distinctive.

In order to counteract species decline and biodiversity loss, specific programs aimed at population and habitat conservation, as well as habitat improvement, have been conceived. An important prerequisite for the implementation of any conservation measures is a good level of knowledge about the quality and area of the species' reproduction habitats. Species Action Plans for threatened dragonflies, with information about occurrence, habitat requirements, endangerment factors and suggested measures exist, for example *Coenagrion ornatum* and *Oxygastra curtisii* in Germany; *A. viridis* in the Netherlands and *Leucorrhinia pectoralis* in Switzerland (Burbach & Winterholler, 2001; De Jong & Verbeek, 2001; Ott, Schorr, Trockur, & Lingenfelder, 2007; Wildermuth, 2013).

The aim of this study was to analyse habitat preferences of *A. viridis* beyond the association to *S. aloides* as oviposition substrate and as larval habitat. Therefore, we conducted a multiyear field study in marshland ditches to test if the vegetation structure in ditch morphology and/or

physico-chemical water parameters influence the occurrence of *A. viridis*. We analysed the significance of these habitat parameters for the presence or absence and abundance of population using habitat modelling. In order to be able to make a statement on the required patch size of *A. viridis*, the threshold of *S. aloides* coverage for the 50% and/or 90% probability levels was calculated for the presence of *A. viridis*.

## Methods

### Study area

The study sites were divided into eight sub-areas located in the river basin of the Hunte and Weser Rivers, between the cities of Oldenburg, Lower Saxony and Bremen, North Western Germany (53.158543° N 8.277195° E and 53.110279° N 8.872268° E, Figure 1), with an east–west extension of 39 km. The study was in the marshlands of NW Germany and can be characterised as a river floodplain situated at an elevation of 1–2 m below and above sea level (Meisel, 1959–1962). The landscape is largely dominated by wet grasslands with a high density of drainage ditches (6.8 km km<sup>-2</sup>; Kiel, Kastner, Lühken, & Schröder, 2012) with different types of ditch vegetation, including, amongst others, *S. aloides*. Due to siltation, the ditches (mean width of about 2 m) have to be maintained frequently.

The *A. viridis* population in the Weser lowlands of Bremen has been known since 1905 and is considered one of the largest populations in Germany (Geissler, 1905; Klugkist et al., 2015). The populations in the Hunte-Weser lowland areas between Oldenburg and Bremen have been known since 1977 (sub-area 5), since 1985/86 (sub-area 3, 4 and 7) and since 2007 (sub-area 1 and 2),

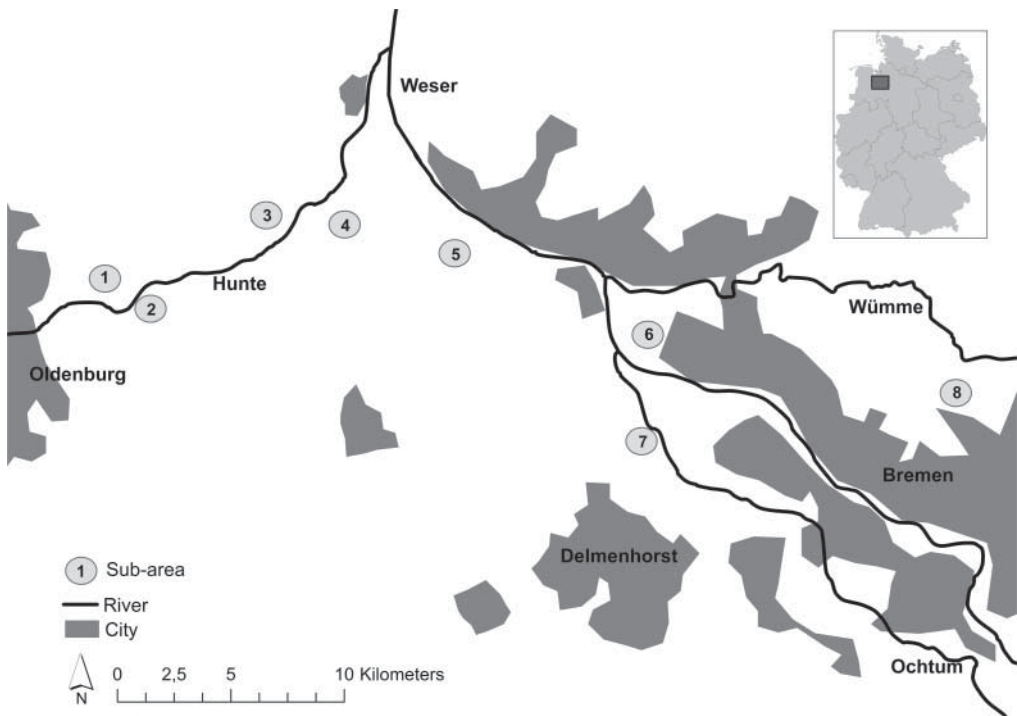


Figure 1. Study area with eight sub-areas between Oldenburg and Bremen in North Western Germany.

respectively (Kastner et al., 2011; Ziebell & Benken, 1982; written message Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz) and are not as large as those around Bremen.

### *Field methods and ecological parameters*

In 2011, 2012 and 2013, we studied 69 ditches (study plots) with *S. aloides* vegetation in eight sub-areas (2011 = 40, 2012 = 62, 2013 = 63; total plots = 165). Each year, from the middle of June until the middle of August, we collected *A. viridis* exuviae once a week in sections of 25 m. In order to examine the entire spectrum of existing characteristics of *S. aloides* stands, the sections were distributed in the ditches in such a way that dense and loose plant populations were included. The collection of exuviae was completed in August, if we found no further exuviae after two consecutive visits. If the weather forecast announced bad weather (heavy rain and/or wind), the exuviae were collected before the rainfalls, as far as possible. Afterwards, the species were determined using identification keys according to Bellmann (2007), Gerken and Sternberg (1999) and Heidemann and Seidenbusch (2002).

In order to characterise the quality of the habitat, we recorded various parameters (Table 1) for each plot in 2011, 2012 and 2013. The physico-chemical water parameters (pH, conductivity, oxygen content, oxygen saturation, chloride, total hardness, calcium, magnesium, total nitrogen, nitrite, nitrate, ammonium, total phosphate, ortho-phosphate, sulphate and iron) were measured three times a year (in March, August and November/December) and the mean for each year was calculated for statistical analyses. The water quality was classified by Länderarbeitsgemeinschaft Wasser (LAWA, 1998) and Pott and Remy (2000). The water temperature was also measured in March, August and November/December. Conductivity, oxygen, pH and water temperature were measured in the field, while all other chemical water parameters were measured in the laboratory. The vegetation cover, as well as the remaining habitat parameters, were measured once a year in August. Due to the two-year larvae development of *A. viridis* (Münchberg, 1930; Wesenberg-Lund, 1913; Wittenberg, Kastner, & Buchwald, 2015), we considered “ditch cleaning” as a yes/no variable for each investigated year, and “ditch” if this event took place during the last two years.

### *Statistical analyses*

Since some plots within the study area were not independent of each other and the density data are count data and did not fit a normal distribution, we conducted generalised linear mixed-effect models (GLMM, Zuur, Hilbe, & Ieno, 2013; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) using R-2.15.3 (R Core Team, 2013) to analyse which parameters affected the data best (Table 1). Since the data collection took place from the middle of June until the middle of August, and thus did not cover the entire hatching period of all Aeshnidae, the accompanying species were not included in the models.

To reduce the number of the 16 physico-chemical water parameters and deal with correlation between them (pH, conductivity, oxygen content, oxygen saturation, chloride, total hardness, calcium, magnesium, total nitrogen, nitrite, nitrate, ammonium, total phosphate, ortho-phosphate, sulphate and iron), a principal component analysis (PCA, Leyer & Wesche, 2008; Quinn & Keough, 2002) for Model 1 ( $N_{\text{plots}} = 165$ ) and Model 2 ( $N_{\text{plots}} = 78$ ) was conducted to create new variables as summarising factors. The new variables for Model 1 (PCA 1) represents four independent principal components (PCs) with an eigenvalue  $> 1$  and explains 76% of the total variance in the dataset. The new variable one, referred to as the geogenic factor (PC 1), was positively correlated with iron (Spearman's rho: 0.7,  $p < 0.001$ ) and negatively correlated with

Table 1. Habitat parameters used in the generalised linear mixed-effect models (GLMM) for *Aeshna viridis*. PCA: principle component analysis, VIF: variance inflation factor.

Parameter	Response variable	
	Variable used in Model 1a	Variable used in Model 2a
Presence or absence of <i>A. viridis</i> exuviae	yes	no
Number of <i>A. viridis</i> exuviae	no	yes
<b>Predictor variable</b>		
<b>Fixed effects</b>		
Year (2011, 2012, 2013)	yes	no (VIF > 3)
Water maintenance (ditch cleaning during the last two years) (Yes/No)	yes	yes
Total coverage of <i>S. aloides</i> (%) <sup>a</sup>	no (VIF > 3)	no (VIF > 3)
Coverage of submerged <i>S. aloides</i> stands (%) <sup>a</sup>	yes	no (VIF > 3)
Coverage of emerged <i>S. aloides</i> stands (%) <sup>a</sup>	yes	yes
Total coverage of aquatic vegetation (%) <sup>b</sup>	yes	yes
Coverage of submerged vegetation (%) <sup>b</sup>	no (VIF > 3)	no (VIF > 3)
Coverage of emerged vegetation (%) <sup>b</sup>	no (VIF > 3)	no (VIF > 3)
Emerged vegetation height (cm)	yes	yes
Sediment thickness (cm)	yes	yes
Water depth (cm)	yes	yes
Width of the ditches (m)	yes	yes
Shading (%)	yes	yes
Water temperature in March (°C)	no (VIF > 3)	yes
Water temperature in August (°C)	yes	yes
Water temperature in November/December (°C)	no (VIF > 3)	no (VIF > 3)
Physico-chemical water parameters <sup>c</sup> , used the new variables build by PCA 1 <sup>d</sup>	yes	–
New variable one (PC1) called geogenic factors		
New variable two (PC2) called nitrogen		
New variable three (PC3) called chloride and oxygen		
New variable four (PC4) called phosphate		
Physico-chemical water parameters <sup>c</sup> , used the new variables build by PCA 2 <sup>e</sup>	–	yes
New variable one (PC1) called geogenic factors		
New variable two (PC2) called nitrogen		
New variable three (PC3) called total phosphate		
New variable four (PC4) called oxygen		
New variable five (PC5) called ortho-phosphate		
<b>Random effects</b>		
Plot	yes	yes
Sub-area	yes	yes

<sup>a</sup> Measured scale (1% = < 5% (1 individual), 2% = < 5% (2 to 5 individuals), 4% = < 5% (6 to 50 individuals), 10% = 5–15%, 20% = 15–25%, 30% = 25–35%, 40% = 35–45%, 50% = 45–55%, 60% = 55–65%, 70% = 65–75%, 80% = 75–85%, 90% = 85–95%, 100% = 95–100%)

<sup>b</sup> Measured scale (2.5% = < 5%, 8.8% = 5–12.5%, 20.0% = 12.5–25%, 37.5% = 25–50%, 62.5% = 50–75%, 87.5% = 75–100%)

<sup>c</sup> Measured physico-chemical water parameters: pH, conductivity, oxygen content, oxygen saturation, chloride, total hardness, calcium, magnesium, total nitrogen, nitrite, nitrate, ammonium, total phosphate, ortho-phosphate, sulphate and iron.

<sup>d</sup> PCA 1: four PCs with eigenvalues > 1 explained 76% of the total variance in the dataset.

<sup>e</sup> PCA 2: five PCs with eigenvalues > 1 explained 82% of the total variance in the dataset.

total hardness (Spearman's rho: –0.9), magnesium (Spearman's rho: –0.9,  $p < 0.001$ ), calcium (Spearman's rho: –0.8,  $p < 0.001$ ) and conductivity (Spearman's rho: –0.9,  $p < 0.001$ ). The second new variable (PC 2), called nitrogen, was positively correlated with ammonium (Spearman's rho: 0.9,  $p < 0.001$ ) and total nitrogen (Spearman's rho: 0.8,  $p < 0.001$ ). The third new variable (PC 3), called chloride and oxygen, was positively correlated with chloride (Spearman's rho: 0.6,  $p < 0.001$ ) and negatively correlated with oxygen content (Spearman's rho: –0.6,  $p < 0.001$ ) and oxygen saturation (Spearman's rho: –0.6,  $p < 0.001$ ). The fourth new variable (PC 4), referred to as phosphate, had a positive correlation with total phosphate (Spearman's rho: 0.8,  $p < 0.001$ ). The new variables for Model 2 (PCA 2) represent five independent

principal components (PCs) with eigenvalues  $> 1$  and explains 82% of the total variance in the dataset. The new variable one, called geogenic factor (PC 1), was positively correlated with iron (Spearman's rho: 0.8,  $p < 0.001$ ), and negatively correlated with conductivity (Spearman's rho:  $-0.9$ ,  $p < 0.001$ ), total hardness (Spearman's rho:  $-0.9$ ,  $p < 0.001$ ), magnesium (Spearman's rho:  $-0.9$ ,  $p < 0.001$ ), calcium (Spearman's rho:  $-0.9$ ,  $p < 0.001$ ) and pH (Spearman's rho:  $-0.7$ ,  $p < 0.001$ ). The second new variable (PC 2), referred to as nitrogen, was positively correlated with total nitrogen (Spearman's rho: 0.7,  $p < 0.001$ ) and ammonium (Spearman's rho: 0.7,  $p < 0.001$ ). The third new variable (PC 3), named total phosphate had a positive correlation with total phosphate (Spearman's rho: 0.7,  $p < 0.001$ ). The fourth new variable (PC 4) called oxygen was negatively correlated with oxygen content (Spearman's rho:  $-0.5$ ,  $p < 0.001$ ) and the fifth new variable (PC 5), called ortho-phosphate was negatively correlated with ortho-phosphate (Spearman's rho:  $-0.5$ ,  $p < 0.001$ ).

In the first model (Model 1), we calculated a GLMM with a binomial distribution (function *glmer*, package "lme4", version 1.0.4; Bates, Bolker, Maechler, & Walker, 2013;  $N_{\text{plots}} = 165$ ) to analyse the effect of the habitat parameters on the presence or absence of *A. viridis* (Table 1: Model 1). In the second model (Model 2), using only presence data, we calculate a GLMM with a negative binomial distribution (function *glmmadmb*, package "glmmADMB", version 0.8.0; Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2014;  $N_{\text{plots}} = 78$ ) to analyse the relationship between the number of *A. viridis* and habitat parameters (Table 1: Model 2). For both GLMMs we used the study plot within the sub-area as a nested random factor. The time factor (represented in this study as year) was used as a predictor variable because the number of levels ( $n = 3$ ) was too small to use the factor as a random effect (Zuur et al., 2013). In order to deal with multicollinearity between the habitat parameters in Model 1 and Model 2, we analysed all variables including the PCs by the variance inflation factor; variables with values  $> 3$  are not included in the model and the calculation was repeated until all values were below this threshold (Zuur et al., 2009). The variables in the final models were checked again for correlation by Kendall's rank correlation. We used stepwise backward selection to remove non-significant variables ( $p < 0.05$ ) from the full model. Because *S. aloides* is an important habitat factor for *A. viridis*, Model 1 and Model 2 also were built only with coverage of emerged *S. aloides* (Model 1b and 2b) and the models were compared (a with b) using *anova* and the Akaike information criterion (AIC), which measured goodness of fit and model complexity. The lower the AIC, the better the model fits the data (Zuur et al., 2009, 2013). For the final models, we produced residual plots for validation (Zuur et al., 2009, 2013). For evaluation of the final models, a conditional coefficient of determination ( $R^2$ ) was calculated (function *r.squaredGLMM*, package "MuMIn", version 1.9.13, Barton (2013) and as this cannot calculate the  $R^2$  for the negative binomial GLMM, the function *r2beta*, package "r2glmm", version 0.1.1, Jaeger (2016) was also used).

## Results

In total we collected 2225 *A. viridis* exuviae (2011 = 563, 2012 = 561, 2013 = 1101), as well as 53 *Aeshna cyanea* (Müller, 1764), 614 *Aeshna grandis* (Linnaeus, 1758), 38 *Aeshna isosceles* (Müller, 1767), 8 *Aeshna juncea* (Linnaeus, 1758), 669 *Aeshna mixta* Latreille, 1805 and 1 *Anax imperator* Leach, 1815 exuviae. *Aeshna viridis* was present in 80 (48.5%) samples (2011 = 22, 2012 = 29, 2013 = 29). The mean abundance of *A. viridis* exuviae per 25 m was  $13.5 \pm 36.3$  (mean  $\pm$  SD,  $n = 165$ ) and varied from 0 to 284 exuviae. The results of the habitat parameter recording are available as supplementary data (Supplement 1). The occupied plots were characterised by a high cover of emerged *S. aloides* stands (Figure 2, Supplement 1). The waterbody was classified according to LAWA (1998, median of quality class) and Pott and Remy (2000) as moderately polluted and meso- to eutrophic.



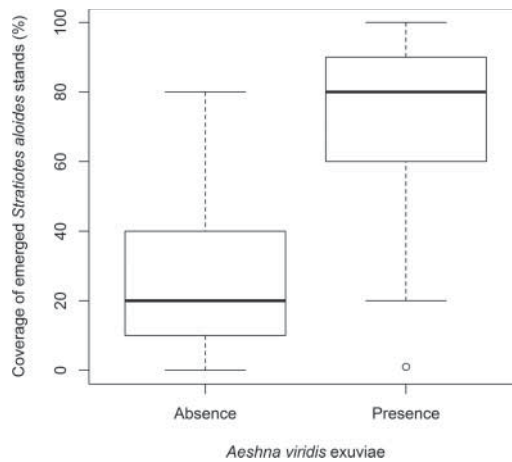


Figure 2. Boxplot of the coverage of emerged *Stratiotes aloides* stands (%) in plots against the presence or absence of *Aeshna viridis* exuviae (absence [n = 85], presence [n = 80]).

Table 2. Relationship between the presence of *Aeshna viridis* exuviae (binomial response variable: presence [n = 80] vs. absence [n = 85]) and environmental parameters (predictor variable, Table 1) in the binomial generalised linear mixed-effect models (GLMM). Random factor was “plot” nested within “sub-area”. Non-significant predictors were excluded from the final model by stepwise backward selection ( $p > 0.005$ ). N: number of observations analysed, AIC: Akaike information criterion.

Predictor variable/ model coefficients	N	Estimate	Z-value	p-value	AIC	R <sup>2</sup>	50%/90% probability of presence of <i>A. viridis</i>
<b>1a) Model with habitat parameters</b>	165				121.4584	0.71	
Intercept		-4.26989	-4.457	< 0.001			
Width of the ditches (m)		0.46248	2.319	0.02			mean: 2.4
Coverage of emerged <i>S. aloides</i> stands (%)		0.06863	6.251	< 0.001			9/14
<b>1b) Model with only <i>S. aloides</i></b>	165				125.069	0.67	
Intercept		-3.21534	-4.22	< 0.001			
Coverage of emerged <i>S. aloides</i> stands (%)		0.06998	6.42	< 0.001			46/77

The presence of *A. viridis* analysed in a binomial GLMM (Model 1a), was positively affected by the coverage of emerged *S. aloides* and the width of the ditches. The new variables of the physico-chemical water factors (PC 1 to PC 4), water temperature, as well as the other habitat parameters, did not contribute to the model (Table 2: Model 1a, Figure 3). The percentage of emerged *S. aloides* and width of the ditches did not correlate with each other (Kendall’s rank correlation tau: 0.25,  $p < 0.001$ ). The researched length of ditches was 25 m and the average width was 2.4 m; the 50% and/or 90% probability of the presence of *A. viridis* was achieved with a coverage of 9% (5.4 m<sup>2</sup>) and/or 14% (8.4 m<sup>2</sup>) emerged *S. aloides* (Figure 3). The model with only the coverage of emerged *S. aloides* (Table 2: Model 1b, Figure 4) was significantly different from the model with the two parameters (Model 1a) ( $\chi^2 = 5.6106$ , df = 1,  $p = 0.018$ ). The AIC of the model with only *S. aloides* was larger than that of the model with the two parameters, and the coefficient of determination (R<sup>2</sup>) was lower. In the model with one variable, i.e. the coverage of *S. aloides* alone, the 50% and/or 90% probability of the presence of *A. viridis* was achieved with a coverage of 46% (27.6 m<sup>2</sup>) and/or 77% (46.2 m<sup>2</sup>) of emerged *S. aloides*.

The number of *A. viridis* (Model 2a) was best explained by a combination of five habitat parameters. The number of exuviae was positively affected by the coverage of emerged *S. aloides* stands and negatively affected by sediment thickness, water maintenance and water temperature

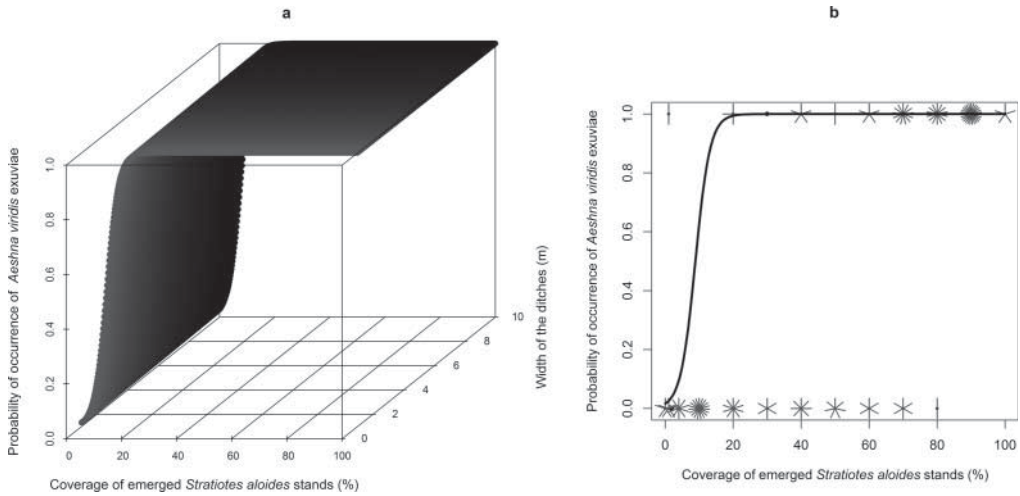


Figure 3. Visualisation of the relationship between the presence and absence of *Aeshna viridis* exuviae (binomial response variable: presence [n = 80] vs. absence [n = 85]) and habitat parameters (predictor variable) by the binomial generalised linear mixed-effect models (GLMM, Model 1a). Random factor was “plot” nested within “sub-area”. Non-significant predictors were excluded from the final model by stepwise backward selection ( $p > 0.005$ ). (a) Width of the ditches from 1 to 10 m. (b) Mean width of the ditches from 2.4 m. Sunflower plot: Repeated values of y are counted and the numbers of cases are represented at each point as scatter.

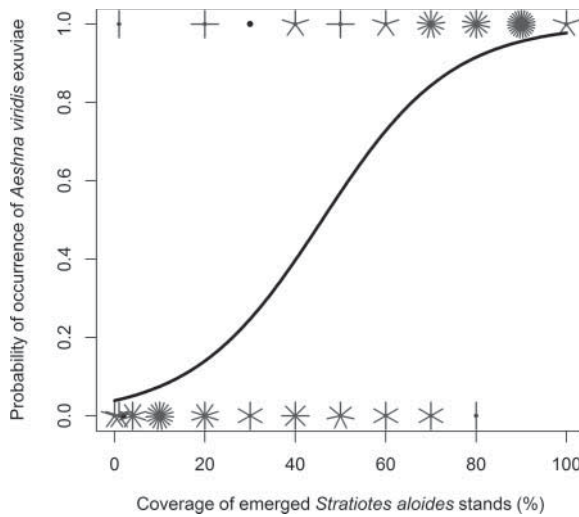


Figure 4. Visualisation of the relationship between the presence and absence of *Aeshna viridis* exuviae (binomial response variable: presence [n = 80] vs. absence [n = 85]) and coverage of emerged *Stratiotes aloides* stands exclusively (predictor variable) by the binomial generalised linear mixed-effect models (GLMM, Model 1b). Random factor was “plot” nested within “sub-area”. Sunflower plot: Repeated values of y are counted and the numbers of cases are represented at each point as scatter.

in March and August (Table 3: Model 2a, Figure 5). The sediment thickness and water temperature (Kendall’s rank correlation tau (temperature March): 0.07,  $p = 0.184$ ; tau (temperature August):  $-0.07$ ,  $p = 0.167$ ), as well as sediment thickness and percentage of emerged *S. aloides* (Kendall’s rank correlation tau:  $-0.14$ ,  $p = 0.078$ ); or water temperature and percentage of emerged *S. aloides* (Kendall’s rank correlation tau (temperature March): 0.06,  $p = 0.432$ ; tau



Table 3. Relationship between the number of *Aeshna viridis* exuviae ( $n = 78$ ) and environmental parameters (predictor variable, Table 1) in the negative binomial generalised linear mixed-effect models (GLMM). Random factor was “plot” nested within “sub-area”. Non-significant predictors were excluded from the final model by stepwise backward selection ( $p > 0.005$ ). SD: standard deviation of the random effect, N: number of observations analysed, AIC: Akaike information criterion.

Predictor variable/ model coefficients	N	Estimate	Z value	p-value	AIC	Negative binomial dispersion parameter $\pm$ SD	R <sup>2</sup>
<b>2a) Model with habitat parameter</b>	78				612.9	1.734 $\pm$ 0.43118	0.493
Intercept		6.78726	4.17	< 0.001			
Water maintenance (ditch cleaning during the last two years) (yes)		-0.62416	-2.47	0.014			
Sediment thickness (cm)		-0.01451	-2.86	0.004			
Coverage of emerged <i>S. aloides</i> stands (%)		0.02879	4.77	< 0.001			
Water temperature March (°C)		-0.0925	-3.36	0.001			
Water temperature August (°C)		-0.23563	-3.21	0.001			
<b>2b) Model with only <i>S. aloides</i></b>	78				627.3	1.2247 $\pm$ 0.25387	0.283
Intercept		0.23612	0.43	0.66			
Coverage of emerged <i>S. aloides</i> stands (%)		0.03229	4.86	< 0.001			

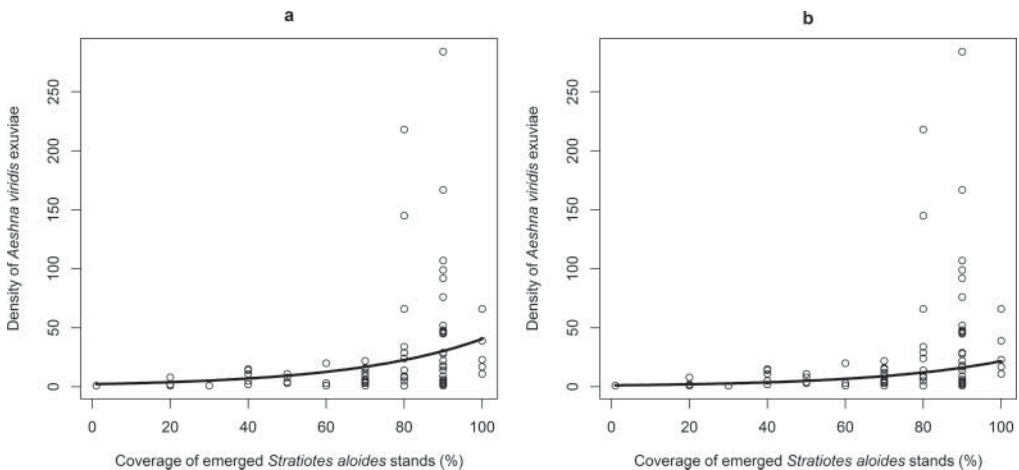


Figure 5. Visualisation of the relationship between the number of *Aeshna viridis* exuviae ( $n = 78$ ) and environmental parameters (predictor variable) by the negative binomial generalised linear mixed-effect models (GLMM, Model 2a). Random factor was “plot” nested within “sub-area”. Non-significant predictors were excluded from the final model by stepwise backward selection ( $p > 0.005$ ). (a) Model parameter: no ditch cleaning, mean sediment depth 67 cm, as well as mean water temperature in March 7.6°C and in August 18.2°C. (b) Model parameter: ditch cleaning, mean sediment depth 67 cm, as well as mean water temperature in March 7.6°C and in August 18.2°C.

(temperature August): 0.001,  $p = 0.986$ ) did not correlate with each other. All other parameters, as well as the new variables of the physico-chemical water factors (PC 1 to PC 5) were excluded from the final model. The model with only the coverage of emerged *S. aloides* as the predicted variable (Table 3: Model 2b, Figure 6) was significantly different from the model with the five habitat parameters (Model 2a) (deviance = 22.442,  $df = 4$ ,  $p < 0.001$ ). The AIC of Model 2b was larger than that of Model 2a, and the R<sup>2</sup> of Model 2b was lower.

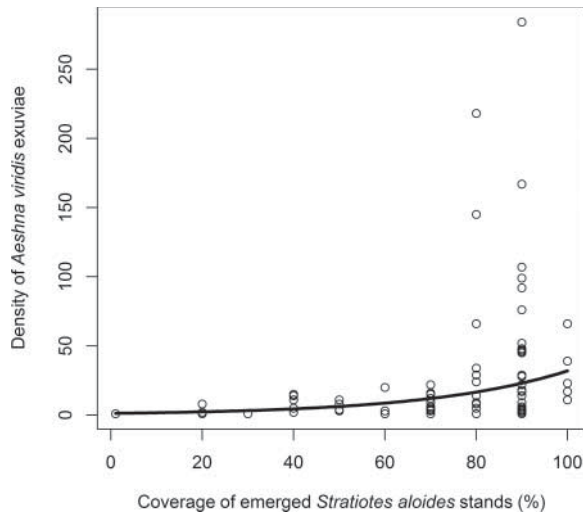


Figure 6. Visualisation of the relationship between the number of *Aeshna viridis* exuviae ( $n = 78$ ) and coverage of emerged *Stratiotes aloides* stands exclusively (predictor variable) by the negative binomial generalised linear mixed-effect models (GLMM, Model 2b). Random factor was “plot” nested within “sub-area”.

The comparison of the coefficient of determination of the two final models indicates a lower value for Model 2a ( $R^2 = 0.49$ ) than for Model 1a ( $R^2 = 0.71$ ).

## Discussion

The presence of *A. viridis* exuviae is determined predominantly by the coverage of emerged *S. aloides* stands in combination with the width of the ditches. The positive effect of ditch width may be explained by the fact that the dragonfly is able to better identify *S. aloides* stands in wide waters than in narrow ones in the course of habitat selection. Habitat selection is a step-by-step process in which biotope, waterbody type and the oviposition site are selected sequentially (Wildermuth, 1994). The selection of the macro-habitat is by visual recognition, for example, by the growth form and distribution of plants in the water and the exact selection of the oviposition site may also be of tactile, thermal and possibly olfactory nature (Wildermuth, 1994). Furthermore, the potential growth area of *S. aloides* will be larger in wider ditches than in narrow ones. Suhonen et al. (2013) also found a positive correlation between *A. viridis* occupation and the area of the *S. aloides* patch. In our study, the minimum coverage of emerged *S. aloides* to accompany a 50% and/or 90% probability of the presence of *A. viridis* in the model using habitat parameters was 5.4 m<sup>2</sup> (9%) and/or 8.4 m<sup>2</sup> (14%), respectively. These values correspond partly with the minimum size of 5 m<sup>2</sup> found by Glitz et al. (1989) and 8–10 m<sup>2</sup> found by Mauersberger et al. (2005). Small *S. aloides* stands are used for oviposition by *A. viridis* if they are spatially connected with larger *S. aloides* stands in the same ditch (Fliedner, 1996; Kastner et al., 2011). However, in our model with only *S. aloides* as the predicted variable, the required coverage to accompany a 50% and/or 90% probability of the presence of *A. viridis* was higher (27.6 m<sup>2</sup> and/or 46.2 m<sup>2</sup>). Large populations of *A. viridis* are found as part of a growth area of the host plant from 50 m<sup>2</sup> onwards (Lohr, 2011), and *S. aloides* stands of about 20 plants per m<sup>2</sup> are ideal for the presence of *A. viridis* (De Jong, 1999).

The coverage of emerged *S. aloides* stands also had a positive effect on the abundance of *A. viridis* exuviae. The other parameters – sediment thickness, water temperature and water maintenance – had a negative effect. Moreover, Suhonen et al. (2013) showed that the density of

*A. viridis* larvae increases with the patch area of *S. aloides*. The better protection against predators, in particular fish, is a possible explanation for the correlation of large *S. aloides* patches with a high number of *A. viridis* (De Jong, 1999; Mauersberger et al., 2005; Rantala et al., 2004; Suhonen et al., 2013; Suutari et al., 2004). The presence or absence of predators, especially fish, is an important habitat condition for larvae (Suhling, Sahlén, et al., 2015); therefore, the protection by *S. aloides* plants is an important habitat factor for *A. viridis*. In this study, detailed conclusions about fish predation cannot be made, although fish occur in the investigated ditches (Brunken, Hein, & Klugkist, 2012; own observation). Sediment thickness and water temperature are indirectly affected by *S. aloides* and are typical for *S. aloides* stands in the silting phase. Most distinctive *S. aloides* stands are found in the optimal phase of ditch succession (Jordan, Kesel, & Kundel, 2010). *Stratiotes aloides* stands, in the beginning of the silting phase of ditch succession, are characterised by increasing sedimentation and lower water depth, therefore the *S. aloides* plants can no longer hibernate at the bottom of the waters and are increasingly replacement by reeds (Jordan et al., 2010). These *S. aloides* stands, however, are no longer selected as oviposition sites by *A. viridis* (pers. comm. H. Klugkist, Ch. Brochard). A relationship between high temperature and concomitant unfavourable oxygen content (Pott & Remy, 2000), which may negatively affect the number of *A. viridis* larvae, was not expected for this study. Aeshnidae larvae are able to absorb oxygen on the water surface with the anal pyramid (Corbet, 1999, p. 76). One assumption is that high temperatures occur at low water depths and in highly silted waters. Furthermore, the temperature influences chemical processes and degradation or accumulation rates in the waters, which in turn influence the *S. aloides* population (Netten, van der Heide, & Smolders, 2013; Roelofs, 1991; Smolders et al., 2003; Zak, Kleeberg, & Hupfer, 2006). Moreover, water temperature, in addition to food supply, is an important factor for larval growth (Krishnaraj & Pritchard, 1995). Temperature response curves of larval growth by dragonflies follow a species-specific optimum course in which larval growth is warm adapted. The optimum temperature for growth is species-specific (Suhling, Suhling, & Richter, 2015). Also, other dragonfly species can benefit by higher temperatures and the intraguild interactions affect the abundance of *A. viridis* negatively, because dragonfly communities are affected by predation between the species (Johansson, 1993). Water maintenance – ditch cleaning during the last two years in which the larvae develop (Münchberg, 1930; Wesenberg-Lund, 1913; Wittenberg et al., 2015) negatively affects the abundance of *A. viridis*, as cleaning removes *S. aloides* plants, as well as the eggs and larvae of *A. viridis* from the ditches (Brunken et al., 2012; Klugkist et al., 2015; Mauersberger et al., 2005). As water maintenance takes place in winter when eggs and larvae hibernate in the plants (Münchberg, 1930; Wesenberg-Lund, 1913), they are probably removed by these procedures.

Both the presence and the number of *A. viridis* exuviae were mostly positively affected by the coverage of emerged *S. aloides* stands. Moreover, the number of exuviae was influenced by water maintenance, as well as by other factors, which are associated with *S. aloides*. All in all, the quality of *A. viridis* habitats is defined by the occurrence, quality and coverage of the *S. aloides* patches. Furthermore, *S. aloides* stands are diverse and individually rich in aquatic macroinvertebrates and thereby serve as important habitats, and indicators of valuable habitats (Obolewski, Strzelczak, & Glinska-Lewczuk, 2014; Suutari et al., 2009; Tarkowska-Kukuryk, 2006). The selection pressure emanating from a habitat affects mainly eggs and larvae (Wildermuth, 1994). Therefore, possible reasons for the strong association between the occurrence of *A. viridis* and *S. aloides* are (1) improved conditions of hibernation in submersed plants (Mauersberger et al., 2005; Münchberg, 1956); (2) optimal protection against predation (Rantala et al., 2004; Suutari et al., 2004); (3) a thermally favoured larval habitat and thereby optimal conditions for pre-adult development (Mauersberger et al., 2005); (4) ease of egg laying in the succulent leaves (Münchberg, 1956); and (5) a rich food supply consisting of a specific zoocenosis on *S. aloides* (Suutari et al., 2009; Tarkowska-Kukuryk, 2006).

## Conservation

Due to the strong dependency of *A. viridis* on *S. aloides*, the degradation and destruction of the latter poses an imminent threat to the persistence of *A. viridis* populations. A possibility for survival in fragmented landscapes is the networking and exchange of individuals between populations. Andersen, Nilsson, and Sahlén (2016) showed that 93% of the locations with *S. aloides* are connected by a dispersal capability of 40 km for the *A. viridis* population in Sweden. *Aeshna viridis* populations, at least in Western and Central Europe, can only be safeguarded by the continuous protection of *S. aloides* stands. In an optimal situation, the *S. aloides* populations occur in a mosaic of different states of siltation, which is managed by adapted water maintenance. The main threats to *S. aloides* populations include: (1) intensive water maintenance, accompanied by the destruction of water vegetation; (2) inadequate water maintenance and concomitant sedimentation/silting; (3) changes in water chemistry and eutrophication; (4) water level reductions and drying up; and (5) damage caused by animals (nutria, muskrats, water birds or cattle) (Kastner et al., 2016; Klugkist et al., 2015; Mauersberger et al., 2005; Roelofs, 1991; Smolders et al., 2003). Several successful conservation measures, such as adapting water maintenance to the growth of ditch vegetation and the developmental period of the dragonfly larvae, or resettlement of *S. aloides* stands, are currently being carried out for the protection or reintroduction of *A. viridis* populations (Brunken et al., 2012; De Vries, 2010; Kastner et al., 2016; Kunze et al., 2012; Mauschering, Jödicke, Neumann, & Winkler, 2011; Nagler and Müller, 2012).

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## Conflict of interest

The authors declare that they have no conflict of interest.

## Supplementary data

Supplemental data for this article can be accessed here <https://doi.org/10.1080/13887890.2018.1531065>

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