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Spatio-temporal patterns of dragonfly occurrence on meadows in the Donau-Auen National Park, Lower Austria

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Abstract

Dispersal is a characteristic trait in Odonata. While dispersal behavior of dragonflies and damselflies between waterbodies has generally received a great deal of attention, dispersal processes subjected to terrestrial habitats and hence, Odonate's use in the context of foraging activities, have previously only attracted limited interest. This study aimed to investigate the dispersal of dragonflies and damselflies to floodplain meadows used for foraging or as refuge. The primary focus was on assessing species-specific dispersal characteristics influencing the spatial distribution of species, species richness and community structure on meadows. Therefore, dragonflies and damselflies were sampled between May and September 2016 at 16 meadow and eight waterbody sites in the Donau–Auen National Park (DANP), Eastern Austria near Orth an der Donau. In total, 1.427 dragonflies were recorded, including 667 observed on meadows. Anisopterans were more likely to disperse long distances from waterbodies than zygopterans, and females showed proportionally higher abundances on meadows than at waterbodies. Species composition, species richness and occurrence of dragonflies were highly influenced by the distance meadows were situated away from waterbodies. Moreover, the results from this study demonstrated that occurrence of Odonata, species richness and the structure of species assemblages are associated with structural characteristics of forest margins adjacent to meadows. For most Odonata species, a positive relationship between heterogeneity in forest margin vegetation structure and occurrence could be found. This study provides important insight into odonate's utilization of meadows embedded in floodplain systems and provides some basis for potential conservation management considerations with the aim to protect terrestrial habitats of rare dragonflies.

Keywords

Odonata, Anisoptera, Zygoptera, Eastern Austria, Danube floodplain, dispersal

Introduction

So far, several ecological studies have focused on the dispersal of Odonata, as a response to seasonal changes or movements between neighboring waterbodies (CONRAD, et al., 1999). However, spatial movements to non-aquatic foraging habitats situated in larger distances to the larval habitats have received little attention. Only few studies have addressed dispersal of dragonflies to distanced meadows in floodplains for the purpose of foraging, mate-seeking, pairing or seeking of refuge (CONRAD, et al., 1999; HYKEL, et al., 2016). In this study, we assessed the importance of meadows, embedded in a river-floodplain system, as foraging habitats for adult Odonata. In particular, we addressed the following questions:

1. **Are species composition, species richness and abundance influenced by the distance meadows are situated away from waterbodies?**
   Abundance of Anisoptera is expected to be high at meadows located at larger distances to waterbodies, while abundance of Zygoptera is expected to be greater at meadows more closely situated to waterbodies due to the varying flight ability of species (CORBET, 1999). Moreover, we expect a shift in species composition at meadows with increasing distance to waterbodies. We also expect that meadows located at great distance from waterbodies are more likely to be visited by habitat generalists since the chance of finding a suitable aquatic habitat is greater for such species (CORBET, 1999). Furthermore, we also assume a female-biased sex-ratio on meadows since females are reported to spend most of their adult life away from aquatic habitats as a result of harassment by males (CORBET, 1999; SUHONEN, et al., 2008).

2. **Are species composition and species richness of Odonata species influenced by the structural quality of forest margins on floodplain meadows?**
   Densely branched trees, shrubs and meadows covered with tall grass provide perching opportunities for odonates between foraging flights and provide shelter between periods of high wind, rain or dense cloud cover (CORBET, 1999). Therefore, we expect that species composition and species richness are influenced by structural characteristics of meadows. Since structural demands on habitats vary between Odonate species, it is assumed that species richness is higher at meadows characterized by structurally diverse forest margins. Moreover, species composition is expected to differ between structurally diverse and structurally uniform vegetation.

Methods

This study was conducted in the Eastern part of the DANP north of the Danube river in the area of Orth an der Donau (48° 9′ N, 16° 42′ E). A levee (Marchfeldschutzdamm) divides the study area into a northern part, an area that is protected against flooding events during periods of high water levels and the southern part, an area that is regularly flooded due to summer inundations. A total of 16 meadows were sampled from the beginning of May until September 2016. Six study sites were situated in the northern part of the area, seven sites were situated south of the Marchfeld levee and three study sites were located directly on the Marchfeld levee. Eight waterbody sites alongside Danube River's side arms and one lentic waterbody in the northern part of the study area were selected as reference sites.

Sampling of dragonflies

On each meadow, adult Odonata were sampled by slowly walking along 100 m transects placed close to the forest margins. All dragonflies and damselflies encountered within a 10m radius of walking direction were counted. Reference data was collected at waterbodies by sampling stretches of 50 m along river banks. All adults observed on the bank and over the waterbody were recorded. Field collections were performed between 10:00–16:00 CEST (SCHINDLER, et al., 2003) when dragonflies are most active. Surveys lasted between 30 and 40 minutes at each site. Sampling was performed on sunny days with low or no wind. To cover all phenological groups of Odonata, each sampling site was visited 7 times, spread over the flight season from May to September (SCHMIDT, 1985). Influence of daytime on sampling results was avoided by systematically changing the daytime a site was visited (CHOVANEC, 1999). Dragonfly and damselfly specimens were observed with binoculars (10 x 40) or caught with a sweep net and identified by sight or photographs (SCHINDLER, et al., 2003) using identification keys of BELLMANN (2013) and DIJKSTRA (2014). Caught dragonflies and damselflies were released immediately after identification.

Habitat parameters on meadows

In order to determine dispersal distances of Odonata to surrounding terrestrial habitats, meadows were located at varying distances from waterbodies. Distances ranged from 95 to 1205 meters. Structural diversity of meadows was categorized based on the availability (presence or absence) of 'big trees', 'small trees' and 'shrubs'. Sites were then assigned to three categories (category 3 represented sites were all three variables were present), resulting in a categorical structural diversity index ranging from 3 (diverse) to 1 (uniform), hereinafter referred to as 'SDIa'. Additionally, we quantified structural complexity of forest margins. Therefore, the length of the forest margin of each site was measured along the 100 m transects using a measuring tool implemented in the programme GoogleEarth version 7.1.8.3036. Values of the calculated lengths of forest margins were then divided by the length of the 100 m transects. Resulting index values ranged from 1-1.15, hereinafter referred to as 'SDIb'.

Results

In the course of this study, a total of 1.427 dragonflies and damselflies were recorded (Zygoptera: 11 species; Anisoptera: 18 species). At meadow sites, 667 individuals, representing 20 Odonata species, were counted. The most frequent Odonata species at surveyed meadow sites was *Platycnemis pennipes* (35% of counted total at meadow sites), followed by *Aeshna isoceles* (19%), *Aeshna mixta* (10%) and *Orthetrum cancellatum* (6%). Anisoptera species (62% of all individuals recorded at meadow sites) were more abundant on meadows than Zygoptera (38% of individuals). At waterbody sites, zygopterans were more abundant than anisopterans.

Species richness

Fig. 1 shows species accumulation curves, calculated for meadow sites and waterbody sites. Recorded species richness was higher at waterbodies than on meadows. However, the extrapolated part of the curve for the Odonata assemblage on meadows indicates similar species richness of both habitat types.

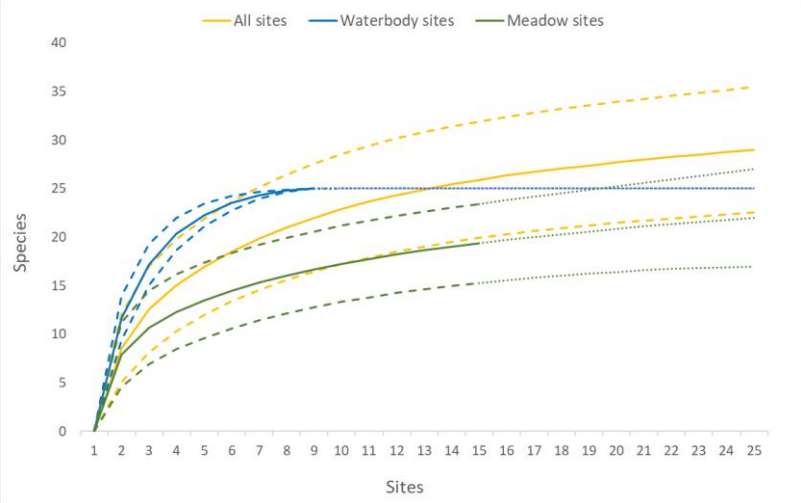

Figure 1: Species-accumulation curves (± 95% CI) calculated for all sites, waterbody sites and meadow sites. Dotted lines represent extrapolated values.

With respect to the relationship between species richness and distance, Zygoptera species richness declined significantly with increasing distance to waterbodies (r = -0.56, p = 0.02). In contrast, no significant relationship was found between Anisoptera species richness and distance to waterbodies (r = -0.19, p = 0.46). Pearson's product-moment correlation shows that overall species richness is significantly associated with SDIb (r = 0.61, p = 0.01). If taxonomical groups are considered individually, species richness of Anisoptera showed a strong positive correlation with SDIb (r = 0.69, p = 0.002), species richness of Zygoptera on the other hand was not significantly influenced by SDIb (r = 0.26, p = 0.31).

Abundance

While no significant correlation between the total number of recorded individuals and the distance to the closest waterbody could be observed (r = 1.14, p = 0.62), models that test Anisoptera and Zygoptera separately, yielded highly significant results. Anisoptera counts increased significantly with increasing distance to waterbody (r = 0.50, p = 0.05), by contrast, counted individuals of the suborder Zygoptera showed a highly significant negative correlation with increasing distance from a waterbody (r = -0.65, p = 0.006; Fig. 2).

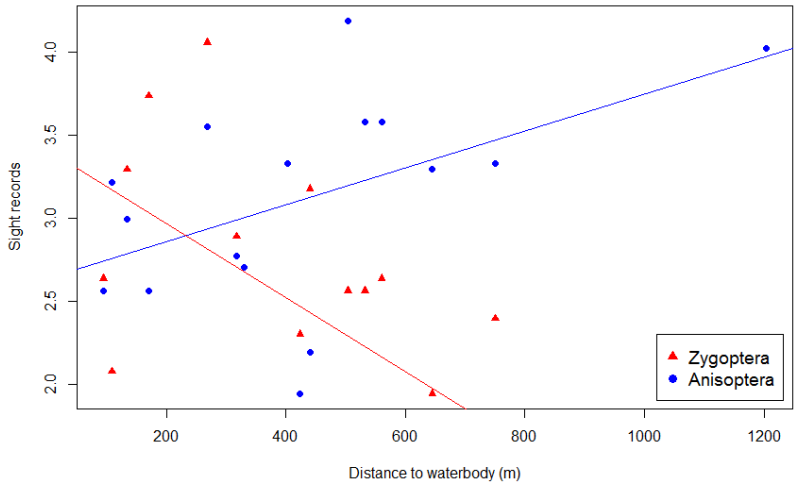

Figure 2: Relationship between recorded number of individuals (log-transformed) and distance to closest waterbody.

A comparison of relative abundances of Zygoptera and Anisoptera specimens recorded at meadow and waterbody sites illustrates that Anisoptera species were more abundant on meadows than Zygoptera. In comparison, Zygoptera were more dominant at waterbodies. Notably, *Platycnemis pennipes* was equally distributed on meadows and waterbodies. Effects of several habitat variables on the abundance of dragonflies were tested. A Kruskal-Wallis rank sum test shows that the number of individuals (H = 6.41, p = 0.04) can be significantly associated with structural diversity of the forest margin (SDIa). A post-hoc Kruskal-Nemenyi test shows that the mean number of dragonfly records at habitats with intermediate and highest structural diversity differ significantly (H = 3.40, p = 0.04). Testing for effects of structural diversity (SDIa) on the occurrence of zygopterans and anisopterans separately, showed that occurrence of Anisoptera species was significantly influenced by the structural diversity of the forest margin (H = 6.22, p = 0.04), however no significant results could be found for Zygoptera species (H = 0.54, p = 0.75).

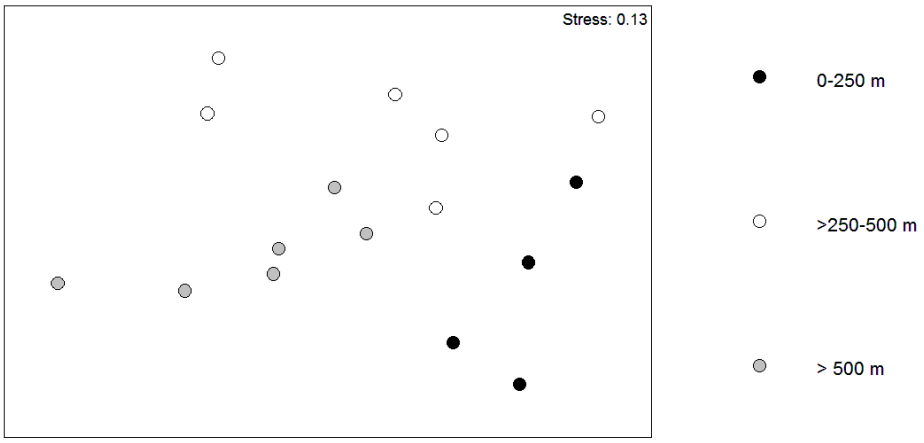

Figure 3: NMDS ordination of meadow sites based on Bray-Curtis similarities. Black points represent sites with a distance to the closest waterbody between 0-250 m, white dots represent waterbody distance of >250-500 and grey dots represent sites with waterbody distance of >500 m. Stress: 0.13.

Species composition

The NMDS ordination based on Bray-Curtis similarities (Fig. 3) shows that species composition of sites can be grouped according to their distance from a waterbody. Sites located at greatest distance from a waterbody (indicated by grey-colored dots) show a similar pattern in species composition and form a distinct group. Communities of sites with intermediate distance from a waterbody (indicated by white dots) are slightly interspersed with sites of lowest distance to waterbody (indicated by black dots).

Dimension 1 values of the NMDS ordination visualizing similarity relationships of species assemblages on meadows were significantly related the distance to waterbodies (r = -0.71, p = 0.002). A one-way ANOSIM showed that species composition differs significantly between categories of distances to waterbodies (0-250 m, > 250-500 m, >500 m) (r_{global} = 0.49, p = 0.001). Pairwise comparisons illustrate a highly significant difference between all distance groups. It was tested whether structural diversity of habitats (SDIa) influences species composition. A one-way ANOSIM showed that species composition differs significantly between categories of structural diversity (r_{global} = 0.27, p = 0.009). While pairwise comparisons revealed that sites showing high diversity and intermediate diversity each differ significantly from structurally less diverse sites, a pairwise test between diversity classes SDIa 2 and SDIa 3 did not yield a significant result.

Sex-specific differences in spatial distribution

Only a subset of species allowed identification of the sex in the field. A list of species that were included in the following calculations can be found in the appendix A5. Male dragonflies (75%) were generally more dominant in the study area than females (25%). A comparison of relative abundances of males and females shows that male Odonata were generally more dominant on meadows than females. With respect to waterbody sites, 88% of recorded Odonata were males and 11% females, resulting in a male-biased sex ratio at both types of sampling sites. The recorded sex ratio at meadows was 2.3:1, the sex ratio at waterbodies was 10:1.

Discussion

Odonata species observed in this study represent 88% of the dragonfly and damselfly fauna recorded for the study area at Orth an der Donau (RAAB, 2000) and 38% of Austria's Odonata fauna (RAAB, 2006).

Species richness

Species richness was slightly higher at waterbodies than on meadows. Only three Zygoptera species (*Ischnura elegans*, *Platycnemis pennipes and Sympecma fusca)* observed at waterbodies could be found on meadows. Also, the rheophilic species *Calopterix splendens* and *Gomphus vulgatissimus* (DIJKSTRA, 2014) were present at sampled waterbodies but could not be recorded on meadows. Zygoptera species richness declined with increasing distance from waterbodies. Given the assumption that zygopterans generally display poorer flight ability than anisopterans (CORBET, 1999), it is not surprising that fewer dragonfly species of the suborder Zygoptera were found on meadows. Moreover, also intraguild predation risk may come into place, preventing zygopterans from foraging in habitats where anisopterans are abundant (CORBET, 1999).

Other than expected, no relationship between structural diversity of forest margins and species richness could be found, however the significant correlation detected between heterogeneity of forest margin structure reflected in SDIb and species richness suggests that increased species richness can be expected if structural diversity of forest margins is high. This assumption is applicable for anisopterans, albeit, no such relationship could be found for zygopterans.

Sex-specific dispersal patterns

It is generally assumed that males and females differ in their tendency to disperse. Various authors describe that sex ratios at reproductive sites are mostly male-biased, once sexual maturity has been reached. Males spend most of their time at breeding sites awaiting females, females on the other hand visit reproductive sites predominantly to mate and oviposit, suggesting that they spend a great deal of time away from waterbodies and are more likely to disperse (SUHONEN, et al., 2008). Our study found that male-biased sex ratios exist at both, waterbody sites and meadow sites, however, the sex ratio at waterbodies was substantially more biased towards males than on meadows. Patterns in sex ratio at waterbodies can be the result of intraspecific faunal interactions. At breeding sites with high male density, females were reported to move away from waterbodies in an attempt to avoid excessive matings or harassment of males (SUHONEN, et al., 2008). In territorial dragonflies with male density at reproductive sites assumed rather low, females may benefit in that harassment during copulation or oviposition is reduced. Also, predation risk may be reduced in high-quality territories, hence areas were territorial males are present (SUHONEN, et al., 2008). Higher abundances of females in such territories are a logical consequence.

Abundance

Our results suggest that dispersal is strongly associated with Odonata suborder. Anisoptera records increased significantly with increasing distance from a waterbody. The opposite could be confirmed for zygopterans, which were present in great abundance, if meadows were located in close vicinity to a waterbody and decreased steeply with increasing distance from waterbodies. If distances moved by single species are considered, only few zygopterans moved long distances from meadows. With the exception of *Platycnemis pennipes* (recorded on meadows in distances of up to 750 meters from waterbodies) and *Sympecma fusca* (up to 645 meters from waterbodies), none of the Zygoptera species dispersed more than 350 meters. Anisoptera species on the other hand were recorded on meadows up to 1205 meters away from waterbodies. Quality of vegetation, such as

structure or density are generally assumed to influence abundance of dragonflies (HYKEL, et al., 2016). Our results suggest that heterogeneity of vegetation structure in terrestrial habitats is of major importance for dragonflies and damselflies. High structural diversity of forest margins was significantly associated with occurrence of dragonflies. Differences in dragonfly abundance was most significant between habitats with intermediate and highest structural diversity. High abundances of *Orthetrum cancellatum* were found on the Marchfeld levee. Sampling sites on the levee were all classified uniform in terms of forest margin diversity because big trees characterize the landscape. *Orthetrum cancellatum* is not as dependent of perching or refuge opportunities in shrubs as other species and uses stony trails for resting between flights (DIJKSTRA, 2014). While it was hypothesized, that dragonflies would be more abundant if the mean height of herb layer was high, no such relationship could be observed within this study. Cover of tall vegetation. instead of height thereof and vegetation cover in general may more likely have an effect on overall dragonfly occurrence (HYKEL, et al., 2016), thus presence of fairly tall vegetation seems more relevant than height.

Species composition

Species composition on meadows was strongly affected by the distance to waterbodies. Meadow sites with similar distance characteristics were similar in species assemblage composition. These results do not only reflect differences in dispersal behavior between zygopterans and anisopterans, but also exhibit species-specific dispersal properties within suborder and family. Community structure may be shaped by faunal interactions such as interspecific competition. Interspecific aggression may force individuals of subdominant species to move to other, less preferred habitats (TYNKKYNEN, et al., 2008) or even lead to the exclusion of some species from certain waterbodies (MOORE, 1964). Whereas such aggressive interactions have mainly been described at reproductive sites (MOORE, 1964; Suhonen, et al., 2008), interspecific competition is also assumed to play a prominent role in terrestrial habitats (CORBET, 1999). Structural characteristics of forest margins also seem to shape community structure on meadows. Composition of dragonfly assemblages on meadows with intermediate and high heterogeneity differed from meadows with uniform forest margin structure, potentially reflecting species with varying demands on vegetation structure at terrestrial habitats. Whereas habitat generalists and specialists have been described in terms of reproductive habitat requirements (RAAB, 2006), knowledge on the demands of Odonata on vegetation structure at terrestrial habitats is limited. Other than expected, species composition north and south of the levee did not differ significantly.

Conclusion

The high conservation value of the DANP floodplain meadows is confirmed by the large number of species utilizing floodplain meadows for foraging or as refuge, as demonstrated in this study. A number of specimens observed during the study are classified 'vulnerable' according to the Austrian's Red List of dragonflies (RAAB, 2007), *Sympecma fusca, Coenagrion hastulatum, Gomphus vulgatissimus, Aeshna affinis, Aeshna isoceles,* and *Brachytron pretense* among them.

Effective management of threatened dragonflies takes into account ecological requirements of dragonflies at all stages of their life cycle (CORBET, 1999), and do not only concentrate on aquatic habitats but also surrounding terrestrial habitats (HYKEL, et al., 2016). As demonstrated in this study, dragonflies spend considerable time away from waterbodies (CORBET, 1999) and respond positively to rich vegetation structure on meadows. In order to maintain plant diversity and to avoid encroachment of shrubs, meadows in the DANP are mown twice annually (NATIONALPARK DONAU-AUEN, 2009). It is widely assumed that mowing affects dragonfly abundance. Lack of suitable areas for roosting during night-time or shelter during inclement weather can be the result of lower abundances of dragonflies (ROUQUETTE & THOMPSON, 2007). Recently mown habitats are largely avoided by dragonflies (DOLNÝ, et al., 2014). Mowing can increase mortality considerably, especially if mowing is done when odonates are inactive during cloudy or cold weather or periods of rain or high wind (DOLNÝ, et al., 2014). Management measures of threatened dragonflies must therefore take into account species' period of emergence; mowing regime on meadows located in close vicinity to habitats where the focal dragonfly species is present must be adapted so that first mowing is done before the emergence of adults. Second mowing should be done after the majority of Odonata completed oviposition (HYKEL, et al., 2016). Since the flying season of dragonflies observed in the study area varies significantly between species, fulfilling such requirements seems hardly possible and is possibly highly unpractical. Alternatively, a probably more economical management measure is to maintain mosaic-like mowing regimes (HYKEL, et al., 2016).

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