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Succession of the Odonata fauna at a small wetland in an overflow and seepage reservoir: results of a six-year study

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Abstract

An unintentionally created, small, permanent, groundwater-fed, and shallow wetland in Lower Austria was subject of an odonatological study carried out from 2016 to 2021. The water body (size 1.200 m^2) was situated in an overflow and seepage reservoir created in 2014. As nobody – apart from the author – had access into the fenced area and as, therefore, there were no measures carried out, successional processes ran totally undisturbed. Main target of the study was to examine the odonate community´s response to changing habitat conditions, in particular as far as the rapid development of helophyte stands is concerned. A high number of observation days (236) within the investigation period of six years allowed detailed phenological analyses, for example of emergence, maturation, and flight periods. Investigations were primarily focused on counting tenerals, juveniles, and adults and on recording pairing wheels, tandems, and egg depositions. Exuviae, predominantly of Anisopterans, were sampled in the years 2016 and 2017. In the subsequent years, sampling of exuviae was widely waived in order to prevent damage to the reed stands associated with a "rejuvenation" of parts of the wetland and the unintentional creation of new small pioneer habitats. In 2016, the site could be characterised as a mosaic consisting of open water areas, open, sparsely and densely vegetated riparian areas, floating submerged macrophytes, and emergent amphibious vegetation of different heights. As of the summer 2018, the wetland was completely covered by the high-growing Broadleaf Cattail *Typha latifolia*, Great Hairy Willowherb *Epilobium hirsutum*, and reed *Phragmites australis*. Within the six years, a total of 32 species were recorded with the highest number (27) in 2016. Species with highest abundances were *Ischnura pumilio* with about 350 individuals in 2016 (sum of both generations), and *Sympetrum striolatum* with about 150 individuals also in 2016. *Orthetrum coerulescens*, in turn, was the only species colonising the site when completely covered by helophytes. Based on the findings of the study, it can be concluded, that *Pyrrhosoma nymphula* was the only species classified as permanently autochthonous in the period under scrutiny – even if only as a small population. The dragonfly community responded in various ways on changing, for most species deteriorating habitat conditions: decrease of the number of individuals and of the number of breeding species; increase of the species´ number recorded only by single records; decrease of the duration of the species´ presence at the site and, thus, reduction of the site-specific flight period compared with the species-specific flight period. In the third and fourth year of its appearance, the bivoltinous *I. pumilio* produced only the spring/early summer generation; the same occurred in *Ischnura elegans* in its second and third year. In several species changes in the reproductive behaviour were observed. In this connection, key stimuli inducing and factors limiting pairing and egg deposition behaviour are discussed.

Keywords: Odonata, Lower Austria, wetland, population structure, species inventory, abundance, reproductive behaviour, short-term change, species turn-over, habitat conditions, helophyte canopy

Zusammenfassung

In der vorliegenden Arbeit wird eine libellenkundliche Sukzessionsstudie präsentiert, die von 2016 bis 2021 durchgeführt wurde und sich somit über sechs Jahre erstreckte. Untersuchungsort war ein etwa 1.200 m^2 großes grundwassergespeistes, permanentes und seichtes Feuchtgebiet in Maria Enzersdorf (Niederösterreich). Das Gewässer entstand unbeabsichtigt in einem Überlauf- und Versickerungsbecken, das im Jahr 2014 errichtet worden war. Da außer dem Autor niemand Zutritt in das umzäunte Areal hatte und daher auch keinerlei Maßnahmen in dem Becken umgesetzt wurden, konnten Sukzessionsvorgänge ungestört ablaufen. Hauptziel der Studie war die Dokumentation der Reaktion der Libellenfauna auf die sich rasch verändernden Habitatbedingungen, die sich insbesondere im vollständigen Zuwachsen des Feuchtgebietes durch hochwüchsige Helophyten äußerte. Die hohe Anzahl von Begehungen (236) ermöglichte detaillierte phänologische Analysen, Vergleiche der Anwesenheitsdauer der Arten am Standort mit den art-spezifischen Flugzeiten sowie Erhebungen der Emergenz- und Reifungszeiten. Die Arbeiten konzentrierten sich auf die Sichtung und Zählung frisch emergierter, juveniler und adulter Individuen sowie auf die Beobachtungen von Paarungsrändern, Tandems und Eiablagen. Exuvien, insbesondere von Anisoptera, wurden in den Jahren 2016 und 2017 gesammelt. In den Folgejahren wurde darauf verzichtet, um durch Betritt des dichten Röhrichts keine kleinräumigen Verjüngungsprozesse zu initiieren. Im Jahr 2016 war das Gewässer durch ein Mosaik von offenen Wasserflächen, aufschwimmenden submersen Makrophyten, Helophyten unterschiedlicher Höhe sowie offenen, spärlich und dicht bewachsenen Ufern geprägt. Ab dem Sommer 2018 war das Feuchtgebiet vollständig von hoch wachsenden Helophyten – Breitblättrigem Rohrkolben *Typha latifolia*, Zottigem Weidenröschen *Epilobium hirsutum* und Schilf *Phragmites australis* – überwuchert. Im Rahmen der gesamten Untersuchung erfolgte der Nachweis von 32 Libellenarten. Mit 27 war die Artenzahl im Jahr 2016 am höchsten. Mit 350 Exemplaren im Jahr 2016 (Summe der Individuen aus beiden Jahresgenerationen) war *Ischnura pumilio* die Zygopteren-Art mit der höchsten Abundanz, *Sympetrum striolatum* war ebenfalls im Jahr 2016 mit 150 Tieren die individuenreichste Anisopteren-Spezies. *Orthetrum coerulescens* war die einzige Art die das Feuchtgebiet erst besiedelte, als es vollkommen zugewachsen war. Die Datenlage lässt vermuten, dass *Pyrrhosoma nymphula* als einzige Art über die gesamte Untersuchungsdauer hinweg durch eine kleine bodenständige Population vertreten war. Die Libellenfauna reagierte auf vielfältige Weise auf die rasch, sich für die allermeisten Arten negativ entwickelnden Habitatfaktoren: Einbrüche der Individuenzahlen; Abnahme der Zahl reproduzierender Arten; Zunahme der Zahl von Arten, die ausschließlich durch Einzelnachweise belegt wurden; Abnahme der Dauer der Nachweisbarkeit am Gewässer verglichen mit den art-spezifischen Flugzeiten. Die zu Beginn der Studie bivoltin auftretenden *Ischnura elegans* und *I. pumilio* waren nur mehr durch die Frühjahrsgeneration vertreten. Bei mehreren Arten traten Veränderungen der Muster des Reproduktionsverhaltens auf. In diesem Zusammenhang werden Konfigurationen von Schlüsselreizen und das Reproduktionsverhalten limitierende Faktoren diskutiert.

Schlagworte: Odonata, Niederösterreich, Feuchtgebiet, Populationsstruktur, Arteninventar, Abundanz, Fortpflanzungsverhalten, kurzfristige Veränderung des Arteninventars, Lebensraumbedingungen, Einfluss des Deckungsgrades von Helophyten

Introduction

The longitudinal and lateral fragmentation of rivers and their regulation, large-scale landscape drainage in order to clear and develop land for agricultural purposes, and urban development are the main pressures on dragonfly habitats and the most important reasons for their isolation and loss in Central Europe. Furthermore, the impacts of climate change deeply affect Odonate communities and their habitats (e. g. Chovanec et al., 2004; Hassall & Thompson, 2008; Ott, 2010; Hassall, 2015; Goertzen & Suhling, 2019; Bowler et al., 2021; Hogreve & Suhling, 2022; Neff et al., 2022; Pinkert et al., 2023). The rehabilitation of water bodies, such as the dynamisation of floodplains (Chovanec et al., 2004), river restructuring (e. g. Chovanec & Waringer, 2015; Chovanec, 2018a, 2021a), peat bog restoration (Bönsel, 2006; Elo et al., 2015; Wildermuth, 2016; Vallat et al., 2020), and the creation of ponds (Wildermuth & Krebs, 1983a; Hübner, 1988; Kadoya et al., 2004; Bried & Ervin, 2005; Chovanec, 2017a; Maynou et al. 2017; Vilenica et al., 2020; Worthen & Chamlee, 2020; de Paz et al., 2021) play an essential role in compensating habitat loss and isolation. In that context it is important to emphasise how important site management plans are at a time when resources are in shorter supply (Wildermuth & Küry, 2009; Wildermuth, 2020).

Due to the lack of suitable water bodies fulfilling species-specific habitat requirements, some “anthropophilous species” (Buczyńsky, 2015) preferably colonise artificial substitute habitats. Even in urban and semi-urban areas, man-made water bodies may play an essential role as breeding sites for Odonates (Laister, 1996; Chovanec & Raab, 2002; Brandt & Buchwald, 2011; Goertzen & Suhling, 2013, 2015; Villalobos-Jiménez et al., 2016; Kietzka et al., 2021; Perron et al., 2021).

Technical facilities, such as gravel pits, drainage ditches, and irrigation ponds, often provide suitable habitats for dragonflies (e. g. Bilek, 1952; Gerken, 1983; Wildermuth & Krebs, 1983b; Buchwald, 1985; Ott, 1991; Holzinger & Brunner, 1993; Glaser et al., 2003; Willigalla et al., 2003; Schiel, 2008; Staufer & Höttinger, 2016; Rychła, 2017). Other types of technical constructions, e. g. flood or stormwater detention and retention basins (Meier & Zucchi, 2000; Ott, 2008; Le Viol et al., 2009; Chester & Robson, 2013; Hassall, 2014; Chovanec, 2017b), even allow dynamic hydrological processes to a certain degree and, in a small scale, the formation of temporary ponds (Scher & Thièry, 2005; Willigalla & Fartmann, 2009; Simaika et al., 2016; Šigutová et al. 2022). In most cases, the origin of anthropogenic ponds and wetland sites is the result of targeted measures. However, when setting up technical systems the creation of dragonfly habitats may also occur unintentionally: After digging basins, the groundwater table may rise to the land surface and, thus, establishes the basis for the development of shallow wetlands.

Most aquatic and semi-aquatic habitat types are subject to successional processes influencing dragonfly communities. Hence, investigations of the dragonfly fauna over longer periods provide useful information on species-specific habitat requirements, population size, association patterns, and the relevance of those factors responsible for the “coming and going” of certain species (Rudolph, 1979; Martens, 1983, 1991; Moore, 1991, 2001; Willigalla, 2001, 2007; Chovanec & Raab, 2002; Schiel, 2008; Wildermuth, 2008a, 2017; Suhling et al. 2009; Shiffer & White, 2014; Rychła, 2019; Nicolai, 2020; Borkenstein & Jödicke, 2023; Koene, 2023). Furthermore, those studies represent an important basis for the management and conservation of valuable dragonfly habitats (Suh et al., 2005; Wildermuth & Küry, 2009; Janssen et al., 2018). Especially in landscapes, where factors initiating dynamic hydrological processes are lacking (floods, changing groundwater levels, beaver populations …), anthropogenic measures are often essential for creating or rejuvenating aquatic and semi-aquatic habitats.

The present six-year study was carried out at a small wetland in an overflow and seepage reservoir situated in a semi-urban area near Vienna (Austria) and deals with the development of the odonate fauna during a rapid overgrowth process. A high number of field trips (236) allowed the analyses of phenological features and the documentation of when species left the wetland in the case of deteriorating species-specific habitat conditions. On the other hand, this research has addressed the question, whether, and if so which species appears when habitat conditions became suitable. On the basis of a large set of observations, behavioural responses on changing habitat parameters were detected in several species.

Study area

The investigated wetland (48°05’47’’N, 16°17‘54“E; 209 m a.s.l.) had a size of about 1,200 m^2 and was situated in an overflow and seepage reservoir with a length of about 100 m and a width of 30 m. In the north, west and east, the basin was surrounded by agricultural areas, in the south by a campus (“Sankt Gabriel”) consisting of a monastery, a small cemetery, an organic farmer, a hotel, a school, an art market, and some shops “far from the mainstream”, such as a book binding shop and a coffee-roasting establishment, as well as a pond (Fig. 1). The study area belongs to the municipality Maria Enzersdorf, a small town in the Austrian Province Lower Austria with about 9.000 inhabitants in the south of the Austrian capital Vienna. Maria Enzersdorf is classified as “intermediate region” according to the urban-rural typology (Eurostat, 2019) and situated in the western part of the landscape unit “Wiener Becken” and of the Austrian bioregion Eastern Ridges and Lowlands, which belongs to the European ecoregion Hungarian Lowlands (Illies, 1978; Fink et al., 2000; Wimmer et al., 2000; Moog et al., 2004). The nearest standing water bodies were the above mentioned campus pond at a distance of 300 m (Fig. 1) and a wetland in a flood retention basin as well as water-filled former clay pits and ponds on a golf court at a distance of about 1,000 m (see also Chovanec, 2020).

Constructed in 2014, the reservoir was key element of a dewatering system to balance high water levels in the pond situated on the campus and high groundwater levels. In case of high water levels, water flowed through a pipe from the pond into the basin. Heavy rainfalls also influenced the water regime of the reservoir. Within the investigation period from 2016–2021, it was filled between two (2021) and seven times (2016) per year up to a depth of about 40 cm in times of heavy rainfall (Fig. 2, taken from photopoint Ph1 in Fig. 1). After such bad weather periods, the water in the basin completely seeped always within a few days, of course with the exception of the small permanent area with groundwater contact. Hence, the temporarily inundated areas of the basin were not suitable for odonate reproduction. The longest period the basin was completely filled lasted from early December 2018 to early March 2019.

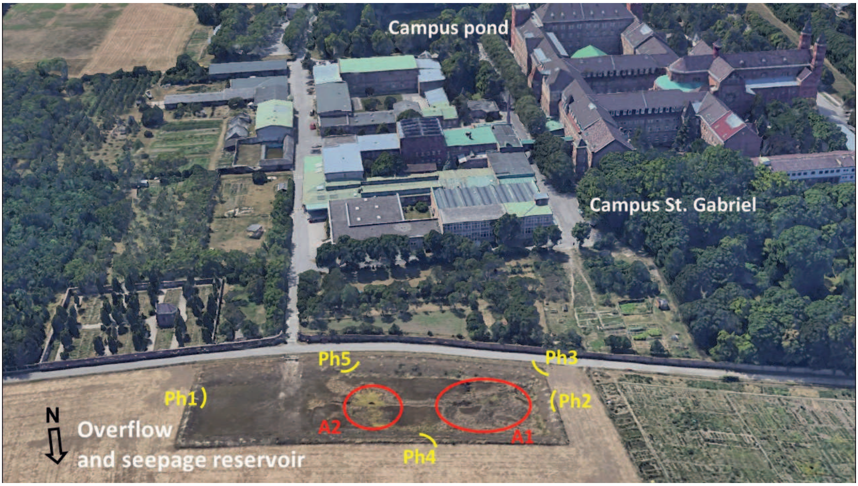


Figure 1. Overflow and seepage reservoir of the St. Gabriel Campus in Maria Enzersdorf, Lower Austria, with the wetland consisting of two areas A1 (permanent) and A2 (temporary). Ph1-5: Points where the photos were taken. Source: Google Earth.

Figure 2. Reservoir filled after a period of heavy rainfall. Photo taken from point Ph1 in Fig. 1, 21-iv-2017, Photo: Andreas Chovanec. The complete set of following photos in this publication was taken by the author.

The reservoir, which has a depth of about 2 m, was surrounded by a wire mesh fence with a locked gate. Therefore, the succession processes within the basin were completely undisturbed from anthropogenic activities, even from walkers or bikers. There were neither initial plantings nor management measures carried out. The wetland was situated in the western half of the basin and consists of two hydrologically connected areas. The western area (Area 1, A1, with a size of about 900 m^2, Fig. 1) can be classified as “Groundwater Associated Aquatic Ecosystem” (Hinsby et al., 2015) due to permanent groundwater contact preventing this zone from drying out and from totally freezing over even in very cold winter periods (Fig. 3). According to Moser (2006) the groundwater level at “St. Gabriel” is at 207 m a.s.l.. The eastern Area 2 (A2), situated in the centre of the basin, with a size of about 300 m^2 (Fig. 1), was superficially fed with water from A1 by a thin trickle with a length of 10 m. The longest period A2 was covered with water lasted from winter 2018/2019 to summer 2021.

Figure 3: Permanent ice-free areas in the western water body (Area 1) in winter 2016/17 at a temperature of -8° C (22-i-2017). Photo taken from Ph2.

In times when the basin was not filled, the maximum water depth at A1 and A2 was about 20 cm. Values of electrical conductivity of the water in both zones measured in 2020 ranged between 1,320 and 1,480 µS/cm. Occasional measurement of water temperatures mostly showed lower temperatures in the groundwater-fed A1 compared to those measured in A2. In August 2019 both water bodies had a temperature of 22° C. Measurements in July and August were made in periods with maximum air temperatures >30° C. Water temperature was measured during the years when the wetland was totally covered by helophytes and therefore the water surface was shaded.

08-iv-2020: Area 1 (A1): 12° C, Area 2 (A2): 16° C
14-vi-2019: A1: 17° C, A2: 22° C
27-vi-2019: A1: 19° C, A2: 22° C
10-vii-2020: A1: 19.3° C, A2: 21.2° C
01-viii-2019: A1: 22° C, A2: 22° C
24-viii-2019: A1: 22° C, A2: 22° C

Water samples taken at 10-vii-2020 at both areas were analysed for tritium isotopes to determine the origin of the wetland´s water. Values of about 7.4 TU (Tritium Units) indicate ground water close to the surface primarily influenced by precipitation (F. Humer, written communication; see also Kralik et al., 2015). The study site is situated in a border area of two small-scale geological units: "quaternary sands/gravels" and "clays, marls, sands, and gravels of the molasses zone" (https://secure.umweltbundesamt.at/webgis-portal/isotopen/map.-xhtml).

In 2016 and 2017, especially A1 was characterized by a mosaic of numerous aquatic and amphibious plants (Fig. 4; in alphabetical order): *Alisma plantago-aquatica, Epilobium hirsutum, Juncus effusus, Lemna minor, Myriophyllum verticillatum, Persicaria hydropiper, Phragmites australis, Potamogeton nodosus, Schoenoplectus tabernaemontani, Sparganium erectum, Typha latifolia, Veronica anagallis-aquatica,* and *Veronica beccabunga*. Open water areas were also covered by filamentous algae and algae mats.

Figure 4: Area 1 in 2016: a mosaic consisting of submerged and emergent macrophytes, helophytes, and open water areas (27-viii-2016).

Particularly the rapid development of *Epilobium hirsutum* (at A1), *Typha latifolia* (at both areas), and *Phragmites australis* (only at A2) led to dense coverage of both areas, which was completed in autumn 2018. Subdominant species at A1 were *Alisma plantago-aquatica, Juncus effusus, Schoenoplectus tabernaemontani,* and *Sparganium erectum*. The last “larger” open area with a size of about 10 m^2 remained until spring / early summer 2018. Since late summer / autumn 2018, access to the water surface for most odonate species was reduced to small patches (Figs. 5–7).

Figures 8–14 illustrate the development of the vegetation at A1. Pictures were taken from the south-western corner of the basin, above the inlet pipe (Figs. 8–13, Ph3 in Fig. 1) and from Ph4 situated at the northern border of the basin (Fig. 14).

Figure 5. Small “open water” patches near the inlet pipe in spring and early summer (15-v-2021).

Figure 6. Remaining access to the water surface in late summer 2018 (13-ix-2018).

Figure 7. Another small access to the water surface (29-viii-2019).

Figure 8. Western water body (Area 1) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 16-iv-2016. Photo taken from Ph3.

The development of the vegetation at A2 is documented in Figures 15–18; pictures were taken at point Ph5 marked in Figure 1.

The sloped sidewalls of the basin and the dry parts of its ground were colonised by ruderal vegetation with the following dominating species (in alphabetical order): *Arctium* sp., *Carduus acanthoides, Carlina vulgaris, Cichorium intibus, Cirsium arvense, Cirsium vul-*

Figure 9. Western water body (Area 1) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 15-ix-2016. Photo taken from Ph3.

Figure 10. Western water body (Area 1) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 25-vi-2017. Photo taken from Ph3.

Figure 11. Western water body (Area 1) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 13-ix-2017. Photo taken from Ph3.

Figure 12. Western water body (Area 1) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 26-vi-2018. Photo taken from Ph3 in Fig. 1.

Figure 13. Western water body (Area 1) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 01-viii-2019. Photo taken from Ph3.

Figure 14. Western water body (Area 1) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 06-vii-2021. Photo taken from Ph4.

Figure 15. Eastern water body (Area 2) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 05-v-2016; in the background on the left Area 1 and the thin trickle connecting both areas. Photo taken from Ph5.

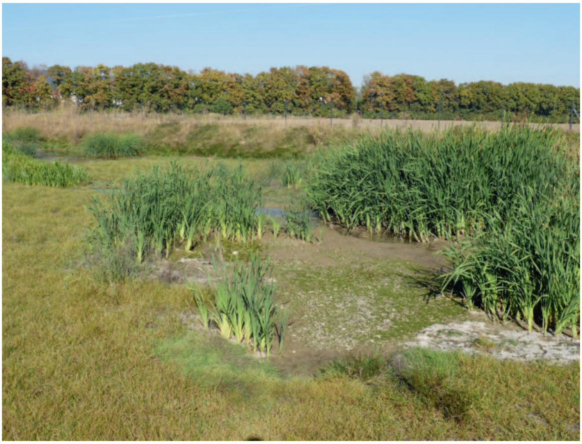


Figure 16. Dried out eastern water body (Area 2) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 30-ix-2016. Photo taken from Ph5.

Figure 17. Eastern water body (Area 2) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 09-ix-2017. Photo taken from Ph5.

Figure 18. Eastern water body (Area 2) in the overflow and seepage reservoir in Maria Enzersdorf, Lower Austria, 20-vii-2019. Photo taken from Ph5.

gare, Clematis vitalba, Convolvulus arvensis, Conyza canadensis, Coronilla varia, Picris hieracioides, Daucus carota, Dipsacus fullonum, Erigeron annuus, Hypericum perforatum, Hyssopus officinalis, Lactuca sonchus oleraceus, Mellilotus officinalis, Oenothera biennis, Papaver rhoeas, Potentilla reptans, Rosa canina, Rumex sp., *Securigera varia, Solidago* sp., *Symphotrichium lanceolatus*, *Taraxacum* sp., *Tragopogon* sp., and *Verbascum* sp. Tree seedlings particularly of *Juglans regia* emerged within the six years and reached heights of several meters, other emerging tree species were *Acer platanoides, Elaeagnus angustifolia*, *Populus* sp., *Prunus* sp., *Robinia pseudoacacia*, and *Salix* sp.

Particularly in 2016 and 2017, when there were still open water areas, the fish-free wetland was colonised by amphibians. Dominant species was *Pelophylax* sp., other species found were *Bufo bufo, Bufotes viridis,* and *Rana dalmatina*. In 2021, also *Lissotriton vulgaris* was detected. Because of the rapid expansion of helophyte stands the wetland lost its role as valuable spawning habitat for amphibians. Aquatic macroinvertebrates detected were, for example, *Asellus aquaticus, Helophilus pendulus, Helophilus trivittatus, Stratiomys chamaeleon,* and *Limnephilus lunatus*. Particularly in 2016–2018, large population of *Argiope bruennichi* and *Tetragnatha extensa* exercised predation pressure on the damselfly and dragonfly populations at the wetland (Figs. 19–21). Spiders and their webs were predominantly found in lower helophyte stands at A1 above the water surface. On 10-vi-2018, for example, about 20 specimens of young *A. bruennichi* were found in 1 m^2 covered by *Sparganium erectum*. In the dry areas of the basin both species appeared in significantly lower abundances.

The Common Snipe *Gallinago gallinago* chose the wetland as winter habitat and may also have had a predatory influence on larval Odonata populations. Two specimens of this species were found from 9-x-2016 to 10-xii-2016 and on 22-iii-2019, one individuum was detected from 08-i-2017 to 27-iii-2017, from 18-xi-2017 to 18-iii-2018, on 13-x-2018 and 16-ii-2020. Another predator, the Red-backed Shrike *Lanius collurio* was often observed at the basin.

Figure 19. ***Argiope bruennichi*** **with its prey: a male *Ischnura elegans*… (13-viii-2016.)**

Figure 20. … and an immature male *Sympetrum striolatum*, 31-vii-2016.

Figure 21: A male *Ischnura pumilio* as prey of *Tetragnatha extensa*, 08-viii-2016.

Climate situation

The study site is situated in a spatial transition zone, mainly influenced by the Pannonian (Continental) climate, but it is also affected by the Illyrian (Mediterranean/Continental), Atlantic (Oceanic), and the Alpine climate (Auer & Böhm, 2011; Galí Reniu, 2017). Data provided by the meteorological monitoring station Vienna/Hohe Warte (198 m a.s.l., 17 km away from the study site), which is run by the Zentralanstalt für Meteorologie und Geodynamik (ZAMG), were used to describe both the historical and the current climate of the region where the study site is located (www.zamg.ac.at/cms/de/klima): The mean annual precipitation for this region, calculated for the "normal climate period 1961–1990" (defined by the World Meteorological Organization), is about 610 mm, the annual average temperature 10.3° C. The annual precipitation in the years 2016–2021 ranged between 582 mm (2021) and 717 mm (2018), the annual average temperature between 11.6° C (2021) and 13.0° C (2018 and 2019). The Figures 22 and 23 illustrate the increased air temperatures over the investigation period compared to the reference period 1961–1990: Figure 22 shows the mean monthly temperatures, Figure 23 the mean temperature of the meteorological seasons (winter: 1-xii – 28/29-ii; spring: 1-iii – 31-v; summer: 1-vi – 31-viii; autumn: 1-ix – 30-xi).

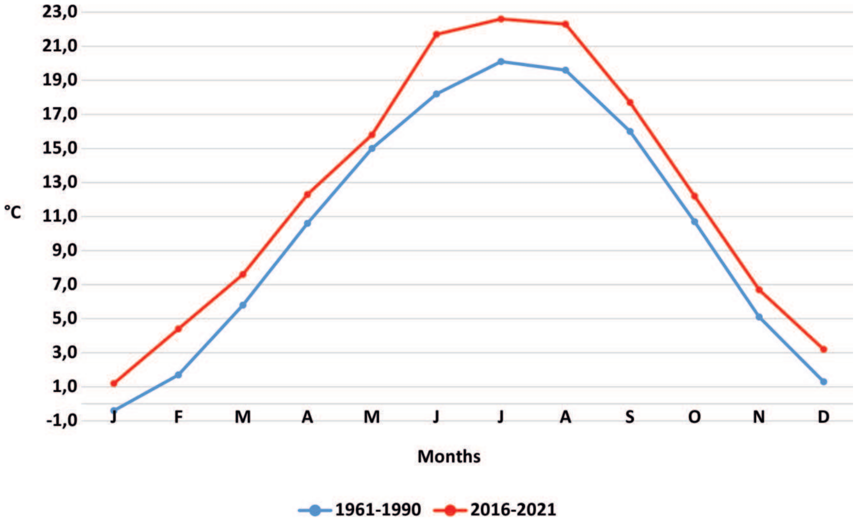


Figure 22. Mean monthly air temperatures (in °C) for the period 2016–2021 (red dots and line) and for the period 1961–1990 (blue dots and line). Source: https://www.zamg.ac.at/cms/de/klima/klima-aktuell/klimamonitoring/.

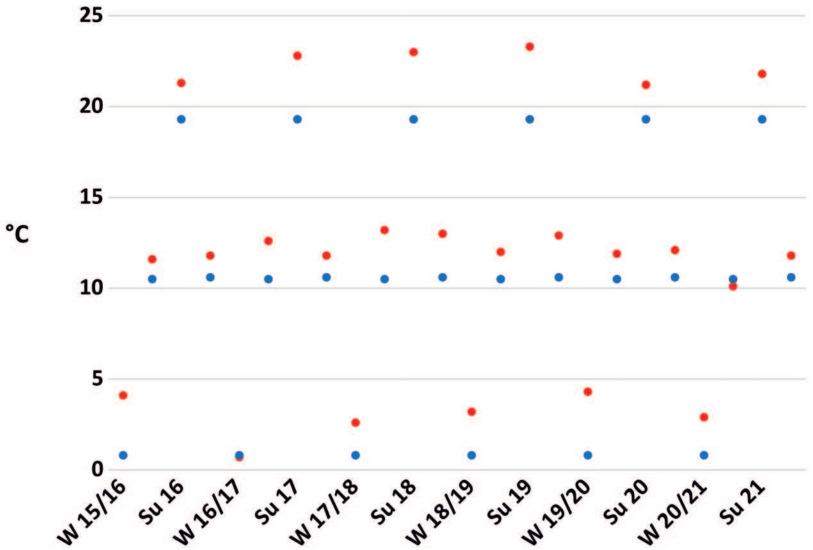


Figure 23. Mean air temperatures (in °C) of the meteorological seasons of the period 2016–2021 (red dots) and of the period 1961–1990 (blue dots), W: winter, Sp: spring, Su: summer, A: autumn. Source: https://www.zamg.ac.at/cms/de/klima/klima-aktuell/-klimamonitoring/.

Field work

Due to the vicinity of the author's home, the performance of a high number of excursions was possible. A total of 236 site visits were carried out between 28-iii-2016 and 04-x-2021 – 2016: 46 visits, 2017: 42, 2018: 30, 2019: 33, 2020: 43, and 2021: 42. Each field trip took between one and three hours and was carried out in warm and sunny weather conditions with no or only gentle wind, between 11:00 and 15:00 CEST. Surveys concentrated on the detection of teneral, juvenile, and adult imagines and on the observation of reproductive behaviour (copulae, tandem, egg deposition). The high number of field trips allowed evaluations of phenological aspects and of the length of the species´ presence at the site compared with the species-specific flight periods.

Individuals were identified by sight and by photographs. When necessary, specimens were caught with a handnet and immediately released after identification. With the exception of *Aeshna isoceles*, photos of all species detected are available taken at the study site. For the summarising documentation of the results, the maximum number per species and per recording day in a year was transferred into a five-class system. In the definition of those five abundance classes dragonfly family-specific habitat requirements (e.g. due to territorial behaviour patterns) were taken into account (Tab. 1; Chovanec et al., 2015). Abundance classes are referred to a 100 m shore-line length, which approximately corresponds to the mean circumference of the wetland. For a better differentiation in the results, abundance class 1 (single record) shows either one single individual recorded at one single field trip in a year or one specimen recorded at more than one trip (indicated by the + in Tab. 2). Single individuals of different sex recorded at different excursions were classified in abundance class 2. Data of Odonata found at the temporarily flooded basin were treated separately (Tab. 2). Hence, the data concerning the role of A1 as reproduction habitat were not biased.

Table 1. Allocation of numbers of specimens/100 m to abundance classes.

	1 Single	2 Rare	3 Frequent	4 Abundant	5 Extr. abund.
Zygoptera without Calopterygidae	1	2-10	11-25	26-50	>50
Calopterygidae and Libellulidae	1	2-5	6-10	11-25	>25
Anisoptera without Libellulidae	1	2	3-5	6-10	>10

Exuviae, predominantly of Anisopterans (Moore & Corbet, 1990), were sampled particularly in the years 2016 and 2017. In the subsequent years sampling of exuviae has been widely waived, in order to prevent damage to the reed stands associated with a “rejuvenation“ of parts of the wetlands and the unintentional creation of small new habitats.

The following data set was subject to assessment, interpretation, and discussion: list of recorded species, evidenced reproduction by detection of tenerals and exuviae, observation of reproductive behaviour (copula, tandem, egg deposition), and annual duration of the species´ presence at the site (site-specific flight period). Total numbers of individuals per year were calculated on the basis of the highest number of specimens per species recorded at one of the field trips of a given year. In the case of bivoltinous species, the maximum numbers of both generations were summarized. The detected species were also assessed considering the Austrian Red List of endangered Odonata (Raab, 2006).

Results of the year 2016 were documented by Chovanec (2017c), different ecological aspects observed at the study site were already published during the investigation period: unguarded oviposition in *Coenagrion scitulum* (Chovanec & Wildermuth, 2017), interrupted oviposition in *Orthetrum brunneum* (Chovanec, 2017d), heterospecific pairing attempts (Chovanec, 2017e), selection of emergence substrate in *O. brunneum* (Chovanec, 2018b), perching behaviour of *O. brunneum* and of other Libellulinae (Chovanec, 2018c), and strong thoracic pruinescence in males of *Orthetrum coerulescens* (Chovanec, 2021b, 2023) and *Orthetrum cancellatum* (Chovanec, 2021c, 2023). Detailed presentations of the findings concerning *Ischnura pumilio* and *Sympetrum striolatum* were given by Chovanec (2022a, b).

Results

General overview

The investigations from 2016 to 2021 revealed a total spectrum of 32 species (14 Zygoptera, 18 Anisoptera) which corresponds to 41% of the Austrian Odonata fauna comprising 78 spp. (Tab. 2). Fourteen out of these 32 species are listed in the Red List for Austria: *Coenagrion scitulum* (detected in 2016; Fig. 24) and *Sympetrum meridionale* (2016 and 2019; Fig. 25) are classified as “critically endangered”. *Lestes barbarus* (“endangered”) was recorded in 2017 and 2019 (Fig. 26). *Libellula fulva* (Fig. 27) was the second “endangered” species

Figure 24. Egg deposition of *Coenagrion scitulum* at A1, 02-vii-2016.

Figure 25. Male of *Sympetrum meridionale* with a total of 32 larvae of *Arrenurus* sp. attached to both wings, 08-viii-2016.

Figure 26. Male of *Lestes barbarus* with a larva of *Arrenurus* sp. attached to the thorax, 19-vii-2019.

Figure 27. Female of *Libellula fulva*, 24-vi-2021.

found (single record in 2021). “Vulnerable” Odonata recorded were *Sympecma fusca, Coenagrion pulchellum, Aeshna affinis, Aeshna isoceles,* and *O. coerulescens. Calopteryx splendens, Calopteryx virgo, O. brunneum,* and *Sympetrum fonscolombii* are classified as “near threatened”.

There was no species found with a “complete set” of records and observations proofing an autochthonous and stable population during all study years: abundance class ≥ 2, records of exuviae and/or tenerals, observation of reproductive behaviour, duration of the presence at the site corresponds to the species-specific flight period. *Sympetrum striolatum* was the only species with this set found during four years (2016-2019). The pattern of records and observations suggests that *Pyrrhosoma nymphula* is the only species autochthonous during the whole investigation period 2016–2021. *Orthetrum coerulescens* was the only species colonising the wetland when it was already totally covered by helophytes and forming a population rich in individuals (Tab. 2). Exuviae and/or tenerals were found in four zygopteran species (*Coenagrion puella, Ischnura elegans, I. pumilio,* and *P. nymphula*), and in seven anisopteran species (*Libellula depressa, Libellula quadrimaculata, O. brunneum, O. coerulescens, S. fonscolombii, S. striolatum,* and *S. vulgatum*). Seven species were not detected in the year following an observed egg deposition (*C. puella, C. scitulum, Enallagma cyathigerum, Erythromma viridulum, Crocothemis erythraea, O. cancellatum,* and *S. meridionale*). The findings of the study are summarised in Table 2 by listing the species found with the abundances, records of tenerals and/or exuviae, observations of reproductive behaviour, and the presence at the site compared with the species-specific flight periods. Species documented exclusively at the temporarily flooded parts of the basin are separately marked.

Sympecma fusca, *P. nymphula*, *L. quadrimaculata*, *S. sanguineum*, *S. striolatum*, and *S. vulgatum* were recorded in each year of the investigation period at A1 and/or A2 (Tab. 2). *Sympetrum striolatum* was the species with the highest number of records: At 108 of the 236 field trips *S. striolatum* was sighted – 2016: 31; 2017: 24; 2018: 16; 2019: 16;

Table 2. Species recorded at the investigated site in Maria Enzersdorf (Lower Austria): abundance class, records of exuviae and/or tenerals, observations of reproductive behaviour, presence at the site, records solely at the flooded area.

	2016	2017	2018	2019	2020	2021
Pyrrhosoma nymphula	🟩 ○	🟩 ○	🟨 ○	🟨 ●○	🟩	🟩 ●○
Sympecma fusca	🟩 ○	🟩 ○	🟦 +	🟩 ○	🟦 +	🟩
Sympetrum striolatum	🟥 ●○	🟧 ●○	🟧 ●○	🟧 ●○	🟧 ●○	🟨 ○
Libellula quadrimaculata	🟧 ●○	🟧 ●○	🟦 +	🟦 +	🟦 +	🟦 ●+
Sympetrum sanguineum	🟨 ○	🟩	🟩 ○	🟩	🟩	🟦
Sympetrum vulgatum	🟨 ●○	🟩 ●○	🟦	🟦	🟦 +	🟩
Aeshna mixta	🟩	🟩	🟦	🟦	🟦 +	
Coenagrion puella	🟥 ●○	🟥 ●○	🟧 ●○	🟨 ●○	▭	🟦
Ischnura pumilio	🟥 ●○ ●○	🟨 ●○ ●○	🟨 ●○	🟩 ●	▭ ○	
Ischnura elegans	🟥 ●○ ●○	🟩 ●○	🟩 ●	🟦 +	▭ +	▭
Libellula depressa	🟨 ○	🟩 ○	🟩 ●	🟦		
Aeshna cyanea	🟦	🟦	🟦	🟦		
Anax imperator	🟧 ○	🟦 +	🟦 +		🟦 +	🟦 +
Orthetrum brunneum	🟧 ●○	🟧 ●○	🟦 +		🟦	🟦
Lestes sponsa	🟩 ○	🟩 ○	🟦			
Aeshna isoceles	🟦	🟦				
Orthetrum cancellatum	🟩 ○			🟦	🟦	🟦 +
Sympetrum fonscolombii	🟦			🟦 +	🟦 +	🟩 ●
Crocothemis erythraea	🟩 ○			🟦 +		🟦 +
Sympetrum meridionale	🟩 ○			🟦 +		
Chalcolestes viridis	🟩				🟦	
Calopteryx splendens	🟦				🟦	
Erythromma viridulum	🟨 ○					
Coenagrion scitulum	🟩 ○					
Enallagma cyathigerum	🟩 ○					
Coenagrion pulchellum	🟩					
Calopteryx virgo	🟦 +					🟦
Lestes barbarus		🟦		🟦		
Aeshna affinis			🟨	🟦		🟦
Anax parthenope			🟦		▭	🟦
Orthetrum coerulescens				🟨 ●○	🟨 ●○	🟥 ●○
Libellula fulva						🟦

🟦	one single record per year	▨	no records at the beginning of the flight period
🟦 +	multiple sporadic single records per year	▨	records only in the middle of the flight period
🟩	rare	▨	missing records at the end of the flight period
🟨	frequent	▭	record only at the flooded area of the basin
🟧	abundant	●	exuvia(e), teneral(s)
🟥	extremely abundant	○	copula(e), tandem(s), egg deposition(s)

2020: 13 and 2021: 8. Three species were found during five years: *Coenagrion puella*, *Aeshna mixta*, and *Anax imperator*. *Coenagrion pulchellum*, *C. scitulum*, *Enallagma cyathigerum,* and *Erythromma viridulum* were found only in 2016. The record of *L. fulva* was restricted to the single record of a female in 2021.

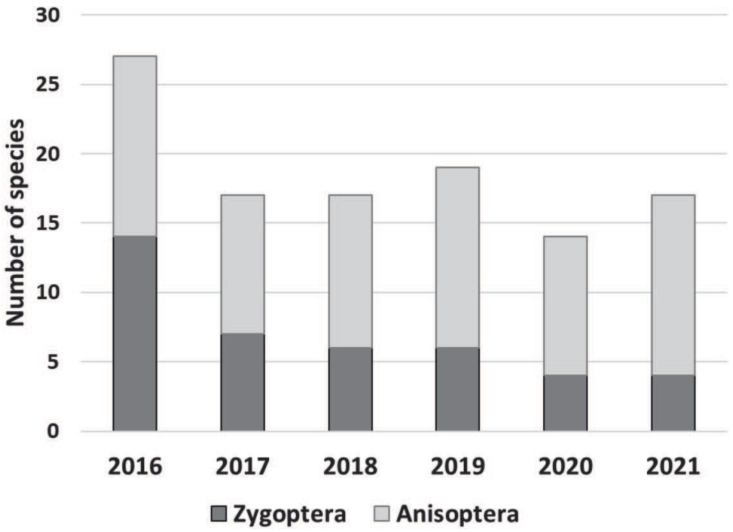


Figure 28. Numbers of species recorded at the areas A1 and A2 in the reservoir in Maria Enzersdorf (Lower Austria).

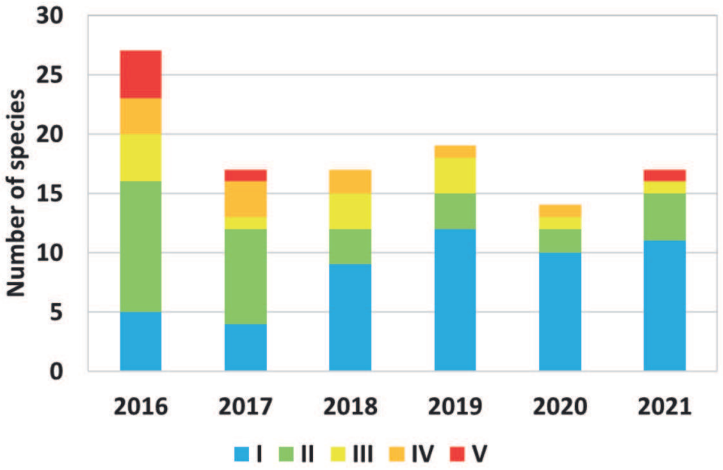


Figure 29. Number of species per abundance class (I–V).

The total number of species decreased from 27 (in 2016) to 14 in 2020 and 17 in 2021, respectively (Fig. 28). Species recorded only at the flooded area in the case of inundation (Tab. 2) are not considered in these analyses. Exclusively in 2016, the number of zygopteran species exceeded that of anisopteran species.

The portion of single records (one record per year and multiple sporadic single records of non-territorial males and/or females) increased during the six-year investigation period whereas the number of species detected in higher abundance classes decreased (Fig. 29). In 2016, four species occurred “extremely abundant” (abundance class V): *Coenagrion puella*, *I. elegans*, *I. pumilio*, and *S. striolatum*. In the following year, only *C. puella* was recorded in abundance class V. Later on, it was only in 2021, that one species (*O. coerulescens*) was assigned to class V.

The total number of individuals decreased from 882 in 2016 to 40 (in 2020) and 74 (in 2021), respectively (Fig. 30). In 2016, *I. pumilio* was the most abundant damselfly with 350 individuals with the maximum numbers of both generations aggregated. From 2017 to 2019, *C. puella* was the dominant zygopteran species. In 2020 and 2021, the numbers of Zygoptera was very low with highest numbers in *S. fusca* and *P. nymphula*. From 2016 to 2020, *S. striolatum* was the anisopteran species with highest numbers of specimens with a significantly decreasing trend from 150 in 2016 to 13 in 2020. *Orthetrum coerulescens* showed increasing numbers of individuals from 2019 to 2021 with a maximum of 40 specimens in the last year of the study. In this year, *O. coerulescens* was the most abundant anisopteran species.

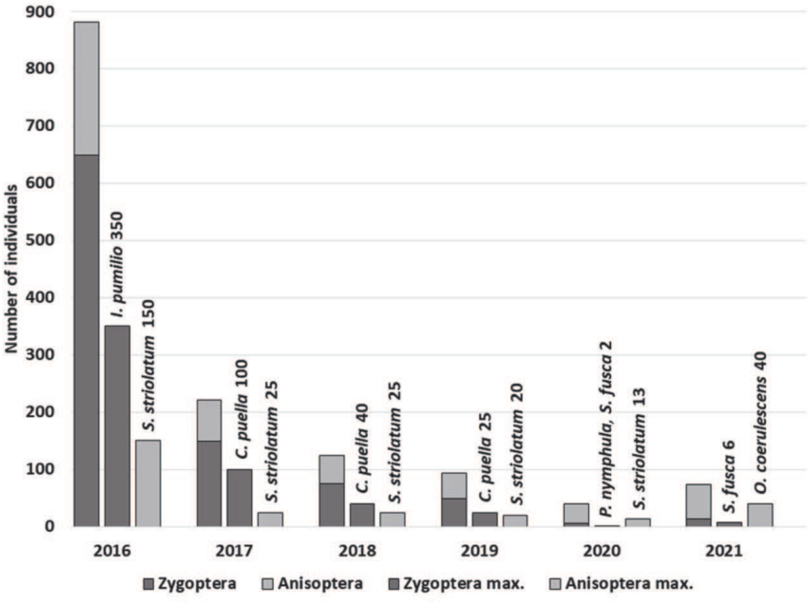


Figure 30. Total numbers of individuals and maximum numbers of individuals of the most abundant Zygoptera and Anisoptera per year.

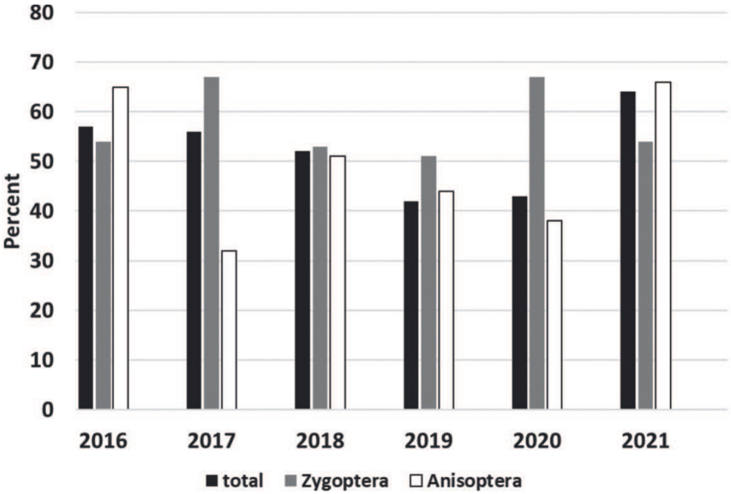


Figure 31. Share of the sum of the individuals of dominant zygopteran species and anisopteran species of the total number of individuals (total); share of the specimens' number of the dominant zygopteran species of the total sum of damselflies; share of the specimens' number of the dominant anisopteran species of the total sum of dragonflies.

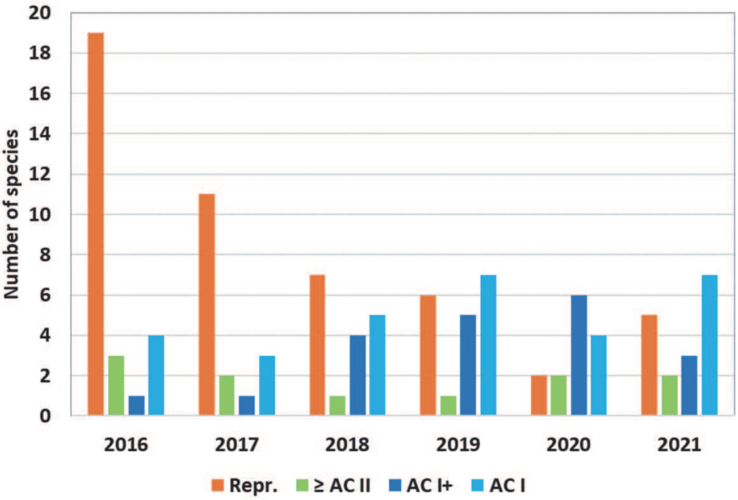


Figure 32. Number of species with proof of reproduction (exuviae and/or tenerals and/or observed reproductive behaviour): Repr.; number of species at least in abundance class (AC) II with no proof of reproduction: ≥ AC II; number of species detected by multiple sporadic single records with no proof of reproduction: AC I+; number of species detected by a single record with no proof of reproduction: AC I.

The sum of the individuals of the most abundant dragonfly and damselfly species accounts for 42–64% of the total number of individuals. In the case of Zygoptera, the dominant species accounts for 51–67% of the total number of damselflies. The dominant anisopteran species has a share of 32–66% of the total dragonfly specimen's number (Fig. 31).

Figure 32 shows a decrease of species with exuviae and/or tenerals found and/or reproductive behaviour observed from 2016 to 2020, with an increase in the final year. The number of species detected in abundance class II or higher with no evidence of reproduction was approximately constant. The sum of the numbers of species detected by multiple sporadic single records and by a single record was lowest in 2016 (5 spp.) and 2017 (4 spp.). The highest value (12 spp.) was reached in 2019 and 2021.

In each year, the sum of species recorded by a single record and by multiple sporadic single records was dominated by anisopteran species. The number of zygopteran species constantly ranged between one and three. The number of anisopteran single records increased from three (2016 and 2017) to ten in 2019 and nine in 2021, respectively (Fig. 33). The multiple sporadic single records of 2021 comprised one freshly emerged *L. quadrimaculata* (Tab. 2).

Figure 33. Number of zygopteran and anisopteran species recorded by both single records and multiple sporadic single records.

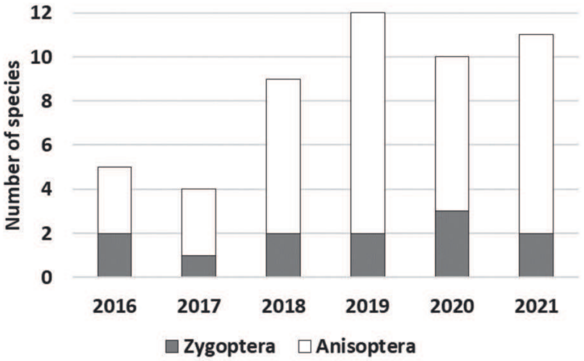


Table 3 shows a detailed phenological analysis based on the records made in 2016 (Tab. 3; see also Chovanec, 2017c).

In the following pages, selected and representative species are covered in detail.

Coenagrion puella:

Coenagrion puella (Fig. 34 and 35) was recorded from 2016 until 2019 at A1. In 2020, the species was solely sighted at temporarily flooded areas of the basin, in 2021 only one individuum was sighted at A1. Deteriorating habitat conditions were reflected in decreasing numbers of individuals, in the shortening of the species´ presence at the wetland compared to its flight period (Fig. 36), and in a decrease in the share of days with observed reproductive behaviour of the total number of days with records of this species. The portion of days with observed tandems and/or pairing wheels decreased from 75% (2016), 86% (2017), and 85% (2018) to 55% (2019). The number of days with observed egg deposition significantly declined one year earlier: 2016: 65%, 2017: 71%, 2018: 23%, 2019: 27%. In Figure 37 the absolute number of observation days is depicted.

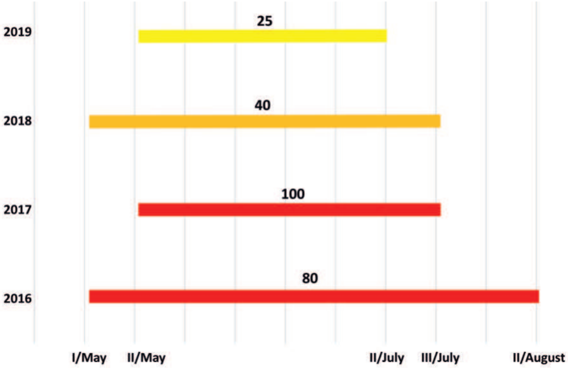
Table 3. Phenology of the species recorded in 2016 (order according to their temporal appearance); blue: single record; green: rare; yellow: frequent; orange: abundant; red: extremely abundant (cf. Tab. 1); ●: records of exuviae and/or tenerals; ○: observation of tandems, copulae, and/or egg deposition.

	S. fusca	*I. pumilio*	*I. elegans*	*C. puella*	*L. quadr.*	*P. nymph.*	*L. depr.*	*O. brunn.*	*A. imp.*	*S. fonsc.*	*C. pulch.*	*S. striol.*	*C. splend.*	*A. isoc.*	*O. canc.*	*C. scit.*	*C. eryth.*	*S. vulg.*	*E. cyath.*	*E. virid.*	*L. sponsa*	*S. sang.*	*C. virgo*	*C. viridis*	*Sy. merid.*	*A. mixta*	*A. cyanea*
10-xii																											
27-xi																											
22-xi												🟧 ○															
13-xi																											
09-xi												🟧 ○															
31-x												🟥 ○															
17-x												🟥 ○												🟦			
09-x												🟥 ○															
01-x	🟦											🟥 ○										🟩				🟦	
30-ix	🟦											🟥 ○														🟦	🟦
24-ix		🟩										🟥 ○										🟩		🟦		🟦	
22-ix								🟦				🟥 ○						🟦									
21-ix								🟦				🟥 ○														🟦	
15-ix		🟩	🟦					🟩				🟥 ○						🟨 ○			🟦	🟨 ○		🟦		🟦	
10-ix		🟩	🟩					🟨 ○				🟥 ○						🟨 ○			🟩	🟨 ○					
03-ix		🟩 ○	🟩 ○					🟩				🟥 ○						🟨 ○			🟦	🟨 ○		🟦	🟦	🟦	
30-viii		🟨 ○	🟩					🟩 ○				🟥 ○						🟩 ○			🟩	🟨 ○				🟩	
27-viii		🟨 ○●	🟩 ○					🟩				🟥 ○●						🟨 ○			🟩	🟨 ○				🟩	
20-viii		🟧 ○●	🟨 ○					🟨 ○				🟥 ○●						🟩			🟩	🟨 ○	🟦				
18-viii		🟥 ○●	🟥 ○●	🟩				🟨 ○				🟧 ○●								🟩	🟩	🟩			🟩		
14-viii		🟥 ○●	🟥 ○●	🟩				🟨	🟦			🟨			🟩			🟦		🟩	🟩	🟩		🟦			
13-viii		🟥 ○●	🟥 ○●	🟩 ○				🟨 ○	🟦			🟧 ○			🟦			🟦		🟨 ○	🟩 ○	🟩					
08-viii		🟥 ○●	🟥 ○●	🟨 ○				🟨 ○	🟩			🟧 ○						🟩		🟨 ○	🟩	🟩	🟦	🟩	🟦		
07-viii		🟥 ○●	🟥 ○●	🟧 ○				🟨 ○	🟨			🟧 ○			🟩 ○			🟩		🟨	🟩	🟩					
31-vii		🟥 ○●	🟥 ○●	🟥 ○	🟩			🟨 ○	🟨			🟧 ○●			🟩 ○		🟦	🟩 ●		🟨 ○	🟩	🟦					
23-vii		🟥 ○●	🟧 ○●	🟥 ○	🟨			🟨 ○	🟨 ○			🟧 ●			🟩 ○		🟦	🟦		🟩 ○	🟩						
22-vii		🟥 ○●	🟧 ○	🟥 ○	🟨			🟨 ○	🟨 ○			🟥 ●			🟩 ○		🟦		🟩	🟩 ○	🟦						
10-vii		🟧 ○●	🟧 ○	🟥 ○	🟨 ○			🟧 ○	🟨			🟥 ●			🟩	🟩 ○			🟩 ○	🟩 ○	🟦						
02-vii		🟨 ○●	🟧 ○●	🟥 ○	🟧 ○			🟧 ○	🟨		🟦	🟧 ●			🟩	🟩 ○		🟦 ●	🟩	🟩							
01-vii		🟧 ○●	🟧 ○	🟥 ○	🟧			🟧 ○	🟨			🟧 ●			🟩 ○		🟦	🟦 ●	🟩								
23-vi		🟧 ○	🟨 ○●	🟥 ○	🟧 ○		🟩	🟧 ○●	🟨 ○			🟧 ●			🟩	🟩 ○	🟦 ○										
19-vi		🟧 ●	🟨 ○	🟧 ○	🟧 ○●	🟦	🟩	🟨 ○	🟦			🟨 ●															
11-vi		🟥 ○●	🟨 ○●	🟧 ○	🟧 ●	🟩	🟨 ○	🟨 ●	🟨		🟦	🟨 ●															
08-vi		🟥 ○●	🟨 ○●	🟥 ○●	🟧 ○●	🟩	🟨 ○	🟧 ○●	🟧 ○		🟦	🟦 ●	🟦	🟦	🟦												
05-vi		🟧 ○●	🟩 ●	🟧 ○	🟨 ○	🟩	🟩	🟨 ○	🟧 ○		🟩																
29-v		🟥 ○●	🟩 ●	🟨 ●	🟩 ●		🟦	🟩 ●	🟦	🟦																	
26-v		🟥 ○●	🟩	🟨 ○	🟩 ●	🟩	🟩	🟩 ●	🟦																		
21-v		🟧 ○●	🟩	🟩 ○●	🟩 ○●	🟩	🟦																				
14-v		🟧 ○●	🟩		🟩 ●	🟦		🟦 ●																			
09-v	🟩 ○	🟨 ●			🟩 ●	🟩 ○	🟩 ○																				
05-v		🟨 ●	🟦	🟦 ●	🟦 ●																						
23-iv		🟩 ●																									
20-iv		🟩 ●																									
16-iv																											
03-iv	🟩																										
28-iii	🟦																										

Figure 34. Egg deposition of *Coenagrion puella* in A1, 26-v-2016.

Figure 35: Two males of *Coenagrion puella* fighting for a female of *Coenagrion pulchellum*, 02-vii-2016.

Figure 36. Presence of *Coenagrion puella* at the site and yearly maximum number of individuals. I, II, III decades of the month.



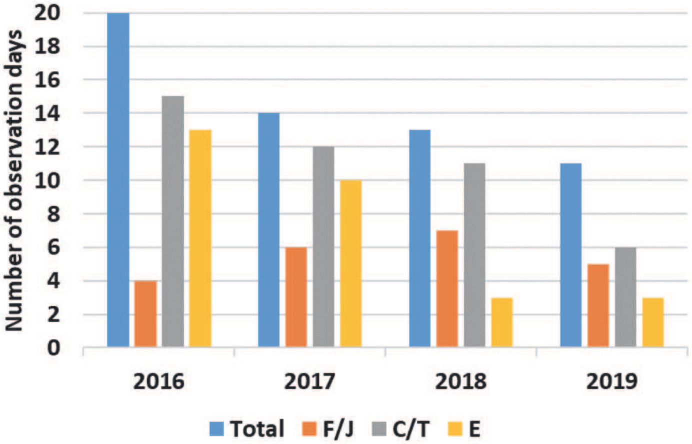


Figure 37. Total number of observation days with *Coenagrion puella* recorded (Total); number of observation days with records and observations of freshly emerged (F) and/or juvenile (J) individuals; number of observation days with observed copulae (C) and/or tandems (T); number of observation days with observed egg deposition (E).

Figure 38. A male *Ischnura elegans* probably of the first generation preying on a freshly hatched conspecific of the second generation, 23-vii-2016.

***Ischnura elegans*:**

In 2016, the second generation of the bivoltinous *I. elegans* was rich in individuals (Fig. 38 and 39). The following years (2017 and 2018) were characterised by decreasing numbers of individuals and by the formation of only the spring/early summer generation. The slight peak in Fig. 39 resembling a second generation in 2017 is explainable by records of a maximum of two “visitors” in August. But in the summer of this year, no freshly emerged individuals were found at all. In July 2017, the species could not be detected. In the same year, a significant decrease of surveys with observed tenerals and reproductive behaviour is remarkable (Fig. 40). In 2018, reproductive behaviour was not observed at all. In the following years, only multiple sporadic single records of this species were made at A1 (2019) and in the flooded parts of the basin (2020 and 2021; see also Tab. 2).

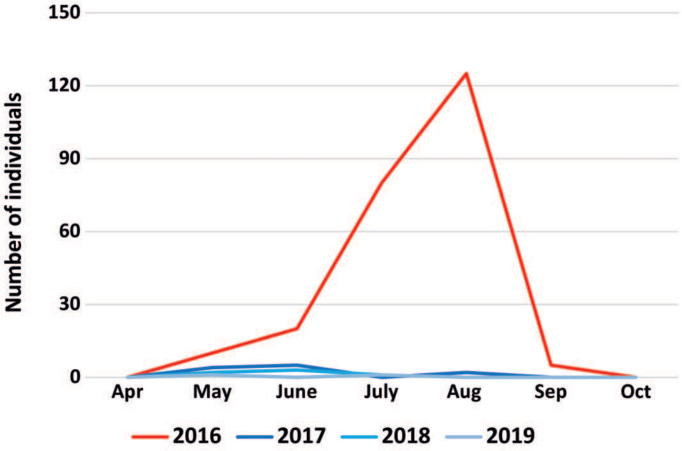


Figure 39. Number of individuals of *Ischnura elegans* at A1 and A2.

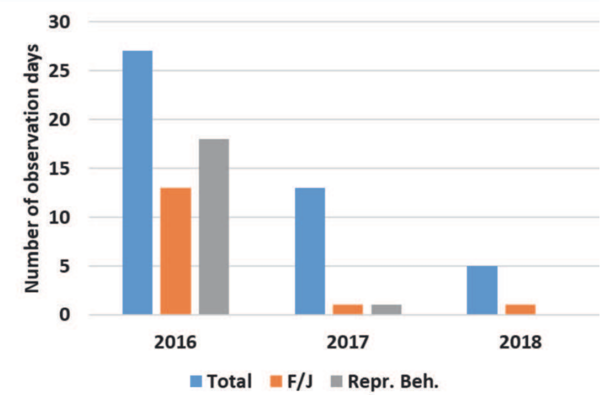


Figure 40. Total number of observation days with *Ischnura elegans* recorded (Total); number of observation days with records and observations of freshly emerged (F) and/or juvenile (J) individuals; number of observation days with observed reproductive behaviour (Repr. Beh.).

Ischnura pumilio:

A detailed analysis of this species´ records at the investigated site is given by Chovanec (2022a). Figure 41 shows an unguarded egg deposition, which is typical of *Ischnura* spp.; a triple tandem with a male *I. pumilio* included is depicted in Figure 42. Different female colour morphs are shown in Figures 43–46. *Ischnura pumilio* was recorded at A1 from 2016 to 2019.

In each year, tenerals and juvenile specimens were found. In 2016, open water areas and low-growing amphibious vegetation characterised the wetland. In that year, *I. pumilio* was the most abundant species within the odonate community comprising 27 species (Tab. 2, Fig. 30). As in *I. elegans*, its development was bivoltinous with higher numbers of specimens in the second generation: The spring/early summer generation comprised about 100 individuals, the midsummer generation about 250. In the following years, the rapid expansion especially of high-growing *Typha latifolia* and *Epilobium hirsutum* led to a complete and dense coverage of the water body. The response of *I. pumilio* to changing habitat conditions was a significant decline in the number of individuals: 2016 – total number 350; 2017 – 30; 2018 – 18; 2019: 5. In contrast to the population structure in 2016, the second generation in 2017 was smaller than the first one. In 2018 and 2019, *I. pumilio* was represented by only the spring/early summer generation. The second generation of 2017 and the single generations of 2018 and 2019 occurred during a shorter time compared to the species-specific flight period (Fig. 47). The continuous collapse of the population was also accompanied by a decreasing number of survey days with observed reproductive behaviour: In 2016, at 23 of the 31 days with records of *I. pumilio* copulae and/or tandems were observed, which corresponds to 74 %. This percentage decreased to 55 % in 2017, and 10 % in 2018. In 2019, the final year of its occurrence at A1 and/or A2, neither copulae, nor tandems, nor egg depositions were observed at any day (Fig. 48). In 2020, *I. pumilio* appeared only at temporarily flooded areas in the reservoir (one copula at 6-vi-2020; Tab. 2).

Figure 41. Egg laying androchromous *Ischnura pumilio*, 13-viii-2016.

Figure 42. A male *Ischnura pumilio* linked to a tandem of *Erythromma viridulum*, 08-viii-2016. (see also Chovanec, 2017e).

Figure 43. Copula of *Ischnura pumilio* with an immature female, forma *aurantiaca*, 22-vii-2016.

Figure 44. Copula of *Ischnura pumilio* with a gynochromous mature female, 21-v-2016.

Figure 45. Copula of *Ischnura pumilio* with an androchromous female, 08-viii--2016.

Figure 46. Copula of *Ischnura pumilio* with an old, pruinescent female, 18-viii-2016.

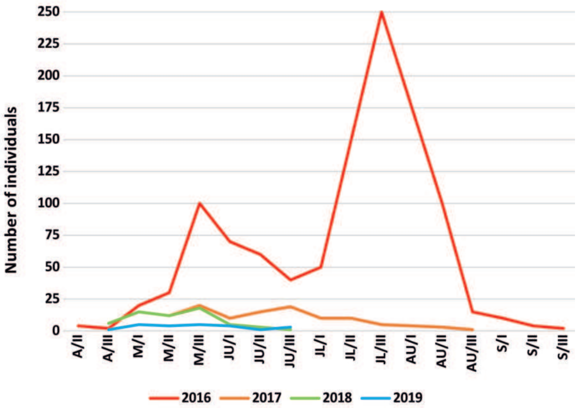
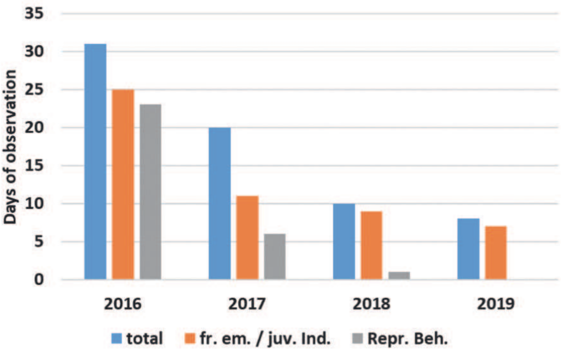


Figure 47. Number of individuals of *Ischnura pumilio*; I, II, III decades of the months; A April, M May, JU June, JL July, AU August, S September.

Figure 48. Total number of observation days with *Ischnura pumilio* recorded (Total); number of observation days with records and observations of freshly emerged and/or juvenile individuals (fr. em / juv. Ind.); number of observation days with observed reproductive behaviour (Repr. Beh.).



***Pyrrhosoma nymphula*:**

Site-specific flight periods of *P. nymphula* (Figs 49–51) started between 22-iv (2019) and 19-v (2017) and ended between 31-v (2018) and 19-vi (2016). The duration of the presence at the site varied between four (2017) and 8 weeks (2019). The maximum numbers of individuals

Figure 49. A tandem of *Pyrrhosoma nymphula*, 01-vi-2021.

Figure 50. A tandem of *Pyrrhosoma nymphula*, 09-v-2016.

recorded in a year ranged from two (2020) to 15 (2019). Numbers of site visits with records of this species ranged from four (2020) to ten (2019). Although the abundance was continuously low, the Large Red Damselfly is probably the only species forming a breeding and, therefore, autochthonous population during the whole investigation period. In 2020, only one or two individuals, respectively, were recorded at four site visits with no sexual behaviour observed. Nevertheless, freshly emerged specimens were detected in 2021.

Figure 51. A female *Pyrrhosoma nymphula* with a preyed crane fly, 11-v-2019.

***Aeshna affinis*:**

A maximum of four males (Fig. 52) were observed in July 2018 continuously patrolling over patches with a size of about 20-30 m^2 situated in A1 characterised by pressed down vegetation (Figs. 53 and 54). This species seemed to be attracted by light reflections caused by the horizontal plant patterns. These impacts, only occurring in 2018, were possibly caused by mammals like foxes or rabbits (both observed in the basin) and provided sunny perching sites used, for example, by frogs. In 2019 and 2021, only single records of *A. affinis* were made (Tab. 2).

Figure 52. A male *Aeshna affinis*, 20-vii-2019.

Figure 53. Pressed down reeds in Area A1, 26-vi-2018.

Figure 54. A1 with pressed down reeds, 04-vii-2018.

Figure 55: Freshly emerged female *Libellula depressa* with a damaged wing and exuding hemolymph, 21-vii-2018.

Libellula depressa:

In 2016, a maximum of eight individuals of *L. depressa* were found, in 2017 five. In both years, reproductive behaviour was observed, exuviae or tenerals were not found. In 2018 some exuviae, freshly emerged specimens and three adults were found, but the small population early left the already densely vegetated site (Fig. 58). Late records of an immature male of *L. depressa* at 26-vi-2018, and of a freshly emerged female at 21-vii-2018 (Fig. 55) are rather remarkable.

Libellula quadrimaculata:

In 2016, the population of *L. quadrimaculata* (Fig. 56, 57) comprised about 20 individuals with exuviae and tenerals found and a presence at the site corresponding to the species-specific flight period. Reproductive behaviour was also observed. One year later, 2017, exuviae and tenerals were also found and the species performed reproductive behaviour. The maximum number of individuals was slightly reduced (15). The most obvious proof of deteriorating habitat conditions was a significantly shortened duration of the presence at the site. Records in the following years were limited to single records (Fig. 58).

Figure 56. Freshly emerged male of *Libellula quadrimaculata*, 14-v-2016.

Figure 57. *Libellula quadrimaculata* forma. *praenubila*, hidden behind a *Typha*-spike, 10-vi-2018.

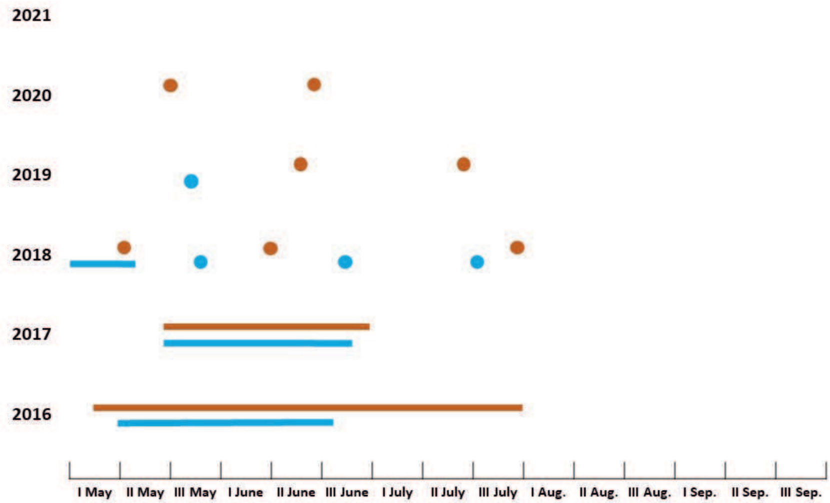


Figure 58. Presence at the site (lines) and single records (dots) of *Libellula depressa* (light blue) and *Libellula quadrimaculata* (brown). I, II, III: decades of the months.

Orthetrum brunneum:

In 2016, the population of *Orthetrum brunneum* (Fig. 59) comprised 15 individuals; the set of proofs of a vital breeding population indicating suitable habitat conditions was complete: presence at the site corresponding to the species-specific flight period, sightings of exuviae and tenerals, and observations of reproductive behaviour (Fig. 60) at 17 of a total of 27 days with records of this species. One year later, the population was of the same size with tenerals found and observed reproductive behaviour at 8 of 12 days, but the presence at the wetland was significantly shorter. In 2018, 2020, and 2021 exclusively single records of

Figure 59. Obelisk posture of a male *Orthetrum brunneum* in order to prevent over-heating, 08-viii-2016 (see also Castillo-Pérez et al., 2023).

Figure 60. Copula of a male *Orthetrum brunneum* with the four-leg perching position of the male, which is typical of Libellulinae. The female embraces the male´s abdomen with only two legs (see also Chovanec, 2018c), 31-vii-2016.

females were made (Fig. 64). Behavioural aspects of egg deposition, perching, and emergence of *O. brunneum* observed during this study have already been published by Chovanec (2017d, 2018b, c).

***Orthetrum coerulescens*:**

Orthetrum coerulescens (Fig. 61–63) was the only species in the investigation period colonising the wetland when it has become totally covered with helophytes. The population of the Keeled Skimmer showed an increasing population size (Fig. 64): In 2019 and 2020 a maximum of 10 individuals were recorded, in 2021 40 specimens. In that year, *O. coerulescens* was classified as the most abundant odonate species at the site (see also Fig. 30). As tenerals were already found in 2019, egg deposition must have been taken place the year before, but was not observed. In the first two years of occurrence, at one of 13 (2019) and

Figure 61. Male of *Orthetrum coerulescens* with a rather pruinose thorax, 20-vii-2019.

at one of 17 (2020) days with records of *O. coerulescens* a copula was sighted. In 2021, at ten of 21 days with records of this species a total of 14 copulae, 12 tandems, and 3 egg depositions were observed. In this year, maximum numbers of individuals were recorded on 25-vii-2021 (35) and 29-vii-2021 (40). The majority of the observed individuals were males, the highest numbers of females were counted on 6-vii-2021 (six from 26 specimens) and 29-vii-2021 (five from 40). Late records of juvenile individuals on 24-viii-2019 and on 2-ix and 5-ix-2021 were rather surprising (Fig. 65). Strong thoracic pruinosity of males recorded at this site (Figs. 61, 62) was discussed by Chovanec (2021b, 2023): This colour variation is interpreted as response to the increased temperatures due to climate change and enables males to hold their territories over a longer period.

Figure 62. Another male of *Orthetrum coerulescens* with a pruinose thorax, 16-viii-2020.

Figure 63. Copula of *Orthetrum coerulescens*, 29-vii-2021.

Figure 65 shows the duration of *O. coerulescens´* presence at the site and the temporal distribution of records of tenerals and juveniles. The dot beside the 2021-line indicates the record of a female at 16-ix-2021, 11 days and 5 sites visits after the last preceding record of the species at 05-ix-2021.

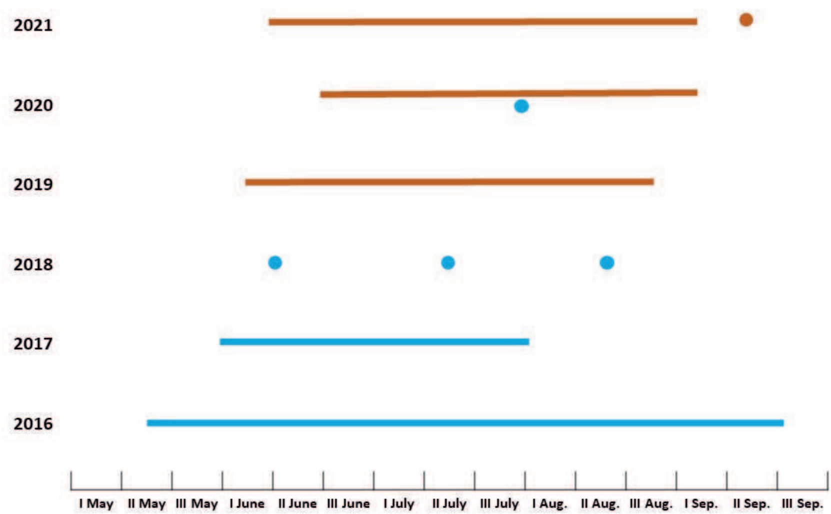


Figure 64. Presence at the site (lines) and single records (dots) of *Orthetrum brunneum* (blue) and *Orthetrum coerulescens* (brown). I, II, III: decades of the months.

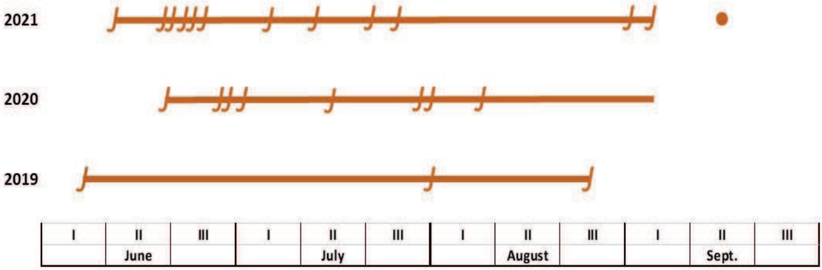


Figure 65. Presence at the site and records of tenerals and/or juveniles (J) of *Orthetrum coerulescens*; brown dot: late record of a female; I, II, III: decades of the months.

***Sympetrum fonscolombii*:**

The number of this species´ records was low. Observations of males were restricted to the first half of the respective year: One male was detected on 29-v-2016 at A1, two males were recorded on 23-vi-2020 at the flooded area (Figs. 66, 67). Females were only found in the second half of the year at the dry, not flooded area of the basin: one specimen on 26-vii and 12-viii-2019 and on 1-viii and 20-viii 2020. Two females, one of them freshly emerged, were detected on 10-ix-2021, probably the same individuals were found one day later, one of them also on 12-ix (Fig. 68, 69).

Figure 66. Male *Sympetrum fonscolombii* …

Figure 67. …found at the temporarily flooded area of the basin, 23-vi-2020.

Figure 68. Female of *Sympetrum fonscolombii*, 10-ix-2021.

Figure 69. Dry area of the basin, where females of *Sympetrum fonscolombii* appeared, 12-viii-2019.

Figure 70. Basking male *Sympetrum striolatum* pressing its thorax on a dry *Typha*-leaf for warming up, 21-ix-2016 (see also Borkenstein & Jödicke, 2020, 2022).

Figure 71. Female of *Sympetrum striolatum* with egg clutch, 13-viii-2016.

***Sympetrum striolatum*:**

A detailed presentation of the data on *Sympetrum striolatum* is given by Chovanec (2022b). The Common Darter (Fig. 70–75) was found in each year with decreasing numbers of individuals from 150 (2016) to 6 (2021). With the exception of 2021, *S. striolatum* was the most abundant anisopteran species (Fig. 30). The longest presence at the site was measured in 2016 lasting from 8-vi to 22-xi (see also Tab. 2 and 3). The last sightings on 22-xi were made after several nocturnal frosts (up to -5.1° C at 15-xi) with observed egg deposition over partly frozen water surface. Records were made almost exclusively at A1, only in 2019 larvae (in June) and freshly emerged specimens (in July) were detected at A2. Table 4 shows the earliest and latest records of tenerals, juveniles, and adult individuals.

Figure 72. Tandem of *Sympetrum striolatum*, resting after an unsuccessful search for egg deposition sites, 06-ix-2018.

Figure 73. Copula of *Sympetrum striolatum*, 29-viii-2019.

The rapid development of helophyte stands represented an obvious habitat degradation for *S. striolatum*. This fact is clearly illustrated by several finding of the study. There was a significant decrease of the number of adults starting in 2017 with the strongest decline from 150 individuals in 2016 to 25 in 2017. Another sign was the short time period in 2020 with

Figure 74. Female of *Sympetrum striolatum* in an interspecific tandem with a male of *Sympetrum sanguineum*, 30-viii-16 (Chovanec, 2017e).

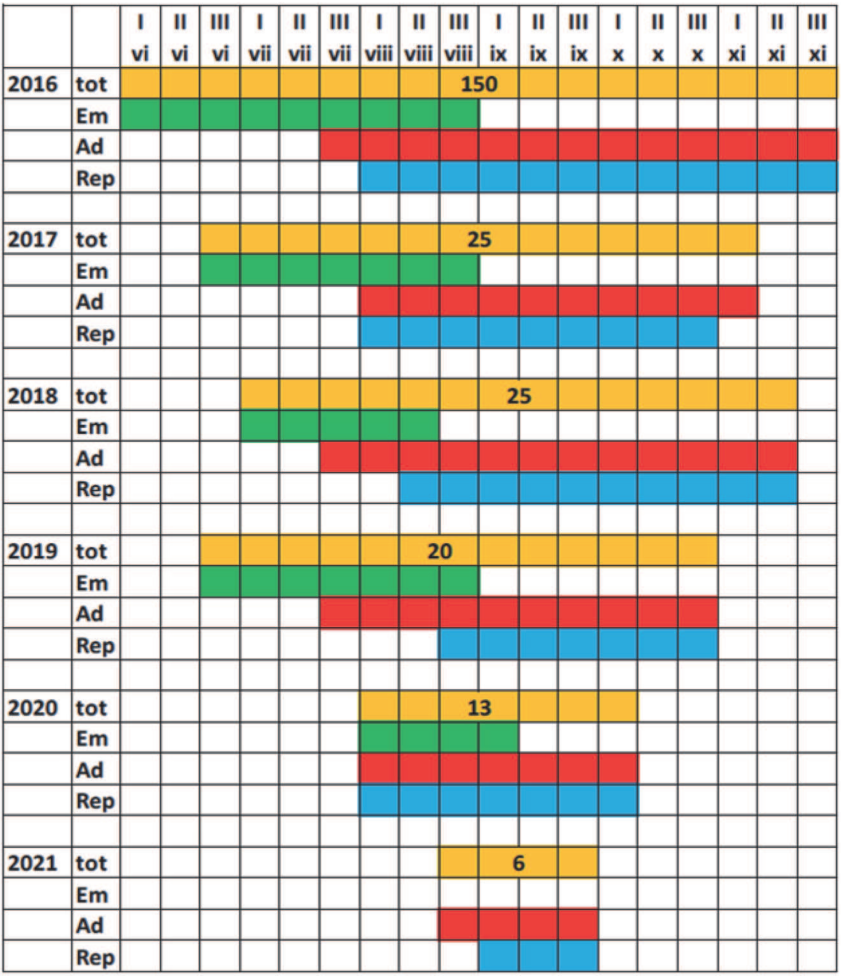
Figure 75. Exuvia of *Sympetrum striolatum* on a nearly horizontal section of a *Schoenoplectus*-stem (see also Straub, 1943), 03-viii-2017.

	earliest record	latest record
Tenerals	08-vi-2016	03-ix-2020
Juveniles	27-vi-2019	24-ix-2020
Adults	22-vii-2016	22-xi-2016

Table 4. Earliest and latest records of teneral, juvenile, and adult *Sympetrum striolatum* at the investigated site in Maria Enzersdorf (Lower Austria).

tenerals found; in 2021, no tenerals were found at all. In 2020, a striking shortening of the presence at the site was observed: It only started in the first decade of August and ended in the first decade of October. In 2021, adults were present at the site from 29-viii to 25-ix (Tab. 5).

Table 5. Total (tot) period of *Sympetrum striolatum* spent at A1 and A2 with maximum number of individuals, emergence period (Em; records of exuviae and tenerals), flight period of adults (Ad) and period with observed reproductive behaviour (copulae, tandems, and/or egg depositions; Rep).



		I	II	III	I	II	III	I	II	III	I	II	III	I	II	III	I	II	III
		vi	vi	vi	vii	vii	vii	viii	viii	viii	ix	ix	ix	x	x	x	xi	xi	xi
2016	tot	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨 150	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨
	Em	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩									
	Ad						🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥
	Rep							🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
2017	tot			🟨	🟨	🟨	🟨	🟨	🟨	🟨 25	🟨	🟨	🟨	🟨	🟨	🟨	🟨		
	Em			🟩	🟩	🟩	🟩	🟩	🟩	🟩									
	Ad							🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥		
	Rep							🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦			
2018	tot				🟨	🟨	🟨	🟨	🟨	🟨	🟨 25	🟨	🟨	🟨	🟨	🟨	🟨	🟨	
	Em				🟩	🟩	🟩	🟩	🟩										
	Ad						🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	
	Rep								🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	
2019	tot			🟨	🟨	🟨	🟨	🟨	🟨 20	🟨	🟨	🟨	🟨	🟨	🟨	🟨			
	Em			🟩	🟩	🟩	🟩	🟩	🟩	🟩									
	Ad						🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥			
	Rep									🟦	🟦	🟦	🟦	🟦	🟦	🟦			
2020	tot							🟨	🟨	🟨 13	🟨	🟨	🟨	🟨					
	Em							🟩	🟩	🟩	🟩								
	Ad							🟥	🟥	🟥	🟥	🟥	🟥	🟥					
	Rep							🟦	🟦	🟦	🟦	🟦	🟦	🟦					
2021	tot									🟨	🟨 6	🟨	🟨						
	Em																		
	Ad									🟥	🟥	🟥	🟥						
	Rep										🟦	🟦	🟦						

Analyses of the data revealed changes in in the quantity and quality of reproductive behaviour in connection with habitat degradation. There was an overall decline of site visits with observed copulae, tandems and/or egg depositions: 2016: 21, 2017: 12, 2018: 7, 2019: 8, 2020: 8, 2021: 3. But there were also obvious changes in the different consecutive phases of reproductive behaviour: In optimal or suboptimal habitat conditions, most copulae were followed by egg deposition. In the years 2016–2018 the number of site visits with observations of egg deposition were (nearly) as high as the number of visits with observed copulae and/or tandems. In 2019 and 2020, a significant decrease of site visits with observed egg laying behaviour was documented, in 2021 this behaviour was not observed at all (Fig. 76).

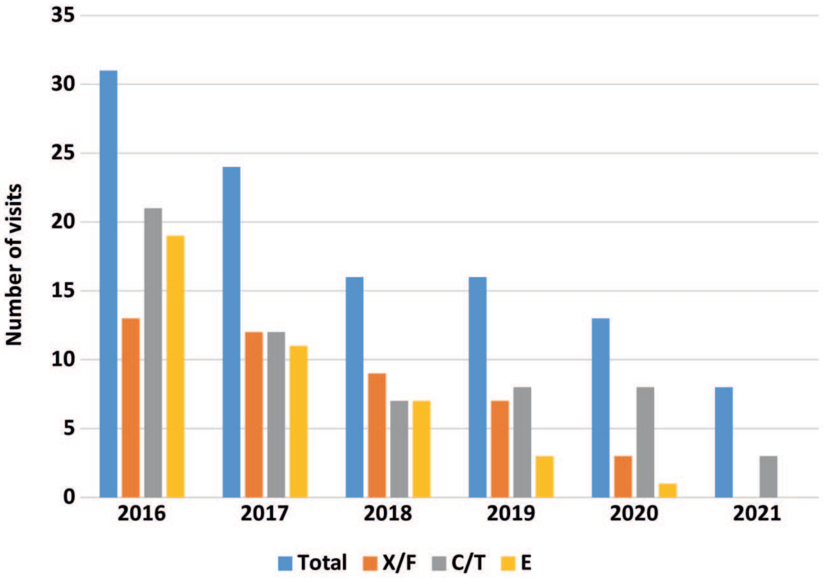


Figure 76. Total number of site visits with records of *Sympetrum striolatum* at A1 and A2 (Total), number of visits with exuviae and/or freshly emerged individuals (X/F) found, number of visits with copulae and/or tandems observed (C/T), number of visits with egg deposition observed (E).

Table 6. Number of recorded tenerals and/or juvenile *Sympetrum striolatum* per site visit carried out in the „emergence and juvenile period".

Year	Emergence and juvenile period (EJP)	Number of site visits in the EJP	Number of tenerals and/or juveniles found per site visit in the EJP
2016	08-vi – 27-viii	17	8,2
2017	20-vi – 23-ix	12	6,2
2018	4-vii – 19-viii	9	4,7
2019	27-vi – 12-ix	12	2,8
2020	31-vii – 24-ix	12	0,6
2021	no tenerals and/or juveniles found	–	–

As can be seen from Table 6, the decrease of both the numbers of adult *S. striolatum* and of egg deposition activities coincide with the numbers of records of tenerals and/or juvenile individuals. In this table the periods with occurring tenerals and juveniles (“emergence and juvenile period”), the number of site visits within this period, and the mean number of recorded tenerals and/or juveniles per site visit are listed.

Discussion

While several long-term studies were carried out at sites subjected to management measures (e. g. Wildermuth, 2008a, 2016, 2017), the water body investigated in the present study was allowed to develop naturally without any disturbances. The main study area, A1, was characterised by constant framework settings as far as the permanent water level is concerned (in contrast to this, see for example Nicolai, 2020). Therefore, the only parameter which had to be related to the changes in the odonate community in this “outdoor laboratory” was the fast development of helophyte coverage. Temporary and sporadic short-term flooding events concerning the whole basin seemed not to affect the odonate community of A1, but, on the other hand, allowed to gain an impression on rapid colonisation of new habitats by dragonflies.

A considerable amount of literature has been published on the fast recognition and colonisation of suitable new habitats by dragonflies (e. g. Martens, 1991; Bönsel, 2006; Buczyńsky et al., 2016; Wildermuth, 2017; Bogan et al., 2020). This fact is well supported by the data provided by the study at hand. Successful reproduction was proved in seven of the 27 species recorded in 2016, the first year of the study. Thus, in those species egg deposition must have already taken place in 2015, soon after the construction of the basin. A more impressive proof for rapid colonisation processes is given by the records made at the flooded area of the basin. Some examples may illustrate this: On 17-viii-2021, the mostly dry parts of the basin were under water for about one week due to heavy rainfall. On the first site visits after the rainfall on 19-viii and 21-viii, individuals of *S. striolatum* were recorded at the flooded parts with pairs in tandem position and copulation wheels; egg depositions were also observed. These sightings were the first records of the Common Darter in that year in the reservoir, furthermore the only copulation wheels and egg depositions performed of *S. striolatum* in 2021 in the basin at all. The records of *S. striolatum* at the flooded parts in 2021 represented the highest numbers of individuals of this species detected in the reservoir in that year. In the following weeks, a maximum of only six individuals were detected at A1 and/or A2. The only records of *I. elegans* in the basin in 2021 were made on 19-viii and they were restricted to the flooded areas. As seen from Table 2, in 2020, records of *C. puella*, *I. elegans*, *I. pumilio*, and *A. imperator* in the basin were limited to observations at the flooded area made on 06-vi after heavy rainfall on 05-vi and on 23-vi after rainfall the day before. As been seen from these data, the detection and colonisation of newly emerging water bodies took place within hours (see Bogan et al., 2020).

Due to the small size and to the shallow depth of the investigated wetland, the consecutiveness of successional processes was rather condensed. At the start of the study in 2016, the successional status of the wetland has to be defined as transition between the pioneer stage, which started in 2014 after the termination of the basin´s construction, and a short developmental stage (Moore, 1991). Developmental stages are described to be those with the highest species diversity (e. g. Moore, 1991; Wildermuth, 2017; Rychła, 2019). Already in the second half of 2018, the developmental stage was followed by the climax stage, characterised by complete reed coverage. Following the rapid alteration of habitat conditions, the Odonata community also changed in short time. Based on the collected data, it can be concluded that only *P. nymphula* established a small breeding and successfully reproducing population during the whole investigation period. Due to methodological reasons explained above, the central parts of densely vegetated patches of A1 were not entered since 2018. As these areas are the preferred habitat of the Large Red Damselfly (Sternberg, 1999; Wildermuth & Martens, 2019), an underestimation of the number of individuals cannot be excluded. *Pyrrhosoma nymphula* is described as a comparatively philopatric species with low mobility (Sternberg, 1999; Wildermuth & Martens, 2019). The source of colonisation by *P. nymphula* was probably represented by the pond on the campus.

In 2016, the first year of the study, the odonate community was characterised by both, pioneer species such as *I. pumilio*, *L. depressa*, *O. brunneum*, and *S. striolatum* (Martens, 1991; Moore, 1991; Wildermuth, 2010a; Kolar et al., 2021) as well as by species typical of advanced successional stages (e. g. *L. sponsa*, *L. quadrimaculata*, *S. vulgatum*, and *S. sanguineum*). This fact is likely to be due to the transition of the site from the pioneer stage into the developmental stage mentioned above. The sum of the pioneer species´ individuals accounted for the highest portion of the total number of individuals. In that year, the highest total number of species (27) and the highest number of species with successful reproduction and/or observed reproductive activities (19) were recorded. 2016 was also the year with the highest total number of individuals and with the highest numbers of individuals belonging to the dominant damselfly and dragonfly species.

In 2016, habitat heterogeneity was high due to the existence of open water areas, open, sparsely, and densely vegetated shallow banks, a specific plant architecture consisting of low- and high-growing helophytes, and floating submerged macrophytes (Banse & Banse, 1985; Lenz, 1991; Moore, 1991; Wildermuth, 2017). The sunny location, the existence of permanent areas, the lack of fish, and the near-natural immediate terrestrial hinterland of the basin were other factors promoting the dragonfly community rich in species in that year. The extensively used park in close vicinity of the wetland provided suitable roosting and maturation physiognomy away from the breeding habitat (Bried & Ervin, 2005).

The lowest number of single records (5) can be interpreted as another indicator of suitable habitat properties. Some species performing reproductive behaviour in 2016 did not appear in 2017, but occasionally occurred later as single specimens (*O. cancellatum*, *C. erythraea*, and *S. meridionale*). Some species showing reproductive behaviour were found only in 2016 at all (*C. scitulum*, *E. cyathigerum*, and *E. viridulum*). Wildermuth (2017) also reported on observed reproductive behaviour in some species (e. g. *E. viridulum*), which were not detected in the following year.

Changes in habitat properties were also obvious in the composition and reaction of ecological guilds. Already in 2017, increasing coverage by helophytes caused the loss of species occurring in 2016 and typical of open water (Chovanec et al., 2015): *Enallagma cyathigerum* and *E. viridulum* were not recorded, *A. imperator* – recorded in abundance class IV in 2016 – appeared only occasionally and was detected as multiple sporadic single record in the following years. Species preferring open or sparsely vegetated banks disappeared (*O. cancel-*

latum) or occurred in significantly reduced abundances (*S. striolatum*). And even species characteristic for helophyte stands, such as *L. quadrimaculata* and *S. sanguineum*, disappeared from this site.

Orthetrum brunneum, a species with pioneer character, started to leave the water body in 2017. It was “replaced” by *O. coerulescens*, a species typical of densely vegetated habitats. A syntopic occurrence of these two species is possible in habitats providing suitable habitat features for both species spatially separated or in water bodies of an intermediate successional stage (Heymer, 1969; Chovanec, 2018d). At the investigated site in Maria Enzersdorf, *O. coerulescens* appeared in 2019, when the wetland was completely overgrown by plants and observations of *O. brunneum* were restricted to single records. As freshly emerged individuals of *O. coerulescens* were detected in 2019, egg deposition must be preceded in 2018, but was not observed. The permanent water level of A1 was dependent on the contact with groundwater. This fact caused marginal flows prevented A1 from complete freezing. This hydrologic situation supported the occurrence of both rheophilous *Orthetrum*-species (Buchwald & Schmidt, 1990; Schorr, 1990; Wildermuth, 2008b; Chovanec et al., 2015; Chovanec 2018b). The source of the colonisation by both *Orthetrum*-species was probably a wetland situated in a flood retention basin a distance of about 1,000 m and a small brook, the Krotenbach, which is situated at a distance of about 700 m. At both sites *O. brunneum* and *O. coerulescens* syntopicly appeared (see also Chovanec, 2020). *Calopteryx splendens* and *C. virgo*, two other rheophilous species, were detected as single records. Both species also occured at the Krotenbach (Chovanec, 2020; see also Stettmer, 1996).

Whereas most of the species detected in 2016 left the site due to reduced habitat quality, the development of helophyte density has proved to be favourable for its colonisation by *O. coerulescens*. According to Buchwald & Schmidt (1990) and Sternberg & Buchwald (2000), the Keeled Skimmer prefers, inter alia, small spring mires and marshes with a coverage of 25–60% by vegetation with heights of 20–70 cm. *Orthetrum coerulescens* is often found at sites with stands of *Sparganium erectum*, which probably indicate not freezing habitats (Buchwald & Schmidt, 1990). However, especially in 2016 and 2017, those habitat conditions were realized at the wetland. Although the appearance of *O. coerulescens* would have been expected sooner, it took place when the A1 was totally covered with high *Typha*-, *Epilobium*-, and *Phragmites*-stands and significantly reduced stands of *Sparganium erectum*.

As highlighted by the photos presented in the results-section, a colour variation of *O. coerulescens* untypical for Central Europe was detected during the study and discussed by Chovanec (2021b, 2023). Climate change has manifold effects on dragonfly communities. Range expansions in many species within the last decades are the most obvious responses to increased temperatures. Both, dragonfly observers and scientific odonatologists also prove changes in phenological shifts. And, furthermore, first studies deal with influences on interspecific interactions and competition (e. g. Hogreve & Suhling, 2022). In the central and northern parts of their range, males of *O. coerulescens* are characterised by a brownish thorax, with slight pruinescense only in older specimens at the end of the flight period. At the wetland in Maria Enzersdorf, a high number of male *O. coerulescens* with an intensively pale blue thorax – similar to adult males of *Orthetrum brunneum* – were observed. Even in young mature and middle-aged males, the thorax was wax-covered to a degree known especially from the southern parts of the species’ distribution range. Moreover, frons, veins at the wing base, and femora were also covered with wax and, thus, appeared blue.

This – for Central Europe – extraordinary pruinosity is interpreted as species-specific variation and thermoregulatory adaptation to increasing air temperatures in Central Europe due to climate change. Meteorological data for the study region presented in this study support this hypothesis by showing significantly higher air temperatures compared with long-term meteorological monitoring data. Pruinescense on the body supports thermoregulation by reflecting UV radiation (see discussion in Chovanec 2021b). In this context, the thorax seems to play a major role, because the protection of the abdomen can also be enabled by postural adjustments, such as the obelisk posture (Corbet, 1999; Wildermuth, 2006; Wildermuth et al., 2018, 2019; Borkenstein & Jödicke, 2020, 2022). The stronger development of the wax-based colouring in populations inhabiting hotter environments underlines this interpretation of the role of pruinescense (see also Pinkert et al., 2023). By reacting on higher temperatures with stronger pruinescence, males probably are able to hold their territories over a longer time without overheating. At the investigation site, the same colour morph was detected in *O. cancellatum* (Chovanec, 2021c, 2023).

Whereas area A1 was groundwater-fed and permanent, the hydrological regime of A2 was dependent on precipitation and increased water levels at A1 allowing an overflow from A1 to A2. Therefore, the temporary A2 was not relevant as breeding site for Odonata. Only in 2019, larvae (in June) and tenerals (in July) of *S. striolatum* were found due to an adequate duration of water coverage and humidity lasting from autumn 2018 to autumn 2019.

The record of a freshly emerged female of *S. fonscolombii* in 10-ix-2021 suggests the successful development of this species at the site. Egg deposition probably took place in mid-July when the reservoir was water-covered for the first time in that year. Taking into account the short development times (less than two months) described for this species (Jödicke & Borkenstein, 2022), emergence at the end of the first September-decade is possible. However, the preconditions for this are both, the completion of the embryonic development at the site of egg deposition and the movement of the larvae timely to water covered areas in A1 or A2. Wildermuth & Martens (2019) described larvae of *S. fonscolombii* as rather mobile.

The large number of site visits allowed a close look on phenological patterns. In 2016, several species were detected quite early at the site compared with data on their flight period available from literature (Raab & Pennerstorfer, 2006; Boudot & Kalkman, 2015; Wildermuth & Martens, 2019). This is evident, for example, in *I. pumilio* (20-iv), *O. brunneum* (14-v), and *S. striolatum* (8-vi). Increasing temperatures due to climate change may cause general shifts in phenological patterns and have to be considered when discussing phenological groups (e. g. Schmidt, 1985; Moore, 1991; Laister, 1996; Chovanec, 1998; Corbet, 1999). In 2016, the population structure of most detected species was rather intact and not influenced by reactions on unsuitable habitat conditions. The chronology of their appearance at the wetland including data on their emergence (Tab. 3) allows a species´ classification in winter-, spring/early summer-, and high summer/autumn-species. Besides the winter-species *S. fusca*, data rather show a cluster of spring/early summer-species starting their flight period in April and May consisting of the first generation of *I. pumilio* and *I. elegans*, of *L. quadrimaculata*, *P. nymphula*, *L. depressa*, *O. brunneum*, and *A. imperator* (in chronological order acc. to Tab. 3). High summer/autumn-species with emergence starting in June or later are *I. pumilio* and *I. elegans* with their second generation, *S. striolatum*, *O. cancellatum*, *S. vul-*

gatum, *E. viridulum*, *L. sponsa*, *S. sanguineum*, and *A. mixta* (in chronological order acc. to Tab. 3).

Data recorded for *S. striolatum* enable a sound analysis of emergence, maturation, and flight periods (Chovanec, 2022b). According to Sternberg (2000), the flight period lasts for 18–22 weeks. The longest presence at the investigated wetland with 24 weeks was recorded in 2016 (from 08-vi to 22-xi). A significantly reduced presence of the Common Darter species was observed in 2020 (10 weeks) and 2021 (four weeks). The longest emergence period in *S. striolatum* was also recorded in 2016 lasting from 08-vi to 27-viii. *Sympetrum striolatum* maturates often kilometres away from water bodies (Sternberg 2000). Sternberg (2000) defines the maturation period as the time span between records of the first tenerals and the first adults at a water body. According to literature, in *S. striolatum* this period lasts between three and six weeks, in hot summers it can be extended to eight weeks (Sternberg, 2000; Horne, 2012; Wildermuth & Martens, 2019). Within the present study, the longest maturation periods were measured in 2017 with seven weeks and in 2016 with six weeks. Data gained in the year 2021 show that *S. striolatum*´s presence at A1 and A2 lasted from 29-viii to 25-ix. In that year no tenerals and juveniles of the Common Darter species were found. As a result of this, it may be concluded that populations of this species appearing at a water body generally consist of both, specimens returning to their "home water" after maturation and new colonisers.

In 2016, exuviae and/or tenerals of *L. quadrimaculata* were found between 5-v and 19-vi. In the same year, *O. brunneum*´s emergence period lasted from 14-v to 23-vi. These data represent a deviation from the generally rather synchronised emergence in spring odonate species (Wildermuth, 1994a; Corbet, 1999).

The present study with the high frequency of excursions was designed to determine the different impacts of habitat changes on the dragonfly community. At the community level, an obvious effect was the increasing number of species recorded by single records or multiple single records within the investigation period. These records consisted of females, chasing non-territorial males, and individuals warming up or just passing by. The increased number of single records in the years 2018–2021 compared to 2016 and 2017 are explainable by the appearance of anisopteran species with a – compared to Zygoptera – larger radius of action, which left the site in the case of inappropriate habitat conditions (Angelibert & Giani, 2003). Near natural, sunny sites rich in prey are used for maturation, chasing, or as sub-habitat especially for females away from the breeding sites (Wildermuth, 2010b; Chovanec, 2020). All single records of *O. brunneum* in 2018, 2020, and 2021 were exclusively represented by females. Several species appearing in abundance class ≥ 2 during the first year of the study and showing sexual behaviour, were recorded only as (multiple sporadic) single records later on (e. g. *A. imperator, C. erythraea*, *O. cancellatum*, *S. meridionale*) or did not occur anymore (*C. scitulum*, *E. cyathigerum*, *E. viridulum*). It can therefore be concluded, that records of several individuals and observations of reproductive behaviour indicate the species´ autochthony especially in the case of constant, and not rapidly changing habitat conditions (e. g. Schmidt, 1985; Höppner, 1999; Wildermuth, 2010a; Chovanec et al. 2015; Bried et al., 2015; Patten et al., 2015).

Deteriorating habitat conditions for the dragonfly community at the investigated site were reflected in several key figures and processes. In all species detected in 2016 and appearing for several years, a decrease of individuals´ numbers throughout the years was obvious. The strongest decrease was observed in *I. elegans*, *I. pumilio*, and *S. striolatum* from 2016 to 2017, which underlines the pioneer character of those species. In several univoltinous species appearing even in higher abundances, their last year of occurrence – apart from single records in the following years – was characterised by a reduced duration of presence at the water body (*C. puella*, *L. depressa*, *L. quadrimaculata*, *O. brunneum*, and *S. striolatum*). This fact indicates that individuals actively migrate out of inappropriate habitats in order to colonise better ones at the end of their flying period. *Ischnura elegans* and *I. pumilio* showed a bivoltinous development at the investigation site (Inden-Lohmar, 1997; Burbach, 2000; Chovanec, 2017c). A response of *I. pumilio* to deteriorating habitat conditions was, that – in contrast to the population structure in 2016 – the second generation in 2017 was smaller than the first one. In 2018 and 2019, *I. pumilio* was represented by only one generation. The second generation of 2017 and the single generations of 2018 and 2019 occurred at the site during a shorter time compared to the species-specific flight periods (Chovanec, 2022a). A similar pattern, starting one year earlier than in *I. pumilio*, was observed in the bivoltinous *I. elegans*. The reduced presence of the first generation of both species was probably due to both, emigration out of the site and mortality by predation. Especially in very small populations the effects of predation may also be a cause for their disappearance (e. g. Cordero, 1994; Padeffke & Suhling, 2003).

The number of days with records of copulations wheels, tandem formations, and egg depositions turned out to be a meaningful parameter to illustrate behavioural changes due to habitat alterations. Days with observed reproduction activities decreased in *C. puella*, *I. elegans*, *I. pumilio*, and *S. striolatum* compared to the total number of days with records of those species. The records of copulation wheels and/or tandems on the one hand and egg deposition on the other in *S. striolatum* showed an obvious decline in the frequency of egg deposition behaviour following preceding copulation. In 2021, only pairing behaviour, but no egg deposition was observed. A similar behavioural pattern was shown by *C. puella*. As published by Cordero (1994), *Coenagrion scitulum* showed significantly reduced sexual behaviour in unsuitable habitat conditions.

The fact of reduced sexual behaviour is likely to be due to decreased encounter rate of males and females explainable by low abundances. Especially in the case of *I. pumilio* with its short-range movements this factor is probably of major relevance (Allen et al., 2014; Chovanec 2022a). The limited availability and accessibility of suitable sites due to the high and dense helophyte stands may be one of the reasons for reduced egg laying activities in *C. puella*. A detailed analysis of behavioural patterns of *S. striolatum* was carried out by Chovanec (2002b). In 2018, this species was observed in performing flights in tandem position over water areas moderately covered by reed in A1. Dipping movements were carried out about 30 to 40 cm over the water surface at the top margin of helophytes, which prevented the tandems to reach the water surface. The not completely overgrown area allowed recognising the horizontally polarised light reflected by the water surface, and, thus, performing all stages of reproductive behaviour including egg laying movements (see also Wildermuth & Spinner, 1991; Wildermuth, 1993, 2007; Corbet, 1999; Horváth et al., 2007). But successful egg deposition did probably not take place, because water has to be touched in order for eggs to be extruded (Ottolenghi, 1987). However, this observed behaviour was interpreted as “attempted” egg deposition and has to be differentiated from "pre-copulatory dipping" described for *S. striolatum* (Ottolenghi, 1987; Sternberg, 2000; see also Miller et al., 1984; McMillan et al., 1996). In the following years 2020 and 2021, reed coverage made light reflections and the recognition of egg deposition sites nearly impossible. Therefore, egg laying movements were hardly (2020) and no longer (2021) observed. Pairs failed to find appropriate egg deposition sites, sometimes rested for a while (Fig. 72), and finally left the basin (furthermore in tandem position). Thus, it seems that the "programme" of egg deposition movements are induced by both key stimuli, tactile stimuli by grasping the female and the reflections of horizontally polarised light indicating suitable egg deposition sites.

The relatively small size of the wetland and the low water depth did not allow spatial niche partitioning of the larval communities to a large extent. Thus, intra- and interspecific competition and predation also may have influenced the size of damsel- and dragonfly populations (Crowley & Martin, 1989; Worthen & Horacek, 2015; Choi et al., 2020; Clark et al., 2021).

The data from this study underline, how fast small and shallow habitats become inappropriate for a large number of dragonfly species due to the expansion of helophytes. Only one species (*O. coerulescens*) benefited from the rapid development of the vegetation. The species´ response on deteriorating habitat conditions is complex and comprises different aspects, such as habitat recognition, active migration out of the area, reduced abundances making populations unstable and more vulnerable to predation and competition, and changes in the behavioural traits leading to less pairing behaviour and egg deposition. The complete helophyte coverage caused not only shading of the site and a loss in crucial habitat features essential for behavioural traits of Odonata (territorialism, reproduction, perching …), but also prevented the reflection-polarisation patterns at flat water surfaces, which are essential for dragonflies for recognising rendevouz and oviposition sites (Wildermuth, 1994b, 1998).

The results of the study clearly show, that new water bodies are quickly recognised and colonised by damselflies and dragonflies and may represent important breeding habitats for an odonate community rich in species. Low water depth promotes plant growth. Thus, shallow waters are subject to fast successional development and spreading of vegetation influencing the odonate fauna. Particularly at wetlands, management measures are indispensable to maintain heterogeneous habitat structures and to favour a diverse odonate community (Angelibert & Giani, 2003; Wildermuth & Küry, 2009). The data obtained in this investigation show how Odonata respond on deteriorating habitat conditions and which parameters are necessary to understand this complex process of migrating away and disappearing from the habitat. However, whereas the changing vegetation structures for most species represented a fast and significant degradation of the site conditions, they favoured the colonisation of the wetland by *O. coerulescens*.

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