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Populační dynamika a struktura druhů *Coenagrion puella* a *Pyrrhosoma nymphula* v
urbanizovaném centru Prahy

Population dynamics and structure of *Coenagrion puella* and *Pyrrhosoma nymphula* in the
urbanised centre of Prague

Diplomová práce

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ABSTRACT

As many other species, also dragonflies can inhabit suitable urban habitats even in the centre of big cities. This study has been focused on population dynamics of two species of damselflies (*Coenagrion puella* and *Pyrrhosoma nymphula*) in urban environment. Main goal has been to experimentally study dispersal of populations and migration between these populations in the Prague city centre using mark-release-recapture (MRR) method to observe whether the urban environment does somehow act as a barrier for population dynamics. Lentic bodies located in the broader centre of the city were chosen as sufficient study sites, situated mostly in green areas. Field study took place in 2023 from the end of May to beginning of July. Every individual was given a unique code and the information about locality of every encounter was included to track movement of individuals. In total, around 1800 individuals of both species were marked in the experiment. Results of the analysis suggest that individuals from zygopteran populations are mostly connected to their parent site. Occasional migration in *C. puella* species and almost no migration in *P. nymphula* species was observed. The putative metapopulation structure of both species is discussed further. MRR also allowed to assess some basic population parameters (separately for both sexes), i.e. the population size and survivorship of each species. From a broader perspective, our study belongs to very few of those dealing with dispersal and population patterns of dragonflies in urban landscape.

Key words: dispersion, population dynamics, dragonflies, urban habitats

ABSTRAKT

Stejně jako mnoho jiných druhů mohou i vážky obývat vhodná městská stanoviště i v centru velkých měst. Tato studie byla zaměřena na populační dynamiku dvou druhů šidélek (*Coenagrion puella* a *Pyrrhosoma nymphula*) v městském prostředí. Hlavním cílem bylo experimentálně studovat disperzi populací těchto druhů a migraci mezi těmito populacemi v centru města Prahy pomocí metody mark-release-recapture (MRR). Cílem bylo sledovat, zda městské prostředí nějakým způsobem představuje bariéru pro dynamiku populací. Jako výzkumné lokality byly vybrány vodní plochy umístěné v širším centru města, situované převážně v městské a soukromé zeleni. Terénní práce probíhaly v roce 2023 od konce května do začátku července. Každý jedinec byl označen unikátním kódem a do protokolu byly zahrnuty informace o místě všech odchyťů, aby bylo možné zpětně sledovat pohyb jedinců mezi lokalitami. Celkem bylo označeno kolem 1800 jedinců od obou druhů. Výsledky analýzy naznačují, že populace těchto šidélek jsou většinou vázané na svou mateřskou lokalitu. Zaznamenána byla občasná migrace jedinců u *Coenagrion puella*, naopak téměř žádná migrace mezi lokalitami nebyla pozorována u *Pyrrhosoma nymphula*. V práci se dále u obou druhů posuzuje, zda se v jejich populacích objevuje metapopulační struktura. V rámci analýzy byly též stanoveny různé odhady o vlastnostech populací, zvláště pro obě pohlaví. Tato práce je v současné době jedna z mála studií, které se zabývají populační dynamikou vážek v urbanizované krajině.

Klíčová slova: disperse, populační dynamika, vážky, Odonata, městské prostředí

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1 Introduction

In this thesis we take a step towards understanding how dragonflies live and possibly thrive in intensively modified environments such as urbanised centres of cities. We will describe how we studied dispersal and population dynamics of selected species of dragonflies using standard and well-known ecological methods and how it can be used in further research of urban aquatic environment and urban populations of dragonflies. It could be important for conservation of aquatic habitats in these regions because dragonflies represent an important umbrella taxon (Kietzka, 2019; Bried et al., 2007).

1.1 Dispersal in Odonata

Movement and dispersal (movement of organisms between habitat patches) are very important mechanisms in ecology and evolutionary processes. We can talk about migration meaning movement of the entire groups of animals at various geographical scales, in some cases on long distances throughout the whole continents or across the globe. On smaller scales we talk about dispersal – dragonflies and other animals (mostly individuals) move or disperse for various reasons, such as foraging, avoiding predators, mating, aggressive interactions, etc (Pyke, 1983; Corbet, 1999). Dispersal affects species distribution, determines the level of gene flow and strength of species interactions (McCuley, Baines and Mabry, 2023).

Adult dragonflies are mostly day-flying insects and flying is their primary mode of dispersal. Dragonflies use flying for foraging, holding territory, seeking out mating spots and sometimes (and only in some species) for long-distance migration (Corbet, 2004). For that, in connection with their hand able population sizes, their conspicuousness and a (relative) ease of catching and marking, odonates are often used as taxon for effective monitoring of invertebrate dispersal movements.

Dispersal is a complex process and even if we knew the (most of) driving factors, we do not entirely understand all the mechanisms and triggers underlying the entire process. Dispersal in Odonata is shaped by the particular species abilities and state of individual (phenotype-dependence) in combination with environmental and social factors (condition-dependence) (Clobert et al., 2009). One of the most crucial factors is species-dependent flight performance. Typically, anisopterans (dragonflies *sensu stricto*), with broader wings attachments and larger muscles to power flight are capable of greater speeds and greater distances than zygopterans with their petiolate wings, which may though increase

manoeuvrability, but come with the cost of reduced power output and flight speed (McCuley, Baines and Mabry, 2023). This general suborder trait split is also described by Harabiš and Dolný (2011) in the case of central european dragonflies and damselflies which were rated by experienced odonatologists by their ability to disperse. In this case, damselflies were overall described as species with lower dispersal abilities.

Dispersal ability in dragonfly populations can be also sex biased. In that case either females (Corbet, 1999; Conrad et al., 2002; Angelibert and Giani, 2003) or males (Damm and Hadrys, 2012) can have greater dispersal probability or range than the other. This sex difference could be linked either to specific species mating systems or to differential costs of dispersal between sexes (summarised in McCuley, Baines and Mabry, 2023). It is also worth noting that some odonate species may exhibit negative density-dependent dispersal (i.e. dispersal rate decreases with increasing population density). Attempts to explain this counterintuitive phenomenon rely mostly on the idea that high population density advertises better habitat (Allen and Thompson, 2010) or there might be sex-driven differences in dispersal response to density (McCuley, Baines and Mabry, 2023).

1.2 Population ecology of Odonata, metapopulation approach

Odonates are bound to aquatic habitats as they serve as their breeding sites; actually, the longest part of dragonfly's life takes place underwater. Aquatic habitats are usually patchily distributed which determines spatial structure of dragonflies' larval "populations." The adults represent the dispersal stage as they may freely move between local sites providing connections (i.e. gene flow) and thus shaping the regional population structure. As mentioned above, this "connectivity" is species-specific and Odonates can exhibit a wide range of population structures (McCuley, Baines and Mabry, 2023), even within a single genus, from patchy, rather isolated patterns (i.e. *Sympetrum depressiusculum* with strong connection to their natal site with routine movements to other patches in surrounding landscape, see Dolný et al., 2014) over metapopulation structure (*Calopteryx splendens* and *Calopteryx virgo*, see Stettmer, 1996) to intracontinental movements (*Sympetrum fonscolombii* in the Middle Asia, see Borisov et al., 2020; Popova and Haritonov, 2014). Some species go even intercontinentally (*Pantala flavescens*, considered as one of the species with global panmictic population with worldwide gene flow among the populations, see i.e. Troast et al., 2016; Ware et al., 2022). Dispersal abilities of species in connection with their ecological valence and structure of the surrounding landscape interact to shape odonate population structure. However, metapopulation patterns

may be considered a prevailing mode as aquatic habitats have patchy distribution in the landscape (Michiels and Dhondt, 1991) and can lower the extinction risk of dragonflies in the region (Korkeamäki and Suhonen, 2002). The concept of metapopulations says that populations of animals may spatially structure into a network of local breeding populations and provides a theoretical framework based on original Levins models (see review in Hanski, 1991; Hanski and Simberloff, 1997). The metapopulation theory describes how species occupy, colonise and abandon habitat patches in the landscape. Migration of individuals among these patches provides connectivity and has some effect on population dynamics. The persistence of local populations depends critically on parameters influencing extinction, e.g. the number of habitat patches and populations, the rates, and patterns of interpatch migration, and propagule delivery (Harrison, 1991). Besides the Levins concept where all the patches are same (size, quality, attractivity, etc.) Harrison (1991) suggested few scenarios which we can observe in the: (i) source-sink metapopulation system where persistence depends on stronger, more resistant populations, (ii) patchy populations where dispersal rate is so high the whole system could be taken for one single population and (iii) non-equilibrium metapopulation in which local extinction happens due to overall regional decline.

Obviously, these patchy populations networks are - by their nature - vulnerable to habitat loss and to connectivity barriers. In recent world, these aggravations are mostly of anthropogenic origin. Humans have altered landscapes nearly anywhere in the world, causing landscape fragmentation, thus increasing cost and risk of dispersal. It is observed especially in urbanised regions where - beside the habitat loss - the penetrability of landscape might be severely hampered. The reduction of dispersal rates in cities is thus expected (Jonsen and Taylor, 2000). This seems to be supported by more pronounced genetic differentiation in populations living in urbanised regions in comparison to those living in rural regions (Sato et al., 2008).

We can therefore expect that that in more modified and fragmented landscape populations of odonates tend to show more metapopulation structure (more isolated groups connected via restricted dispersal of individuals), while in rural population they are more likely to have though also patchy but well-connected population structure (McCuley, Baines and Mabry, 2023).

1.3 Odonata and urbanisation

1.3.1 Urbanisation

Urbanisation is a man-made process transforming landscape to totally serve human needs. It includes deforestation, reduction of green area, covering of land in impervious materials and building of infrastructure (roads, buildings, etc). From the point of aquatic habitats urbanisation leads to modification of hydrological systems (water bodies, streams, rivers) for human use. All of this has many effects on landscape such as increasing fragmentation, disruption of pathways, ability of landscape to retain water, and on ecological and evolutionary processes in species living there (Grimm et al., 2008; Alberti, 2015). Today more than 50% of the global human population live in cities and in the developed industrialised countries, it could be more than 80% (Ritchie et al., 2024).

Expansion of cities has a negative impact on biodiversity which leads to degradation and homogenization of communities. Generally, plant species richness is often bigger in cities due to import of exotic species. Plant diversity is also more easily controlled by humans than animals. In animals, species richness declines (leading to homogenization) but we can see a rise in abundances of some groups, especially arthropods or birds, which can benefit from human activities (Faeth et al., 2011). On the other hand, a lot of studies are reporting that presence of secondary habitats (often relics after human activities, frequent in cities and surrounding sites) can induce presence of habitat specialists, including endangered species (Ives et al., 2016; Bobrek, 2020).

Urbanisation also affects the aquatic environment. Main threats for freshwater urban aquatic biodiversity worldwide are mostly flow modification, anthropogenic pollutants (road salt, heavy metals, oils, etc.), invasive species and mismanagement (Dudgeon et al., 2006).

1.3.2 Studies on dragonfly dispersal and diversity in urbanised areas

There are many studies focusing on dragonfly populations and communities. Some of them are focused on the influence of environmental warming and climate change on distribution of species (Hassall and Thompson, 2008; Cerini, 2020) and some of them on long-distance migration (Suhling et al., 2017 et al.). Number of studies focused on dispersal of dragonflies is growing but most of them are focused on endangered species, such as *Coenagrion mercuriale* (Purse et al., 2003; Rouquette & Thompson, 2007; Hassall & Thompson, 2012) or *Coenagrion hylas* (Landmann et al., 2021) and few of them on common

species (i.e. *Calopteryx splendens* and *Calopteryx virgo*, see Stettmer, 1996). There are also a few articles about Odonata assemblages and population dynamics at secondary habitats (Harabiš a Dolný, 2012; Harabiš, 2016; Šigutová et al., 2022). Overall, the number of studies focusing on dragonflies occupying habitat patches in heavily modified/urbanised landscape is low. Study of odonates in urban regions has potential for future research. Dragonflies are not an exception as their diversity is observed to be reduced in cities, especially in built-up city cores (Villalobos-Jimenez et al., 2016). In this study were focused mainly on lentic species, living especially in urban man-made ponds and pools. The most important drivers for Odonata diversity at urban ponds are composition of plant communities, then water quality and land cover (for both dragonflies and damselflies and both larvae and adults, see Perron et al., 2021). There is also evidence that cities can host a substantial Odonata species richness (Goertzen and Suhling, 2015). This was recorded especially in Europe and in Northern America but that and the higher number of papers on these continents is probably caused by lack of research and insufficient funding in other parts of the world.

1.4 Mark-Release-Recapture experiment (MRR)

Experiments working with marked individuals are one of the most common methods used in population ecology when there is a need for tracking and distinguishing individuals from each other during the study. Odonates are good model organisms for mark-release-resight/recapture experiments. They can be easily marked (usually on the wings or the abdomen by colourful marker) and they concentrate more around water bodies, which is better for recapture rates (Cordero-Rivera and Stoks, 2008). Marking part of the population during one occasion and continuous resampling and additional marking in following occasions can provide reliable estimates of many population parameters such as survival, encounters, emigration and recruitability.

Few assumptions need to be met (as reviewed in Cordero-Rivera and Stoks, 2008). All estimates of population parameters depend on the ratio of marked and unmarked or animals marked on a given occasion compared with those marked on the other occasion. That means marking must not affect the survival, emigration, or recapture rates. Luckily, there is no (yet) evidence that marking of odonate individuals (if implemented properly) could somehow affect movement (McCuley, Baines and Mabry, 2023). On the other hand, the change of coloration patterns of an individual due to marking might be responsible for changing behaviour because the coloration is important for polymorphic dragonflies (Huang et al., 2014; Suárez-Tovar,

2022). Unmarked animals in the population must have the same probability of capture as marked animals in the population, i.e., that newly captured marked and unmarked animals are a random sample of all animals in the population. This is the most crucial assumption for Jolly-Seber models. Animals must retain their tags throughout the experiment. Tags must be read properly. Sampling must be instantaneous. Survival probabilities must be the same for all animals (marked and unmarked) between each pair of sampling occasions (homogeneous survival). The study area must be constant (Cooch and White, 2023).

2 Aims

This study aims to provide some insights to populations ecology of dragonflies inhabiting patchy and isolated waterbodies in urbanised ecosystems. For that, we have chosen two species from suborder Zygoptera, family Coenagrionidae: *Coenagrion puella* and *Pyrrhosoma nymphula*. We expect that using these two common generalist species should provide sufficient number of collected data to assess:

- Population dynamics (species abundances and their change during the season), sex ratios
- Survivorship estimations (incl. sex differences)
- An extent of dispersion. Do patches communicate in the city? Can we expect functional metapopulation structure even in the build-up city centre?
- Despite both species being common and generalist, do they differ in these patterns?

Motivation for this study comes from a study made by Sato (2008). Sato studied genetic differentiation and isolation of populations in three species of damselfly populations in Tokyo, Japan, using AFLP (Amplified Fragment Length Polymorphism) technique. He discovered that populations in urbanised regions were more isolated and more genetically distant to each other than the ones situated in more rural environment.

3 Methods and materials

3.1 Studied species

Generalist species with lower habitat quality requirements and a wide distribution in the Czech Republic with recorded occurrence in Prague (Šťastný et al., 2015) needed to be selected for the experiment to guarantee enough data for processing. With these requirements two Odonata species were chosen as research objects in my thesis – Large Red Damselfly (*Pyrrhosoma nymphula*) and Azure Bluet (*Coenagrion puella*).

3.1.1 *Pyrrhosoma nymphula*

Pyrrhosoma nymphula (Large Red Damselfly, šidélko ruměnné; Sulzer, 1776) is a common damselfly species from the family Coenagrionidae, quite unique by its red colouring among Czech damselflies. It is widely distributed throughout the Czech Republic from the lowlands to the mountains. It is mostly found in smaller overgrown ponds, but it can also be found in bogs, the edges of larger bodies of water, etc., as it is pretty generalist species. This damselfly appears early in the spring, towards the end of April, and can be found in nature until late July (Waldhauser and Černý, 2014).



FIGURE 1: *PYRRHOSOMA NYMPHULA*, MALE (AUTHOR: HANS HILLEWAERT; SOURCE: WIKIPEDIA COMMONS)



FIGURE 2: *PYRRHOSOMA NYMPHULA*, FEMALE (AUTHOR: CHARLES JAMES SHARP; SOURCE: WIKIPEDIA COMMONS)

3.1.2 *Coenagrion puella*

Coenagrion puella (Azure Damselfly, šidélko páskované; Linnaeus, 1758) is a damselfly species from the family Coenagrionidae. This damselfly is also widely distributed throughout the Czech Republic as one of the Czech most common odonates. *C. puella* can be seen at nearly all altitudes and inhabits all types of lentic and slow lotic waters. Most abundant is in more overgrown habitats. These damselflies are flying in riparian vegetation most of the time. In nature, we can see it from May to August with peak season in June and July (Waldhauser & Černý, 2014).



FIGURE 3: *COENAGRION PUELLA*, MALE (AUTHOR: L. B. TETTENBORN; SOURCE: WIKIPEDIA COMMONS)



FIGURE 4: *COENAGRION PUELLA*, FEMALE (AUTHOR: CHARLES JAMES SHARP; SOURCE: WIKIPEDIA COMMONS)

3.2 Study sites

Lentic bodies located in the broader centre of the city were chosen as sufficient study sites, situated mostly in parks and in the botanical garden. There were few features important for the study sites selection. Study sites should be in the city centre. They should maintain some water level during the entire year. There should be some percentage of shading from the surrounding vegetation. And they should provide sufficient microhabitats for dragonfly larvae and for the adults.

Study area had approximately 11,5 km² and included about fourteen water bodies, of which three did not have stable water level throughout the season. From that, twelve localities were selected for field work (86 %, see Figure 5). Each site was labelled with a letter code (going from letter A to letter L) for easier protocol logging purposes. Almost all water bodies which met conditions mentioned above were added to the experiment. In addition, few localities which did not meet these conditions were added for comparison (Locality B and C). It is important to say that chosen study sites probably represent the majority of water bodies available in the build-up city centre as almost no other stable lentic habitats are present and connection with other water bodies in the landscape (situated more to the outskirts of the city) is possible, but questionable.

For the data collection we split study sites into two zones (zone 1 and zone 2) divided by the Vltava River. This categorization was used only for the field work and was not considered in the analysis whatsoever. Maximum distance between study sites was 3,5 km, minimum distance was 50 metres. Mean distance was 1,5 km (specific distances between individual

localities are in Table 1). The description of all localities is provided further in detail (see below). Coordinates to all study sites are in Table 2 and some the photos of some of them are pictured below (see Figures 6 to 10).

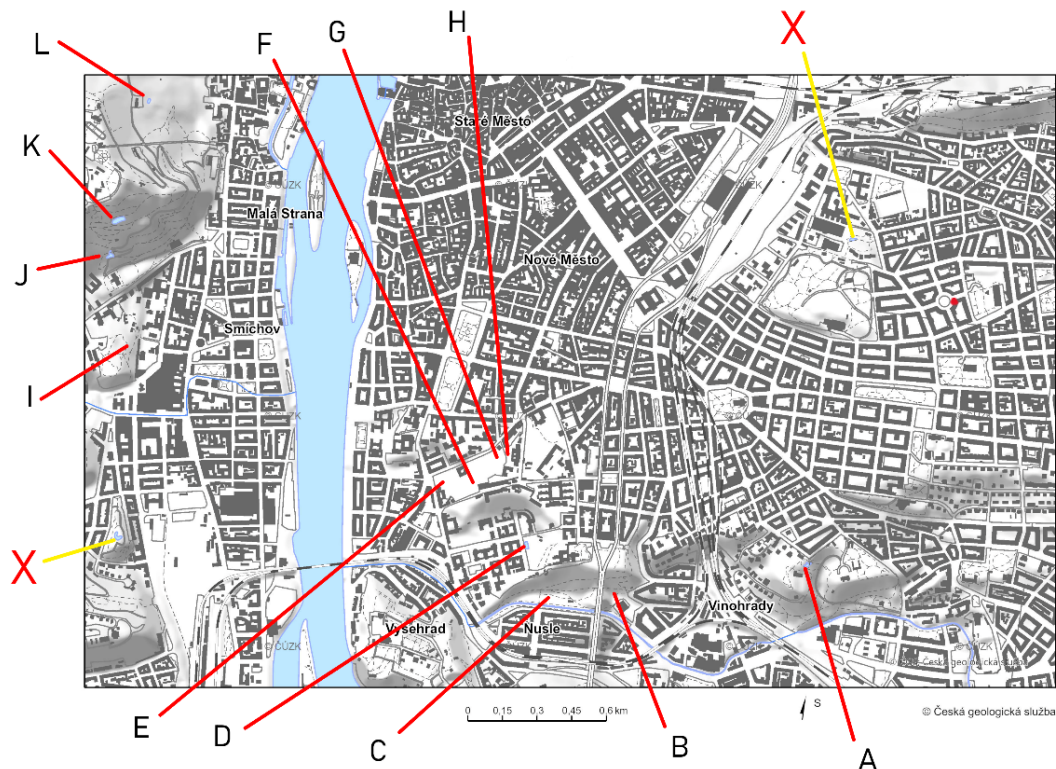


FIGURE 5: STUDY AREA WITH STUDIED LOCALITIES (RED LINES) MARKED WITH A LETTER CODE AND LOCALITIES IN THE STUDY AREA WHICH WERE NOT INCLUDED IN THE EXPERIMENT (SOURCE: ČESKÁ GEOLOGICKÁ SLUŽBA, MODIFIED USING GIMP)

Distances between study sites (km)		ZONE 1								ZONE 2			
		A	B	C	D	E	F	G	H	I	J	K	L
ZONE 1	A		0,9	1,1	1,2	1,5	1,5	1,5	1,5	3,1	3,3	3,3	3,5
	B			0,3	0,4	0,8	0,8	0,8	0,8	2,4	2,6	2,7	2,9
	C				0,25	0,6	0,6	0,7	0,7	2,2	2,4	2,5	2,8
	D					0,4	0,4	0,4	0,4	2	2,2	2,3	2,5
	E						0,1	0,2	0,3	1,6	1,8	1,9	2,2
	F							0,15	0,2	1,6	1,9	1,9	2,2
	G								0,05	1,7	1,9	1,95	2,2
	H									1,7	1,9	2	2,2
ZONE 2	I									0,3	0,45	1	
	J										0,15	0,7	
	K											0,5	
	L												

Table 1: Distances between individual study sites (km), marked minimal distance (orange) and maximal distance (yellow)

	Study site	Longitude North [°]	Latitude East [°]
ZONE 1	A	50.06983	14.44312
	B	50.06735	14.43107
	C	50.06699	14.42756
	D	50.06888	14.42554
	E	50.07078	14.42015
	F	50.07082	14.42171
	G	50.07213	14.42316
	H	50.07232	14.42371
ZONE 2	I	50.07543	14.40014
	J	50.07783	14.39812
	K	50.07921	14.39852
	L	50.08401	14.39921

Table 2: Coordinates of individual study sites

3.2.1 A – Havlíčkovy sady

This water body is situated in the northern edge of Havlíčkovy sady (see Figure 6). Its area of water surface is approximately 300 m². Even though the banks of the pond are made of stone, rich littoral vegetation, and aquatic plants (emerged and submerged) are present, providing anchorage points for emerging dragonflies. Among the animals, wild ducks (*Anas platyrhynchos*) and several types of exotic carp species were spotted. Waterfall connected to the pond supplies the place with water. The surrounding trees create partial shading of the water surface. The place was probably built as an aesthetic feature of a park in which a pond is situated.

3.2.2 B and C – Folimanka

Area of these two neighbouring localities is 190 m² (loc. B) and 5 m² (loc. C). They were chosen as not suitable localities for comparison with other, more natural localities. These were built as water features of the recreational park. Site B consists of several shallow concrete tanks with no vegetation, natural banks or shading. Also, water was not present during the whole season. The locality marked with the letter C is a fountain located in the same park, a few hundred metres away from locality B. It probably does not dry out during the season, but it is also entirely made of concrete with little to no shading and no vegetation.

3.2.3 D – Genetic Garden

Study site marked with letter D is in the genetic garden which is part of the Faculty of Natural Sciences of Charles University (see Figure 7). The water pond situated in this garden is approximately 250 m² large water reservoir which, despite having concrete walls, is densely surrounded by littoral vegetation, and partially shaded on one side by trees.

3.2.4 E, F, G and H – Botanical Garden

These are study sites marked E, F, G and H. They are part of the botanical garden of the Faculty of Natural Sciences. Locality E is a complex of little ponds and a stream. Little water pond near the greenhouses in the lower part of the garden and has area of approximately 250 m². The entire pool is densely overgrown with vegetation and shaded by trees. The second one is rather isolated pond by the park road with area about 12 m² with little littoral vegetation. The locality includes a stream, stretching from the pool to the faculty building in Benátská Street. The presence of diverse vegetation and rocks ensures enough space for dragonflies to move.

Site F corresponds to the system of little water reservoirs for water plants which are part of the exhibition of the botanical garden. It is situated in the upper level of the botanical garden, partially shaded by trees.

Locality G is a small pond (circa 15 m²) located on the hill side near the faculty buildings (see Figure 8). The pond is shaded by the surrounding trees. The shore and the bottom of the pool is made of stones. Emerging vegetation was present in the water.

The last part was locality H, which is located directly behind the faculty building in Viničná Street and consists of four small water ponds (whole pond area has circa 100 m²) which are rich in vegetation and partially shaded by the trees. The bottoms and sides of the pools are made of concrete.

3.2.5 I – Station of young naturalists

Locality I is part of the station of young naturalists in Smíchov. Water pond (circa 20 m²) has concrete bottom and banks, dense vegetation and is almost completely shaded by trees.

3.2.6 J and K – Kinského zahrady

Locality J is a pond connected to a waterfall, both accessible by park pathways (see Figure 9). Together, the pond and the waterfall have circa 400 m² in area. The pond is

surrounded by a stone wall, the banks and bottom are also made from stone blocks. Vegetation emerging from the water covers roughly a third of the pond banks. Part of the pond is shaded by trees.

Study site K is also a park pond in the same gardens with area of 980 m². The banks, the bottom and the islands in the middle are made of stone. Part of the bank is shaded by trees. Vegetation presence in the water is minimal.

3.2.7 L – Pod Petřinkou

Locality L is a small pond (see Figure 10) with are about 190 m², called “Pod Petřinkou.” There we can see a thick growth of littoral vegetation and almost complete shading by the surrounding tree vegetation.



FIGURE 6 (LEFT): STUDY SITE A (HAVLÍČKOVY SADY, AUTHOR: PB0305, SOURCE: WIKIPEDIA COMMONS)

FIGURE 7 (RIGHT): STUDY SITE D (GENETIC GARDEN, AUTHOR: BOHUMIL RONALD FIALA)

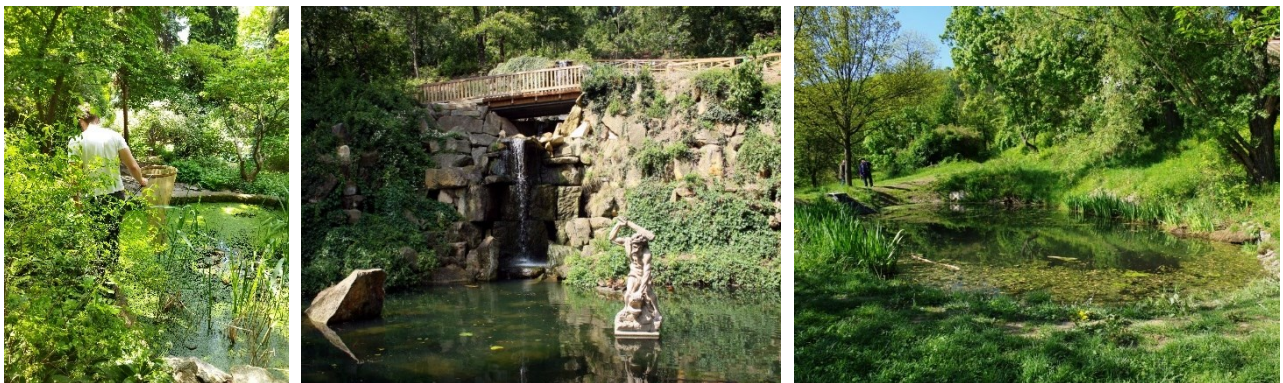


FIGURE 8 (LEFT): STUDY SITE G (BOTANICAL GARDEN, AUTHOR: BOHUMIL RONALD FIALA)

FIGURE 9 (MIDDLE): STUDY SITE J (KINSKÉHO ZAHRADY, AUTHOR: NINA HAVLOVÁ)

FIGURE 10 (RIGHT): STUDY SITE L (POD PETŘINKOU, SOURCE: PRAHA-PRIRODA.CZ)

3.3 Data collection

In our experiment we used the typical MRR method. In principle it involved regular visits at the study sites, capturing and marking studied individuals visibly on the wings with colour or numerical codes. At each such visit, the number of tagged and untagged individuals was recorded.

The aim of the experiment was to investigate the populations of selected species of odonates at studied localities. Here we used the MRR method not only to acquire the data necessary to assess population estimates, but also to map the movement of individuals in the investigated area (the city centre of Prague).

The work in the field consisted of individual sampling occasions. Due to the time restriction of individual researchers, we split localities into two zones, zone 1 - loc. A, B, C, D, E, F, G, H; and zone 2 – localities I, J, K and L (As shown in Tables 1 and 2). It was necessary to organise the monitoring during the species adult's activity. The seasons of adult activity of *C. puella* and *P. nymphula* are rather similar so their movement was monitored from the second half of May (first occasion on 20th May 2023) to beginning of July (last occasion on 7th of July 2023) during individual occasions in which all the locality were visited and data received. Each zone had different schedule (as shown in Table 3).

The gap between sample days was set to be two to three days with a maximum of four to five days when extraordinary circumstances occurred (unsuitable weather, indisposition of researchers, etc.). In this case, conditions suitable for data collecting are a temperature around/above 20°C with a clear to slightly cloudy sky with none to mild wind. Day time of the visits was chosen variably from early morning to late afternoon. However, the zones have been used only for sampling organisation, they were not considered (i.e. not treated separately) in the analyses of data.

ZONE 1			ZONE 2		
occasion	date	Interval from previous occ.	occasion	date	Interval from previous occ.
1	20.5.		1	20.5.	
2	22.5.	1	2	24.5.	3
3	25.5.	2	3	26.5.	1
4	29.5.	3	4	30.5.	3
5	1.6.	2	5	2.6.	2
6	5.6.	3	6	5.6.	2
7	7.6.	1	7	8.6.	2
8	11.6.	3	8	11.6.	2
9	13.6.	1	9	14.6.	2
10	16.6.	2	10	17.6.	2
11	19.6.	2	11	20.6.	2
12	22.6.	2	12	23.6.	2
13	25.6.	2	13	26.6.	2
14	28.6.	2	14	29.6.	2
15	1.7.	2	15	2.7.	2
16	4.7.	2	16	5.7.	2
17	7.7.	2	17	8.7.	2

Table 3: List of individual occasions for both zones in the study area

An entomological net was used to catch unmarked and marked individuals. At each locality we moved around water bodies and their surroundings, visually searching for individuals. To keep the sampling effort balanced among sites, we adjusted the time spent on each locality according to its size. This way, all marked and unmarked individuals had same probability of recapture, which is especially important for experiment design.

Every caught individual was given a unique code (see Figure 11). The code consisted of a three-digit number, starting with the number 001 counting all the way to 999. If the number of marked individuals exceeded this number, the counting started again from 001 but with a different colour to avoid errors. We have chosen this simple coding scheme to avoid errors and also because of the small size of damselflies wings for including the whole alpha-numerical code. All species were marked the same way together with one numerical system to spare time during the sampling.



FIGURE 11: EXAMPLE OF MARKED INDIVIDUAL, FEMALE OF *PYRRHOSOMA NYMPHULA*
(AUTHOR: BOHUMIL RONALD FIALA, 2023)

Everything was written down using field protocols. Each record contained the information on the species, sex, used code and information about the place and time where the recorded individual was caught. A separate protocol was created for each sampling day and for each researcher (there were two of us). For the safety, the paper protocols were digitalized (photographed) and stored in a cloud after each day.

3.4 Data analysis

As we wanted to make assumptions about the city centre, data from all study sites are analysed together.

3.4.1 MARK analysis

For analysis we used the MARK program (version 9.0, Cooch & White, 2023, White & Burnham, 1999). MARK is a Windows-based program used for analysis of data from experiments with marked individuals. We have chosen the Jolly-Seber method for open populations, specifically the built-in module POPAN (Schwarz and Arnason, 1996) based on the POPAN formulation of the original Jolly-Seber principle (Crosbie and Manly, 1985). POPAN formulation works with so-called super-population which consists of all animals that would ever be born to the population and parameters b_i which represented the probability that

an animal from this hypothetical super-population would enter the population between occasions i and $i + 1$ (Cooch and White, 2023). It was better for us to work with open population model as we could not rule out emigration or immigration from outside of the study area.

There are few assumptions for the POPAN data and overall, for all types of data analysed by Cormack-Jolly-Seber based models (as presented in Cooch & White, 2023, White & Burnham, 1999). In the experiment our data need to meet all the assumptions for the POPAN models. These data consist of individual encounter histories. In our dataset, every individual has its own history tagged with the individual's code. Sex of the individual was also included, dividing the dataset for each species into two groups (males and females). In the beginning we input our data and information about number of occasions, intervals between the occasions and groups of data (in this case corresponding to two groups – males and females). For the purposes of the field work we did split our study area to two parts, as stated above, but in the analysis, we have been using both zones combined so the analysis includes all the study sites. Different intervals between occasions in the individual zones are similar, so we used intervals from the zone 1 (see Table 3). Also, in this type of analysis, the fate of individuals after the last capture is expected to be unknown, either it died or was simply not seen after the last encounter.

In this study we needed to get few hundreds of individuals for our dataset to effectively answer our research goals. From that we could estimate needed parameters. We wanted to know how abundant the populations in the city centre are and how this number fluctuates. Then how long individuals survive and how effectively we can encounter them. In the MARK analysis we can get these estimates using models with several parameters. First one is "Phi", which corresponds to the survival probability, which means it describes the probability that both marked and unmarked individuals in the population will survive in the time between the two following occasions. Then there are parameters "p" which means probability of encountering live (again, both marked and unmarked) individuals during each sampling occasion and parameter "pent", meaning probability of entry, meaning probability that individual enters the population in the time between sampling occasions, either by immigration or by birth (in our case by emergence of dragonfly from the parental water site). Last parameter is N, which means abundance. These parameters could be either dependent upon time (t), group (g, in our case referencing to two groups: males and females) or be constant (*). Dependence on both sex and time and their interaction was also included (g*t). For purposes of our research, from these outputs we estimate the number of individuals and the survival.

Because the model(s) can vary in the degree of dependencies (see above), we should be looking for the model which fits our data the most. From the variety of possible models we have chosen the one(s) which has the lowest AICs (Akaike's Information Criterion; see Akaike, 1998) which is also provided in the analysis in the MARK software (see Figure 12). Sometimes a situation occurred when model with the lowest AICc could not be used because of very high standard errors, giving unreasonable estimates not corresponding with the reality (eg. going in negative abundancies etc.). In that case we used a second criterion that we have chosen a model with reasonable standard errors for estimates of abundance and survival, even when the model was not the one with lowest AICc. In this combination, the model with reasonable estimates and the lowest possible AICc has been chosen for following interpretation. Analysis was also performed for every species separately, so for each of them the different model could be chosen. Even then, the estimates are still intercomparable.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance	-2Log(L)	Time Stamp
Check Par. Crt. (Phi(tln) p(g^1) pent(g^1) N(g^1)a)	2230.5527	0.0000	1.00000	1.0000	32	-6988.4831	2165.2911	24:01:26:17:31:23
Check Par. Crt. (Phi(g^1ln) p(g^1) pent(g^1) N(g^1)a)	2267.4231	36.8704	0.00000	0.0000	62	-7015.1030	2138.6712	24:01:26:17:41:47
Check Par. Crt. (Phi(.) p(g^1+) pent(g^1) N(g^1)a)	2272.3501	41.7974	0.00000	0.0000	44	-6971.8068	2181.9674	24:01:26:16:58:58
Check Par. Crt. (Phi(g^1tpoly) p(g^1) pent(g^1) N(g^1)a)	2276.0478	45.4951	0.00000	0.0000	63	-7008.6345	2145.1397	24:01:26:18:09:45
Check Par. Crt. (Phi(.) p(g^1tpoly) pent(g^1) N(g^1)a)	2281.8671	51.3144	0.00000	0.0000	32	-6937.1687	2216.6054	24:01:26:13:31:34
Check Par. Crt. (Phi(tln) p(g^1+) pent(g^1) N(g^1)a)	2282.0786	51.5259	0.00000	0.0000	45	-6964.1880	2189.5861	24:01:26:17:09:38
Check Par. Crt. (Phi(.) p(t) pent(g^1) N(g^1)a)	2283.5257	52.9730	0.00000	0.0000	43	-6958.5238	2195.2503	24:01:26:17:01:23
Check Par. Crt. (Phi(.) p(g^1ln) pent(t) N(g^1)a)	2284.3648	53.8121	0.00000	0.0000	19	-6907.8599	2245.9143	24:01:26:12:53:30
Check Par. Crt. (Phi(tln) p(t) pent(g^1) N(g^1)a)	2284.7442	54.1915	0.00000	0.0000	44	-6959.4127	2194.3615	24:01:26:17:07:05

FIGURE 12: EXAMPLE OF THE RESULT BROWSER IN THE MARK INTERFACE

3.4.2 Sex ratio

Sex ratios were calculated using Microsoft Excel by simply filtering individual species, then in every one of them taking all individuals and separating them by filtering into two groups, male and females, counting all results to get sex ratio and calculating percentage.

3.4.3 Recapture rates

Recapture rates were computed using Microsoft Excel and Rstudio (version 2024.04.2, build 764; Posit Software, PBC, 2024) from the collected data. In the result table will be stated number of recaptures at each locality, including recaptures of individuals marked on these locality and immigrants from another localities.

3.4.4 Migration, migration routes

Migration of individuals is visualised using QGIS (version 3.22.0 – Białowieża) using coordinates of each locality and information about individual occurrence from collected data. We do not visualise any terrain profile, instead we are interested only in movement of the individuals between the study localities. Also, the number of moving individuals was calculated.

3.4.5 Dragonfly diversity in the studied area

During the intensive fieldwork we have also inevitably encountered other species of dragonflies, which indeed provides quite accurate information about the overall diversity of dragonflies in the Prague's city centre. This was an extra addition for this thesis as we are able to do that during individual marking occasions. No equipment except determining key was used to reliably determine all species of dragonflies which we encounter at study sites.

4 Results

4.1 Raw data: numbers of marked and recaptured

Together, 1821 individuals of both species were caught and marked. We were able to cover all planned study sites in the designated area. From this number 403 (22,13 %) were females and 1418 (77,87 %) were males. Overall, 1534 marked individuals were not seen again and 287 individuals were recaptured, thus calculating recapture rate at 15,76 percent (individually 14,3 % for *C. puella* and 22,3 % for *P. nymphula*). Most of the individuals were caught at two areas – first at study sites E to H, all situated at Botanical Garden and second at study sites J to K, consisting of two big water bodies in the gardens of Kinski. Three of the study sites were not inhabited by damselflies (study sites B, C, and I). We also received one record of sighting of marked individual from outside of the Botanical Garden from one other faculty member (see Figure 13).



FIGURE 13: INDIVIDUAL ENCOUNTERED BY FACULTY MEMBER (GPS COORDINATES 50°04'09.2"N 14°25'29.3"E)

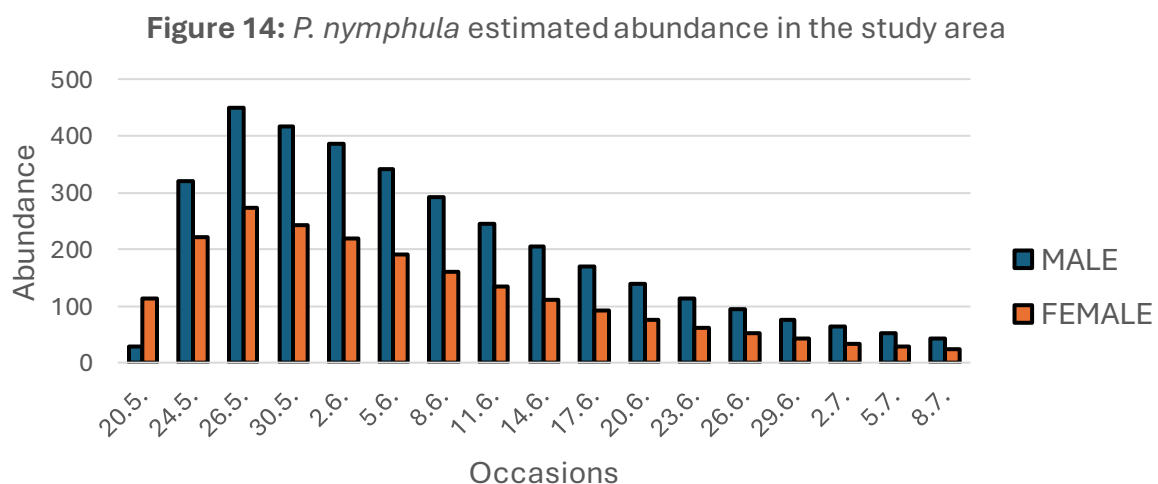
Exactly seventeen occasions were conducted for both studied species. The more abundant of all species was *Coenagrion puella*, counting 1462 individuals, 317 (21,7%) females and 1145 (78,3 %) males. Recapture rate was 14,16 % with 207 recaptured individuals. Some of them were seen more time (180 ind. twice, 20 ind. three times and 7 ind. four times). Approximately four times less individuals were marked for *Pyrrosoma nymphula* species with

359 marked damselflies. Of those 359 individuals with 86 (24 %) females and 273 (76 %) males. From that, 80 individuals were recaptured, making recapture rate 22,3 percent. As in the case of *C. puella*, some individuals of *P. nymphula* were recaptured multiple times (62 ind. two times and 18 ind. three times). The longest period between recaptures of one individual was 31 days (first one on 25th of May, second one on 25th of June) in both species, which we consider as a total coincidence.

4.2 Population parameters and seasonal dynamics

4.2.1 *Pyrrhosoma nymphula*

For *Pyrrhosoma nymphula* model $\phi(.)p(g*tlin)pent(g+tlin)N(g*t)a$ was chosen. In this model the survival probability is constant (it is not dependent on time, neither on group effect or interaction of both, which means it doesn't change between the occasions), the encounter probability is dependent on linear time, group and their interaction and probability of entry is dependent on linear time and group but without their interaction. From this model, the total number of individuals has been estimated to be 752 ± 80 (\pm SE) for males and 446 ± 126 (\pm SE) for females. Survival was $90,4 \pm 1,6$ % (\pm SE) and it was the same for all the occasions, as it was characterised as a constant in the model parameters. We also got estimates of abundance for each occasion (see Figure 14). Obviously, the population peaked in late May/ early June, experienced steady decline afterwards. There is no dynamics difference in sexes over the whole season as females were consistently about $\frac{1}{3}$ less numerous than males, the only “glitch” in this pattern appears on the very first day of sampling when females dominated over males.



4.2.2 *Coenagrion puella*

For *Coenagrion puella* model $\phi(g^*tlin)p(g^*t)pent(g^*t)N(g^*t)a$ was chosen. In this model the survival probability is dependent on linear time, group and their interaction, other parameters are dependent on normal time, group, and their interaction. From this model, the total number of individuals was estimated to be 5048 ± 596 (\pm SE) for males and 3951 ± 2342 (\pm SE) for females. This (very) large standard error comes likely from the fact that females comprised only a small part of all individuals marked with low recapture rates. Figure 15 shows estimate of abundance and Figure 16 shows estimates of survival over the season. From this, we can see that there is a rather pronounced disparity between sexes though, in general, they seem to follow the same seasonal pattern. As in *Pyrrhosoma nymphula*, also here there is a dominance of females at the beginning of the season which may point to their earlier emergence (see Chapter 5).

Figure 15: *Coenagrion puella* estimated abundance in the study area

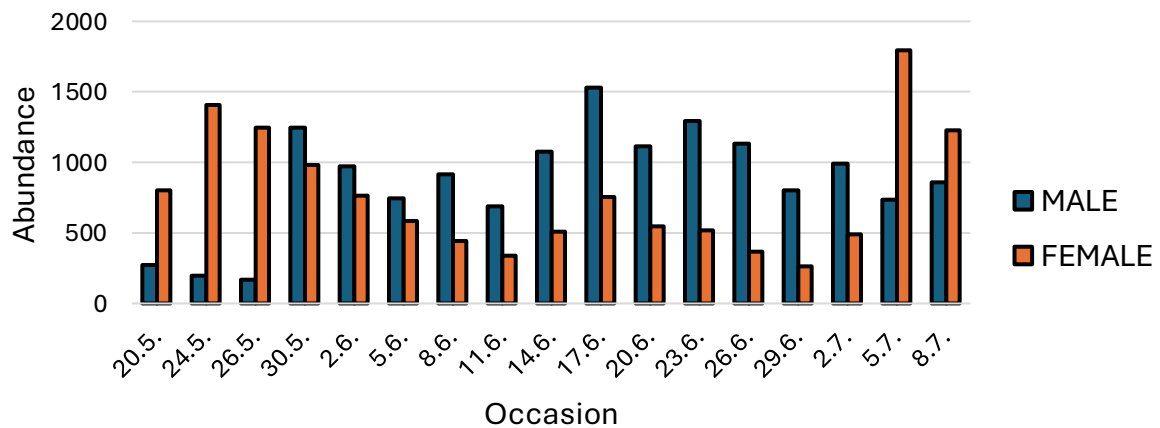
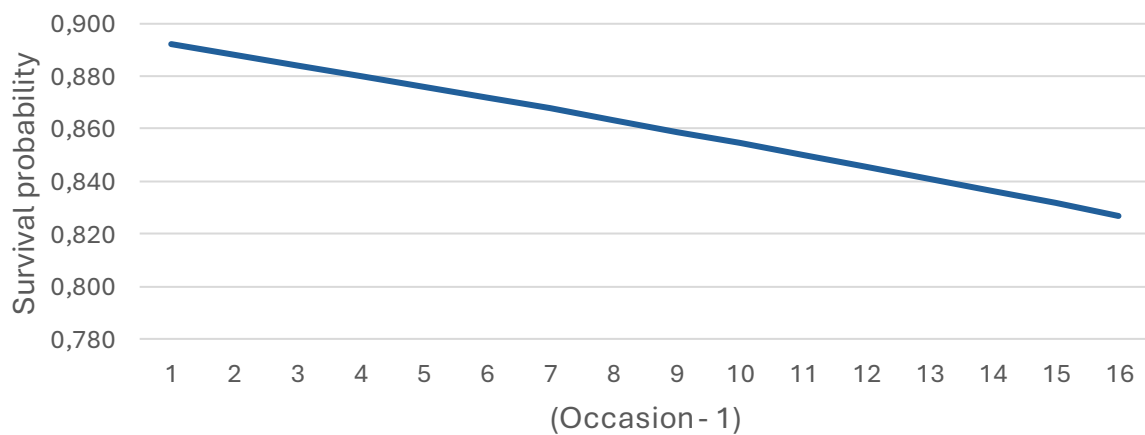


Figure 16: Survival probability estimate for *Coenagrion puella*



4.3 Dispersal and movement pattern

Here, we categorized migration of individuals to two categories – long-distance and short-distance. As long-distance we count all dispersal movement across the Vltava River and all the movements from the site A to other sites on the same side of the river. As short-distance we count all the other dispersal movements, meaning movement among nearby study sites (between J, K and L on one side and between D, E, F, G, H on the other side of the river). It is worth to note that in all long-distance flights the large parts of the journeys go over/through build-up areas and there is no way to avoid them even if much longer paths are considered. In the case of short-distance movement there are almost no city-built barriers. All distances are calculated from the straight aerial distances on the map.

There was a significant difference in the dispersal activity and individual movement among the species. *Pyrrhosoma nymphula* showed to be species with low dispersal activity in our urban study area. Only 3 individuals were seen to disperse between the study sites, making dispersal rate of 0,84 percent. All of these 3 individuals were males. All the dispersion was observed only among the closest ones (short-distance) with the longest distance of 400 metres (from the site D to the site H; see Figure 17). No long-distance flights were recorded.

On the other hand, *Coenagrion puella* was more vagile, as 26 individuals were seen to disperse throughout the whole study area (see Figure 18). Dispersal rate in this case is calculated to be 1,58 % with 3 females and 23 males. The longest recorded distance was approximately 3,3 km (from the site A to the site K). Overall, there were 8 such long-distance flights recorded and 16 short-distance flights.

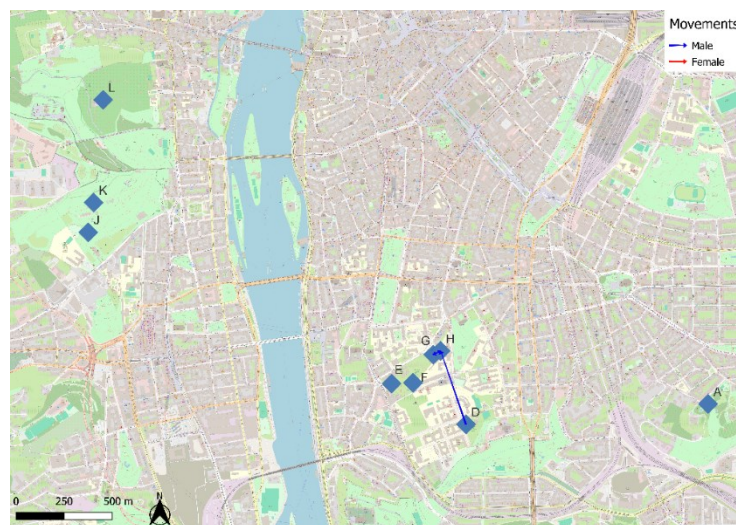


FIGURE 17: VISUALISED RECORDED MOVEMENT OF INDIVIDUALS BETWEEN STUDY SITES IN *PYRRHOSOMANYMPHULA* SPECIES (AUTHOR: TOMÁŠ JOR)

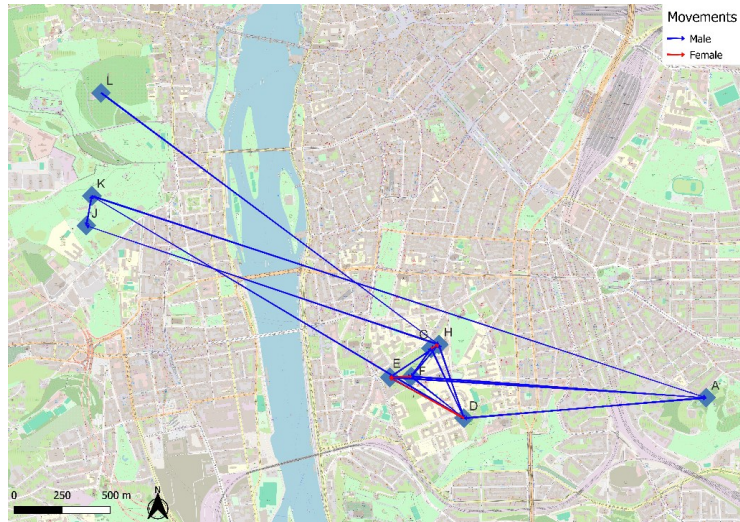


FIGURE 18: VISUALISED RECORDED MOVEMENT OF INDIVIDUALS BETWEEN STUDY SITES IN *COENAGRION PUELLA* SPECIES (AUTHOR: TOMÁŠ JOR)

4.4 Diversity of dragonflies

As an extra “byproduct” addendum to this study, we did explore diversity of odonate assemblages in the Prague city centre. It is likely not a final list of this diversity for Prague’s centre but definitely a representative one as we visited the sampling sites quite intensively in this part of flying adult’s season. Overall, twelve species were recorded at study sites. The relative abundance was evaluated subjectively by the researchers on the scale from “(seen) rarely,” to “(seen) sometimes,” to “(seen) repeatedly.” The total list is stated below in Table 4:

#	SPECIES	FAMILY	RL STATUS	SEEN
suborder <i>Zygoptera</i>				
1	<i>Coenagrion puella</i>	Coenagrionidae	LC	repeatedly
2	<i>Pyrrhosoma nymphula</i>	Coenagrionidae	LC	repeatedly
3	<i>Ischnura elegans</i>	Coenagrionidae	LC	rarely
4	<i>Calopteryx splendens</i>	Calopterygidae	LC	rarely
5	<i>Calopteryx virgo</i>	Calopterygidae	LC	rarely
6	<i>Lestes sponsa</i>	Lestidae	LC	rarely
7	<i>Sympecma fusca</i>	Lestidae	NT	repeatedly
suborder <i>Anisoptera</i>				
8	<i>Anax imperator</i>	Aeshnidae	LC	sometimes
9	<i>Aeshna cyanea</i>	Aeshnidae	LC	rarely
10	<i>Libellula depressa</i>	Libellulidae	LC	sometimes
11	<i>Orthemtrum cancellatum</i>	Libellulidae	LC	rarely
12	<i>Crocothemis erythraea</i>	Libellulidae	LC	rarely

Table 4: Species encountered during the study in the Prague city centre

5 Discussion

5.1 Use of MRR method

The MRR method used in this study was effectively used for tracking movement of the individuals. The marking of the individuals was successful as marks were big enough to be recognised and still suitable for little damselfly wings. They also remained permanent during the whole period of research.

Marking season of the year 2023 followed after the season 2022 where we tried to compare rural and urban landscape. For that, control study site was established, situated in Prague, Komořany (GPS coordinates 49.9927169N, 14.4012717E). It consists of system of small water bodies with rich vegetation, partial shading and with connection to Vltava River. The whole area is also declared a protected area. We only studied *Pyrrhosoma nymphula* in that year, hoping to obtain data because the habitat corresponded with usual preferred habitat of this species. The research in 2022 was unsuccessful as we were not able to find enough data for the analysis and this season was not included in this study. Only tens of individuals were caught and marked, most of them in the city centre at one study site (in the 2023 season marked with letter A – Havlíčkovy sady, see Chapter 3.2.1). Only two individuals were encountered at ponds in Komořany with one recapture. For the next season (2023) we focused more on the city centre core and added second species, *Coenagrion puella* to ensure the success of the research.

5.2 Population parameters and seasonal dynamics

Firstly, based on the data, we could calculate and estimate some basic population parameters for studied species. The recapture rate was little higher for *Pyrrhosoma nymphula* (22,3 %) than for *C. puella* (14,6 %) but the comparison could be problematic because of the quite different number of marked individuals. More than 84 % of marked individuals from both species were not seen again. We can only hypothesize about their fate. It could be caused by mortality due to predation (by birds for example, see Kennedy, 1950; Kuchata and Svensson, 2014), parasites or anthropogenic factors. In this case, insufficient number of available water bodies and a lot of reflective surfaces (cars, windows, gravestones etc.) in the surrounding area could be responsible for death of individuals due to confusion and following exhaustion as it was recorded before (Horváth et al., 2007, Kriska et al., 2009). Last reason could be that we simply did not encounter the individuals again, even if they were present in the population.

Another parameter was sex ratio. Firstly, from gross MRR data can we observe uneven number of marked females and males, with three to four times more marked males than females in both species. Smaller number of marked females in both species and thus less precise estimates of their population parameters could be connected with their general lower encounter probability at study sites (Garrison and Hafernik, 1981). This was already experienced and described by Bennet and Mill (1995) with explanation for that could be longer maturation of females, happening away from the parental site or other aquatic habitats, thus causing smaller detectability for marking and smaller recapture rates. On the other hand, it could also be caused by higher mortality of immature females and their higher predation in comparison to males, giving male-biased sex ratio (Stoks, 2001; Johansson et al., 2005). Also, as the result of this capturing probability bias, the model estimates of abundance for both species shows that females are less abundant than males (see Figures 9 and 10). One exception was for both species in the beginning and then only for the *C. puella* species at the end of the season. Here, the estimated abundance of females spiked and exceeded the abundance of the males. It could be caused by earlier emergence of females, which would explain this spike in female occurrence and also decrease in their abundance later during the sampling season, as they take more time to mature and have also probably higher mortality in that time (as stated above). This female-biased shift in sex ratio during the emergence in territorial density-dependent population has been hypothesized and predicted in models (Crowley and Johansson, 2002), and also observed in some populations (Dolný et al., 2010). Beside this phenomenon we can observe that population dynamics, taken from abundance, are stable for both species, as none of them experienced big fluctuations during their assumed flying-adult season.

The city centre of Prague hosts a few valuable populations of damselflies, which we explored in this thesis, but not all study sites could be considered as suitable localities. In Folimanka park we did not find any damselflies as the locality B did not have any water during the summer and locality C, even when containing sufficient water levels (supplied by the city water systems), was found to be very sterile. Another unsuitable locality was the one marked with letter I (in the Station of young naturalists). This water body had enough littoral vegetation and shading but concrete banks and bottom prevented any damselfly occurrence.

The probability of survival tells us what the probability is for an individual to survive the period between individual collection days, i.e. from any occasion i to occasion $(i+1)$. For the *Pyrrhosoma nymphula* species it was approximately 90,5 percent. The probability of survival, expressed in the analysis by the Phi parameter, was constant, i.e. it had the same value between

any two occasions. This could mean that the newly marked individuals had a pretty high probability of survival until the next occasion. But it also means that an individual marked on the first occasion could still have a probability of survival of some 20,25 % at the end of data collection (that is, between the 16th and 17th occasion). For the *Coenagrion puella* species, the probability of survival was not constant (as visualised in Figure 11), but it decreases with each following occasion. Even so, at the beginning it is estimated to be circa 89.2 %, and towards the end it dropped to 82.7 %, which is still remarkably high. Of course, the estimation of the survival probability is affected by migration, thanks to which we could lose a lot of individuals, even to the geographically unknown place. From this survival probability we could also derive mortality. However, this number would be biased by the fact that we could not objectively monitor the fate of individual damselflies outside of the surroundings of our study sites, either because they moved to another locality, or we simply could not encounter them. We could have lost a lot of individuals by migrating outside the monitored area, even though the area we monitored and the system of localities we monitored represent the vast majority of water bodies in the urbanized centre (pointing to the lack of water elements in the landscape of the centre of Prague).

In the analysis, the addition of individuals to the population, expressed in POPAN models by the parameter p_{ent} , is also important. In our case, it consists of number of the newly emerged adults and individuals which immigrated to the population from elsewhere. However, we cannot separate these two phenomena from each other. This total increase is represented as an increase in abundance (see Table 9 and 10).

Both studied species differed in the abundance. *Pyrrhosoma nymphula* was approximately 7,5 times less abundant than *Coenagrion puella*. If we take the approximate abundance estimate for each studied species (this time without calculated standard errors), i.e. 1198 individuals (males and females) for *P. nymphula* and 8999 individuals (also including males and females) for *C. puella*, the total area we monitored (in km²) and the number of study sites (here we count only 9 study sites, given the fact that not all of localities were occupied by damselflies), we can get to the estimation that there's an average of 133 individuals of *P. nymphula* and 1000 individuals of *C. puella* per site and 104 individuals of *P. nymphula* and 783 of *C. puella* individuals per 1 km². These numbers, together with other estimates of abundance, survival and population dynamics during the season indicate that in the centre of Prague both species have stable and robust populations with fairly regular dynamics.

5.3 Dispersal and influence of the urban landscape

In this study, we recorded relocality of some individuals and movement across the whole study area. However, the majority of these dispersal events was recorded within the short distances. Reason for that could be that it is just easier to move among suitable habitat at short distances, probability of success is greater, and energy consumption is lower. Another explanation, relatable to our research, could be that on long-distance tracks, the character of landscape is far more built-up and constitutes unnatural barriers with no natural paths through. In our study area, this urbanised region consists of typical inner-city blocks and heavy-traffic streets, usually with little to no vegetation and almost no water elements along the way. This could make the probability of dispersal success very low and energy consumption higher, especially in the summer period when the temperature of some impervious surfaces could be remarkably high.

Big differences were recorded between the studied species. *Coenagrion puella* had 1,88x higher recorded dispersal rates than *Pyrrhosoma nymphula* in relation to the total number of marked individuals. If we take the estimates of abundance for these species and recorded dispersal rate, we can calculate number of potential successful dispersal flights in the whole population. In this case this would be only 10+ individuals for *P. nymphula* and 161+ individuals for *C. puella*. These numbers are just approximating because we cannot really say there is a restriction for the maximum number of these dispersal events and also that we encountered all of the migrating individuals.

This low dispersal rate in *P. nymphula* species could be explained by its generally low dispersal abilities as a main factor of its observed isolation, but unfortunately that is not well studied in this species (see for example Corbet, 1952). It is then debatable whether the city environment could represent extra barrier for this species dispersal. In the case of *C. puella*, there was almost two times higher dispersal rate recorded and as it seems, it is no problem for this species to disperse even through the urbanized landscape. Both species are generalists with broad spectrum of preferred habitats, so in the light of these differences in dispersal rate we cannot generalize influence of urbanisation level on dispersal of damselflies and more research needs to be done in the future. Comparison with the similar system of habitat patches in rural environment could reveal whether the urban environment plays a bigger role as a barrier for damselfly dispersal.

5.4 Metapopulation structure

Our data show that there is some degree of dispersal in both species (though significantly higher in *C. puella*) which offers some insights into their population structure. In the case of *Coenagrion puella* it is possible to say that all the study sites with present populations and dispersal ability of this species could somehow maintain metapopulation structure. Above, we calculated number of possible successful dispersal flights in the entire population with the result of 161 individuals (males and females). From that, 36+ flights could be long-distance. With these results it is quite feasible to say that metapopulation structure is being maintained by connection and the gene flow via dispersal is present because it probably takes only one fertilised female or one pair which successfully mates at new locality, which can be achieved with these type of population dynamics. *Coenagrion puella* also seems to be able to overcome the problems issued by the urbanisation as individuals of this species were able to fly among even the distant study sites. Another interpretation could be (according to Harrison, 1991), that in this situation we can talk about two main “source” populations with good conditions and greater abundances – botanical garden and gardens of Kinski – creating clusters of habitats to host viable, abundant populations. Other few little localities (A, D and L) could be supported by these main populations via dispersal. However, at the moment we can only speculate, whether this dispersal rate could be sufficient to maintain metapopulation structure. Exploration of genetic structure of these populations would be appropriate to uncover possible correlation with MRR experiment results.

On the other hand, *Pyrrhosoma nymphula* demonstrated strong fidelity to its parental site with minimal dispersal among study sites. MRR data indicate that adults are strongly connected to their parent site with minimal interpatch movement and even then, this movement was restricted to short distance and close neighbouring water bodies. It could be a similar case to the study by Watts et al. (2004) on rare damselfly *Coenagrion mercuriale*. This damselfly was explored to have sedentary life with restricted dispersal. According to this article, a strong genetic clustering and differentiation between populations was proved. There was also strong correlation between habitat fragmentation and isolation of *C. mercuriale* populations (recorded also in Rouquette and Thompson, 2007). Our case with *P. nymphula* species could be similar. Also then, lower abundance of *P. nymphula* could be explained by the fact, that this species has lower dispersal rate and hypothetically more restricted dispersal abilities, thus making its populations less dynamical and resilient against disturbances. If the recorded isolation is a norm for the urban populations of this species, then we have a few rather isolated populations in the

Prague city centre. It would be also appropriate to explore the genetic structure of these populations, possibly to uncover genetic isolation correlating with the ecological one. However, no recent studies on *P. nymphula* dispersal and population dynamics are known, so this study is one of the first in the last years.

5.5 Diversity of dragonflies

During the field work we encountered some other species than the ones included in the study. Twelve species of dragonflies were encountered during the sampling season (see Table 4). This number of species (according to Šťastný et al., 2015) makes up circa 29,3 percent of 41 odonates historically encountered or even periodically observed in the Prague city and circa 16,2 percent of all 74 odonate species occurring in the Czech Republic. From these twelve species, most of them are common species with wide distribution. One exception is *Crocothemis erythraea* as this dragonfly was rare in Czechia in the last century, but in recent decades it is also experiencing expansion. Today is *C. erythraea* starting to be a common species, especially in the lowlands (Waldhauser and Černý, 2014). Another damselfly, *Sympecma fusca*, is categorized as “near threatened.”

Overall, we can say that Prague city centre can maintain a pretty sustainable environment for quite a lot of species of dragonflies. However, our point of view was very narrowed by time restriction as we covered only first half of the season (from the end of May to the first half of July) and we didn't explore the greater perimeter of the city centre and also the outskirts of Prague so we couldn't get the whole image of diversity of dragonflies in Prague.

6 Summary

The present study showed population dynamics and dispersal patterns of two generalist damselfly species – *Pyrrhosoma nymphula* and *Coenagrion puella* - and differences between them. For that, the mark-release-recapture method (MRR) was used to track the movement of individuals. Analysis of the population parameters was performed using POPAN module in the open-source programme MARK. Main question was whether urban environment somehow acts as a barrier for damselflies dispersal. Beside that, basic parameters (survival, abundance, and recapture rates) were estimated from MRR experiment. Additional information from the field work was observation of dragonfly diversity in studied area.

We can say that Prague city centre can host viable populations of odonates. Together, 1821 individuals from both species were marked during seventeen marking occasions, around 16 percent of them were encountered and recaptured again. In both species there was male-biased sex ratio. Both species had high survival probability (approximately 90,4 % for *P. nymphula* and 86,1 % for *C. puella*). Studied damselflies differed significantly in their dispersal rate and reaction to the urbanised matrix. *Coenagrion puella* had almost two times (1,54 %) higher dispersal rate in relation to the number of marked individuals than *Pyrrhosoma nymphula* (0,84 %) and it included long-distance flights across the urbanised landscape. We can presumably say that this dispersal could maintain metapopulation structure in the aquatic habitats in the Prague city centre. We can also say that *P. nymphula* species is rather sedentary and individuals are connected with their parental site with occasional short-distance dispersal to the nearby water bodies. It could be connected with their restricted movement in fragmented landscape. It was explored in this study that urban landscape can act as a barrier in species with worse dispersal abilities, as we observed in *Pyrrhosoma nymphula* species. On the other hand, *Coenagrion puella* had no problem, even with long-distance flights through the built-up city core. Due to these facts – that two generalist species had quite different response in dispersal behaviour to the urbanisation of landscape – we can't really generalize influence of urbanisation level on the dispersal of damselflies as there probably are more factors in play. We also suggest that further research on the genetics of these populations and relations between them is needed to explore either stable connection or isolation of population in both species. Overall, we consider this study as a fine example of MRR study of population dynamics and dispersal abilities of damselflies in the urbanised regions.

7 References

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