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Ecology of endangered damselfly *Coenagrion ornatum* in post-mining streams in relation to their restoration

Master thesis

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Annotation

The thesis explores various aspects of ecology of endangered damselfly *Coenagrion ornatum*, the specialists for lowland headwaters, in post-mining streams of Radovesicka spoil. The first part of thesis is manuscript which has been already submitted in *Journal of Insect Conservation*. In the first part, we focused on population estimate of the local population using capture-recapture method, and explored its habitat requirements across life stages and spatial scales. In the next part, I assess mobility of the focal species and reveals basic distribution patterns. Finally, the thesis suggest various implications for restoration of post-mining freshwaters and conservation of the studied species.

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Filip Tichanek has come with the research idea, has substantially contributed to its designing and planning, has fully organised the data sampling and analyses, and has substantially contributed to the results interpretations and the manuscript writing.

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1 A brief commentary and aims

This thesis follows my bachelor thesis which figured out that post-mining streams attract valuable communities with several threatened odonates associated with endangered habitats of lowland small streams. Results of my bachelor thesis were already published in the *Journal of Insect Conservation* and brought new view to the ongoing debate on restoration of post-mining sites. Here, in my master thesis, I focused more deeply on the endangered damselfly *Coenagrion ornatum*, one of the threatened species occupying one of the studied spoil heap. The species is protected in whole Europe, but in spite of the official protection, it is still declining.

The thesis have two main parts. The first is a manuscript already submitted into the *Journal of Insect Conservation*. It focuses on questions relevant for restoration of the local habitats, especially on the total size of the population and habitat requirements for the species. The second part is focused on the *C. ornatum*'s spatial ecology and its implications for the species monitoring and conservation.

More specifically, the main aims of the master thesis are:

i) to estimate population size of *Coenagrion ornatum* in the Radovesicka spoil heap;
ii) to explore its habitat requirements for different life stages and sexes;
iii) to explore the species mobility and adult dispersion patterns;
iv) to suggest the most effective monitoring of the species
v) to suggest basic implications for restoration of post-mining streams, as well as for conservation of the protected species.

2 Literature review

2.1 Conservation of headwaters

2.1.1 Importance and degradation of headwaters

Headwaters (i.e. first-order and second-order streams) and small streams are the most common components of the whole riverine system. In Europe, they flow almost everywhere, from alpine to lowland areas, and represent crucial component of whole riverine system (Dodds and Whiles 2010). Due to their abundance and tight connection to the terrestrial environment, they crucially affect nutrient dynamics, bio-complexity and water quality of the whole riverine system (Gomi et al. 2002; Alexander et al. 2007; Wiplfli et al. 2007). Moreover, headwaters also represent an extremely heterogeneous environment with high within-stream (small-scale), as well as inter-stream heterogeneity, creating thus plenty of ecological niches for highly specialized organisms (Meyer et al. 2007). Due to the headwater heterogeneity and high proneness of the headwater specialists to geographical isolation, headwaters serve as essential resource of biodiversity for the riverine systems (Gomi et al. 2002; Lowe and Likens 2005).

Unfortunately, changes in land use along with the high sensitivity of the headwaters to various disturbances (and low potential to buffer pollution) led to a serious degradation of the vast majority of headwaters flowing in European landscape, especially in lowlands (Malmqvist and Rundle 2002; Lowe and Likens 2005). Almost 90 % of the lowland small streams and headwaters have been channelized (i.e. became drainage ditches) in the last decades, losing thus their natural heterogeneity, aquatic-terrestrial connectivity, biodiversity, retention and other ecosystem functions (Muotka et al. 2002; Pedersen et al. 2006). Some were even piped. Moreover, other factors, such as both organic and inorganic pollutions, invasions of non-native species and damming, have had a negative impact on the conservation value of the headwaters and small streams (Allan and Flecker 1993). Such degradation was stronger in lowland areas where the human impact was especially severe and pervasive, whilst (sub)montane headwaters are in much better conditions in many European areas (Lowe and Likens 2005).

The degradation of the lowland headwater streams has been aggravated mainly by intensive agriculture and urban influences (Janse and Van Puijenbroek 1998; Moore and Palmer 2005). Both agricultural fertilizers and urban sewer seepages cause eutrophication (i.e. increased input of some nutrients, mainly phosphates and ammonium), which has had a direct negative (i.e. toxic) impact on physiology of substantial part of headwater invertebrates (Janse and Van Puijenbroek 1998; Watson and Ormerod 2004; Clarke 2014). Moreover, eutrophication has often led to anoxic instream conditions lethal for majority of headwater specialists. In addition, the eutrophication prevents development of diversified emergent and aquatic vegetation favourable for most species whereas it supports pervasive, high and homogeneous vegetation (e.g. common reed monocultures; Riis and Sand-Jensen 2001). Besides the eutrophication, various pesticides and herbicides from agriculture also had a negative impact on the headwater biota via their direct toxicity to organisms (Moore and Palmer 2005).

Similarly, the headwater streams in agricultural landscape are also harmed by erosion of fine sediments into the streams and their consequent colmation (Painter 1999; Descloux et al. 2013). It was repeatedly shown that pervasive fine sediments suppress the microhabitat heterogeneity of streams and leads to more eutrophic and anaerobic conditions, as well as to substantial reduction of free water columns and thus a reduction of habitat suitable for various freshwater organisms (Buffington and Montgomery 1999; Yarnell et al. 2006; Descloux et al. 2013; Burdon et al. 2013). Moreover, movement of invertebrates is extremely difficult in the fine sediments. Therefore, very high sediment supply decreases habitat quality and thus overall biodiversity.

On the one hand, effect of sediment erosion and input of fertilizers and herbicides could be partially reduced via keeping sufficient buffer strips around the streams (Moore and Palmer 2005). However, vegetation should not induce complete shading of the stream. As a big proportion of lowland headwater specialists require sunny streams, the shading, caused by overgrowth along the stream via dense shrubs and other high bank vegetation, leads to further reduction of habitat quality of the lowland streams (Rouquette and Thompson 2005; Harabiš and Dolný 2015).

As a result, widespread degradation of the headwater streams have led to extinction or decline of a substantial part of headwater biota and headwaters are therefore currently considered as one of the most threatened habitats within Europe (Allan and Flecker 1993; Malmqvist and Rundle 2002; Meyer et al. 2007). The dramatic decline of headwater biota can be well illustrated by the best known group of insects associated with freshwaters – odonates (Odonata, i.e. both dragonflies and damselflies). Substantial part of the threatened odonates are restricted to small streams and headwaters (Kalkman et al. 2007; Kalkman et al. 2010). In the Czech Republic, there are 8 species primarily associated with small streams and headwaters (Waldhauser and Černý 2015; Dolný et al. 2016). Unsurprisingly, six of them are listed as threatened in Czech red-list status (Dolný et al. 2016), one species is even extinct (*Coenagrion mercuriale*, the typical representative of sunny springs and headwaters of lowland non-forest landscape). The only remaining species (*Somatochlora meridionalis*) is known from a single locality in the Czech Republic and its current status is now highly uncertain (Dolný et al. 2016).

2.1.2 Conservation of headwaters

Recently, there has been growing numbers of restoration projects focused on small streams in Europe (Muotka et al. 2002; Muotka and Laasonen 2002; Pedersen et al. 2006). The projects have mostly aimed at improving physical structure of the streams: increasing roughness of the bottom, development of stream sinuosity and establishing riffle-pool structures. Altogether, these arrangements lead to higher small-scale heterogeneity in stream velocity, increased terrestrial-aquatic connectivity and decreased sediment transfer. However, reported efficiencies of these projects, in terms of biodiversity, are inconsistent with both positive (Muotka et al. 2002; Muotka and Laasonen 2002; Pedersen et al. 2006) and negative (Ernst et al. 2011) results. However, the inconsistent short term results are at least partially explainable by limited dispersion of model groups and restricted species pool in the studied areas.

Fortunately, even some already channelized streams were documented to re-establish a quasi-natural state spontaneously and to serve as a biodiversity refuge (Vermonden et al. 2009). The channelized streams could be particularly valuable if they are surrounded by area with non-intensive land use, or at least with limited use of fertilizers (Painter 1998; Painter 1999; Harabiš and Dolný 2015). In addition, the conservation potential could be greatly supported by mowing the bank vegetation, establishing wide buffer strips of semi-natural habitats around the stream, and by careful rotational cleaning of sections with high sediment input (Painter 1998; Moore and Palmer 2005). Despite the artificial state, even these already channelized streams could represent secondary habitat for some threatened organisms primarily associated with natural headwaters (Chester and Robson 2013; Harabiš and Dolný 2015).

Finally, a recently published study (Tichanek and Tropek 2015) showed that post-mining streams flowing in drainage ditches of a large lignite spoil heap attract extraordinarily dense populations of some threatened odonates restricted to streams and headwaters, including these which had not been found in the studied region recently. It indicates substantial potential of post-mining sites for headwater conservation. However, more studies must be done to evaluate the potential properly.

2.2 Post-mining sites as refuges for threatened species

2.2.1 Occurrence of rare species in post-industrial sites

Various post-industrial sites have been repeatedly documented to represent refuges for numerous threatened organisms. The high conservation potential was documented in many types of post-industrial sites and for wide variety of organisms (reviewed by Tropek and Řehounek (2012) and Řehounek et al. (2015)). For example, many rare plants were reported from limestone quarries (Tropek et al. 2010), spoil heaps (Řehounek et al. 2015; Tropek et al. 2012, 2013), and sandpits (Šebelíková et al. 2015; Řehounková et al. 2016). Even critically endangered birds were documented from the North-Bohemian spoil heaps (Šálek 2012). Amphibians were found in many types of post-mining sites, namely spoil heaps and various quarries (Vojar et al. 2016). Rare butterflies were documented from ash deposits (Tropek et al., in review), various spoil heaps and quarries (Beneš et al. 2003; Tropek et al. 2010, 2012, 2013). Threatened odonates were found to be very common in standing freshwaters of spoil heaps (Harabiš et al. 2013), mine subsidence (Dolný and Harabiš 2012) and sandpits (Hesoun and Dolný 2011). Various other critically endangered invertebrates were found in spoil heaps (Hendrychová et al. 2012; Tropek et al. 2012; Kolář et al. 2015), quarries (Tropek et al. 2010; Tropek et al. 2008), sandpits (Řehounková et al. 2016) and ash deposits (Tropek et al. 2013, 2014, 2015). Post-industrial sites are especially important for aculeate hymenopterans: many critically endangered species of Czech hymenopteran is associated exclusively with post-industrial sites (Srba and Heneberg 2011; Tropek et al. 2013). Interestingly, Tropek et al. (2013, 2016) revealed that the ash deposits offer habitats to some hymenopteran species that had previously been considered to be extinct in the Czech Republic. Finally, not only do post-mining sites offer habitats to rare species, they also host high overall biodiversity, largely exceeding biodiversity in surrounding landscape (Řehounek et al. 2015).

The immense conservation potential of the post-industrial sites can be attributed to several characteristics of the post-industrial sites, mainly oligotrophic environment and presence of early-successional habitats (Prach and Walker 2011; Tropek et al. 2012; Tropek et al. 2015). Changes in land use in last century, including termination of traditional extensive agricultural, caused large-scale eutrophication and overgrowth of the Central European landscape (Thomas et al. 1994). These factors thus triggered a rapid decline of the oligotrophic and early-successional species. In contrast to the surrounding landscape, the post-mining sites are often early-successional and the succession is often even blocked by unsuitable substratum or disturbances (Frouz et al. 2008). Moreover, they are not affected by fertilizers and various toxins from intensive agriculture. In addition, some post-mining sites offer extraordinarily dense net of small oligotrophic pools (Harabiš et al. 2013), which are rarely seen in agricultural and urban landscape, and are especially important for amphibians and freshwater insects. As occurrence of all these factors in one site is very rare in the Central European landscape, the post-mining sites represent unique and valuable environments.

2.2.2 Post-mining restoration

However, conservation potential and biodiversity strongly depend on the restoration method applied (Řehounek et al. 2016). There are basically two main prevailing methods: technical reclamation and spontaneous succession (Prach and Hobbs 2008, Tropek et al. 2010, 2012). During the technical reclamation, the terrain is flattened, covered by rich topsoil and consequently planted by the trees or grass mixture. Sometimes, crop fields are established on some bigger post-mining sites. In addition, water is often drained via a system of drainage ditches and retention reservoirs in the reclaimed post-mining sites. However, sometimes the draining was not applied and technical flattening was not carried out intensively, thus partially retaining landscape heterogeneity (Harabiš et al. 2013). In contrast to technical reclamation, the spontaneous succession approach allowed the site to spontaneously development, keeping thus huge environmental heterogeneity with numerous bare patches, erosive slopes and generally oligotrophic soil condition (Prach and Pysek 2001). There are numbers of studies comparing these two main approaches in terms of terrestrial biodiversity and conservation potential. These include broad multi-taxa studies in limestone quarries (Tropek et al. 2010), spoil heaps (Tropek et al. 2012; Hendrychová et al. 2012), fly ash deposits (Tropek et al. 2014, 2016), and sandpits (Řehounková et al. 2016); plant studies in spoil heaps (Hodačová and Prach 2003; Mudrák et al. 2010) and sandpits (Šebelíková et al. 2015); an ant study in spoil heaps (Holec and Frouz 2005); and a comparison of bird communities in spoil heaps (Šálek 2012). All have brought the same conclusion: technical reclamations damage biodiversity and conservation value of the post-mining sites. Moreover, the most recent multi-taxa study of sandpits have shown that spontaneous succession with additional non-intensive disturbances is even better approach of restoration than spontaneous succession alone (Řehounková et al. 2016).

2.2.3 Restoration of post-mining stagnant freshwaters

Unfortunately, all the mentioned studies were focused solely on terrestrial communities, although freshwaters and wetlands are considered to be of the most important post-mining habitats. The first study comparing both prevailing restoration approaches focused on physical structure and the density of stagnant freshwaters at spoil heaps in north Bohemia (Doležalová et al. 2012). This study found pools at spontaneously developing sites having more heterogeneous banks and that their density is higher when compared to the technically reclaimed sites. The first study comparing the restoration methods in terms of biological communities was provided via studying odonates in spoil heaps in North Bohemian lignite basin (Harabiš et al. 2013). The study compared communities in three distinctive types of freshwaters: i) pools of spontaneously developing sites; ii) pools of spontaneous origin (inundated terrain depressions), but in reclaimed sites; iii) artificial reservoirs in reclaimed sites (with artificial inflow, outflow, or even water gate). Surprisingly, results of the study were different from the studies of terrestrial communities: all the three types attracted some rare and threatened species, but all the types were comparable in terms of the species richness and the conservation value of their communities.

In contrast, results of a recent study of amphibian communities in the same study area have brought discordant results: spontaneous succession has been shown to support amphibian diversity, whereas technical reclamation had a negative impact on it (Vojar et al. 2016). However, comparing both studies is difficult because of the different classification of the pools. Specifically, some sites defined as inundated depression in reclaimed spoil heaps in the study of odonates (Harabiš et al. 2013) were treated as spontaneously developing sites in the study of amphibians. A particularly important discrepancy includes parts of the Kopistská and Růžodolská spoil heaps, which had been extensively flattened and consequently planted by dense trees, but no draining had been applied (F. Tichánek, pers. observ.). As these sites are especially valuable in terms of freshwater habitat quality (Harabiš et al., 2013; V. Kolář, F. Tichánek & R. Tropek, unpubl. data), the different definitions could partially explain the contrasting conclusions of the two mentioned studies. However, a group-specific response is still possible. Based on these results, we can conclude that the relationship between applied restoration methods and conservation value of the post-mining freshwaters does not seem to be straightforward, especially when compared to terrestrial communities.

2.2.4 Post-mining streams

Although mining could destroy groundwater, springs and whole stream systems in the wider surroundings of excavated areas (Mutz 1998), it simultaneously creates another freshwater habitat: headwater streams in the ditches draining the reclaimed spoil heaps and mines (Tichanek and Tropek 2015). The post-mining stream biodiversity was not studied in Europe, but they were generally not viewed as beneficial for biodiversity conservation. However, these streams have several characteristics highly favourable for some stream and headwater species: low nutrient level, very limited shading and sometimes also (ir)regularly mown banks. Moreover, they are intact from various pesticides and also tend to have more favourable physical properties, such as wider bed and low bankside inclination (compared to agricultural ditches). On the other hand, they are sometimes polluted by heavy metals influencing the stream life (Mebane et al. 2015) and sometimes show extreme chemical properties, such as pH and conductivity (Mutz 1998). The only study that has focused on biodiversity and water chemistry of post-mining streams and their comparison to natural headwaters was provided in Virginia, USA (Petty et al. 2013). The study found that diversities of both studied groups – water macroinvertebrates and amphibians – were comparable, but mining streams had lower proportion of stream specialists. Moreover, although the metals were low in both stream types, mining streams had greater conductivity and dissolved solid concentrations.

The first study examining diversity and conservation value of post-mining headwaters in Europe (Tichanek and Tropek 2015) was focused on odonate communities at drainage ditches of the Radovesicka spoil heap (North Bohemia). Interestingly, the study revealed high conservation value of the studied ditches, with high densities of three threatened odonates primarily associated to small streams (*C. ornatum*, *Orthetrum coerulescens* and *Orthetrum brunneum*; Tichanek and Tropek 2015). Moreover, two other threatened species were found: the endangered *Sympetrum pedomontanum* was even recorded for the first time in the studied region. When compared the studied post-mining stream communities (one spoil heap) with the stagnant waters (9 spoil heaps) in the studied region, it is evident that post-mining streams offer habitat to species at higher risk of extinction and thus have substantially higher conservation value (Harabiš et al. 2013; Tichanek and Tropek 2015). As the studied stream system flows in the reclaimed sites only, the results of the study indicate that the technical reclamation creates the most valuable freshwater habitats in the spoil heaps, at least in terms of odonate communities of North Bohemia. However, more studies of post-mining headwater biodiversity, ideally using other organismal groups and other study areas, are strongly needed. Moreover, as the study of Tichanek and Tropek (2015) was carried out using adult odonates only, the real value of the streams, even for odonates, is still questionable because adult odonates are not generally accepted as an indicator of habitat quality by some researchers, especially in local studies (Raebel et al. 2010; see chapter 2.3.3).

2.3 Odonates as model organisms in ecology and conservation biology

2.3.1 General information on odonates

Odonates group of insects, consisting of over 5,680 species worldwide (Clausnitzer et al. 2009). The order includes two phylogenetically separated sub-orders – mostly smaller, finer and slower damselflies (*Zygoptera*), and mostly larger, more robust and agile dragonflies (*Anizoptera*). Although being hemimetabolous insects, larval and adult habitats are separated: larval development is strictly associated with aquatic environments, whereas adults are terrestrial fliers (Dolný et al. 2016). In spite of that adults spend majority of their lifetime close to breeding habitats, it is known that their niche is much wider as they hunt and even overnight elsewhere (Rouquette and Thompson 2006; Dolný et al. 2012; Kutcher and Bried 2014; Šigutová et al. 2015). Development of larvae vary in its duration length from one to five years in species living in the Czech Republic (Waldhauser and Černý 2014). Czech dragonflies overwinter as larvae, except for two species (both belong to genus *Sympecma*).

Both larvae and adults are predators. Larvae hunts small invertebrates, but older larvae of bigger dragonfly species are able to prey on tadpoles or even small fish (Dolný et al. 2016). Odonate larvae are also frequent cannibals or hunt smaller stages of other odonates. Adult dragonflies prey on various flying insects. Fish and many predator macroinvertebrates hunt them as larvae, birds and some insect predators (e.g. wasps) hunt them as adults, with the latter preying more so on smaller species.

In the Czech Republic, there are around 74 odonate species with various habitat associations. The major threat for almost all odonate is eutrophication and degradation of heterogeneity of their habitats. Lentic species strongly suffer due to intensive fish harming (Dolný et al. 2016).

2.3.2 Odonates as bioindicators

As odonates are aesthetically highly attractive, relatively “easy to study” and thus relatively well-known (especially, but not only, when compared to other freshwater insect), they were successfully used in macroecology (Hof et al. 2006; Keil et al. 2008; Heino 2011; Grewe et al. 2013) and as indicators of long-term conservation trends (Kalkman et al. 2007; Clausnitzer et al. 2009). Similarly, they were shown to be sensitive on large-scale environmental processes, such as climatic changes (Bush et al. 2013). More importantly, they are one of the most frequently used indicators of freshwater habitat quality, environmental health and biodiversity changes in the freshwater communities (D’Amico et al. 2004; Silva et al. 2010; Simaika and Samways 2011; Acquah-Lamptey et al. 2013; Kutcher and Bried 2014).

Besides easy field determination, the odonates have several other attributes of highly useful environmental indicators. First of all, dragonfly communities were shown to be very sensitive to habitat changes, even more than other water macroinvertebrates (Simaika and Samways 2011). Moreover, they have relatively good dispersal abilities enabling them to rapidly colonize newly restored habitats and thus accurately indicate the outcome of the conservation treatment (Silva et al. 2010). In contrast, using a poor disperser in studies of habitat recovery leads to false negative results (Ernst et al. 2011). In addition, because of odonates‘ complex life cycle, they are believed to be good indicators of environmental changes across both aquatic and surrounding (terrestrial) environment (Dolný et al. 2012; Kutcher and Bried 2014). They occupy a relatively wide spectrum of environments as a group, but often have specific narrow habitat requirements as species (Djikstra 2006). Finally, as odonates are charismatic, relatively well-known, relatively easy to study and were repeatedly documented to indicate overall freshwater biodiversity, at least some of them could successfully serve as umbrella species (i.e. the species, whose protection have positive impact on whole threatened communities, including those of other taxonomic groups; Bried and Ervin 2014; Dutra and De Marco 2015; Patten et al. 2015).

2.3.3 Accuracy of assessments based on adults

Although the majority of the ecological studies use adult odonates as a model organism, there are general concerns about the accuracy of the indication when only adults are used in local studies (Raebel et al. 2010; Patten et al. 2015). Adult odonates were repeatedly found to oviposit in sites unsuitable for larval development (Horváth et al. 2007; Šigutová et al. 2015). Presence, including breeding, of adults thus does not necessarily imply residency of the species in the given site (Raebel et al. 2010). However, there are significant differences in spatial ecology and distribution patterns of adults among species, suggesting that adult indicatory qualities are variable across odonate groups. For example, it was suggested that adult damselfly (Zygoptera) have generally more specific distribution restricted to particular microhabitats whereas adult dragonflies (Anisoptera) operate on a larger landscape scale, having more diffuse distributions and thus smaller indication value when only adults are used for local habitat assessments (Dutra and De Marco 2015). However, even closely related species could substantially differ in adult distribution patterns and connection to larval habitat (Dolný et al. 2013). Such information about spatial ecology and larva-adult distribution correlation is thus needed when adults of the species are frequently used for assessments. This is especially important in species protected by the "Natura 2000", which are commonly used as umbrella species and bioindicators, but the large part of data on their distribution are provided by citizens without sufficient training in larvae/exuviae determination. Although using larvae and/or exuviae is ideal, it is not always feasible because of sampling effort and determination difficulties (Bried et al. 2015). Moreover, exuviae surveys were reported to be biased toward underestimation of the diversity and/or abundance of focal species/communities, because of their low detectability (Bried et al. 2012a). On the other hand, the species residency could be accurately estimated even using adults, if additional information about sampled populations are considered (Bried et al. 2012a). Recently, several studies have revealed that the evidence of breeding and high abundance of juveniles could be a good proxy of species residency (Bried et al. 2012b). Similarly, other methodological study found that repeated recording of adults, high adult abundancy and presence of juveniles in the site is the very accurate indication of the species' local residency (Bried et al. 2015).

2.4 Coenagrion ornatum

Coenagrion ornatum is a small damselfly distributed across Southeastern Europe, Asia Minor and Caucasus countries, and also in Central Europe and some parts of West Europe (Kalkman et al. 2010). However, in Central and West Europe, the species is very rare or even locally extinct (e.g. in Italy and Switzerland) and is declining across the whole of Europe (Boudot 2014). Although the species was considered to be extinct in the Czech Republic, it has been found in new localities since 2002 (Waldhauser and Mikát 2010). Until recently, the species was considered as critically endangered (Hanel et al. 2005; Dolný et al. 2007), but recently was requalified as endangered in the Czech Republic (Dolný et al. 2016). On the other hand, in the past few years, decline of its known population has been observed (Waldhasuer personal communication).

The species is closely associated with small lowland streams and headwaters, including those which were partly channelized but still with some beneficial properties, such as low water velocity, rich vegetation and absence of shading and eutrophication. In Central Europe, *C. ornatum* is restricted to the warm areas only. Because of its rare occurrence in Central/West Europe, together with its general population decline and its association with the threatened habitats of headwaters and small streams, *Coenagrion ornatum* is treated as near threatened in the whole Europe. It is also included in the Appendix II of the European Habitat Directive ("Natura 2000"; Kalkman et al. 2010). Because it is the only officially protected odonate species associated with sunny lowland streams living in the Czech Republic, as well as in other European countries, *C. ornatum* has immense potential as an umbrella species for other threatened (but not officially protected) lowland headwater species. The species has several attributes of the suitable umbrella species for the headwater specialised communities: namely, its adults are easily recognisable and catchable, it shows specific requirements toward small streams and headwaters, and it reacts negatively to some factors representing main threats for substantial proportion of the headwater biota (i.e. shading, high eutrophication, homogenous or missing aquatic vegetation and oversimplified streambeds with high velocity). On the other hand, the habitat requirements were not studied in details and with respect to larval (micro)habitat associations (Harabiš and Dolný 2015; Tichanek and Tropek 2015). Similarly, mobility and distribution of its adults in relation to their larval habitat is not known. However, acquiring the information about spatial ecology of the species would be very valuable to assess the indicatory qualities of its adults.

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Chapter 3 could not be published online due to copyright issues

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4 Part two – spatial ecology

4.1 Methods and results

Study area and sampling of adults by the capture-mark-recapture is described in Methods of the chapter 3. Similarly, numbers of the captured and/or observed individuals are the same as in the submitted manuscript (chapter 3). Numbers of the recaptured individuals, however, differ as the numbers in the first part of the study included captures from the different *capture occasions* only. For the second part of the study I have defined *recapture* as the repeated capture after at least 30 minutes even within the same *capture occasion*. Considering such definition, the number of recaptured individuals was 240 (45 females and 195 males) which were recaptured altogether 334 times. However, majority of the recaptures were after a short time only (half of recaptures was realized after less than 4 hours). The number of individuals recaptured in a different day, than they were captured, was 137 (18 females, 119 males). Interestingly, two male individuals were recaptured after 17 days. The average time between capture and the last recapture was 58 hours (median 24 hours). With a single exception, all individuals were sampled only at the same stream, only a single male was detected to flight across a retention basin to another section of the same channel. Beside the adults, we also observed 104 juvenile individuals.

To reveal which factors influence *individual dispersal range* (i.e. distance between the two most distant places where a particular individual was captured-recaptured; the distance was measured along the stream, not by air), I performed generalized linear model with negative-binomial errors distribution and log-link function using the *MASS* package (Venables and Ripley 2002) in R (R Development Core Team 2016). The chosen errors-distribution was used because of a huge over-dispersion in the *individual dispersal range*. The tested factors included: i) *time range* (i.e. time between the capture and the last recapture; logarithmically transformed); ii) *number of recaptures*; iii) *phenology* (i.e. the middle day between the first capture and last recapture); iv) *sex*. The factors for the final models were selected via backward selection using Bayesian information criterion (BIC). The GLM identified *time range* (Δ BIC= 19) and *phenology* (Δ BIC= 5) as important factors with linear positive effects (Table 5).

Table 5 Effects of important variables selected by backward selection based on BIC.

Variable	estimate± SE	Δ BIC
individual dispersal range	0.2914± 0.0598	19
phenology	0.0277± 0.0001	5

The median *individual dispersal range* was 11 m (third quartile 61 m), suggesting an extremely low mobility of *C. ornatum* individuals in the studied population. However, if I have considered only individuals recaptured after at least one day (137 individuals), the median grew to 16 m (third quartile 80 m). After at least four days it was 47 m (third quartile 102 m; 75 individuals); individuals recaptured at least one week after the first capture had median individual dispersal range 74 m (third quartile 124 m; 36 individuals).

Generalized linear mixed models (GLMM) with the binomial-errors distribution and logit function were used to reveal a probability of emigration from the studied 81 m sections (see Methods in chapter 3 for details; individuals recaptured in different sections repeatedly are considered as different observations; n= 334)), provided using the *lm4* package (Bates et al. 2015) in R (R Development Core Team 2016). I used these variable (all are describing 40.5 m adjacent stream sections): i) *time range* (time between capturing and recapturing; log-transformed); ii) *phenology* (defined in previous paragraph); iii) *sex* (male/female); three environmental factors important for at least two measures of adult abundance (for description of individual factors see Table 1 in chapter 3): iv) *bankside height*; v) *emergent vegetation;* vi) *Eleocharis*; and three measures of adult abundance (all log-transformed): vi) *female abundance*; vii) *male abundance;* vii) *juvenile abundance.* All variables were scaled using the *scales* package in R to have zero mean and unit variance. Damselfly individuals represented a random factor. Variables were chosen using BIC. The GLMM revealed that the probability of the site emigration increased by *time* (effect= 1.73 ±0.6; Δ BIC= 4) and, much more importantly, strongly decreased by *Eleocharis* (effect= –2.6 ±0.65; Δ BIC= 25).

To evaluate an importance of the potential spatial autocorrelations and range of its effect for *C. ornatum* adult abundance, I performed the Moran's I of residuals from the individual habitat models (see Methods and Results in chapter 3). Besides the scales of 81 and 27 meters, I performed also models explaining abundances of the adults on the 9 m scale (*male-9* and *female-9* models), using the same set of environmental variables and same procedure of their selection. After the models fitting, their residuals were tested for spatial autocorrelation using the *ape* package (Paradis 2004), semivariograms were reconstructed using the *geoR* package (Riberio and Digle 2002) in R. Males showed very significant spatial autocorrelation ($p < 0.001$) whereas females showed only weakly significant spatial structure ($p = 0.026$). The semivariogram for both male and females models indicate that the spatial autocorrelation affect the adult abundances on distance of 100 to 150 m, but the signal is weak in females (Fig 3).

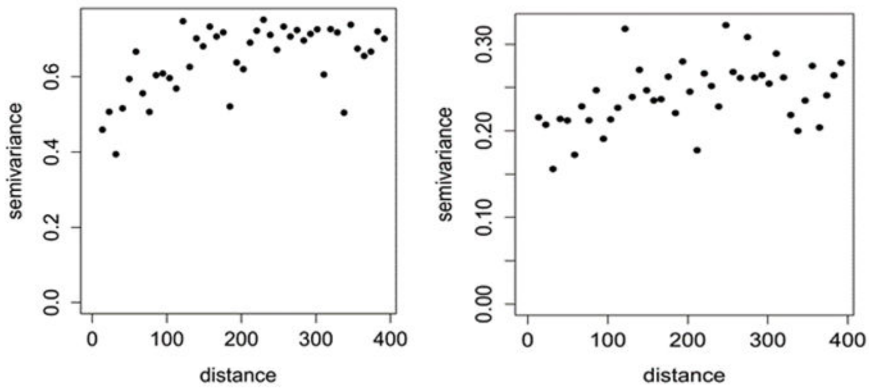

Fig. 3 Semivariograms showing similarity in model residuals in relation to their spatial distance. Residuals from both male (left) and female (right) model are shown.

To figure out how can be suitability of habitats for larvae predicted by abundances of adults, *larval* model was fitted by *female*-27, *male-27* and *adult-27* (total number of both males and females in 27 m sections) as predictors (all were log-transformed). Consequently, the models were compared by AICc and additional bootstraps simulation (1000 simulations); all using the *AICcmodavg* package (Mazerolle 2016) in R (R Development Core Team 2016). At the same time, the *mgcv* package (Wood 2011) was used to estimate adjusted R^2 of the models. The results showed that the *female-27* abundance is much better predictor of *larval* abundance than *adult-27* and *male-27* abundances, based on all three parameters – AICc, bootstrap simulation (i.e. the relative frequencies of model selection from the bootstrap) as well as adjusted R^2 (Table 6).

Table 6 Comparison of models via their AIC, bootstrap simulation and explained variability

Variable	K	AICc	Δ AICc	AICc weights	PiWt[a]	R^2 (adjusted)
female_27	2	170.67	0	1	0.72	0.71
adult_27	2	183.73	13.06	0	0.19	0.43
male_27	2	187.86	17.19	0	0.09	0.36

Legend: a) the relative frequencies of model selection from the bootstrap.

Consequently, the same methods were used for comparison the *female-27* prediction ability alone with records *breeding* behaviour (i.e. average number of the observed ovipositions or pairs in tandem or copulation; log-transformed) and *juvenile-27* abundances (average numbers of juveniles with poor ability to fly), as well as interactions of these variables. The results showed that combination of *breeding* and *juvenile-27* is the most accurate predictor of larval abundance (Table 7)

Table 7 Comparison of models via their AIC, bootstrap simulation and explained variability

Variable	K	AICc	Δ AICc	AICc weights	PiWt[a]	R^2 (adjusted)
juveniles+breeding	3	157.05	0	0.67	0.52	0.79
females+breeding+juveniles	4	159.16	2.11	0.23	0.14	0.78
female+juveniles	3	161.2	4.14	0.08	0.19	0.74
breeding	2	165.77	8.72	0.01	0.08	0.75
females+breeding	3	167.41	10.35	0	0.02	0.76
juveniles	2	250.44	93.39	0	0.06	0.01

Legend: a) the relative frequencies of model selection from the bootstrap.

4.2 Discussion

The revealed pattern of females being much better proxy of larval abundances brings an interesting contribution to the current intensive debates on using of adult odonates as environmental indicators (Raebel et al. 2010; Bried et al. 2012a). The sex-dependent indicatory qualities, however, have not been studied in damselflies so far. On the other hand, it well corresponds with empirical experiences from field and with knowledge about differences in behaviour of males and females (Dijkstra and Lewington 2006). Nevertheless, it has repeatedly been documented that abundances of juvenile adults and presence of breeding behaviour are accurate indicator of local species residence (Bried et al. 2012a; Bried et al. 2015; Patten et al. 2015). As *C. ornatum* is protected in the EU countries and its monitoring should be performed regularly, this result brings important implications. From many objective reasons, majority of monitoring and assessments of the protected odonates are focused on adults only. Moreover, majority of such projects consider even simply presences of individual species as an evidence of a suitability of the present habitats for it. My results shows that as males bring more "noisy" and less spatially specific data, they are much poorer predictor of the microhabitat quality and species residence. Therefore, the both sexes should be counted separately in any local project and its habitats should be assessed only on abundances of females if larvae are not recorded at all. As another option, recording of breeding behaviour and juveniles is also highly useful, especially because it is much easily recognisable by non-odonatologists. On the other hand, such behaviour is relatively rare to be observed. In addition, the numbers of juveniles are declining during June (Fig 4), and I thus recommend to monitor adults of *C. ornatum* from the start of their flight period.

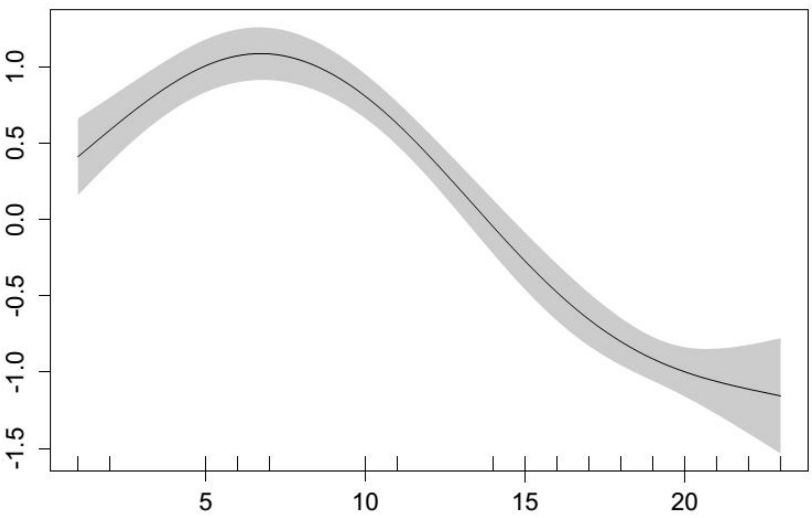

Fig. 4 Schematic figure showing trend in density of juvenile adults. X-axe represent individual days of June 2012. Y-axe shows density of the juvenile individuals (their partial residuals derived from GAMM model respectively).

As our recapture rate of *C. ornatum* was relatively low, estimates of its life span would be highly questionable. However, the recaptures of two males 17 days after its marking could be seen highly interesting because a middle life span of *Coenagrion mercuriale,* the related and ecologically similar species, was estimated for 7-8 days (Allen and Thompson 2014). On the other hand Allen and Thompson (2014) experienced also a few records in 19 days after the specimen marking, suggesting that our records are not unique within the genus. On the other hand, even without sophisticated estimates it seems that its life span is probably shorter than what was reported in other damselflies, especially from the Lestidae family whose life span could be over 9 months in case of *Sympecma* spp. overwintering as adult (Waldhauser and Černý 2014)

The relatively very short median individual dispersal range (11 m), shows *C. ornatum* as an extremely sedentary species. Although it was strongly dependent on the time between first and last captures (only 41 hours in average), even if only the individuals recaptured after at least one week (the median life span in *C. mercuriale*) would be considered the median individual dispersal range is lower than 100 m. As most studies of damselfly dispersion did not calibrate the distance according time between captures and recaptures, the results are hardly comparable with other research. However, dispersion patterns in *C. mercuriale* seems to be similar as it also tends to stay within tens of meters sections in most of the recorded cases. Another study on damselfly dispersion (Conrad et al. 1999) was performed in a system of ponds which offers a different distribution of suitable habitats than linear streams. Nevertheless it revealed that besides a majority of sedentary individuals a scarce guild of mobile individuals was documented. Such patterns could be indicated also in my study, as I have recorded six individuals flying for more than 1,000 m, but more data would be necessary even for such speculations. On the other hand, in the majority of damselfly studies, the highest individual dispersal ranges were comparable (Rouquette and Thompson 2007) or even lower than those in my study (Conrad et al. 1999; Purse et al. 2003; Hassall and Thompson 2011). Moreover, it has been reported that the dispersal characteristics could be highly variable among populations of the same species (Rouquette and Thompson 2007; Watts et al. 2007; Hassall and Thompson 2011), which makes interspecific comparisons much more difficult without more detailed inter-population studies.

Dependency of the individual dispersal range on period between first and last captures is trivial and has been repeatedly documented in damselflies, including the related *C. mercuriale* (Purse et al. 2003; Rouquette and Thompson 2007; Hassall and Thompson 2011).

Because we do not know what individuals do between the last recapture and death, the individual dispersal area is surely underestimated. The positive relationship between mobility and phenological season in *C. ornatum* was also reported for *C. mercuriale.* It could be easily explained by generally more stable weather with higher temperatures from during the second half of my sampling, which gives the species more opportunities to disperse. An alternative explanation could be through a higher ratio of older specimens in later season, as older and fully mature individuals have better flying abilities than very young adults.

The very strong reluctance of *C. ornatum* to leave sections with relatively high cover of *Eleocharis* spp. strongly underlines the importance of the plant for forming the crucial microhabitat of the species already revealed in the analyses of habitat preferences of both adults and larvae (see Chapter 3). To the best of my knowledge, such strong influence of a single environmental factor on dispersion of any damselfly species has not been observed so far. On the other hand, the real mechanism of such effect is difficult to discuss as a strong negative relationship between dispersion and population density was described (Rouquette and Thompson 2007). Because the plant is the only relatively abundant narrow-leaved small and densely growing plant in the studied streams, it also cannot be claimed as the crucial plant for the species. Following the resource-based habitat view (Dennis 2012) and no obvious direct relationship between the damselfly's development and any particular plant species, I rather expect that *C. ornatum* needs microhabitat of any narrow-leaved emergent plants. This should be surely considered during any management plans supporting this damselfly.

The significantly more diffused distribution of males, compared to females, has not been, to my best knowledge, reported in damselflies. It indicates that the females are more restricted to the specific microhabitats used for potential oviposition and development of larvae. Males, however, tend to search for females in a wider adjacent area. The effect of spatial autocorrelation on the distance of 100 to 150 meters fits very well to the observed dispersal characteristics of the species, it again confirms that 100 to 150 m is the spatially relevant distance for the species. Therefore, any habitat management should consider this and restrict any temporarily negative actions (e.g. removing the sediments) to maximal length of 100 m, followed by at least the same length of stream untouched by the action. This would avoid a fragmentation of the population. These results again revealed females as more useful indicators of suitable habitats than males which is important for any monitoring or habitat evaluation.

5 Summary and synthesis

As the thesis results confirmed, the Radovesicka spoil heap represents a regionally important secondary habitat for endangered *Coenagrion ornatum*. Although the high conservation value of the post-mining streams was already suggested (Tichanek and Tropek 2015), various opponents have been sceptical about residency of the threatened headwater species in the post-industrial freshwater sites. According to our results on the population size, the larval occurrence, and the species' spatial ecology, the population is confirmed to be resident. This detailed study of the endangered species shows that at least some of the habitat most specialised species are able to create rich and relatively stable local populations in human-made sites. It also supports indication, that the most interesting and valuable odonate communities are being formed in reclaimed parts of spoil heaps, contrasting thus to threatened terrestrial biota.

Similarly, both studying the spatial ecology and detailed habitat requirements revealed the huge importance of small-scaled microhabitats formed by fine-leaved emergent vegetation (*Eleocharis* spp. in our study). Such microhabitats are favoured by both life stages, both sexes, and on both studied spatial scales. The patches without the microhabitat are colonized by fewer specimens which tend to emigrate soon. Supporting such microhabitats is thus extremely useful for the species conservation and should represent one from the main tools in restoration of post-mining flowing freshwaters.

Because the species is sedentary, mostly operating within 100 m long sections, all conservation action potentially degrading the habitat from short-term point of view should be provided in maximally 100 meters long sections. Even short-term damage of longer sections via management suggested by the species' habitat preferences (removing sediments or too grown vegetation) could lead to fragmentation of the local population. Moreover, it would be highly desirable to establish good microhabitats at least with the frequency one short section per 100 m long section. This will keep a higher connectivity and thus viability of the population.

Our results confirmed that sampling of larvae is still optimal. Larval response slightly differ from adults, mainly because of requiring finer-scale habitat heterogeneity, whereas they are not influenced by the banks characteristics. However, despite this, *C. ornatum* females have still relatively narrow distribution restricted to specific microhabitats which are very important also for larvae. Females and juveniles thus can be monitored as a very accurate proxy of the larval development and species residency. Finally, as number of present juveniles is decreasing shortly after start of the season, sampling should be provided in early species flight period to record sufficient abundances of the generally hardly detectable juveniles.

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