

**The impacts of urbanisation on the ecology
and evolution of dragonflies and damselflies
(Insecta: Odonata)**

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

The work in Chapter 1 of the thesis has appeared in publication as follows:

Villalobos-Jiménez, G., Dunn, A.M. & Hassall, C., 2016. Dragonflies and damselflies (Odonata) in urban ecosystems: a review. Eur J Entomol, 113(1): 217–232.

I was responsible for the collection and analysis of the data with advice from co-authors, and was solely responsible for the literature review, interpretation of the results, and for writing the manuscript. All co-authors provided comments on draft manuscripts.

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I was responsible for the data analysis, interpretation of results, and for writing and structuring the manuscript. Data was provided by the British Dragonfly Society (BDS). The co-author provided advice on the data analysis, and also provided comments on draft manuscripts.

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The impacts of urbanisation on the ecology and evolution of dragonflies and damselflies (Insecta: Odonata)

Abstract

Urbanisation is one of the main drivers of ecosystem change. The impacts of urban land use on biodiversity have been investigated, but other aspects of ecology have been overlooked, as well as the effects of urban stressors. Understanding the effects of specific urban stressors is crucial in order to appropriately manage urban areas and conserve their biodiversity.

Dragonflies and damselflies (the Odonata) are a suitable taxon for evaluating the impacts of urbanisation on both terrestrial and aquatic ecosystems. Here, using a combination of field and laboratory data, I study the ecological impacts of urban stressors on odonates. I found that the urban heat island has negligible impacts on the phenology of odonates compared to climate change. Moreover, noise disturbance reduces significantly the feeding rate of the damselfly *Ischnura elegans*, although anthropogenic noise has no significant impact. Regarding the impacts of polarised light pollution (PLP), the strength of polarotaxis increased significantly with age in laboratory-reared specimens, but there was no significant differentiation between urban and rural populations. However, field-caught urban specimens showed less preference to polarised light compared to rural populations, suggesting strong selective pressures are acting upon urban populations, but no adaptation has occurred. Flight-related traits

showed no significant differentiation among urban and rural populations of *I. elegans*. Lastly, biodiversity patterns did not differ among urban and rural areas, although aquatic vegetation and presence of fish were the main drivers of community composition.

These results show odonates can tolerate a wide range of urban stressors, notably *I. elegans*. However, PLP, fish, and absence of aquatic vegetation in urban ponds can have a negative impact on odonate biodiversity, which has important implications on conservation and management of urban areas. Urban ecosystems are complex, thus an integrative approach is necessary in order to understand in depth the impacts of urbanisation on biodiversity.

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Chapter 1: Dragonflies and damselflies (Odonata) in urban ecosystems: a review

The following paper, *Villalobos-Jiménez, G., Dunn, A.M. & Hassall, C., 2016. Dragonflies and damselflies (Odonata) in urban ecosystems: a review. Eur J Entomol, 113(1): 217–232*, is a modified version of this chapter.

I was responsible for the collection and analysis of the data with advice from co-authors, and was solely responsible for the literature review, interpretation of the results, and for writing the manuscript. All co-authors provided comments on draft manuscripts.

Abstract

The expansion of urban areas is one of the most significant anthropogenic impacts on the natural landscape. Due to their sensitivity to stressors in both aquatic and terrestrial habitats, dragonflies and damselflies (the Odonata) may provide insights into the effects of urbanisation on biodiversity. However, while knowledge about the impacts of urbanisation on odonates is growing, there has not been a comprehensive review of this body of literature until now. This is the first systematic literature review conducted to evaluate both the quantity and topics of research conducted on odonates in urban ecosystems. From this research, 79 peer-reviewed papers were identified, the vast majority (89.87%) of which related to studies of changing patterns of biodiversity in urban odonate communities. From the papers regarding biodiversity changes, 31 were performed in an urban-rural gradient and 21 of these reported lower diversity towards built up city cores. Twelve of the cases of biodiversity loss were directly related to the concentrations of pollutants in the water. Other studies found higher concentrations of pollutants in odonates from built-up catchments and suggested that odonates such as *Aeshna juncea* and *Platycnemis pennipes* may be candidate indicators for particular contaminants. I conclude by identifying current research needs, which include the need for more studies regarding behavioural ecology and life-history traits in response to urbanisation, and a need to investigate the mechanisms behind diversity trends beyond pollution.

Introduction

Urbanisation is one of the main drivers of ecosystem change. The expansion of urban areas is a main cause of many environmental stressors: (i) removal of native vegetation leading to degradation and fragmentation of the natural landscape, (ii) modification of hydrological systems through water extraction for human use, (iii) increase of local minimum temperature creating a “heat island” effect, and (iv) accumulation of pollutants to a point at which the environment cannot fully process and degrade them, causing eutrophication and affecting biogeochemical cycles (Grimm et al., 2008; McDonald, 2008). Moreover, the estimated percentage of the world population living in urban areas now exceeds 50% (Grimm et al., 2008) and almost 60% will be living in urban areas by the year 2030 (Güneralp and Seto, 2013; Seto et al., 2012). Given the range of impacts and rapid growth of urban development, it is essential that we understand in depth the implications for natural systems both in and around cities. Dragonflies and damselflies (the Odonata) have been suggested as barometers for environmental change due to their sensitivity to other anthropogenic stressors such as climate change (Hassall, 2015) and variation in habitat quality (Clark and Samways, 1996). However, the impacts of urbanisation on odonates remain poorly understood. In this review, I will investigate current research on the impacts of urbanisation using odonates as a model group. First, I will present a brief overview on the impacts of urbanisation on terrestrial and freshwater ecosystems, then I conduct a systematic literature review regarding odonates in urban environments and outline the plausible effects on odonates, followed by the use of odonates as bioindicators, the conservation

value of urban wetlands for odonates, a summary of evolutionary strategies for species to cope with urban stressors, and finally I conclude by identifying research needs.

The effects of urban stressors on terrestrial and freshwater ecosystems

The wide range of impacts associated with urbanisation indicates that it exerts a considerable effect on terrestrial biodiversity. Most studies show that species richness and evenness is reduced in highly urbanised regions, depending on the taxonomic group observed, degree of urbanisation, and spatial scale of analysis (McKinney, 2002; McKinney, 2008). For example, butterflies (Blair and Launer, 1997; Ruszczyk, 1987; Ruszczyk and De Araujo, 1992) and ground arthropods (McIntyre et al., 2001) show this tendency. The general pattern of biodiversity decrease in cities is probably due to the fact that over 80% of land in city cores is covered by buildings and pavements, with the remaining area used for lawns, trees, and shrubs (Blair and Launer, 1997), thus fragmenting the landscape and homogenising vegetation composition (Blair and Launer, 1997; Faeth et al., 2011; Faeth et al., 2012; McKinney, 2002). However, plant biodiversity peaks at intermediate levels of urbanisation, perhaps due to the high numbers of species associated with suburban gardens (McKinney, 2008).

Urban freshwaters have not been explored as much as terrestrial urban ecosystems, despite the high degree of vulnerability that freshwaters exhibit to the pressures of urbanisation (Dudgeon et al., 2006; Paul and Meyer, 2001). Urban streams, for example, are usually modified to carry out storm water into natural streams, washing away industrial and human wastes, as well as road runoff (Forman, 2014). Streams are

subjected to toxins, temperature change, siltation, organic pollutants, and the replacement of riparian vegetation and substrate for rocks or concrete and, consequently, insects, molluscs, crustaceans, and annelids tend to have decreased species richness and abundance (Forman, 2008; Forman, 2014; Paul and Meyer, 2001; Vaughan and Ormerod, 2012). The presence of organic pollution has been associated with increased abundance of chironomids and oligochaetes, making them the dominant members of urban stream communities (Campbell, 1978; Paul and Meyer, 2001; Seager and Abrahams, 1990).

Ponds are very frequent in parks and gardens for aesthetic purposes and to improve human well-being (Forman, 2014; Hassall, 2014), and are greatly influenced by a variety of factors such as the land use of the surroundings, the runoff to the pond, subsurface groundwater flow, and shoreline conditions (Forman, 2014). Parks and gardens are heavily managed and fertilisers are commonly used, and due to their limited capacity for the processing of pollutants and nutrients, ponds often suffer from eutrophication with an accompanying decline in biodiversity (Forman, 2014). However, the relative isolation of urban ponds generates a substantial degree of habitat heterogeneity. Each pond possesses its own physical, chemical, and hydrological features, facilitating the presence of a range of species of specialised habitat requirements, hence increasing the differentiation among these ecosystems and the landscape diversity (beta and gamma diversity, respectively) (De Meester et al., 2005). They also work as “stepping stones”, thus allowing landscape connectivity and potentially acting as metapopulations (De Meester et al., 2005; Hassall, 2014).

The biodiversity of odonates in urban areas is expected to be different from their rural counterparts, as is the case for other taxa. However, as already discussed, urbanisation is a complex process that encompasses a wide range of selective pressures, and each of them is expected to have a different impact on odonates according to the species and the life stages. Sensitive odonate species may be severely affected by stressors such as contaminants from sewage input, but generalist species are expected to tolerate these conditions, leading to decreased species richness. Moreover, generalist species would exploit the resources available due to decreased interspecific competition, resulting in high abundance of tolerant species. This variation in sensitivity to a range of urban stressors means that odonate communities have the potential to act as barometers of environmental change in urban areas, as has been demonstrated successfully in South Africa for habitat quality (Clark and Samways, 1996) and as has been suggested for climate change (Hassall, 2015). In this review I outline the stressors associated with urban environments that have the potential to affect odonates considerably across their life cycle.

Dragonflies and damselflies as a model system

Dragonflies and damselflies (the Odonata) are highly suitable model organisms for the study of urban ecosystems because (a) they are sensitive to different stressors, such as pollutants (Ferrerias-Romero et al., 2009) and temperature changes (Hassall and Thompson, 2008), therefore can be a powerful tool to assess the general conditions of the city environment; (b) they are aquatic as larvae and terrestrial as adults, hence can be used as bioindicators in both aquatic and terrestrial habitats (Oertli, 2008); (c) they

have an important role as predators, hence have a wide range of interactions with different organisms in both aquatic and terrestrial ecosystems (Knight et al., 2005); (d) they are ideal for studying movement through the landscape, as their adult stage can disperse due to their flying capacity and are very conspicuous (Conrad et al., 1999), and (e) their biodiversity, ecology and evolutionary biology is well-documented, providing a robust foundation for drawing general conclusions (Córdoba-Aguilar, 2008).

Literature review

I conducted a literature review of the prior work regarding urbanisation and odonates, in order to evaluate the potential of odonates as a model system for studying urbanisation.

During January-April 2014, I used standardised search terms with three online databases: Web of Science, Scopus and ScienceDirect. The words “urban” and “Odonata OR dragonfl* OR damselfl*” were searched in title, keywords and abstract (except in Web of Science, where the search was in Topic). Only peer-reviewed papers including odonates in an urban environment were selected, reviews were excluded.

According to the nature of the study, each paper was classified into one, two or three of the following categories: diversity (variables considered here were taxa richness, abundance, probability of occurrence for creating habitat suitability models, diversity indices such as Shannon-Wiener, etc.), toxicology (such as physicochemical features of the water bodies and heavy metal concentration), behavioural ecology (dispersal, trophic dynamics), and life-history traits (reproduction, life growth). I went on to examine the references from the papers found in the standardised search and also added those to the analysis where appropriate.

The search returned a total of 79 papers, most of which (65.82%) were published after 2004 (see Figure 1.1, and Table A.1 in the Appendix for a complete list of papers with categories). I was also interested in analysing geographical patterns in research regarding odonates in urban ecosystems and found most studies were conducted in United States and Brazil, though plenty were from Austria, South Africa, Germany, Japan, and others (see Figure 1.2).

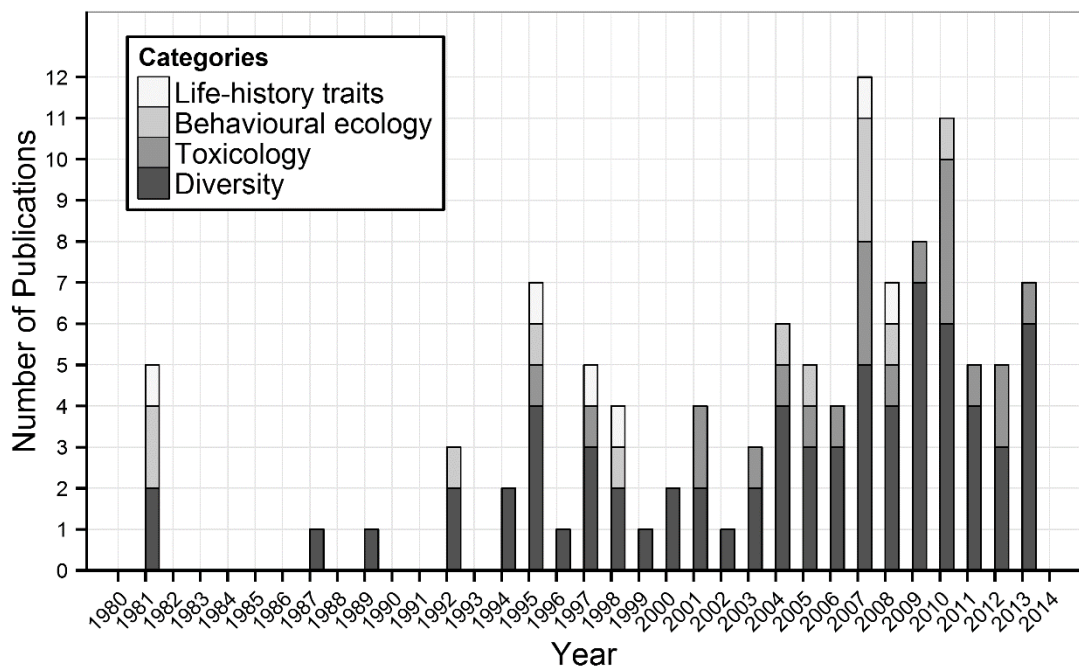


Figure 1.1. Urban odonate peer-reviewed publications found by year and category.

Of the 79 papers found, 71 (89.87%) investigated patterns in biodiversity, of which 31 were executed in an urban-rural gradient or compared diversity in streams before and after the water flow reached an urbanised area. Of the studies regarding biodiversity in an urban-rural gradient, 21 reported less diversity in cities, and 12 cases of diversity loss were related to pollutant concentration in the water (see Table 1.1). Below, I discuss the

general trend within these papers and give example studies to illustrate those trends; a comprehensive list of studies and summaries of findings can be found in Table A.1 in the Appendix.

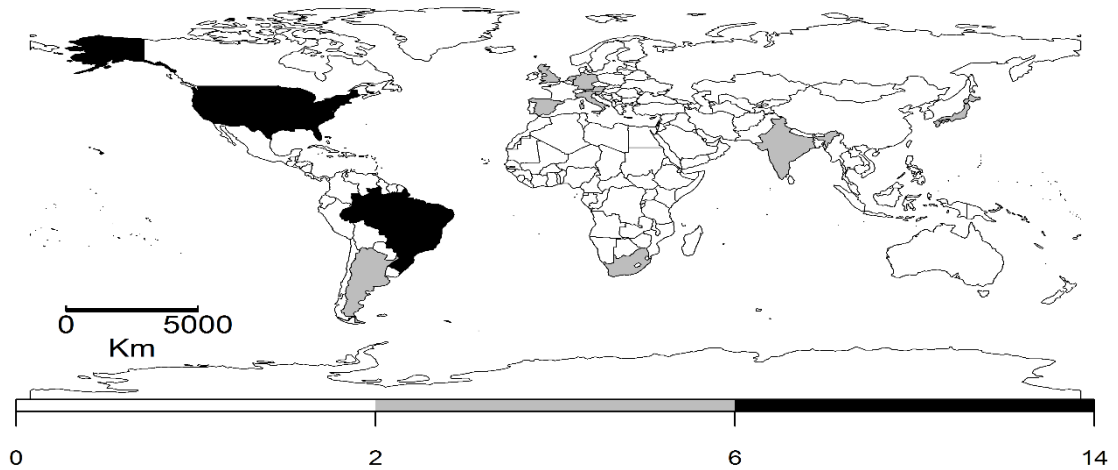


Figure 1.2. Map of urban odonate peer-reviewed publications found per country

Table 1.1. Urban odonate peer-reviewed papers found related to diversity

	No urban-rural gradient	Less diversity	More diversity	No change
Urban odonate diversity publications	38	21	3	7
Diversity related to increased pollutants	4	12	---	1

The effects of urban stressors on odonates

These results suggest that increasing urbanisation seems to affect odonate diversity negatively, on the whole, as has been shown in other groups (McKinney, 2008).

However, urbanisation is a multi-faceted problem and the studies reviewed herein offer some perspectives on which aspects of urbanisation are having the greatest impacts on

Odonata across their life cycle and how this may reflect the biodiversity loss in cities (see Figure 1.3). It is worth mentioning that the stressors listed may not only have a considerable impact in a given stage of their life cycle, but the effects can also be transferred to other stages via carry-over effects (e.g. maternal effects from adult to larva, or persistence of impacts between life history stages from larva to adult), except when a decoupling mechanism interferes (for a detailed review see Stoks & Córdoba-Aguilar, 2012).

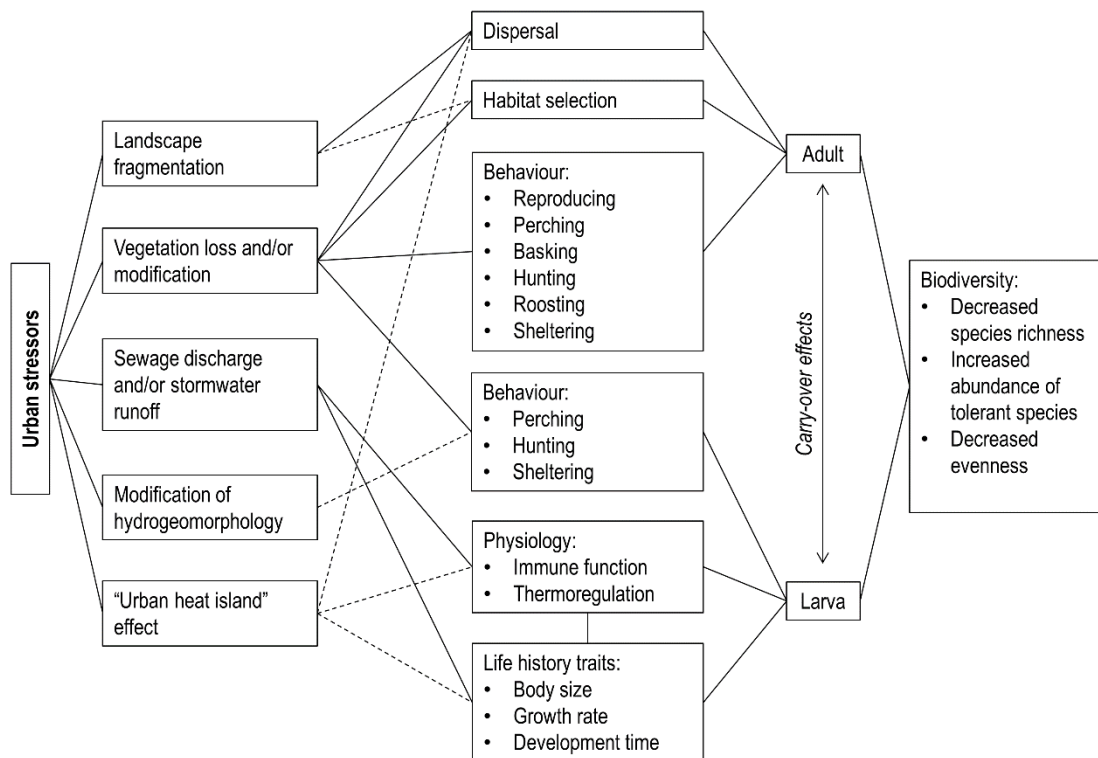


Figure 1.3. Summary of drivers of odonate biodiversity in cities due to heavy management. Dashed lines represent hypothetical effects, since no studies were found to investigate the association between the specified stressor and the corresponding trait(s) on odonates. Behavioural traits are separated according to their effects on either the larval or adult phase.

Fragmentation: Fragmented landscapes with little vegetation cover and few water bodies may not provide sufficient corridors to facilitate dispersal, thus limiting odonate connectivity within cities (Chovanec et al., 2000; Sato et al., 2008; Watts et al., 2004). Urban landscapes were found to function as barriers for *Paracercion calamorum*, *Ischnura senegalensis*, and *I. asiatica* in Japan when the genetic differentiation among populations was analysed (Sato et al., 2008), showing that the effect of fragmentation in urban areas is consistent within at least three zygopteran species. These results are also consistent between methods of dispersal analysis: Watts et al. (2004) provide evidence from genetic techniques and a mark-release-recapture study that urban areas cause a strong negative effect in the dispersal of *Coenagrion mercuriale* in UK. Although I did not find any studies using odonates linking habitat selection and urban landscapes, fragmentation may also affect habitat selection negatively by constraining access to optimal sites, as has been shown in a study using two model species representing territorial animals (van Langevelde, 2015).

Vegetation removal and/or modification: Increased vegetation cover and biodiversity of plants was associated with increased odonate richness and overall evenness in Austria (Chovanec et al., 2002), Germany (Goertzen and Suhling, 2013), France (Jeanmougin et al., 2014), and South Africa (Pryke and Samways, 2009; Samways and Steytler, 1996), among others. For example, Goertzen & Suhling (2013) studied odonate diversity patterns in ponds across an urban-rural gradient using a multivariate approach and found that vegetation was not only one of the major drivers of alpha diversity, but also trampling vegetation had a significant negative effect. Other studies have reported similar results, but suggested percentage cover of submerged macrophytes was the main

component of vegetation affecting odonate diversity (Jeanmougin et al., 2014). Additionally, indigenous plant species have also been highlighted as a key factor shaping odonate communities in urban wetlands, and leaving a strip of indigenous riparian vegetation of at least 20 m between the stream edge and commercial plantations seems to facilitate the presence of sensitive odonate species such as *Chlorolestes tessellatus* in South Africa (Samways and Steytler, 1996).

The strong management of vegetation in terrestrial ecosystems in cities has a considerable impact on the adult phase of odonates (Silva et al., 2010) because vegetation is one of the main cues used for habitat selection and it influences a vast range of behaviours such as basking, foraging, roosting, sheltering, among others (Buchwald, 1992). Removal or modification of aquatic vegetation from urban freshwater habitats also might have a considerable effect on the behaviour of odonates not only on the adult phase, but throughout their life cycle (Gee et al., 1997). Adults use aquatic vegetation as an oviposition substrate (Buchwald, 1992), often by inserting eggs into submerged plant stems (Corbet, 1999). Once the eggs hatch, the larvae use the submerged plant stems for perching, hiding from predators, and for sit-and-wait ambush hunting (Buchwald, 1992). During emergence, the larva climbs upwards out of the water along vertical plant stems and proceeds to full metamorphosis once it leaves the water. The composition of plant communities may also exclude some specialist species that rely on particular plants, such as *Aeshna viridis* that only oviposits on *Stratiotes aloides* (Dijkstra and Lewington, 2006). However, it is worth mentioning that sensitivity to aquatic vegetation loss may vary across odonates, since not all species require aquatic vegetation for oviposition.

Sewage discharge and stormwater runoff: Sewage is formed primarily of domestic, commercial, and industrial waste. Wastewater is collected through the sewage system and treated before releasing into freshwater. However, sewer overflows are not uncommon, and some countries lack these facilities or treat wastewater only partially (Rosa & Clasen, 2010) and in many occasions, treatment is not enough to remove all the contaminants (Paul and Meyer, 2001).

Several studies found in this literature search examined the effects of sewage input or “urban pollutants” in general rather than particular contaminants. In these cases, diversity was negatively related to sewage input (Henriques-de-Oliveira et al., 2007; Solimini et al., 1997), although most of the papers from the search were focused on aquatic macroinvertebrates and the overall group of odonates as bioindicators rather than particular species. Urban pollution was associated with increased abundance and dominance of Libellulidae and other taxa (see Table 1.2), but decreased abundance of Gomphidae (Ferrerias-Romero et al., 2009) and overall evenness (Henriques-de-Oliveira et al., 2007). However, it is worth mentioning that even though there are many tolerant species within Libellulidae and sensitive species in Gomphidae (Ferrerias-Romero et al., 2009), the sensitivity or tolerance of a stressor depends on the particular species rather than a larger taxon, therefore caution must be taken when considering libellulids or gomphids as bioindicators.

Table 1.2. Bioindicators of urbanisation.

Indicator taxon	Response to urbanisation	Urban stressor	Reference
<i>Aeshna</i> spp.	Tolerant	Urban land use	Brazner et al. (2007)
Gomphidae	Sensitive	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009); Malherbe et al. (2010)
<i>Ischnura graellsii</i>	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
<i>Anax parthenope</i>	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
<i>Aeshna mixta</i>	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
<i>Orthetrum cancellatum</i>	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
Libellulidae	Tolerant	Urban development (deforestation and water pollution)	Ferreras-Romero et al. (2009)
<i>Aeshna juncea</i>	Tolerant	Manganese, lead and nickel	Girgin et al. (2010)
<i>Platycnemis pennipes</i>	Tolerant	Cadmium, boron, iron and total hardness	Girgin et al. (2010)
<i>Erythrodiplax fusca</i>	Tolerant	Urban development (deforestation)	Monteiro et al. (2013)
<i>Argia</i> sp.	Tolerant	Urban development (deforestation)	Monteiro et al. (2013)
<i>Argia modesta</i>	Sensitive	Urban development (water pollution)	Silva et al. (2010)
<i>Ischnura elegans</i>	Tolerant	Urban development (water pollution)	Solimini et al. (1997)
<i>Erythromma lindenii</i>	Tolerant	Urban development (water pollution)	Solimini et al. (1997)

Wastewater contains a wide variety of contaminants ranging from metals, organic and inorganic fertilisers and pesticides to polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs) (Paul and Meyer, 2001), forming a cocktail of pollutants which may affect odonate larvae – and other aquatic macroinvertebrates – in a number of ways. First, high contents of organic matter and fertilisers cause eutrophication, leading to algal and bacterial blooms and decreasing levels of dissolved oxygen in water (Forman, 2008). Second, organic and inorganic contaminants from both sewage discharge and stormwater runoff may be toxic for some species. For example, pesticides have been shown to increase mortality in odonate larvae and in sublethal concentrations, it also increases fluctuating asymmetry (e.g. Chang et al., 2007). A study looking at the life history of *Coenagrion puella* under pesticide stress suggested that the sensitivity of life-history traits depends on the type of pesticide and the exposure time, being increased development time the only life-history trait which showed consistency across pesticide treatments in the long-term exposure experiment (atrazine, carbaryl and endosulfan in this case) (Campero et al., 2007). On the other hand, exposure of *Ischnura elegans* larvae to a pesticide (chlorpyrifos) decreased immune function significantly, and adult heat stress caused a stronger decrease in immune function, indicating that temperature and pesticide stress interact across metamorphosis (Janssens et al., 2014). Moreover, urban populations of *C. puella* larvae showed increased activity levels when exposed to chlorpyrifos at 20° and 24°C while showing decreased food intake under pesticide stress at 24°C, compared to rural populations which showed decreased activity and food intake in all treatments (Tüzün et al., 2015). These results suggest that urban larvae populations are locally adapted to higher contaminant levels (Tüzün et al., 2015). These studies are particularly useful when analysing the impacts of

urbanisation due to their multiple-stressor approach, which highlight the effect of interactions between urban stressors and contribute to a more integral understanding of urban ecosystems.

Certain contaminants such as PCBs and heavy metals may bioaccumulate in tissues. There are 209 different types of PCBs, and the mid-chlorinated congeners (e.g. PCB-153 and PCB-138) have been found in high concentrations among chironomids and dragonflies in an urban riparian ecosystem in Beijing (Yu et al., 2013). Similar results have been found with other organic persistent pollutants such as polybrominated diphenyl ethers (PBDEs) and hexachlorobenzene (HCB) in *I. elegans* larvae in several ponds across Flanders, Belgium (Van Praet et al., 2012). Heavy metals may come from both sewage input and road runoff, and they also tend to accumulate in the exoskeleton of odonate larvae (Meyer et al., 1986). Although lead and copper can cause deformities in other insects, e.g. *Chironomus mentum* (de Bisthoven et al., 1998), *Aeshna juncea* showed tolerance of high concentrations of manganese, and nickel, while *Platycnemis pennipes* showed a sensitivity to cadmium, boron, and iron (Girgin et al., 2010), providing evidence of their use as suitable candidates for biomonitoring programmes.

Odonates as bioindicators in urban environments

Aquatic biomonitoring programmes are aimed at evaluating water quality and identify water pollution in an early stage before it leads to decreased environmental health and ultimately affect human health and the security of public water supplies, which is particularly important in cities (Jones et al., 2010). Odonates have been used extensively

as a bioindicator group of habitat quality (Clark and Samways, 1996; Clausnitzer et al., 2009; Dolný et al., 2011; Foote and Rice Hornung, 2005; Sahlén and Ekestubbe, 2001; Subramanian et al., 2008) and are one of the taxa included in the Biological Monitoring Working Party (BMWP) score system (Biological Monitoring Working Party, 1978). The BMWP score system has been used as a biological classification system for river pollution surveys in UK since 1980 (Paisley et al., 2014). The revised BMWP system, which is now called the Whalley, Hawkes, Paisley & Trigg (WHPT) index (Wilkes et al., 2017), includes Calopterygidae, Platycnemididae, Coenagrionidae, Cordulegastridae, Aeshnidae and Libellulidae (see Paisley et al., 2014 for the scores of each group). However, some species from these groups seem to be tolerant to urban stressors, such as *Ischnura elegans*, *I. graellsii*, *Erythrodiplax fusca*, among others (see Table 1.2). The presence of tolerant taxa in this system, as well as the absence of sensitive taxa such as *Gomphus vulgatissimus* (Brooks and Levington, 2007), might result in a misleading WHPT score. For instance, if in a given freshwater habitat there are abundant odonates, but 50% of the abundance includes tolerant species such as *I. elegans*, the result would be a high WHPT score which might not indicate water quality appropriately. Conversely, if there were abundant *G. vulgatissimus*, the WHPT score would be low, although the water quality in fact might be high. Unfortunately, there was insufficient data to include Gomphidae in the current WHPT system (Paisley et al., 2014). Nevertheless, in order to reduce error using the current WHPT score system, this system should include sensitive species and reduce the value of tolerant taxa. It has also been suggested that water quality indices relying on Odonata might be influenced by shifting distributions under climate change (Hassall et al., 2010).

Ecological traps in cities

Several studies have demonstrated that ecological traps can arise for dragonflies within urban areas, reducing the fitness of urban populations (e.g. Horváth et al., 2007). The term “ecological trap” refers to situations in which unsuitable sites unable to sustain a population are preferred over the suitable sites or the unsuitable habitats mimic the cues that species use for selecting ideal habitats, leading species to choose unsuitable habitats over the optimal sites for roosting, feeding, and mostly reproducing (Donovan and Thompson, 2001; Robertson and Hutto, 2006; Schlaepfer et al., 2002). Ecological traps are often induced by anthropogenic modifications of the environment (Schlaepfer et al., 2002), hence urban locations could be used as model sites for studying ecological traps (Hale et al., 2015). Alongside anthropogenically-modified water bodies that might be sub-optimal for odonates (Hale et al., 2015), human activity also produces a range of surfaces that reflect polarised light to an equal or greater extent than water (Horváth et al., 1998). Since odonates (and other semi-aquatic insects) use polarised light as a cue for oviposition site selection, such surfaces represent important ecological traps. For example, it was found in Brazil that the reflectance of cars imitates the reflectance pattern of ponds, encouraging the presence of *Pantala flavescens* in parking areas and even causing them to oviposit on the car’s surfaces, representing an important energy loss (Van de Koken et al., 2007). This behaviour has not only been observed in response to cars (Blahó et al., 2014; Gunther, 2003; Watson, 1992; Wildermuth and Horváth, 2005), but also to black plastic foil (Wildermuth, 1998), crude oil ponds (Horváth et al.,

1998) and grave stones (Horváth et al., 2007). However, this behaviour may be a result of the greater availability of strongly-polarising artificial surfaces relative to natural habitats, so odonates would use these surfaces in proportion to their availability. There needs to be active selection for the highly polarising surfaces for these systems to work as true ecological traps in urban areas, independently of availability, although there is currently limited evidence in the literature regarding the relative selection of artificial, strongly-polarising surfaces over suitable habitats, which are naturally polarising surfaces. According to Kokko & Sutherland (2001), true ecological traps could produce an Allee effect in low population densities. In high densities where there is increased competition, most individuals would compete for the preferred but unsuitable habitats, whereas the losing rivals would settle in the less preferred, high-quality habitat. However, in low population densities, the lack of competition will allow most individuals to make poor decisions on choosing proper habitats, therefore decreasing population density even more and eventually leading to extinction (Kokko and Sutherland, 2001; Schlaepfer et al., 2002).

The conservation value of urban water bodies for odonates

Although most studies showed a decrease in biodiversity as a result of urbanisation, there is evidence suggesting that urbanisation *per se* is not necessarily negative, but rather the negative impacts on biodiversity arise from highly intensive management associated with urban environments. Urban sites with a variety of vegetation composition, along with a proper management to minimise water pollution, were found to host more diverse communities of dragonflies and damselflies than those with limited

vegetation diversity and increased water pollution (Colding et al., 2009; Goertzen and Suhling, 2013). For example, urban drainage systems in The Netherlands with low nutrient content and rich vegetation have been shown to have comparable macroinvertebrate diversity to rural drainage systems (Vermonden et al., 2009). In the Austrian Danube River floodplain system located within the city limits of Vienna, a water enhancement programme was implemented (which consisted of restructuring the embankments of an artificial island by creating shallow water areas, gravel banks, small permanent backwaters and temporary waters) and showed increased vegetation, odonate diversity and connectivity in the landscape in a long-term monitoring programme (e.g. Chovanec et al., 2000; Chovanec et al., 2002). A study conducted in South Africa compared odonate diversity (and other invertebrate taxa) in natural and recovering forests and fynbos to alien pine plantations and botanical gardens rich in indigenous plants, and surprisingly the botanical gardens presented the highest species richness and abundance, especially compared with alien pine plantations (Pryke and Samways, 2009), providing evidence that botanical gardens represent a major refuge for invertebrate species. Parks in South Africa have shown high odonate diversity, whereas alien plantation forests where *Eucalyptus* sp. was the most abundant had the lowest odonate richness (Samways and Steytler, 1996). From a social perspective, increased biodiversity of odonates in urban green areas such as botanical gardens and parks is also important because they help attract tourists and increase awareness of the role of wetlands (Lemelin, 2007).

Additionally, urban ecosystems offer a vast diversity of pond types, ranging from ornamental ponds to drainage systems, each of these being subjected to different

management plans (Hassall, 2014). This heterogeneity of pond types provides different hydrological and ecological conditions which may promote a higher beta and gamma diversity of odonates, not only generalist species (Goertzen and Suhling, 2013).

Likewise, ponds are abundant mostly in suburban areas in Central Europe (Willigalla and Fartmann, 2012), perhaps due to garden ponds. Garden ponds are also common in UK, between 2.5 and 3.5 million garden ponds are estimated in UK (Davies et al., 2009), providing abundant aquatic habitats which facilitate connectivity and promote metapopulations (Hassall, 2014).

In spite of generalist species being abundant in cities, there are some specialist species that can also find refuge in urban habitats. For example, the threatened damselfly *Coenagrion ornatum* has been reported to inhabit drainage systems (Harabiš and Dolný, 2015), and golf courses in Sweden have demonstrated to serve as a refuge for endangered species e.g. *Leucorrhinia pectoralis*, a dragonfly considered “near threatened” in the Appendix II of the Bern Convention (Colding et al., 2009).

An interesting case is presented by *Ischnura gemina*. This species is endemic to the San Francisco Bay area, USA, which is highly urbanised. Even though *I. gemina* has been able to survive despite the stressors in the region (Garrison and Hafernik, 1981a; Garrison and Hafernik, 1981b), populations are decreasing and now it is threatened by urban development, in spite of repatriation efforts (Hannon and Hafernik, 2007). This species is currently under protection, which is predicted to benefit the species under climate change scenarios as well (Sánchez-Guillén et al., 2014). This situation represents an important case study in urban invertebrate conservation not only for

conservation biologists, but also for the regional authorities and urban planners with whom conservationist must work, since *I. gemina* and other odonates, as previously discussed, are helpful indicators of habitat quality and can work as “umbrella species” (Bried et al., 2007; Clausnitzer et al., 2009). This is particularly important in cities because by meeting the conditions required for odonates to survive, other species’ requirements will be met as well (Bried et al., 2007), thus saving time and effort in developing biodiverse, sustainable cities. They also work as “flagship species” for wetlands due to their attractiveness (Lemelin, 2007), which may help attract visitors to urban green areas.

Adapting to urbanisation

As I have mentioned throughout this review, some odonate species may be more tolerant of urban stressors. In order to unravel the specific traits driving the success of species in urban ecosystems, some studies have examined the role of the life history of odonates in light of the stressors caused by urbanisation. For example, a study in Italy observed the life history patterns of *Erythromma lindenii* and *Ischnura elegans* along an urban tract of a river and suggested the key factors to allow these species to cope with organic pollution is a longer reproductive period, absence of diapause, and tolerance of low oxygen concentration (Solimini et al., 1997). Studies performed in Japan demonstrated that the life cycle of *Sympetrum striolatum imitoides* was synchronised with the use of swimming pools; this species laid eggs in autumn, the larvae hatched in mid-winter and most adults emerged before the pools were drained and cleaned (Matsura et al., 1995; Matsura et al., 1998). However, the mechanisms underlying the

life history of these species in both studies are uncertain, i.e. whether the species possessed pre-adaptations to urban habitats or exhibit plastic responses that allow them to persist despite urban stressors.

However, the Odonata represent one group within which common garden rearing experiments using multiple stressors have yielded considerable insights (Stoks et al., 2015). These studies allow the partitioning of genetic and environmental factors to investigate the relative contributions of plasticity and adaptation, and have suggested that local adaptation to temperature (Arambourou and Stoks, 2015; Dinh Van et al., 2014) and pesticide stress (Tüzün et al., 2015) is common in odonates. Hence, studying phenotypic variation in urban environments represents a great opportunity for researchers in ecology and evolution to observe the complex, underlying processes of how species adapt to new circumstances through the use of urban habitat patch networks as “natural experiments”.

Research needed

While general patterns of diversity are well described and some of the mechanisms underlying those patterns have been quantified, a number of important areas of research are under-represented in the current literature. Below, I outline some key of these key areas:

Trophic interactions: I found very few studies regarding trophic interactions of odonates in cities, in spite of being considered key predators in both aquatic and terrestrial

ecosystems (Knight et al., 2005). Some studies using turtles (Martins et al., 2010) and bats (Kalcounis-Rueppell et al., 2007; Srinivasulu and Srinivasulu, 2005) encountered odonates as prey, in both urban and non-urban habitats. However, there is little information regarding how their role as predators changes in urban ecosystems. Possible intraguild predation has been suggested, but not observed in detail (Agüero-Pelegín and Ferreras-Romero, 1994; Sacha, 2011). Other than that, it is commonly known that they feed on chironomids (Matsura et al., 1998). Thus, there is no comprehensive knowledge regarding the diet of dragonflies and damselflies in cities. Given the fact that aquatic macroinvertebrate communities (i.e. prey) differ in cities from their rural counterparts (Azrina et al., 2006), there might be a significant impact on the energy flow in both aquatic and terrestrial habitats from urban environments (Knight et al., 2005) and the potential role for control of disease vectors in densely populated areas (Saha et al., 2012). Moreover, given the fact that odonate larvae tend to bioaccumulate contaminants such as heavy metals and PCBs that come from human activities, odonate larvae can transfer the contaminants to other organisms via trophic interactions, either in aquatic or terrestrial ecosystems, that is, in absence of a decoupling mechanism preventing the transfer of contaminants from larvae to adults (Yu et al., 2013).

Behaviour: Research on behaviour in relation to urban odonate populations has focused on dispersal and the selection of oviposition sites, but a much wider suite of behavioural traits would be expected to vary across urban-rural gradients. Considering, for example, the different stressors from urban areas (reviewed above), it is common to find tolerant species in cities (i.e. urban adapters and exploiters; McKinney, 2002) such as *I. elegans* (Solimini et al., 1997). Urban adapters and exploiters among invertebrates would be

predicted to exhibit syndromes involving multiple behavioural responses such as increased boldness, that is, being willing to take more risks (Lowry et al., 2013) like those exhibited by vertebrates (e.g. song sparrows, Evans et al., 2010). Increased boldness has been associated with increased dispersal in invasive *Gambusia* species (Rehage and Sih, 2004), therefore bold adult odonates may also show increased dispersal in urban areas, where disturbance is frequent, although bolder individuals are also at higher risk of predation, representing a trade-off between dispersal and predation risk. However, human disturbance in freshwater habitats is much less frequent compared to terrestrial habitats, therefore boldness is not expected to differ among urban and rural odonates in the larval phase. Only one study to my knowledge has investigated the behavioural response of odonates to urban stressors, and found that exploration behaviour, activity, and food intake of *C. puella* larvae were affected by pesticide stress except for boldness, although urban populations in general showed increased activity rate compared to rural populations (Tüzün et al., 2015). Therefore, there is a current lack of studies regarding behavioural syndromes in odonates and other invertebrates in response to other urban stressors along urban-rural gradients and the ecological and evolutionary consequences of those syndromes. Further studies regarding odonate behavioural ecology could also provide important insights into how odonates and other animals interact with urban ecosystems and test for a generalisation of urban evolutionary pressures across taxa.

Urban thermal ecology: Furthermore, we must consider that temperature increases in urban environments, creating a regional climate change effect called “Urban Heat Island” (UHI, Grimm et al., 2008). This temperature increase is most noticeable during

the night (Karl et al., 1988), and operates both in terrestrial areas where pavements and rooftops absorb and radiate heat to increase the ambient air temperature, and in aquatic systems where heated runoff that passes over hot concrete and asphalt enters water bodies (Jones et al., 2012). Temperature is a major driver of odonate phenology (Hassall et al., 2007), polymorph frequency (Gosden et al., 2011), and body size (Hassall, 2013; Hassall et al., 2014). Additionally, temperature has a great impact on many physiological processes, such as metabolism, respiration, muscular activity, immunology, development, reproduction, and – naturally – thermoregulation (i.e. pigmentation, basking, wing-whirring) (Hassall and Thompson, 2008; Neven, 2000). Therefore, there may be phenological, morphological and physiological shifts in odonates caused by the urban heat island effect, as well as interactions between these shifts. However, the effect of the UHI might not necessarily be negative. Most odonates are likely to tolerate such warm conditions due to their tropical evolutionary origin (Pritchard and Leggott, 1987), although thermal stress can be lethal if the temperatures exceed upper tolerance thresholds. In fact, the UHI may facilitate dispersal of odonates, as has been found in scale insects (Meineke et al., 2013) and mosquitoes (Araujo et al., 2015). It has been suggested that cities in temperate regions may benefit from the increased temperature, particularly during winter, although the UHI can also increase thermal and drought stress in tropical, subtropical and desert cities (Shochat et al., 2006). The UHI also has a great impact on freshwater habitats, because during storms in urban areas, rainwater makes contact with paved surfaces that can reach extremely high temperatures, which causes an abrupt temperature increase in freshwater habitats and, subsequently, a high mortality rate of sensitive organisms to thermal stress (Somers et al., 2013). However, there is no research regarding these topics in odonates.

Modified hydrogeomorphology of freshwaters: Rivers and ponds are frequently subjected to human alterations mostly by increasing imperviousness, which increases temperature, decreases infiltration of water and increases stormwater runoff drastically (for a detailed review see Paul & Meyer, 2001). Sediment is also coarser in urban water bodies as a result of alteration of sediment supply and velocities, and also tends to accumulate high metal contents such as lead, zinc, and cadmium (Paul and Meyer, 2001). The lack of natural substrate may interfere with microhabitat use, habitat selection, and a variety of behaviours (e.g. sheltering, hunting). However, to my knowledge no studies have yet been carried out on the importance of flow regimes and sediment change to odonates within urban rivers and ponds.

Urban genomics: As mentioned previously, the intraspecific variation throughout an urban gradient may be driven via phenotypic plasticity or genetic adaptation. Other than studies looking at dispersal (Sato et al., 2008; Watts et al., 2004), there are no investigations to my knowledge that link genetics to the phenotypic variation in urban odonate populations. Thus, the underlying mechanisms that drive phenotypic variation of odonates in cities are not well-documented. While one study has looked at population differentiation across an urban landscape (Sato et al., 2008), there could be far greater insights through a combination of gene-flow models, cost surfaces, and corridor analyses to use odonate movement as an indicator of large-scale habitat connectivity in cities. Modern advances in transcriptomics and metabolomics also offer opportunities to explore the stressors experienced by urban populations through the differential expression of genes (e.g. Chapman et al., 2009).

Noise pollution: noise is another form of anthropogenic disturbance which is now ubiquitous because of the expansion of urban land use (Morley et al., 2014).

Anthropogenic noise has been shown to have deleterious impacts on a wide range of taxa from terrestrial, marine, and to some extent, freshwater ecosystems (see Kight and Swaddle, 2011). However, current research has focused almost exclusively on vertebrates, despite the crucial role of invertebrates in trophic interactions and ecosystem functioning (Morley et al., 2014). Noise can have physiological, anatomical, developmental, and behavioural impacts in organisms (Kunc et al., 2016), and is expected to have similar outcomes in odonates. In addition, odonate larvae locate their prey using tarsal hairs and antennae which detect the low-frequency vibration cues produced by the prey (Vasserot, 1957). Hence, noise disturbance may interfere with the larval mechanism for prey detection, and can have knock-on effects on trophic interactions. However, no research has been conducted on this topic so far, thus further studies are encouraged to discover the effect of environmental noise on odonates.

To summarise, this review illustrates that odonate diversity is generally lower in built-up city cores than in surrounding areas. However, with suitable management and design, urban areas could increase diversity and landscape connectivity, which has various promising implications for ecology, evolutionary biology, conservation biology and urban planning. While patterns in diversity are well-documented, there has been a lack of research into the behavioural, genetic, and life history processes that might act as mechanisms to drive those diversity patterns. The literature reviewed here provides a strong case for the use of odonates as a model taxon in both the lab and field for the

study of a wide range of phenomena related to urbanisation. In order to achieve an integrated understanding of urban ecosystems, I encourage further research, specifically using odonates due to their versatility as bioindicators in both aquatic and terrestrial habitats.

Thesis outline

In this thesis, my aim is to evaluate in more depth the impacts of urbanisation on the ecology of odonates and their response to urban stressors. In particular, the effects of different forms of pollution, specifically thermal, acoustic, and polarised light pollution (PLP), as well as the impacts of landscape fragmentation due to the expansion of urban land use, and the combined effect of urban stressors on biodiversity patterns across an urban gradient.

In Chapter 2, I will investigate the phenological response of odonates to the urban heat island (UHI).

In Chapter 3, I will study the impact of environmental noise on the predation rates of the larvae of *Ischnura elegans*.

In Chapter 4, I will analyse the susceptibility of urban and rural populations of *I. elegans* to polarotactic ecological traps and the ontogenetic variation in the preference to horizontally polarised light.

In Chapter 5, I will study the morphometric variation in flight-related traits in urban and rural populations of *I. elegans* in response to urbanisation.

In Chapter 6, I will explore the odonate biodiversity patterns across an urban-rural gradient using a multivariate approach to investigate the effect of modification of riparian vegetation and other urban stressors on aquatic macroinvertebrate biodiversity and community composition.

In Chapter 7, I will discuss my findings from Chapters 2-6 in the context of wider literature to identify the response of odonates to these urban stressors and the implications of these results for the conservation of biodiversity and the management of urban green/blue areas. I will also conclude by highlighting research needs.

Chapter 2: Effects of the urban heat island on the phenology of Odonata in London, UK

The following paper, *Villalobos-Jiménez, G. & Hassall, C., 2017. Effects of the urban heat island on the phenology of Odonata in London, UK. International Journal of Biometeorology, 61(7): 1337–1346*, is a modified version of this chapter.

I was responsible for the data analysis, interpretation of results, and for writing and structuring the manuscript. Data was provided by the British Dragonfly Society (BDS). The co-author provided advice on the data analysis, and also provided comments on draft manuscripts.

Abstract

Urbanisation is one of the major drivers of ecosystem change, and includes increased temperatures in cities leading to an urban heat island (UHI). This study quantified the phenological response of odonates across London, UK, from 1990 to 2012 using a database of 1,031,277 historical sightings. The ordinal flight dates of each species were used to calculate the leading edge, middle, and trailing edge of the flight period (P5, P50, and P95, respectively). The results suggest that the phenology of odonates is affected by the UHI only at a community level: no significant changes in the P5 or P50 of the flight period were found, although the P95 shows a mean advance of 4.13 days compared to rural areas, thus suggesting a contraction of the flight period in urban areas. However, only one individual species (*Sympetrum striolatum*) exhibited an advance in the P95 of the flight period in urban areas compared to rural areas. On the other hand, climate change (minimum temperature) had a much stronger impact on the phenology of odonates at the community level with a significant advance of 6.9 days·°C⁻¹ in the P5 of the flight period, 3.1 days·°C⁻¹ in the P50, and 3.3 days·°C⁻¹ in the P95 flight date. Similarly, a significant advance in P5 was found in 7 of the 15 species tested in response to minimum temperature and 2 species showed a significant advance in P50 in response to minimum temperature, but no species showed a shift in the P95 flight date due to minimum temperature. As shown in previous studies, life history influences the phenological response of odonates, with spring species and those species lacking an egg diapause being the most responsive to increased temperatures, although summer species and species with obligate egg diapause also respond to the UHI by advancing the P95 by 3.8 days and 4.5 days respectively compared to rural areas, thus contracting the flight

period. The present study shows that the UHI has negligible impacts on emergence patterns of odonates compared to climate change, which may result from the capacity of aquatic habitats to buffer the microclimatic conditions of the surrounding terrestrial habitats. I conclude by highlighting the importance of climate change on freshwater habitats over the impacts of the UHI.

Introduction

With over 50% of people now living in cities (Grimm et al., 2008) and the impacts extending beyond the metropolitan borders (Faeth et al., 2011), studying the effects of urbanisation has become crucial in order to understand urban ecosystems and mitigate the negative impacts of cities. The many impacts of urbanisation include a significant increase in temperature in urbanised areas compared to the rural surroundings, referred to as the “urban heat island” (UHI) effect. This effect is mainly caused by the increased areas of dark, impervious surfaces in cities, as well as the low abundance of vegetation (Jochner and Menzel, 2015). The increase in temperature ranges on average from 0.5 to 3.0 °C depending on weather conditions (Jochner and Menzel, 2015), although the strength of the UHI effect is also positively correlated with city size (Oke, 1973). The effect of the UHI is greater during the night (Karl et al., 1988) and even more so in winter (Parker, 2004). The UHI effect also increases water temperature by transferring heat from rooftops and asphalt roads to stormwater runoff, leading to increased thermal pollution once it enters water bodies (Jones et al., 2012).

Such a substantial change in local climate is likely to have knock-on effects for biological processes. One of the most common indicators of climate variation is the timing of biological events, known as “phenology” (Menzel et al., 2006; Walther et al., 2002), and this phenomenon has been acknowledged as an indicator of changing climate by the UK Government (Cannell et al., 1999). Over 80% of terrestrial, marine and freshwater species in UK have advanced their phenology due to climate change (Thackeray et al., 2010), while at a global scale almost 60% of the species studied (including plants, birds, butterflies and amphibians) showed significant changes in their phenology over the past 30 to 150 years (Parmesan and Yohe, 2003), which suggest that phenological responses to climate change are highly coherent at a global scale. Likewise, phenology is also influenced by the UHI effect. It has been shown that the UHI advances the flowering and leaf unfolding of plants (e.g. Jochner et al. 2013) and the reproductive phenology of birds (Deviche and Davies, 2014) and amphibians (Cook et al., 2006). However, currently there is a lack of studies regarding the impact of the UHI effect on aquatic organisms.

Dragonflies and damselflies (Odonata) represent an aquatic insect group which has been proposed as a candidate barometer of climate change (Hassall, 2015). British odonate species have advanced their flight season by 1.5 days each decade between 1960 and 2004 (Hassall et al., 2007). In the Netherlands, odonates have also advanced their flight seasons towards the spring (Dingemanse and Kalkman, 2008). The phenological response of odonates to increasing temperatures has also been studied in the laboratory: larvae reared at 5°C above ambient temperature had emerged approximately 3 weeks before the larvae reared at ambient temperature (McCauley et al., 2015). Predictive

models also suggest the emergence of *Gomphus vulgatissimus* is likely to advance by 6-7 days per 1°C increase (Richter et al., 2008), especially at higher latitudes where increased development speed is expected to occur due to climate change (Braune et al., 2008). The impact of climate change on the phenology of odonates is explained by the fact that their life history is greatly influenced by temperature (Hassall and Thompson, 2008). First, temperature dictates the success and duration of the embryonic development (Pilon and Masseur, 1984) and egg diapause, a period of developmental stasis (Sawchyn and Church, 1973). Second, increased temperatures tend to accelerate the growth rate of larvae (Pritchard et al., 2000) and also play a key role in ecdysis (Lutz, 1974). In the adult phase, warm temperatures also increase reproductive success (Banks and Thompson, 1987).

This study examines the phenology of odonates in the context of the UHI in the city of London, UK. I hypothesise that, as is the case with temporal trends in climate, higher temperatures caused by the UHI will lead to an advance in the phenology of odonates in urban areas relative to the surrounding non-urban areas. This phenological advance would be reflected in earlier observations of adult odonates in the city compared to rural areas.

Methods

The urban area of London and the surrounding rural areas were extracted from the Ordnance Survey (OS) Meridian 2 data (Ordnance Survey, 2013). London was chosen

as a study site for a number of reasons: (i) the size of the city means that it should have a high degree of urban warming, (ii) recording of odonates is greatest in the south of the UK and so there should be a large number of records, and (iii) there is a moderately-rich odonate fauna present in the south of England which allows straightforward identification. The “developed land use areas” layer (DLUA) was used from the OS Meridian 2 data to define the extent of the urban area. A buffer of 40 km was created around the city polygon and the sample area was defined as a 5km x 5km grid (540 grid cells in total), since climate data was also available at this resolution. Grid squares were defined as urban depending on whether over 50% of the grid cover was within the DLUA region (Figure 2.1). Once the urban and rural areas were defined, the annual mean minimum temperatures for each grid square were calculated from the UKCP09 gridded data sets (UK Climate Projections, 2009) (Figure 2.2). Air temperatures are not only influential during the adult phase of odonates, but also tend to be correlated to surface water temperatures (Livingstone and Lotter, 1998; McCombie, 1959), which influence the development of the larvae, therefore is a suitable measure for predicting the phenology of odonates. Moreover, air temperatures have already been used as a surrogate for studying phenological shifts in odonates (e.g. Hassall et al. 2007). In this study, minimum temperature was selected as a quantitative measurement of the UHI effect because (i) the increase in temperature in cities is greater at night when the temperatures are cooler (Karl et al., 1988), (ii) atmospheric and surface temperatures in cities show similar patterns during the night (U.S. Environmental Protection Agency, 2008); (iii) night temperatures are not influenced by solar radiation, and (iv) the development of insects is more likely to be hindered by lower temperatures which may fall below critical thermal thresholds. The urban grids sampled were significantly

warmer than the rural grids by 0.8°C ($t = -47.01$, $df = 3733.764$, $P < 0.001$). From this step onwards, the analysis was performed in R 3.0.2 (R Core Team, 2013).

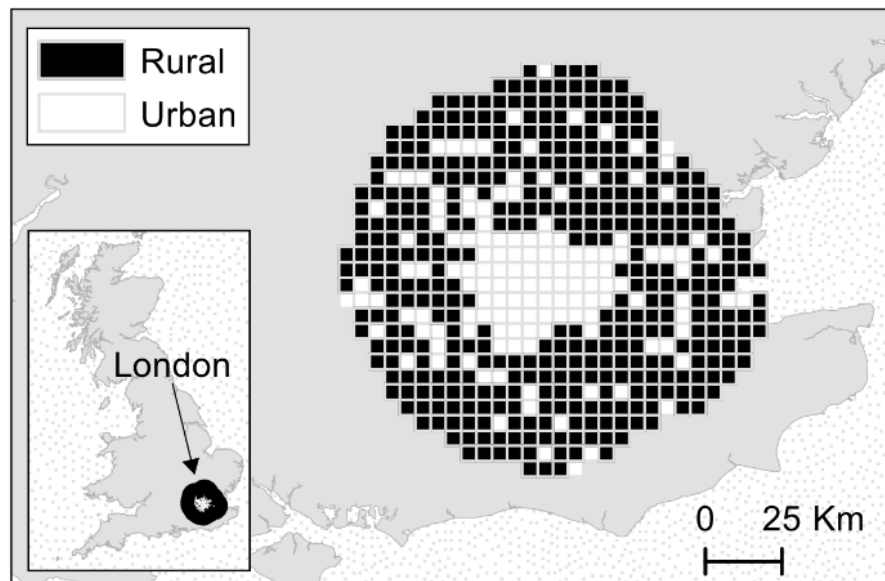


Figure 2.1. Location of urban (*white*) and rural (*black*) grid squares sampled for the phenological analysis in London, UK.

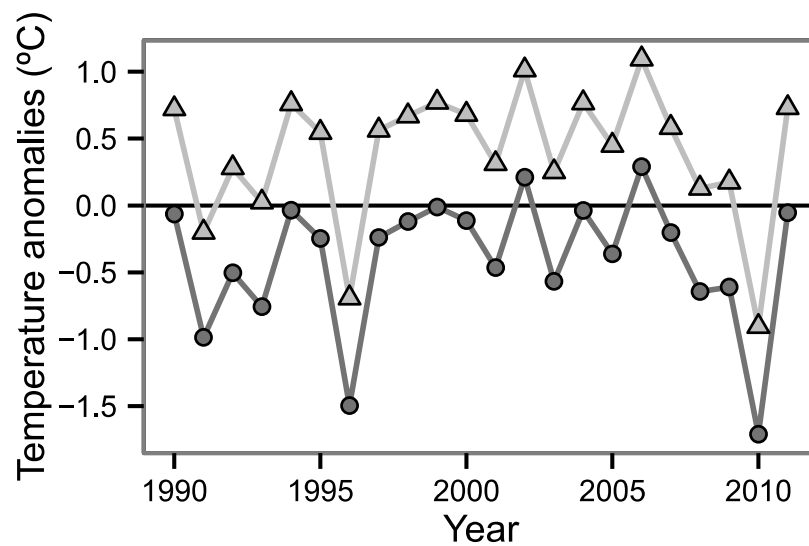


Figure 2.2. Anomalies in minimum temperature in urban (*triangle*) and rural (*circle*) areas sampled. Anomalies were calculated from the mean minimum temperature from the sampled areas from 1990 to 2012.

To analyse phenological shifts, the British Dragonfly Society (BDS) database was used, which contains 1,031,277 records of sightings of odonates (date accessed: 20/01/2015). Species considered migratory or not established in the UK according to the BDS species list (<http://www.british-dragonflies.org.uk>) were excluded *a priori*. Furthermore, only adult records within the urban and rural grid squares with an exact flight date from 1990 to 2012 were selected. This period of time was chosen to minimise temporal variation in urban development and in temperature.

Ordinal dates from records for each species were collated for each year from rural and urban sites. Three percentiles (P5, P50, and P95, corresponding to the leading edge, middle, and trailing edge of the flight period, respectively) were calculated from the distributions of these ordinal dates. However, only species with over 30 records in each type of land use per year in a period of at least 10 years were used to ensure the percentiles were representative of the true flight-period trends. This led to the selection of 96,366 records from the following species: *Aeshna cyanea*, *Aeshna grandis*, *Aeshna mixta*, *Anax imperator*, *Calopteryx splendens*, *Coenagrion puella*, *Enallagma cyathigerum*, *Erythromma najas*, *Ischnura elegans*, *Libellula quadrimaculata*, *Orthetrum cancellatum*, *Pyrrosoma nymphula*, and *Sympetrum striolatum* (Table 2.1).

The BDS database represents a valuable collection of observations of odonates from volunteers throughout UK. However, recording is executed without a standardised sampling method, resulting in uneven recorder effort, which may bring some complications for any analysis (Hassall and Thompson, 2010). In the present study, the

data showed more records from rural areas. Given that the amount of records was highly unbalanced between urban and rural areas ($N_{urban}= 22,047$; $N_{rural}= 74,319$) and the data was heteroskedastic, a feasible generalised least squares (FGLS) model was used (Gregoire, 1987) to test whether the flight season of each species was more advanced in the city compared to rural areas. Unlike the common GLS, FGLS calculates the structure of heteroskedasticity from OLS instead of assuming the structure of heteroskedasticity, which was necessary given that the heteroskedasticity in this dataset may have been due to minimum temperature, land use, or a combination of these two factors. Each of the percentiles by species was used as the response variable, whereas land use (urban vs rural), year and minimum temperature were used as the predictor variables. Ideally, urban cover would be included as a continuous variable, although the urban land cover data is not available per year and is expected to increase with time. Treating land use as a categorical variable may be less precise, but is also less susceptible to variation in time due to urban development. On the other hand, minimum temperature and year are expected to be collinear variables as a result of climate change. Therefore, to test for multicollinearity, variance inflation factors (VIF) were used. All P-values were adjusted using the false discovery rate (FDR) correction to account for the number of tests executed (1 test for each of the 3 percentiles across 13 species gives a total of 39 tests).

To assess the impact of the UHI on community-level phenology shifts (i.e. pooling all Odonata), the coefficients from the FGLS models (year, temperature and urban land use) were tested using a one-sample, two-tailed t -test (Hassall et al., 2007). A significant difference from zero in the mean change in flight dates would imply a

phenological shift across all the species tested. All 9 *P*-values obtained from the community-level tests were also adjusted using the FDR correction. In order to take into account the inherent correlation of traits among closely related species, a phylogenetic approach is necessary. However, phylogenetic comparative methods require a reliable phylogeny (Felsenstein, 1985; O'Meara, 2012) and, despite the great efforts to describe the phylogeny of European odonates, such phylogeny has not been fully resolved (Dijkstra and Kalkman, 2012). In such conditions, ideally the evolutionary correlation of traits would be partially controlled using an ANOVA with type I (sequential) sum of squares (Hof et al., 2006). However, the sub-branching of life history traits in the phylogenetic groups considered in this study lead to such a high collinearity that the effects of phylogeny and life history were indiscernible between each other. Therefore, this study is focused exclusively on life history traits and I cannot rule out an effect of phylogenetic relatedness *per se*. Similar to the community-level phenological analysis in the present study, the coefficients from the FGLS were tested against their life-history traits (Hassall et al., 2007) using a one sample, two-tailed *t*-test and also adjusting the *P*-values using the FDR correction to account for multiple testing. Such traits include the presence/absence of egg diapause (although facultative egg diapause was excluded considering it was represented by only one species, *S. striolatum*), as well as the classification of spring/summer species. The term “spring species”, coined by Corbet (1954), refers to odonates which have a larval diapause in the last instar of their life history and emerge during the spring in a synchronous manner; whereas “summer species” emerge asynchronously during the summer and, if a larval diapause is present, occurs during any other instar. These life-history traits were chosen since they influence

the phenology directly and are likely to respond to the consequent temperature changes of the UHI.

Using adult records instead of emergence patterns offers various advantages for studying phenology, most importantly the ability to evaluate changes throughout the flight period rather than only the leading edge of the flight period. However, adult odonates tend to disperse and therefore it is likely that an individual recorded in a site may not have developed and emerged there. Nevertheless, most species do not disperse more than 1 Km from their emergence site (Angelibert and Giani, 2003; Bennett and Mill, 1995; Conrad et al., 1999; Stettmer, 1996; Ward and Mill, 2007) and though anisopterans are commonly known to have long-distance dispersal, particularly in the case of aeshnids, unfortunately there is insufficient data to estimate the maximum distance dispersal in this group. Therefore the phenology analysis at a community level was repeated but excluding species that are more likely to disperse long distances – the Anisoptera – to test the validity of the study. Accounting for life history in this case was not possible due to the fact that all zygopterans in this study have no diapause and only 3 spring species and 3 summer species were left to compare these traits.

Results

Regarding the community-level shifts in response to urbanisation, a small but statistically significant advance of the P95 flight date of 4.1 days ($t = -5.066$, $df = 12$, $P = 0.002$) was found after using the FDR correction, and no significant change was found

in P5 or P50 (P5: mean = 2.4 days, $t = 2.190$, $df = 12$, $P = 0.063$; P50: mean = -0.3 days, $t = -0.429$, $df = 12$, $P = 0.675$), representing a contraction of the flight period of odonates in cities (**¡Error! No se encuentra el origen de la referencia.**). However, in response to changing minimum temperature, a mean advance was observed in all flight dates at a community level, even after the FDR correction (P5: mean = -6.9 days·°C⁻¹, $t = -4.748$, $df = 12$, $P = 0.002$; P50: mean = -3.1 days·°C⁻¹, $t = -2.855$, $df = 12$, $P = 0.026$; P95: mean = -3.3 days·°C⁻¹, $t = -2.988$, $df = 12$, $P = 0.025$; **¡Error! No se encuentra el origen de la referencia.**). Regarding the phenological shifts by year, changes in the P5 and P50 flight dates at a community level were significant after using the FDR correction (P5: mean = -0.3 days·year⁻¹, $t = -4.461$, $df = 12$, $P = 0.002$; P50: mean = -0.4 days·year⁻¹, $t = -2.694$, $df = 12$, $P = 0.029$; P95: mean = 0.1 days·year⁻¹, $t = 0.559$, $df = 12$, $P = 0.660$). These results suggest that climate change is advancing the flight period, while the UHI is contracting the flight period.

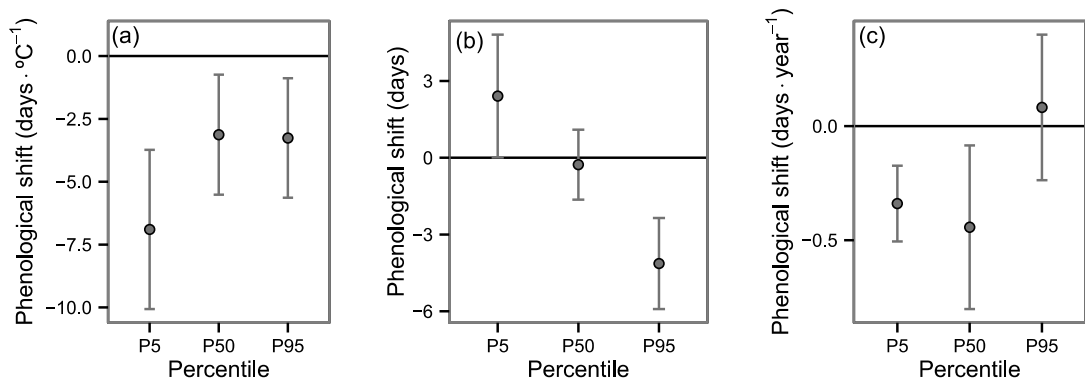


Figure 2.3. Community-level shifts in flight dates (*P5*, *P50*, *P95*) in relation to (a) minimum temperature, (b) urban land use compared to the rural surroundings and (c) year. Error bars represent 95% confidence intervals.

Table 2.1. Estimates of the coefficients of year, minimum temperature and urban land use on the flight dates of each species analysed. Each coefficient value includes their corresponding *P*-values adjusted using the FDR correction. Significant results are highlighted in bold.

Species	Predictor	P5		P50		P95	
		Coefficient	<i>P</i>	Coefficient	<i>P</i>	Coefficient	<i>P</i>
<i>Aeshna cyanea</i>	Year	-0.371	0.687	0.522	0.246	0.810	0.314
	Min. temp.	0.816	0.962	-3.457	0.687	0.895	0.962
	Land use	8.484	0.435	0.702	0.957	-4.629	0.701
<i>Aeshna grandis</i>	Year	-0.476	0.130	-0.186	0.378	0.113	0.701
	Min. temp.	-1.701	0.715	-3.955	0.131	-2.620	0.516
	Land use	5.595	0.198	4.000	0.142	-3.933	0.272
<i>Aeshna mixta</i>	Year	-0.581	0.077	0.307	0.169	0.758	0.035
	Min. temp.	2.567	0.602	-1.899	0.542	-0.959	0.886
	Land use	0.423	0.962	0.288	0.962	-4.956	0.313
<i>Anax imperator</i>	Year	-0.431	0.173	-0.764	0.025	-0.291	0.479
	Min. temp.	-5.966	0.108	1.830	0.701	2.877	0.583
	Land use	2.966	0.542	0.136	0.978	-1.766	0.745
<i>Calopteryx splendens</i>	Year	-0.637	0.043	-0.868	0.080	0.001	0.996
	Min. temp.	-8.014	0.040	1.030	0.923	-2.792	0.674
	Land use	2.381	0.636	-1.288	0.886	0.140	0.978
<i>Coenagrion puella</i>	Year	-0.011	0.968	-0.129	0.701	-0.047	0.957
	Min. temp.	-11.352	<0.001	-9.030	0.019	-4.408	0.397
	Land use	-2.986	0.311	-2.412	0.602	-4.325	0.395
<i>Enallagma cyathigerum</i>	Year	-0.688	0.015	-1.065	0.001	0.015	0.968
	Min. temp.	-8.930	0.015	-1.740	0.712	-6.612	0.080
	Land use	1.743	0.701	0.342	0.962	-1.966	0.687
<i>Erythromma najas</i>	Year	-0.352	0.184	-1.007	0.041	0.070	0.886
	Min. temp.	-11.687	0.001	-2.606	0.715	-4.730	0.246
	Land use	0.682	0.886	-1.410	0.886	-7.206	0.064
<i>Ischnura elegans</i>	Year	0.187	0.602	-0.409	0.272	0.109	0.604
	Min. temp.	-8.698	0.013	-2.026	0.701	-3.771	0.061
	Land use	-4.023	0.280	-3.689	0.498	-3.170	0.146
<i>Libellula quadrimaculata</i>	Year	-0.505	0.535	-1.032	0.204	-0.893	0.314
	Min. temp.	-13.072	0.064	-9.454	0.254	-11.227	0.225
	Land use	9.328	0.197	1.640	0.886	-2.524	0.857
<i>Orthetrum cancellatum</i>	Year	-0.198	0.625	-0.863	0.040	-0.580	0.064
	Min. temp.	-9.018	0.040	-1.389	0.881	-4.939	0.246
	Land use	5.228	0.246	2.878	0.687	-1.077	0.881
<i>Pyrrhosoma nymphula</i>	Year	-0.420	0.121	-0.792	0.013	0.026	0.962
	Min. temp.	-12.678	<0.001	-9.474	0.014	-6.552	0.157
	Land use	1.825	0.674	-1.777	0.701	-8.272	0.064
<i>Sympetrum striolatum</i>	Year	0.070	0.886	0.521	0.008	0.973	0.014
	Min. temp.	-1.926	0.692	1.511	0.573	2.456	0.674
	Land use	-0.321	0.962	-2.911	0.246	-10.032	0.043

After excluding the Anisoptera, the results confirm the community-level advance of the

P5 and P95 flight dates in response to minimum temperature (P5: mean = -10.2 days·°C

¹, $t = -13.087$, $df = 5$, $P < 0.001$; P50: mean = $-4.0 \text{ days} \cdot ^\circ\text{C}^{-1}$, $t = -2.275$, $df = 5$, $P = 0.094$; P95: mean = $-4.8 \text{ days} \cdot ^\circ\text{C}^{-1}$, $t = -7.736$, $df = 5$, $P = 0.003$; see Figure A.1 in the Appendix). In response to the UHI, the advance in the P95 flight date was confirmed (P5: mean = -0.1 days , $t = -0.056$, $df = 5$, $P = 0.957$; P50: mean = -1.7 days , $t = -3.132$, $df = 5$, $P = 0.047$; P95: mean = -4.1 days , $t = -3.186$, $df = 5$, $P = 0.047$; see Figure A.1 in the Appendix), which suggests a contraction of the flight period in the city. Regarding phenological shifts by year, only the advance in P50 flight date was confirmed (P5: mean = $-0.3 \text{ days} \cdot \text{year}^{-1}$, $t = -2.265$, $df = 5$, $P = 0.094$; P50: mean = $-0.7 \text{ days} \cdot \text{year}^{-1}$, $t = -4.749$, $df = 5$, $P = 0.015$; P95: mean = $0.03 \text{ days} \cdot \text{year}^{-1}$, $t = 1.303$, $df = 5$, $P = 0.280$; see Figure A.1 in the Appendix). It is worth mentioning, however, that even though all the P -values were adjusted using the FDR correction, only 6 species were included for this part of the analysis, thus limiting statistical power. Nevertheless, these results suggest that the advance of the flight period of odonates in response to minimum temperature and the contraction of the flight period in response to the UHI are robust whether or not species with higher dispersal were included.

After the FDR correction, no significant effects of the UHI were found on the P5 or P50 flight dates of any individual species of odonates. However, there was a significant effect of urban land use found on the P95 flight date of only one species (*Sympetrum striolatum*), with an advance of 10.03 days in the city compared to surrounding rural areas (Table 2.1), thus shortening the flight period of this species in cities. On the other hand, minimum temperature had a significant effect in the flight dates of 7 of the 13 species tested (see Table 2.1). All the species affected by minimum temperature showed an advance in the P5 flight date and 2 of these species also showed an advance in the

P50 flight date (Table 2.1). No species presented any significant difference in the P95 flight date due to minimum temperature. Phenological shifts across the years were shown to be statistically significant in 8 species, of which 2 species showed an advance in the P5 flight date, 4 species advanced the P50 flight date, one species showed a delay in P50 (*Sympetrum striolatum*) and 2 species showed a delay in the P95 flight date (see Table 2.1 for details). The rates of the statistically significant shifts per year showed a maximum value of 0.97 days·year⁻¹ (Table 2.1). All models showed a low VIF value (see Table A.2 in the Appendix), therefore the results of the models were not affected by multicollinearity.

When the life history of odonates was included in the analysis, the presence or absence of a diapause was found to influence significantly the phenological response of odonates in relation to minimum temperature. Species without egg diapause showed a strongly significant advance in the P5 and P95 flight date compared to species with obligate egg diapause in response to minimum temperature (see Table 2.2; Figure 2.4), as well as a small, but statistically significant shift in the P5 and P50 flight date according to year (Table 2.2). Species with and without egg diapause showed a significant advance in the P95 flight date in response to the UHI. However, all species with an obligate egg diapause tested belong only to the family Aeshnidae, therefore it is difficult to ascertain the effects of an obligate egg diapause from the effects of phylogeny.

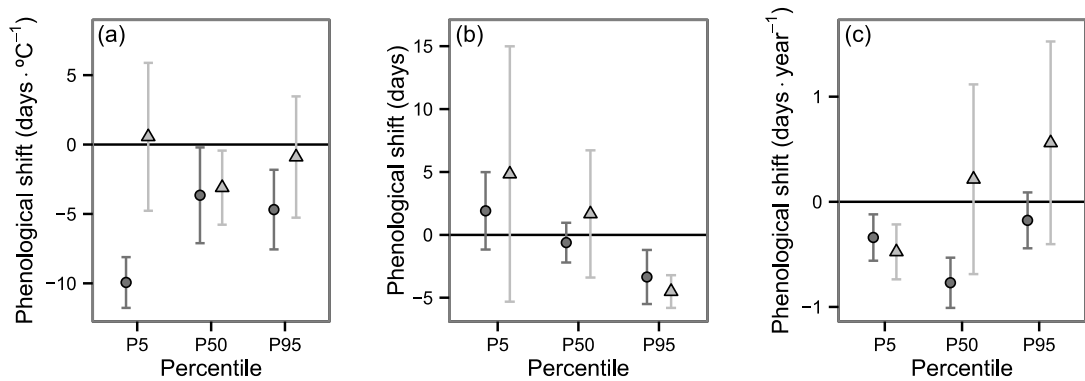


Figure 2.4. Shifts in flight dates (*P5*, *P50*, *P95*) in species with no egg diapause (*circle*), and obligate egg diapause (*triangle*). Shifts are in relation to (a) minimum temperature, (b) urban land use compared to the rural surroundings and (c) year. Error bars represent 95% confidence intervals.

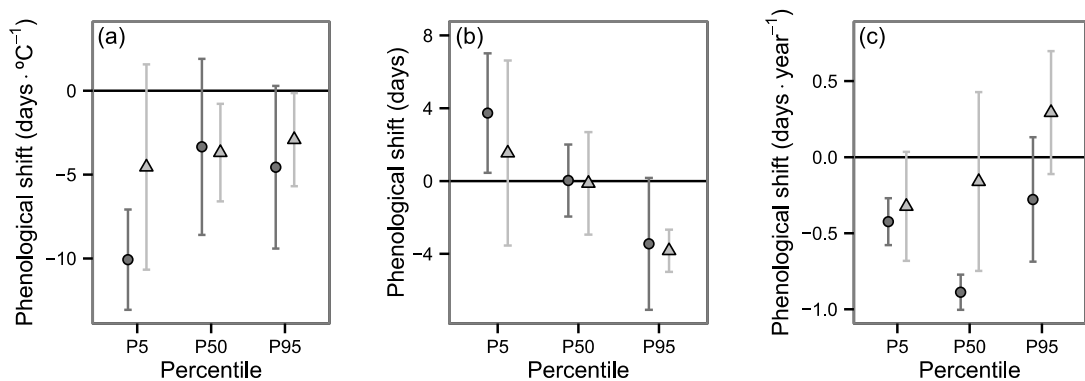


Figure 2.5. Shifts in flight dates (*P5*, *P50*, *P95*) in spring species (*circle*) and summer species (*triangle*). Shifts are in relation to (a) minimum temperature, (b) urban land use compared to the rural surroundings and (c) year. Error bars represent 95% confidence intervals.

Regarding spring and summer species, spring species advanced their P5 flight date significantly in response to minimum temperature (Table 2.2; **Error! No se encuentra el origen de la referencia.**), as well as a significant advance in the P5 and P50 flight

dates by year. On the other hand, summer species showed an advance in the P95 flight date in response to the UHI (Table 2.2; **¡Error! No se encuentra el origen de la referencia.**), thus suggesting a minor contraction of the flight period in the city within this group (**¡Error! No se encuentra el origen de la referencia.**). Summer species showed no significant shifts in their phenology in response to minimum temperature or year.

Table 2.2. Estimate of the mean phenological shift in days due to minimum temperature, urban land use and year according to life history traits. Such traits considered are presence/absence of egg diapause, and spring/summer species. Each estimate of the phenological shift includes their corresponding *t*-values and *P*-values, which were adjusted using the FDR correction. Significant results are highlighted in bold.

	No egg diapause					Obligate egg diapause				
	N	Mean	SE	<i>t</i>	<i>P</i>	N	Mean	SE	<i>t</i>	<i>P</i>
<i>Min. temperature</i>										
P5	9	-9.93	0.79	-12.530	< 0.001	3	0.56	1.24	0.453	0.736
P50	9	-3.65	1.50	-2.442	0.097	3	-3.10	0.62	-5.010	0.097
P95	9	-4.68	1.25	-3.760	0.025	3	-0.89	1.02	-0.881	0.531
<i>Urban land use</i>										
P5	9	1.91	1.33	1.428	0.255	3	4.83	2.36	2.050	0.245
P50	9	-0.62	0.69	-0.904	0.487	3	1.66	1.17	1.416	0.376
P95	9	-3.35	0.93	-3.597	0.027	3	-4.51	0.30	-14.942	0.023
<i>Year</i>										
P5	9	-0.34	0.10	-3.552	0.027	3	-0.48	0.06	-7.844	0.052
P50	9	-0.77	0.10	-7.438	0.001	3	0.21	0.21	1.023	0.497
P95	9	-0.18	0.12	-1.533	0.236	3	0.56	0.22	2.502	0.212
	Spring species					Summer species				
	N	Mean	SE	<i>t</i>	<i>P</i>	N	Mean	SE	<i>t</i>	<i>P</i>
<i>Min. temperature</i>										
P5	6	-10.07	1.16	-8.658	0.003	6	-4.55	2.38	-1.910	0.206
P50	6	-3.34	2.04	-1.637	0.236	6	-3.68	1.13	-3.256	0.068
P95	6	-4.56	1.89	-2.414	0.121	6	-2.91	1.08	-2.694	0.097
<i>Urban land use</i>										
P5	6	3.74	1.28	2.925	0.091	6	1.54	1.98	0.778	0.531
P50	6	0.03	0.77	0.039	0.971	6	-0.13	1.10	-0.117	0.938
P95	6	-3.45	1.41	-2.449	0.121	6	-3.83	0.45	-8.512	0.003
<i>Year</i>										
P5	6	-0.42	0.06	-7.047	0.005	6	-0.32	0.14	-2.320	0.129
P50	6	-0.89	0.04	-19.761	< 0.001	6	-0.16	0.23	-0.700	0.562
P95	6	-0.28	0.16	-1.744	0.222	6	0.29	0.16	1.862	0.209

Discussion

These results suggest that, contrary to what might be predicted based on observations of the impacts of temperature on odonate phenology, the UHI only causes a slight advance in the trailing edge of the flight period at a community level with no change in the leading edge or middle flight date, and one species (*Sympetrum striolatum*) presented this advance in the P95 flight date. However, annual variation in minimum temperature appears to have a much stronger impact, with a clear advance of the flight period across the whole taxon and also in 50% of the species tested. Moreover, the life history of odonates imposes a great influence on the phenological response of the species to minimum temperature and, to a lesser extent, the UHI. In particular, both spring species and species without egg diapause tend to strongly advance their P5 flight date due to minimum temperature, whereas species with and without egg diapause advance the P95 flight date in response to the UHI to a minor extent. Additionally, summer species show an advance in their P95 flight date due to the UHI.

In previous studies, the UHI has demonstrated to have a strong impact on the phenology of terrestrial taxa (Cook et al., 2006; Deviche and Davies, 2014; Jochner et al., 2013). However, spatio-temporal patterns in temperature, which was the quantitative measurement of the UHI used in this study, are driven by both the UHI and climate

change. It is important to emphasize that the UHI implies a “local” temperature increase — although the extent of the UHI may depend on the city size and can be shifted by wind and topography (California Environmental Protection Agency, 2015) — as opposed to climate change, the effects of which extend globally (IPCC, 2013). The results from this investigation suggest that the UHI is only a minor contributor to thermal ecology of freshwaters, especially when compared to climate change. One explanation for this observation may be the presence of microclimates formed within and around urban freshwater ecosystems, which can buffer the effects of the UHI (Coutts et al., 2013; Hathway and Sharples, 2012). Even though a study found the phenology of mosquitoes advanced in cities due to the UHI (Townroe and Callaghan, 2014), this may be a result of the size of the water bodies investigated, which were only 80 litre black plastic dustbins. The capability of water bodies to buffer the surrounding temperature depends greatly on the size of the water body (Jacobs et al., 2008). The external elements of urban water bodies may also contribute to buffer the impacts of the UHI. For example, a ring of trees around a pond provide a cooling effect (Forman, 2014), therefore ponds found within parks and/or woodlands will be less responsive to the UHI compared to other urban water bodies lacking surrounding vegetation. On the other hand, microclimates within urban water bodies are influenced by presence of aquatic vegetation and the impervious surface cover in the catchment (Paul and Meyer, 2001). Despite urban water bodies often lacking riparian vegetation (Paul and Meyer, 2001; Villalobos-Jiménez et al., 2016) to help regulate temperature, urban ponds in particular have a wide variety of features and are subject to different management plans, ranging from garden ponds to nature reserves (Hassall, 2014) and contain a wide variety of invertebrate taxa as a result (Hill et al., 2017). Some urban ponds might be more

effective at buffering the effects of the UHI, especially large urban ponds with abundant vegetation and decreased impervious cover in the catchment, and land managers can take advantage of this buffering capacity while preventing the establishment of invasive species and disease vectors (Hassall et al., 2016). The findings from this study may be a result of the *average* effectiveness of urban freshwater ecosystems at regulating the impacts of the UHI. However, the buffering capacity of water bodies would only be effective whilst the odonates develop in the aquatic environment, therefore the adult phase – which is terrestrial – is more vulnerable to the impacts of the UHI, which may explain the advance of the P95 flight date in cities. However, the present study only considers one city (London) and its surroundings, therefore further research is needed to analyse the biological implications of microclimatic conditions in urban water bodies in other cities.

Another factor to take into account is that urban climate is not only defined by increased temperatures – although it may be the most prominent feature – but it is also influenced by decreased insolation due to the buildings and other structures blocking the solar radiation (Terjung and Louie, 1973). Likewise, the UHI is less intense in large areas dominated by green space (Forman, 2014), where urban water bodies may have been found. Although the air temperature is still higher in cities despite having decreased insolation (Terjung and Louie, 1973), this could potentially decrease the flight activity of odonates, which may in turn decrease detectability and recorder effort in urban areas.

Despite the fact that the community as a whole was advancing phenology in relation to changing temperature, and showed a contraction of the flight period in urban areas, these patterns were not consistent across species. However, when the phenology was tested in the context of variation in life history traits, the results were more informative. For instance, species without egg diapause were found to be much more responsive to changes in minimum temperature compared to species with an egg diapause. The P5 flight date of species with no egg diapause advanced conspicuously in response to minimum temperature with a mean advance of 9.9 days·°C⁻¹. Likewise, the P95 flight date of species lacking an egg diapause showed a mean advance of 4.7 days·°C⁻¹, which suggests a shift of the flight period in response to minimum temperature. The lack of phenological shift in response to minimum temperature found in species with an egg diapause may be explained by the fact that the diapause protects the species from stressful conditions over winter, but may also impede the species' capacity to respond to increased warming in spring. Even though the sample size of species with an obligate egg diapause is rather small in this study – only 3 species, thus lacking statistical power – similar differences have been observed in the phenology of odonates in relation to climate change (Hassall et al., 2007) and even in other insect taxa such as aphids that overwinter in different stages (Harrington et al., 2007). On the other hand, species with and without an egg diapause responded similarly to the UHI by advancing the P95 flight date, suggesting this trait does not help counteract the impacts of the UHI in the adult phase of odonates.

Similarly, spring species, which undergo a larval diapause in the last instar, show a considerable advance in the P5 flight date due to minimum temperature, which is in line

with Hassall et al. (2007). However, the advance in the P95 flight date found in summer species in urban areas, as negligible as it may be, is somewhat unexpected since it is not in accordance with minimum temperature. The consequent temperature increase from the UHI is expected to extend the flight period instead of contracting the phenology. This contraction of the flight period of summer species in cities could be explained by increased mortality in the adult phase due to thermal stress, which is more noticeable in the summer compared to spring, or other stressors commonly found in urban areas, such as the presence of contaminants in water (Villalobos-Jiménez et al., 2016) that can also interact with the thermal stress even across metamorphosis (Janssens et al., 2014). However, the mechanisms underlying this response are not known. Additionally, other life-history traits that may have a significant impact on the phenological response of odonates are voltinism and body size. Voltinism – the number of generations completed in a year – may have a similar effect to larval diapause in response to the UHI and buffer the effect of increased temperatures. However, higher temperatures tend to increase voltinism in odonates (Corbet, 1999), which may decouple the phenology of odonates in temperate regions. Similarly, body size decreases as the growth rate increases due to increased temperatures (Chown and Gaston, 2010). Therefore, the UHI is expected to decrease body size in odonates and other aquatic macroinvertebrates. Further research is encouraged in order to decipher the relationship between voltinism, body size, and the UHI.

This investigation shows that the UHI does advance the final stage of the phenology of odonates, but only to a certain extent. However, the impacts of climate change on their phenology are far greater, with 50% of the species tested showing a clear advance in

response to minimum temperature. The findings of this study provide evidence that climate change is the most important factor responsible for the increased temperatures and the subsequent phenological trends observed, whereas the UHI contributes only negligibly to the overall phenological trends. The present study also increases the current understanding of freshwater habitats and how their vulnerability towards climate change is probably higher than expected compared to the UHI. However, it is important to emphasize other factors in cities which can interact with increased temperatures and potentially alter the phenology of odonates and other aquatic insects, such as the presence of contaminants. Most importantly, the microclimatic conditions of urban water bodies can play an important role in regulating the effects of the UHI. Therefore, the biological impacts of the UHI can be dependent upon urban design and management (Hassall et al., 2016).

Chapter 3: Environmental noise reduces predation rate in an aquatic invertebrate

Abstract

Noise is one of a wide range of disturbances associated with human activities that have been shown to have detrimental impacts on a wide range of species, from montane regions to the deep marine environment. Noise may also have community-level impacts via predator-prey interactions, thus jeopardising the stability of trophic networks.

However, the impact of noise on freshwater ecosystems is largely unknown. Even more so is the case of insects, despite their crucial role in trophic networks. Here, I study the impact of underwater noise on the predatory functional response of damselfly larvae. I compared the feeding rates of larvae under anthropogenic noise, natural noise, and silent conditions. The results suggest that underwater noise (pooling the effects of anthropogenic noise and natural noise) decreases the feeding rate of damselflies significantly compared to silent conditions. In particular, natural noise increased the handling time significantly compared to the silent treatment, thus reducing the feeding rate. Unexpectedly, feeding rates under anthropogenic noise were not reduced significantly compared to silent conditions. This study suggests that noise per se may not necessarily have negative impacts on trophic interactions. Instead, the impact of noise on feeding rates may be explained by the presence of nonlinearities in acoustic signals, which may be more abundant in natural compared to anthropogenic noise. I conclude by highlighting the importance of studying a diversity of types of acoustic pollution, and encourage further work regarding trophic interactions with insects using a functional response approach.

Introduction

Human activities have exerted substantial pressures on a wide range of ecosystems, from montane regions to the deep marine environment. Many such impacts have been categorised, evaluated, and quantified in great detail (Sala et al., 2000). However, many such studies have focused on those threats that are easiest to quantify and study, based on broad assessments of community diversity and structure with and without the threat, such as habitat fragmentation (Fahrig, 2003) and climate change (e.g. Chen et al., 2011). However, other stressors do not offer such clear records of their impacts on the environment.

This is the case of noise pollution. While some research into the impacts of noise on animals has achieved a high profile, particularly research carried out on cetaceans (Weilgart, 2007) and in urban birds (Slabbekoorn and Peet, 2003), research is only just beginning to explore the wider impacts on ecosystems. Additionally, at an individual level, anthropogenic noise can have considerable anatomical, physiological, and behavioural impacts (Kunc et al., 2016; Kight and Swaddle, 2011). For example, exposure to road traffic noise reduced foraging and increased vigilance significantly in the prairie dog *Cynomys ludovicianus* (Shannon et al., 2014). Even though some species have developed mechanisms to cope with noise disturbance (Halfwerk and Slabbekoorn, 2009; Parris et al., 2009; Fuller et al., 2007), the potential of anthropogenic noise to impact the conservation of wildlife populations (Slabbekoorn and Ripmeester, 2008; Brumm, 2010; Chan and Blumstein, 2011; Aguilar de Soto,

2016), as well as the wellbeing of human populations (WHO, 2011), is nonetheless concerning.

In marine environments, where the impact of noise is even stronger given the fact that sound waves travel nearly five times quicker in water than through air (USA Office of Scientific Research Development and National Defense Research Committee, 1946), acoustic masking due to anthropogenic noise can impair the reception of information through various “acoustic spaces”, such as echolocation, intraspecific communication, predator avoidance and prey detection (Clark et al., 2009). However, little is known about the impact of anthropogenic noise on freshwater habitats. Freshwater ecosystems account for 0.01% of global water and yet support almost 6% of all described species (Dudgeon et al., 2006) and provide a wide range of ecosystem services (Millennium Ecosystem Assessment, 2005). However, these habitats are also susceptible to various sources of noise, most notably boats in canals, lakes, and rivers. Only a few studies have investigated the impact of noise on freshwater species, e.g. foraging efficiency in sticklebacks (Purser and Radford, 2011; Voellmy et al., 2014) and European eels (Simpson et al., 2015). Such studies show the impacts of noise may go beyond single species and have community-level effects via trophic interactions. Noise may disrupt predatory mechanisms in various ways, either by (i) inducing stress (Simpson et al., 2015), (ii) masking the acoustic cues produced by predators and/or prey, thus complicating detection (Siemers and Schaub, 2011), (iii) inducing attention shifts on the predator (Purser and Radford, 2011), or (iv) by compromising antipredator behaviour in the prey, which may in turn increase predation risk (Simpson et al., 2015). Possible disturbances in predator-prey interactions in freshwater ecosystems via anthropogenic

noise may lead to sudden shifts in predator and/or prey populations and compromise the stability of trophic networks. It is essential to understand the effects of noise on predator-prey interactions in order to implement mitigation programmes for the management and conservation of species and ecosystems (Chan and Blumstein, 2011).

However, the impact of noise on insects has been largely overlooked (Morley et al., 2014), despite the fact that insects are hugely diverse and comprise the vast majority of species worldwide (Mora et al., 2011) and thus have a crucial role in trophic networks (Schoenly et al., 1991). The impacts of underwater noise on aquatic insects are likely to have a stronger effect at a community level compared to vertebrates in freshwater ecosystems due to the great contribution of aquatic invertebrates to a wide range of ecosystem functions (Wallace and Webster, 1996). Moreover, in the case of semi-aquatic insects, the potential impacts of noise in freshwater habitats can also impact terrestrial ecosystems through cascading trophic interactions across ecosystem boundaries (Knight et al., 2005).

A useful method for predicting the ecological impacts of predator-prey interactions is the functional response (Dick et al., 2014). The functional response was first described by Holling (1959) and is defined as the relationship between a predator's feeding rate and the prey density. This method predicts three parameters which dictate the amount of prey eaten according to prey density: the attack rate (also called searching time or attack coefficient), the handling time, and the total time available for predation. The attack rate is defined as "the instantaneous rate of discovery", whereas the handling time is referred

to as the time taken to process the prey, including all stages of the predatory sequence and the digestive pause. In other words, the time elapsing from the pursuit of one prey to the next (Holling, 1959). Functional responses can be classified into three types: type I assumes a linear increase of number of prey eaten with prey density; type II assumes a maximum number of prey eaten as prey density increases according to a satiation point, where the curves reaches an asymptote; type III is similar to the aforementioned, except the number of prey eaten is low at lower prey densities, forming a sigmoid curve (Holling, 1959). The functional response approach takes into account important ecological factors such as prey density, searching time and satiation levels, which makes it more realistic compared to other methods for estimating the relationship between predator and prey populations. Most importantly, this approach explicitly considers demographic consequences for prey populations (Dick et al., 2014), which is key for understanding ecological and conservation issues (Brumm, 2010; Morley et al., 2014).

This study aims to investigate the impact of natural and anthropogenic underwater noise on predator-prey interactions in freshwater ecosystems using a functional response approach in damselfly larvae, which are aquatic predatory insects. Damselflies (Zygoptera) represent a semi-aquatic taxon with an aquatic larval phase and a terrestrial adult phase. Larval damselflies are found in lotic and lentic habitats feeding on smaller invertebrates such as *Daphnia* (Thompson, 1978a) and, at the same time, are prey of larger predators (Martins et al., 2010). Damselfly larvae can locate prey using their compound eyes and mechanoreceptors –such as the tarsal hairs and antennae– to detect the vibrations produced by the prey (Vasserot, 1957). Hence, noisy environments can potentially interfere with their mechanism for prey detection.

My two hypotheses – which are not mutually exclusive – are: (i) underwater noise causes larvae to take longer to detect their prey, therefore decrease the attack rate and the total prey consumed; (ii) underwater noise increases handling time, thus decreasing the total prey consumed.

Methods

Study species

The model species selected for this study is *Ischnura elegans* (Figure 3.1). *I. elegans* is one of the most common zygopteran species in Europe, is found mostly in lentic habitats or very slow-moving waters such as canals, and can tolerate high levels of eutrophication and salinity, although it cannot inhabit acidic sites such as bogs (Dijkstra and Lewington, 2006; Dow, 2010). *I. elegans* is univoltine across most of its range, with some evidence of semivoltinism in more northerly regions (Thompson, 1978b), and can occupy habitats with and without fish (McPeck, 1998). This species was chosen due to its prevalence in disturbed, urban environments where noise may be a stressor (Goertzen and Suhling, 2013).



Figure 3.1. Larva of *Ischnura elegans* in instar 12.

Collection of adults and larvae rearing

To control for phenotypic plasticity, I conducted a common garden rearing experiment. I obtained *I. elegans* eggs from field-caught adult females from sites in an urban to rural gradient (see Table A.3 in the Appendix) during July-August 2015. Originally, the response to noise was going to be compared between urban and rural populations. However, due to small sample sizes this was not possible and, even though sampling in an urban-rural gradient increases geographic variation and reduce the risk of pseudoreplication, I cannot overrule an effect of urban land use. Once the eggs hatched, the larvae were reared at 20°C at a photoperiod of 14L:10D with aerated tap water and fed with *Artemia* sp. and *Daphnia magna ad libitum*.

Experimental design

For the functional response experiments, three treatments were used: (1) anthropogenic noise, recorded from the diesel engine of a narrowboat in the Leeds-Liverpool canal, UK (53.794°N, 1.559°W) with an underwater recorder (condenser hydrophone connected to a Zoom H1 portable digital recorder); (2) natural noise, represented by water flowing on a rocky river (track “river-6.wav” downloaded from <http://www.soundjay.com/river-sounds-1.html>), and (3) the control treatment, conducted in silence. All audio stimuli were normalised to make sure that the sound levels in the experimental setup were as close to the original recordings as possible. Posteriorly, audio stimuli were saved in WAV format with 32-bit floating point (Figure 3.2a and b). Spectral power density was analysed in Audacity 2.1.0 (<http://www.audacityteam.org/>) using Fast Fourier Transform (FFT) with Hann evaluation window, FFT size 512, averaged from a 20 s sample of each recording (Figure 3.2c).

Prior to the experiments, larvae were selected based on their head width to standardise size, since larger larvae are known to have higher predation rates (Thompson, 1975). Only larvae with head width of 2.5-3.1 mm (mean=2.86 mm \pm 0.013 SE) were used in the experiments, which were most likely to be on the 11th instar (Thompson, 1975; Thompson, 1978b). The larvae selected were starved for 48 hrs to empty their gut before the experiment (Thompson, 1975).

During the experiments, the larvae were transferred to individual meshed cylindrical containers (0.5 mm mesh size, 6 cm diameter, 14 cm long) with a wooden stick for the larva to perch to reduce stress, inside a 28 L fish tank (24 x 39 x 30 cm) covered on all sides in a 5 cm layer of polystyrene to isolate against noise. The tank was filled with 9 L of aged tap water. Two sound transducers (Adin B1BT 10W vibration speakers) were laid on two opposite sides of the tank to produce the acoustic stimulus synchronously (Figure 3.3). Sound transducers produce vibration alongside playing the tracks to recreate the effect of boat passage. Even though the transducers were located outside the tank, which may limit considerably the particle motion produced by sound waves, the vibrations produced by the transducers are transferred to the tank walls and, subsequently, the water, thus facilitating to a certain extent the particle motion alongside the pressure waves. Larvae were fed with *Daphnia* (the prey model). Size of *Daphnia* was also controlled: only *Daphnia* that were able to pass through a 1.4 mm Endecotts Test Sieve, but not a 1 mm mesh sieve were used in the experiments.

Different densities of *Daphnia* were placed inside the meshed containers alongside the larvae. Prey densities were 5, 10, 15, 20, 30, 40, and 50 individual *Daphnia*. Sample sizes per prey density in each treatment ranged from 4 to 7 due to the death of some experimental animals (see Table A.4 in the Appendix). Each larva was only used once, so animals represent individual, independent replicates. Considering the transducers were located on the sides of the tank, the strength of the stimuli varied spatially within the tank according to the distance from the transducers, so the position of the larvae inside the experimental setup can have an influence on the perception of noise and the resulting predation response. In order to avoid any bias in the analysis due to this issue,

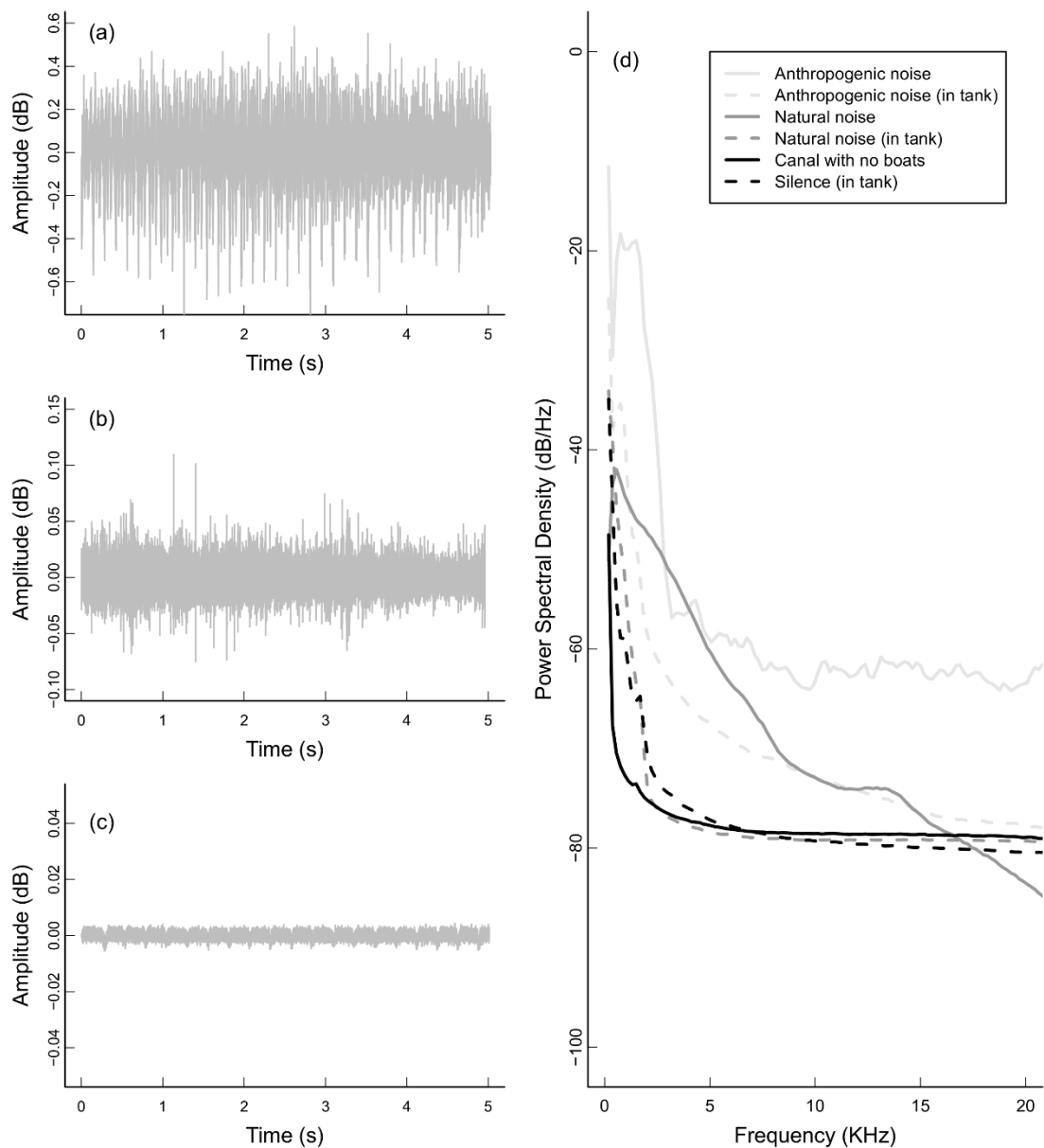


Figure 3.2. Properties of the audio cues used in the functional response experiment. **(a)** Segment of 5 seconds of the audio cue used in the anthropogenic treatment, recorded from the diesel engine of a narrowboat; **(b)** segment of the audio cue used in the natural treatment, represented by a rocky river, also 5 seconds; **(c)** segment of the sound levels in the Leeds-Liverpool Canal with no boats passing by, also 5 seconds; **(d)** power spectral density of the original audio cues used in the anthropogenic and natural treatments, the re-recordings of the original audio cues in the fish tank used as part of the experimental setup, the sound levels of the canal with no boats, and the recording of the sound levels in the silent (control) treatment.

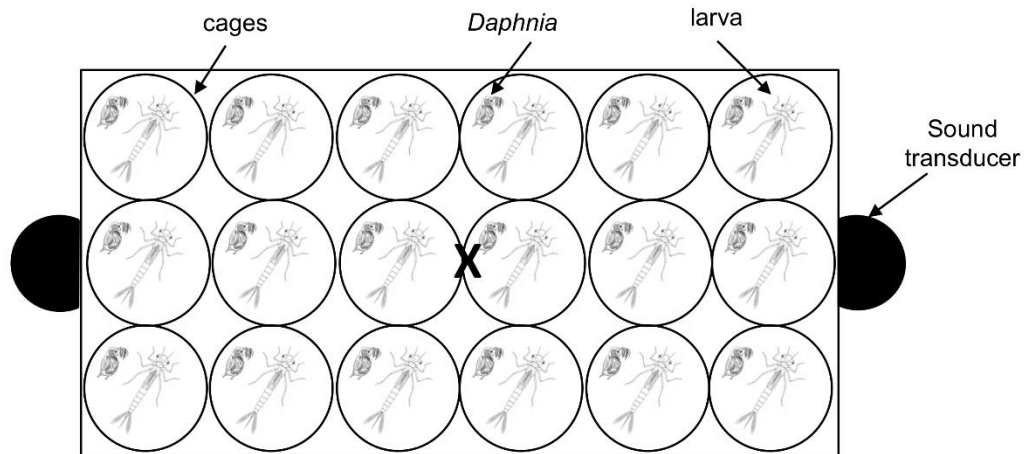


Figure 3.3. Downward view of the experimental setup for estimating the functional response of *Ischnura elegans*. The cross indicates where the microphone was placed to do the recordings in the tank.

the position of each larvae and prey density replicate was randomised prior to running the experiments. Each experiment was left running for 24 hrs in an incubator at 20°C in the dark. Using the incubator also ensured that the temperature was constant, which is a crucial driver of the functional response of odonates (Thompson, 1978b), and even though the incubator might have produced additional noise, this noise was consistent across all experiments. The experiment was left in the dark for two reasons: (i) to ensure that prey were not detected visually, but merely by the vibrations produced by the prey, (ii) to avoid photic effects in the water that may cause behavioural changes in *Daphnia* (Thompson, 1975). The acoustic stimuli were looped over the 24 hrs, except in the control treatment where there was no sound produced. The sound transducers were left in place during the control treatment. After the 24 hr-period, the larvae were removed and the *Daphnia* counted. To account for the fact that damselfly larvae engage in “wasteful killing” (Johnson et al., 1975) or also called “partial consumption” (Paterson

et al., 2015), the *Daphnia* that had more than 50% of their bodies missing were considered as “eaten”, whilst the ones that had less than 50% missing were recorded as a result of “wasteful killing”.

Statistical analysis

I performed two separate analyses: first, I tested the differences in the attack rates and the handling times with and without acoustic stimuli by pooling the data from the anthropogenic noise and natural noise treatments and compared the coefficients against the control (silence) treatment. In the second analysis, I compared the attack rates and the handling times of each treatment explicitly, that is, anthropogenic noise, natural noise, and control (silence) treatments. The statistical analysis was performed using the *frair* package (Pritchard, 2014) in R 3.0.2 (R Core Team, 2013). The functional response of *I. elegans* larvae has been previously described as type II (Thompson, 1978b; Thompson, 1975). Given that the prey were not replaced during the experiment, the attack rates and handling times were calculated using Rogers’ type II formula (Rogers, 1972):

$$N_a = N_0(1 - e^{-a(T-h \cdot N_a)}) \quad \textbf{Equation 3.1}$$

Where N_a = number of prey eaten, N_0 = prey density, T = total time prey are exposed to predation, a = attack rate, and h = handling time.

However, the frair package utilises maximum likelihood estimation within the bbmle package (Bolker and R Development Core Team, 2014) and a modified version of Equation 3.1 with Lambert's W function (Bolker, 2008) to make the equation solvable:

$$N_a = N_0 - \frac{\text{lambertW}(a \cdot h \cdot N_0 \cdot e^{-a(T-h \cdot N_0)})}{a \cdot h} \quad \text{Equation 3.2}$$

The fitted curves were bootstrapped to visualise variability ($n = 999$), and both the attack rate and handling time were compared between treatments using indicator variables (Juliano, 2001) using the function “frair_compare” in the frair package. The “indicator variable” approach only allows pairwise comparisons between groups (Juliano, 2001), but this approach has been widely used in functional response studies (e.g. Paterson et al. 2015; Taylor and Dunn 2016).

To ensure that all individuals considered had a stable feeding rate, I conducted an *a posteriori* analysis by identifying and eliminating potential outliers. In order to do so, the residuals were obtained from the fitted functional response curve. All residuals that were below the first quantile – 1.5 interquartile range (IQR) or above the third quantile + IQR were excluded, leading to the exclusion of three data points. Once all potential outliers were removed, the attack rates and handling times were recalculated using the same procedure previously described and the functional response curves were refitted.

Results

As described by Thompson (1978b; 1975), the functional response of *I. elegans* in all treatments was type II (Figure 3.4). In the first analysis, I compared the control (silence) treatment against the pooled noise treatments to evaluate the effect of noise *per se* on feeding. The functional response of *I. elegans* had a lower maximum feeding rate with noise ($1/hT = 10.6 \text{ prey}\cdot\text{day}^{-1}$; Figure 3.4a) compared to the feeding rate in silent conditions ($1/hT = 16.7 \text{ prey}\cdot\text{day}^{-1}$; Figure 3.4a). Specifically, the handling time increased significantly with noise (Table 3.1; Figure 3.5a), whereas the difference in the attack rates with noise and no noise was not significant (Table 3.1; Figure 3.5a). These results support my hypothesis that underwater noise decreases the feeding rate of *I. elegans*, particularly by increasing the handling time.

In the second analysis, I compared the control (silence) treatment to each of the two different types of acoustic stimuli (anthropogenic and natural). The outcomes differed when the functional responses of *I. elegans* were analysed under different types of noise. The maximum feeding rate of *I. elegans* in the anthropogenic noise treatment was lower than the maximum feeding rate in the control treatment (anthropogenic noise: $1/hT = 12.0 \text{ prey}\cdot\text{day}^{-1}$; control: $1/hT = 16.7 \text{ prey}\cdot\text{day}^{-1}$), but neither the attack rate nor the handling time in the anthropogenic noise treatment were significantly different from the control treatment (Table 3.1; Figure 3.5b). Unexpectedly, the natural noise treatment showed the lowest feeding rate of all treatments ($1/hT = 9.4 \text{ prey}\cdot\text{day}^{-1}$). In particular, the handling time in the natural noise treatment was significantly higher than the control

and the anthropogenic noise treatment (Table 3.1; Figure 3.5b). The attack rates were not significantly different among treatments (Table 3.1; Figure 3.5b).

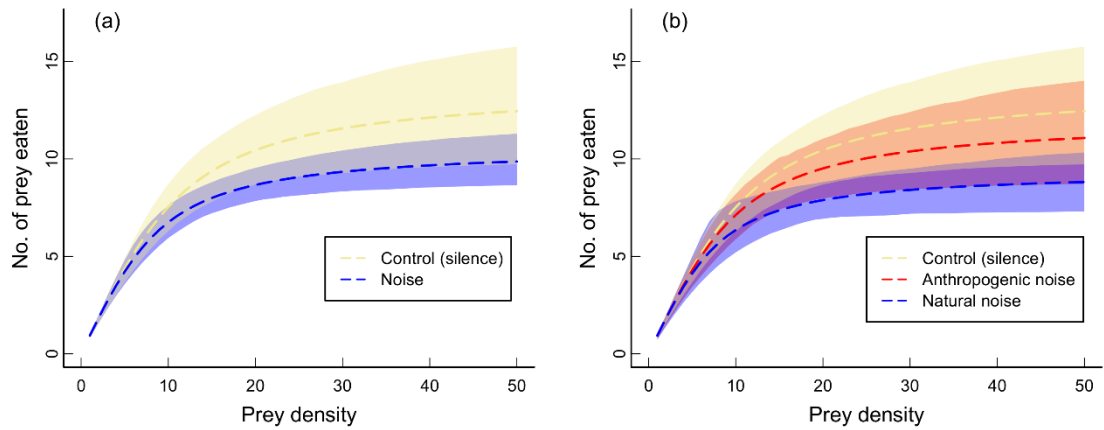


Figure 3.4. Fitted functional response curves from all the experiments obtained from the frair package (Pritchard, 2014), comparing (a) the control treatment (silence) against noise (grouping anthropogenic and natural noise treatments), and (b) the control treatments. Shaded areas represent 95% confidence intervals.

Table 3.1. Comparison between functional response parameter estimates for *I. elegans* among the treatments used. D represents the difference between the attack rates (Da) and handling times (Dh) among treatments. Significant values are highlighted in bold.

Treatment 1	Treatment 2	D	Estimate	SE	z	P
Noise	Control (silence)	Da	-0.016	0.803	-0.020	0.984
		Dh	0.021	0.008	2.757	0.006
Anthropogenic noise	Control (silence)	Da	-0.044	0.918	-0.048	0.962
		Dh	0.010	0.009	1.138	0.255
Natural noise	Control (silence)	Da	-0.014	1.036	-0.014	0.989
		Dh	-0.033	0.010	-3.270	0.001
Anthropogenic noise	Natural noise	Da	-0.060	1.117	-0.054	0.957
		Dh	-0.023	0.011	-2.097	0.036

Discussion

The results from this study suggest that, in general, the presence of acoustic stimuli decreased the number of prey eaten compared to silent conditions even at high prey densities. The results also suggest that the attack rate did not change with underwater noise, but instead the handling time increased, thus decreasing the feeding rate of the larvae in the presence of noise. The finding supports my general hypothesis that noise interferes with feeding behaviour. However, I found that natural and anthropogenic noise had different outcomes: natural noise decreased the number of prey eaten by the larvae significantly, while anthropogenic noise had no significant effect. These results suggest that *I. elegans* larvae do not take longer to detect or process their prey with anthropogenic noise, which therefore does not decrease the amount of prey eaten compared to silent conditions. However, the number of prey eaten under natural noise is significantly less than in silent conditions. Specifically, I found increased handling time with natural noise, which suggests that the larvae take longer to catch and/or process their prey compared to silent conditions. No difference in attack rate was found in any of the treatments.

The fact that anthropogenic noise does not affect the attack rate or handling time suggests that either the *I. elegans* larvae and/or the *Daphnia* – predator and prey in this study – can tolerate anthropogenic noise. This is the first evidence of aquatic macroinvertebrates being tolerant to anthropogenic noise. However, it is not possible to ascertain the drivers of this response from the data obtained in this study; more research

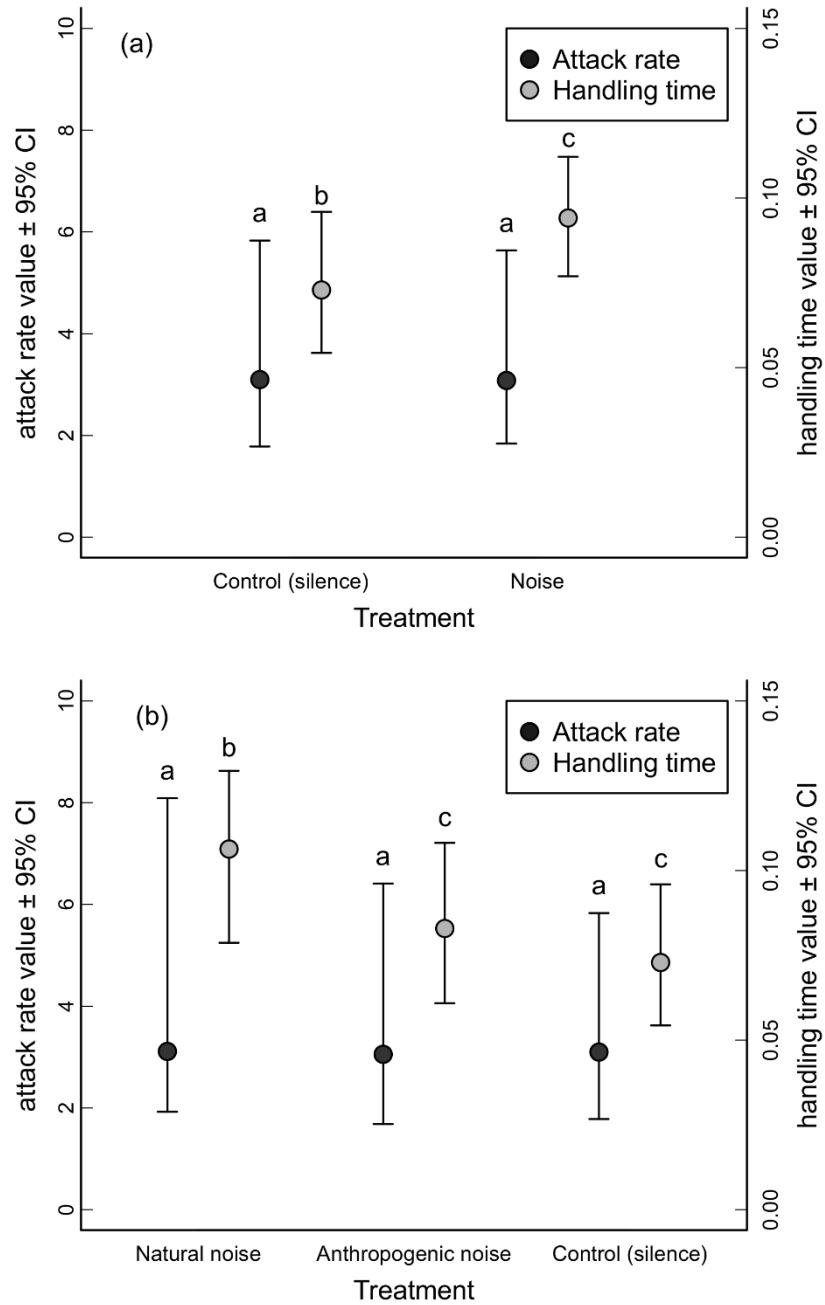


Figure 3.5. Estimates of the attack rates and the handling times in each treatment, comparing (a) control treatment (silence) against noise (grouping anthropogenic and natural noise treatments), and (b) control treatment (silence) against anthropogenic and natural noise treatments. Letters represent significant difference. Error bars represent bootstrapped studentized 95% confidence intervals.

is needed to discover the mechanism driving this tolerance to anthropogenic noise. Paradoxically, natural noise had a negative impact on the functional response of the larvae; this type of noise was found to decrease the number of prey eaten due to increased handling time. While *I. elegans* is mostly found in lentic habitats such as ponds, the species is also abundant around running waters (Dijkstra and Lewington, 2006; Dow, 2010). The greater prevalence in lentic habitats may explain why natural noise had a significant impact on the amount of prey eaten by larvae compared to the low noise treatment that may be representative of the preferred still water habitat.

Another plausible explanation as to why natural noise had a greater effect than anthropogenic noise on the functional response of *I. elegans* is due to the presence of nonlinearities in the audio cues used in the experiment. The power spectrum of the anthropogenic noise recorded showed high-amplitudes (maximum -11.55 dB) only at low frequencies (maximum 3 KHz), and then the amplitude decreased drastically (-54 dB) and became relatively stable at higher frequencies. The stimuli used in the natural noise treatment, on the other hand, had lower amplitude levels (maximum -51.1 dB) compared to the anthropogenic noise, but the amplitude levels were highest at low frequencies (maximum 3 KHz) and then decreased gradually as the frequencies increased (see Figure 3.2). This can be interpreted as natural noise having high amplitude levels at low frequencies with some degree of nonlinearity at different frequencies compared to anthropogenic noise. A wide range of invertebrates have adapted to detect particle motion at frequencies below 1 KHz (Morley et al., 2014), and stimuli of higher frequencies have been shown to be less relevant in other animals such

as fish (Popper and Fay, 1993; Fay and Popper, 2012). However, nonlinearities in acoustic phenomena have been shown to increase unpredictability and result in a heightened behavioural response in meerkats (Karp et al., 2014; Townsend and Manser, 2011), marmots (Blumstein and Récapet, 2009), and red deers (Reby and Charlton, 2012). An accessible example of the difference between a simple and nonlinear acoustic signal is in the vocalization of primates, ranging from “coo” calls (relatively pure tones with minimal noise) through to nonlinear sounds such as “screams” (highly complex sounds produced with subharmonics and deterministic chaos; see Fig. 1 in Fitch et al. (2002) for an example). This is in accordance with the ‘unpredictability hypothesis’, which suggests that nonlinearities prevent habituation and may induce fear, since “unfamiliar” noises (i.e. nonlinearities) can be perceived as a threat, e.g. a predator (Karp et al., 2014; Blesdoe and Blumstein, 2014). In this study, my recording of anthropogenic noise is more predictable than natural noise, despite having high amplitude levels at low frequencies, thus it is more likely that the damselfly larvae become habituated to anthropogenic noise, whereas nonlinearities in natural noise may be misconceived as a threat.

One can argue that natural noise can mask the vibrations produced by the prey, particularly since in *Calopteryx splendens* – another zygopteran – the optimal stimulus is a sequence of stochastic, small-amplitude pressure waves resembling those produced by *Daphnia* (Vasserot, 1957), which is similar to the nonlinear, low-amplitude pattern found in natural noise. However, this seems unlikely considering that masking the vibrations produced by prey would affect the attack rate rather than the handling time, as was found in the present study. According to Holling (1959), the handling time

includes catching, processing, and digesting the prey. I speculate the impact of natural noise can occur on any of these phases through one of the following mechanisms: (i) natural noise distracts the predator and thus complicates the catchment and/or processing of prey, as has been found in European eels (Purser and Radford, 2011); (ii) natural noise increases the movement of prey (frequency or distance of movement), therefore delaying the catchment of prey; (iii) natural noise induces stress via hormones, which may alter the predator's metabolism and prolong the processing of food (Kight and Swaddle, 2011). Additionally, it is important to mention only one audio file of each stimuli was used per treatment, so it is impossible to separate the effects of the stimuli used from the noise types *per se*. Moreover, despite efforts to make the noise treatments as close to the environmental conditions as possible, I cannot guarantee that the results are identical to what occurs in the environment, particularly regarding particle motion, which is the cue that insects use to detect sound instead of sound pressure. Further research is encouraged to describe in detail the particle motion with different types of noise and the impact on aquatic insect behaviour, which can be done using an accelerometer.

The results from this study provide evidence that underwater noise may impose a threat to the stability of trophic networks. *I. elegans* is known to feed on oligochaete worms, chironomids and other dipterans, coleopteran larvae, copepods, daphniids, isopods, ostracods, ephemeropterans, and even other zygopterans (Thompson, 1978a).

Considering underwater noise reduces the maximum feeding rate, then it is within reason to expect declines in the strength of trophic link between damselflies and these prey taxa in noisy areas – which may or may not be associated with human activities.

This has considerable impacts on population dynamics of the predator (*I. elegans* in this case) and prey, which may also have substantial implications on the management and conservation of freshwater biodiversity (Chan and Blumstein, 2011).

Most studies have focused on the impacts of anthropogenic noise. However, to my knowledge, this is the first study showing that other sources of noise, such as noises generated in complex flowing water environments, may have even a higher impact on aquatic macroinvertebrates and can be a factor in determining the stability of trophic interactions. This study highlights the importance of studying the impact of not only anthropogenic noise, but also natural sources of noise.

This study has effectively shown that underwater noise can significantly alter predator-prey interactions. However, anthropogenic noise may not necessarily have a negative impact on predator-prey interactions, but rather the characteristics of the type of noise itself. Additionally, this is the first study to my knowledge that explores the role of noise in the functional response of an aquatic invertebrate predator and compares natural and anthropogenic noise. However, further research is encouraged and needed to discover the underlying mechanisms of this response, and should focus on the characteristics of environmental noise within the context of prey capture to understand the effects on conservation of biodiversity.

Chapter 4: Ontogenetic variation in susceptibility to ecological traps among urban and rural damselflies

Abstract

Ecological traps arise when the environmental cues that were once adaptive for habitat choice become unreliable mostly due to anthropogenic disturbance in the environment, or when a novel element mimics the cues for suitable habitat choice, which leads to poor habitat choices. This in turn decreases population fitness and may ultimately lead to extinction. Therefore, strong selective pressures may be found in areas where anthropogenic changes are frequent, such as cities. Localised adaptations to ecological traps have considerable implications for conservation of a wide variety of taxa.

Dragonflies and damselflies (the Odonata) are one of the many taxa vulnerable to ecological traps. Odonates use horizontally polarised light as a cue of suitable water bodies. However, some artificial surfaces such as car hoods, black plastic, and solar panels reflect horizontally polarised light strongly, thus luring these insects to oviposit on these unsuitable surfaces. Here, I compare the behavioural response to horizontally polarised light between urban and rural populations of the odonate *Ischnura elegans* to test the potential for localised adaptations to ecological traps. I used individuals reared in controlled conditions in the laboratory as well as field-caught adults to evaluate the role of phenotypic plasticity. I also studied the association between ontogeny and polarotaxis that has been suggested – but not empirically tested – by other studies. The results from this study show a strong preference for horizontally polarised light with increasing age, but no difference between urban and rural populations. However, the results differed vastly when the field-caught individuals were tested: rural individuals showed a significantly stronger preference for horizontally polarised light in comparison with urban individuals. The results from the field-caught individuals

suggest there is strong selection against polarotaxis in urban areas. However, due to the fact that ecological traps have occurred for a relatively short time compared to the evolutionary history of odonates, and the fact that British odonate species have up to one generation per year, there has not yet been adaptation in urban odonate populations. Possible mechanisms driving this response are further discussed.

Introduction

Ecological traps occur when environmental cues used by organisms for habitat choice are no longer reliable but instead lead to maladaptive behaviour (Schlaepfer et al., 2002). This term was coined by Gates and Gyles (1978) to describe the preference of passerines for nesting in field-forest edges induced by anthropogenic disturbance, where eggs and nestlings were more susceptible to predation and cowbird parasitism (*Molothrus ater*). Forest edges are heterogeneous and provide a wide variety of resources for mixed-habitat birds (Gates and Gysel, 1978). On the other hand, artificial field-forest edges are much narrower and yet show the same heterogeneity and variety of structural cues of these species for settling and nesting (*idem*), therefore are perceived as a suitable habitat. However, narrow forest edges increase bird density by concentrating nests, which in turn increases density-dependent mortality, i.e. predation and parasitism (*idem*). From an evolutionary perspective, anthropogenic field-forest edges are recent, thus passerines have not evolved to associate narrow man-made forest edges with increased predation and parasitism. The species becomes constrained by its evolutionary past to choose poorly, despite having suitable conditions available

elsewhere, and ultimately decreases fitness and may lead to population declines or even extinction (Schlaepfer et al., 2002).

Ecological traps can be created by rapid environmental change that decouples cues from the aspects of the habitat from which organisms benefit. Land use change, such as during urbanisation, is the most significant anthropogenic impact (Sala et al., 2000) and is continuing at a rapid pace. Moreover, ecological traps may also arise when a novel element mimics the cues for suitable habitat choice, which misleads the organism to choose the unsuitable habitat and leads to maladaptive behaviour (Schlaepfer et al., 2002). This is the case of odonates.

It is well-established that odonates are attracted to horizontally polarised light since it is one of the main cues for detecting suitable water bodies (Bernáth et al., 2002).

However, many surfaces also reflect horizontally polarised light, such as crude oil ponds (Horváth and Zeil, 1996; Horváth et al., 1998), cars (Blahó et al., 2014; Kriska et al., 2006; Wildermuth and Horváth, 2005), asphalt (Kriska et al., 1998), gravestones (Horváth et al., 2007), even solar panels (Horváth et al., 2010). In addition, these surfaces reflect horizontally polarised light more strongly than water, making them potentially more attractive (Horváth et al., 1998). This leads to odonates drowning in the oil pools or ovipositing on other unsuitable surfaces instead of ovipositing on water, thus drying out the eggs and ultimately decreasing fitness. Many of these horizontally-polarised-reflecting surfaces are common in cities (Horváth et al., 2009; Villalobos-Jiménez et al., 2016), although some species of odonates seem to thrive in urban areas

(Villalobos-Jiménez et al., 2016), suggesting there may be a mechanism for odonates to cope with these ecological traps.

Mitigating the negative effects of ecological traps requires an understanding of their strength, mechanism, and evolution, but this is often lacking (Hale et al., 2015). Studies instead focus on measuring traps in the field with inferences about selective pressures (Robertson and Hutto, 2006). Even though these studies contribute to understanding the impact of ecological traps, they do not control for phenotypic plasticity, therefore it is difficult to ascertain whether the (now) maladaptive behaviour has a genetic basis, whether it will contribute to the gene pool and continue the maladaptive trait in future generations, or perhaps more interestingly, if there is a mechanism which can decouple this maladaptive behaviour.

Even though strongly polarising surfaces are preferred over suitable habitats (Horváth et al., 1998), this has not been studied in the context of urbanisation. It is true that suitable habitats are not as frequent in urban areas compared to their rural counterparts, whereas polarising surfaces are more frequent in urban environments compared to undisturbed habitats (Horváth et al., 2009). Therefore, odonates may be more susceptible to ecological traps in cities merely due to the increased availability of polarising surfaces and reduced availability of suitable habitat in urban areas. In order to look at habitat selection and ecological traps in urban ecosystems, a student explored the potential for localised adaptations to ecological traps in odonates as part of an unpublished MSc dissertation at the University of Leeds, conducted in June-July 2015. The study in question consisted of (i) multiple-choice field experiments around Leeds and Bradford

in an urban-rural gradient using test surfaces reflecting light in various degrees of polarisation; (ii) laboratory dual-choice experiments using horizontally-polarised, vertically-polarised and non-polarised light on field-caught specimens of the blue tailed damselfly (*Ischnura elegans*). The results from the field experiments suggested that individuals from more urbanised environments were deceived less by unsuitable habitat cues compared to individuals from less urbanised environments ($P < 0.001$). However, there was no significant difference found between populations of various degrees of urbanisation in the laboratory experiments when presented with horizontally polarised light and light of other polarisations in the laboratory choice experiments. Nonetheless, these results confirm positive polarotaxis in *I. elegans* and suggest that odonates from more urbanised populations can potentially adapt to polarised light pollution (PLP) and, therefore, ecological traps. However, the mechanism driving this phenomenon is unknown to this date. Additionally, the study was conducted with field-caught specimens, meaning phenotypic plasticity was not controlled for. The work described in this chapter explores those unpublished findings, and will be combined with that other project in a manuscript at a later date.

Additionally, preference to horizontally polarised light may vary according to ontogeny, since immature odonates tend to disperse away from water bodies until they reach maturity, and then return to breed (Horváth et al., 2007; Wildermuth, 1998). This behaviour can be a result of a preferential shift from unpolarised to horizontally polarised light: sexually immature adults may show a negative polarotaxis (i.e. they avoid horizontally polarised light), but when these individuals reach sexual maturation, they could become attracted to horizontally polarised light instead (Corbet, 1999). Thus,

sexual maturation may intervene in the behavioural response to horizontally polarised light in odonates, and may also be a mechanism driving adaptation of urban odonates to ecological traps. Here, I examine the behavioural response of odonates to horizontally polarised light across different ages in the adult phase and compare between urban and rural populations. Contrary to other studies, this investigation will make use of laboratory rearing to control for phenotypic plasticity and examine the ontogeny of the trait.

Methods

Collection of adults and larvae rearing

I used individuals from common rearing conditions to evaluate the ontogenetic variation in the polarotactic response in adult odonates. I obtained *I. elegans* eggs from field-caught adult females from 5 sites in an urban to rural gradient (Table 4.1) during July-August 2015. Once the eggs hatched, the larvae were reared at 20°C at a photoperiod of 14L:10D with aerated tap water and fed with *Artemia* sp. and *Daphnia magna ad libitum*. Once the larvae emerged, the adults were kept in an insect net cage and fed with *Drosophila melanogaster ad libitum*. However, due to a large mortality rate in the larvae and low numbers of emerged adults reaching sexual maturity in the lab – particularly males – some of the individuals tested were collected as larvae from the field instead of being reared in the laboratory since the egg stage (reared from the egg stage: $N_{urban} = 9$, $N_{rural} = 28$; reared from the larval stage: $N_{urban} = 36$, $N_{rural} = 10$).

Therefore, the individuals used in the tests that were reared in the laboratory are part of a semi-controlled rearing experiment ($N_{urban} = 45$, $N_{rural} = 38$).

I also captured adult *I. elegans* from the field to compare the results with the lab-reared individuals ($N_{urban} = 21$, $N_{rural} = 24$). In this case, it was not possible to control for the mating status of the individuals (virgin vs. mated) or to analyse the changes in different ages, but instead the response of only sexually mature individuals to polarised light was tested. One of the advantages of using *I. elegans* is that sexually mature adults – both males and females – have a different colouration to their immature counterparts, thus the identification of mature adults in the field was based on their colouration.

Table 4.1. Sampling sites used for collecting *Ischnura elegans*. Land use classification of sampling sites was based on the percentage of urban cover (according to the Land Cover Map (LCM) 2007) at a distance of 1 Km around the ponds.

Location	Land use	Latitude	Longitude
ASD Metal Services	urban	53° 46' 04.2" N	1° 30' 41.2" W
Freemans Grattan Holdings (FGH) Ltd Listerhills Warehouse	urban	53° 47' 50.5" N	1° 46' 14.6" W
Kemira Chemicals UK	urban	53° 46' 43.0" N	1° 44' 46.4" W
Letchmire Pastures Nature Reserve	rural	53° 44' 27.2" N	1° 21' 26.1" W
Middleton Park	rural	53° 45' 16.1" N	1° 32' 41.9" W
Roundhay Park	rural	53° 50' 26.1" N	1° 29' 43.4" W
Paull Holme Strays Nature Reserve	rural	53° 42' 40.0" N	0° 12' 51.9" W
St. Aidan's Country Park	rural	53° 45' 05.4" N	1° 23' 58.6" W

Laboratory choice experiments

The adult *I. elegans* were introduced into a dual-choice chamber made of matte cardboard (57 x 30 x 8 cm; Figure 4.1). Each individual was tested three times under three different conditions: (1) horizontally polarised light vs. unpolarised light (H-U test); (2) horizontally polarised light vs. vertically polarised light (H-V test); and (3) vertically polarised light vs. unpolarised light (V-U test). Polarised light was created using a common linearly polarising filter (DyanSun 58mm slim linear polarising filter) positioned to reflect the required angle of polarisation.

To ensure a constant light intensity throughout the experiments, unfiltered light sources used in tests 2 and 3 were covered by a semi-transparent material and measured using a light meter to within 10 lx of the light intensity of the filtered light source. Light measurements were taken in the centre of the experimental chamber. Light variation within the chamber was not measured, although given the length of the chamber (57 cm), variation is likely to be low. External light surrounding the apparatus remained constant and was blocked from the view of the individual as much as possible. A ruler was placed inside the apparatus for recording movement over time. The choice chamber was covered in netting material to prevent any individuals escaping. Two markers were drawn intermediately between the centre of the apparatus and the two terminal light sources (Figure 4.1). Individuals were deemed to have chosen a preferred light source upon reaching either of the markers. The time taken for the individual to reach the marker was recorded as well as the position of the individual within the apparatus at 20, 40, and 60 seconds and then at 30 second intervals for 10 minutes or until the animal

reached a marker. If no marker was reached within the 10 minutes of observation then the individual was deemed as showing no preference. The lab-reared individuals were tested every 2 days, starting from day 2 after emergence until they died; the field-caught individuals were only tested once.

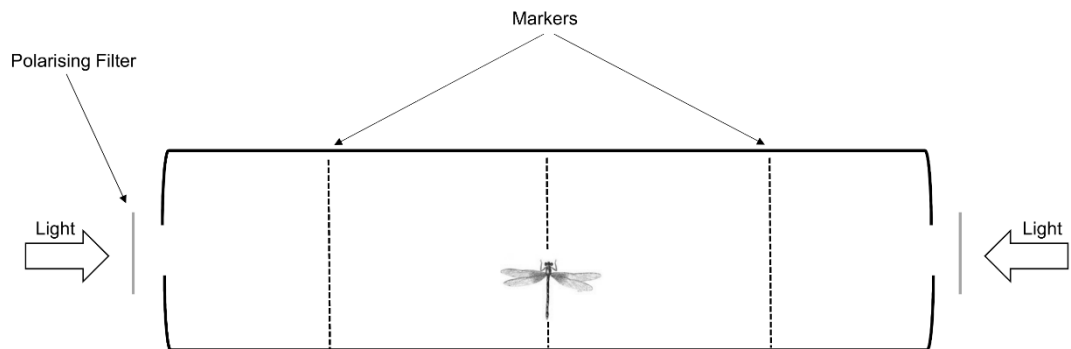


Figure 4.1. Experimental apparatus for testing individual preferences between two light sources of various angles of linear polarisations.

Statistical analysis

All statistical analyses were performed using R 3.0.1. (R Core Team, 2013). To test the differences in the behavioural response to polarised light across different ages in urban and rural populations, I used a Generalised Linear Mixed Model (GLMM) with binomial error using the lme4 package (Bates et al., 2014), where light choice in each type of test used in the experimental setup was the response variable, age and land use (urban and rural) were used as explanatory variables and individual ID was the random effect to account for repeated measurements. However, in field-caught specimens, I used only a Generalised Linear Model (GLM) with binomial distribution, since all measurements were independent. In this model, the light choice was also the response variable, but only

land use was the explanatory variable. Initially, sex was also considered as an explanatory variable for the analyses with individuals reared in the laboratory as well as the field-caught adults. However, sex did not contribute significantly to the models and was therefore eliminated.

I also tested the latency of choice making as a measurement of the strength of attraction to polarised light across different ages in urban and rural populations. In this case, I used the Cox proportional hazards method using the survival package (Therneau, 2015), with time of decision-making and light choice as the response variables, land use and age as explanatory variables, and clustering the data by the individual ID to account for repeated measurements in lab-reared odonates. With the field-caught specimens, only land use was the explanatory variable and clustering of data was not necessary since the measurements here are independent. Once again, sex was not included as an explanatory variable in these analyses given that it did not contribute significantly to the models.

Results

After analysing the preference for horizontally polarised light in the H-U test with the individuals reared in the laboratory, age had a significant effect (see Table 4.2; Figure 4.2), with older individuals having a stronger preference for horizontally polarised light. However, the response of urban individuals reared in the laboratory was not significantly different to the response from rural individuals (Table 4.2; Figure 4.2). In the H-V test, urban individuals reared in the laboratory showed a significantly higher

probability of selecting horizontally polarised light compared to rural individuals (Table 4.2; Figure 4.2), although this response did not change significantly across ages (Table 4.2; Figure 4.2). In the V-U test, the difference was not significant between urban or rural individuals reared in the laboratory at any age (Table 4.2; Figure 4.2).

Unexpectedly, the results from these tests were different when field-caught individuals were used. In the H-U test, urban individuals had a significantly lower probability of selecting horizontally polarised light compared to rural individuals (Table 4.2; Figure 4.2), contrary to the results from the test using individuals reared in the laboratory. Individuals caught from urban locations showed no significant difference compared to rural individuals in their preference for polarised light in H-V test (Table 4.2; Figure 4.2) nor in V-U test (Table 4.2; Figure 4.2).

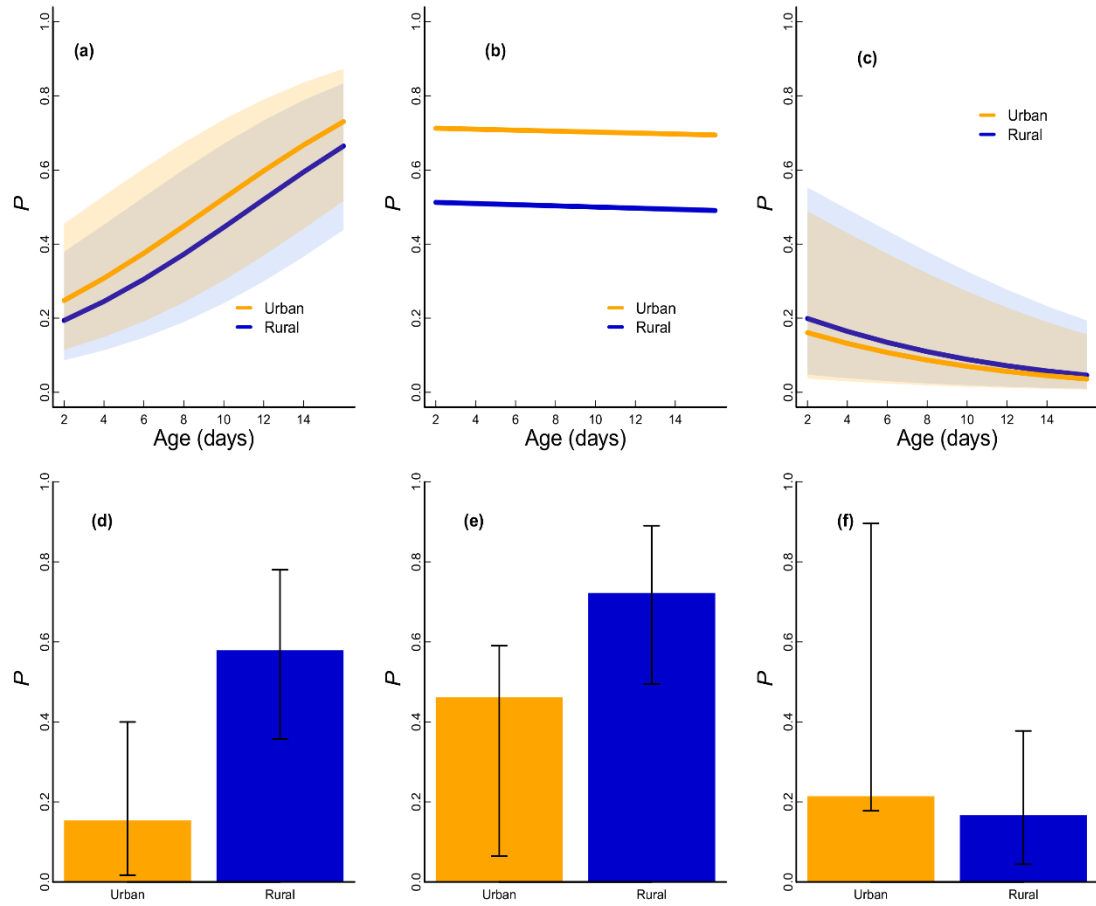


Figure 4.2. Results from the binomial models showing the preference for polarised light between urban (*orange*) and rural (*blue*) populations. Graphs from a-c represent the relationship in lab-reared individuals between age and the probability (P) of choosing (a) horizontally polarised light over unpolarised light; (b) horizontally polarised light over vertically polarised light, and (c) vertically polarised light over unpolarised light. Shaded areas represent 95% CI. Graphs from d-f represent the preference of field-caught adults for (d) horizontally polarised light over unpolarised light; (e) horizontally polarised light over vertically polarised light, and (f) vertically polarised light over unpolarised light. Error bars represent 95% CI.

Regarding the latency of decision-making in the H-U test using the laboratory-reared individuals, age had a significant impact, with older individuals taking less time to choose horizontally polarised light (Table 4.3; Figure 4.3). No difference between urban and rural individuals was found in this test (Table 4.3; Figure 4.3). However, there was

no significant effect of age or urbanisation on the latency of decision-making in the H-V test (Table 4.3; Figure 4.3) or in the V-U test (Table 4.3; Figure 4.3). On the other hand, once the tests were conducted with the field-caught specimens, the results varied. Firstly, urban individuals took significantly longer to make a decision in H-U test (Table 4.3; Figure 4.3) compared to rural individuals. However, there was no significant difference between urban and rural individuals caught in the field in the latency of decision-making in H-V test (Table 4.3; Figure 4.3) or in V-U test (Table 4.3; Figure 4.3).

Table 4.2. Predictors of preference for horizontally polarised light (or vertically polarised light in testing vertically polarised light against unpolarised light) in the damselfly *Ischnura elegans*. Significant values are highlighted in bold.

	Parameter	β	SE	z	P
<i>Reared in laboratory</i>					
H-U test	Urban land use	0.314	0.424	0.741	0.459
	Age	0.151	0.068	2.215	0.027
H-V test	Urban land use	0.858	0.374	2.296	0.022
	Age	-0.006	0.060	-0.105	0.916
V-U test	Urban land use	-0.259	0.546	-0.474	0.636
	Age	-0.117	0.099	-1.186	0.236
<i>Caught in the field</i>					
H-U test	Urban land use	2.023	0.898	2.252	0.024
H-V test	Urban land use	1.110	0.766	1.449	0.147
V-U test	Urban land use	0.310	0.908	0.342	0.733

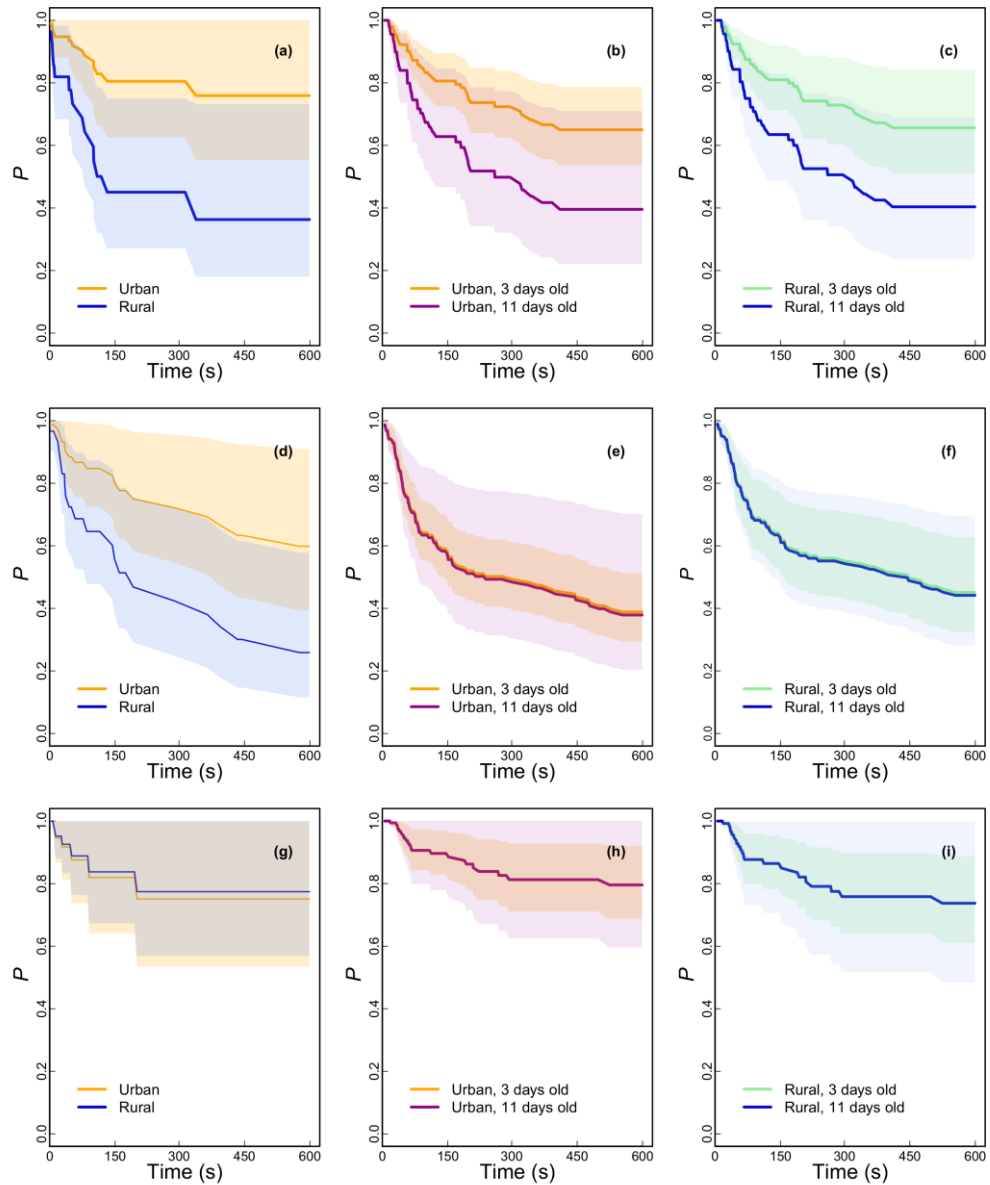


Figure 4.3. Latency of decision-making in urban and rural individuals. Subfigures a-c show the probability (P) of choosing horizontally polarised light over time in H-U test in (a) field-caught adults from urban and rural areas; (b) immature (3 days old) and mature (11 days old) urban individuals reared in the laboratory, and (c) immature (3 days old) and mature (11 days old) rural individuals reared in the laboratory. Subfigures d-f show the probability (P) of choosing horizontally polarised light over time in H-V test in (d) field-caught adults from urban and rural areas; (e) immature (3 days old) and mature (11 days old) urban individuals reared in the laboratory; (f) immature (3 days old) and mature (11 days old) rural individuals reared in the laboratory. Subfigures g-i show the probability (P) of choosing vertically polarised light over time in V-U test in (g) field-caught adults from urban and rural areas; (h) immature (3 days old) and mature (11 days old) urban individuals reared in the laboratory, and (i) immature (3 days old) and mature (11 days old) rural individuals reared in the laboratory. Shaded areas represent 95% CI.

Table 4.3. Predictors of latency to approach horizontally polarised light (or vertically polarised light in V-U test) in the damselfly *Ischnura elegans*. Significant values are highlighted in bold.

	Parameter	β	Hazard Rate (HR)	SE	z	P
<i>Reared in laboratory</i>						
H-U test	Urban land use	0.022	1.022	0.326	0.064	0.949
	Age	0.096	1.100	0.043	2.699	0.008
H-V test	Urban land use	0.173	1.118	0.233	0.713	0.476
	Age	0.003	1.003	0.042	0.085	0.932
V-U test	Urban land use	-0.288	0.750	0.429	-0.713	0.476
	Age	-0.002	0.998	0.626	-0.003	0.998
<i>Caught in the field</i>						
H-U test	Urban land use	-1.303	0.272	0.656	-1.984	0.047
H-V test	Urban land use	-0.969	0.380	0.496	-1.953	0.051
V-U test	Urban land use	0.115	1.122	0.817	0.140	0.888

Discussion

Ecological traps represent a subtle and insidious threat to biodiversity, by uncoupling environmental cues from fitness benefits. However, this is the first study to explore the possibility of adaptation to ecological traps. The results suggest that age has a significant impact on the behavioural response to horizontally polarised light, with older individuals preferring horizontally polarised light over non-polarised light, regardless of land use (urban or rural). After analysing the latency of decision-making in individuals reared in the laboratory, age also had a significant impact, with older individuals taking less time to choose horizontally polarised light compared to non-polarised light, though

no significant difference between urban and rural individuals was found in this test. Unexpectedly, field-caught individuals from urban areas showed a significantly lower probability of selecting horizontally polarised light compared to individuals caught from rural areas, contrary to the results from the lab-reared individuals. Likewise, field-caught individuals from urban areas took significantly longer to make a decision in this test. The individuals tested did not show a preference for vertically polarised light. In the following lines, I will provide possible mechanisms driving the behavioural responses found to horizontally polarised light.

Preference for horizontally polarised light has developed in odonates as a cue for suitable habitat, which elicits reproductive behaviour such as oviposition in females or patrolling in males (Horváth and Varjú, 1997; Wildermuth, 1998; Bernáth et al., 2002). In *I. elegans* there is a positive correlation between age and sexual maturation (Parr, 1973); therefore, it is within reason that preference for horizontally polarised light increased with age. The empirical demonstration of an ontogenetic switch from negative to positive polarotaxis from this study fits with the theory that polarotaxis is associated with reproductive behaviour. This ontogenetic switch has also been found in other aquatic insects, such as mayflies (Szaz et al., 2015). However, this switch has considerable implications for population-level responses to ecological traps since mature individuals are more susceptible to ecological traps. There is also a consequence for the understanding of the mechanism underlying the response, since there may be physiological factors associated with sexual maturity that are potentially involved in polarotaxis, e.g. juvenile hormone (JH). JH is key in regulating a range of physiological, behavioural, and life-history traits such as mating, immune response, senescence and

survival (Córdoba-Aguilar and González-Tokman, 2014). JH promotes egg production in females (Flatt et al., 2005) and increases territorial behaviour in males (Contreras-Garduño et al., 2009), but also promotes rapid senescence (González-Tokman et al., 2013) and decreases immune response (Contreras-Garduño et al., 2009). Thus, JH may play an important role in facilitating the polarotactic response of odonates, though the detailed mechanism is unknown to date.

Importantly, this study demonstrated the behavioural discrepancy between the individuals from the common rearing experiment and field-caught adults. The results show there is no genetic basis underlying the decreased preference for horizontally polarised light found in odonates from urban areas. However, natural selection can be driving this response in adult individuals caught in urban areas: given that artificial horizontally-polarising cues are less frequent in rural areas (Horváth et al., 2009), natural selection has not acted upon these populations, whereas in urban areas the increased presence of ecological traps will favour individuals that show decreased preference for horizontally polarised light. The results suggest that even though there is no genetic mechanism underlying this response yet, there is still strong selection already acting upon urban populations, therefore there is potential for future generations to genetically develop resistance to ecological traps. However, ecological traps have existed for a relatively short time period which may be insufficient for adaptation to occur in a trait that has had such an important role in the semi-aquatic lifestyle of these insects (Gates and Gysel, 1978; Schlaepfer et al., 2002). According to Schlaepfer et al. (2002), if populations cannot adapt rapidly to ecological traps or the population is too small to persist until adaptation occurs, ecological traps lead to abrupt population

declines or even extinction. Therefore, urban odonate populations may act as sinks in wider metapopulations unless odonates can adapt promptly to ecological traps.

However, I was unable to control for the mating status in the field-caught individuals, which may have had an effect on the results.

The results also showed that rural field-caught adults were significantly quicker in choosing horizontally polarised light compared to their urban counterparts. The aim of decision making is to evaluate the advantages and disadvantages of all the alternative options available in order to avoid or minimise risks (McFarland, 1977). This action depends on many factors, both external (weather conditions, predators) and internal (prior experiences, weight, etc.) (McFarland, 1977). The time invested in decision-making is crucial for acquiring the best outcome possible with increased accuracy and minimal risks (Zenger and Fahle, 1997; Skorupski et al., 2006). However, there may be a trade-off between latency of decision-making and the benefit of such decision (Skorupski et al., 2006; Chittka et al., 2009). For example, damselflies that take longer to decide to approach a potential mate may have increased accuracy and avoid risks such as predation, but on the other hand they lose more opportunities for mating (Hilfert-Rüppell, 1999). In various circumstances, natural selection may be in favour of bold individuals, which take less time to make a decision despite the presence of risks (Kurvers et al., 2011). This is the case of some invasive *Gambusia* species, which owe their success in novel environments to increased boldness (Rehage and Sih, 2004). Likewise, many species have been successful colonisers of urban areas due to increased boldness (Evans et al., 2010; Lowry et al., 2013). Predation risk is not expected to differ among urban and rural damselflies given that their predators are generalistic. However,

in this case, individuals that take longer to make a decision are less susceptible to ecological traps, particularly in urban areas. There may be a trade-off between boldness in urban odonates and susceptibility to ecological traps. Bold urban organisms may be more prone to ecological traps. Thus, selective pressures may be already driving resistance to ecological traps found in field-caught urban odonates. However, as previously mentioned, these results were not found in lab-reared individuals, so there appears to be no behavioural adaptation yet.

On the other hand, individuals reared in the laboratory showed decreased latency of decision-making with increased age, which suggests there is a mechanism associated with sexual maturation and senescence that influences this behaviour. Studies have shown that testosterone in vertebrates, for instance, increases boldness (Raynaud and Schradin, 2014) and also aggressiveness (Boudreau, 2011). The invertebrate homologue, JH, has shown similar results in damselflies (e.g. Contreras-Garduño et al., 2009). Considering JH increases with age (González-Tokman et al., 2013), it is within reason that older individuals took less time to make a decision. Even though it is very likely that JH is the main regulator driving the latency of decision-making in odonates, the empirical evidence supporting this idea does not exist to this date. Further studies could provide valuable insights into the role of JH in latency of decision-making and preference for horizontally-polarised light in odonates.

Despite the fact that urban and rural individuals reared in the lab showed no difference in their preference for horizontally-polarised light, there is indirect evidence which may suggest that urban odonate populations in the wild have a shorter life span compared to

rural populations. Villalobos-Jiménez and Hassall (2017) showed that the trailing edge of the flight period of odonates is shorter in cities than in rural areas, which suggests a contraction of the flight period and that the adult phase has a shorter life span. This may explain why rural individuals caught in the field showed a stronger preference for horizontally polarised light compared to the field-caught individuals.

Interestingly, the results found in this study differ from the MSc dissertation conducted on the same topic. In the dissertation, there was no difference reported in the preference for horizontally polarised light between urban and rural individuals, whereas in this case the urban field-caught specimens showed a distinct avoidance to horizontally polarised light. This may be because the study in question did not control for sexual maturation, the individuals used could have been mature or immature, whereas all the field-caught adult individuals tested in this study were mature.

To conclude, this study demonstrates that there are considerable differences in the susceptibility to polarised light pollution, and that these manifest more strongly in urban odonate populations. However, there is no evidence that this selection pressure has produced a genetic adaptation in urban populations. Ontogenetic variation in polarotaxis means that adult odonates are more susceptible to ecological traps than younger animals, which suggests that there may be subtle demographic effects on populations and implies a role for juvenile hormone in driving the response to polarised light. The findings from odonates may well extend to other semi-aquatic insects which exhibit similar behavioural responses to PLP, with significant consequences for the aquatic and terrestrial food webs in which such invertebrates play a fundamental role.

Chapter 5: Differentiation of wing shape patterns among urban, suburban, and rural populations of a damselfly

Abstract

Dragonflies and damselflies (the Odonata) are among the most efficient flying insects. However, fragmentation of the landscape can increase distance between habitats and affect costs of dispersal, thus shaping phenotypic patterns of flight-related traits, such as wing shape, wing loading and wing size. Urban landscapes are highly fragmented, which limits dispersal among aquatic habitats. Hence, strong selective pressures can act upon urban populations in favour of individuals with increased flight performance, or may lead to the reduction in dispersal traits. Here, I explore differentiation in morphological flight-related traits among urban, suburban, and rural populations of the damselfly *Ischnura elegans*, which is one of the most abundant species in both urban and rural ponds in Europe. I sampled 20 sites across Leeds and Bradford, UK, in an urban-to-rural gradient from June to August 2014 and 2015 ($N_{\text{males}}=201$, $N_{\text{females}}=119$). I compared wing shape among different land use types using geometric morphometrics. Other wing properties analysed were wing aspect ratio, wing loading, and wing centroid size. Unexpectedly, I found no significant effect of urban land use on wing shape. However, wing shape differed significantly between males and females. Additionally, females showed significantly larger wing centroid sizes ($P < 0.001$), increased wing loading ($P < 0.001$) and aspect ratio ($P < 0.001$) compared to males across all land use types. Possible mechanisms driving these results are further discussed.

Introduction

As aerial predators, dragonflies and damselflies (the Odonata) are adapted to fly efficiently in order to catch prey in the air, and also use their flight ability to disperse, migrate, mate, defend territories, and flee from predators (Marden, 2008). Many morphological traits dictate the flight performance in odonates and other insects, such as wing shape and size, body size, wing loading (i.e. the ratio of body mass to wing area), and thoracic muscle mass (Dudley, 2000; Marden, 2008). Body size and muscle mass influence flight performance strongly, since smaller individuals may need less energy to move and show increased agility (Serrano-Meneses et al., 2007), although their muscle mass and fat reserves are more limited (Marden, 1989; Serrano-Meneses et al., 2007; Samejima and Tsubaki, 2010), therefore representing a trade-off between flight performance and energetic costs (Serrano-Meneses et al., 2007). However, for this study, I will focus on the main functional organs for flight: the wings.

Larger wings produce more lift and carry heavier loads (Marden, 1987; Wootton, 1992). The ratio of wing length to width, known as aspect ratio, has also a strong influence on flight performance, although the resulting effect in insects can be quite different to that in vertebrates. In vertebrates, higher aspect ratio (i.e. longer, narrower wings) decreases the lift-to-drag ratio, which in turn decreases energetic costs and facilitates gliding and long-distance dispersal (Norberg, 1989). High aspect ratios have been found in a wide range of migratory birds (Mönkkönen, 1995). On the other hand, lower aspect ratios (shorter, wider wings) improve manoeuvrability (Norberg, 1989), a trait that is

particularly important when escaping predators, catching prey, or fighting against a rival male. However, studies regarding the role of aspect ratio in insects have found rather contrasting results. Firstly, insects operate at very low Reynolds numbers (a measure used to predict the flow patterns of fluids), and it has been proposed that the benefits of higher aspect ratios are in fact reversed in such cases (Wootton, 1992) so that long, narrow wings increase manoeuvrability, whereas short, wide wings allow long-distance movements with low energetic costs. However, marginal populations of *Calopteryx splendens* and *Coenagrion puella* – both damselflies with expanding range margins – have shown longer, narrower wings, which may suggest that higher aspect ratios reduce energetic costs in a similar way to vertebrates, although the costs and benefits have not been demonstrated (Hassall et al., 2008; Hassall et al., 2009). Importantly, aspect ratio is not the only element of wing shape driving flight efficiency. For instance, petiolated or narrow-based wings –such as the wings of many zygopterans– are associated with slow flight and hovering because the base shows low angular velocity and contributes little force, whereas broad-based wings allow a wider range of speeds, from gliding to high-speed flight (Wootton and Newman, 2008). This is particularly true in anisopterans, which have wide-based hind wings that permit efficient gliding and fast flight (Wootton and Newman, 2008; Bomphrey et al., 2016). Wing loading, on the other hand, influences the amount of thrust generated per wing beat (Dudley, 2000).

Certain species have shown adaptations in these morphological traits to improve flight performance in order to disperse to environments of limited access, e.g. Taylor and Merriam (1995) show that wing shape of *Calopteryx maculata* is affected by habitat fragmentation. More recently, Outomuro et al. (2013) show that habitat type influences

wing shape of *Trithemis* spp., with long, narrow wings being more abundant in forested areas.

Urban environments represent heavily fragmented habitats, with low vegetation cover and frequent barriers such as roads and buildings (Grimm et al., 2008; Forman, 2014), all of which may impede dispersal to other aquatic habitats. Hence, the strong selective pressures acting upon urban odonate populations may drive wing patterns in favour of individuals with increased flight performance. Such a result has been found in the damselfly *Coenagrion puella* (Tüzün, Op de Beeck and Stoks, 2017), although this study only analysed phenotypic patterns among urban and rural males.

Here, I study the intraspecific variation in wing size, shape and wing loading of the damselfly *Ischnura elegans* in an urban-to-rural gradient to investigate which wing pattern is more successful in urban areas where dispersal may be limited. This species shows slow-speed flight (Bomphrey et al., 2016), but is widely distributed in Europe and is abundant in urban and rural wetlands (Goertzen and Suhling, 2013). Considering this species presents heavily petiolated wings, which generate considerable lift distally, this species may benefit from having longer wings by increasing flight efficiency and reducing energetic costs (Wootton and Newman, 2008; Dudley, 2000; Bomphrey et al., 2016). Hence, I hypothesize that large wings with high aspect ratios will be more abundant in urban areas to decrease the energetic costs of long-distance dispersal, whereas in rural areas, the smaller wings with low aspect ratios will be predominant due

to the facilitation of movement in the highly vegetated areas. Suburban populations will show an intermediate form of wing shape between urban and rural populations.

Methods

Field survey

I surveyed 20 ponds across Leeds and Bradford (Table 5.1; **¡Error! No se encuentra el origen de la referencia.**) in an urban to rural gradient from June to August 2014 and 2015. Classification of sampling sites was according to the proportion of urbanisation within 1 Km around each pond, which was calculated using the 25m Land Cover Map 2007 (Centre for Ecology & Hydrology, www.ceh.ac.uk/services/land-cover-map-2007) in ArcGIS 10.1 (ESRI, 2011). Because morphometric traits have shown small-scale spatial variation (e.g. Taylor and Merriam, 1995; Outomuro et al., 2013), sites were classified in three categories: urban, suburban, and rural. Sites with an urban cover of >45% in a 1 Km buffer were classified as urban; sites with a suburban cover of >45% in a 1 Km buffer were classified as suburban, and sites with an urban and suburban cover of <45% in a 1 Km buffer were classified as rural. Urban areas are typically heavily fragmented (Grimm et al., 2008), therefore sites classified as “urban” in this study are expected to be strongly fragmented compared to the “suburban” areas (moderately fragmented) and the “rural” areas (low fragmentation). However, the configuration of the landscape (i.e. fragmented vs continuous) was not directly assessed in this study. A total of 320 specimens of *Ischnura elegans* ($N_{\text{males}}=201$, $N_{\text{females}}=119$) were collected with a net, which were then fixed with 70% ethanol.

Geomorphometric analysis

Wings were dissected from the body as close to the thorax as possible and mounted on matte adhesive tape. Wings were scanned using the slide scanner on a Canon CanoScan LiDE 25 flatbed scanner with fixed exposure at 1200dpi. Left wings were reflected so that both left and right wings had the same orientation. After dissecting the wings, the specimens were weighted to the nearest 0.1 mg to obtain body mass.

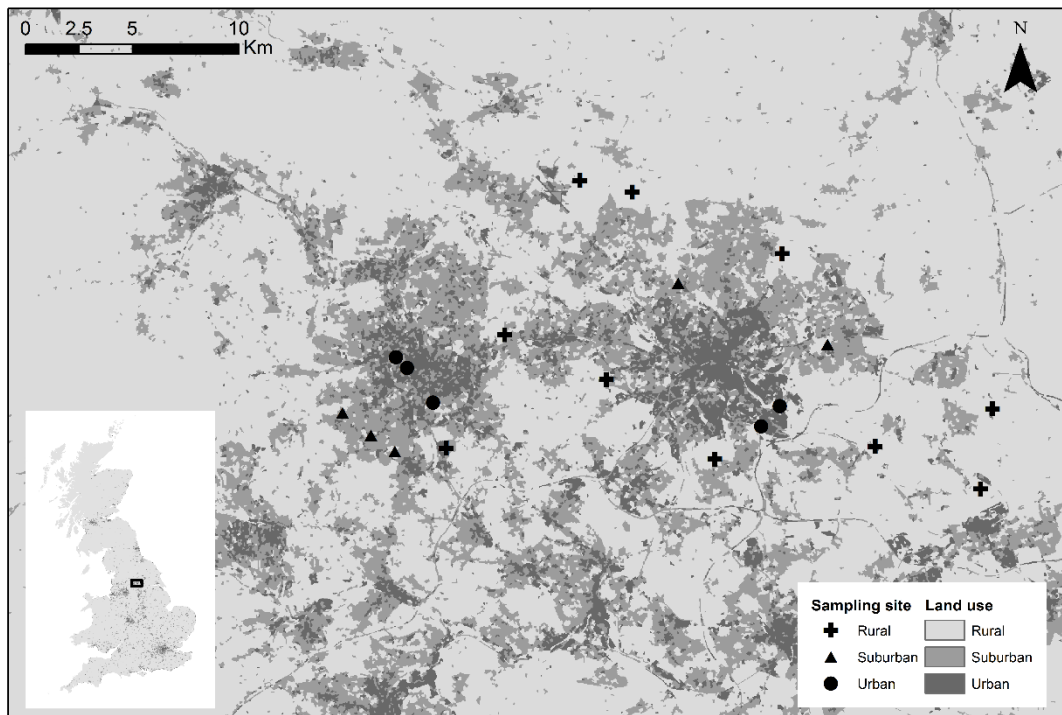


Figure 5.1. Map of the sampling sites for the morphometric analysis in Leeds (right) and Bradford (left), indicating the degree of urbanisation and classification of the sampling sites.

Table 5.1. Sampling site locations, land use classification of each site, proportion of urban, suburban, woodland, and grassland cover in a 1 Km buffer around the sampling sites, and sample sizes of female fore wings (N_{FFW}), female hind wings (N_{FHW}), male fore wings (N_{MFW}), and male hind wings (N_{MHW}) of *Ischnura elegans* per site.

Location	Latitude	Longitude	Land use	Urban cover (%)	Suburban cover (%)	Woodland cover (%)	Grassland cover (%)	N_{FFW}	N_{FHW}	N_{MFW}	N_{MHW}
ASD metal services	53° 46' 4.71" N	1° 30' 46.70" W	urban	45.80	23.55	4.25	10.47	10	9	17	17
FGH Ltd Listerhills Warehouse	53° 47' 52.21" N	1° 46' 21.69" W	urban	62.79	35.09	0.00	2.12	9	9	13	11
Kemira Chemicals	53° 46' 43.22" N	1° 44' 47.02" W	urban	45.35	43.09	3.39	8.17	26	24	23	23
Skelton Grange Environment Centre	53° 46' 35.18" N	1° 29' 58.65" W	urban	49.02	14.06	4.47	17.31	6	8	4	3
University of Bradford Main Campus	53° 47' 35.98" N	1° 45' 53.68" W	urban	64.78	33.05	0.00	2.16	4	4	2	3
Harold Park	53° 45' 29.16" N	1° 46' 25.74" W	suburban	11.47	67.87	0.15	18.72	10	9	15	16
Hollin Lane	53° 49' 42.57" N	1° 34' 17.41" W	suburban	7.60	64.08	10.38	13.85	2	2	25	26
Horton Bank Country Park	53° 46' 28.07" N	1° 48' 39.11" W	suburban	7.62	66.07	2.95	22.22	21	20	23	23
Primrose Valley Park	53° 48' 8.07" N	1° 27' 55.26" W	suburban	12.34	62.43	2.54	22.32	17	15	22	21
Reevy Mill Dam	53° 45' 53.80" N	1° 47' 26.75" W	suburban	10.95	80.29	0.00	8.76	2	2	6	6
Bierley Hall Wood	53° 45' 33.81" N	1° 44' 13.48" W	rural	13.43	25.12	5.17	52.48	10	11	18	17
Farnley Hall Fish Local Nature Reserve	53° 47' 17.14" N	1° 37' 22.50" W	rural	8.16	28.72	11.66	33.08	6	6	7	8
Ledston Luck	53° 46' 28.25" N	1° 20' 53.97" W	rural	1.04	3.83	3.94	15.71	8	10	8	8
Letchmire Pastures Nature Reserve	53° 44' 27.09" N	1° 21' 26.44" W	rural	5.33	5.93	4.97	26.32	6	6	13	12
Middleton Park	53° 45' 15.48" N	1° 32' 46.23" W	rural	2.18	31.46	28.36	31.66	37	34	69	72
None Go Bye Farm	53° 52' 18.74" N	1° 38' 28.14" W	rural	2.10	6.97	5.29	75.06	6	6	16	15
Paul's pond	53° 52' 0.68" N	1° 36' 13.40" W	rural	0.28	12.80	9.36	71.97	9	9	37	40
Roundhay Park	53° 50' 26.18" N	1° 29' 49.87" W	rural	4.20	21.54	17.23	39.46	13	14	27	33
Swillington Organic Farm	53° 45' 28.01" N	1° 26' 0.96" W	rural	2.64	10.29	16.55	33.79	12	12	13	14
Woodhall Lake	53° 48' 25.55" N	1° 41' 42.78" W	rural	8.43	37.10	5.27	43.36	2	1	7	7

In order to analyse wing shape, I used geometric morphometrics, which uses a multivariate approach to estimate the qualitative properties of wing shape and transform them to a quantitative measure (Bookstein, 1991). I digitised nine type 1 landmarks (Bookstein, 1991) defined as the intersection between the main veins (Figure 5.2) according to Arambourou et al. (2017) using the geomorph package (Adams and Otárola-Castillo, 2013) in R 3.4.0 (R Core Team, 2013). As a proxy of wing size, the wing centroid sizes were calculated as the square root of the summed squared distances from each landmark to the geometric centre of each wing (Bookstein, 1991). I also quantified (1) wing area as the area of the polygon defined by the landmarks 1–8, and (2) wing length as the distance between landmarks 1 and 4 (Arambourou et al., 2017). Wing loading was calculated as body mass/wing area and wing aspect ratio was calculated as wing length²/wing area (Gilchrist et al., 2000; Berwaerts et al., 2002). Both wing length ($r = 0.99$, $P < 0.001$) and area ($r = 0.96$, $P < 0.001$) were highly correlated with wing centroid size.

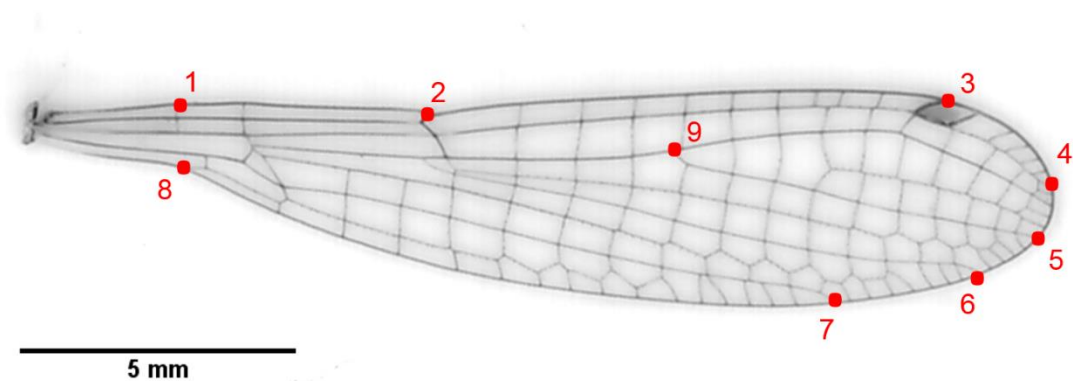


Figure 5.2. Localization of the nine landmarks digitised on the wings of *Ischnura elegans* according to Arambourou et al. (2017).

Wing shape was estimated using the landmarks previously digitised, with any differences among wing configurations other than shape differences (i.e., position, orientation and size) removed using the generalized Procrustes superimposition method (Rohlf and Slice, 1990). To confirm that wing shape is independent of wing size, or in other words, that there were no allometric effects, I calculated a linear regression with the Procrustes coordinates as the response variables and wing centroids as the explanatory variable. To assess the significance of this relationship, 100 permutations were conducted by randomly reassigning observations for Procrustes coordinates to observations for centroid sizes. I found a significant allometric effect ($F_{1, 1224} = 141.7, P = 0.009$), as has been observed previously in insect wings (Gilchrist et al., 2000; Debat et al., 2003). Because the shape variables were strongly dependent on wing centroids, I used the residuals of this regression as the non-allometric shape component. Principal components analysis (PCA) was then carried out on the non-allometric landmarks to obtain the shape variables as principal components scores. Considering the first four PC scores accounted for 88% of the overall variation (PC1: 60.58%, PC2: 12.11%, PC3: 10.82%, PC4: 4.49%), I used only these as a measure of wing shape.

Statistical analysis

To test the effect of land use on flight related traits, I used a linear mixed model using the lme4 package (Bates et al., 2014) with each of the flight-related traits as dependent variables (PC1, PC2, PC3, PC4, aspect ratio, wing loading, and wing centroids); sex and

types of land use (urban, suburban, rural) were the grouping explanatory variables, and the sex \times land use interaction was also tested. Before running the analyses, I compared the flight-related traits (PC1, PC2, PC3, PC4, aspect ratio, wing loading, and wing centroids) among types of wing (left and right, fore and hind wings) using a MANOVA to test whether all wings could be pooled together for the analysis. The results suggested fore and hind wings had significantly different flight-related traits (Wilk's $\lambda = 0.157$, $df_N = 7$, $df_D = 1159$, approximate $F = 887.95$, $P < 0.001$), but no significant differences were found among left and right wings (left and right fore wings: Wilk's $\lambda = 0.99$, $df_N = 7$, $df_D = 573$, approximate $F = 0.803$, $P = 0.59$; left and right hind wings: Wilk's $\lambda = 0.99$, $df_N = 7$, $df_D = 578$, approximate $F = 0.827$, $P = 0.57$). Therefore, the analyses were separated by fore wings and hind wings, but because the left and right wings were repeated for each specimen, the individual ID was used as a random effect. Additionally, to account for spatial variation, each sampling site nested within land use type was also added as a random effect. The P -values were obtained using the Satterthwaite approximation to calculate denominator degrees of freedom. I calculated the Variation Inflation Factors (VIF) to account for multicollinearity (see Table A.5 in the Appendix), and the resulting P -values from the linear mixed models were transformed using the False Discovery Rate (FDR) to account for multiple testing. Significant interactions were further analysed by conducting pairwise comparisons of least-square means using contrast analysis with the Tukey post-hoc test.

Results

Aspect ratio was significantly higher in females than males, both fore and hind wings (Table 5.2; Figure 5.3a,d), but no significant differences were observed among land use types (Table 5.2; Figure 5.3a,d). Wing loading, on the other hand, was only significantly larger in fore wings of females compared to fore wings of males (Table 5.2; Figure 5.3b), although in hind wings, there were no significant differences between males and females (Table 5.2; Figure 5.3e). Wing loadings were not significantly different across the different land use types (Table 5.2; Figure 5.3b,e). Wing centroid size was also significantly larger in fore and hind wings of females than males (Table 5.2; Figure 5.3c,f), and though the sex \times land use interaction was significant for wing size in hind wings (Table 5.2), the Tukey post-hoc test showed no significant differences in pairwise comparisons between land use types within males or females (Table 5.3).

Regarding the wing shape variables, all PC scores represented subtle changes in the wing planform (see Figure 5.4i-p), with very little shape variation ($\sigma^2 = 0.001$). All PC scores were significantly correlated with aspect ratio, although the strength of the correlation was weak except for PC3 (PC1, fore wings: $r = -0.242$, $P < 0.001$; PC1, hind wings: $r = -0.293$, $P < 0.001$; PC2, fore wing: $r = -0.292$, $P < 0.001$; PC2, hind wing: $r = -0.296$, $P < 0.001$;

Table 5.2. Results of the linear mixed-effects models testing the effect of land use, sex, and the resulting interaction of sex \times land use on the PC scores, wing aspect ratio, wing loading, and wing size of fore and hind wings. P-values were obtained using the Satterthwaite approximation to calculate denominator degrees of freedom. P-values presented here have been adjusted for multiple testing using the FDR correction. Significant differences are in bold.

	<i>df_N</i>	Fore wings			Hind wings		
		<i>df_D</i>	<i>F</i>	<i>P</i>	<i>df_D</i>	<i>F</i>	<i>P</i>
<i>PC1</i>							
Sex	1	298.07	88.359	<0.001	312.81	113.241	<0.001
Land use	2	13.29	1.477	0.410	11.32	3.025	0.219
Sex \times land use	2	297.80	0.616	0.668	311.95	1.573	0.374
<i>PC2</i>							
Sex	1	301.51	1.943	0.345	305.74	8.536	0.022
Land use	2	14.64	4.807	0.104	13.26	3.332	0.177
Sex \times land use	2	301.16	2.051	0.304	305.14	3.322	0.130
<i>PC3</i>							
Sex	1	300.72	1.348	0.398	301.69	0.487	0.638
Land use	2	15.40	1.383	0.420	15.97	0.078	0.987
Sex \times land use	2	300.43	0.062	0.987	301.33	0.004	0.996
<i>PC4</i>							
Sex	1	300.12	0.000	0.996	302.63	0.308	0.695
Land use	2	14.82	2.224	0.316	18.26	0.645	0.668
Sex \times land use	2	299.67	0.299	0.842	302.41	0.268	0.846
<i>Wing aspect ratio</i>							
Sex	1	299.83	106.912	<0.001	308.89	89.439	<0.001
Land use	2	14.68	3.509	0.170	12.16	1.766	0.374
Sex \times land use	2	299.44	2.732	0.177	308.02	3.246	0.130
<i>Wing loading</i>							
Sex	1	289.12	7.794	0.029	296.38	4.303	0.130
Land use	2	15.45	1.258	0.436	15.60	1.264	0.436
Sex \times land use	2	289.07	0.364	0.811	296.28	0.860	0.575
<i>Wing centroid size</i>							
Sex	1	280.75	462.474	<0.001	284.62	477.507	<0.001
Land use	2	15.87	1.866	0.374	15.54	1.607	0.390
Sex \times land use	2	280.89	1.551	0.374	284.53	5.154	0.030

PC3, fore wing: $r = -0.654$, $P < 0.001$; PC3, hind wing: $r = -0.625$, $P < 0.001$; PC4, fore wing: $r = 0.245$, $P < 0.001$; PC4, hind wing: $r = 0.171$, $P < 0.001$). PC1 showed significant differences between sexes (Table 5.2), with females showing larger PC1 values in both fore

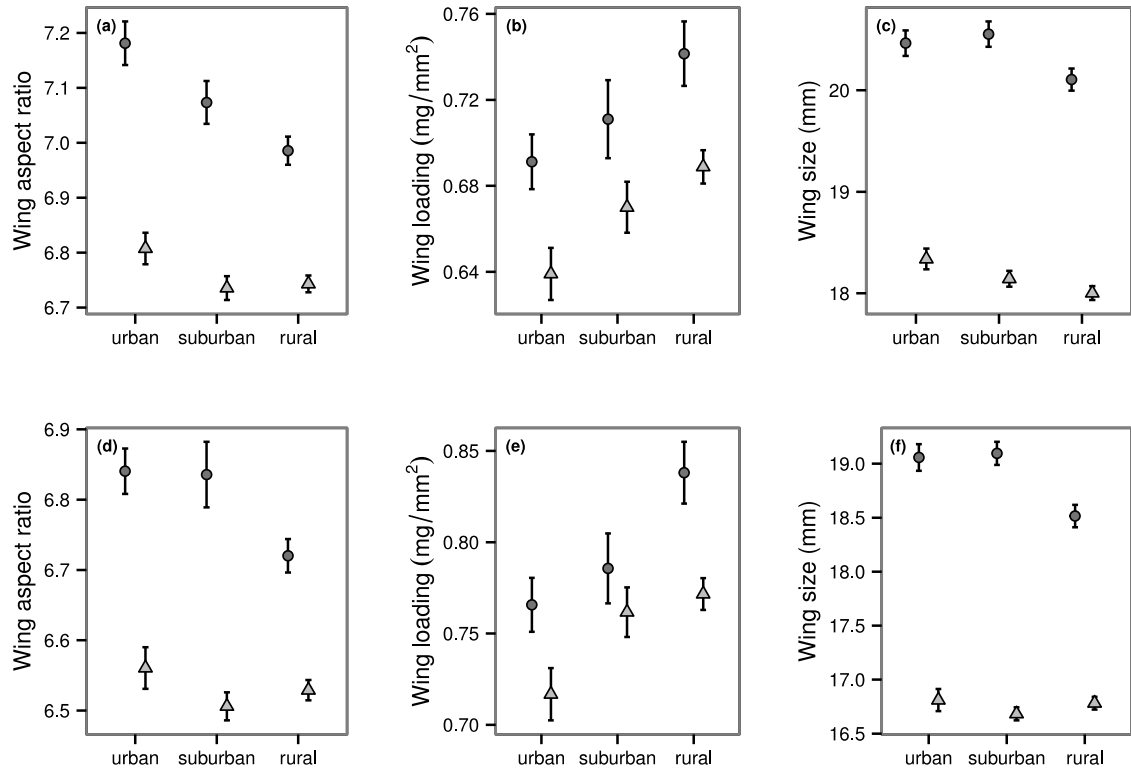


Figure 5.3. Mean morphological flight-related traits by males (*triangle*) and females (*circle*) from the urban, suburban, and rural populations sampled. **(a)** Wing aspect ratio in fore wings, **(b)** wing loadings in fore wings, **(c)** wing centroid size in fore wings, **(d)** Wing aspect ratio in hind wings, **(e)** wing loadings in hind wings, **(f)** wing centroid size in hind wings. Error bars represent ± 1 SE.

(Figure 5.4a; Figure 5.5) and hind wings (Figure 5.4; Figure 5.4. **Results** e). Females also exhibited significantly larger PC2 values than males in hind wings (Table 5.2; Figure 5.4f; Figure 5.5). PC3 and PC4 was not significantly different among sexes (Table 5.2). No significant effect of land use was found in any of the shape variables (Table 5.2).

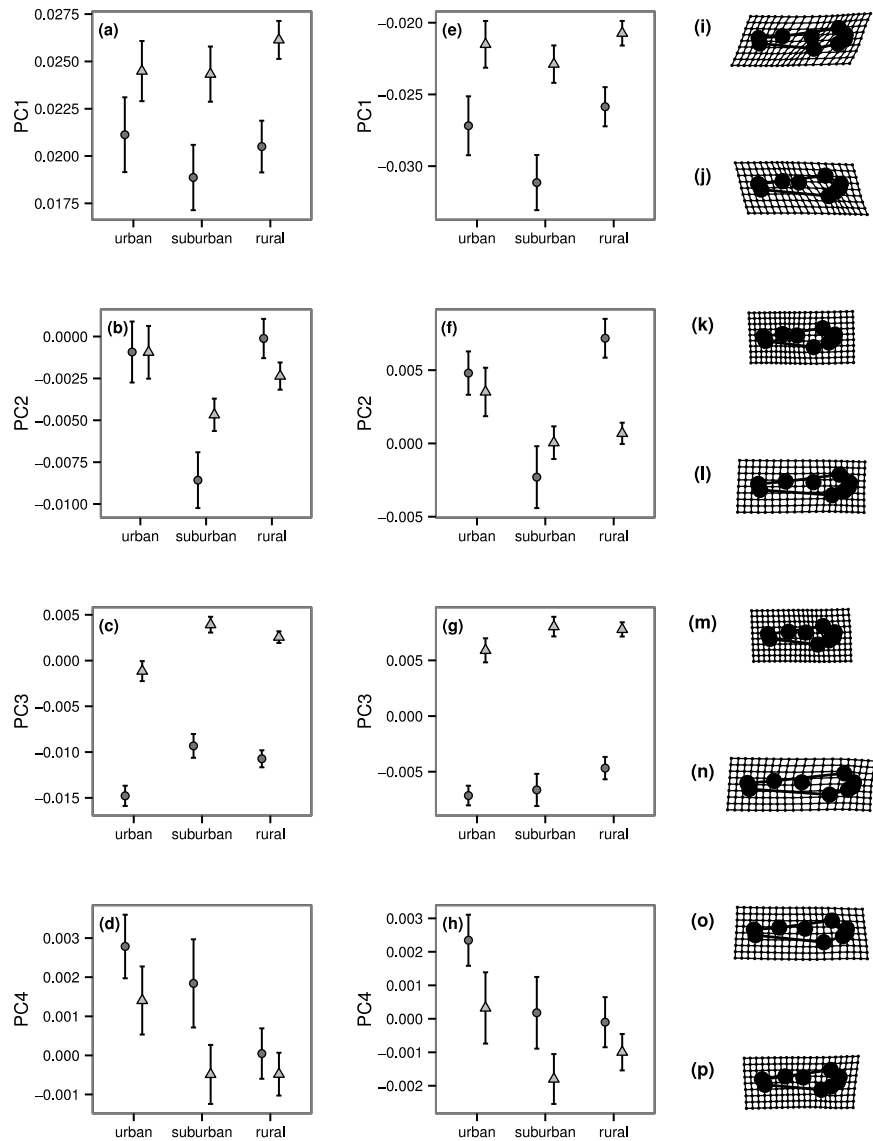


Figure 5.4. Results of the geometric morphometric analysis showing mean PC scores by males (*triangle*) and females (*circle*) from the urban, suburban, and rural populations sampled, and the deformation grids showing the changes in mean shape represented by the PC scores. **(a)** PC1 in fore wings, **(b)** PC2 in fore wings, **(c)** PC3 in fore wings, **(d)** PC4 in fore wings, **(e)** PC1 in hind wings, **(f)** PC2 in hind wings, **(g)** PC3 in hind wings, **(h)** PC4 in hind wings, **(i)** wing shape with maximum PC1 score, **(j)** wing shape with minimum PC1 score, **(k)** wing shape with maximum PC2 score, **(l)** wing shape with minimum PC2 score, **(m)** wing shape with maximum PC3 score, **(n)** wing shape with minimum PC3 score, **(o)** wing shape with maximum PC4 score, **(p)** wing shape with minimum PC4 score. Error bars represent ± 1 SE. To better visualize shape variations in the deformation grids, an amplification factor of 2 was applied.

Table 5.3. Results of the Tukey post-hoc analysis to analyse the sex \times land use interaction in the wing size of hind wings, showing the pairwise comparisons between males and females across land uses. Significant results are in bold.

	Δ Mean	SE	df	t	P
Rural females - suburban females	-0.69	0.30	27.04	-2.276	0.238
Rural females - urban females	-0.63	0.30	25.50	-2.110	0.314
Rural females - rural males	1.77	0.12	296.89	14.963	<0.001
Rural females - suburban males	1.76	0.28	20.95	6.205	<0.001
Rural females - urban males	1.55	0.30	25.13	5.193	<0.001
Suburban females - urban females	0.06	0.35	26.72	0.179	1.000
suburban females - rural males	2.46	0.30	24.55	8.314	<0.001
suburban females - suburban males	2.45	0.19	299.54	13.141	<0.001
suburban females - urban males	2.24	0.35	26.43	6.402	<0.001
urban females - rural males	2.40	0.29	23.06	8.270	<0.001
urban females - suburban males	2.39	0.33	22.12	7.188	<0.001
urban females - urban males	2.18	0.19	297.42	11.280	<0.001
rural males - suburban males	-0.02	0.28	18.72	-0.058	1.000
rural males - urban males	-0.23	0.29	22.72	-0.775	0.969
suburban males - urban males	-0.21	0.33	21.88	-0.630	0.987

Discussion

In this study, I found no evidence of differentiation of flight-related morphological traits in *I. elegans* due to urbanisation. Instead, there were subtle, but significant differences between males and females (see Figure 5.4 and Figure 5.5), particularly females having larger wing centroid sizes in fore and hind wings, higher aspect ratios in fore and hind wings, increased wing loadings in fore wings, higher PC1 values in fore and hind wings, which is associated with an increased distance between the pterostigma and the nodus (see Figure 5.4i, j), and higher PC2 values in hind wings, which represents a shorter distance between the nodus and the radial section (Figure 5.4k, l). In the following text, I will suggest plausible mechanisms driving these responses.

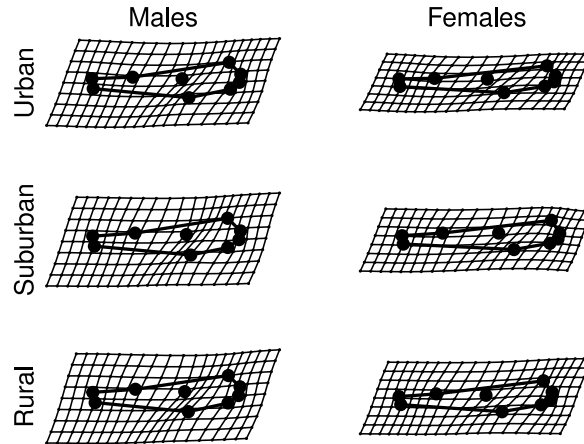


Figure 5.5. Deformation grids showing the mean wing shape of males and females in urban, suburban, and rural populations. To better visualize shape variations, an amplification factor of 5 was applied.

Urban areas can be heavily fragmented (Grimm et al., 2008) and fragmented habitats can affect morphological flight-related traits in odonates (Taylor and Merriam, 1995; Outomuro et al., 2013). However, in this study I found no significant difference in morphological traits associated with flight performance and dispersal among urban, suburban, and rural populations. This result is unexpected since it contrasts with other studies which have shown significant differences in flight-related traits in odonate populations due to urbanisation (e.g. Tüzün, Op de Beeck and Stoks, 2017). However, I only focused on the morphological differences in flight-related traits, I did not measure flight endurance, flight muscle mass, fat content, metabolic rate, or account for genetic variation, all of which influence flight performance and dispersal (Marden, 2008). Petiolated wings, as mentioned, do not allow gliding, therefore large energy storage could be advantageous for long-distance dispersal. In fact, another study (Tüzün, Op de Beeck and Stoks, 2017) did find

higher flight endurance in urban males of another damselfly (*Coenagrion puella*), though females were not assessed. However, *C. puella* is more likely to disperse to other ponds compared to *I. elegans* (Conrad et al., 2002), which may explain why the former species showed differences in flight-related traits between urban and rural populations, and the latter did not. Despite the fact that no differentiation was found in the phenotypic traits of *I. elegans* associated to flight, strong genetic differentiation was found among urban and rural populations of other *Ischnura* species, namely *I. senegalensis* and *I. asiatica*, which suggests dispersal is indeed limited in the urban landscape, thus isolating urban populations (Sato et al., 2008). Even though the genetic differentiation of urban and rural populations of *I. elegans* has not been investigated, urban populations are expected to be heavily isolated due to increased habitat fragmentation in cities and the low mobility of this species. Further studies are encouraged to explore the intraspecific variation of flight performance, dispersal, and genetic diversity within an urban landscape in *I. elegans* and other species, particularly linking flight morphology and function.

One of the main findings in this study is the conspicuous distinction of flight-related traits among males and females of *I. elegans* (Figure 5.5). Sexual wing dimorphism has been reported previously in *I. elegans* (Arambourou et al., 2017), and can be attributed to the difference in selection pressures to which males and females are subject to. Both males and females disperse away from their native water body after emerging to feed until they reach sexual maturity (Corbet, 1999). However, after becoming sexually mature, females only return to breeding sites when they are receptive (Corbet, 1999) and undergo stronger

selective pressure to forage (Anholt, 1992), whereas males tend to stay close to breeding sites in order to find a mate (Corbet, 1999; Beirinckx et al., 2006), therefore females may need to be more dispersive than males (Beirinckx et al., 2006). In such case, the larger, longer, and narrower wing pattern found in females could be of aid for long-distance dispersal, since the angular velocity increases towards the wing tip in flapping wings, notably in petiolated wings where the velocity gradient from base to tip is more pronounced (Dudley, 2000; Bomphrey et al., 2016), thus providing more lift per wingbeat (Bomphrey et al., 2016). The increased wing loadings found in females also promote dispersal by increasing the thrust generated per wingbeat (Dudley, 2000). However, more studies are needed to confirm the effect of increased aspect ratio in the flight performance of *I. elegans*.

Urbanisation is one of the main drivers of ecosystem change (Grimm et al., 2008; Faeth et al., 2011; McKinney, 2008), and the resulting fragmentation of the landscape can shape phenotypic patterns to facilitate dispersal (e.g. Tüzün, Op de Beeck and Stoks, 2017). However, *I. elegans* is a widespread species and one of the most abundant damselflies in Europe (Dijkstra and Lewington, 2006; Dow, 2010), which can tolerate a wide range of stressors (Dow, 2010). The results of this study suggest that this species' dispersal is not affected by increased fragmentation in the urban landscape and may also explain why this species thrives in urban ponds (Goertzen and Suhling, 2013). However, more studies are needed to analyse intraspecific and interspecific variation of flight-related traits in order to disentangle the effects of urbanisation at a population and community level. This, in turn,

will allow a better understanding of which species are more susceptible to land use change and how organisms and communities respond to novel environments.

Chapter 6: The effect of urbanisation on biodiversity and composition of aquatic macroinvertebrate communities, with an emphasis on riparian vegetation and odonates

Abstract

Urbanisation is one the major threats to biodiversity worldwide, representing one of the main causes of degradation, fragmentation and homogenisation of the landscape.

Freshwater ecosystems are no exception and are severely altered by urban development.

While there has been research suggesting low vegetation cover – among other environmental stressors – can affect biodiversity, the impact of specific urban stressors driving biodiversity loss, such as the modification of riparian vegetation on the biodiversity of urban ponds, has not been deeply explored. Here, I assess in more detail the impacts of urbanisation on adult dragonflies and damselflies, which are well established as a suitable group for studying these effects since they exhibit strong responses to environmental change. Specifically, I explore the particular components of the urban environment that mediate odonate diversity and community structure, with a focus on riparian vegetation structure, in Leeds and Bradford, UK. I also study the patterns of aquatic macroinvertebrate biodiversity to test the role of odonates as bioindicators of aquatic biodiversity in urban ponds. Riparian vegetation structure was quantified by identifying vegetation types by height and measuring density using two different, complementary methods: drop disc (used for measuring vegetation density of grasslands), and Robel pole (which can be used for grasslands and bushes). Unexpectedly, the results suggest urban land use has no impact on the biodiversity of odonates in the adult phase, nor on aquatic macroinvertebrates.

Additionally, riparian vegetation density does not change significantly across the urban-rural gradient, and riparian vegetation has no significant effect on the assemblage of

odonate species and aquatic macroinvertebrates. However, presence of fish and submerged vegetation were significant drivers of species composition, with taxa such as *Ischnura elegans* and Chironomidae showing tolerance to fish. The odonates *Coenagrion puella* and *Pyrrhosoma nymphula*, as well as members of the families Gammaridae (Amphipoda) and Gerridae (Hemiptera) were highly associated with increased cover of submerged vegetation. On the other hand, the presence of adult odonates was not strongly associated with the biodiversity of aquatic macroinvertebrates. These results indicate that urban ponds can maintain the same levels of biodiversity of aquatic macroinvertebrates (including odonates) as rural ponds, providing these ponds are adequately managed with abundant aquatic vegetation.

Introduction

Urbanisation is one of the main drivers of ecosystem change, having strong impacts on ecosystems which extend far beyond metropolitan borders (Faeth et al., 2011). Urban landscapes are highly fragmented, characterised by residential, commercial and industrial areas, while green areas mainly consist of city parks and gardens (Goertzen and Suhling, 2013). Biodiversity changes have been well investigated in urban areas in a wide range of taxa, including butterflies (Ruszczyk, 1987; Ruszczyk and De Araujo, 1992; Blair and Launer, 1997), birds (e.g. Marzluff, 2005), and plants (McKinney, 2008). Most of these studies show that biodiversity is reduced in highly urbanised areas (McKinney, 2002;

McKinney, 2008), although certain groups such as birds (Marzluff, 2005) and plants (McKinney, 2008) show increased biodiversity in suburban areas or where low to intermediate disturbance occurs. However, very few studies have investigated the underlying determinants of the spatial and temporal variation in patterns of biodiversity in urban areas (Werner, 2011).

Aquatic biodiversity in cities has been particularly overlooked, despite its vulnerability to urban stressors such as eutrophication (Paul and Meyer, 2001). Small water bodies such as ponds are frequently found in parks and gardens in urban areas for aesthetic purposes and to promote human well-being (Forman, 2014; Hassall, 2014). Ponds provide important habitats for biodiversity (Biggs et al., 2017) and, due to the great variety of pond types and functions (Hassall, 2014), ponds also contribute substantially to beta and gamma diversity (Céréghino et al., 2014; Hassall, 2014). Ponds also increase landscape connectivity by acting as “stepping stones” for species and support the formation of metapopulations (De Meester et al., 2005). Lentic water bodies in cities, however, are not sufficiently studied despite their value for conservation (Goertzen and Suhling, 2013).

Dragonflies and damselflies (the Odonata) have been shown to be a useful and well-used model system to study the drivers of biodiversity change in urban water bodies (Villalobos-Jiménez et al., 2016). Odonates are considered to be suitable bioindicators of habitat quality in both aquatic and terrestrial habitats (Oertli, 2008), they represent an important umbrella taxon for wetlands (Bried et al., 2007), and are considered “charismatic”, which in turn

increases recreation and tourism in wetlands (Lemelin, 2007) as well as engagement of the general public in citizen science (e.g. Hassall et al., 2007). Therefore, odonates may not only be of aid in identifying the main drivers of aquatic macroinvertebrate biodiversity in city ponds, but also play a key role in promoting biodiversity conservation in urban ponds. Additionally, biotic indices using benthic macroinvertebrates are versatile and robust tools for evaluating and monitoring freshwater ecosystem health, and odonates have been used extensively as part of these indices in biomonitoring programmes such as the Biological Monitoring Working Party (BMWP) scoring system (Paisley et al., 2014), which ranks benthic macroinvertebrates at a family level according to their sensitivity to environmental stressors, and the Dragonfly Biotic Index (DBI) in South Africa (Simaika and Samways, 2009; Simaika and Samways, 2012), which ranks odonate species according to their IUCN conservation status. Of these two biotic indices, the latter is faster and easier to use since it solely uses odonate species as barometers of environmental health. Thus, odonate biodiversity can potentially be used to develop a rapid ecosystem assessment similar to the DBI in the UK as well, providing these species show a strong association with overall freshwater health and macroinvertebrate biodiversity. Odonate biodiversity in urban ponds has already been studied (e.g. Samways and Steytler, 1996; Willigalla and Fartmann, 2012; Goertzen and Suhling, 2013; Jeanmougin et al., 2014), and many of these studies show that presence of vegetation in urban ponds determines to a great extent the biodiversity patterns (Villalobos-Jiménez et al., 2016). This is explained by the fact that vegetation is one of the main cues for habitat selection and intervenes in a wide range of behavioural patterns, from foraging to sheltering and roosting (Buchwald, 1992). However, increased vegetation density is likely to provide greater shelter and attract a wider range of prey species.

Considering the important role of vegetation in the behavioural repertoire of odonates, vegetation density may be a more suitable predictor of odonate biodiversity –and other aquatic macroinvertebrates– in urban ponds, rather than presence or absence of vegetation, especially due to common practices in urban areas such as mowing. In other words, a three-dimensional measure of vegetation – such as vegetation density – is a more accurate depiction of natural resources for odonates in urban areas, than a two-dimensional measure of vegetation such as vegetation cover.

In this study, I investigated the effect of riparian vegetation and other stressors associated with urban ponds on odonate biodiversity. Using a multivariate approach, I analysed the spatial variation of biodiversity patterns in an urban-to-rural gradient. Residents usually prefer wetlands with visibly mown lawn and low macrophyte cover so that the pond substrate is visible (Hassall, 2014). Therefore, urban green areas are often subject to heavy management plans which include practices such as mowing and introduction of non-native plant species (Kowarik, 1995; McKinney, 2006). Decreased vegetation cover and biodiversity has already been found in urban areas due to intensive gardening activities, which had a negative impact on odonate biodiversity in urban ponds (Goertzen and Suhling, 2013). Therefore, I hypothesize that the riparian vegetation around urban ponds will be strongly manipulated against other land use types, particularly due to mowing, which in turn will show decreased vegetation density. The decreased vegetation density and the presence of anthropogenic stressors in urban areas will impact odonate biodiversity

negatively. Additionally, the patterns of odonate biodiversity will be strongly associated with aquatic macroinvertebrate biodiversity.

Methods

Study area

This study was conducted in Leeds and Bradford, UK. A total of 21 ponds were selected throughout Leeds and Bradford (Figure 6.1). Each pond was categorised *a priori* by creating a buffer of 1 km in ArcMap 10.1 (ESRI, 2011) and calculating the extent of urban, suburban and rural area in the buffer, based on the LCM2007 land use classification (Morton et al., 2011). Sites with an urban cover of >45% in a 1 Km buffer were classified as urban; sites with a suburban cover of >45% in a 1 Km buffer were classified as suburban, and sites with an urban and suburban cover of <45% in a 1 Km buffer were classified as rural. This resulted in 5 urban, 8 suburban, and 8 rural sites. Local land use was classified into 4 categories, according to their management: parks and gardens (14 ponds with green areas, intense management and human disturbance), industrial (4 ponds with intense management, medium human disturbance), farms/ruderal (2 ponds, medium vegetation management and disturbance), and nature reserves (1 pond with low human disturbance levels).

Data collection

This part of the project was divided into three methods, the vegetation survey (where the riparian vegetation density was assessed), the odonate survey, and the aquatic macroinvertebrate survey. As a general description of the sampling sites, I recorded local land use, tree shading (%), proportion of the pond covered by aquatic vegetation (submerged, floating-leaved, and emergent vegetation), presence of fish and waterfowl (determined by observation or by asking the manager), pH and conductivity (Environment Agency and Ponds Conservation Trust, 2002). Both vegetation and odonate surveys were in a 30 m buffer around the ponds, as this was considered to be the salient riparian habitat for the odonates (Samways and Steytler, 1996).

The vegetation survey occurred from June to October in 2014 and 2015. The vegetation surrounding the ponds was subdivided into “patches”, each of these patches was divided into three vertical layers (herbaceous cover, bushes, and trees) and then evaluated using height of each layer as the main criteria: herbaceous cover (0-20 cm, <1 m, >1 m), bushes (0, <1 m, >1 m) and trees (0, <5 m, >5 m). In each patch, a 40-step transect was established. Vegetation density was measured every 5 steps using 2 different methods: a 30 cm drop disc – which measures vegetation density in grasslands, and a 1.8 m Robel pole with stripes every 10 cm (modified from Robel et al., 1970), which can measure vegetation density in grasslands, as well as more complex structures such as bushes.

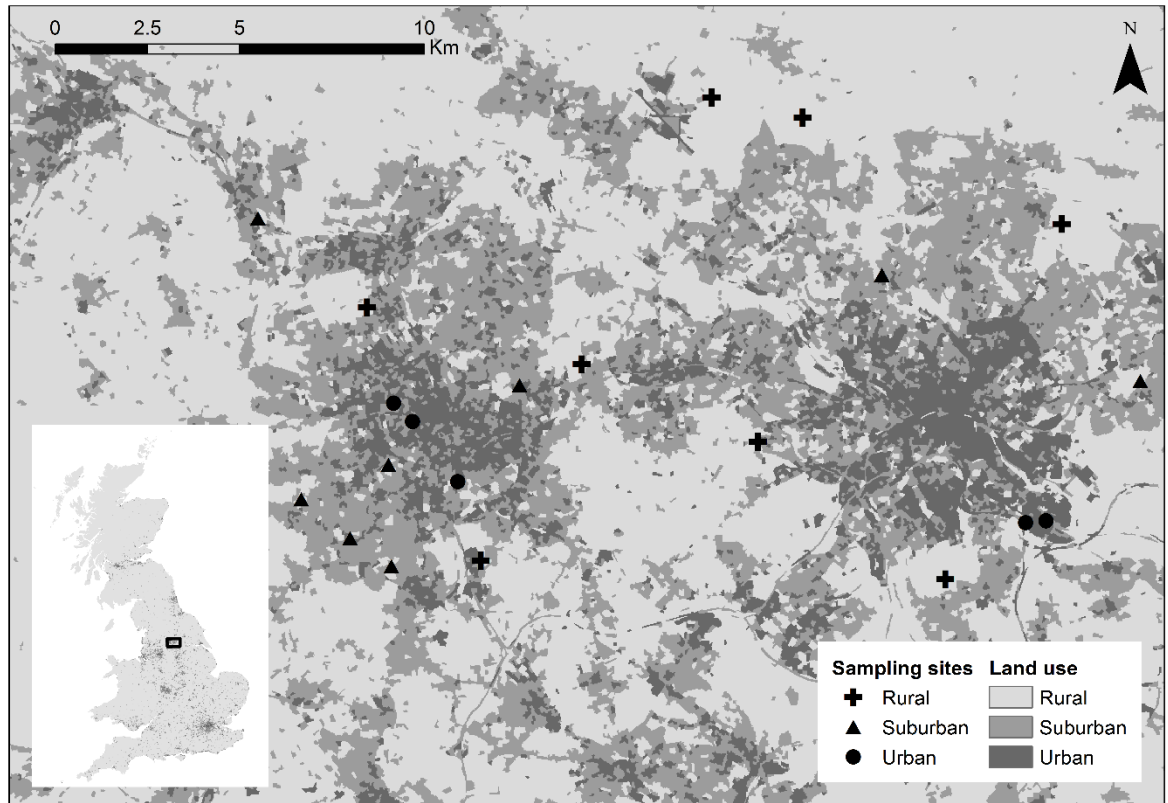


Figure 6.1. Map of the sampling sites in Leeds (right) and Bradford (left), indicating the degree of urbanisation and classification of the sampling sites.

The odonate survey was executed from July to August 2015, at a time between 10:00 am to 5:00 pm, only under specific weather conditions (temperature > 17°C, wind speed < 18 mph, no rain, preferably cloud cover < 60%) based on the British Dragonfly Society (BDS) monitoring scheme (<https://british-dragonflies.org.uk/content/monitoring-dragonflies-and-damselflies-britain>). Adult odonates were caught using the sweep-net method with an insect net in each of the vegetation patches, then identified to species level, marked to avoid double-counting, and then released. Each pond was visited only once.

The aquatic macroinvertebrate survey was conducted from July to August 2015 and was based on the Predictive System for Multimetrics (PSYM) method (Environment Agency and Ponds Conservation Trust, 2002). Samples were collected by sweep-netting with a pond net (1 mm mesh size, 25 × 25 × 30 cm) during 3 minutes in each pond, and sampling was subdivided by mesohabitats in each pond to account for small-scale spatial variation. Sampling time was also subdivided according to mesohabitats. For instance, if three mesohabitats were identified in a pond, then a subsample was taken from each mesohabitat for 1 minute. The collected benthic macroinvertebrates were identified to family level.

Statistical analysis

All statistical analyses were performed using R 3.0.2 (R Core Team, 2013). Considering that two measurements of vegetation density were used in the vegetation surveys in the same sites, I used a Principal Component Analysis (PCA) to account for multicollinearity. The Principal Components (PC) obtained were used as a measure of vegetation density in the odonate and aquatic macroinvertebrate biodiversity analyses. To assess whether vegetation density varied across an urban-to-rural gradient, I used a Canonical Correspondence Analysis (CCA) with the vegetation density measures (Robel, drop-disc) as response variables, and land use (urban, suburban, and rural), location, and transects as the constraining terms. Then, as a significance test to assess differences of vegetation density among urban, suburban, and rural sites, a permutation-based ANOVA was used with 999 random permutations of the residuals from the CCA nested within transects. Finally, a post-hoc test was performed by calculating Tukey's Honest Significant

Differences (HSD) with 999 permutations of the data nested by transect to do pairwise-comparisons of vegetation density between urban, suburban, and rural sites.

The adult odonate and aquatic macroinvertebrate biodiversity analyses were based on species occurrence rather than abundance, considering each site was only visited once. Therefore, species richness was calculated and then bootstrapped from each sample to estimate α -diversity using the vegan package (Oksanen et al., 2013). Tukey's HSD was also used to compare species richness in among urban, suburban and rural ponds. In order to analyse species composition and the interaction with all the variables measured, Non-metric Multidimensional Scaling (nMDS) was used in the vegan package as well (Oksanen et al., 2013). The Gower dissimilarity index was used and nMDS was run 3 times starting from the previous best solution to reduce ordination stress as much as possible. Environmental variables were fitted in the model with 999 random permutations of the data.

Finally, to test odonates as bioindicators of aquatic macroinvertebrate biodiversity, the relationship between odonate biodiversity and aquatic macroinvertebrate biodiversity was estimated by using Generalised Linear Models (GLM) with Poisson distribution (log link), with aquatic macroinvertebrate richness as the response variable, and presence of each species of odonates found as the predictor variables, as well as the overall odonate species richness. Additionally, I tested odonates as bioindicators of freshwater quality by assessing the relationship between odonate biodiversity and the BMWP scores (Paisley et al., 2014) using GLM with negative binomial distribution error due to overdispersion.

Results

Vegetation survey

The results from the ANOVA using permutations of the residuals from the CCA suggest there is no significant difference in vegetation density along an urban-rural gradient ($\chi^2 = 0.031$, $F_{2,600} = 154.06$, $P = 0.157$), although there was a significant difference found among sampling sites ($\chi^2 = 0.054$, $F_{19,600} = 28.39$, $P = 0.001$) and transects ($\chi^2 = 0.044$, $F_{26,600} = 16.94$, $P = 0.001$). Both vegetation density measurements (Robel and drop-disc) were significantly correlated ($t = 17.073$, $df = 646$, Pearson's $r = 0.557$, $P < 0.001$), and the PCA used to aggregate the vegetation density measurements resulted in only 2 PC scores, accounting for 77.88% and 22.12% of the variation, respectively. PC1 had an Eigenvalue of 1.55, whereas PC2 showed an Eigenvalue of 0.44. Considering only PC1 had an Eigenvalue over 1, this is the only PC score used as a measure of vegetation density in the rest of the analyses.

Adult odonate and aquatic macroinvertebrate biodiversity surveys

A total of 5 species and 238 adult odonates were found in the surveyed ponds (Table 6.1). Bootstrapped species richness resulted in 5.36 ± 0.48 SE across all sites. The most frequent species were *Ischnura elegans* (71.43%), followed by *Coenagrion puella* (33.33%). However, the Tukey test showed no significant pairwise differences among urban,

suburban, or rural ponds (Figure 6.2; Table 6.2). Regarding the aquatic macroinvertebrate survey, a total of 46 taxa were identified and 3603 specimens were collected (Table 6.1), the most frequent being Asellidae and Planorbidae (Table 6.1). Bootstrapped richness of aquatic macroinvertebrate taxa resulted in 51.97 ± 3.38 SE. Similarly to the adult odonates, the Tukey HSD test showed no significant pairwise differences among urban, suburban, or rural ponds (Figure 6.2; Table 6.2).

Table 6.1. List of odonates encountered as adults (species level) and aquatic macroinvertebrates (family level) found in the sampling sites.

	Total abundance	Number of ponds	Frequency (%)
Odonata			
<i>Coenagrion puella</i>	40	7	33.3
<i>Coenagrion</i> sp.	2	1	4.8
<i>Enallagma cyathigerum</i>	21	6	28.6
<i>Ischnura elegans</i>	159	15	71.4
<i>Pyrrosoma nymphula</i>	16	6	28.6
Aquatic macroinvertebrates			
Turbellaria, Tricladida*	6	3	14.3
Annelida, Hirudinea			
Glossiphoniidae	324	11	52.4
Piscicolidae	7	3	14.3
Erpobdellidae	10	1	4.8
Annelida, Oligochaeta*	126	10	47.6
Mollusca, Gastropoda			
Hydrobiidae	111	5	23.8
Planorbidae	253	17	80.9
Physidae	151	10	47.6
Bithyniidae	9	4	19.0
Lymnaeidae	228	13	61.9
Mollusca, Bivalvia			
Sphaeriidae	384	9	42.9
Crustacea, Isopoda			
Asellidae	889	17	80.9
Crustacea, Amphipoda			
Crangonyctidae	64	6	28.6

Table 6.1 (continued).

	Total abundance	Number of ponds	Frequency (%)
Gammaridae	163	5	23.8
Arachnida, Araneae			
Cybaeidae	11	2	9.5
Arachnida, Acari			
Hydrachnidea	33	9	42.9
Insecta, Ephemeroptera			
Baetidae	19	6	28.6
Caenidae	14	6	28.6
Insecta, Trichoptera			
Polycentropodidae	1	1	4.8
Leptoceridae	33	2	9.5
Ecnomidae	1	1	4.8
Limnephilidae	2	1	4.8
Insecta, Coleoptera			
Dytiscidae	17	4	19.0
Elmidae	2	2	9.5
Scirtidae	2	1	4.8
Hydrophilidae	4	3	14.3
Helophoridae	8	5	23.8
Halipidae	31	9	42.9
Chrysomelidae	7	4	19.0
Staphylinidae	1	1	4.8
Insecta, Hemiptera			
Corixidae	299	14	66.7
Gerridae	8	5	23.8
Nepidae	2	1	4.8
Naucoridae	10	1	4.8
Notonectidae	71	14	66.7
Insecta, Diptera			
Culicidae	1	1	4.8
Chironomidae	236	15	71.4
Dixidae	5	4	19.0
Empididae	8	1	4.8
Ephydriidae	1	1	4.8
Syrphidae	1	1	4.8
Ceratopogonidae	7	3	14.3
Insecta, Megaloptera			
Sialidae	7	1	4.8

* Not identified to family level.

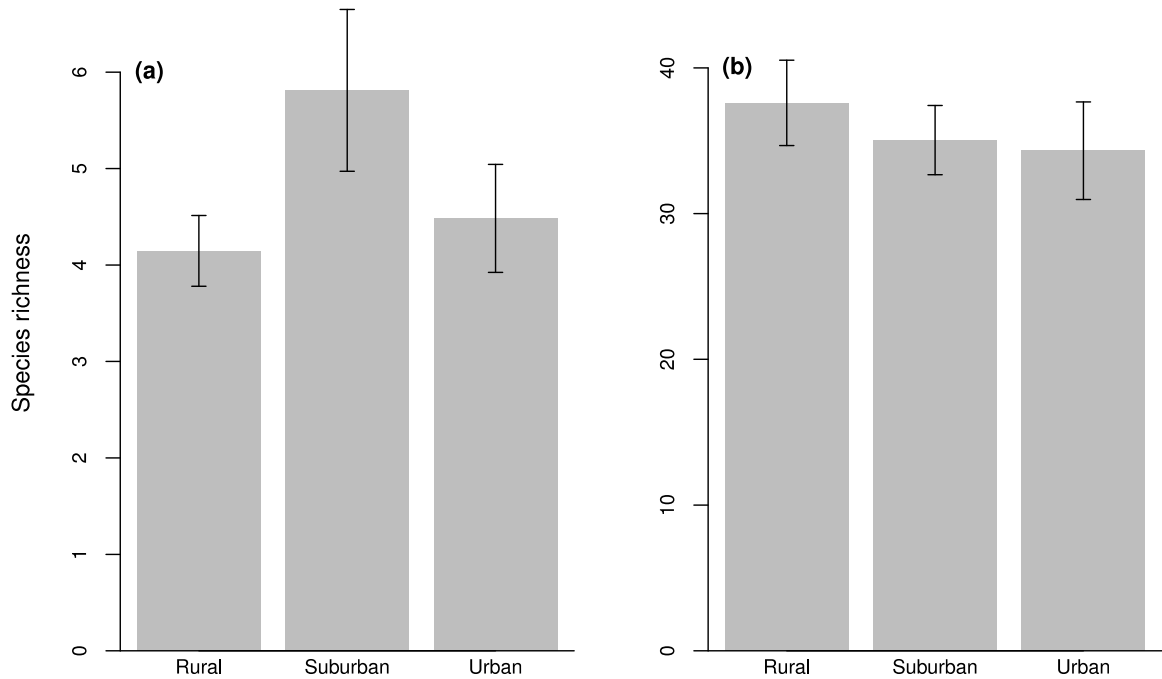


Figure 6.2. Bootstrapped α -diversity of (a) odonates, and (b) aquatic macroinvertebrates, in an urban-rural gradient. Error bars represent ± 1 SE.

Table 6.2. Results of the Tukey HSD test for estimating β -diversity, all pairwise comparisons of adult odonate community composition and aquatic macroinvertebrates among urban, suburban, and rural sites.

Pairwise group comparison	Δ mean	95% CI	<i>P</i>
<i>Adult odonates</i>			
Suburban - rural	0.000	0.168	1.000
Urban - rural	-0.139	0.190	0.171
Urban - suburban	-0.139	0.195	0.185
<i>Aquatic macroinvertebrates</i>			
Suburban - rural	-0.002	0.106	0.998
Urban - rural	-0.043	0.121	0.645
Urban - suburban	-0.040	0.121	0.675

Table 6.3. Scores of factors (categorical variables) in nMDS1 and nMDS2 for the community analysis including adult odonates and aquatic macroinvertebrates. *P*-values are based on 999 permutations. Significant values are in bold.

FACTORS	NMDS1	NMDS2	GOODNESS OF FIT	
			R ²	<i>P</i>
<i>Classification</i>			0.007	0.992
Urban	-0.010	-0.025		
Suburban	0.002	0.004		
Rural	0.004	0.012		
<i>Local land use</i>			0.159	0.391
Farm/ruderal	-0.168	-0.009		
Industrial	-0.004	0.015		
Parks and gardens	0.017	0.012		
Reserve	0.116	-0.212		
<i>Presence of fish</i>			0.156	0.037
Yes	0.006	0.053		
No	-0.012	-0.106		
<i>Presence of waterfowl</i>			0.070	0.247
Yes	-0.016	0.028		
No	0.040	-0.069		

Table 6.4. Scores of vectors (numeric variables) in nMDS1 and nMDS2 for the community analysis including adult odonates and aquatic macroinvertebrates. *P*-values are based on 999 permutations. Significant values are in bold.

VECTORS	NMDS1	NMDS2	R ²	<i>P</i>
pH	-0.132	0.066	0.022	0.856
Conductivity	0.034	0.287	0.083	0.449
Tree overhang	-0.302	0.071	0.097	0.397
Submerged vegetation	0.024	-0.569	0.324	0.031
Floating-leaved vegetation	0.065	-0.453	0.209	0.136
Emergent vegetation	-0.033	-0.085	0.008	0.932
Riparian vegetation density (PC1)	-0.232	-0.225	0.105	0.364

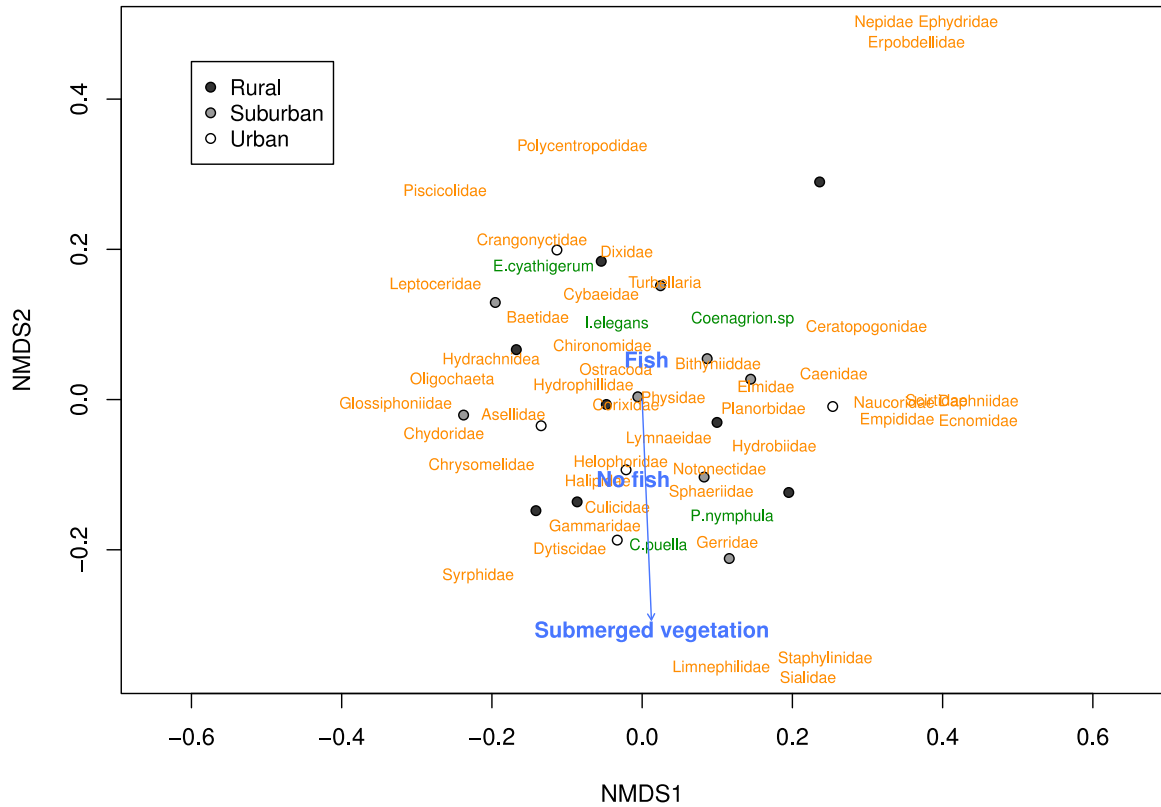


Figure 6.3. nMDS ordination of odonate species (*green*) and aquatic macroinvertebrates (*orange*) in surveyed ponds in an urban-gradient (*circles*), and significant ($P < 0.05$) environmental variables (*blue*). Numeric variables have an additional arrow indicating direction and strength of correlation with nMDS 1 and 2.

Regarding the nMDS model, the Root Mean Square Error (RMSE) and the Maximum Residual obtained after running the nMDS 3 times was $1.321e-05$ and $3.329e-05$, respectively. The results from the nMDS revealed that the species assemblage is not constrained by the *a priori* classification of urban, suburban and rural areas, nor the local land use of these sites (Table 6.3). Instead, the presence of fish has a significant effect on the species assemblage (Table 6.3), as well as the percentage of submerged vegetation (Table 6.4). In particular, *I. elegans* and Chironomidae showed tolerance to fish (Figure

6.3), whereas Haliplidae and Notonectidae showed high sensitivity to the presence of fish (Figure 6.3). Additionally, crustaceans from the family Gammaridae, hemipterans from Gerridae, and the odonates *P. nymphula* and *C. puella* showed a strong association with increased cover of submerged vegetation.

Table 6.5. Results of the GLM models showing the relationship between the presence of each of the odonate species found and overall richness of odonates, with the taxonomic richness of aquatic macroinvertebrates, as well as water quality (measured by the BMWP scores).

Taxon	Coefficient (β)	SE	Z	P
Aquatic macroinvertebrate biodiversity				
<i>Coenagrion puella</i>	-0.115	0.140	-0.821	0.412
<i>Enallagma cyathigerum</i>	0.089	0.140	0.633	0.527
<i>Ischnura elegans</i>	0.205	0.150	1.365	0.172
<i>Pyrrhosoma nymphula</i>	-0.032	0.144	-0.225	0.822
All odonates	0.013	0.057	0.229	0.819
Water quality				
<i>Coenagrion puella</i>	-0.071	0.194	-0.367	0.714
<i>Enallagma cyathigerum</i>	0.104	0.200	0.516	0.606
<i>Ischnura elegans</i>	0.342	0.191	1.792	0.073
<i>Pyrrhosoma nymphula</i>	0.042	0.202	0.205	0.837
All odonates	0.062	0.080	0.767	0.443

Adult odonates as bioindicators

The results of the GLM models suggest that the relationship between each of the odonate species found in the sampling sites and the aquatic macroinvertebrates is not significant (Table 6.5). Likewise, the relationship between odonate species richness and aquatic macroinvertebrate taxa is not significant (Table 6.5). Regarding the relationship between

odonates and water quality, the results of the GLM models showed no significant association between odonate species and the BMWP scores for each site (Table 6.5).

Discussion

The results from this study indicate that biodiversity patterns do not vary significantly across the urban-rural gradient. Riparian vegetation density also did not vary significantly across the urban-rural gradient, only according to the sampling sites and transect. Additionally, riparian vegetation density did not have a significant impact on the community assemblage of odonates or aquatic macroinvertebrates. However, presence of fish and submerged vegetation had a strong impact on the community composition of these taxa. Finally, adult odonate biodiversity did not show a strong association with aquatic macroinvertebrate biodiversity.

Perhaps one of the reasons why there was no differentiation in biodiversity across the urban-rural gradient was that only 5 odonate species were found, all of which were zygopterans. This bias towards zygopterans could be a result of the sweep-net method, since anisopterans are harder to catch using this method. However, the same results were found in aquatic macroinvertebrates, where 46 different taxa were encountered. These results suggest that urban built-up area does not have a strong influence on the biodiversity patterns of urban ponds (Hill et al., 2017). Instead, the aquatic vegetation and fish in these

water habitats is the main factor determining the biodiversity and community composition of urban ponds. Other studies have shown similar results, e.g. Goertzen and Suhling (2013) and Jeanmougin (2014). The vast majority of the surveyed sites had a variety of vegetation types despite their land use, from mowed lawn to natural grassland and woodland, which may also explain why there were no significant differences in riparian vegetation density across the urban-rural gradient. Even though riparian vegetation has been shown to have an significant role in odonate biodiversity and behaviour (Buchwald, 1992; Samways and Steytler, 1996; Monteiro et al., 2013), this was not supported by this study. However, this is more likely a result of the lack of differentiation of vegetation density across the urban gradient.

The results of the nMDS analysis suggests presence of fish and submerged vegetation have a significant impact on the community assemblage of odonates and other aquatic macroinvertebrates. Fish are one of the main predators of odonate larvae and play a key role in shaping species distributions (McPeck, 2008). However, the susceptibility of odonates to fish predation is largely dependent on their activity levels, and active species have a higher predation risk compared to species with lower activity levels (Johansson, 2000). Larval *I. elegans* and *E. cyathigerum* are less active and can coexist with fish predators (Crumrine et al., 2008), which may explain the fact that these species were abundant in ponds with fish. In contrast, members of the family Notonectidae showed high vulnerability to presence of fish, which is a result of their activity levels, size and colour patterns (Cook and Streams, 1984).

Submerged vegetation was another key factor driving community assemblage in the surveyed ponds, particularly for the odonates *C. puella* and *P. nymphula*, as well as other taxa such as Gerridae and Gammaridae. Aquatic vegetation acts as a refuge for larval odonates to protect themselves from predators, and to ambush their prey (Buchwald, 1992). In the case of *C. puella* and *P. nymphula*, the adults use aquatic vegetation as a substrate for oviposition (Dijkstra and Lewington, 2006). Goertzen and Suhling (2013) also found aquatic vegetation to be one of the main drivers of biodiversity in urban ponds. This has important implications on urban management, since increasing submerged vegetation in urban ponds may be of aid in order to promote biodiversity in urban areas.

Unexpectedly, biodiversity of odonates was not strongly associated with aquatic macroinvertebrate biodiversity or water quality. Odonates have been widely used as bioindicators in biomonitoring programmes due to their sensitivity to environmental stressors (Clark and Samways, 1996; Oertli, 2008; Simaika and Samways, 2009; Simaika and Samways, 2012). However, the species of odonates found in this survey are mostly generalists with a high tolerance to a wide range of stressors, particularly *I. elegans* (Dijkstra and Lewington, 2006), and all species found were only zygopterans from one family, Coenagrionidae. Perhaps the use of other survey methods which allow the sampling of a wider range of odonates which are sensitive to environmental stressors and are more suitable for indicating habitat quality (Villalobos-Jiménez et al., 2016) may be needed for developing a method for a rapid assessment of freshwater ecosystems using odonates. Such

field methods may include the use of larval or exuvial records. However, the DBI was developed for the evaluation of habitat quality in South Africa, a country with a rich biodiversity (Simaika and Samways, 2009), and since the UK has relatively low levels of odonate biodiversity compared to other countries which are in the tropics, the use of only one taxon (the Odonata) may not be sufficient to assess habitat quality here in the UK.

This study shows that urban land use does not have a significant influence on biodiversity in urban wetlands. However, the urban management dictates to a great extent the biodiversity patterns in ponds (Goertzen and Suhling, 2013). An adequate management programme would need to integrate increased aquatic vegetation in urban ponds to promote biodiversity. This in turn would increase the conservation value of urban ponds for aquatic macroinvertebrates.

Chapter 7: General Discussion

The aim of this thesis is to describe the ecological impacts of urban development on odonates, and the results suggest that odonates respond to urbanisation in various ways, depending on the anthropogenic stressor involved and the taxon. Chapter II investigates the effects of the urban heat island (UHI) – one of the main urban stressors which affect odonates (see Figure 1.3) – and shows it has negligible impacts on the phenology of odonates compared to climate change, although summer species are more susceptible to increased temperatures from the UHI. Chapter III demonstrates noise disturbance reduces significantly the feeding rate of the damselfly *Ischnura elegans*, although anthropogenic noise has no significant impact. Regarding the impacts of polarised light pollution (PLP), which were studied in Chapter IV, the strength of polarotaxis increased significantly with age in laboratory-reared specimens, but there was no significant differentiation between urban and rural populations, suggesting urban populations are not adapted to PLP. However, field-caught urban specimens showed less preference to polarised light compared to rural populations, suggesting strong selective pressures are acting upon urban populations. In Chapter V, I studied the effects of urbanisation on dispersal-related traits of odonates, but the results indicate urbanisation has no significant effect on the dispersal of *I. elegans*, since flight-related traits showed no significant differentiation among urban and rural populations. Lastly, biodiversity patterns did not differ among urban and rural areas in Chapter VI, although aquatic vegetation and presence of fish were the main drivers of community composition. Here, I discuss how these findings contribute to the knowledge on the ecology and evolutionary biology of odonates in an urban ecosystem, as well as the

practical implications of these findings on the management of green and blue spaces in cities.

Tolerance of odonates to urban stressors

Cities are places which have been perceived as having negative impacts on ecosystem health and biodiversity, and whilst there are many stressors associated with urban areas which have detrimental effects on biodiversity (reviewed in Chapter I, see Figure 1.3), other anthropogenic disturbances have little to no impact on odonates, particularly on generalist odonate species which can tolerate a wide range of stressors (see Table 1.2). The results of this thesis further demonstrates that there are a wide range of negative stressors in urban ecosystems, but on the other hand, there are other anthropogenic stressors which odonates can tolerate. Here, I highlight the findings from this thesis that show tolerance of odonates to urban stressors.

Urban heat islands are one of the main stressors in cities, and given that increasing temperatures due to climate change have been shown to affect the phenology of odonates (Hassall et al., 2007; McCauley et al., 2015), the UHI is also expected to have a similar impact on odonates. However, odonates showed a negligible response to increased temperatures in urban areas, especially when compared to climate change, possibly due to the presence of microclimates in water bodies which have a buffering capacity to

counteract the UHI (Coutts et al., 2013; Hathway and Sharples, 2012). Despite the fact that spring species advanced their phenology considerably in response to climate change, a high tolerance to the UHI was presented in species with this life history trait. As the name suggests, spring species have an adult phase which is active during the spring (Corbet, 1954), which may help avoid the increased thermal stress found during the summer. However, the atmospheric UHI is more intense during the winter (U.S. Environmental Protection Agency, 2008), which might trigger the cessation of diapause over winter if temperatures surpass a given threshold, in which case spring species can be at risk of having a decoupled phenology due to the UHI, as has already been suggested due to climate change (Hassall et al., 2007). Hence, further empirical studies are needed to describe the drivers of this response in spring species and possible outcomes due to warming temperatures.

While urbanisation can have various negative impacts at a small scale, urban stressors may not have the same effect at a landscape level. In this thesis, urban land use at a large scale did not have a significant impact on the species richness and community structure of odonates. Previous studies conducted in birds (Clergeau et al., 1998; Aronson et al., 2014; Shochat et al., 2010), plants (McKinney, 2008; Aronson et al., 2014), butterflies (Blair and Launer, 1997; Ruszczyk, 1987; Ruszczyk and De Araujo, 1992), and even odonates (e.g. Cleto Filho and Walker, 2001; Ferreras-Romero et al., 2009) have reported urban areas have lower biodiversity levels compared to rural areas. The results in the literature review in Chapter I further supports this finding (see Table 1.1). However, other studies using a

multivariate approach have demonstrated that urban land use itself does not contribute significantly to biodiversity patterns in an urban-to-rural gradient (e.g. Goertzen and Suhling, 2013). These observations are further supported by the results in Chapter VI. Instead, other factors associated with urbanisation can determine biodiversity levels in odonates, such as city size (Willigalla and Fartmann, 2012), decreased aquatic vegetation cover and biodiversity (Goertzen and Suhling, 2013; Jeanmougin et al., 2014), and modification of riparian vegetation (Ferrerias-Romero et al., 2009; Goertzen and Suhling, 2013; Hassall et al., 2014; Monteiro et al., 2013; Samways and Steytler, 1996; Subramanian et al., 2008). Given that certain practices in urban green spaces – such as gardening activities - can reduce riparian vegetation density, I investigated the effects of riparian vegetation density on biodiversity in urban areas. However, vegetation density did not have a strong impact on the biodiversity patterns in ponds in an urban-to-rural gradient. Vegetation has been well-documented as a key component in odonate biology (Buchwald, 1992) and, therefore, one of the main determinants of odonate biodiversity (Goertzen and Suhling, 2013; Subramanian et al., 2008), so it is difficult to ascertain the drivers of the rather contrasting findings presented in this thesis. On one hand, aquatic vegetation cover has already been reported as one of the main drivers of odonate biodiversity in urban areas (Goertzen and Suhling, 2013; Jeanmougin et al., 2014), and such results are further supported by this thesis, although riparian vegetation density in particular had no effect, which suggests that the modification of riparian vegetation – such as that caused by gardening activities – has no impact on odonate communities even if it decreases vegetation density, providing the vegetation cover is not decreased and there is abundant aquatic vegetation in the water bodies.

Another stressor commonly found in urban areas is anthropogenic noise, and though underwater noise had a significant effect on the feeding behaviour of the odonate *I. elegans*, this species showed no significant response to anthropogenic noise in particular. This is the only study which has investigated the impact of anthropogenic noise on a freshwater macroinvertebrate using a functional response approach, and the first evidence of an aquatic macroinvertebrate being tolerant to anthropogenic noise disturbance. The fact that noise disturbance had a significant impact on feeding rates, and anthropogenic noise did not, may be due to the fact that the organisms can easily become habituated to anthropogenic noise disturbance, since there are low levels of nonlinearities in the anthropogenic acoustic signals that reduce the habituation to the acoustic stimuli (Blesdoe and Blumstein, 2014; Karp et al., 2014). However, only one file of each acoustic stimulus was used in each treatment because the functional-response approach necessitates small numbers of treatment levels, therefore it is difficult to partition the effects of the file from the acoustic stimulus *per se*. Additionally, particle motion was not assessed in this thesis. Further studies are required using multiple audio stimuli to confirm the effect of anthropogenic noise on feeding rates of *I. elegans* and to validate these findings by assessing the particle motion produced by noise disturbance.

Landscape fragmentation is also one of the main drivers of biodiversity loss in cities (Faeth et al., 2012; Grimm et al., 2008) and can have a negative impact on the dispersal of odonates (e.g. Taylor and Merriam, 1995; Outomuro et al., 2013). However, no

differentiation in the flight-related traits was found among urban, suburban, and rural populations of *I. elegans*, which suggests that at least this species can tolerate urbanisation. These findings are in contrast to those from other species. For example, other studies have found urbanisation to have an effect on flight-related traits of *Coenagrion puella* (Tüzün, Op de Beeck and Stoks, 2017). This contrasting finding may be due to the fact that *C. puella* has a higher tendency to disperse to other ponds compared to *I. elegans* (Conrad et al., 2002). However, the low dispersal tendencies of *I. elegans* may affect the genetic diversity, since decreased migration rates to other breeding sites are expected to limit the gene flow among populations. Similar results have already been reported in urban populations of other *Ischnura* species in Japan, namely *I. senegalensis* and *I. asiatica*, where urban populations showed a higher genetic differentiation compared to rural populations due to habitat fragmentation (Sato et al., 2008). Thus, increasing landscape connectivity in urban areas is still encouraged to avoid future complications in the conservation of urban odonate populations. Habitat fragmentation due to urbanisation also increases isolation among populations and can promote the formation of metapopulations (Hanski, 1998). In the context of freshwater ecology, ponds represent suitable patches in a matrix of unsuitable habitat, which is considered a classic metapopulation model (De Meester et al., 2005). However, the continuous land use change due to urbanisation can further fragment these suitable habitats, decrease patch size and/or habitat quality, or cause suitable habitat loss and increase the distance between other suitable patches, therefore increases the complexity of metapopulation dynamics (Hanski, 1998). On the other hand, newly-formed artificial ponds are common in urban areas to alleviate key issues of water management and climate change such as rainfall interception (Céréghino et al., 2014), and

garden ponds are also increasingly popular for aesthetic purposes (Davies et al., 2009). The creation of more suitable habitats in urban areas can contribute to balance habitat loss. However, further research is needed to analyse how urban ponds contribute to odonate metapopulation dynamics and migration patterns in the urban matrix.

It is important to mention the studies conducted in Chapter III and V (which investigated the effects of noise disturbance on feeding rates and landscape fragmentation on flight-related traits, respectively) were performed using *I. elegans* as a model species, which is known to tolerate hostile conditions, including ponds with high salinity (Dow, 2010; Dijkstra and Lewington, 2006). This species was chosen as the study model because (i) it is one of the most common species across Europe and is abundant across urban and rural ponds (Goertzen and Suhling, 2013), which facilitates the comparison of traits among urban and rural populations, (ii) it is relatively easy to rear in laboratory conditions (Piersanti et al., 2015), and (iii) being one of the most abundant odonates in urban areas, it plays the ecological role of predators of other invertebrate populations in urban freshwaters, such as mosquitoes. However, further studies comparing other species are encouraged in order to have a more comprehensive understanding of the impacts of urbanisation on the ecology of odonates and other semi-aquatic macroinvertebrates.

Sensitivity of odonates to urban stressors and suggestions for management of urban areas to promote biodiversity conservation

Despite the aforementioned tolerance to urban stressors in odonates, there is substantial variation in the vulnerability to these stressors within odonates (see Chapter I), particularly specialist species, e.g. *Aeshna viridis*, which is prone to changes in plant community composition since this species only oviposits on *Stratiotes aloides* (Dijkstra and Lewington, 2006). However, even generalist species can be susceptible to urban stressors. For instance, pesticide stress has been shown to decrease immune function on *I. elegans* larvae (Janssens et al., 2014) and increased development time in *C. puella* (Campero et al., 2007). In this thesis, I have also identified other urban stressors to which odonates show a strong, negative response, which are summarised below.

Even though the UHI did not advance the emergence of odonates in urban areas, at a community level odonates advanced the trailing edge of their flight period in urban areas, which suggests a contraction of their activity period in the adult phase. When investigating the effects of life-history traits on this response, egg diapause did not show any significant influence. However, when investigating the effects of larval diapause, summer species were particularly sensitive to the UHI and had a contracted flight season in urban areas compared to spring species, which present a larval diapause during the last instar and emerge synchronously during the spring. Recent research studying the thermal performance curves

(TPCs) of the summer species *Coenagrion puella* has found that rural populations of this species show an increased growth rate, but lower survival with increased temperatures compared to urban populations, which shows that urban populations of this species are well-adapted to the UHI (Tüzün, Op de Beeck, Brans, et al., 2017), although this study only analysed the effects on the larval stage. Moreover, water bodies can buffer the increased temperatures from the UHI (Coutts et al., 2013; Hathway and Sharples, 2012), which may explain why the UHI did not advance the emergence of odonates, although this effect only occurs whilst the odonates are in the aquatic, larval stage. Once these larvae emerge, the adult phase is much more prone to the increased temperatures from the UHI, especially for summer species because thermal stress is higher in summer than in spring. Additionally, aquatic pollutants such as the pesticide chlorpyrifos can interact with thermal stress across metamorphosis (Janssens et al., 2014). Despite the fact that thermal stress in UK is not as intense as in the southern regions of European species' range, this may be an issue for species that show less tolerance to increased warming and are becoming relict in the southern range, such as *Leucorrhinia dubia* (Dijkstra and Lewington, 2006). Therefore, mitigating measures are needed to increase the presence of thermal refuge through enhanced heterogeneity, or minimise thermal stress around urban water bodies. Such mitigating measures may include, among others, increased canopy cover to provide a cooling effect (Baker et al., 2002; Dreistadt et al., 1990).

On the other hand, underwater noise was associated with reductions in the feeding rate of *I. elegans* through increasing in handling time, providing evidence that underwater noise may

pose a threat to the stability of trophic interactions. Unexpectedly, instead of anthropogenic noise having a negative impact as predicted, it was natural noise which decreased the feeding rate of *I. elegans*, despite this species being tolerant to a wide range of stressors. This is perhaps one of the most novel contributions to knowledge in this thesis. As previously discussed, this may be due to the presence of nonlinearities in this particular acoustic stimulus, which prevent habituation and induce an exacerbated behavioural response (Blumstein and Récapet, 2009; Karp et al., 2014; Reby and Charlton, 2012; Townsend and Manser, 2011). These results suggest the effects of noise depend on the acoustic properties of the noise disturbance, rather than the source of noise. Similarly to the results from Chapter VI – which show that human-modified areas do not have a negative impact *per se*, but specific characteristics of these areas can have deleterious impacts on biodiversity, such as lack of vegetation and presence of fish – I demonstrate in this thesis that anthropogenic noise is not necessarily negative, but certain features of noise disturbance can have negative impacts, in this case, on the feeding behaviour of *I. elegans*. Additionally, underwater noise and, in particular, natural noise decreased the handling time, which represents the time during which the predator catches, processes, and digests the prey (Holling, 1959). However, it was not possible to identify which of these phases is affected in this study, therefore further research is needed to describe in more detail the effects of noise disturbance on predator-prey interactions. These studies may incorporate the removal of vibration sensors –the antennae and/or tarsal hairs, repeating the work in light and dark conditions, high-speed video to track the capture success, among others.

One of the main findings of the research conducted as part of this thesis is regarding the effects of PLP on urban odonate populations. PLP is becoming increasingly frequent in urban areas due to the increasing abundance of cars and other polarising surfaces such as solar panels and black plastic trays, all of which can lead to ecological traps (Horváth et al., 2009). In Chapter IV, PLP was found to have a significant impact on the biology of adult *I. elegans*, with older individuals being more susceptible to horizontally polarised light compared to sexually-immature individuals. Most importantly, the field-caught specimens from rural areas showed a significantly stronger response to horizontally polarised light compared to urban populations, which shows there are strong selective pressures acting upon urban populations, whereas the laboratory-reared individuals showed no significant differentiation among urban and rural populations, showing urban populations have not adapted to PLP. These results suggest that strong selective pressures are present in urban areas due to PLP, but no adaptation has occurred to this point in urban populations.

Odonates are among the oldest insect orders (Corbet, 1999) along with Ephemeroptera, which are also strongly attracted to horizontally polarised light (Horváth et al., 2009; Boda et al., 2014), therefore the positive polarotaxis presumably has been an adaptive trait over millions of years in these insects to detect suitable habitats. On the other hand, ecological traps have only existed since the appearance of anthropogenic changes in the environment and have increased exponentially over the past several decades as a by-product of the rapid spread of urban development, road systems, and industrial agriculture (Horváth et al., 2009), which in an evolutionary context is a relatively short time period compared to the time during which the formerly adaptive trait – in this case, preference to horizontally polarised light – has evolved (Gates and Gysel, 1978; Schlaepfer et al., 2002). The failure

to adapt promptly to ecological traps can lead to sudden population sinks or even extinction (Schlaepfer et al., 2002). This represents a major concern for the conservation of odonates in cities, and management efforts should be directed towards mitigating the impacts of PLP in urban areas (Horváth et al., 2009). Unfortunately, some management practices increase the frequency of ecological traps (Hale et al., 2015), as well as other activities which were expected to decrease PLP, such as the use of matte car paint (Blahó et al., 2014). However, some studies have found positive results when testing methods for mitigating polarotactic ecological traps. For example, adding a white non-polarising grid to solar panels decreases the attractiveness of these surfaces to polarotactic insects (Horváth et al., 2010). Another effective mitigation method consists of deploying horizontally polarizing water-filled black or red trays along the edge of the road during the flight period so that the polarotactic insects are lured by these surfaces - instead of cars and other polarotactic traps – and lay their eggs, which can then be transferred to suitable water bodies (Egri et al., 2017). These two methods can be used in urban blue areas to mitigate the negative effects of ecological traps and promote the conservation of urban populations.

The modification of surrounding anthropogenic structures may reduce ecological traps, but ponds of poor quality can still be ecological traps themselves if they appear to be of high quality but lack key characteristics for odonate survival and reproduction. For example, the presence of fish can be one of the main drivers of community assemblage of not only odonates, but other aquatic macroinvertebrates as well. Fish are the predominant predators of odonate larvae and play a key role in shaping species distributions (McPeck, 2008). The

activity patterns of each species determines how susceptible the species are to being detected by fish, therefore active species have a higher predation risk and are commonly found in fishless water bodies, compared to sedentary species which can coexist with fish (Corbet, 1999; McPeck, 2008). Examples of “fishless species” include *Anax junius*, *A. longipes*, *Archilestes grandis*, and *Enallagma aspersum* (Corbet, 1999). In urban ponds, studies have shown fish stock can lead to decreased evenness, since presence of fish excludes active odonates and only benefits sedentary species such as *I. elegans* (Goertzen and Suhling, 2013). Moreover, fish have been found to cause declines in macroinvertebrate biomass (Dorn, 2008), which in turn can affect habitat quality and ecosystem functioning (Wallace and Webster, 1996). This is a particularly concerning issue in urban ponds, where the introduction of ornamental, non-native fish such as *Carassius auratus* has negative impacts on native populations (Copp et al., 2005).

Submerged vegetation was another major determinant of community composition of odonates and other macroinvertebrates in the surveyed ponds. Similar results have been described in other studies investigating biodiversity in odonates in urban ponds (Goertzen and Suhling, 2013). Aquatic vegetation acts as a refuge for larval odonates to hide from predators, as well as a perch for larvae to ambush their prey (Buchwald, 1992).

Additionally, endophytic species use aquatic vegetation as a substrate for inserting the eggs (Corbet, 1999). Several restoration programs (e.g. Chovanec, 1994; Chovanec et al., 2000; Suh and Samways, 2005) have successfully promoted odonate biodiversity by increasing

submerged vegetation. Therefore, increased submerged vegetation can increase the conservation value in urban ponds and promote biodiversity in urban areas.

The value of using an integrative approach to urban ecology

Urbanisation, being one of the main threats to biodiversity, has received much attention in recent research, although studies have generally been limited to describing the biodiversity change patterns across an urban gradient and analysing the toxicological effects of urban wastewater on biodiversity and life-history traits (Villalobos-Jiménez et al., 2016).

However, urban ecosystems comprise a wide range of stressors and, therefore, need to be analysed in an integral, multidisciplinary manner in order to understand in depth the effects of cities on biodiversity patterns, and to mitigate the negative impacts in urban areas. In addition to some anthropogenic stressors already described as contributors to odonate biodiversity loss, the studies performed as part of this thesis have allowed the identification of other stressors that affect the biology and conservation of odonates, of which PLP, noise disturbance, thermal stress from the UHI (in the case of summer species), presence of fish, and absence of aquatic vegetation are of utmost importance. Some of these findings, particularly the studies regarding the impacts of noise disturbance and PLP, represent novel areas of research and have important contributions to the theory of urban ecology and odonate biology.

There has been a considerable body of literature investigating the evolutionary ecology of odonates (see Córdoba-Aguilar, 2008), and this body of literature is also growing in the context of odonates in urban landscapes (Villalobos-Jiménez et al., 2016), which may enable some predictions as to how odonates could respond to urbanisation in the future. The results from this thesis may also contribute to such predictions. In order to thrive in urban areas, odonates should be able to tolerate or become adapted to increased thermal stress from the UHI, noise disturbance, ecological traps, the spatial configuration of the urban matrix (which is usually heavily degraded and fragmented), decreased submerged vegetation and presence of fish. In the context of the UHI, odonates are better adapted to tolerate heat given their tropical origin (Pritchard and Leggott, 1987), and it is likely that their tolerance to increased temperatures improves in the future in urban areas given the selective pressure that the UHI imposes on urban populations. However, the adult phase is more susceptible to the UHI since no developmental adaptations to temperature changes are found in this life stage, therefore other adaptations in the adult phase would be necessary to be resistant to the UHI. While there has been more research regarding the effect of temperature on odonates (see Hassall and Thompson, 2008), the impact of noise disturbance on odonates had not been investigated until this thesis, and the results suggest larvae can withstand anthropogenic noise, thus noise disturbance should not be a limiting factor for odonates in urban areas. The typical “patchy” configuration of urban landscapes should not affect odonates either, since some species such as *I. elegans* already show limited dispersal (as shown in Chapter V), whilst others adapt their wing morphology to improve their flight performance in urban landscapes or increase their flight endurance (Tüzün, Op de Beeck and Stoks, 2017). On the other hand, some urban ponds have a

particular set of features which can have a detrimental effect on odonates, such as the presence of fish. However, other species have already developed mechanisms to minimise predation by fish (McPeck, 2008), therefore coexistence with fish may be possible for some odonate species in urban areas in the future. Unfortunately, absence of submerged vegetation and presence of polarotactic traps are two features which are much more difficult to overcome since the association of odonates with aquatic vegetation and polarised light has a very early origin in the evolutionary past of odonates (Corbet, 1999) and, in the case of aquatic vegetation, this relationship is found throughout the life cycle of odonates (Buchwald, 1992). Perhaps odonates in urban areas can avoid ecological traps by increasing the time of decision-making, as was shown in Chapter IV. However, more research is encouraged in order to make more firm predictions regarding the response of odonates to urbanisation in the future.

While the Odonata are a well-established barometer for multiple aspects of environmental change, further work incorporating other species is encouraged in order to evaluate the impact of these stressors in a wider range of taxa. Other organisms may have distinct ecological niches, therefore studying other taxa may help to have a better understanding of the pathways through which urban stressors impact biodiversity, ecosystem functioning, and trophic networks. Moreover, many of these stressors may interact, which can result in antagonistic or synergetic effects on odonates and other taxa (Matthaei et al., 2010; Piggott et al., 2012; Piggott et al., 2015). Despite the difficulty that studying multiple-stressors may imply, this is necessary in order to have a more realistic understanding of the combined

effects of urban stressors, which in turn will also help improve the mitigation of the negative effects and enhance the management, design, and restoration in urban ecosystems in order to promote the conservation of biodiversity.

Urban ecology, being an applied, multidisciplinary science linking human civilizations and ecosystems, has the ability to have a direct benefit on ecosystem health and human wellbeing. The findings reported in this thesis have practical implications on the improvement of management, planning, and designing of urban green and blue areas. Urban freshwater ecosystems may be improved substantially by increasing aquatic vegetation cover, adding thermal refugia through increased canopy cover to provide shade, and maintaining PLP-sources away from breeding sites or mitigating the negative impacts of PLP by adding black trays with freshwater alongside urban water bodies and then laying the contents back into the urban water bodies (Egri et al., 2017), which may take time to do, but it is inexpensive and does not require any specialist skills, so could be feasible in sites of conservation importance or those managed by wildlife conservation groups. Additionally, having noise-free areas in urban blue spaces is particularly important in protected areas, such as locations classified as Sites of Special Scientific Interest (SSSI), which comprise, among others, 25 canals in UK (<https://designatedsites.naturalengland.org.uk>). The implementation of these measures can prevent biodiversity loss in urban areas and increase the conservation value of urban freshwaters.

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Appendix

Table A.1. Summary of publications considered in the literature review and the categories in which they were included.

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Agüero-Pelegrín & Ferreras-Romero (1994)	Odonates	Spain	Urban pond	Species richness, abundance, exuviae dry weight, sex ratio	Diversity	<i>Anax imperator</i> , <i>Crocothemis erythraea</i> , <i>Sympetrum fonscolombii</i> and <i>Trithemis annulata</i> were found. <i>T. annulata</i> was the most abundant and male exuviae were heavier. There were slightly more males than females.
Alvarez & Pardo (2007)	Aquatic macroinvertebrates	Spain	Temporary streams	Taxa richness, abundance, community assemblage, flow permanence, riparian land use	Diversity	Taxa richness was higher in undisturbed riparian land use in all aquatic invertebrates including odonates; Abundance was related to flow permanence, independent from land use.
Azrina et al. (2006)	Aquatic macroinvertebrates	Malaysia	River	Physicochemical features upstream (undisturbed) and downstream (highly urbanised) sites, taxa richness and abundance, BMWP scores	Diversity Toxicology	In all aquatic invertebrates including odonates, upstream pollution indices were significantly lower than downstream, where urban pollution was discharged. Diversity measurements were also correlated with pollution indices.
Bracken & Lewis (2004)	Odonates	Canada	Highly urbanised Conservation area	Taxa richness	Diversity	Fifty species of odonates encountered, which represents 47.2% of the county richness.
Brandt & Buchwald (2011)	Odonates	Germany	Ponds	Taxa richness and abundance	Diversity	A total of 28 species of odonates was recorded, 21 of them were native from the area.

Table A.1 (*continued*)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Brazner et al. (2007)	Birds, fish, amphibians, aquatic macroinvertebrates, wetland vegetation, and diatoms.	USA	Coastal wetlands	Human disturbance factors (agriculture, urban development, contaminants), non-stressor variables (vegetation, watershed), taxa richness	Diversity Toxicology	Non-stressor variables were a better predictor of diversity than human disturbance factors; fish (<i>Ambloplites rupestris</i>) and <i>Aeshna</i> spp. were the strongest indicators of urban development.
Burton (1995)	Plants and animals	United Kingdom	Woodland and parkland (now golf-course)	Taxa richness	Diversity	A total of 210 species of higher plants; 24 species of mammals, reptiles and amphibians; 82 species of birds; 101 species of lepidopterans, and some more records of other insect orders, including odonates.
Chovanec (1994)	Amphibians and odonates	Austria	Artificial urban pond	Taxa richness and abundance	Diversity	Richness was considerably high; all amphibians found were included in the Red List of Endangered Species and the odonate species were native from the area.
Chovanec & Raab (1997)	Odonates	Austria	Canals and urban pond	Taxa richness and abundance	Diversity	Overall odonate diversity had increased since the implementation of the canal system and creation of artificial pond

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Chovanec et al. (2000)	Plants, odonates, amphibians, reptiles, waterfowl.	Austria	River-floodplain systems	Taxa richness, abundance, community assemblage	Diversity	Shallow sites without direct connection to the main river (Danube) were rich in odonates, amphibians, and riparian vegetation. The new presence of <i>Ischnura pumilio</i> demonstrates the connectedness created by the new landscape.
Chovanec et al. (2002)	Odonates, amphibians and fish	Austria	River-floodplain systems	Taxa richness, abundance, community assemblage	Diversity	Ponds were inhabited mostly by amphibians and odonates, whereas fish richness was related to connectivity. New floodplain system facilitated migration paths for amphibians and dragonflies, but no suitable breeding sites were found.
Cleto Filho & Walker (2001)	Aquatic macroinvertebrates	Brazil	Streams	Water quality measurements, taxa richness, diversity and similarity indices	Diversity Toxicology	Water quality was lower in streams with urban input, which negatively affected overall diversity, including odonates.
Colding et al. (2009)	Amphibians and odonates	Sweden	Golf-course and off-course ponds	Taxa richness in golf courses and off-course ponds, diversity and similarity indices	Diversity	Species composition was not significantly different between ponds. <i>Leucorrhinia pectoralis</i> , an endangered species, was found exclusively in golf course ponds.
Craves & O'Brien (2013)	Odonates	USA	Lotic and lentic waterbodies	Taxa richness and abundance	Diversity	Ninety species of odonates encountered within a highly-urbanised county.
Dombrovskiy & Kharchenko (2005)	Aquatic macroinvertebrates	Ukraine	Urban lake	Taxa richness, abundance, diversity and saprobic indices	Diversity Toxicology	Both diversity and saprobic indices were inversely related. Zygopterans were the dominant predators.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Edokpayi et al. (2004)	Aquatic macroinvertebrates	Nigeria	Lagoon	Water quality measurements, taxa richness and diversity index.	Diversity Toxicology	Low diversity in all sampling sites, elevated pollution rates. BOD and TDB content were significantly different among sites. No anisopterans were found.
Ferreras-Romero et al. (2009)	Odonates	Spain	River	Physicochemical features, ecological quality and land use upstream (undisturbed) and downstream (highly urbanised) sites, taxa richness, abundance, IBMWP scores	Diversity Toxicology	Species composition was negatively related to physicochemical values and modification of land use. Communities in sites less affected by human impact were dominated by semivoltine anisopterans.
Fischer et al. (2000)	Aquatic insects	Argentina	Urban rain pools	Meteorological parameters, taxa richness and abundance along seasons.	Diversity	The highest richness of adults was recorded during the warmer months; immatures were out of phase. Most ponds accounted less than 25% of the recorded taxa. Only two odonate taxa recorded.
Fontanarrosa et al. (2004)	Aquatic insects	Argentina	Temporary, urban pools and permanent, rural lagoons	Taxa richness and diversity index	Diversity	Odonate richness was higher where floating vegetation was found. Taxa richness in temporary pools wasn't significantly different from permanent ponds, but overall diversity was lower. Only four odonate taxa recorded.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Funk et al. (2009)	Aquatic molluscs, dragonflies and fish	Austria	River-floodplain systems	Taxa richness, abundance, and species composition was assessed before and after a water enhancement scheme.	Diversity	Molluscs and dragonflies were positively affected; fish showed no change. Dragonflies had increased taxa richness and abundance, but no significant change in species composition.
Funk et al. (2013)	Reptiles, amphibians, fish, snails and odonates	Austria	River-floodplain systems	Probability of occurrence with connected and isolated conditions.	Diversity	Most of the species selected had a higher probability of being found in connected conditions. Odonate species included in the model were <i>Leucorrhinia pectoralis</i> and <i>Ophiogomphus cecilia</i> .
Garrison & Hafernik (1981b)	<i>Ischnura gemina</i>	USA	Urban park creek	Population dynamics	Diversity Behavioural ecology Life-history traits	Dispersal was mostly local, but potential for larger dispersal was detected. Constant population size, short life span, quick maturation rate, slightly more males than females; one satellite population found.
Garrison & Hafernik (1981a)	<i>Ischnura gemina</i>	USA	Urban park creek	Geographic range	Diversity Behavioural ecology	Range is limited to small urban area, may have adapted to disturbance. Andromorphic female was described.
Girgin et al. (2010)	Aquatic insects	Turkey	Streams	Heavy metal concentration related to taxa richness, abundance and diversity index.	Diversity Toxicology	<i>Aeshna juncea</i> was a good bioindicator for Mn, Pb, and Ni; <i>Platycnemis pennipes</i> for Cd, B, Fe, and total hardness.

Table A.1 (*continued*)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Goertzen & Suhling (2013)	Odonates	Germany	Ponds	Habitat variables (human disturbance, vegetation, substrate types, percentage of detritum, mud, etc.) related to taxa richness, abundance, diversity indices.	Diversity	Vegetation increased taxa richness and evenness, but decreased dominance. Human disturbance was not a significant factor.
Hannon & Hafernik (2007)	<i>Ischnura gemina</i>	USA	Urban park creek	Population size, survivorship, longevity, oviposition, and dispersal.	Diversity Behavioural ecology Life-history traits	Reintroduction of the endangered damselfly was successful only one year. Reintroduced males moved longer distances than the ones recorded in 1979 and 1983, before their local extinction. No oviposition observed at the end of the year.
Henriques-de-Oliveira et al. (2007)	Aquatic macroinvertebrates associated to <i>Typha domingensis</i>	Brazil	Lagoon	Taxa richness, abundance, community assemblage, diversity and similarity indices in sites with urban sewage input	Diversity Toxicology	Richness increased in site with less sewage input, but evenness decreased; trichopterans and ephemeropterans were characteristic of these sites. Abundance was positively related to sewage input; chironomids and oligochaetes were present in such sites. <i>Micrathyria</i> spp. and <i>Miathyria</i> sp. were found exclusively in the site with less sewage input.

Table A.1 (*continued*)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Jara et al. (2013)	Predatory aquatic insects	Argentina	Pools	Relation of richness and abundance with hydroperiod of the ponds, physical features, vegetation and presence of fish.	Diversity	Taxa richness peaked in early summer in ponds surrounded by forest. Presence of fish did not alter taxa richness significantly. The most frequent odonate species were <i>Rhionaeschna variegata</i> and <i>Cyanallagma interruptum</i>
Kalcounis-Rueppell et al. (2007)	Insectivorous bats and insects	USA	Urban stream system	Taxa richness, abundance, community structure (insects and bats) and foraging behaviour (bats) related to wastewater treatment plant effluent.	Diversity Behavioural ecology	Dipterans, coleopterans, and lepidopterans were more abundant upstream; odonates were more abundant downstream. Wastewater effluent affected bat community structure, but not their foraging behaviour.
Karouna-Renier & Sparling (2001)	Aquatic macroinvertebrates	USA	Stormwater ponds	Metal concentrations in invertebrates, sediments, and water in relation to watershed land use	Toxicology	Zn and Cu concentrations in odonates were significantly higher in watersheds with commercial development. All concentrations were below lethal for fish diet. No differences in sediments and water concentration.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Kulkarni & Subramanian (2013)	Odonates	India	River	Taxa richness, relative abundance, diversity and similarity indices, and community assemblage along different land use types	Diversity	Community assemblage was significantly different among land use types and season, presenting high diversity and abundance in urbanised regions during the post monsoon season.
Kury & Christ (2010)	Odonates	Switzerland	Lotic and lentic waterbodies	Taxa richness and abundance	Diversity	A total of 42 species encountered, including two endangered (<i>Gomphus pulchellus</i> and <i>Gomphus simillimus</i>)
Lenders et al. (2001)	Higher plants, odonates, butterflies, fish, amphibians, reptiles, birds and mammals	The Netherlands	River floodplains	Taxa richness, diversity, protection status using BIO-SAFE method	Diversity	The BIO-SAFE biodiversity assessment method was developed based on several species of rivers and their floodplains, including 14 species of odonates. This method was tested in different ecotopes from urban floodplains, and showed that ecotope saturation (TES) and the actual ecotope importance (ATEI) scores must be taken into account to gain insight in the value of ecotopes for endangered species.
Lubertazzi & Ginsberg (2010)	Odonates	USA	Ponds	Community assemblage, taxa richness, and diversity indices along an urban-to-rural gradient	Diversity	Richness and evenness did not differ significantly between urban and rural sites; many species were more commonly found in urban sites with fish.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Lunde & Resh (2012)	Aquatic macroinvertebrates	USA	Ponds	Physicochemical features, habitat variables (vegetation composition, substrate, urbanisation percentage), taxa richness and abundance	Diversity Toxicology	The Index of Biotic Integrity (IBI) was developed using percent Ephemeroptera, Odonata, and Trichoptera (EOT); EOT richness; percent Tanypodinae/Chironomidae; Oligochaeta richness; percent Coleoptera; and predator richness. This method was negatively related to percentage of urbanisation and showed no significant bias with environmental gradients.
Mahato & Kennedy (2008a)	Aquatic macroinvertebrates	USA	Streams	Physicochemical features, taxa richness and abundance	Diversity Toxicology	Abundance was significantly higher in the urban stream, no differences in richness. Two odonate taxa found.
Mahato & Kennedy (2008b)	<i>Erpetogomphus designatus</i>	USA	Ponds	Survival, head width, total width, wing pad length and wet weight	Life-history traits	No survival in three sites (all of them in summer, two in spring). Growth rate was significantly higher in one of the urbanised sites
Majumder et al. (2013)	Aquatic insects	India	Lakes	Taxa richness, abundance, diversity indices.	Diversity	Hemipterans and odonates had the highest taxa richness.
Malherbe et al. (2010)	Aquatic macroinvertebrates	South Africa	River and tributaries	Physicochemical features, taxa richness, abundance, and community assemblages	Diversity Toxicology	Community assemblage in the main stem and its tributaries was significantly different due to abundance of chironomids and oligochaetes and low water quality. The polluted river had decreased sensitive taxa such as Atyidae, Naucoridae, Gomphidae and Leptoceridae.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Martins et al. (2010)	<i>Phrynops geoffroanus</i> (Chelidae) and its prey	Brazil	River	Composition of stomach contents	Behavioural ecology	<i>Chironomus</i> sp. was the most frequent and abundant prey; odonate larvae, molluscs, fish and plants were present as well.
Matsura et al. (1998)	Odonates	Japan	Swimming pools	Taxa richness, abundance, life-history traits	Diversity Behavioural ecology Life-history traits	A total of 11 species were found, <i>Sympetrum striolatum imitoides</i> was abundant in all pools, since chironomids (their prey) are very abundant. Females lay their eggs directly on water and eggs hatch before other dragonfly species, which also increases their abundance.
Matsura et al. (1995)	Odonates	Japan	Swimming pools	Taxa richness and abundance, survival, predation	Diversity Life-history traits	<i>Sympetrum striolatum imitoides</i> was the most abundant in all pools, which fed on chironomid larvae. They emerge in May-June and deposit eggs directly on water in October, coinciding with non-use period of the pools. Male established their territory for 1-18 days.
Monteiro et al. (2013)	Odonates	Brazil	Streams	Taxa richness, abundance and community assemblage with and without riparian vegetation	Diversity	A total of 32 species were found. <i>Erythrodiplax basifusca</i> and <i>Argia</i> sp. were associated with deforested streams, hence could potentially be used as bioindicators for deforestation from creation of new roads.
Moreno et al. (2009)	Aquatic macroinvertebrates	Brazil	River and tributaries	Taxa richness, abundance, and community assemblage using BEAST method	Diversity	Community assemblage allowed site classification in four categories according to its conditions: natural, altered, highly altered and degraded. The former being near urban sites.

Table A.1 (*continued*)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
						Calopterygidae and Gomphidae represented non-impacted sites.
Mostert (1998)	Odonates	The Netherlands	Waterbodies in meadows, arable land, nature reserves, recreational areas and urban areas	Taxa richness, population density, water turbidity	Diversity	Taxa richness and density were negatively related to turbidity and positively related to riparian vegetation. Natural areas were the most diverse. However, richness was higher in urban sites than in agricultural areas.
Murdoch (1989)	Odonates	United Kingdom	Lotic and lentic waterbodies	Taxa richness	Diversity	A total of 11 species were found, five of them were probably breeding there.
Neiss et al. (2008)	<i>Microstigma maculatum</i>	Brazil	Pond	Not defined	Diversity	The larval description of the species was made.
Nelson (2011)	Aquatic macroinvertebrates	USA	Drainage	Taxa richness, abundance, community assemblage, hydrology features (velocity, depth, width) and water quality measurements before and after a treatment plant	Diversity Toxicology	Wastewater input increased flow and abundance, but decreased conductivity and taxa richness. Tributary communities, which were associated with high conductivity, were taxa-rich compared with other groups and tended to contain odonates and a variety of dipteran and beetle taxa.

Table A.1 (*continued*)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Nummelin et al. (2007)	Predatory aquatic insects	Finland	Ponds	Heavy metal concentration in dragonflies, antlions, waterstriders and ants, both polluted and control sites.	Toxicology	All demonstrated to be good indicators for heavy metal pollution, although ants were the least effective. Waterstriders displayed high levels of Fe and Mn; antlions and odonates for Fe and Cd; antlions and ants for Pb and Mn.
Osada & Tabata (1992)	Odonates and aquatic plants	Japan	Pond	Taxa richness and abundance, succession (hydrophytes) and dispersal (odonates)	Diversity Behavioural ecology	Odonate richness increased after improvement of the pond, aquatic plants established there as well. Five distribution patterns were described.
Poulton et al. (2003)	Aquatic macroinvertebrates	USA	River	Water quality metrics, taxa richness and diversity indices.	Diversity Toxicology	One third of the taxa collected belonged to the sensitive EPOT insect orders (Ephemeroptera, Plecoptera, Odonata, and Trichoptera). However, Trichoptera abundance decreased downstream, next to a large city, whereas Oligochaeta relative abundance increased. Water quality metrics were particularly low downstream as well.
Principe & Corigliano (2006)	Aquatic macroinvertebrates	Argentina	River	Biomass, taxa richness, and diversity indices in rural and urban sites.	Diversity	Marginal fauna was more diverse than in benthos and drift. Rural sites had higher biomass and abundance, yet urban sites showed higher richness. Odonates were mostly representative of marginal fauna, both in urban and rural sites, except for <i>Aeshna</i> sp., which was only found in urban sites.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Pryke & Samways (2009)	Plants and invertebrates	South Africa	Natural and recovering forests (riverine and non-riverine), natural and recovering fynbos, botanical gardens and alien pine plantations	Taxa richness and abundance, species accumulation curves, non-parametric estimators of richness, community assemblage.	Diversity	Pines had low taxa richness and abundance. Gardens provided refuges in urban areas for invertebrate diversity. Odonates and lepidopterans were more commonly found in fynbos and botanical gardens.
Pujol-Luz (1987)	Odonates	Brazil	Urban water cisterns	Taxa richness and abundance	Diversity	Twenty species of odonates were found, mostly during the month of November.
Rivera Rondón et al. (2010)	Algae, zooplankton and aquatic macroinvertebrates	Colombia	River-floodplain systems	Physicochemical features, community assemblage, taxa richness, abundance, and diversity indices.	Diversity Toxicology	Most systems showed low levels of pH, nutrients and ions. Dominant algae were Bacillariophyceae and Zygnemaphyceae; coleopterans, odonates and ephemeropterans were the most abundant in all communities, and were more diverse in substrates rich in leaf litter.
Rizzoni et al. (1995)	Aquatic macroinvertebrates and <i>Vicia faba</i>	Italy	River	Community assemblage, diversity indices, taxa richness, biomass and	Diversity Toxicology	Micronucleus frequency increased towards the city centre, as well as invertebrate biomass, but diversity decreased. Only two odonate taxa were reported.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
				micronucleus frequency		
Sacha (2011)	Odonates	Slovakia	Garden pond	Taxa richness, abundance, and population size	Diversity	Three species were found at first, <i>Aeshna cyanea</i> was the most abundant. After a year, the other species were outcompeted or eliminated by predation. Abundance grew up to 1 individual per litre.
Saito & Owada (2005)	Odonates	Japan	Garden pond	Taxa richness and abundance	Diversity	A total of 18 species were enlisted, including the rare damselfly <i>Ceriagrion nipponicum</i> .
Samraoui et al. (1992)	Plants, odonates and birds	Algeria	Lake	Taxa richness and vegetation composition	Diversity	A description of the vegetation composition and structure was made, as well as an inventory of 45 bird species and 23 odonates.
Samways & Steytler (1996)	Odonates	South Africa	A river through plantation forests, residential areas, parklands, and industrial areas.	Environmental data, taxa richness and abundance, species accumulation curves, non-parametric estimators of richness, community assemblage.	Diversity	Industrial areas were the second lowest taxa richness, but had the highest abundance in anisopterans. Parks, on the other hand, were the highest in zygopteran richness and abundance.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Sato et al. (2008)	Zygotera	Japan	Rice paddies, natural and man-made ponds	Genetic variability	Diversity Behavioural ecology	No significant differences in genetic diversity in urban and rural populations. However, genetic differentiation was significantly higher in urban populations, meaning that dispersal is limited.
Scolozzi & Geneletti (2011)	<i>Muscardinus avellanarius</i> , <i>Sitta europaea</i> , <i>Erinacaeus europaeus</i> , <i>Lanius collurio</i> , <i>Rana synklepton esculenta</i> , and <i>Calopteryx virgo</i> .	Italy	Valley	Probability of occurrence according to their breeding, survival, dispersal, habitat unsuitability and hostility	Diversity	Habitat suitability models were used for mapping the impact of urban land use
Silva et al. (2010)	Odonates	Brazil	River	Physicochemical features, ecological quality, taxa richness and abundance up- and downstream	Diversity Toxicology	<i>Argia modesta</i> was abundant upstream; taxa richness and abundance were affected by seasonality and lack of riparian vegetation.
Sinclair et al. (2012)	Invertebrates	Canada	River	Methylmercury concentration in sediment, water and invertebrates	Toxicology	MeHg concentration in sediment, water and invertebrates was higher in the newest (urban) wetlands. Odonates were significantly greater in wetlands equal to or less than 2 years old. Odonate MeHg concentrations from new and old wetland were not significantly different.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Smith & Lamp (2008)	Aquatic insects	USA	Streams	Community assemblage, taxa richness, abundance, diversity and similarity indices in urban and rural watersheds.	Diversity	Taxa richness and diversity were lower in urban sites. However, urban sites had high similarity in both headwater and main-stem communities, unlike rural sites. The unique headwater taxa in urban headwater streams belonged only to Odonata (<i>Ischnura</i> spp. and <i>Calopteryx maculata</i>) and Diptera (<i>Aedes</i> and <i>Odontomyia</i>).
Solimini et al. (1997)	Zygoptera	Italy	River	Water quality metrics, community assemblage and life-history traits	Diversity Toxicology Life-history traits	Damselfly assemblage was mostly formed by generalist species found in lentic habitats. <i>Ischnura elegans</i> and <i>Erythromma (=Cercion) lindenii</i> were the most abundant in highly polluted wetlands, presenting a longer reproductive period, absence of diapause, and tolerance of low oxygen concentration.
Srinivasulu & Srinivasulu (2005)	Bats and their prey	India	Forest caves and urban sites	Composition of faecal pellets	Behavioural ecology	All studied samples contained mostly insects and spiders, including odonates. Forest bats presented opportunistic feeding behaviour, while urban ones were selective with their prey.
Steytler & Samways (1995)	Odonates	South Africa	Artificial park pond	Biotope preference, taxa richness	Diversity Behavioural ecology	Stenotopic species were highly sensitive to changes in sunlight, water flow and vegetation structure. Yet, taxa richness increased over 100% after the creation of the pond

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
Suh & Samways (2005)	Odonates	South Africa	Stream in an urban reservoir	Taxa richness, community assemblage, habitat variables (shade, vegetation structure and composition, substrate, etc.)	Diversity	Taxa richness doubled after implementation of the reservoir. The most important factors determining species assemblage were vegetation structure and composition, percentage shade, submerged vegetation, water flow and amount of open water.
Suhling et al. (2009)	Odonates	Germany	Lotic and lentic waterbodies	Species richness, abundance and population trends	Diversity	A total of 51 species were found. <i>Sympetrum pedemontanum</i> , <i>Coenagrion pulchellum</i> , <i>Ischnura pumilio</i> and <i>Sympetrum danae</i> had declined, although species like <i>Sympecma fusca</i> , <i>Gomphus vulgatissimus</i> , <i>Ophiogomphus cecilia</i> , <i>Orthetrum brunneum</i> and <i>Orthetrum coerulescens</i> had increased in a period of almost 30 years
Uboni et al. (2006)	<i>Cordulegaster heros</i>	Italy	Stream	Not defined	Diversity	A population of <i>Cordulegaster heros</i> was found in an urban stream, where it co-occurs with <i>Cordulegaster bidentata</i> and <i>Calopteryx virgo</i> .
Van de Koken et al. (2007)	<i>Pantala flavescens</i>	Brazil	Parking areas	Eggs laid, occurrence frequency, amount of cars in the parking area, light/dark car ratio	Behavioural ecology	<i>P. flavescens</i> occurrence was positively related to the amount of cars found in the parking area. There was also a preference towards light coloured cars. Oviposition was recorded on the hood surfaces, which represents an energy loss for the females.

Table A.1 (continued)

Ref.	Studied group	Location	Habitat type	Variables	Categories	Results summary
van Laar (1999)	<i>Calopteryx splendens</i>	The Netherlands	Streams	Population density	Diversity	<i>C. splendens</i> had disappeared around 1970 due to pollution and deforestation. After mitigation measures, the species recolonised the area, including urban sites.
Watts et al. (2004)	<i>Coenagrion mercuriale</i>	United Kingdom	River	Genetic variability	Diversity Behavioural ecology	Genetic differentiation was significant throughout sampling area, thus species is mostly sedentary. Urban areas made a barrier effect and limited their dispersal.
Willigalla & Fartmann (2012)	Odonates	Central Europe	Cities	Taxa richness and city area	Diversity	Taxa richness is positively related to city size, but decreases towards city centres.
Willigalla & Fartmann (2009)	Odonates	Germany	Rain-storage ponds	Taxa richness, abundance, community assemblage and similarity index	Diversity	A total of 32 species were recorded. Richness increased in suburban ponds and was positively related to pond size. Similarity index was negatively related to distance between ponds.
Willigalla et al. (2003)	Odonates	Germany	Rain-storage ponds	Taxa richness	Diversity	A total of 27 species were recorded. Exposure to sunlight and vegetation structure defined odonate diversity.
Wilson (1997)	Odonates	China	Streams	Taxa richness and abundance	Diversity	Two sites were particularly rich in Gomphidae and Macromiidae species
Yu et al. (2013)	Zooplankton and aquatic macroinvertebrates	China	River	Polychlorinated biphenyl (PCB) concentration in invertebrates	Toxicology	Zooplankton presented the highest PCB levels, followed by soil-dwelling invertebrates. Chironomids and odonates had high concentrations of mid-chlorinated congeners (PCB-153 and PCB-138)

Table A.2. Variance Inflation Factors (VIF) of the predictor variables used in the FGLS models by species in the phenology analysis.

Species	Urban land use	Minimum temperature	Year
<i>Aeshna cyanea</i>	1.232	1.796	1.564
<i>Aeshna grandis</i>	1.095	1.124	1.029
<i>Aeshna mixta</i>	1.082	1.217	1.134
<i>Anax imperator</i>	1.171	1.283	1.112
<i>Calopteryx splendens</i>	1.064	1.112	1.048
<i>Coenagrion puella</i>	1.036	1.086	1.050
<i>Enallagma cyathigerum</i>	1.064	1.128	1.064
<i>Erythromma najas</i>	1.038	1.095	1.057
<i>Ischnura elegans</i>	1.097	1.228	1.131
<i>Libellula quadrimaculata</i>	1.057	1.108	1.051
<i>Orthetrum cancellatum</i>	1.092	1.094	1.002
<i>Pyrrhosoma nymphula</i>	1.068	1.160	1.092
<i>Sympetrum striolatum</i>	1.173	1.307	1.134

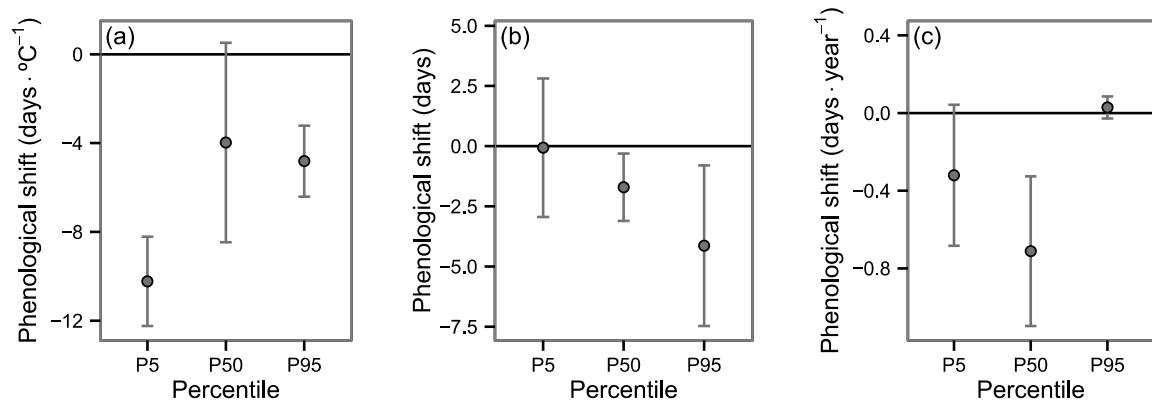


Figure A.1. Community-level phenological shifts excluding anisoptera in flight dates (P5, P50, P95) in relation to (a) minimum temperature, (b) urban land use compared to the rural surroundings, and (c) year. Error bars represent 95% confidence intervals.

Table A.3. Sampling sites used for collecting adult females from *Ischnura elegans*. Land use classification of sampling sites was based on the percentage of urban cover (according to the Land Cover Map (LCM) 2007) at a distance of 1 Km around the ponds.

Location	Land use	Latitude	Longitude
ASD Metal Services	urban	53° 46' 04.19" N	001° 30' 41.16" W
Freemans Grattan Holdings (FGH) Ltd Listerhills Warehouse	urban	53° 47' 50.54" N	001° 46' 14.62" W
Harold Park	suburban	53° 45' 28.16" N	001° 46' 20.86" W
Middleton Park	rural	53° 45' 16.12" N	001° 32' 41.85" W
Roundhay Park	rural	53° 50' 26.07" N	001° 29' 43.39" W
St. Aidan's Country Park	rural	53° 45' 05.40" N	001° 23' 58.58" W

Table A.4. Number of replicates per prey density in each treatment of the noise experiments.

Treatment	Prey density	N
<i>Anthropogenic noise</i>	5	6
	10	6
	15	5
	20	5
	30	4
	40	5
	50	6
<i>Natural noise</i>	5	5
	10	6
	15	6
	20	5
	30	6
	40	5
	50	6
<i>Control (silence)</i>	5	5
	10	6
	15	5
	20	5
	30	7
	40	6
	50	4

Table A.5. Variance Inflation Factors (VIF) obtained from the linear mixed-effects models for the geomorphometric analysis.

	Sex	Suburban land use	Urban land use	Sex × Suburban land use	Sex × Urban land use
<i>Fore wings</i>					
PC1	1.83	2.00	1.75	2.31	1.94
PC2	1.84	2.24	1.92	2.55	2.09
PC3	1.83	2.15	1.86	2.46	2.03
PC4	1.84	2.43	2.06	2.74	2.21
Wing aspect ratio	1.83	2.20	1.90	2.51	2.06
Wing loading	1.81	1.44	1.35	1.74	1.58
Wing size	1.81	1.37	1.30	1.67	1.54
<i>Hind wings</i>					
PC1	1.81	2.38	1.99	2.69	2.13
PC2	1.81	2.29	1.93	2.59	2.07
PC3	1.81	2.12	1.81	2.43	1.97
PC4	1.80	1.97	1.70	2.28	1.88
Wing aspect ratio	1.81	2.43	2.03	2.73	2.16
Wing loading	1.79	1.43	1.33	1.72	1.56
Wing size	1.79	1.46	1.35	1.76	1.57

